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ORIGINAL ARTICLE

Growth and functional leaf traits of coppice regrowth of *Bertholletia excelsa* during an *El Niño* event in the central Amazon

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ABSTRACT

The most severe drought of this century in the Amazon rainforest, which was caused by *El Niño,* occurred from 2015 to 2016. With a focus on the ecophysiology of the regrowth of the Brazil nut tree, *Bertholletia excelsa*, it was investigated how the progression of the drought of 2015-2016 affected the physiological traits of the coppice regrowth of *B. excelsa*. The experiment was carried out in a ten-year-old plantation of Brazil nut trees, which had been subjected to thinning and coppice regrowth two years earlier. In the sprouts grown on the stumps of cut trees, the following treatments were applied: (T1) thinning to one sprout per stump; (T2) thinning to two sprouts per stump, and (T3) maintenance of three sprouts per stump. Thinning treatments did not alter the growth and ecophysiological traits of the Brazil nut tree sprouts, though the phosphorus content of the leaves was higher in T1. However, the progression of the drought in 2015-2016 negatively affected the growth (height) and gas exchange of sprouts of all treatments. In addition, an increase of around 37% was observed in the intrinsic water-use efficiency. Concerning photochemical performance, no alterations were observed. Therefore, drought stress promoted a negative effect on sprout growth and affected traits related to the photosynthesis of the *B. excelsa* sprouts independently of the number of sprouts per stump.

KEYWORDS: Brazil nut tree, drought, plant stress, silviculture, sprout, tree physiology

Crescimento e características funcionais foliares de rebrotas de *Bertholletia excelsa* durante um evento de *El Niño* na Amazônia Central

RESUMO

A seca mais severa deste século na floresta amazônica, causada por *El Niño*, ocorreu de 2015 a 2016. Com foco na ecofisiologia da rebrota da castanheira da Amazônia, foi investigado como a progressão da seca de 2015-2016 afetou as características fisiológicas das rebrotas de uma talhadia de *B. excelsa*. O experimento foi realizado em uma plantação de castanheiras com dez anos, a qual havia sido submetida a um desbaste e rebrota de talhadia dois anos antes. Nas rebrotas crescidas sobre os tocos das árvores cortadas foram aplicados os seguintes tratamentos: (T1) desbrota para manter um broto por cepa; (T2) desbrota para manter dois brotos por cepa; e (T3) manutenção de três brotos por cepa. Os tratamentos de desbrota não alteraram o crescimento e as características ecofisiológicas dos brotos da castanheira, exceto para o teor foliar de fósforo, que foi maior em T1. Porém, a progressão da seca em 2015-2016 afetou negativamente o crescimento em altura e as trocas gasosas dos brotos de todos os tratamentos. Além disso, foi observado um aumento de cerca de 37% na eficiência intrínseca do uso da água. Quanto ao desempenho fotoquímico, não foram observadas alterações. Portanto, o estresse hídrico promoveu efeito negativo no crescimento da brotação e afetou características relacionadas à fotossíntese das brotações de *B. excelsa*, independentemente do número de brotações por cepa.

PALAVRAS-CHAVE: castanheira-do-Brasil, seca, estresse vegetal, silvicultura, broto, fisiologia de árvores

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INTRODUCTION

Productive forest plantations represent approximately 0.42% of the soil use classes in deforested areas in the Brazilian Amazon (INPE 2016). One of the most commonly recommended tree species for plantations in disturbed areas of the Amazon is *Bertholletia excelsa* Humb. & Bonpl., since this species exhibits adequate stem characteristics, high survival rates, and high growth rates (Bertwell et al. 2018; Andrade et al. 2019). Additionally, it produces wood and fruit that have ecological and socioeconomic importance (Thomas *et al*. 2018; Staudhammer *et al*. 2021). These properties are probably due to the functional plasticity and stress tolerance of *B.excelsa* (Lopes *et al*. 2019; Schimpl *et al*. 2019; Costa *et al*. 2020, Scoles and Gribel 2021; Da Costa *et al*. 2022).

Another important characteristic of *B. excelsa* is the ability to emit sprouts (Scoles et al. 2011). The second rotation of planting can occur through seedlings or by regrowth coppice growing on the stumps, and because seed predation by rodents is high for *B. excelsa*, coppice regrowth can be a means of preventing such damage and improving survival (Peres *et al*. 1997; Drake *et al*. 2012). It is known that coppice regrowth enables more early and vigorous growth than when using seedlings (Drake *et al*. 2009; Ferraz Filho and Scolforo 2014); however, there is a need for further studies on thinning and coppice regrowth of *B. excelsa*.

Generally, the adoption of the coppice regrowth system for forestry stand management requires the implementation of thinning treatments, in which between one and three sprouts per stump are retained with the objective of greater growth of the dominant stem and improved product quality. This method is favorable because it decreases competition for primary resources and water loss by evapotranspiration (Drake *et al*. 2012; Xue *et al*. 2013; Souza *et al*. 2015). Therefore, thinning treatments may represent an important technique for encouraging coppice regrowth under anomalous climate conditions and when resources are scarce (Cabon *et al*. 2018). Such treatments may become increasingly relevant in face of climate change, which is projected to increase the severity and frequency of droughts, as well as the extent of areas that are affected as a result of the *El Niño* phenomenon or heat anomalies that are maximized by deforestation due to human actions (Duffy *et al*. 2015).

