



Comparative study on different planting systems of the Brazil nut trees established in a degraded area of the Amazon

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Abstract

The allocation and distribution of primary resources in planting systems can significantly influence the physiological and growth performance of *Bertholletia excelsa*, an Amazonian tree of significant socioeconomic and ecological importance. This study was carried out for two years to investigate the resource availability and ecophysiological responses of *B. excelsa* cultivated in different planting systems in 3 × 3 spacing: (1) pure plantation, (2) mixed plantation using *B. excelsa* and *Inga edulis* and (3) an agroforestry system (AFS); the AFS with intercropping of *Theobroma cacao* and *Musa* sp. between *B. excelsa* and *I. edulis* trees, respectively. Planting systems (Pure, Mixed and AFS) were evaluated based on site resource availability, growth rate, gas exchange, nutrient use efficiency, and nutritional status of *B. excelsa*. This study showed greater availability of light in pure plantations and a better soil quality index in the AFS. The Brazilian nut trees in the AFS showed higher values of photosynthesis (P_N), stomatal conductance (g_s), transpiration (E), foliar content of phosphorus, calcium, and magnesium, and greater efficiency in the use of nitrogen and potassium. Brazilian nut tree saplings showed greater investment in light capture, with greater height growth, and no difference in diameter growth rates. From the present study, it can be concluded that in the initial growth phase relating to the first installation years of field plantings, the AFS favors the ecophysiological performance and height growth of *B. excelsa* saplings in degraded areas of Eastern Brazilian's Amazon.

Keywords Agroforestry system · Brazil nut tree · Gas exchange · Mixed plantations · Nutrient use efficiency · Physiological plasticity

Introduction

The Brazilian Amazon has lost approximately 20% of its original forest area, and its degradation has reached 1,104,533 ha (INPE 2023). This area includes the state of Pará, where the so-called “polygon of Brazil nut trees” is located, named after the high abundance of Brazil

nut trees (*Bertholletia excelsa* Bonpl.), and the region's history of the species extractivism (Homma 2014; Guariguata et al. 2017). Intensive deforestation, together with changes in occupational dynamics and land use, has fragmented *B. excelsa* populations. This has led to individual isolation, and consequently, high mortality rates. The groves underwent significant ecological degradation and are now referred to as "Brazil nut cemeteries" (Bentes et al. 1988; Guariguata et al. 2017).

Degraded areas have high irradiance levels, low soil cover, and a low availability of primary resources (Santos Junior et al. 2006; Jaquetti et al. 2021). There is a need to select physiologically plastic species with high biomass production, silvicultural adjustments, and ecosystem services (Jaquetti et al. 2016, 2021; Jaquetti and Gonçalves 2017; da Costa et al. 2022; da Silva Ceretta et al. 2025). However, it is not possible to find a single species that brings together all the desirable characteristics, and it is necessary to associate a group of species that meet the needs of degraded sites (Caetano et al. 2014; Santos and Ferreira 2020). Thus, a combination of plant species is a viable alternative to meet such demands, for example through agroforestry systems (AFSs) and mixed plantations formed by economically important nitrogen-fixing legumes (de Souza et al. 2023; Reid et al. 2024).

Inga edulis is a legume tree that associates with nitrogen-fixing bacteria and shows rapid growth, tolerance to acidic and nutrient-poor soils, high leaf biomass production, besides being used for soil fertility improvement by the deposition of nitrogen-rich litter (Lojka et al. 2010; Joslin et al. 2024). The species also attracts small animals to forage for fruit, and its canopy structure is attractive to birds, functioning as a natural perch (Melo et al. 2015; Rodrigues et al. 2021). Because of these characteristics, *I. edulis* is considered a facilitator species in the ecological succession processes (Lojka et al. 2010; Melo et al. 2015). Therefore, they have been used to recover degraded areas and integrate AFSs and mixed plantations (Joslin et al. 2024).

The AFS and mixed plantations are considered alternatives to pure plantations or monocultures, in which a single species is cultivated in the production area (de Souza et al. 2023). AFSs and mixed plantations restore soil fertility, reduce water and nutrient loss, and contribute to soil organic matter. Other environmental benefits include fruit and seed dispersal, commercial products, and income promotion (Ferreira and Tonini 2009). These planting systems are economic alternatives to constitute a legal reserve, as ensured by Brazilian legislation (Homma et al. 2014; Souza et al. 2017; de Souza et al. 2023).

Site edaphoclimatic factors, such as rainfall regime, soil acidity, and low natural fertility, represent another critical challenge for species establishment and growth. The Amazon biome predominates in the southeastern region of Pará, characterized by intense solar irradiation throughout the year, water availability varying from 377 mm/month in the wettest period (December to April) to 11 mm/month in the driest period (June to September) (INMET 2019). Reforestation of degraded areas in this region is strongly affected by water dynamics and nutrient availability. This results in poor establishment and survival of plants in the Eastern Brazilian Amazon, as these stressor effects become even more severe in altered areas. Therefore, it is important to consider how abiotic factors affect the juvenile phase of trees, which coincides with their growth phase when they are planted in the field. Perennial trees often undergo a long and complex juvenile phase that can last for several years (Pan et al. 2023).

Among the Amazon forest species, *B. excelsa* exhibits biological and economic characteristics that reflect its great potential for integrating planting systems to recover altered

or degraded areas (Costa et al. 2009; da Costa et al. 2022). This species contributes to ecosystem functioning by sequestering carbon and attracting animals that facilitate pollination and seed dispersal (Fauset et al. 2015; Santos-Silva et al. 2017; de Souza et al. 2023). The forestry industry shows strong interest in products like wood and fruits, which are well-established in international markets (Salomão et al. 2020; de Souza et al. 2023). Furthermore, studies have demonstrated *B. excelsa* is tolerant of reduced soil water and nutrient availability. In addition, the physiological plasticity of the species to changes in light availability promotes growth and carbon assimilation, even under stressful conditions, such as altered or degraded areas (Souza et al. 2017; Lopes et al. 2019; Melo et al. 2019; Schimpl et al. 2019; da Costa et al. 2022; de Souza et al. 2023; Oliveira et al., 2024b).

However, the response of *B. excelsa* under different planting systems, in the same degraded site conditions, remains unclear. In this study, we sought to understand the growth performance and ecophysiological responses of *B. excelsa* in pure plantations, mixed plantations, and AFSs installed in a degraded pasture area in the Amazonian region. Within this context, a pivotal question emerges: do variations in environmental factors play a determining role in *B. excelsa* performance during the initial phase within each planting system? We investigated the effects of pure and mixed plantations and AFSs on *B. excelsa* growth responses and physiological characteristics in the first two years of planting. To achieve this goal, we formulated the following hypotheses: (1) different planting systems will promote different growth rates for *B. excelsa* saplings, and (2) the physiological plasticity of *B. excelsa* will minimize the potential negative impacts of variations in primary resources (light, nutrients, and water) within planting systems.

Materials and methods

Study area

The study area is located within the campus of the Federal University of the South and Southeast of Pará (UNIFESSPA), between the coordinates 5°21'49.5" S and 49°01'11" W, Marabá, in Pará state, Brazil. The climate is Am, sub-humid tropical (Köppen 1948), with an average annual temperature of 28 °C and annual precipitation of approximately 1,400 mm (INMET 2019). The predominant soil is the Red-Yellow Argisol type, with dystrophic conditions (Santos et al. 2011). The site is located in a river plain area (Araguaia depression, Tocantins), with the experimental terrain being predominantly flat, which favors flooding and groundwater elevation. The area was originally a native *B. excelsa* grove, and around the 1970 s, the vegetation was removed and replaced by pasture for cattle raising and agricultural activities and was subsequently abandoned (Fig. 1).

