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Brazil nut tree increases photosynthetic activity and stem diameter growth after thinning

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Abstract *Bertholletia excelsa* Bonpl. is widely planted in the Amazon and information about thinning effects is poorly documented. Here, we investigate thinning effects on the ecophysiology of *B. excelsa* plantations. The thinning trial was set up as a randomized complete block design (RCBD) with two treatments (unthinned and thinned to 50% basal area removal). The canopy openness of plots thinned was two times higher than the unthinned treatment (control). *B. excelsa* under thinning growed three times in relation to trees of control. One week after thinning, we observed increase of 25% photosynthesis (P_N), 100% respiration (R_d), 35% stomatal conductance (g_s), and 25% transpiration (E). After thinning, we verified reduction of the maximum photochemical efficiency of photosystem II (F_V/F_M), with subsequent recovery. At the end of 5 months after thinning, the trees on thinned plots achieved values of leaf mass per area (LMA), nitrogen (N_a), phosphorus (P_a), and potassium (K_a) about 27% higher than trees of unthinned plots. Thinning did not affect the midday leaf water potential (Ψw). Thinning increased the growth of *B. excelsa* influenced by photosynthetic performance and regulated by the g_s, LMA, leaf N_a, and P_a concentrations. Our findings demonstrated that thinning can be recommended for timber production under the dense planting of Brazil nut trees cultivated in degraded Amazonian areas.

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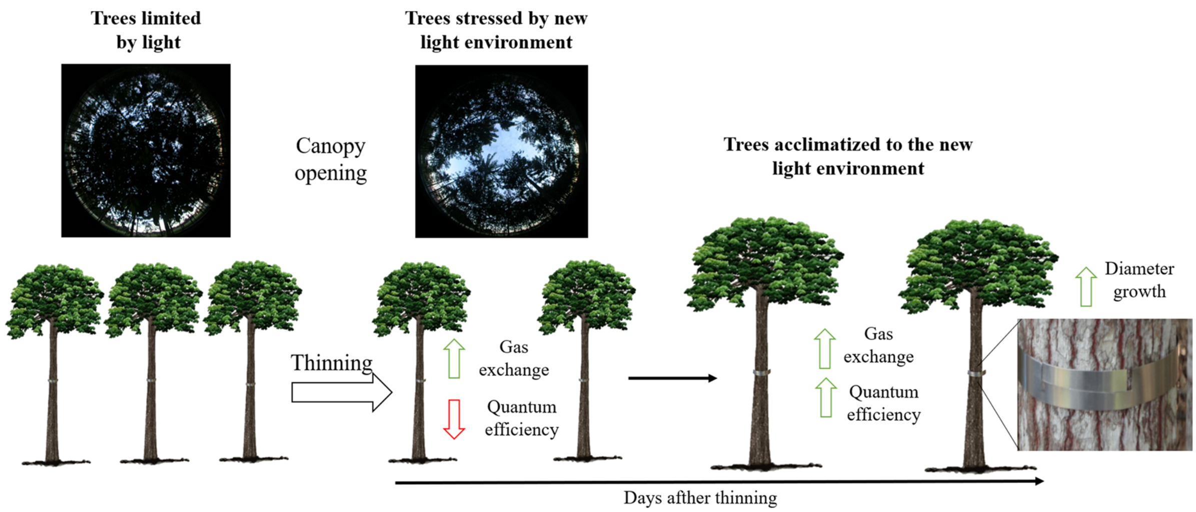
Graphical abstract



Keywords Photosynthesis · Chlorophyll *a* fluorescence · Leaf water potential · Nutrient · Silvicultural treatment

1 Introduction

In the "Legal Amazon" region, the productive plantations until 2020 year represented about 1% of the classes of use of deforested areas, and most of this area is occupied by exotic species from the genus *Eucalyptus* and *Pinus* (INPE 2020; IBGE 2020). The small area occupied by productive plantations in the "Legal Amazon" region and the significant number of exotic species planted resulted, in part, from a lack of knowledge of the silvicultural and ecophysiological characteristics of native species (FAO 2023).

The Brazil nut tree (*Bertholletia excelsa*) is one of the most used native species in silvicultural experiences in the Amazon (Costa et al. 2022; Souza et al. 2022; Fortes et al. 2023). The main market product is the Brazil nut, but this species also has great potential for the timber industry due to its excellent features silvicultural and high-quality wood (Ferreira and Tonini 2009). The techniques related to seedling production and the process of establishment of plantation of this culture are already relatively well established (Costa et al. 2022). However, aspects related to plantation management for timber production are still unknown (Souza et al. 2022).

The management of forest plantations for timber production must contemplate the adoption of specific silvicultural treatments such as thinning, pruning, and fertilization (Allen 2008; West 2014; Souza et al. 2022). In this sense, the forest thinning assumes a prominent role, in the increase in yield and quality of the final product, and still may increase the revenue generated in the enterprise (West 2014; Tanger et al. 2021; Peng et al. 2022; Benedetti-Ruiz et al. 2023). In summary, the thinning changes the stand's competitive environment and may redirect the disponibility of the site's primary resources (light, nutrients, and water) among the residual trees (Moreau et al. 2022).

