Current Forestry Reports (2022) 8:90–110
https://doi.org/10.1007/s40725-022-00158-x

# Advances in Brazil Nut Tree Ecophysiology: Linking Abiotic Factors to Tree Growth and Fruit Production

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Accepted: 17 December 2021 / Published online: 10 February 2022

## Abstract

**Purpose of the Review** The Brazil nut tree (*Bertholletia excelsa*) is a symbolic tree in the Brazilian Amazonian. In a broad sense, it plays a crucial role in its social, economic, and environmental importance. This species contributes on a large scale to the equilibrium of the biological processes related to the biogeochemical cycles in the Amazon biome, and its nuts sustain a multi-million-dollar extractive economy, which supports small farmers and traditional populations. Brazil nut is also becoming one of the most important species in silviculture and is increasingly used in agroforestry systems and the recovery of degraded areas. In this review, we deepened our understanding of the growth performance of the Brazil nut tree and its ecophysiological traits, both in native trees and commercial forest plantations. Based on the literature for this species, we discuss the concepts of plasticity and other functional traits that may help to increase Brazil nut plantation and conservation, which in turn will increase nut production, forest sustainability, and social welfare.

**Recent Findings** The Brazil nut tree is a dominant species and is found throughout the Amazon region. Due to its ecophysiological traits, it can be cultivated as a commercial monoculture, in the enrichment of forest plantations, used in the recovery of degraded areas and the implementation of agroforestry systems. Recent evidence suggests that their dominance of natural forests and their high functional performance under cultivated conditions may be associated with their physiological plasticity and tolerance to abiotic stresses.

**Summary** Aspects related to phenotypic variation, genetic diversity, population characteristics, cultivation, and ecophysiological performance of *Bertholletia excelsa* are revised and linked to growth and nut production. We demonstrate that Brazil nut exhibits phenotypical plasticity in response to light, water, and nutrient availability. This trait can be explored for improvements in nut production in native trees and agroforestry plantations. In both cases, the availability of these resources influences population structure, tree growth, and fruit production. These results reinforce the importance of the use of Brazil nut tree as an attractive alternative for improving programs that involve the recovery of degraded areas in the continental Amazon. Lastly, the ecophysiological performance of the Brazil nut tree suggests its resilience to environmental change.

**Keywords** Forest plantation · Photosynthesis · Plasticity · Resources use efficiency · Tree physiology · Sustainability

## Introduction

Historically, the gigantic Brazil nut (*Bertholletia excelsa*) tree has contributed to the development of complex societies in the Amazon region and its domestication dates from

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This article is part of the Topical Collection on *Physiological Processes*

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the first millennium of the Common Era [1]. Currently, this species is one of the main non-timber forest products marketed in Brazil. Additionally, it supports the livelihoods of populations throughout the Amazon basin by producing Brazil nuts, which drives a multi-million-dollar extractive economy in Bolivia, Brazil, and Peru [2]. Brazil nut also plays a fundamental role in carbon sequestration, ranking first among economically important Amazonian species while coming in third place among 3458 species evaluated for biomass accumulation [3]. In sum, Brazil nut can be considered a biocultural keystone species [4] due to its critical multi-faceted role.

This important tree species belongs to the Lecythidaceae (Poiteau 1825) family. It was first catalogued in Western science by Alexander von Humboldt and Aimé Bonpland in their natural history expedition to the New World from 1799 to 1804. It was subsequently named as *Bertholletia excelsa* by Bonpland in 1808 [5]. The genus terminology is dedicated to the chemist Claude Louis Berthollet in reference to his scientific stature, while the epithet refers to the grandiosity (*excelsa* = noble) of the adult trees [6]. The social, economic, and ecological importance of Brazil nut is due, in part, to its extensive distribution throughout the Amazon basin and its high rates of survival and growth, even in adverse conditions such as sites with acidic soils, low water and nutrient availability, and variations in availability of irradiance [7–11]. In addition, Brazil nut is a large tree with a great capacity to sequester carbon and can play an important role in mitigating the effects of climate change on Amazon forests [12, 13].

This review synthesizes the natural history and the ecophysiological evidence that may explain the vigorous performance and relative dominance of Brazil nut in Amazon forests. We first demonstrate that the natural history of this species indicates phenotypic plasticity, which is defined as an organism’s ability to change, adapt, or respond to stimuli or inputs from the environment such as low soil fertility or water, light, and temperature stresses [14]. We then integrate studies on phenotypic variation, genetic diversity, and a natural population’s characteristics to infer the influence of abiotic factors on phenotypic changes in Brazil nut and the relationships between this ability and its vigorous performance and relative dominance in Amazon forests.

The variation in the phenotypic characteristics of the Brazil nut tree may be attributed partially to human selection because humans commonly select phenotypes that have larger crowns, fruits, and seeds during incipient domestication phases. Nonetheless, the characteristics of natural populations such as seed production, above-ground biomass, regeneration, the density of individuals, and growth in diameter appear to be directly affected by the availability of water, light, and nutrients [15–19]. Light seems to be one of the most critical factors in the physiological performance of this species in natural forests and plantations, directly influencing the density of individuals, biomass gain, fruit yield, population distribution patterns, and wood production [16, 20–25]. Water availability, on the other hand, may influence fruit or seed production. Nutrients, especially phosphorus, also seem to be a key determinant of growth and fruit yield in natural forests and plantations [11, 26, 27].

In reviewing the relationship between abiotic factors and phenotypic characteristics, we posit that the Brazil nut tree has adaptive plasticity to resource availability. This species adjusts its morphophysiological traits (photosynthesis, leaf morphology, resource use efficiency) to favor its survival and growth under different environmental conditions. In addition, the Brazil nut tree also tolerates stresses caused by the low availability of water and nutrients in the soil and by variations in light availability. These characteristics help us understand its vigorous performance and relative dominance in the Amazon forest and help explain why this species has performed well when planted in pure plantations, agroforestry systems, mixed plantations, enrichment plantings, and plantings to recuperate degraded areas.

Nonetheless, several important gaps in the ecophysiological understanding of the Brazil nut tree exist. Because this species is one of the principal native species targeted for restoration in the Amazon, addressing these gaps may guide continued wild tree conservation and production, as well as highlight new silvicultural horizons [28]. Currently, it is illegal to sell Brazil nut trees because of their traditional and contemporary non-timber values (i.e., nuts, carbon sequestration, and storage) (Brazilian Law decree No. 5.975/2006). Despite that, some landowners have shown interest in potential future markets for Brazil nut timber, because of its high wood quality.

Thus, considering the current and future social, economic, and environmental roles of Brazil nut, we discuss the effects of resource availability on the functional and phenotypic characteristics of this species. Finally, we also review the application and implications of these ecophysiological characteristics of Brazil nut on its cultivation, closing with a brief conclusion of prospects for conservation and cultivation. The ecophysiological understanding of Brazil nut can be used to refine and improve management techniques, conservation practices, and social sustainability, and to forecast impacts of climate change in the Brazil nut tree–rich Amazon forests.

## The Natural and anthropogenic History of the Brazil Nut Tree Indicates Physiological Plasticity

The origin and distribution of Brazil nut throughout the Amazon basin still intrigue scientists, and it has been linked with high physiological plasticity. The most widespread hypothesis for the location of species origin is based on linguistic and phylogenetic evidence that suggests that Brazil nut originated in the central Amazon, with *Lecythis* as ancestor [29, 30]. However, this hypothesis is difficult to prove, considering that the species has very likely occurred in the region for at least several hundreds of thousands of years [31].