Plant material and planting systems

The planting systems were pure plantations of *B. excelsa* and mixed plantations with intercropping of *B. excelsa* and ingá (*Inga edulis* Mart.); and the AFS with intercropping of *B. excelsa*, *I. edulis*, cocoa (*Theobroma cacao* L.), banana (*Musa* sp.), and maize (*Zea mays* L.) (Fig. 2). *B. excelsa*, *I. edulis*, and *T. cacao* saplings were produced via seminal propagation in a greenhouse located at the UNIFESSPA Campus III. The saplings of *B. excelsa* used



Fig. 1 Experimental area's satellite images: **a** from 2002, showing the area devoid of vegetation cover; and **b** from 2024, two years after the experiment was implemented

in this study were approximately 7 months old, 35 cm in height, and 0.5 cm in diameter. *Musa* sp. saplings were obtained from the Municipal Secretary of Agriculture (SEAGRI) of Marabá, and *Z. mays* seeds were obtained from a local market.

In the pure and mixed plantations, the planting spacing was $3\text{ m} \times 3\text{ m}$, with a density of 25 plants per plot. In the AFS, the spacing between *B. excelsa* and *I. edulis* was $3\text{ m} \times 3\text{ m}$, and *Musa* sp. was inserted into *B. excelsa* lines between the plants. The *T. cacao* were planted in *I. edulis* lines one year later. The total AFS density was 45 plants per plot (Fig. 2). Plant density meets the species' silvicultural recommendations, with 3×3 spacing appropriate for timber productions, and 3×3 during the first few years with posterior thinning

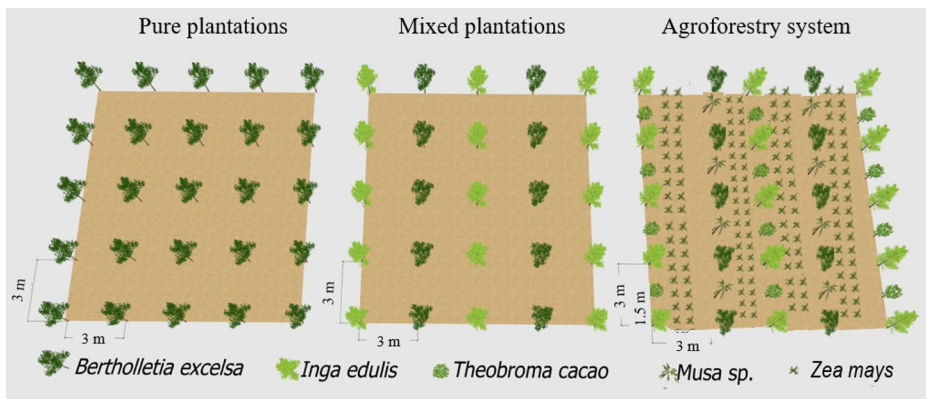


Fig. 2 Experimental design demonstrating planting systems arrangement: pure plantation, mixed plantation, and agroforestry system (spacing between rows and plants)

to favor canopy opening for the nut production systems. The AFS spacing between trees respects the indicated density, since *Musa* spp and *T. cacao* are not trees. These species explore the understory levels, as herbaceous and shrub respectively.

Implementation and management of planting systems

Different planting systems with *B. excelsa* were implemented between January 4 and 15, 2020, corresponding to the beginning of the rainy season at the experimental site. The *B. excelsa*, *I. edulis* and *Musa* sp. saplings were planted simultaneously. The saplings were planted in $40 \times 40 \times 40$ cm holes, and 200 g of dolomitic limestone (90% PRNT), 100 g of NPK 04–14–08, and 4 kg of bovine manure were added to each hole. The necessity for liming and fertilizer application was estimated as proposed by Jaquetti et al. (2022).

In the AFS, the species *B. excelsa*, *I. edulis*, and *Musa* sp. were planted simultaneously. Approximately 30 days later, *Z. mays* seeds were planted between the AFS tree lines directly into the ground using a manual planter. Sowing was carried out in rows at a depth of 5 cm with a spacing of 70×70 cm. Maize crops were harvested during the first area cleaning (April 27–29, 2020), and the remaining biomass was used as soil cover and fertilization. One year later, *T. cacao* saplings were inserted into the AFS and planted in the *I. edulis* lines at a distance of 1.5 m between plants (Figs. 2 and 3).

The management of different planting systems involved only manual cleaning, which was carried out monthly using a brush cutter. Irrigation and fertilization practices were not established throughout the experimental period.

Experimental design and data collect

The study was arranged in a completely randomized block design (RBD). The established factor is planting system represented by pure plantation, mixed plantation, and AFS. The blocks were repeated 5 times. Data on resource availability, ecophysiological traits, and growth were collected from an interior plot of $12 \text{ m} \times 7.5 \text{ m}$ (93.75 m^2), from a total experimental area of 470 m^2 . A total of 25, 25, and 45 saplings were planted in the pure, mixed,

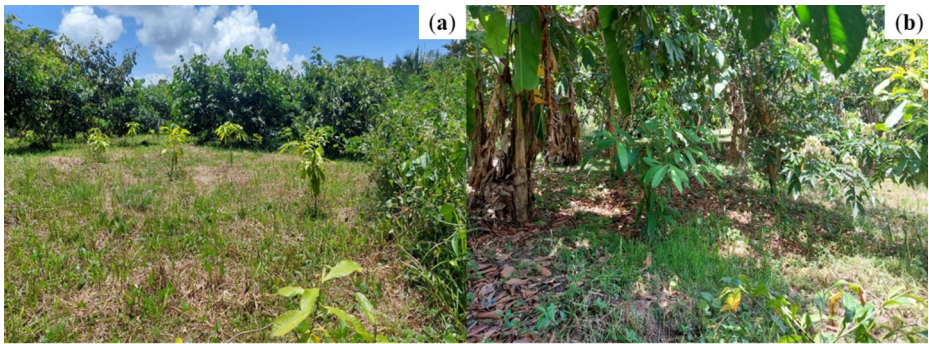


Fig. 3 Planting systems photos during data collection. **a** Pure plantation of *B. excelsa* and **b** Agroforestry system with *B. excelsa*, *I. edulis*, *Musa* sp. and *T. cacao*

and AFS treatments, respectively, totaling 475 plants within the whole experiment (Figs. 2 and 3).

Light availability and soil quality index (SQI)

Light availability was monitored using photosynthetically active radiation (PAR). PAR was measured at 1.5 m using a quantum sensor (LI-190SZ Quantum Sensor; Li-Cor, Inc., Lincoln, NE, USA) attached to a portable infrared gas analyzer (IRGA, Li-6400; Li-Cor Inc., Lincoln, NE, USA). The PAR was measured in 75 randomly selected points per plot from 7 am to 12 am daily over 7 days. Each day, one planting system was randomly selected and a different planting system was measured until the three treatments were covered.

Soil moisture and nutrient availability were obtained from soil cores collected from each plot. Soil cores (5 cm inner diameter) were collected at a depth of 10 cm from three randomly selected locations and combined into one composite sample. This depth was selected to compare the soil coverage and solar irradiation effects of the different plantations during the experimental period. The litter layer was removed before soil cores were collected. The samples were air-dried and sieved using a 2 mm mesh after the manual removal of stones and roots. The soil chemical attributes included total nitrogen (N), organic matter (OM), aluminum (Al), calcium (Ca), magnesium (Mg), potassium (K), iron (Fe), zinc (Zn), manganese (Mn) and pH.