The opening of the canopy as a result of the reduction in stocking density of trees by thinning induces important changes in microclimatic variables (e.g. available soil water and nutrients, irradiance, air temperature, and relative humidity) that should influence the physiological processes of the remaining trees (Gauthier and Jacobs 2010; Forrester et al. 2013a; Dobner et al. 2019; Costa et al. 2020; Domingo et al. 2020). The application of thinning decreases the competition among individuals, distributing the production potential of the site among the remaining trees (Forrester et al. 2013b; West 2014); it has been observed such changes improve the nutritional and water status, and added up to the greater availability of light, may reflect in increased photosynthetic rates and consequently in the growth rates of the remaining trees (Forrester et al. 2013a; Costa et al. 2020; Souza et al. 2022).

The knowledge of the functional changes resulting from the thinning in plantations associated with growth variables and other silvicultural trials can allow us to identify with precision the main factor responsible for the increase of the production of individual trees, as well as contribute to describing the suitable strategies of management for these plantations (Costa et al. 2020; Bosela et al. 2021). However, few studies have been conducted about thinning in certain parts of the world. Studies conducted in Asia and the southern hemisphere are practically nonexistent, and boreal and tropical regions are underrepresented (Moreau et al. 2022).

Due to the high demand for further studies on the effect of thinning applied to forest plantations in the Amazon environment, we investigated whether thinning influences *B. excelsa* plantations' growth and morphophysiological characteristics. To reach this goal, we formulated the following hypotheses: (1) Thinning promotes the fast diameter growth of residual trees of *B. excelsa*; (2) The growth responses of *B. excelsa* plantations subjected to thinning are determined by the photosynthetic performance as affected by the stomatal control, water, and nutritional status of residual trees cultivated in degraded areas in the Amazon.

2 Material and methods

2.1 Site description

A *B. excelsa* plantation selected for this study is located in Itacoatiara, AM, Brazil (3°0′30.63″ S, 58°50′1.50″ E). The local climate is classified as "Amw" (Köppen 1948) with a mean annual temperature of 25 °C and precipitation of 2700 mm (INMET 2022). The elevation is between 120 and 170 m above sea level. The dominant soil type is Ferrasol. The plantation was established in 2005, on an area of 0.3 ha, using seedlings at 7 months old and 15 cm height. Spacing between plants was 2.5 × 1.5 m resulting in a stocking density of 2666 trees per hectare. Weed control was done through mechanized chopping twice a year. Seedlings were not fertilized.

2.2 Field experiment design

The number of blocks was defined from the variable diameter at breast height (DBH, measured at 1.3 m above ground level), obtained by a preliminary pilot inventory. We used the sample size equation to determine how many sample units were needed to have a degree of confidence of 95% and 10% precision. Thus, eight blocks (420 m^2) were established and in each block, the two treatment plots (Control and Thinning) were randomly applied. In the field, the treatment plots were separated by a buffer zone of 4 m.

2.3 Thinning treatment

The selective thinning method was applied and the intensity of basal area removal was 50%. The suppressed and forked trees were eliminated. Thinning was performed between 08/07/2013 and 12/07/2013 when the trees were 8 years old. After thinning, was removed from the planting area the rest of the leaves, twigs, and wood of the trees thinned.

2.4 Sampled trees and sample periods

Considering the impossibility of measuring the physiological variables of all the trees of the treatment plots (35 trees), were selected for each plot, 3 trees, totalizing 25 sample trees per treatment. The following characteristics were taken into account when selecting trees for this study: similarity in diameter, height, form, and crown length.

Ecophysiological variables were collected before thinning (07/07/2013) and after thinning. The data collected after thinning were carried out 1 week (07/14/2013), 1 month (08/31/2013), 3 months (10/05/2013), and 5 months (12/07/2013) after removing the trees.

2.5 Canopy opening

Hemispherical photographs were made after thinning to quantify the percentage of canopy openness (Frazer et al. 1999). For this, we used a Nikon Coolpix 4500 camera with a fisheye lens Nikon LC-coupled ER1

8 mm, producing an angle of 180° and generating images of 2 megapixels. The camera was mounted on a tripod at 1 m height above the ground. The camera was leveled to face exactly vertical using a bubble level and photographs were taken without direct sunlight entering the lens between 17 and 18 h (Frazer et al. 1999). Three photographs were taken of each plot. The hemispheric photographs were processed in Gap Light Analyzer (GLA) software version 2.0 (Frazer et al. 1999).

2.6 Growth measurements

The tree diameter at breast height (DBH, measured at 1.3 m above ground level) was measured to calculate the periodic annual increment (Avery and Harold 2015).

2.7 Leaf gas exchange

Net photosynthesis (P_N) per unit area (*A*), stomatal conductance (g_s), transpiration (*E*), and dark respiration (R_d) were measured using a portable infrared gas analyzer (Li-6400; Li-Cor, Lincoln, NE, USA) with an area of leaf chamber of 6.0 cm^2 and light provided by the red and blue LEDs (665 and 470 nm, respectively).

The measurements were made between 08:00 h and 12:00 h (noon) on healthy and fully expanded leaves from branch segments excised from the middle canopy of trees (Ferreira et al. 2016).

All measurements were made at photosynthetic photon flux densities (PPFD) of 0 and 1500 μmol m^{-2} s^{-1}, the airflow through the chamber was about 400 μmol s^{-1}, the CO_2 concentration [CO_2] of the flow rate into the chamber was 400 ± 1 μmol mol^{-1}, the block temperature was 31 ± 1 °C, and H_2O vapor was about 21 ± 1 mmol mol^{-1} (Ferreira et al. 2016).