The *El Niño* event of 2015–2016 resulted in a prolonged drought in the Amazon rainforest (Jiménez-Muñoz *et al*. 2016). In this context, it is believed that the highest trees are particularly affected by hydraulic stress (Bennett *et al*. 2015), and this appears to be particularly true for *B. excelsa* (Staudhammer *et al*. 2021). Studies of *B. excelsa* plantations have already been carried out regarding ecophysiological measurements and the responses of Brazil nut trees to thinning (Ferreira *et al*. 2016; Costa *et al*. 2020), however, the growth and functional trait responses of coppice regrowth of *B. excelsa* in plantations throughout the drought of 2015-16 has not yet been reported in the literature.

In *El Nino* years, drought has been linked to increased mortality and decreased growth of trees in tropical forests, likely due to reduced water and nutrient availability (Palomo-Kumul *et al*. 2021). Consequently, the photosynthesis process is affected by water and nutrient limitations (whether in the capture of light energy or gas exchange), altering the photochemical traits and stomatal conductance efficiency of plants (Marenco *et al*. 2001; Rice *et al*. 2004; Alfaro *et al*. 2017; Yang *et al*. 2018). The physiological plasticity of *B. excelsa* subjected to different light, water, and nutrient availability (both under controlled conditions and in the field) has already been reported (Morais *et al*. 2007; Ferreira *et al*. 2009: Souza *et al*. 2017; Lopes *et al*. 2019; Schimpl *et al*. 2019; Costa *et al*. 2020; Da Costa *et al*. 2022). However, data on silvicultural treatments in cultivation areas are scarce, and there is no clear understanding of the effect of planting techniques, silvicultural interventions, soil types, or seasonality on the response of *B. excelsa* to drought (Costa *et al*. 2020; Da Costa *et al*. 2022).

This study is one of the first in the Amazon to examine the effects of the progression of the strong *El Niño* drought of 2015-2016 on coppice regrowth in a *B. excelsa* plantation in the Amazon. Although *B. excelsa* is resilient and displays physiological plasticity, it was hypothesized that: i) the progression of the dry season during *El Niño* years adversely affects the aboveground growth and physiological performance of *B. excelsa* regrowth; and ii) higher intensity thinning treatments for sprouts do not affect the growth of the dominant stem and leaf functional traits of the regrowth. We investigated how the progression of the dry season of 2015-2016 affected the growth and leaf functional traits of the coppice regrowth of *B. excelsa* in a productive plantation in the central Amazon. The results obtained are discussed in the context of current models of physiological shifts in trees occurring during stress, which may assist forest management practices, afforestation, and reforestation in the Amazon.

MATERIAL AND METHODS

Study site and experimental design

This study was conducted using field-grown *B. excelsa* trees owned by the company Agriculture Aruanã S.A., located in Itacoatiara, Amazonas State, Brazil (3°0'30.63"S, 58°50'1.50"W). The soil is predominantly a clayey, yellow Latosol, generic Ferrolsol, and the topography presents ripples, with altitudes varying between 120 m and 170 m (FAO-Unesco-ISRIC 1990, Botschek *et al*. 1996, Ferreira *et al*. 2016). The climate of the region is A f under the Köppen classification (Köppen and Hendrichs-Pérez 1948).

According to data from an automated station of the National Institute of Meteorology (INMET), located in the city of Itacoatiara - AM (58ºW; 3ºS) from 1972 to 2014, the average minimum and maximum temperatures were 23.0 °C and 31.9 °C, respectively, and the average rainfall was 2,403 mm. However, in 2015, the average annual minimum and maximum temperatures were 24.7 °C and 33 °C, respectively, and the recorded rainfall was 2,239.9 mm, although with only 3.9 mm in September (Figure 1).

Seven-month-old seedlings of *B. excelsa* were planted in 2005 and distributed at a spacing of 2.5 m x 1.5 m. Fertilizer was not applied, and weeds were controlled by mechanized mowing twice a year. Between July 8th and 12th, 2013, when the trees were eight years old, the plantation was submitted to tree thinning. In May 2015, the diameter (0.05 m at ground level) and total height (m) of individual sprouts growing in the understory of the plantation after tree thinning were measured (Drake *et al.* 2009).