Total N was determined using the Kjeldahl method (Miyazawa et al. 1999). Organic matter content was determined using the Walkley-Black method. Al, Ca, and Mg were extracted using 1 M KCl (Miyazawa et al. 1999), whereas K, Fe, Zn, and Mn were extracted using a Mehlich 1 solution. The nutrient contents were determined using atomic absorption spectrometry (Perkin-Elmer 1100 B, Uberlingen, Germany). Available P was extracted using a Mehlich 1 solution, and the P content was determined via spectrophotometry at 725 nm. The pH of the soil was measured in the supernatant suspension of a 1:2.5, soil: water and 1:2.5 soil: 1 M KCl solution (Miyazawa et al. 1999). The soil attribute values are presented in Table 1.

The soil chemical attributes were used for the SQI calculation according to Abdel-Fattah et al. (2021). The SQI was calculated using Eq. 1.

Table 1 Soil nutrients in different planting systems with *Bertholletia excelsa*

Soil attributes	Pure plantation	Mixed plantation	Agroforestry system
pH	5.09±0.087 a	5.05±0.08 a	5.07±0.041 a
C (g kg ⁻¹)	11.64±1.63 a	11.70±1.30 a	11.60±1.47 a
N (g kg ⁻¹)	0.88±0.09 a	0.99±0.05 a	0.88±0.06 a
M.O. (g kg ⁻¹)	20.02±2.79 a	20.14±2.24 a	19.95±2.53 a
P (mg kg ⁻¹)	12.87±5.43 a	7.72±1.33 b	15.90±5.59 a
K (cmolc kg ⁻¹)	0.10±0.010 a	0.11±0.02 a	0.11±0.01 a
Ca (cmolc kg ⁻¹)	0.77±0.19 a	0.95±0.32 a	1.02±0.18 a
Mg (cmolc kg ⁻¹)	0.42±0.07 a	0.39±0.07 a	0.52±0.10 a
Al (cmolc kg ⁻¹)	0.87±0.09 a	0.81±0.18 a	0.80±0.06 a
Fe (mg kg ⁻¹)	794.4±61.38 a	789.2±56.2 a	764.64±31.95 a
Zn (mg kg ⁻¹)	1.15±0.27 a	0.77±0.17 a	1.04±0.27 a
Mn (mg kg ⁻¹)	15.09±4.19 a	18.00±3.76 a	18.11±4.22 a

Values are mean±standard deviation. Mean followed by the same letter in the line are not statistically different, when the Tukey test is applied at the 5% probability level

$$SQI = \sum_{i=1}^N Wi \times Si$$

(1)

where Wi is the relative weight of each indicator with values ranging between 0 and 1, and Si is the value of each soil indicator. Wi expresses the component score coefficient obtained from the Principal Component Analysis (PCA) results, and Si represents the soil standardized indicators obtained from Eq. 2.

$$z = \frac{x - \bar{x}}{\sigma}$$

(2)

where z , x , $\bar{x}$ and σ refer to the standardized value, the value of a soil indicator, the average of a soil indicator, and the standard deviation of a soil indicator, respectively.

Plant growth

Experimental period comprised 720 days, and height and diameter measurements were performed at 180-day intervals, for a total of five measurements. The height of the saplings (considered up to the apical bud) was measured using a measuring tape graduated in centimeters. The diameter was measured at the base of the plant, close to the ground, using a digital caliper (Mitutoyo, CD-8 CX-B). The height (AGRH) and diameter (AGRD) growth rates were calculated according to Benincasa (1988).

Leaf gas exchange and nutrient use efficiency

Net photosynthesis per unit area (P_N), stomatal conductance (gs), transpiration (E), and dark respiration (Rd) were measured using a portable infrared gas analyzer (Li-6400; Li-Cor, Lincoln, NE, USA) with a leaf chamber of 6.0 cm² and light provided by red and blue LEDs (665 and 470 nm, respectively). Measurements were made between 8:00 am and 12:00 (noon) on healthy, fully expanded, and mature leaves. The airflow through the chamber

was about $400 \mu\text{mol s}^{-1}$, the CO_2 concentration $[\text{CO}_2]$ of the flow rate into the chamber was $410 \pm 1 \mu\text{mol mol}^{-1}$, block temperature was $31 \pm 1^\circ\text{C}$, and H_2O vapor was about $21 \pm 1 \text{ mmol mol}^{-1}$ (Lopes et al. 2019). Nutrient use efficiency is related to net photosynthesis per unit of nutrients in the leaves (Reich et al. 2014).

Leaf nutrient content

Two healthy and fully expanded leaves were collected from the *B. excelsa* saplings. Leaves samples were oven dried at 65°C for constant mass evaluation. Total N content was determined using the Kjeldahl method. Macronutrients (Ca, Mg, P, and K) were extracted with a 3:1 nitric-perchloric solution, and the contents of these nutrients were determined via atomic absorption spectrometry (Perkin-Elmer 1100 B, Uberlingen, Germany); P was determined via spectrophotometry at 725 nm (Miyazawa et al. 1999). P limitation was determined using the N: P ratio (Corrêa et al. 2022).

Data analysis

The data were preliminarily verified and confirmed for assumptions of normality and homogeneity of variance using the Shapiro–Wilk and F tests, respectively. The effects of the planting systems on *B. excelsa* saplings were evaluated using a two-way ANOVA, and the means were compared using Tukey's test 5%. Statistical analysis was performed using the statistical programming language R (R Core Team 2018).

Results

The planting system influenced the availability of resources at the site, providing different levels of ground cover and shade. Pure plantation showed the highest PAR values ($1103\text{--}1415 \mu\text{mol m}^{-2} \text{s}^{-1}$), while the lowest values ($384\text{--}1316 \mu\text{mol m}^{-2} \text{s}^{-1}$) were found in the agroforestry system (AFS). The mixed plantation displayed intermediary PAR values ($852\text{--}1336 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Fig. 4a). In the AFS, the best soil quality (SQI) indexes of 0.33–1.00 were observed (Fig. 4b), and in pure and mixed plantations a lower SQI of