Additionally, theories have been proposed to explain the wide distribution of Brazil nut in the Amazon basin and its remarkable abundance in some regions. Adolphe Ducke in 1946 was the first to propose that pre-Columbian indigenous tribes had a significant role in the promotion of clumped Brazil nut stands. This hypothesis, however, was challenged by Peres and Baider [32] who suggested that seed predators, such as short-range agouti (*Dasyprocta* sp.), are more effective seed dispersers than humans and thus responsible for the establishment of new stands. Nonetheless, over the last decade, beginning with Shepard and Ramirez [30] who emphasized the role of humans in Brazil nut recruitment, several studies using different methodological approaches have supported the hypothesis that the humans have been central in species distribution [22, 33–35]. In our view, these hypotheses are not mutually exclusive. Especially in areas of anthropogenically disturbed forests such as forest clearings for small-scale agricultural plantings, agouti (*Dasyprocta* sp.) is a particularly effective facilitator of Brazil nut seed placement and burial, and ultimately seedling establishment [21].

Range shifts during the Pleistocene may also have strongly influenced the current distribution of Brazil nut [31]. Since the last interglacial period, suitable conditions and areas for species establishment emerged in the western to central Amazon. Following this period, however, when cooler and drier weather predominated during the last glacial maximum (about 20,000 years ago), suitable species habitats were reduced considerably, and Brazil nut distribution may have been primarily restricted to several potential refuges across the southern Amazon [31]. During the mid-Holocene, evidence suggests an expansion of favorable habitats for Brazil nut establishment, which are considered comparable to current distribution conditions [31]. Today, the species is widely distributed and grows across various soil types, seasonality regimes, and topographic conditions [36].

Thus, taking into account the different Brazil nut origin and distribution theories, acclimatization capacity and plasticity of this species to various environmental conditions seem important for explaining Brazil nut distribution throughout the Amazon. Pertinent processes may include agouti seed dispersal, cultivation or favoring by traditional human populations in different regions, and the ability of the species to survive periods of cooling/warming and drying/moistening [30, 31, 34]. One study that characterized the genetic structure of natural populations of Brazil nut across the Brazilian Amazon indicated that it does not follow the pattern expected by neutral processes [37]. The authors argued that factors other than seed dispersal by agoutis may have left footprints in the Brazil nut genome. Indeed, it was confirmed that genetic diversity is more significant in populations located near predicted Pleistocene refuges. All this evidence reinforces the need for further studies to disentangle the relative influences of agouti seed dispersal, local adaptation, historic range shifts, and anthropogenic impacts in natural populations of Brazil nut throughout the Amazon [34].

## Phenotypic Variation and Genetic Diversity

*Bertholletia excelsa* is monospecific, but natural populations display phenotypic variation in tree shape and fruit format [38]. In 1874, these differences led John Miers to describe a species called *Bertholletia nobilis*. Still, the characteristics of collected specimens were not considered valid for a separate classification in the Lecythidaceae family, and consequently, *B. nobilis* was later synonymized with *B. excelsa* [38]. The phenotypic variation is so remarkable in some regions that traditional Amazonian communities recognize different varieties co-occurring in natural stands [39]. They identify some morphological differences in wood color and quality, fruit production, and trunk and crown form. The popular classification varies across Brazilian regions. In lower latitudes within Mato Grosso state, Brazil, which is the southern limit of the distribution of Brazil nut, the most well-known types are named *cor de rosa* (pink), *rajada* (striped), and *mirim* (small) [39]. The popular classification is based on wood color, size of fruit, and quantity of seeds per fruit. When sampled in the same location, the "pink" trees produced heavier fruits and more seeds per fruit than the other popular types [39]. In distant eastern longitudes, in Acre state, the popular classification is based on the color and quality of the wood (red vs. white) and the size and shape of the adult trees [40]. Locals believe the individuals that produce reddish wood to be better for construction than the white-type wood. These "red" individuals also displayed a larger crown and greater fruit production when compared to the "white" type [40]. Nonetheless, when the consistency of phenotypical characteristics of trees, fruits, and seeds in individuals popularly classified as red or white types and genotyped adult trees with molecular markers was evaluated, they concluded that the popular classification is not supported by molecular differences. They also suggested that the phenotypic differences among the types may represent age-related variations [40].

Phenotypical variations of Brazil nut across Amazonian regions have been commonly pointed out as a consequence of human selection because fruit size, wood quality, and shape of the crown are considered typical traits selected by humans in incipient domestication of managed species

[41]. Despite this, the effect of resource availability on the phenotypic variation of Brazil nut cannot be ruled out, and evidence suggests that, at least in small scales (< 50 m), the availability of resources, especially light and nutrients, can directly affect Brazil nut fruit and seed production and above-ground biomass, as well as the shape and size of the crown and crop size [20].

## Brazil Nut Tree Forest Populations

Historical data on the characteristics of natural populations of Brazil nut emanates almost exclusively from the Brazil nut commercial strongholds of Brazil, Peru, and Bolivia (Fig. 1), although it occurs naturally throughout the Amazon biome. Brazilian data is mostly restricted to Acre, Amapá, Amazonas, Pará, and Rondônia Brazilian states.

Phenotypic plasticity is a key point in explaining the dynamics of natural populations [42]. The ability of a plant to colonize different ecosystems, therefore expanding its range and adaptability to diverse environments, can be due to greater (or lesser) degrees of plasticity [42]. Brazil nut trees, for example, are found throughout a large geographic range, from 5° N to 14° S latitude, which comprises areas throughout the Brazilian Amazon and adjacent regions of Bolivia, Peru, Colombia, Venezuela, and the Guianas (Fig. 1). In general, it is found in *terra firme* forests, but there are reports of trees also occurring in floodplains (locally known as "várzeas") [36, 43]. Distribution models estimate that the species occurs most commonly in areas with elevations of 200–400 m [44]. However, studies document that the species can occur from sea level [31] to up to about 562 m above sea level [36].

Brazil nut tree plasticity's observed extensiveness can at least partially explain the wide occurrence of the species in environments with a wide range of abiotic factors. These include air temperatures that range from approximately 24.3 to 27.2℃, total annual rainfall variations between 1400 and 2800 mm, and mean annual relative humidity ranging between 79 and 86% [45]. Edaphic factors, such as particle size, macroporosity, pH, and nutrient content are factors that best predicted spatial variation in Brazil nut occurrence [46]. Additionally, elevation seems to be an important predictor