2.8 Chlorophyll *a* fluorescence

The chlorophyll *a* fluorescence was measured using a portable fluorimeter (PEA, MK2-9600-Hansatech, Norfolk, UK) between 08:00 h and 11:00 h, on healthy, fully expanded mature leaves. The selected leaves were adapted to a dark period for 30 min and then exposed to a 5-s excitation pulse of high irradiance intensity at saturating light (3000 mmol m^{-2} s^{-1}) with a wavelength of 650 nm (Gonçalves et al. 2012). The parameters related to polyphasic chlorophyll *a* fluorescence transient were obtained from a specific software (Handy PEA software—v 1.30) and these values were used for the calculation of the variables of the specific energy fluxes, quantum yields, and performance index (Strasser et al. 2010).

2.9 Leaf mass per area (LMA) and nutrient concentrations

After the leaf gas exchange measurements, the same leaves were collected for LMA and chemical analysis. The LMA was calculated by the ratio between leaf dry mass after oven-dried at 70 °C and the leaf area from leaf discs of a known area (0.283 cm^2). Total N was determined in accordance with the Kjeldahl method (Bremner and Mulvaney 1982). The phosphorus concentration was determined by spectrophotometry (Miyazawa et al. 1999). Macronutrients (Ca, Mg, and K) and micronutrients (Fe, Zn, Cu, and Mn) were determined by spectrophotometric atomic absorption (Perkin–Elmer 1100B, Uberlingen, Germany).

2.10 Leaf water potential and water use efficiency (WUE)

Midday leaf water potential (Ψw) was measured on healthy, fully expanded mature leaves using a pressure chamber (PMS Instruments Company, Corvallis, OR) (Scholander et al. 1965). Water use efficiency (WUE) was calculated as the ratio A/E (Ferreira et al. 2009).

2.11 Data analysis

A RCBD was established in this study. The treatments (T) were randomly applied: (T1) control and (T2) thinning. Thus, the measurements were performed in a plot of 12.5 m × 7.5 m (93.75 m^2) with 25 trees per plot (a total of 400 trees). The data were preliminarily verified for the assumptions of normality and homogeneity of variance by Shapiro Willk and F tests, respectively. The thinning effects on growth and ecophysiological characteristics were tested by *t* test. Linear regressions were tested to verify the effect of physiological and morphological traits on photosynthesis. All analyses were performed using R software.

3 Results

The thinning changed the light availability for *B. excelsa* trees. The percentage of canopy openness of plots thinned (24%) was two times higher than plots unthinned (12%) (Fig. 1).

The changes in light availability due to thinning influenced the photosynthesis of *B. excelsa* trees (Table 1). One week after thinning we verified an increase in non-photochemical dissipation (DI_O/RC), reduction of electron transport rate (ET_O/RC), and reduction of maximum photochemical efficiency values of PS II (F_V/F_M) (Table 1). However, in the second month after thinning, the trees achieved values of DI_O/RC and F_V/F_M near the unthinned treatment (Table 1).

One week after thinning we also measured an increase in all parameters of gas exchange

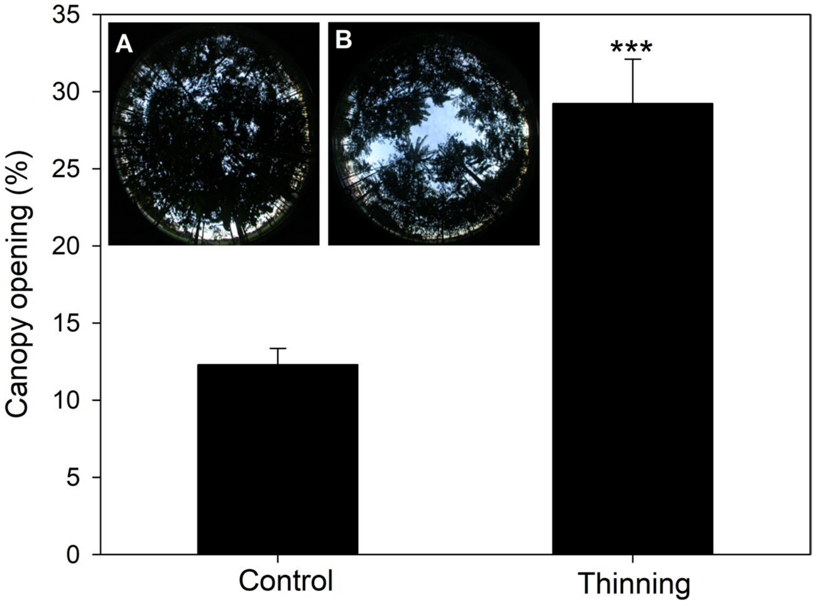


Fig. 1 Opening canopy of *Bertholletia excelsa* plantation in control (A) and thinning treatments (B) ($n=8$) ***$p<0.001$. The bars represent the standard error of the mean

Table 1 Effect of thinning on photochemical efficiency of *Bertholletia excelsa* trees under thinning treatment