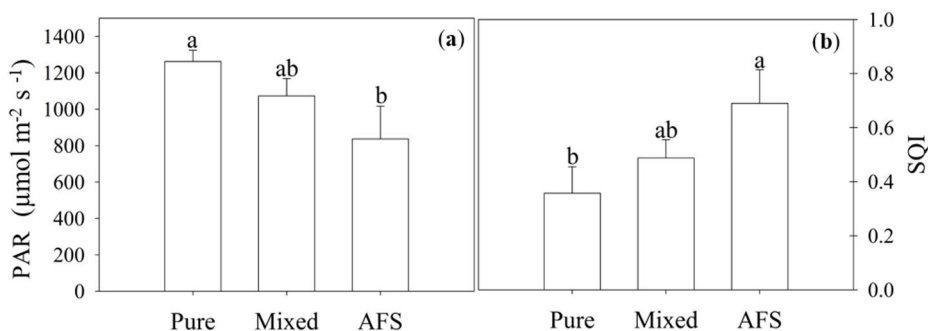
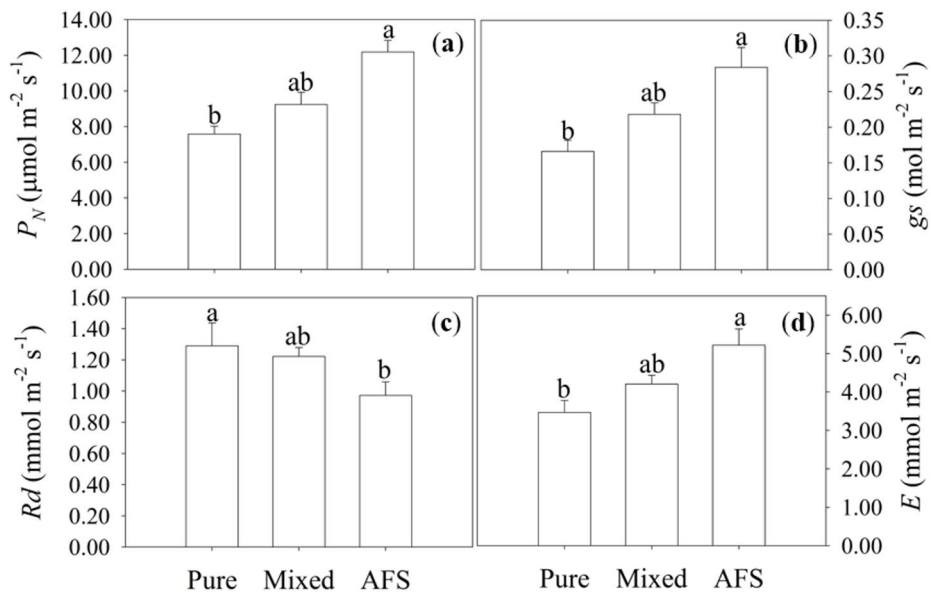


Fig. 4 Availability of light and quality of soil in different planting systems. **a** Photosynthetically active radiation (PAR) and **b** Soil quality index (SQI). Different letters above bars indicate statistical difference at 5% probability

Table 2 Leaf nutrients of *Bertholletia excelsa* saplings in different planting systems

Leaf nutrient	Pure plantation	Mixed plantation	Agroforestry system
N (g kg^{-1})	14.38 ± 0.83 a	14.83 ± 0.43 a	14.31 ± 0.60 a
P (g kg^{-1})	1.49 ± 0.17 b	1.84 ± 0.26 b	2.23 ± 0.19 a
K (g kg^{-1})	6.07 ± 0.49 ab	6.47 ± 0.68 a	4.93 ± 0.56 b
Ca (g kg^{-1})	9.18 ± 0.70 b	7.51 ± 0.58 b	10.28 ± 0.49 a
Mg (g kg^{-1})	2.01 ± 0.16 b	2.09 ± 0.15 b	2.97 ± 0.50 a
Fe (mg kg^{-1})	127.42 ± 10.86 a	141.90 ± 5.51 a	161.65 ± 11.77 a
Zn (mg kg^{-1})	28.92 ± 3.67 a	32.42 ± 5.49 a	35.36 ± 2.52 a
Mn (mg kg^{-1})	67.20 ± 6.90 b	47.88 ± 8.52 b	87.42 ± 1.61 a

Values are mean $\pm$ standard deviation. Mean followed by the same letter in the line are not statistically different, when the Tukey test is applied at the 5% probability level

**Fig. 5** Gas exchanges in different planting systems. **a** photosynthesis, **b** stomatal conductance, **c** dark respiration and **d** transpiration. Different letters above bars indicate statistical difference at 5% probability

0.36—0.57 and 0.12—0.64, respectively. The PAR values in the pure plantation were 17% and 51% higher than those in the mixed plantation and AFS, respectively (Fig. 4a), whereas in the AFS, the SQI was 93% higher than that in the pure plantation and 41% higher than that in the mixed plantation (Fig. 4b).

Differences in PAR and SQI caused by the planting systems were accompanied by changes in the concentrations of phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and manganese (Mn) in the leaves of saplings from different planting systems (Table 2). Saplings from the AFS showed higher P, Ca, Mg, and Mn content (Table 2). On the other hand, in this same planting system, the lowest contents of K were observed (Table 2).

B. excelsa saplings from the AFS showed better gas exchange performance. The potential assimilation, stomatal conductance, and transpiration values were 61, 71, and 50% higher, respectively, in AFS than in pure plantation saplings (Fig. 5). No differences were found in

dark respiration, although the rate in the pure plantation was approximately 33% higher than that in the AFS (Fig. 5). Net photosynthesis per unit area (P_N) means and standard deviations were $7.58 \pm 0.099 \mu\text{mol m}^{-2} \text{s}^{-1}$ in pure plantation, $9.24 \pm 1.53 \mu\text{mol m}^{-2} \text{s}^{-1}$ in mixed plantation and $12.19 \pm 1.43 \mu\text{mol m}^{-2} \text{s}^{-1}$ in AFS. Stomatal conductance (g_s) means and standard deviations were 0.167 ± 0.035 , followed by 0.220 ± 0.033 , and $0.284 \pm 0.059 \text{ mol m}^{-2} \text{s}^{-1}$ in the pure, mixed and AFS plantations, respectively. Transpiration (E) means and standard deviations followed the same trend, with 3.47 ± 0.69 , 4.21 ± 0.52 and $5.22 \pm 0.95 \text{ mmol m}^{-2} \text{s}^{-1}$. For dark respiration (R_d) means and standard deviations the AFS was the lowest with $0.97 \pm 0.19 \text{ mmol m}^{-2} \text{s}^{-1}$, succeeded by mixed plantation with $1.22 \pm 0.13 \text{ mmol m}^{-2} \text{s}^{-1}$ and pure plantation with $1.29 \pm 0.33 \text{ mmol m}^{-2} \text{s}^{-1}$.

B. excelsa saplings from the agroforestry system also had higher nitrogen (PNUE) and potassium (PKUE) use efficiency (Fig. 6). The PNUE found in the saplings of the AFS were 53 and 13% higher than those observed in pure and mixed plantations, respectively, with means and standard deviations of 147.6 ± 31.6 , 130.4 ± 27.8 and $96.2 \pm 17.5 \text{ mmol mol}^{-1} \text{s}^{-1}$. The PKUE observed in the saplings of the AFS were 87 and 63% greater than those in pure and mixed plantations saplings, respectively, with means and standard deviations of 1298 ± 530 , followed by 791 ± 178 , and $691 \pm 185 \text{ mmol mol}^{-1} \text{s}^{-1}$. Regardless of the planting system, the order of nutrient use efficiency of *B. excelsa* saplings was $\text{P} > \text{Mg} > \text{K} > \text{Ca} > \text{Zn} > \text{Mn} > \text{N} > \text{Fe}$ (Fig. 6).