A census of coppice regrowth was conducted on 251 stumps, which were then grouped by the number of sprouts, average diameter class (5 cm wide), and average height class (100 cm wide). Subsequently, biometrically similar subjects were selected from eight samples of coppice regrowth for each sprout thinning treatment (T1 – thinning to one sprout per stump, T2 – thinning to two sprouts per stump, and T3 – maintenance of three sprouts per stump) and arranged in a randomized complete block design (RCBD). The growth and ecophysiological traits of the single sprout or the dominant sprout in T2 and T3 were measured on day 7 (July 2015), day 85 (October 2015), and day 141 (December 2015) after

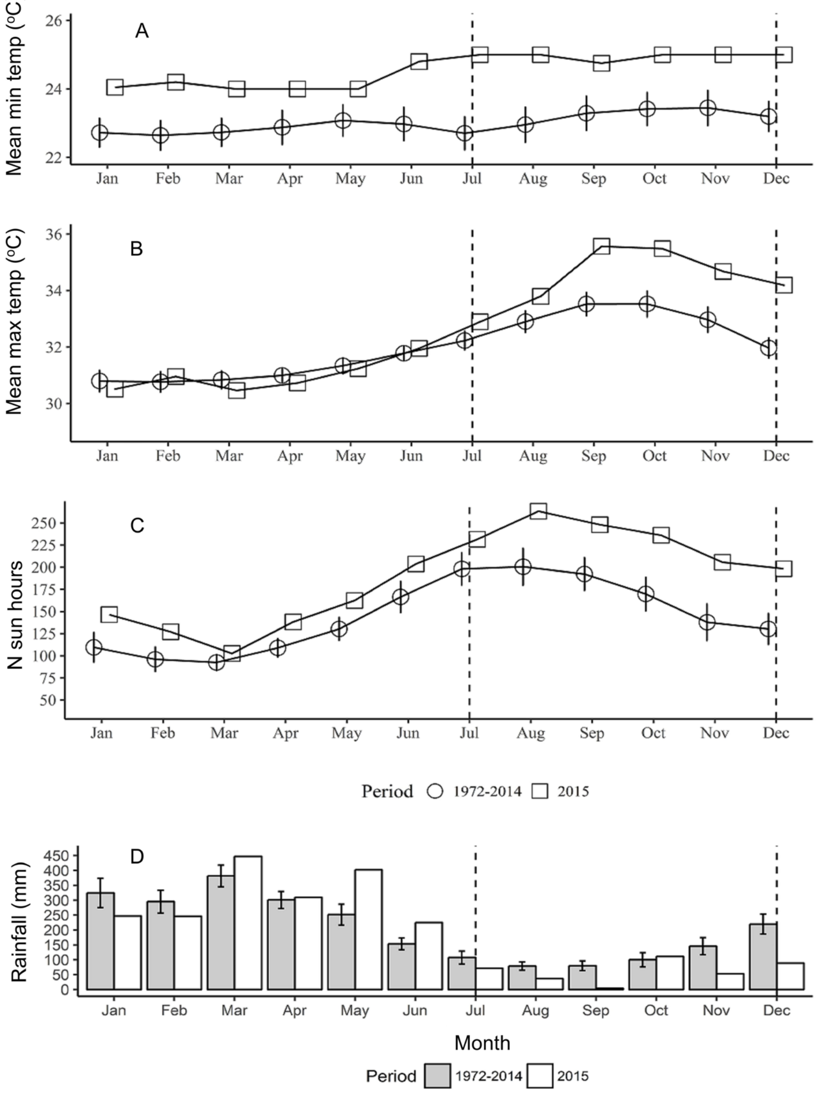

Figure 1. Minimum monthly temperature (A), maximum monthly temperature (B), monthly hours of sunlight (C), and monthly rainfall (D) for the period 1972–2014 (monthly averages) and for 2015 in Itacoatiara, Amazonas, Brazil. Vertical bars represent the confidence interval of 95%, and the vertical dotted lines delimit the experimental period. Source: National Institute of Meteorology (INMET) Brazil.

the sprout thinning treatment, and after the sprouts had experienced a worsening of the dry season caused by the effects of *El Niño*.

Total stem basal area and growth in height and diameter

The total height (*H*, cm) was measured using hypsometric rules, and the diameter (*D*, cm) was measured with digital calipers 0.05 m above the ground surface for each sprout of the sample stump (Drake *et al.* 2009). The total stem basal area was calculated for the sum of the basal area of each coppice stump ($A_{b,}$ cm^2), and the absolute growth rates (AGRs) for height (cm day^{-1}) and diameter (mm day^{-1}) were calculated for two distinct periods of precipitation, from July to August (high precipitation), and from August to December 2015 (low precipitation) (Bugbee 1996; Drake *et al.* 2012).

Leaf water potential

Midday leaf water potential (Ψw, MPa) was determined using a Scholander pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA) (Scholander *et al.* 1965). For each sample, two fully expanded leaves located in the middle third of the branch and canopy in the dominant sprout (greater height) were collected and the measurements were taken between 11:00 am and 12:00 pm. The increment of pressure applied was 0.2 MPa and the waiting time for sieve extrusion was five minutes (Turner 1981; Liberato *et al.* 2006).