Variable	Data collect period				
	Before thinning	After thinning			
		One week	Two months	Three months	Five months
DI_o/RC	0.42 ± 0.04 (−6.0)	0.56 ± 0.14 (+86.8)*	1.77 ± 0.17 (−31.7)	0.54 ± 0.07 (+1.2)	0.57 ± 0.10 (−2.8)
ABS/RC	2.23 ± 0.09 (+1.1)	2.54 ± 0.18 (+22.4)	2.39 ± 0.06 (+5.4)	2.53 ± 0.10 (+1.0)	2.56 ± 0.12 (+2.2)
TR_o/RC	1.81 ± 0.05 (+2.7)	1.98 ± 0.09 (+4.5)	1.95 ± 0.03 (+2.6)	1.99 ± 0.06 (+0.9)	1.99 ± 0.03 (+3.6)
ET_o/RC	0.93 ± 0.02 (+0.9)	1.00 ± 0.07 (−26.4)**	0.89 ± 0.02 (−16.9)***	0.88 ± 0.04 (−16.1)*	0.92 ± 0.03 (−15.8)**
RE_o/RC	0.28 ± 0.01 (−4.0)	0.35 ± 0.08 (−21.9)	0.26 ± 0.01 (+16.2)**	0.26 ± 0.02 (+6.8)	0.28 ± 0.03 (+12.6)
F_V/F_M	0.82 ± 0.01 (+1.1)	0.81 ± 0.01 (−11.7)**	0.82 ± 0.01 (−2.4)	0.79 ± 0.02 (−0.2)	0.80 ± 0.02 (−0.9)

DI_o/RC, non-photochemical dissipation; ABS/RC, effective size of the antenna complex; TR_o/RC, maximum photosystem (PS) II capture; ET_o/RC, electron transport rate; RE_o/RC, electron flow to reduction end acceptors on the acceptor side of the photosystem (PS) I; F_V/F_M, maximum quantum efficiency of the photosystem (PS) II

The values are averages of eight repetitions of trees under unthinned treatment ± standard error and the values in brackets are percentages of changes promoted by the application of thinning (increase +, or reduction −, concerning the values obtained in the control treatment)

*$p<0.05$; **$p<0.01$; ***$p<0.001$

(Fig. 2A–D). In this period, the trees on thinned plots, increased in 25% the rates of photosynthesis (P_N) and transpiration (E), while for stomatal conductance (g_s) and dark respiration (R_d), the increase was 35% and 100%, respectively (Fig. 2A–D). Following months, the trees under thinned plots always showed values of P_N, R_d, g_s, and E higher than trees of unthinned plots (Fig. 2A–D) and at the end of 5 months from thinning, the trees under thinned had 30% most higher values of P_N than trees under unthinned treatment (Fig. 2A–D).

We verified an increase of 20.3% in leaf mass per area (LMA) and 21.2% in leaf nitrogen concentration (N_a) in the second month after thinning (Table 2). Increases in phosphorus (P_a) and potassium (K_a) leaf concentration were observed in the third and fourth months after thinning (Table 2). At the end of 5 months from thinning, the trees under thinned plots achieved values of LMA, N_a, P_a, and K_a higher than in unthinned treatment (Table 2).

The thinning treatment did not change the leaf water potential (ψ_w) of trees. The amplitude of range throughout the trial period for the trees on thinned plots was −1.53 and −1.34 MPa, while for the unthinned control was −1.64 and −1.19 MPa (Fig. 3A, B). However, we measured an increase of 20% in WUE in the second month after thinning, followed by a decrease in October and an increase of 16% in the fifth month (December) (Fig. 3A, B).

After 1 year of application of thinning, the average annual increment in DBH of trees on thinned plots (1.12 cm year^{-1}) was three times higher than unthinned control (0.39 cm year^{-1}) (Fig. 4).