Planting systems influenced the growth height of *B. excelsa* saplings, but no statistical difference was observed in diameter growth. In agreement with silvicultural standards, initial height mean and standard deviation were $42.35 \pm 18.54 \text{ cm}$ and diameter

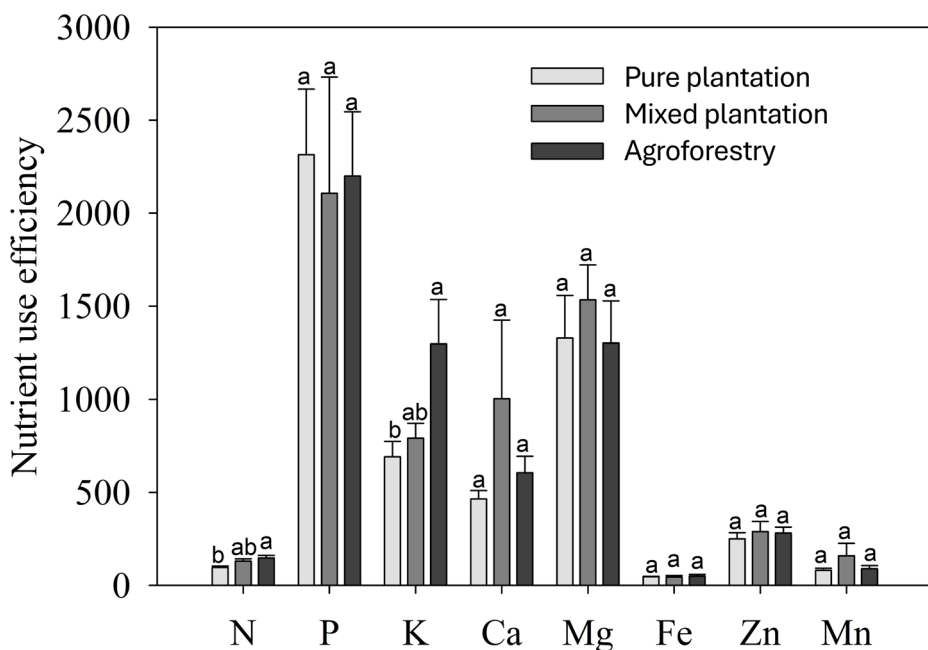


Fig. 6 Photosynthetic efficiency in nutrient use in *B. excelsa* saplings in different planting systems. Different letters above bars indicate statistical difference between efficiency of same nutrient in different planting systems at 5% probability

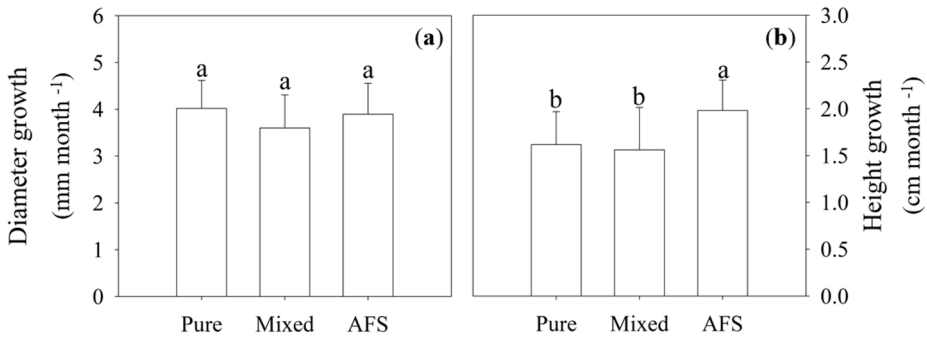


Fig. 7 Growth rate in *B. excelsa* saplings in different planting systems: **a** height growth rates, and **b** diameter growth rates. Different letters above bars indicate statistical difference at 5% probability

were 7.43 ± 2.89 mm according to silvicultural standards. Final absolute heights were 81.96 ± 52.87 , 73.10 ± 51.11 , and 115.40 ± 61.04 I in the pure, mixed and AFS, respectively. Final diameters were 18.42 ± 12.37 , 17.43 ± 10.87 , and 19.66 ± 8.26 , respectively. Therefore, no significant difference was registered for AGRD between planting systems, whereas AGRH was enhanced in AFS (Fig. 7). Surviving plants totaled 55, 20 and 24 in pure, mixed and AFS, comprising for 73, 80 and 96%, respectively.

Discussion

In the degraded Eastern Amazon area, AFS *B. excelsa* saplings showed better ecophysiological performance than the monoculture and mixed plantations. This was represented by higher survival, photosynthesis, leaf nutrient content, and nitrogen (N) and potassium (K) use efficiencies. Different planting systems provide different resource availabilities and competition, resulting in distinct ecophysiological conditions. *B. excelsa* physiological plasticity allowed the plants to respond with height growth and gas exchange improvements in the AFS, probably resulting in higher assimilation and biomass allocation if prolonged over time. The difference in the ecophysiological performance of *B. excelsa* saplings between planting systems is probably due to changes in resource availability and plasticity of the species.

Photosynthetically active radiation (PAR) is a limiting resource; plants grow taller to outfit competitors, and this condition is stimulated in shaded areas such as AFS. Higher investment in height, rather than diameter, demonstrates a priority in the allocation and phenotypical plasticity of *B. excelsa*. A higher H/D relation diminishes biomechanical tolerance, increases photosynthetic capacity in the first few years, and can compensate for greater biomass allocation if it succeeds. PAR also affects soil dynamics because solar irradiance can dry soil and increase local droughts. A higher plant density in AFS increases competition above and belowground; however, the soil benefits from a green cover. Vegetation protects the soil from rain and direct sunlight, preserves the air and water balance, and allows the microbiota to maintain the soil structure. These soil protection, as demonstrated in Fig. 3, are likely to improve SQI. Changes in the availability of primary resources for plant growth caused by different planting systems have also been reported by Thomas et al.

(2021), who attributed the differences in PAR to species density in each system. However, the improvement in the SQI is influenced by the species present in each system and their ability to produce nutrient-rich litter in large quantities (Freitas et al. 2020; Octavia et al. 2024; Souza et al. 2024).

The high PAR values found in the monoculture and mixed plantations could be attributed to the lower density of individual species (Fig. 2). Although the density in monoculture was the same as that in mixed plantations, the lower PAR values found in the latter were due to *I. edulis* presence, which shades the area due to canopy structure and rapid growth. *I. edulis* and *Musa* sp. were responsible for shading the *B. excelsa* in the AFS. *B. excelsa* exhibits phenotypic and physiological plasticity in response to variations in environmental irradiance, which gives it the ability to survive and grow in both shaded and degraded agro-forestry sites. However, higher growth and photosynthetic rates were observed in areas with greater light availability (da Costa et al. 2022; Oliveira et al., 2024a).

The presence of *I. edulis* in the AFS and mixed plantation was probably the determining factor for the improvement in the SQI in these planting systems. *I. edulis* has been indicated for the recovery of degraded areas, mainly because of its ability to produce litter with good chemical quality (high values of N) and in large quantities (Freitas et al. 2020). Although the litter was not evaluated in this study, it is possible to observe a large amount of *I. edulis* leaf residues in AFS soil (Fig. 3).

The SQI improvement reflected increased phosphorus (P), calcium (Ca), magnesium (Mg), and manganese (Mn) leaf contents in the AFS *B. excelsa* saplings. Planting systems intercropped with nitrogen-fixing legumes may favor nutrient availability to plants by influencing the actions of soil fauna, microorganisms, and enzymes (Eka et al. 2022). For example, Aleixo et al. (2020) observed that a eucalyptus and nitrogen-fixing legume consortium in recovery plantations in degraded areas increased all soil P fractions.

Regarding plant nutrition, the higher values of K found in pure plantation saplings can be related to strategies to minimize the water stress effects caused by direct radiation exposure and, consequently, to higher temperatures. The enhanced K rates are probably related to osmoregulation and stomata control functions. Similar behavior has already been observed in *B. excelsa*; when exposed to water stress, the species increases the concentrations of potassium, proline, and carbohydrates in the leaves (Ferreira et al. 2012; Schimpl et al. 2019; da Costa et al. 2022). In the AFS and mixed plantations, the saplings may have benefited from the shading provided by the other species which could result in reduction of water stress. In addition, greater soil coverage by the tree canopy and organic matter can contribute to soil moisture conservation. However, in pure plantations greater exposure causes higher irradiation and temperature.