Leaf gas exchange

Net photosynthesis rate (*A*, μmol CO_2 m^{-2} s^{-1}), dark respiration (R_d,μmol CO_2 m^{-2} s^{-1}), internal CO_2 concentration (*C*i, μmol CO_2 mol^{-1}), stomatal conductance (g_s, molH_2O m^{-2} s^{-1}) and transpiration rates (*E*, mmolH_2O m^{-2} s^{-1}) were determined using a portable photosynthesis system (LI-6400, Li-cor, USA) equipped with an artificial irradiance source (6400-02B Red Blue) from 8:00 am to 12:00 pm for leaves in the same position on the branch and within the canopy as those used to determine the leaf water potential. All measurements were taken at photosynthetic photon flux densities (PPFD) of 0 and 1,500 μmol photon m^{-2} s^{-1}, with the leaf chamber adjusted for a CO_2 concentration, H_2O vapor, and temperature of approximately 400 ± 4 μmol mol^{-1}, 21 ± 1 mmol mol^{-1} and 31 °C ± 1 °C, respectively (Santos Junior *et al.* 2006, 2013). The water-use efficiency (WUE) was calculated as the ratio between *A* and *E*, and the intrinsic water-use efficiency (WUE_i) was calculated as the ratio between *A* and g_s (Farquhar and Richards 1984; Polley *et al.* 1993; Silva *et al.* 2008).

Chlorophyll *a* fluorescence

The chlorophyll *a* (Chl*a*) fluorescence was determined from two completely expanded leaves of the coppice regrowth sample, concurrent with the gas exchange measurements and in a similar location, by using a portable fluorometer (Plant Efficiency Analyser, MK2 – 9600, Hansatech, Norfolk, UK). The selected leaves were submitted to a 30 min period of adaptation to darkness. Subsequently, the leaves were exposed to saturated light at an intensity of 3,000 μmol m^{-2}s^{-1}and a wavelength of 650nm for 5 s (dos Santos Junior et al. 2015). The parameters related to polyphasic chlorophyll *a* fluorescence transient were obtained from specific software (Handy PEA software – v 1.30), and quantum efficiency of PSII (Fv/F_M) and the performance indicators PIabs and total PI were calculated according to the JIP-test (Strasser *et al.* 1995).

Chloroplast pigment content

Chloroplast pigments were measured in leaves with similar characteristics to those used for the leaf gas exchange measurements. Chlorophyll (Chl*a* /Chl*b*) and carotenoid contents (C_{c+x}) were extracted with 80% (V/V) acetone and 0.5% (W/V) magnesium carbonate ($MgCO_3$), and determined spectrophotometrically according to the methodology modified by Lichtenthaler and Wellburn (1983). The concentration of chloroplast pigments in the base area (μmol cm^{-2}) was estimated according to the equations by Hendry and Price (1993).

Leaf nutrient content

In each sample, five fully expanded leaves of the regrowth were collected from the dominant sprout (Drake *et al.* 2009) at the middle third of the branch and canopy. The leaves were oven-dried at 65 ºC for 72 hours. The total nitrogen (N) was determined using the Kjeldahl method (Bremner and Mulvaney 1982). The macronutrients phosphorus (P) and potassium (K) and the micronutrients iron (Fe), zinc (Zn), and manganese (Mn) were extracted by digestion with a 3:1 nitric-perchloric solution. The concentrations of K, Fe, Zn, and Mn were determined via atomic absorption spectrometry (Perkin-Elmer 1100B, Uberlingen, Germany), and P was determined by spectrophotometry at 725 nm (Miyazawa *et al.* 1999).

Data analysis

Each variable was subjected to repeated measures ANOVA. The data were previously submitted to a normality test (Shapiro-Wilk test) and a homogeneity of variance test (Levene's test). Variables that did not comply with the assumptions for parametric analysis were transformed using the logarithmic function (ln) (PI_{abs}, Ca, and Mg), or using the square root function (R_d, Fe, and Mn). Then, the parameters were used to test the sphericity hypothesis using the Mauchly test and, when violated, the degrees of freedom for the measured months were corrected by the Greenhouse-Geisser procedure. In such cases, the height and diameter of the dominant sprout, the R_d, WUE, WUE_i, Chl *b*, N, Fe, and Zn values were fixed and the mean values were compared using the Bonferroni test. Graphs were constructed using the

R platform (R Core Team 2014) and the packages ggplot2 (Wickham 2011a), plotly (Sievert *et al*. 2016), plyr (Wickham 2011b), and Rmisc (Hope 2013), and the statistical analysis was performed using SPSS version 21.0 (IBM, Armonk NY).

RESULTS

Of a total of 251 trees, 98% of the tree coppice regrew two years after thinning. The thinning treatment decreased the total stem basal area by 51% for T1 and 18% for T2, but this treatment did not result in greater absolute growth rates (AGR) in relation to the height and diameter of the dominant sprout (Figure 2). The AGR of the height of the dominant sprout decreased significantly throughout the period of measurement (Table 1) and was 60% lower from October to December than from July to October ($p < 0.002$, Bonferroni test) (Figure 2).

The thinning treatments did not significantly influence the Ψw, gas exchange, and water use efficiency (Table 1), but these variables were significantly affected by the progression of the dry season (Table 1). The Ψw values were significantly lower in October than in July ($p < 0.001$, Bonferroni test), whereas the lowest value was observed in December when Ψw was 156% lower than in July ($p < 0.001$, Bonferroni test) and 27% lower than in October ($p = 0.005$, Bonferroni test) (Figure 3a). *A* and *gs* in December were 28% and 51% lower, respectively, compared to July ($p < 0.001$ (both), Bonferroni test) and 36% and 49% lower, respectively, compared to October ($p < 0.001$ and $p = 0.001$, respectively, Bonferroni test) (Figure 3c).