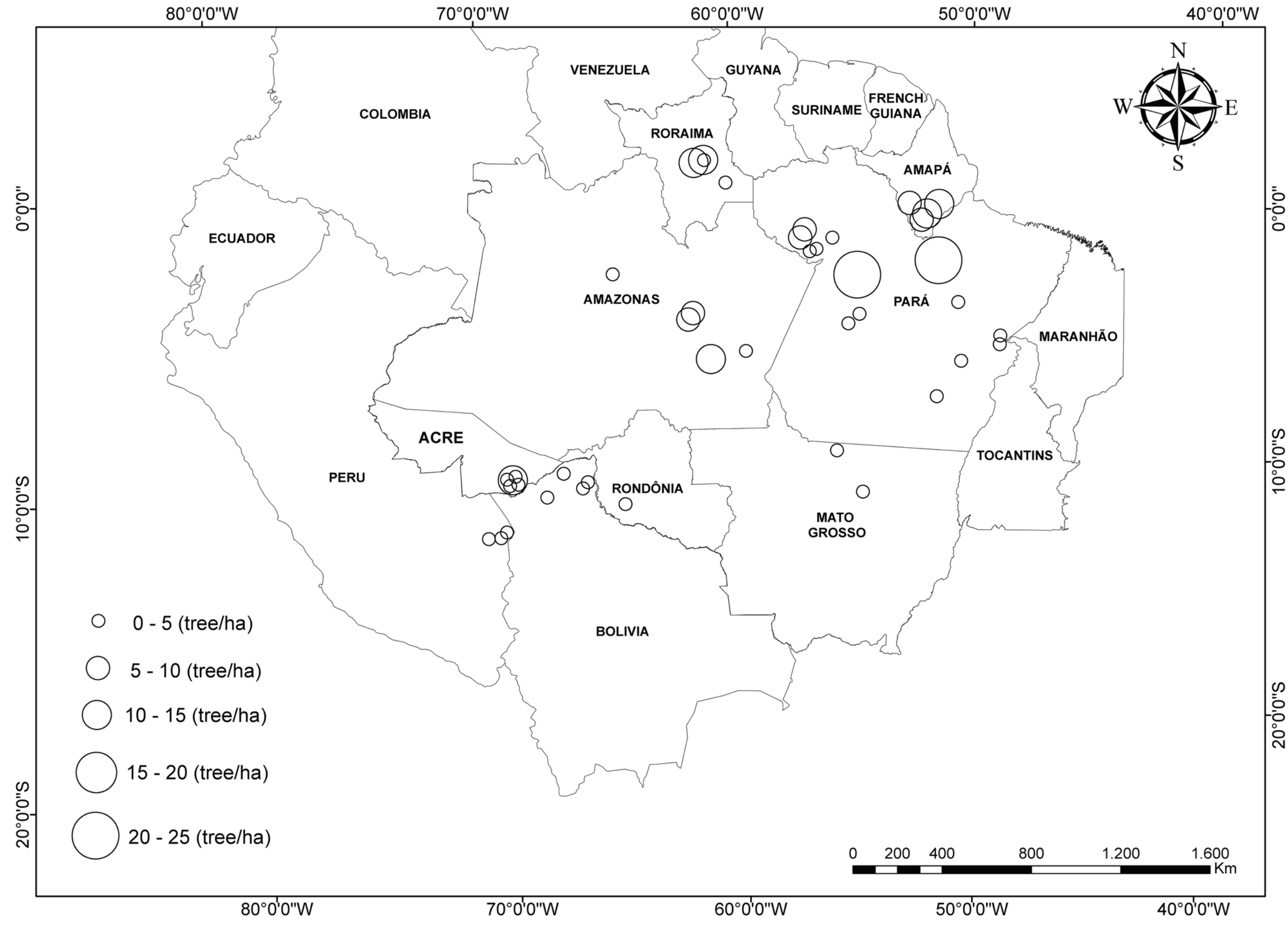

**Fig. 1** Distribution of studies and population densities of Brazil nut in the Amazon region

for explaining the occurrence of Brazil nut in some sites, revealing that lowland areas also are suitable for species establishment [36], although this correlation may not be causal. This species presents better growth performance in soils with a clay to heavy clay texture, and its growth is impaired in sandy soils [43, 47].

Another indicator of the high level of Brazil nut phenotypic plasticity is its long life span that is associated with its ability to reach large diameters in natural forests. Large Brazil nut trees with > 160 cm in diameter at breast height (DBH) may be over 300 years old, while those first entering reproductive sizes (~ DBH > 40 cm) may exceed 100 years of age [48, 49]. In the eastern Amazon, enormous Brazil nut trees (4.46 m DBH) were estimated to be approximately 800 and 1000 years old [50], and radiocarbon dating suggests maximum lifespans can be over 1000 years [51]. The main factors responsible for Brazil nut mortality in natural populations appear to be wind, storms, human-ignited fires, and liana infestations [49]. Like plants with long life spans, Brazil nut may have compensatory mechanisms that bestow plasticity and maintain their photosynthetic capacity and vascular complexity, allowing them to grow and survive for long periods of time [52].

Plastic responses to abiotic factors, such as light, water, and nutrients, can be observed in several population characteristics. For example, Brazil nut trees often are found in groves of 5–100 individuals known as *castanhais* that are separated from other groves by gaps of about 1 km in which the species is entirely absent [38]. However, a random distribution pattern has also been reported [16, 18, 48]. In Acre, individual trees were separated by distances ranging from 1 to 233 m in locations considered to be rich in Brazil nut [16]. Groves versus more scattered distribution patterns may be partially due to differences in forest types, and light seems to exercise an important effect [16]. Perhaps, open forest provides more consistent favorable regeneration conditions, such as high light intensity, which results in a more scattered spatial distribution pattern and more constant seedling establishment over time [16]. Evidence suggests that a grove distribution pattern may be influenced by human dispersal, while the more scattered pattern may result from greater agouti-mediated seed dispersal [34].

Additionally, light availability has been associated with several other population characteristics of Brazil nut, such as seedling density, diameter growth, population structure, and fruit production [18, 21, 33, 48, 53–55]. In natural populations, for example, Brazil nut seedling densities vary from extremes of 0.005 trees ha$^{-1}$ in Oriximiná to 25 trees ha$^{-1}$ in the Caxiunã Reserve, both recorded in the state of Pará (Fig. 1). In Brazil, the largest populations are concentrated in the states of Acre, Amazonas, Amapá, Pará, and Roraima. In Bolivia, recorded densities averaged about 1.7 trees ha$^{-1}$ in Beni to 3.3 trees ha$^{-1}$ in Pando. Nowadays, high densities in Brazil are associated with protected forest areas (Fig. 1). The history of use of the sites and the availability of light have been pointed out as determining factors for the rate of regeneration and seedling densities, and a high mean of regeneration and seedlings density has been observed in environments where there is greater availability of light [21, 33].

Average Brazil nut tree diameters vary from 44.9 cm in Alter do Chão to 159 cm in Oriximiná, both in Pará state, Brazil, where tree populations were among those with the lowest and highest densities of young plants, respectively (Table 5). The increasing availability of light favors the Brazil nut plant's growth rates [21, 48, 53–55] and can also be associated with the time to reach maturity and the beginning of fruit production. Some reports also have shown that light does not seem to influence the survival rate of seedlings [48], but light does affect population structure. For instance, Brazil nut grows best in large forest gaps during the initial developmental stages of its life cycle [38, 53]. The ability of plants to colonize gaps and open areas is an important characteristic of plants that show physiological plasticity [14].

The lack of standardized inventories also hampers more precise information on Brazil nut population structure [16], including the use of sample units of different sizes and shapes, differences in a minimum DBH limits, and criteria for plot locations [16]. Purposefully or unwittingly, inventories may include areas that were modified by humans, and characteristics such as crown shape and height may result from anthropogenic activity over time [33], reflecting the way the forest was occupied and/or exploited by humans.

Sufficient and timely rainfall also increases growth rates in relation to diameter and has a strong relationship with fruit production, but to date, there is no evidence that drought causes changes in survival rates of Brazil nut tree populations [49, 56]. Phenotypic plasticity is beneficial in periods of water stress and favors the emergence and growth of plants even in places where water availability is limited. Nutrient availability is also related to water, and Brazil nut can grow in both low and high fertility soils. However, the increased availability of phosphorus seems to favor species growth and photosynthetic rates [11].

Tree diameter growth and canopy shape (related to canopy size) are positively related to Brazil nut fruit yield [16]. The variation in annual fruit yield of individuals is very large and can range from 9 to 218.5 fruits per tree (Table 6). On average, the annual nut production is 15 kg tree$^{-1}$ with a variation from 3.8 to 39.4 kg tree$^{-1}$ (Table 6), which translates to 30 kg ha$^{-1}$ with variation from 8 to 116 kg ha$^{-1}$. Several factors can be considered alone and in association, such as (1) genetic background, (2) climate, (3) soil fertility, (4) biological competition, (5) tree size and architecture, (6) canopy position, (7) and level of liana infestation (Table 1).

Lianas have a negative effect on nut production based on studies located in the Chico Mendes Reserve in Acre state,

**Table 1** Effects of availability of resources on the population characteristics of Brazil nut

| Population traits | | | Availability of resource | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | -------------------- Soil attributes ------------------ | | | | | | | |
| | Light | Rain fall | Elevation | Clay | Silt | Porosity | Water | CEC | P | Zn | Cu |
| Occurrence | - | - | - | ↗ | - | ↗ | ↗ | ↗ | - | ↗ | ↗ |
| Survival | ➡ | - | - | - | - | - | | - | - | - | - |
| Aggregate spatial distribution | ↘ | - | - | - | - | - | - | - | - | - | - |
| Population density | - | - | - | - | - | - | - | - | - | - | - |
| Regeneration | ⬆ | - | - | - | - | - | - | - | - | - | - |
| Diameter growth | ⬆ | - | ↗ | ⬆ | - | - | - | - | - | - | - |
| Life span | - | ⬆ | - | - | - | - | - | - | - | - | - |
| Age of maturity | ⬆ | - | - | - | - | - | - | - | - | - | - |
| Fruit or seed production | ⬆ | ⬆ | ↗ | ⬆ | - | - | ⬆ | ⬆ | ↗ | - | - |

⬆ = indicates positive effects; ↗ = indicates a predominantly positive trend; ↘ = indicates a predominantly negative trend; ➡ = indicates no effects.