The increase in leaf nutrient content, especially P, may have been the determining factor for finding the highest rates of photosynthesis, stomatal conductance, and transpiration in AFS plants. Phosphorus is involved in several cellular processes, including energy conservation, metabolic regulation, and signal transduction (Kayoumu et al. 2023). Correa et al. (2022) found that increased P availability has beneficial effects on photosynthesis in *B. excelsa* by favoring photochemical efficiency and CO₂ capture. Additionally, studies have found that greater P availability contributes to improvements in light- and nutrient-use efficiency in *B. excelsa* plants (da Costa et al. 2022; Oliveira et al., 2024b).

There was also an increase in Mg, Ca, and Mn concentrations in AFS sapling leaves. Mg can be associated with protein and RuBisCO synthesis, as well as chloroplast ultrastruc-

ture, and acts directly on chlorophyll synthesis and RuBisCO activation (Cunha et al. 2016; Tränkner et al. 2018). Ca and Mn are essential for the oxygen evolution complex (OEC) of the photosynthetic apparatus, which catalyzes the water-splitting reaction in photosystem II (PSII) (Silva et al. 2008; Wang et al. 2019; Alejandro et al. 2020).

Additionally, Souza et al. (2017) demonstrated that the PAR level of 800–1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (levels similar to those found in this study in the AFS) may be more advantageous for *B. excelsa* saplings. At higher irradiance levels, *B. excelsa* has a lower photochemical efficiency, which can compromise photosynthesis, particularly carbohydrate metabolism (Lopes et al. 2019; Costa et al. 2020; Jaquetti et al. 2022). On the other hand, Scoles et al. (2014) demonstrated that irradiance levels lower than 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ can favor *B. excelsa* mortality in the medium and long term.

The increase in photosynthesis in AFS saplings was the main factor contributing to greater K and N use efficiency, as nutrient use efficiency is determined by the availability of nutrients and photosynthesis values (Marenco et al. 2001; Baligar et al. 2001; Nieves-Cordones et al. 2020). Additionally, the nutrient use efficiency values observed in this study were higher than those verified in a study with clones of *B. excelsa* in a degraded area of the Central Amazon, mainly regarding the use of N, K, Mg, and Mn (Ferreira et al. 2016). These factors confirmed the aptitude of the species for cultivation in areas that have undergone degradation. In addition to being tolerant to low nutrient availability, it still adjusts the photosynthetic apparatus so that nutrients are used more efficiently.

Considering that the plants in the pure plantations had the greatest light availability, the highest values of respiration in the dark for *B. excelsa* in this treatment corroborate the findings of an Amazon study on native species (Rodrigues and Gonçalves 2014). High rates of dark respiration are associated with the high cost of maintaining the photosynthetic apparatus. In addition, there is an increase in photoprotection mechanism investment, with an increase in this variable occurring with the increase in irradiance, temperature, and improvement in the nutritional status of trees (Krause 2012; Rodrigues and Gonçalves 2014).

The ability of a species to respond to changes in the availability of environmental resources depends on its level of physiological plasticity (Lopes et al. 2019; da Costa et al. 2022). In the case of *B. excelsa*, da Costa et al. (2022) highlighted that this species has a high level of adaptive plasticity, being able to respond to changes in the light environment, as well as variations in the availability of water and nutrients in the soil. Here, it was observed that the species uses different physiological and structural strategies to support changes in the availability of resources in the environment and favors their survival and growth rates (Lopes et al. 2019; da Costa et al. 2022; Fortes et al. 2023; de Souza et al. 2023).

The greater growth in height of *B. excelsa* saplings in the first two years of plantation in the AFS may have occurred because of the high level of plasticity of this species in response to low irradiance levels, as already observed in a greenhouse (Lopes et al. 2019). Thus, the lower availability of irradiance in the AFS induced the species to invest in strategies to increase survival and light capture and thus increase growth rates in height, but not in diameter. These results were obtained from a study on the juvenile growth and physiological performance of *B. excelsa* grown under different planting systems established in a degraded area in an open field. However, understanding the future of modeling planting systems, particularly in agroforestry, presents major challenges in finding the right balance between model complexity and the range of interactions that can be simulated, as highlighted by Gonçalves et al. (2021).

Conclusion

Different planting systems in the degraded land of the Eastern Amazon show that environmental factors play a determining role in the performance of *B. excelsa* during the initial phase. This study evaluated pure and mixed plantations and the effects of AFS on *B. excelsa* growth and physiological characteristics during the first two years. Different planting systems promoted different growth and gas exchange rates in *B. excelsa* saplings in response to variations in primary resource availability (light, nutrients, and water). The different planting systems promoted different site conditions for *B. excelsa* saplings, with an emphasis on high availability of light in the pure plantations. The AFS exhibited an improved soil quality index, together with lower irradiance levels.

The best ecophysiological responses of *B. excelsa* were observed in the AFS and mixed plantations, mainly in relation to gas exchange (P_N , g_s , and E) and nutritional status (PNUE and PKUE). In addition, this study highlighted the physiological plasticity of *B. excelsa* in response to variations in primary resources, particularly light availability. The results obtained in this study show the ability of *B. excelsa* in juvenile stages to recover altered areas when cultivated in these planting systems; however, it is important to analyze the behavior of the species in mixed plantations and agroforestry systems in the long term and under varying degradation conditions.

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Author contributions IVO, KCPC, and JFCG conceived the conceptualization, methodology, investigation, formal analysis, review, editing, and writing original draft preparation. IVO, ALG, JCC, ARNJ, and DAF contributed to the investigation, formal analysis, and writing original draft preparation. IVO, ALG, JCC, ARNJ, and DAF contributed to the investigation and formal analysis. JFCG contributed to the project administration, supervision, funding acquisition, writing review and editing. All authors read and approved of the final manuscript.

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Data availability The data associated with this article are available at New Forests.

Declarations

Competing interests The authors declare no competing interests.