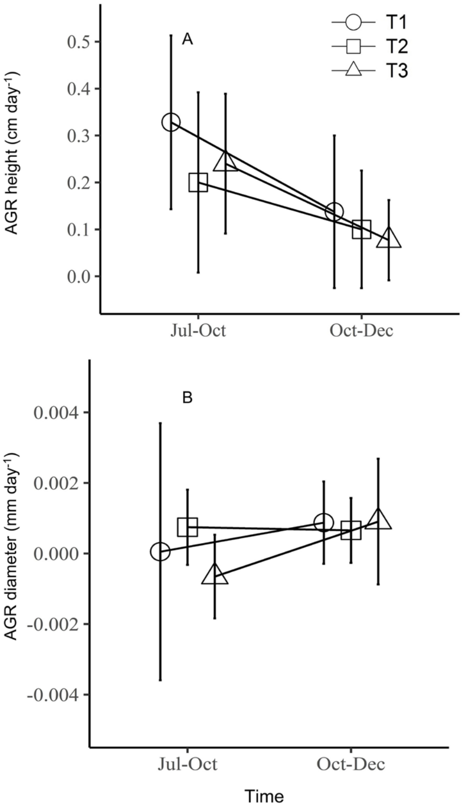

Figure 2. Absolute growth rates in height (A) and diameter (B) of the dominant sprout in coppice regrowth samples of *Bertholletia excelsa* under three thinning treatments measured from July (Jul.) to October (Oct.), and October (Oct.) to December (Dec.) 2015 in a dense forest plantation subjected to thinning. Symbols represent the mean and vertical bars of the standard deviations of the treatments: T1 = thinning to one sprout per stump; T2 = thinning to two sprouts per stump; and T3 = maintenance of three sprouts per stump) ($n = 8$ per treatment).

The thinning treatments and the progression of the dry season did not have a significant effect on F_V/F_M, $PI_{abs,}$ and PI_{total} (Table 1). Among the chloroplast pigments, only the Chl*a*/Chl*b* rate differed significantly among months (Table 1), with 8% and 6% lower values in July than in October ($p = 0.001$, Bonferroni test) and December ($p = 0.014$, Bonferroni test).

Regarding mineral nutrient contents, N and *P* values were 9% and 35% higher in October than in July, respectively ($p = 0.031$ and $p < 0.001$, respectively, Bonferroni test), and 14% and 28% higher than in December, respectively ($p = 0.001$ and $p < 0.001$, respectively, Bonferroni test) (Figure 4a and 4b). Among the macronutrients, only P was significantly affected by the thinning treatment (Table 1), with higher levels in T1 than in T2 ($p < 0.001$, Bonferroni test) and T3 ($p = 0.038$, Bonferroni test) (Figure 4b). However, all macronutrients differed significantly among the months (Table 1). The K content was lower in July than in October (37%) and December (33%) (p < 0.001, Bonferroni test, for both months) (Figure 4c).

Among the micronutrients, Fe differed significantly among months according to the ANOVA (Table 1); although the Bonferroni test did not indicate significant pairwise differences between the months. Mn also differed significantly among months (Table 1), with 38% lower content in October than in July ($p < 0.024$, Bonferroni test). Zn did not vary significantly among the months (Table 1).

DISCUSSION

In this study, we gained valuable insights into the physiology of *B. excelsa* trees grown in plantations under different management strategies and under *El Niño* conditions. Below, we discuss the main physiological mechanisms involved in the response of *B. excelsa* when affected by natural drought stress.

Drought stress and stomatal and non-stomatal limitations

When compared with the historical average, the *El Niño* of 2015 and 2016 showed a 49% reduction in rainfall and an increase in temperature during the dry season, which negatively affected the height of *B. excelsa* coppice regrowth in the understory. This demonstrates the importance of water availability for growth and the capture and use of

Table 1. Repeated measures analysis of variance of the changes in the growth and leaf functional traits of the dominant sprout of *Bertholletia excelsa* copice regrowth in three thinning treatments during the progression of the drought of 2015-2016 (time), and interaction between the factors (time x thinning).