Brazil [17, 20, 26]. The elimination of lianas increased nut production significantly (3×). This increase was attributed to reduced competition for light and below-ground resources, such as water and nutrients [17]. Cation exchange capacity (CEC) and foliar phosphorus have been positively associated with fruit production [26]. On the other hand, in lowland areas, where individuals can spend months in flooded conditions, fruit production seems lower [43, 56]. Other soil attributes, especially the availability of phosphorus ($PO_4^{3-}$), exchangeable aluminum (Al), pH, and potassium (K), seem to influence fruit yield [26, 56, 57], but nutritional research has been limited.

While there are still gaps regarding which abiotic factors determine growth and fruit production of Brazil nut trees in natural forests, recurring results converge on several abiotic factors that seem to influence Brazil nut populations (Table 1). Cumulative research to date indicates that irradiance in natural populations seems to be the factor that most influences Brazil nut tree regeneration, diameter growth, landscape distribution patterns, and time to reach reproductive maturity, as supported by several authors [21, 38, 58–61].

## Cultivating the Brazil Nut Tree

Brazil nut cultivation is not a recent activity, and there are records of plantings by humans dating from the first millennium of the Common Era [1]. Contemporary planting has been attributed to Japanese immigrant settlers in the Brazilian cities of Tomé-Açu, Pará state, and Parintins, Amazonas state, beginning in the 1930s [62]. The Brazil nut tree is currently being cultivated in different planting systems, including monoculture or pure plantations, agroforestry systems, mixed plantations, and enrichment plantings (Fig. 2). Brazil nut plantations have been established throughout and outside the species' natural range, with the highest concentration of Brazil nut plantations occurring in the Brazilian Legal Amazon (Fig. 2).

The wide distribution of Brazil nut plantations throughout very different climatic conditions beyond Amazon biome borders reinforces inferences about phenotypic plasticity. In Lavras, Minas Gerais state, where Brazil nut tree species is also planted (Fig. 2), mean air temperatures range from 18 to 20 °C, and total annual rainfall ranges between 1300 and 1700 mm [63]. These variations in temperature and rainfall are very different from the conditions of the natural species occurrence whereby the mean air temperature ranges from 24.3 to 27.2 °C and total annual rainfall ranges between 1400 and 2800 mm [45]. Brazil nut plants exhibit robust physiological processes (for example photosynthesis) capable to handle functional adjustments in order to ensure higher survival rates and growth in different environments [64].

Researchers and farmers considered several economic and technical aspects before Brazil nut plantations became widespread in the Amazon. Observed low fruit production in previously established plantations coupled with pest and disease risks associated with pure plantations were the main concerns. "Growing *Bertholletia excelsa* in plantations has not been very successful, probably due to the lack of efficient pollinators and the risk of inbreeding" [38, 60] and "*Bertholletia excelsa* monoculture plantations are an option for already capitalized investments, but in the future, they may be limited by the attack of pests and disease." [65] Little was known about *B. excelsa* pollinators and fears that

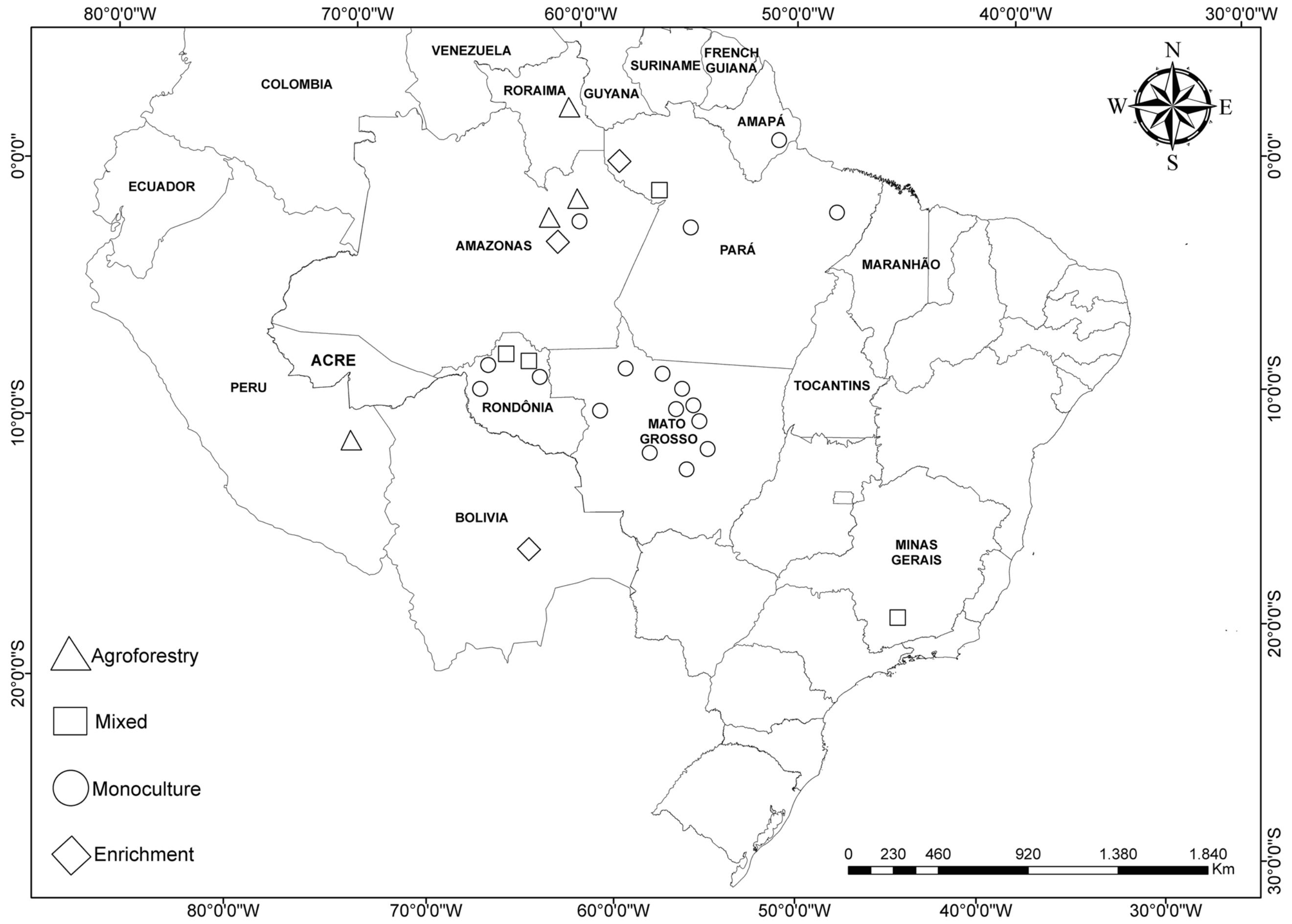

**Fig. 2** Distribution of studies and plantation systems of Brazil nut

concentrated plantings might provide favorable conditions for pest and/or disease development were widespread, as had been observed with the rubber tree and the pathogen *Microcyclus ulei* [66].

Brazil nut trees often are widely recommended for commercial plantations beyond the geographic boundaries of the Amazon region. So far, pests and/or diseases affecting growth or fruit production by this species have been described [67, 68]. Only one disease (brown spot) caused by the fungi *Colletotrichum* sp. has been detected, infecting leaves, but with apparently no damage to growth or fruit production [67, 69]. Species with high levels of genetic plasticity are more tolerant to pests and are also able to recover more quickly after disturbances caused by diseases and pests [70, 71].