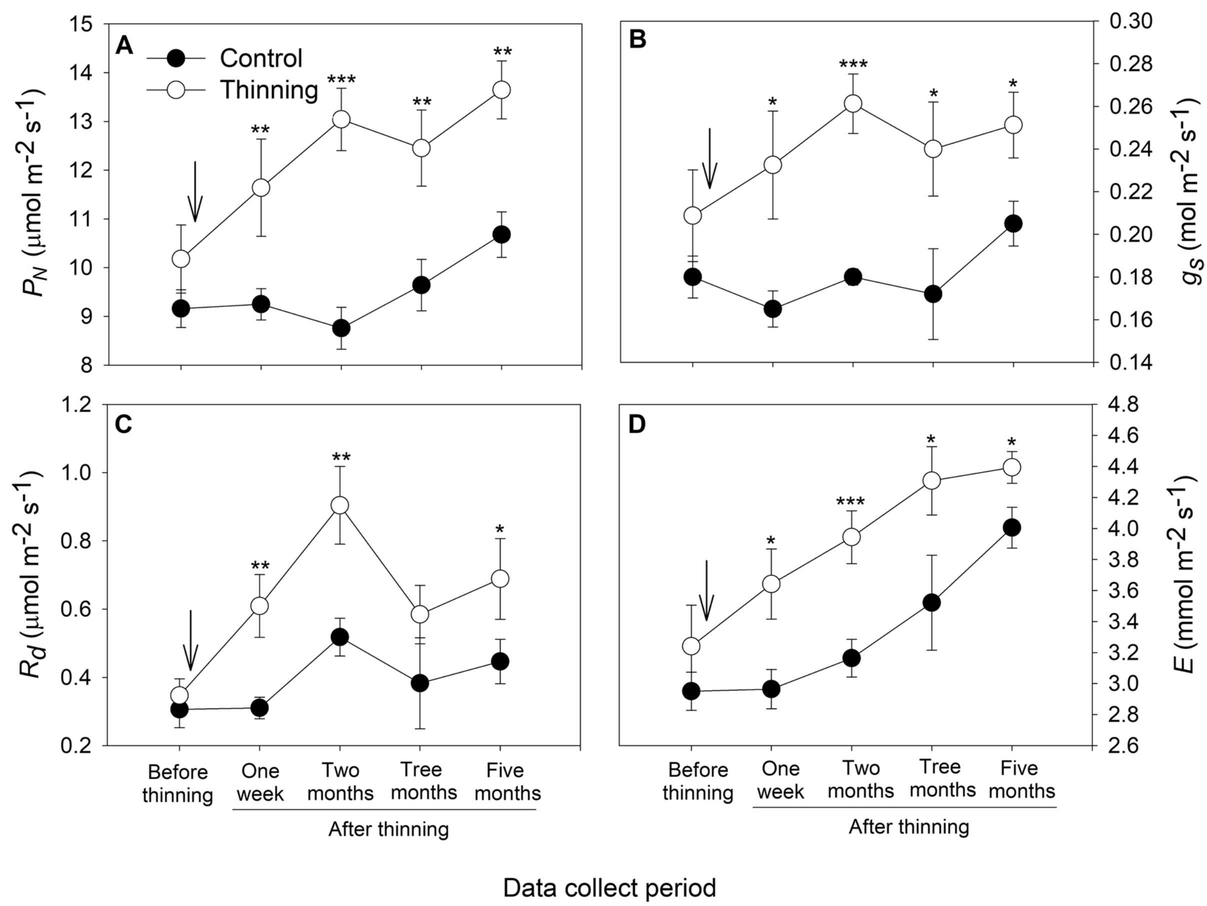


Fig. 2 Leaf gas exchange of *Bertholletia excelsa* trees under thinning ($n = 8$) *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. The bars represent the standard error of the mean. The arrow indicates the time that thinning

Table 2 Effect of thinning on leaf mass per area (LMA) and leaf nutrients concentrations of *Bertholletia excelsa* plantation

Variable	Data collect period				
	Before thinning	After thinning			
		One week	Two months	Three months	Five months
LMA (g m^{-2})	92.2 ± 4.4 (+4.9)	92.2 ± 4.4 (+4.9)	84.3 ± 4.8 (+20.3)*	91.0 ± 4.3 (+15.9)**	87.4 ± 3.9 (+24.9)**
N_a (g m^{-2})	1.37 ± 0.09 (+15.8)	1.37 ± 0.09 (+15.8)	1.39 ± 0.06 (+21.2)**	1.55 ± 0.07 (+20.3)**	1.55 ± 0.06 (+27.0)**
P_a (g m^{-2})	0.05 ± 0.01 (+8.3)	0.05 ± 0.01 (+8.3)	0.05 ± 0.01 (+15.7)	0.06 ± 0.01 (+26.8)**	0.06 ± 0.01 (+31.4)**
K_a (g m^{-2})	0.40 ± 0.04 (+14.6)	0.40 ± 0.04 (+14.6)	0.45 ± 0.03 (+24.8)	0.48 ± 0.04 (−3.8)	0.46 ± 0.03 (+23.2)*
Ca_a (g m^{-2})	0.46 ± 0.06 (+5.5)	0.46 ± 0.06 (+5.5)	0.41 ± 0.06 (+45.9)	0.48 ± 0.04 (+48.3)*	0.54 ± 0.03 (+66.0)
Mg_a (g m^{-2})	0.24 ± 0.06 (+4.6)	0.24 ± 0.06 (+4.6)	0.19 ± 0.02 (+23.9)	0.25 ± 0.01 (+28.7)	0.22 ± 0.01 (+34.1)
Fe_a (mg m^{-2})	1.31 ± 0.26 (+18.6)	1.31 ± 0.26 (+18.6)	4.25 ± 0.42 (+3.4)	5.23 ± 0.40 (+10.4)	5.05 ± 0.27 (+15.1)
Zn_a (mg m^{-2})	1.64 ± 0.11 (+20.5)	1.64 ± 0.11 (+20.5)	1.12 ± 0.07 (+42.2)	1.79 ± 0.13 (+34.1)*	2.26 ± 0.34 (−9.1)
Mn_a (mg m^{-2})	12.83 ± 2.85 (+6.3)	12.83 ± 2.85 (+6.3)	9.32 ± 1.46 (+20.5)	8.61 ± 0.71 (+128.8)*	12.62 ± 2.35 (+45.4)

The values are averages of eight repetitions of trees under unthinned treatment ± standard error and the values in brackets are percentages of changes promoted by the application of thinning (increase +, or reduction −, concerning the values obtained in the control treatment)