Dependent variable	Time			Thinning treatment			Time x Thinning interaction		
	F	df	P	F	df	P	F	df	P
AGR height	13.206	1, 21	0.002	0.417	2, 21	0.665	1.243	2, 21	0.309
AGR diameter	0.955	1, 21	0.340	1.610	2, 21	0.224	0.018	2, 21	0.122
Ψw	57.107	2, 42	< 0.001	0.369	2, 21	0.696	0.201	4, 42	0.110
A	75.657	2, 42	< 0.001	0.336	2, 21	0.719	0.290	4, 42	0.883
R_d	7.861	1.531, 32.153	0.003	1.349	2, 21	0.281	4.270	3.062, 32.153	0.739
Ci	75.657	2, 42	<0.001	0.249	2, 21	0.782	0.836	4, 42	0.510
g_s	16.67	2, 42	<0.001	0.171	2, 21	0.844	0.121	4, 42	0.974
E	18.255	2, 42	<0.001	0.211	2, 21	0.811	0.059	4, 42	0.993
F_V/F_M	1.48	2, 42	0.239	0.072	2, 21	0.931	0.524	4, 42	0.719
PI_{abs}	1.803	2, 42	0.177	0.08	2, 21	0.923	1.618	4, 42	0.188
PI_{total}	2.801	2, 42	0.072	0.002	2, 21	0.998	1.092	4, 42	0.373
Chl_a	0.197	2, 42	0.822	0.347	2, 21	0.711	0.242	4, 42	0.913
Chl_b	0.497	1.518, 31.871	0.562	0.0	2, 21	1.0	0.308	3.035, 31.871	0.822
C_{c+x}	0.449	2, 42	0.641	0.629	2, 21	0.543	0.154	4, 42	0.960
Chl_{total}	0.282	2, 42	0.756	0.668	2, 21	0.524	0.192	4, 42	0.941
Chl_{total} / C_{c+x}	0.294	2, 42	0.747	0.194	2, 21	0.825	0.635	4, 42	0.640
Chl_a /Chl_b	13.510	2, 42	<0.001	0.078	2, 21	0.925	0.739	4, 42	0.571
N	11.741	1.510, 31.707	<0.001	1.641	2, 21	0.218	0.579	3.020, 31.707	0.634
P	42.357	2, 42	<0.001	11.219	2, 21	<0.001	2.042	4, 42	0.106
Ca	17.820	2, 42	<0.001	0.819	2, 21	0.454	0.948	4, 42	0.446
Mg	9.174	2, 42	<0.001	1.811	2, 21	0.188	2.430	4, 42	0.062
K	46.406	2, 42	<0.001	0.476	2, 21	0.628	1.26	4, 42	0.301
Fe	3.941	1.532, 32.179	0.027	0.049	2, 21	0.952	0.345	3.065, 32.179	0.797
Mn	3.779	2, 42	0.031	0.291	2, 21	0.750	0.915	4, 42	0.464
Zn	2.007	1.319, 27.695	0.165	0.594	2, 21	0.561	1.324	2.638, 27.695	0.286

Dependent variable data differ significantly when affected by time, thinning treatment, or interaction between factors (time x thinning treatment) by repeated measures when $p \leq 0.05$. AGR - absolute growth rate.

carbon, particularly for this species (Schimpl *et al.* 2019). The effect resulted in the greatest damage between October and December, because of the gradual increase in stress conditions. The sprouts were more tolerant at the beginning of the experimental period, maybe due to factors such as greater soil moisture at the beginning of the dry period, and adaptation mechanisms of the species, which occurs in areas with a longer dry season, and is thus adapted to these conditions (Ferreira *et al.* 2016; Castellanos-Acuña *et al.* 2018; Li *et al.* 2018).

The inherent decline in aboveground growth and the possible contribution of the reduction in the photosynthetic capacity in December may highlight the sensitivity and stomatal control in relation to PS-II efficiency. This result corroborates studies that show that stomatal conductance is more sensitive to changes in water availability, whereas the structural and functional responses of the thylakoid membrane require a greater stress intensity or a combination of stress factors, as this membrane presents improved protection mechanisms (Gallé *et al.* 2007). Stomatal closure could be a strategy of *B. excelsa* to reduce the risk of xylem dysfunction in response to drought stress at the cost of gas exchange (Chen *et al.* 2010; Lu *et al.* 2020). On the other hand, stomatal limitations are characterized by a faster recovery after re-watering, which suggests that a higher rate of return will be observed under photosynthetic conditions after the onset of rainfall, when under the studied conditions (Gallé *et al.* 2007).

The absence of significant responses of chlorophyll *a* fluorescence is consistent with the results obtained for chloroplast pigments, and only the relationship between Chl*a* and Chl*b* was affected during the study period. The lowest ratio of Chl*a*/Chl*b* was observed in July rather than in October and December, which likely indicates a response to increased levels of irradiance, representing a reduction of the complex antenna and the PSII/PSI relationship (Evans and Poorter 2001). Thus, the understory location of the sprouts likely contributed to lower light radiation levels and a reduction in