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References

- Abdel-Fattah MK, Mohamed ES, Wagdi EM, Shahin SA, Aldosari AA, Lasaponara R, Alnaimy MA (2021) Quantitative evaluation of soil quality using principal component analysis: the case study of El-Fayoum depression Egypt. *Sustainability* 13:es1824. <https://doi.org/10.3390/su13041824>
- Aleixo S, Gama-Rodrigues AC, Gama-Rodrigues EF, Campello EFC, Silva EC, Schripsema J (2020) Can soil phosphorus availability in tropical forest systems be increased by nitrogen-fixing leguminous trees? *Sci Total Environ* 712:136405. <https://doi.org/10.1016/j.scitotenv.2019.136405>
- Alejandro S, Höller S, Meier B, Peiter E (2020) Manganese in plants: from acquisition to subcellular allocation. *Front Plant Sci* 11:300. <https://doi.org/10.3389/fpls.2020.00300>
- Baligar VC, Fageria NK, He ZL (2001) Nutrient use efficiency in plants. *Commun Soil Sci Plant Anal* 32:7–8. <https://doi.org/10.1081/CSS-100104098>
- Benincasa MMP (1988) Análise de crescimento de plantas. FUNEP, Jaboticabal
- Bentes RS, Marin RA, Emmi MF (1988) Os cemitérios Das Castanheiras do Tocantins. *Para Desenvolvimento* 23:18–23
- Caetano AC, Macedo RLG, Souto BAD, Ribeiro SC (2014) Height-diameter equations for Brazil nut intercropped with rubber tree in the south of Minas Gerais. *Floresta* 44:497–504
- Correia V, Gonçalves J, Costa K, Oliveira I, Santos J, Oliveira S, Ferreira M, Lima R, Araújo W, Nunes-Nesi A (2022) The role of phosphate fertilization on physiological responses of the young *Bertholletia excelsa* plants grown in a P-deficient Amazon ferralsol. *Plants* 21:2955
- Costa JR, Castro ABC, Wandelli EV, Coral SCT, Souza SAG (2009) Aspectos silviculturais da castanha-do-brasil (*Bertholletia excelsa*) em sistemas agroflorestais na Amazônia Central. *Acta Amazon* 39:843–850
- Costa KCP, Jaquetti RK, Gonçalves JFC (2020) Chlorophyll *a* fluorescence of *Bertholletia excelsa* Bonpl. plantations under thinning, liming, and phosphorus fertilization. *Photosynthetica* 58:138–145
- Cunha HFV, Gonçalves JFC, Santos Junior UM, Ferreira MJ, Peixoto PHP (2016) Biomassa, Trocas Gasosas e aspectos nutricionais de Plantas jovens de Pau de Balsa (*Ochroma Pyramidale* (Cav. Ex Lamb.) Urb.) submetidas à fertilização Fosfatada Em ambientes contrastantes de irradiância. *Scientia For* 44:215–230
- da Costa K, de Carvalho Gonçalves J, Gonçalves A et al (2022) Advances in Brazil nut tree ecophysiology: linking abiotic factors to tree growth and fruit production. *Curr Forestry Rep* 8:90–110. <https://doi.org/10.1007/s40725-022-00158-x>
- da Silva Ceretta RP, Marques JD, Lima MDR et al (2025) Planted forests of *Tachigali vulgaris* in Eastern Amazonia: how spacing affects the anatomical variations and wood density. *New Forests* 56:26. <https://doi.org/10.1007/s11056-025-10094-w>
- de Oliveira IV, da Costa KCP, da Rocha NAI, de Carvalho JC, Gonçalves JFC (2024a) Brazil nut tree increases photosynthetic activity and stem diameter growth after thinning. *Theor Exp Plant Physiol* 36:251–263. <https://doi.org/10.1007/s40626-024-00317-4>
- de Oliveira SS, da Costa KCP, de Lima RM, Nina Junior AR, de Carvalho JC, Nunes-Nessi A, Araújo WL, Carvalho Gonçalves JF (2024b) *Bertholletia excelsa* saplings respond to seasonal precipitation variations by changing metabolism when fertilized with NPK in different planting systems. *For Ecol Manag*. <https://doi.org/10.1016/j.foreco.2024.122325>
- de Souza JP, de Carvalho Gonçalves JF, Jaquetti RK et al (2023) Silvicultural interventions and agroforestry systems increase the economic and ecological value of *Bertholletia excelsa* plantations in the Amazon. *Agroforest Syst* 97:197–207. <https://doi.org/10.1007/s10457-022-00798-9>
- Eka JW, Ekim ED, Osu SR (2022) Effect of intercropping leguminous tree species on soil nutrient status, growth and yield of arable crops in Ukan Edemaya, Ikot Abasi local government area, Akwa Ibom State, Nigeria. *J Appl Sci Environ Manage* 26:429–437
- Fauset S, Johnson MO, Gloor M, Baker TR, Monteagudo AM, Brienens RJW et al (2015) Hyperdominance in Amazonian forest carbon cycling. *Nat Commun* 6:6857
- Ferreira LM, Tonini H (2009) Comportamento Da castanha-do-brasil (*Bertholletia excelsa*) e Da cupiúba (*Goupia glabra*) Em sistema agrossilvicultural Na região de Confiança, Cantá, Roraima. *Acta Amazon* 39:835–842
- Ferreira MJ, Gonçalves JF, Ferraz JBS (2012) Crescimento e eficiência do Uso Da água de Plantas jovens de castanheira-da-Amazônia Em área degradada e submetida à adubação. *Cienc Florest* 22:393–401

- Ferreira MJ, Gonçalves JFC, Ferraz JBS, Santos Junior UM, Rennenberg H (2016) Clonal variation in photosynthesis, foliar nutrient concentrations, and photosynthetic nutrient use efficiency in a Brazil nut (*Bertholletia excelsa*) plantation. *For Sci* 62:323–332
- Fortes SLK, Gonçalves JC, Costa KCP, Lopes JS, Ferreira MJ, Lima RMB, Nina Junior AR (2023) Growth and functional leaf traits of coppice regrowth of *Bertholletia excelsa* during an El Niño event in the central Amazon. *Acta Amazon* 53:9–19
- Freitas AF, Carneiro JJ, Venturin N, Moreira FMS, Ferreira AIG, Lara GPO, Miranda RM, Siqueira LF, Cardoso IM (2020) *Inga edulis* Mart. intercropped with pasture improves soil quality without compromising forage yields. *Agroforest Syst* 94:2355–2366
- Gonçalves B, Morais MC, Pereira S, Mosquera-Losada MR, Santos M (2021) Tree–Crop ecological and physiological interactions within climate change contexts: A Mini-Review. *Front Ecol Evol* 9:661978. <https://doi.org/10.3389/fevo.2021.661978>
- Guariguata MR, Cronkleton P, Duchelle AE et al (2017) Revisiting the ‘cornerstone of Amazonian conservation’: a socioecological assessment of Brazil nut exploitation. *Biodivers Conserv* 26:2007–2027. <https://doi.org/10.1007/s10531-017-1355-3>
- Homma AKO (2014) Extrativismo vegetal na Amazônia: história, ecologia, economia e domesticação. Embrapa, Brasília
- INMET (2019) Dados climáticos anuais. <http://www.inmet.gov.br/portal/index.php?r=clima>. Accessed 05 June 2020
- INPE (2023) Levantamento de alertas de evidências de alteração da cobertura florestal na Amazônia: degradação. <http://terrabrasil.dpi.inpe.br/downloads>. Accessed 15 July 2023
- Jaquetti RK, Gonçalves JFC (2017) Carbon and nutrient stocks of three fabaceae trees used for forest restoration and subjected to fertilization in Amazônia. *Acad Bras Cienc* 89:1–11. <https://doi.org/10.1590/0001-3765201720160734>
- Jaquetti RK, Gonçalves JFC, Ferraz JBS, Ferreira MJ, Santos Junior UM (2016) Ecofunctional traits and biomass production in leguminous tree species under fertilization treatments during forest restoration in Amazônia. *Forests* 7:76–79
- Jaquetti RK, Gonçalves JFC, Nascimento HEM, Costa KCP, Maia JMF, Schimpl FC (2021) Fertilization and influence of seasonality on the photochemical performance of tree legumes in forest plantations for area recovery in the Amazon. *PLoS One* 16:e0243118
- Jaquetti RK, Nascimento HEM, Zotarelli L et al (2022) Coordinated adjustments of carbohydrates and growth of tree legumes under different fertilization regimes in degraded areas in Amazonia. *New Forests* 53:221–240. <https://doi.org/10.1007/s11056-021-09853-2>
- Joslin AH, Oliveira FA, Kato OR, Vasconcelis SS, Morris L, Markewitz D (2024) Ten years of improved–fallow slash–and–mulch agroforestry in Brazilian amazonia: do nitrogen–fixing trees affect nitrous oxide and methane efux? *Agroforest Syst* 98:2587–2603
- Kayoumu M, Iqbal A, Muhammad N, Li X, Li L, Wang X, Gui H, Qi Q, Ruan S, Guo R, Zhang X, Song M, Dong Q (2023) Phosphorus availability affects the photosynthesis and antioxidant system of contrasting low-P-tolerant cotton genotypes. *Antioxidants* 12:466
- Köppen W (1948) *Climatologia: un estudio de los climas de la tierra*. Fondo de Cultura Económica, México
- Krause GH (2012) Photosynthesis, photoprotection, and growth of shade-tolerant tropical tree seedlings under full sunlight. *Photosynth Res* 113:273–285
- Lojka B, Dumas L, Preininger D, Polesny Z, Banout J (2010) The use and integration of *Inga edulis* in agroforestry systems in the amazon – review article. *Agric Trop Subtrop* 43:352–359
- Lopes JS, Costa KCP, Fernandes VS, Gonçalves JFC (2019) Functional traits associated to photosynthetic plasticity of young Brazil nut (*Bertholletia excelsa*) plants. *Flora* 258:1–9
- Marenco RA, Gonçalves JF, Vieira G (2001) Photosynthesis and leaf nutrient content in *Ochroma pyramidale* (bombacaceae). *Photosynthetica* 39:539–543
- Melo CG, Daronco C, Ré DS, Durigan G (2015) Atributos de espécies arbóreas e a facilitação Da regeneração natural Em plantio heterogêneo de Mata ciliar. *Scientia For* 43:333–344
- Melo VF, Batista AH, Barbosa JZ, Barbeiro L, Gomesc R, Dultra MTM (2019) Soil quality and reforestation of the Brazil nut tree (*Bertholletia excelsa* Bonpl.) after laterite-type bauxite mining in the Brazilian Amazon forest. *Ecol Eng* 125:111–118
- Miyazawa M, Pavan MA, Muraoka T, Carmo CAFS, Melo WJ (1999) Manual de análise química de solos, plantas e fertilizantes. Embrapa, Brasília
- Nieves-Cordones M, Rubio F, Santa-María GE (2020) Nutrient use-efficiency in plants: an integrative approach. *Front Plant Sci* 11:623976
- Octavia D, Murniati, Suhartia S, Hani A, Mindawati N, Suratman, Swestiani D, Junaedi A, Undaharta NKE, Santosa P, Wahyuningtyas Reni, Faubiany V (2024) Smart agroforestry for sustaining soil fertility and community livelihood. *For Sci Technol* 19:315–328