*$p < 0.05$; **$p < 0.01$; $p < 0.001$

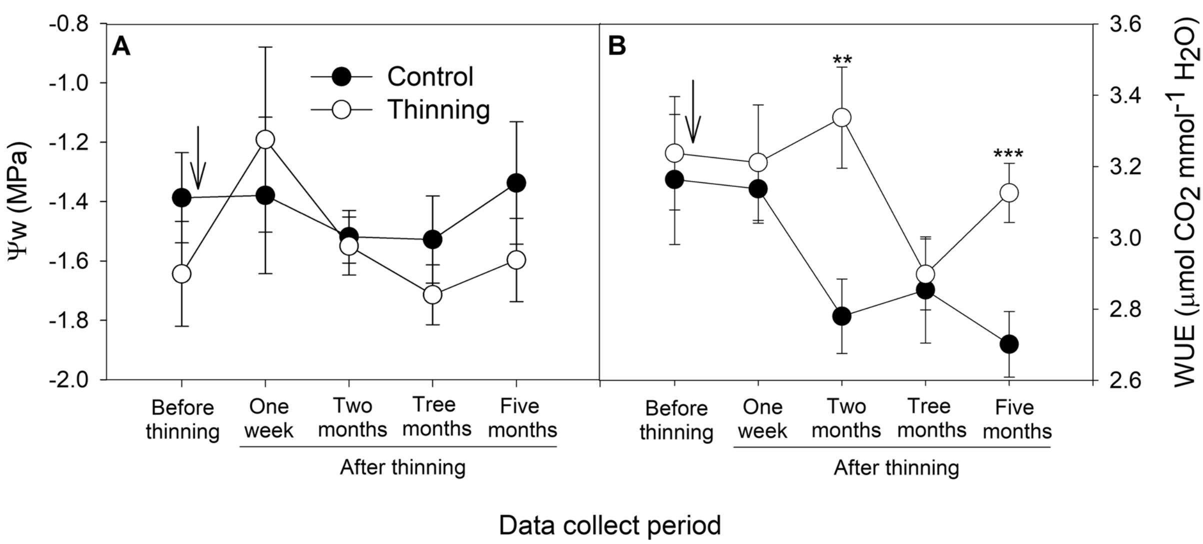


Fig. 3 Midday leaf water potential (ψ_w) (**A**) and water use efficiency (WUE) (**B**) of *Bertholletia excelsa* trees under thinning treatment ($n = 8$) **$p < 0.01$; ***$p < 0.001$. The bars represent the standard error of the mean. The arrow indicates the time that thinning

At the end of 5 months of thinning, we observed that the photosynthesis rates and the increase in diameter were positively related to the dose opening percentage and that the photosynthesis rates in turn were positively correlated with the increase in diameter of *B. excelsa* trees (Fig. 5A–C).

4 Discussion

In the present study, we observed that *B. excelsa* plantations subjected to thinning demonstrated high growth rates in diameter after 1 year, which occurred as a response of the fast increase in photosynthetic

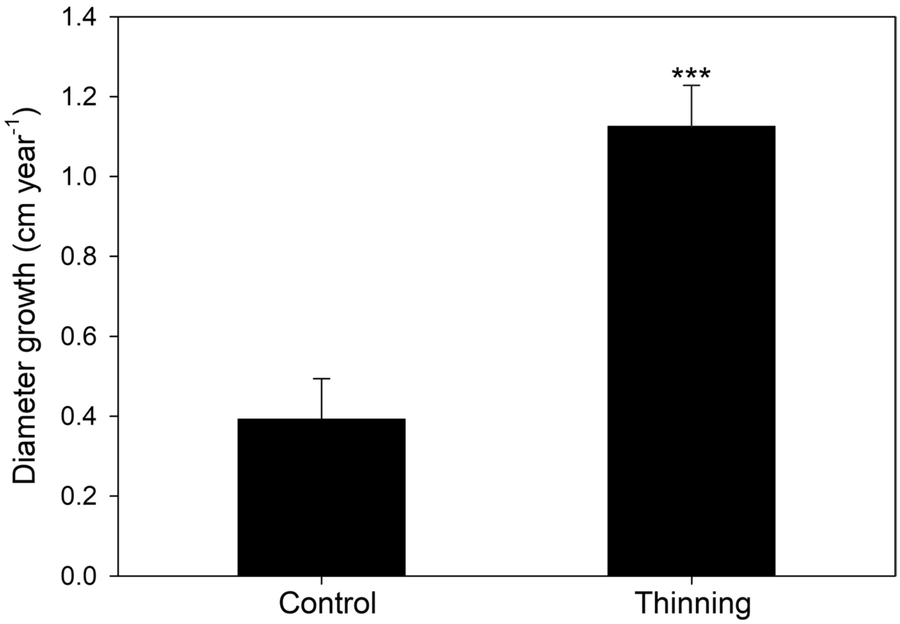


Fig. 4 Effects of thinning on diameter growth of *Bertholletia excelsa* ($n=8$) ***$p<0.001$. The bars represent the standard error of the mean

performance determined by stomatal conductance, LMA, and nutritional status. So, the first hypothesis of this study was endorsed, because the thinning increases the diameter growth of residual trees of *B. excelsa*. However, the second hypothesis was partially endorsed because the growth responses of *B. excelsa* to thinning was determined by the photosynthetic performance that was affected by the stomatal control, nutritional status, and morphological traits, but not by the water status of residual trees.

The greater availability of light has been pointed in a series of studies as the factor that, in the short term, further contributes to the increase in the rates of growth of plantations under thinning (Wang et al. 1995; Forrester et al. 2012, 2013a; Costa et al. 2020). Thus, our results suggest that the greater circulation of energy, due to the canopy opening, associated with the ability of this species to respond to the availability of light has directly influenced the performance of photosynthetic and consequently increased the *B. excelsa* growth rates under thinning treatment. Regarding the species, has been found in studies that the performance of *B. excelsa* is superior in environments with greater availability of light (Myers et al. 2000; Wadt et al. 2008; Paiva et al. 2011; Scoles and Gribel 2012; Sousa et al. 2014; Costa et al. 2022) and that the shading can be detrimental to the good performance of Brazil nut tree, compromising the survival of seedlings in the medium and long term (Scoles et al. 2014).