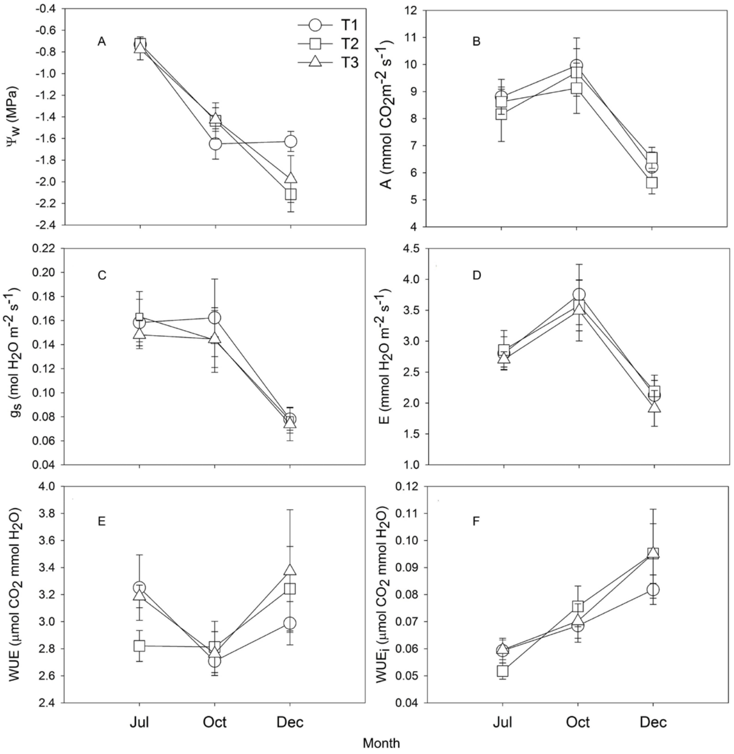

Figure 3. Ecophysiological parameters of the dominant sprout of coppice regrowth samples in a dense plantation forest of *Bertholletia excelsa* under thinning treatments measured in July (Jul), October (Oct), and December (Dec) in 2015. A – leaf water potential (Ψw, MPa); B – net photosynthesis rate (*A*, µmol CO_2 m^{-2} s^{-1}); C – stomatal conductance (g_s, molH_2O m^{-2} s^{-1}); D – transpiration rates (*E*, mmolH_2O m^{-2} s^{-1}); E – water-use efficiency (WUE); F – intrinsic water-use efficiency (WUE_i). Symbols represent the mean and vertical bars are the standard deviations of the treatments. T1 = thinning to one sprout per stump; T2 = thinning to two sprouts per stump; and T3 = maintenance of three sprouts per stump (*n* = 8 per treatment).

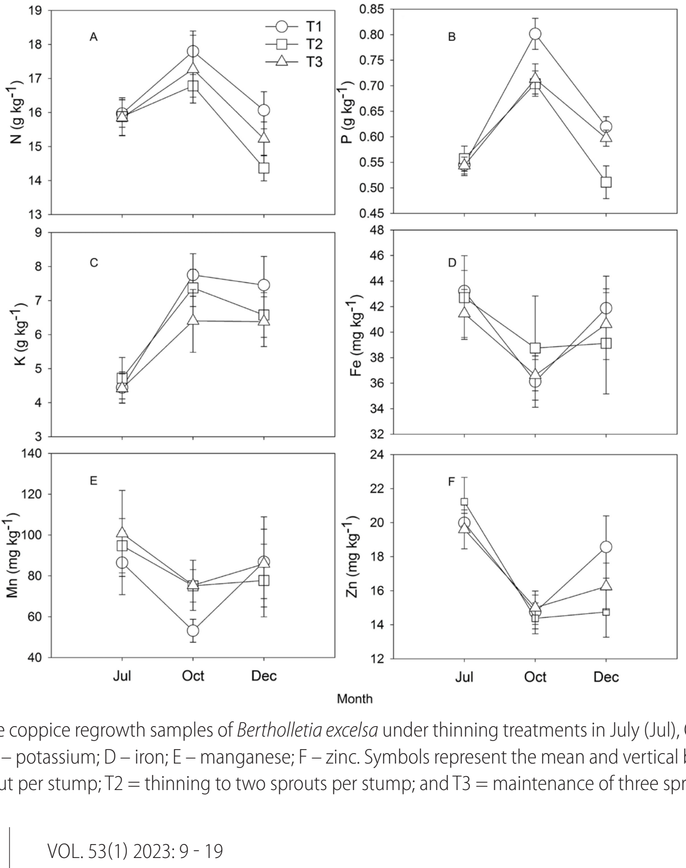

Figure 4. Leaf nutrient content of the coppice regrowth samples of *Bertholletia excelsa* under thinning treatments in July (Jul), October (Oct), and December (Dec) in 2015. A – nitrogen; B – phosphorus; C – potassium; D – iron; E – manganese; F – zinc. Symbols represent the mean and vertical bars are the standard deviations of the treatments. T1 = thinning to one sprout per stump; T2 = thinning to two sprouts per stump; and T3 = maintenance of three sprouts per stump (*n* = 8 per treatment).

stress conditions that are common when plants are exposed to direct sunlight and longer exposure to light stress. In this way, the understory environment contributes to the maintenance of fluorescence parameters. Moreover, the c_{c+x} content does not appear to result in increased energy dissipation (Ferreira *et al.* 2009; Gonçalves *et al.* 2010; Hallik *et al.* 2012).

Additionally, the stomatal control, reduction in g_s and *Ci*, and increase in WUE$_i$ in December compared with that of previous months, as well as the maintenance of K levels and reductions of N and P levels compared with that in October, may be related to increased stomatal regulation against water loss, which was provided by the K content (Fortini *et al.* 2003).

The beginning of the low rainfall period (July and August) did not have a negative effect on the leaf functional traits and did not represent characteristic stress conditions. The maintenance of leaf functional traits at the beginning of the dry season may have contributed to mechanisms that are associated with higher leaf emergence in the low rainfall period, and these mechanisms may explain the higher N, P, and K contents and *E* in October, which are traits observed in younger leaves (Kitajima *et al.* 1997; Ferreira *et al.* 2016).