One study investigated several aspects of Brazil nut tree pollination ecology in plantations [72], but the relationship between pollination success and fruit yield is still unclear. Evidence from mating system studies indicates that lower fruit yield in plantations may be due to genetic incompatibility among trees and inbreeding. The Brazil nut tree predominantly reproduces by cross-pollination and viable seeds are mostly produced after crossing among unrelated trees [73–75]. A study conducted in the Peruvian Amazon demonstrated that fruit yield was negatively affected by conspecific proximity, probably because of biparental inbreeding and resource competition [76].

Low germination rates (of about 25%) and delayed seedling emergence (from 12 to 15 months) also discouraged Brazil nut tree plantations in the past [77]. However, removal of the external integument (testa) from the seeds and treatment with fungicides before sowing have proven to raise germination rates to over 90% [77].

The Brazil nut tree has several silvicultural characteristics that make it one of the most frequently recommended native forest species for restoration of degraded areas, agroforestry systems, forest enrichment, and monoculture plantations for the production of fruits and wood [61, 78–80]. Diameter growth in plantations varies from 9.6 mm year$^{-1}$ in mixed plantations used to restore degraded areas to 31.6 mm year$^{-1}$ in agroforestry systems, and plant survival is over 80% (Table 7) [61, 79–81]. In these planted environments, little is known about fruit production, but light availability has been reported to have a strong positive influence on growth rates (diameter and height) [64].

Seedling establishment in enrichment planting (increasing the number of a specific tree in disturbed or undisturbed areas) has also been examined and Brazil nut trees support the variation in light availability that occurs according to the different sizes of clearings, but better results were seen in large clearings, where the availability of light is more significant. In Bolivia, in an enrichment planting, after 4 years, the survival rate of seedlings varied between 59 and 94% [59]. The results obtained in Trombetas experimental plantations, Pará state, Brazil, followed the pattern observed in trees of enrichment experiments, where the degree of light exposure was the primary determinant for the best performance of the plant, increasing the growth with the size of the canopy opening [82].

In agroforestry systems, it has been observed that Brazil nut trees invested a substantial part of their biomass and nutrients on branches and crowns, it shows a tendency of Brazil nut trees to develop spreading crowns with very large and heavy branches when grown under agroforestry conditions [9]. In addition, the availability of Ca and Mg was associated with higher biomass production in Brazil nut trees in agroforestry systems. The changes in the biomass allocation pattern in plants are an essential strategy of acclimatization and plasticity that gives plants the ability to increase efficiency in capturing or using more limited resources for their survival and growth.

Additionally, differences between the growth rates of the Brazil nut tree in agroforestry systems were mainly attributed to the availability of nutrients in the soil and also the historical use of the areas, since the growth of the species can be favored primarily by the levels of phosphorus and organic matter in the soil [68]. Similar results were observed in fertilized agroforestry systems, in which trees responded to increased levels of nitrogen, phosphorus, and lime, with significantly improved foliar nutrition and growth. Plasticity is partially responsible for determining the responses of plant performance to soil fertilization. The rationale is that functional traits reflect the plants' capacities for resource capture and adaptations to environmental changes.

The effects of silvicultural interventions, such as fertilization and thinning, on the growth rates of the Brazil nut were also tested in pure plantations formed by the species [11]. As a monoculture, the species has shown high growth rates and, in general, in the Amazon region these plantations have been established without the adoption of silvicultural interventions such as the application of fertilizer or correction of soil pH and the control of ants [11]. Even in these conditions, the species has a high rate of survival and growth when compared to other native and even exotic species planted under the same site conditions. In these planting systems, the species has a high capacity both to support and to recover from disturbances caused by changes in the availability of light, water, and nutrients that may occur due to silvicultural interventions such as thinning [11].

Among the native species, Brazil nut is one of the most promising for reforestation and recovery of degraded areas from different activities such as mining and grazing of animals, which are among the main types of degradation in the Amazonian forests [9, 11, 27, 61, 62]. The recommendation to use Brazil nut for the recovery of degraded areas is mainly due to its capacity to tolerate stress caused by the extreme conditions imposed by these adverse environments, such as high irradiance and low availability of water and nutrients. In addition to tolerating the stresses caused by the harsh conditions of the degraded sites, the species also possesses efficiency in the use of the most limiting resources such as water and nutrients. In the case of mined areas, the species' capacity to tolerate high levels of heavy metals in soils demonstrates the high potential of the species for phytoremediation [80].

The fruit production of Brazil nut trees growing in forests normally begins at ages over 70 years [49, 83]. In plantations, the production generally starts between 12 and 15 years [68], but there are reports of Brazil nut trees that fruit at 10 years [38], 8 years [68], 6 years [62], and even at 5 years [84]. In plantations, annual fruit production by tree varies from 1 to 132 fruits tree$^{-1}$ [81, 85], and annual seed production varies from 7.5 to 24.0 kg tree$^{-1}$ [68, 81, 86]. The evaluation of plantations and fruit production in Rondônia showed a variation from 73 to 1,792 fruits ha$^{-1}$ over 14 years of monitoring [86]. Production did not show a clear relationship with the ages of the trees during this period and did not exhibit differences between the production of trees in mixed plantations and pure plantations [86].

In general, ecophysiology studies of Brazil nut trees have been carried out under different forest site conditions and these edaphoclimatic variations make it difficult to restore the linking abiotic factors with tree growth and fruit production in natural conditions. For Brazil nut plantations, we found recurrent information in published studies that showed us that light availability is the most investigated resource regarding the survival and growth of Brazil nut plantations. Light availability favors plant growth in enrichment plantations, agroforestry systems, and monocultures, especially in diameter, but it does not affect the survival of the seedlings in the initial phase of the plantation (Table 2). In addition, edaphic factors, mainly the availability of Ca and Mg, were highlighted for biomass production in Brazil nut trees in agroforestry systems.

**Table 2** Effects of the availability of resources on plantation traits of Brazil nut

| Plantation's traits | Availability of resources | | | | | | |
|---|---|---|---|---|---|---|---|
| | Light | Water | CEC | pH | Ca | Mg | P |
| Survival | ➡ | ↗ | - | - | - | - | - |
| Diameter growth | ⬆ | - | ⬆ | - | - | - | - |
| Height growth | ⬆ | - | ⬆ | - | - | - | - |
| Biomass | - | - | - | - | | ↗ | ↗ |
| Wood production | ⬆ | - | ⬆ | - | - | - | - |
| Fruits production | - | - | - | - | - | - | ↗ |

⬆ = indicates positive effects; ↗ = indicates a predominantly positive trend; ➡ = indicates no effects.

## Brazil nut Tree Functional Traits and Ecophysiology

The description of leaf phenological stages is essential for understanding the functional traits and ecophysiology. These measurements are generally carried out at the leaf level and according to strict data collection protocols. Most commonly, in the field, it is possible to identify at least four leaf phenological stages in the Brazil nut tree: recently released leaves, new leaves, mature leaves, and old leaves. The youngest leaves always occur at the base of the branches and will differentiate into older leaves over time.

Newly released and new leaves are tender and can be larger than mature and old leaves, but this depends on the plant's growing environment. The main difference between the newly released leaves and the new leaves is their color, as recently released leaves have a light brown color. The difference between new and mature leaves is mainly in the texture and color of the leaves. The mature leaves are less tender than the new ones and have a more intense and brighter green color. Regarding the difference between mature leaves and old leaves, the main difference is the leathery appearance and the more opaque green color in the older leaves.

The mature leaves show the leaf area (LA) ranges from 74.8 to approximately 400 $cm^2$ according to their age and the environmental conditions, with higher values occurring in shaded plants [8, 27, 64, 87, 88]. The specific leaf area (SLA) ranges from 91.3 to approximately 200 $cm^2\ g^{-1}$, with higher values found in shaded plants and with lower values observed in plants under full sunlight [8, 27, 64, 87, 88]. In general, changes in leaf area occur due to changes in the light environment and differences in soil fertility. On the other hand, changes in specific leaf area values have been observed relating to changes in the light environment and water availability at the site and less from changes in soil fertility [8, 27, 64, 87, 88].