In relation to a performance photosynthetic, the greater availability of light reduced of maximum photochemical efficiency (F_V/F_M) of trees a week after the application of thinning. Similar behavior was found for this same species by Costa et al. (2020). This reduction probably is related to the increased non-photochemical dissipation (DI_O/RC) added to the reduction in the rate of transport of electrons (ET_O/RC) that were also recorded in the same period. The rapid recovery of F_V/F_M should be a consequence of the increase of N_a and P_a in the leaves of these trees. These nutrients are essential for the maintenance of the integrity of the thylakoid membranes, the structure of chloroplast pigments, and the enzyme activities involved in the electron transport in phase photochemistry of photosynthesis (Marenco et al. 2001; Zivcák et al. 2014; Costa et al. 2020).

The fact that *B. excelsa* has acclimatized to quickly increase in irradiance availability after thinning (represented by the rapid recovery of F_V/F_M values) was a determining factor in the increase in the photosynthetic capacity of this species. The photosynthetic performance of forest plantations subjected to thinning has been explained largely by increased irradiance on the remaining trees (Bréda et al. 1995; Wang et al. 1995; Forrester et al. 2012,

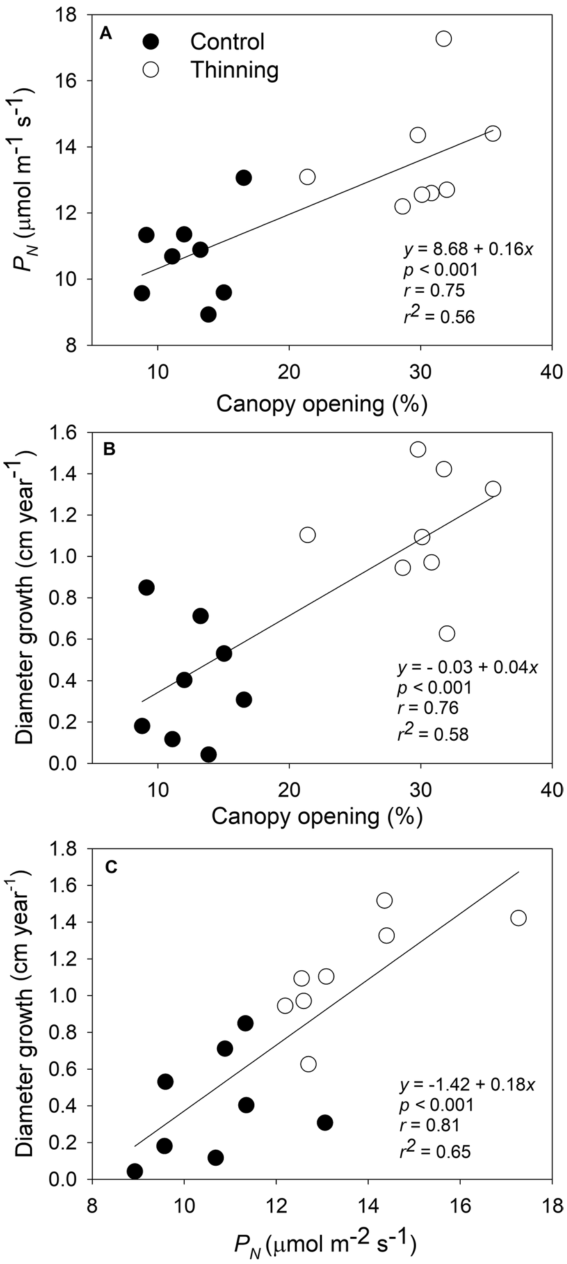


Fig. 5 Relationship between physiological and morphological variables of *Bertholletia excelsa* trees under thinning treatment (n=40) Note that part labels are mentioned in the artworks but not provided in captions of Figs. 2 and 5. Please check and amend if needed. In our opinion, it is not necessary. But if necessary, see the captions to Figs. 2 and 5. Fig. 2. Leaf gas exchange of *Bertholletia excelsa* trees under thinning (n = 8) * p < 0.05; ** p < 0.01; p < 0.001. The bars represent the standard error of the mean. The arrow indicates the time that thinning. Net photosynthesis (*PN*) per unit area (*A*), stomatal conductance (*gs*), transpiration (*E*), and dark respiration (*Rd*). Relationship between physiological and morphological variables of *Bertholletia excelsa* trees under thinning treatment. n = 40. Net photosynthesis (*PN*)

2013a). In this way, the increase in this work is related to the increase in the availability of light, as well as the increase of g_s, MFA, N_a, and P_a.

The increase in g_s and E under natural conditions or in response to thinning treatment has also been appointed as a result of the greatest availability of light associated with greater availability of water in soils and, consequently, appropriate water condition of the plants (Bréda et al. 1995; Habermann et al. 2011; Forrester et al. 2012; Sun et al. 2014). However, we did not observe changes in the water status of trees under thinning, which allows us to infer that instead of water condition, the canopy openness was crucial to the rise of g_s and E.