- Pan T, Fan X, Sun H (2023) Juvenile phase: an important phase of the life cycle in plants. *Ornam Plant Res* 3:18. <https://doi.org/10.48130/OPR-2023-0018>
- R Core Team (2018) R: A Language and environment for statistical computing. Foundation for Statistical Computing, Vienna
- Reich M, Aghajanzadeh T, De Kok LJ (2014) In: Hawkesford MJ, Kopriva S, De Kok LJ (eds) Nutrient use efficiency in plants. Springer International Publishing Switzerland, Versailles, France, p 287
- Reid NM, Wigley K, Nusrath A, Smail SJ, Garrett LG (2024) Use of nitrogen-fixing plants to improve planted forest soil fertility and productivity in New Zealand: a review. *N Z J Forest Sci*. <https://doi.org/10.33494/nzjfs542024x329x>
- Rodrigues JK, Cavalcanti JHF, Silva PO, Borges EEDL, Junior ADRN, Carvalho Gonçalves JF (2021) Unraveling relationships of prompt germination among four species of *Inga* Mill detected by morpho-anatomical and histochemical traits. *Flora*. <https://doi.org/10.1016/j.flora.2021.151941>
- Rodrigues JVFC, Gonçalves JFC (2014) Leaf gas exchange, photon capture and light harvest in *Aldina heterophylla* along a vegetation gradient in the Amazon rainforest. *American J Plant Sci* 5:51477–1488
- Salomão RP, Sousa VG, Brienza Júnior S, Barbosa MG, Hage ALF (2020) Trajetória Da restauração florestal de áreas Mineradas Ao Longo de 17 Anos Em Unidade de conservação Na Amazônia. *Brazilian J Dev* 6:3588–3609
- Santos HG, Carvalho Junior W, Dart RO, Áglío MLD, Sousa JS, Pares JG, Fontana A, Martins ALS, Oliveira AP (2011) O Novo Mapa de solos do Brasil legenda atualizada. Embrapa, Rio de Janeiro. <http://www.infoteca.cnptia.embrapa.br/infoteca/handle/doc/920267>
- Santos Junior UM, Gonçalves JFC, Feldpausch TR (2006) Growth, leaf nutrient concentration and photosynthetic nutrient use efficiency in tropical tree species planted in degraded areas in central Amazonia. *For Ecol Manag* 226:299–309
- Santos VAHF, Ferreira MJ (2020) Initial establishment of commercial tree species under enrichment planting in a central Amazon secondary forest: effects of silvicultural treatments. *For Ecol Manag* 460:117822
- Santos-Silva L, Silva LCDP, Corassa JDN, Battistola LD (2017) The Brazil nut tree (*Bertholletia excelsa* Humb. & Bonpl. (Lecythidaceae)): importance and biological interactions. *Sci Electron Arch* 10:01–14
- Schimpl FC, Ferreira MJ, Jaquetti RK, Martins SCV, Gonçalves JFC (2019) Physiological responses of young Brazil nut (*Bertholletia excelsa*) plants to drought stress and subsequent rewetting. *Flora* 252:10–17
- Scoles R, Klein GN, Gribel R (2014) Crescimento e sobrevivência de castanheira (*Bertholletia excelsa* Bonpl., Lecythidaceae) plantada em diferentes condições de luminosidade após seis anos de plantio na região do rio Trombetas, Oriximiná, Pará. *Bol Mus Para Emílio Goeldi Ciênc Nat* 9:321–336
- Silva CEM, Gonçalves JFC, Feldpausch TR (2008) Water-use efficiency of tree species following calcium and phosphorus application on an abandoned pasture, central Amazonia, Brazil. *Environ Exp Bot* 64:89–195. <https://doi.org/10.1016/j.envexpbot.2008.03.001>
- Souza CSCR, Santos VAHF, Ferreira MJ, Gonçalves JFC (2017) Biomassa, crescimento e respostas ecofisiológicas de plantas jovens de *Bertholletia excelsa* Bonpl. submetidas a diferentes níveis de irradiância. *Ciênc Florestal* 27:557–569
- Souza IMD, Sagrilo E, de Oliveira Júnior JOL, Araújo MDM, Muniz LC, Costa JB, Pompeu RCFF, de Sousa DC, de Andrade HAF, de Oliveira Neto ED et al (2024) Soil chemical quality in integrated production systems with the presence of native and exotic tree components in the Brazilian Eastern Amazon. *Forests* 15:1078
- Thomas A, Priault P, Piutti S, Dallé E, Marron N (2021) Growth dynamics of fast-growing tree species in mixed forestry and agroforestry plantations. *For Ecol Manag* 480:118672
- Tränkner M, Tavakol E, Jákli B (2018) Functioning of potassium and magnesium in photosynthesis, photosynthate translocation and photoprotection. *Physiol Plant* 163:414–431
- Wang Q, Yang S, Wan S, Li X (2019) The significance of calcium in photosynthesis. *Int J Mol Sci* 20:1353

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