In the literature, it is possible to find photosynthesis values (*Pn*) for Brazil nut trees that vary from 0.5 to 15 μmol $m^{-2}\ s^{-1}$ [8, 10, 27, 88]. However, in general, *Pn* values between 7 and 10 μmol $m^{-2}\ s^{-1}$ represent the most common photosynthetic behavior for the species. The dark (Rd) respiration rates found for the Brazil nut vary from 0.12 to 2.9 μmol $m^{-2}\ s^{-1}$, and the range of values for stomatal conductance (*gs*) and transpiration (*E*) is from 0.02 to 0.59 mol $m^{-2}\ s^{-1}$ and from 0.57 to 6.5 mmol $m^{-2}\ s^{-1}$, respectively [8, 10, 27, 88]. In general, the lowest *Pn*, *Rd*, *gs*, and *E* values have been observed in seedlings subjected to severe water deficit [10]. In contrast, the highest values have been observed in plants exposed to direct sunlight and fertilized [8, 10, 27, 64, 88].

A typical photosynthesis curve can indicate a light compensation point ranging from 2.11 to 71 μmol $m^{-2}\ s^{-1}$, saturation point ranging from 190 to 1.032 μmol $m^{-2}\ s^{-1}$, and quantum yield ranges between 0.026 and 0.08 μmol $μmol^{-1}$ [8, 27, 64, 87, 88]. An unusual quantum yield value (0.12 mmol $mmol^{-1}$) was also already found for Brazil nut seedlings in controlled conditions [64]. These values can vary according to the light environment, water availability, soil fertility, and leaf age. There is not a large variation in the photosystem II photochemical efficiency ($F_V/F_M$), which ranges from 0.58 to 0.85, with lower values being found in plants under full sunlight and in nutrient-impoverished soils [7, 8, 10, 84, 85].

Concentrations of macro- and micronutrients in leaves of Brazil nut trees at different ages, growing in different conditions across the Amazon region show little variation (Table 3), with higher values being observed in young plants in the greenhouse and the lowest in plantations in degraded areas. In general, the order of nutrient concentration in the leaves of the Brazil nut tree is N (18 g $kg^{-1}$) > Ca (7 g $kg^{-1}$) > K (5 g $kg^{-1}$) > Mg (2 g $kg^{-1}$) > P (1 g $kg^{-1}$) > Mn (102 mg $kg^{-1}$) > Fe (68 mg $kg^{-1}$) > Zn (28 g $kg^{-1}$) (Table 3). The highest concentrations of macro- and micronutrients are observed in the leaves + fine branches, and the crowns represented about 57% of the total nutrient stock in Brazil nut trees [89].

Brazil nut is considered a tolerant species to the low soil nutrient availability, but fertilization favors the ecophysiological performance and growth of Brazil nut [27]. Higher

**Table 3** Concentrations of macro- and micronutrients in the leaves of Brazil nut at different ages and under different growth conditions in the Amazon region

| Growth condition | Amazon region | N | P | K | Ca | Mg | Fe | Zn | Mn |
|---|---|---|---|---|---|---|---|---|---|
| | | g $kg^{-1}$ | | | | | mg $kg^{-1}$ | | |
| Pure plantation, 8 years[1] | Itacoatiara, AM, Brazil | 17.5 | 0.7 | 6.2 | 4.3 | 2.4 | 57.5 | 25.7 | 94.5 |
| Vegetation house, 9 months[2] | Itacoatiara, AM, Brazil | 20.2 | 1.1 | 5.5 | 4.2 | 1.5 | 39.3 | 36.7 | 52.9 |
| Clonal (606) plantation[3] | Itacoatiara, AM, Brazil | 19.2 | 1.0 | 5.7 | 5.6 | 2.1 | 64.2 | 29.0 | 107.4 |
| Clonal (609) plantation[3] | Itacoatiara, AM, Brazil | 19.7 | 0.9 | 4.4 | 8.4 | 2.2 | 67.4 | 29.2 | 134.5 |
| Clonal (ARU) plantation[3] | Itacoatiara, AM, Brazil | 18.8 | 1.0 | 4.7 | 6.1 | 2.3 | 66.2 | 30.1 | 99.9 |
| Clonal (Manuel Pedro) plantation[3] | Itacoatiara, AM, Brazil | 19.0 | 1.0 | 4.8 | 6.3 | 2.6 | 70.3 | 28.5 | 124.1 |
| Clonal (Santa Fé) plantation[3] | Itacoatiara, AM, Brazil | 19.3 | 1.0 | 4.4 | 7.8 | 2.6 | 68.7 | 30.2 | 149.2 |
| RAD plantations, 1 year[4] | Manaus, AM, Brazil | 10.7 | 1.2 | 3.1 | 11.1 | 2.4 | 119.6 | 19.6 | 32.6 |
| Mixed plantations, 10 years[5] | Manaus, AM, Brazil | 18.5 | 0.7 | 4.1 | 8.8 | 2.7 | 62.3 | 28.2 | 123.2 |
| Agroforestry, 7 years[6] | Manaus, AM, Brazil | 19.4 | 1.1 | 7.0 | 9.5 | 2.7 | - | - | - |
| Pure plantation, 17 years[7] | Itacoatiara, AM, Brazil | 17.2 | 0.9 | 3.6 | 5.5 | 2.5 | 97.1 | 20.5 | 95.2 |
| Pure plantation, 12 years[8] | Itacoatiara, AM, Brazil | 17.1 | 0.7 | 4.6 | 5.6 | 3.7 | 36.6 | 18.9 | 62.4 |
| Pure plantation, 29 years[8] | Claudia, MT, Brazil | 19.3 | 1.1 | 8.4 | 5.2 | 2.7 | 46.4 | 18.7 | 32.4 |

[1]=Costa et al. 2015; [2]=Maia et al. 2015; [3] Ferreira et al. 2015; [4]=Ferreira et al. 2013; [5]=Morais et al. 2007; [6]=Schroth et al. 2015; [7]=Lopes 2018, unpublished data; [8]=Castro 2017, unpublished data

photosynthesis, growth rates, and biomass accumulation in seedlings of Brazil nut have been related to the positive effects of fertilization on stomatal conductance, respiration and the efficiency of uptake, and use of other primary resources, such as water and light [27, 64].

The functional traits of mature leaves of Brazil nut trees growing under controlled and field conditions, thus subjected to variations in the availability of light, water, and nutrients, indicate that plants benefit from an increased irradiance availability. The species is tolerant to the low water availability and is highly efficient in the use of nutrients, especially phosphorus (Table 4). These responses were associated with the plasticity of functional traits that the species develops, favoring the capture and use of these resources [10, 11, 27, 64, 87, 88].

The specific leaf area and the nutrient and water use efficiency are improved in the Brazil nut trees at high light availability, allowing it to keep the stomata open and thus

**Table 4** Physiological responses of Brazil nut to the variation in the availability of light, water, and nutrients

| Physiological traits | Light[1] | | Water[2] | | Nutrients[3] | |
|---|---|---|---|---|---|---|
| | Shade leaves | Sun leaves | Dry season | Rainy season | Without fertilization | Fertilized |
| *Pn* (μmol $m^{-2}$ $s^{-1}$) | 10.34 | 12.61 | 11.21 | 11.74 | 8.23 | 11.60 |
| $g_s$ (mol $m^{-2}$ $s^{-1}$) | 0.24 | 0.30 | 0.28 | 0.24 | 0.26 | 0.37 |
| *E* (mmol $m^{-2}$ $s^{-1}$) | 4.14 | 4.77 | 4.62 | 4.29 | 3.57 | 4.71 |
| $R_d$ (μmol $m^{-2}$ $s^{-1}$) | 1.03 | 1.72 | 1.47 | 1.28 | 0.82 | 0.95 |
| SLA ($cm^{-2}$ $g^{-1}$) | 115 | 95 | 115 | 95 | 142 | 150 |
| Chl *a*/Chl *b* | 2.92 | 3.05 | 2.88 | 3.08 | 3.46 | 3.29 |
| $Chl_{total}$/Car | 2.83 | 2.65 | 2.72 | 2.77 | 3.07 | 2.50 |
| $F_V/F_M$ | 0.82 | 0.78 | 0.81 | 0.80 | 0.74 | 0.76 |
| NUE (mmol mol-1 $s^{-1}$) | 0.56 | 0.70 | 0.61 | 0.66 | 0.66 | 0.62 |
| PUE (mmol mol-1 $s^{-1}$) | 11.02 | 14.45 | 10.83 | 14.64 | 9.27 | 10.30 |
| WUE (μmol $CO_2$ $mmol^{-1}$ $H_2O$) | 2.63 | 2.69 | 2.53 | 2.79 | 2.28 | 2.50 |