About R_d, little is known about its dynamics in thinned plantations. However, native species from the Amazon point that this variable increase with increasing irradiance, temperature, and improving the nutritional status of trees (Rodrigues and Gonçalves 2014; Jaquetti et al. 2016). In this way, the increase of the rates of R_d in *B. excelsa* under thinning can be a reflection of both the increase in irradiance and temperature that are associated with the highest percentage of canopy openness and the increase in concentrations of N_a, P_a, and K_a.

The increase in foliar concentrations of N_a, P_a, and K_a in this work reflects the increase of the MFA. Additionally, it has been verified that in addition to the increase in MFA, the reduction of intraspecific competition for nutrients, the withdrawal of the basal area of planting, and, in the case of N_a, increased rates of transpiration that favors the absorption of this nutrient for mass flow can also contribute to improving the nutritional status of trees under thinning treatment (Gauthier and Jacobs 2009; Han and Chiba 2009). It is important to highlight that the thinning residues (leaves, branches, and stems) were removed from the area, an aspect that allows us to infer the nonexistence of entry of nutrients to the soil via the decomposition of plant material.

The thinning usually results in the improved water status of forest plantations. However, most of these works were held in temperate regions, where the dry period normally imposes the vegetation water deficiency situations (Bréda et al. 1995; Sohn et al. 2013; Domingo et al. 2020; del Campo et al. 2022). The Amazonian species, however, do not seem to introduce water restrictions during months of lower precipitation (Asner et al. 2004; Restrepo-Coupe et al. 2013). The non-occurrence of water limitation may be associated with little pronounced seasonality in some Amazonian regions, the development of a deep root system, as well as hydraulic redistribution strategies, a process in which, the roots extract water from wet soil layers and deposited it in the drier (Nepstad et al. 1994; Oliveira et al. 2005). Although it has not been observed effect of thinning on the water status of trees, the treatment promoted increased efficiency in water use. This result can be explained by the increase in photosynthetic rates, which offset the higher rates of transpiration. In a way, this result although it is a characteristic inherent to the species, can also be seen as the result of the increase in water demands for regular leaf temperature and to keep carbon assimilation.

The increment in foliar mass per area (MFA) of trees under thinning treatment has been linked primarily to greater investment in the mesophyll. However, it has also been reported that plants acclimated to low irradiance, when exposed to high irradiance may also increase the thickness of the epidermis (Poorter et al. 2009). The increase in the proportion of mesophyll results in a greater number of chloroplasts in the base of the leaf area, photosynthetic capacity which favors the plants (Oguchi et al. 2005). While the increase in thickness of the epidermis protects the leaf against the damage caused by exposure to high irradiance (Poorter et al. 2009).

Overall, we found that *B. excelsa* responds to the thinning practice, increasing their rates of growth due to increased availability of light and consequently improving photosynthetic performance. It may be of interest to investigate the long-term effects of thinning on the growth of *B. excelsa*, as well as the suitable age, intensity, and type of thinning to be applied. It is also important to study the effects of thinning on wood properties and fruit production, since some studies have demonstrated that thinning influences these characteristics in other species (Allen 2008; Benedetti-Ruiz et al. 2023).

In summary, the application of thinning resulted in increased availability of light (greater openness of canopy), which favored the growth in diameter of *B. excelsa*. From a physiological point of view, the stomatal conductance, LMA, and nutritional status of *B. excelsa* were crucial to increasing the photosynthetic rates and, consequently, growth in diameter. Thus, our results have provided evidence that light conditions changes play a pivotal role in the growth performance of *B. excelsa* when cultivated in dense plantations. Therefore, implementing a thinning regimen becomes imperative as a strategy to augment the availability of these resources, thereby facilitating the resumption of tree growth. Furthermore, the thinning treatment created favorable conditions for the carbon capture, uptake, and storage capabilities of *B. excelsa*. Our findings indicate that thinning can be recommended for timber production under the dense planting of Brazil nut trees cultivated in degraded Amazonian areas.

5 Conclusion

Overall, we found that *B. excelsa* responds to the thinning practice, increasing their rates of growth due to increased availability of light and consequently improving photosynthetic performance. It may be of interest to investigate the long-term effects of thinning on the growth of *B. excelsa*, as well as the best age, intensity, and type of thinning to be applied.

In summary, the application of thinning resulted in increased availability of light (greater openness of canopy), which favored the growth in diameter of *B. excelsa*. From a physiological point of view, the stomatal conductance, LMA, and nutritional status of *B. excelsa* were crucial to increasing the photosynthetic rates and, consequently, growth in diameter. Thus, our results have provided evidence that light conditions changes play a pivotal role in the growth performance of *B. excelsa* when cultivated in dense plantations. Therefore, implementing a thinning regimen becomes imperative as a strategy to augment the availability of these resources, thereby facilitating the resumption of tree growth. Furthermore, the thinning treatment created favorable conditions for the carbon capture, uptake, and storage capabilities of *B. excelsa*. Our findings strongly indicate that thinning can be recommended for timber production under the dense planting of Brazil nut trees cultivated in degraded Amazonian areas.

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Author contributions IVdO, KCPdC, and JFdCG discussed the original idea. IVdO, and JCdC, carried out the experiments and analyzed the data. IVdO conceived the study and wrote the article with contributions of all authors; AdRNJ research plans and complemented the writing; IVdO and JCdC provided technical assistance to KCPdC and JFdCG supervised the experiments; JFdCG agrees to serve as the author responsible for contact and ensures communication.

Data availability The data associated with a paper is available at Theoretical and Experimental Plant Physiology.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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