The increased levels of N and P in October, compared with those in July, were similar to the results reported by Ferreira *et al.* (2016), who described an increase in the levels of these nutrients in the low precipitation period for adult clone species. This increase, which is due to the function of these nutrients, can be attributed to electron transport, the activity of Rubisco, the availability of phosphate sugars and chloroplast pigment content, and the consequent increase of WUE$_i$ and *A* (Kitajima *et al.* 1997; Carswell *et al.* 2000). Although the highest *E* values were observed in this same month, this may have been due to differences in anatomical and morphological levels linked to leaf ontogeny, such as cell density and cutin and wax deposition and composition, which provides less resistance to the transpiration process in this month than in other months (Aasamaa *et al.* 2005; Pantin *et al.* 2012).

Despite the gradual reduction of the leaf water potential over time, the decrease recorded in October did not represent damage to photosynthetic activity, which led to the maintenance of g_s. These variables are not always strongly related, as leaf water potential can reach lower values without affecting the photosynthetic activity, due to that stomata remain open throughout the day in response to a combination of environmental conditions, as well as ontogenetic factors designed to restore hydration overnight (Niinemets *et al.* 1999; Ferreira *et al.* 2009). However, the increase in *E* and the maintenance of g_s values are not indicative of water stress, because these values usually decrease during water stress conditions with increased concentration of abscisic acid (Niinemets *et al.* 1999; Pou *et al.* 2008). Thus, depending on the emission mechanisms for new leaves or of leaf phenology as a whole, in combination with the ability to mobilize soil resources, the first months of the low rainfall period of anomalous years may not result in a reduction in leaf functionality (Palomo-Kumul *et al.* 2021).

Sprout thinning and growth and leaf functional traits

The thinning of sprouts resulted in a reduction of the total stem basal area of the coppice regrowth, but not in greater height and diameter of the dominant sprout, and the leaf functional traits were not significantly affected by the progression of the dry season. Studies on other species have indicated that the absence of a significant effect of thinning on the growth of sprouts may be caused by a natural reduction in the number of sprouts after treatment (Xue *et al.* 2013; Souza *et al.* 2015). Even so, in terms of growth, our findings may have been due to the short duration of the experiment (Souza *et al.* 2015). Moreover, the conditions of the understory may have been crucial to the lack of significant differences among thinning treatments, and because the low level of irradiance tends to promote less *E* and, consequently, should result in lower stress in the low rainfall period in *El Niño* years. Nonetheless, the lack of effect on growth showed the inefficiency of sprout thinning on *B. excelsa* in our study area.

Stability of the photosynthetic apparatus

Above we highlight our previous findings on the functional characteristics of *B. excelsa* in terms of physiological plasticity, particularly concerning the photochemical traits of the species (Morais *et al.* 2007; Ferreira 2009; Lopes *et al.* 2019; Costa *et al.* 2020). We showed the photochemical stability of understory *B. excelsa* coppice regrowth in a planted forest under different sprout thinning conditions during an *El Niño* year. The nutrient efficiency of N, P, and K (Ferreira *et al.* 2015; 2016) was discussed, emphasizing the importance of nutrient-sensitive manganese in aiding the protection of the photosynthetic apparatus of the leaves of *B. excelsa,* probably through intense redox reactions, and thus avoiding photooxidation effects and protecting the maintenance of photosynthesis in field conditions (Ferreira *et al.* 2016; this study). It is also worth mentioning the effect of Fe, which can corroborate the idea of the intense electron flow mechanism through oxidation and reduction reactions in plants (Zhu *et al.* 2022). Further studies should address water relations and their direct effect on water transport, hydraulic architecture, and gas exchange in *B. excelsa* in long-term field experiments. Under controlled conditions, the value of $\Psi w = -4.7$ MPa in *B. excelsa* seedlings subjected to water deficit and subsequent recovery was found to explain the variations in growth, functional responses, and leaf anatomical characteristics (Schimpl *et al.* 2019). However, field conditions are more complex and variable than controlled conditions. Another aspect to be considered is that the vascular structure of a sapling may not have the same anatomical characteristics of *B. excelsa* coppice regrowth.

CONCLUSIONS

The progression of the dry season in 2015-2016 significantly affected the growth, leaf water status, and gas exchange of coppice regrowth of *B. excelsa* plants subjected to the strongest *El Niño* event in recent decades in the Amazon, while these traits were not affected by thinning treatments. We also observed that the drought stress conditions were not sufficient to impair photochemical performance. Our findings reinforce the concept that *B. excelsa* has high plasticity in its key photosynthetic apparatus traits, such as the chlorophyll *a* fluorescence parameters and chloroplast pigment content. In addition, the potential role of manganese and iron as key micronutrients for the protection of the photosynthetic apparatus in *B. excelsa* is supported. Together, these functional leaf traits may have important implications for the superiority of *B. excelsa* in response to prolonged droughts in plantations in the central Amazon. The physiological variables analyzed here can serve as indicators for improving silvicultural practices aiming at the sustainability of Brazil nut tree plantations in the Amazon.

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