Obs.: The values are means calculated from literature data. *Pn* photosynthesis, $g_s$ stomatal conductance, *E* transpiration, $R_d$ respiration, *SLA* specific leaf area; $Chl_{total}$ chlorophyll total, *Car* carotenoids, $F_V/F_M$ photochemical efficiency, *NUE* nitrogen use efficiency, *PUE* phosphorus use efficiency, *WUE* water use efficiency. Authors: 1 = [83, 84]; 2 = [7, 8, 27, 75, 83]; 3 = [85, unpublished data].

increasing photosynthesis rates [64, 88]. Additionally, due to high light intensity, the species invests in photoprotective strategies, with the possibility of increasing the concentration of carotenoids in the leaves [64, 87]. On the other hand, under shady conditions, a larger leaf area and an increase of chlorophylls are observed, allowing an improvement of light capture [64, 87, 88]. It has also been observed that shaded plants increase their biomass allocation in leaves and branches as a strategy for capturing more light, while plants in full sun invest a greater amount of biomass in the roots, which can favor the capture of water and nutrients [64, 88].

Another interesting aspect of the Brazil nut tree is its ability to recover from stress caused by sudden changes in the availability of light, which is represented by the recovery of the photosystem II photochemical efficiency ($F_V/F_M$) value at levels close to 0.8, such as that which can occur naturally in forests with the opening of clearings or in plantations after thinning [64]. Some research has attributed this response to the efficient capacity of this species to release excess energy in the form of heat and maintain electron transport rates in the transport chain [11]. The maintenance of electron transport rates, even under stress conditions due to high irradiance, seems to be related to the species' ability to develop photoprotective strategies such as increasing iron and carotenoid concentrations in its leaves [11].

The Brazil nut tree is tolerant to water deficit [10]. The water potential values observed for Brazil nut trees range from – 0,19 to – 4.7 MPa [10, 79]. Brazil nut trees under water deficiency increase the concentration of osmoregulatory solutes, such as potassium and proline in the leaves, allowing stomata opening [10]. The Brazil nut tree also alters the allocation of carbon with the increase in root growth, thus favoring the capture of water by the roots [10]. Although the species can also occur in flooded areas, there is still no information in the literature regarding the effects of flooding on the physiological characteristics of the species.

## Seeds Chemical Components with Economic Relevance and Bioperspectives

The climatic conditions of the Amazon Rainforest and the different extreme conditions of cultivation lead to the activation of the functional plasticity of Brazil nut, in particular, a robust photosynthetic apparatus that is a result of its complex and specific genome. This qualifies it as a large "factory" for the production and storage of important chemical components, some of them "compartmentalized" in the Brazil nuts (fruits), which are the main commodity. Among chemical components in the Brazil nuts are the primary metabolites (proteins, lipids, and carbohydrates), secondary metabolites (terpenes, phytosteroids, flavonoids, tannins, and tocopherols) and other nutrients such as selenium and inorganic phosphate (Fig. 3).

Apart from the high protein content (15.7%), Brazil nuts may be considered oilseeds (70.7%) and also an important source of P, Mg, and Zn [90]. Storage proteins derived from albumin isoforms [91] and selenoproteins [92] are important components, in addition to fatty acids [93] and their respective triacylglycerides and phospholipids [94]. Inorganic phosphate and organic phosphate derivatives (phosphatidic acid and phosphatidylinositol lipids) accumulate in the Brazil nuts [94].

Besides being crucial for the biosynthesis of ATP, phosphate is also important in the biosynthesis of amino acids, terpenes, phytosteroids and tocopherols (mainly as organic diphosphates), and simple phenolic compounds, flavonoids, and tannins [93, 95]. The abundant availability of such metabolites qualifies Brazil nut as a promising resource of biologically-active substances, with industrial applications in the cosmetic, food, and biotechnological fields.

## Conclusion and Future Prospects

The importance of the Brazil nut tree in the social, economic, and environmental framework of the Amazon can be attributed, in part, to its plasticity and other biological abilities discussed in this review. How to deal more efficiently with different abiotic factors and plant stresses or cope with their consequences may be the significant differential of this species, explaining the Brazil nut tree's physiological performance.

Thus, following an ecophysiological approach, we aimed to enhance our understanding of the effects of resource availability on the Brazil nut tree's growth performance to highlight the plasticity and other eco-functional characteristics that are potentially useful for improving the production of the species. As a result, we confirm that *B. excelsa* shows phenotypic plasticity in response to light, water, and nutrient availability. In both natural forests and plantations, the availability of these resources influences population structure, tree growth, and fruit production.

Light represents a major factor in determining the structure of populations and growth in both natural forests and plantations. The Brazil nut tree shows tolerance to stresses caused by the reduction of soil water and nutrient availability and variations in irradiance. This supports using this species as an alternative in programs to recover degraded areas in the continental Amazon. We also found robust evidence that increases in irradiance may lead to increased fruit production; however, fruit production is also affected by competition with lianas and edaphic factors, especially phosphorus availability and soil cationic exchange capacity.

Although this review has compiled several reports on the physiology of the Brazil nut tree, such as photosynthesis, biomass gain, vegetative propagation, susceptibility

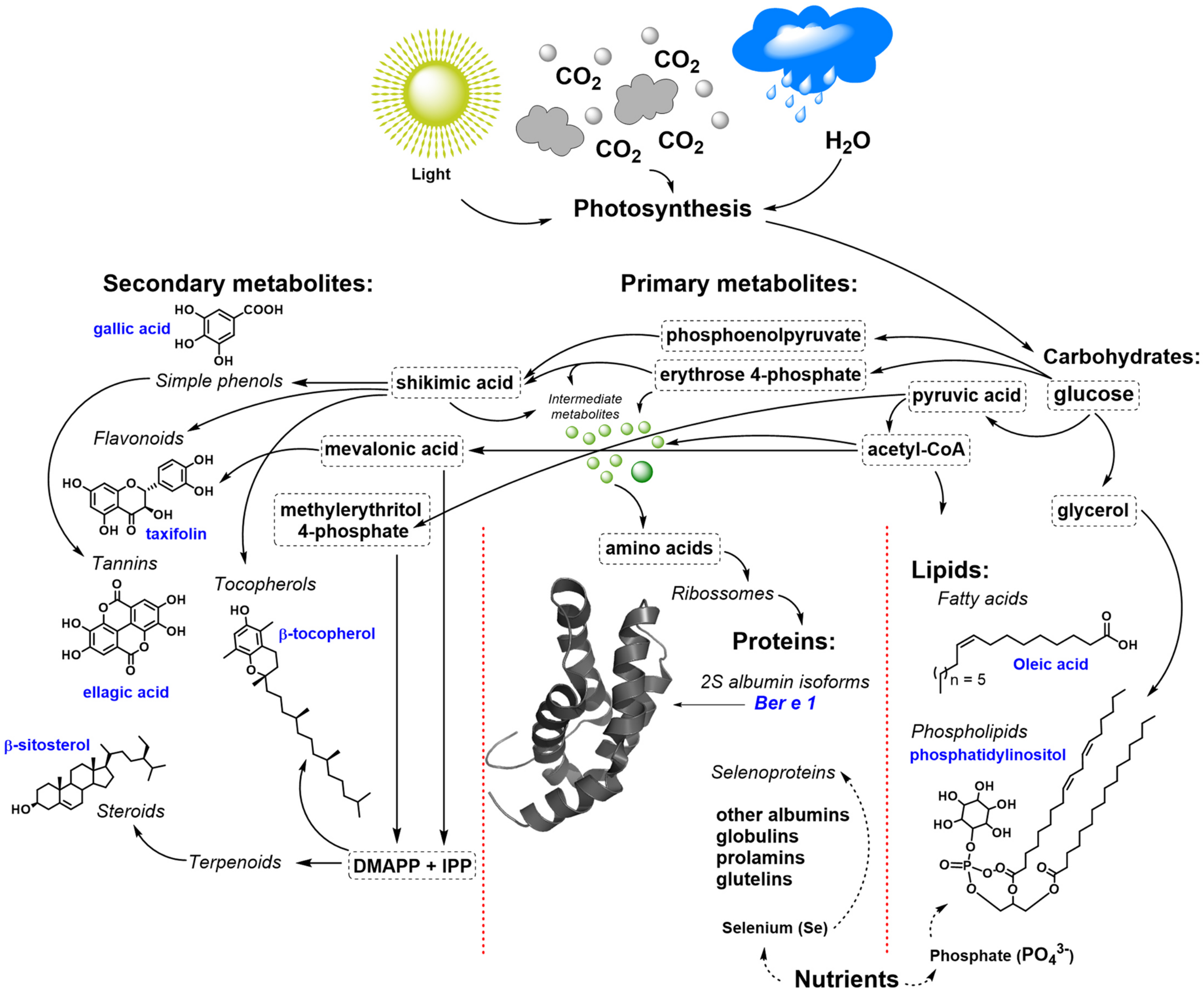

**Fig. 3** Illustrative scheme of primary and secondary metabolic pathways applied to Brazil nut seeds

to climate change, plantation management and modeling, genetic enhancement, ecology, fruit production, Pi accumulation in the nuts, and implications on seed metabolic pathway, we believe that we are still far from understanding the physiological behavior of this species under the different system cultivation possibilities. Further studies are necessary to assist management practices, which will undoubtedly improve Brazil nut production and allow making robust inferences about how to improve the silvicultural interventions. Additionally, research well designed and executed may help to potentiate synergies for sustainable practices, minimizing the impacts of climate change on both native trees and commercial forest plantations.

# Appendix

**Table 5** Population traits of Brazil nut in natural forests in different Amazon regions

| Amazon region | Density (Tree ha$^{-1}$) | Juveniles (%) | DBH (cm) | References |
|---|---|---|---|---|
| Pinkaiti Reserve, Pará, Brazil | 3.30 | - | - | Baider 2000 |
| O Deserto, lower Xingú River, Pará, Brazil | 1.00 | - | - | Campbell et al. 1986 |
| Tapajós Reserve, Pará, Brazil | 0.67 | - | - | Carvalho 1981 |
| Chico Mendes Reserve—Fallow, Acre, Brazil | 12.7 | - | - | Cotta et al. 2008 |
| Chico Mendes Reserve—Forest, Acre, Brazil | 5.30 | - | - | Cotta et al. 2008 |
| Cajari, Amapá Reserve—Forest, Brazil | 7.00 | 21.0 | 112 | Guedes et al. 2014 |
| Cajari, Amapá Reserve—Capoeira, Brazil | 11.00 | 63.0 | 57 | Guedes et al. 2014 |
| Tambopata Reserve, Peru | 1.30 | - | - | Gentry 1988 |
| Alto Cajari—Forest, Amapá, Brazil | 6.70 | - | - | Neves et al. 2015 |
| Alto Cajaria—Capoeira, Amapá, Brazil | 11.00 | - | - | Neves et al. 2015 |
| Filipinas, Acre, Brazil | 1.80 | 28.0 | 74.6 | Neves et al. 2016 |
| Cachoeria, Acre, Brazil | 2.70 | 17.0 | 88.4 | Neves et al. 2016 |
| Água Branca, Amapá, Brazil | 6.80 | 22.0 | 92.9 | Neves et al. 2016 |
| Sororoca, Amapá, Brazil | 11.20 | 10.0 | 108.6 | Neves et al. 2016 |
| Tahuamanu Reserve, Madre de Dios, Peru | 0.86 | - | - | Nunes et al. 2012 |
| Tambopata Reserve, Madre de Dios, Peru | 0.40 | - | - | Nunes et al. 2012 |
| Indigenous land Kayapó, Pará, Brazil | 1.30 | - | - | Peres and Baider 1997 |
| Pinkaiti Kayapó land, Pará, Brazil | 3.30 | 43.3 | 72.6 | Peres et al. 2003 |
| Kranure Kayapó land, Pará, Brazil | 3.40 | 52.5 | 65.7 | Peres et al. 2003 |
| Saracá-Taqüera land, Pará, Brazil | 1.50 | 1.6 | 134.8 | Peres et al. 2003 |
| Marabá, Pará, Brazil | 4.30 | 33.3 | 119.7 | Peres et al. 2003 |
| Tapajós Reserve, Pará, Brazil | 0.70 | 35.7 | 73.8 | Peres et al. 2003 |
| Alto Cajarí Reserve, Amapá, Brazil | 12.00 | 0.7 | 156.4 | Peres et al. 2003 |
| Iratapuru Reserve, Amapá, Brazil | 9.40 | 0.9 | 154.1 | Peres et al. 2003 |
| Aventura, Lago Uauaçú, Amazonas, Brazil | 6.80 | 24.6 | 102.3 | Peres et al. 2003 |
| Ussicanta, Lago Uauaçú, Amazonas, Brazil | 8.50 | 3.8 | 133.5 | Peres et al. 2003 |
| Lago Cipotuba, Rio Aripuanã, Amazonas, Brazil | 1.80 | 22.4 | 116.6 | Peres et al. 2003 |
| Amanã Reserve, Amazonas, Brazil | 1.40 | 5.3 | 123.5 | Peres et al. 2003 |
| Rio Cristalino, Mato Grosso, Brazil | 4.90 | 40.7 | 90.7 | Peres et al. 2003 |
| Cláudia, Mato Grosso, Brazil | 3.60 | 31.2 | 71.0 | Peres et al. 2003 |
| Nova Esperança, Acre, Brazil | 3.10 | 47.2 | 73.9 | Peres et al. 2003 |
| Colocação Tucumã, Acre, Brazil | 1.40 | 12.2 | 108 | Peres et al. 2003 |
| Colocação Rio de Janeiro, Acre, Brazil | 1.40 | 32.4 | 89.8 | Peres et al. 2003 |
| Encontro, Acre, Brazil | 1.40 | 25.1 | 91.4 | Peres et al. 2003 |
| Oculto, Madre de Dios, Peru | 0.70 | 10.9 | 109.9 | Peres et al. 2003 |
| Limón, Madre de Dios, Peru | 0.10 | 10.6 | 108.2 | Peres et al. 2003 |
| El Tigre, Beni, Bolivia | 1.70 | 25.0 | 102.1 | Peres et al. 2003 |
| El Sena, Pando, Bolivia | 3.30 | 21.7 | 111.3 | Peres et al. 2003 |
| Alter do Chão, Pará, Brazil | 23.00 | 75.6 | 44.9 | Peres et al. 2003 |
| Rio Ouro Preto Reserve, Rondônia, Brazil | 2.00 | 4.5 | 127.7 | Peres et al. 2003 |
| Kikretum Kayapó land | 1.7 | - | - | Ribeiro et al. 2014 |
| A’Ukre Kayapó land | 3.5 | - | - | Ribeiro et al. 2014 |
| Moikarakô Kayapó land | 2.4 | - | - | Ribeiro et al. 2014 |
| Brazil nuts conssesions, Madre de Dios, Peru | 0.62 | - | 126.3 | Rockwell et al. 2015 |

**Table 5** (continued)

| Amazon region | Density (Tree ha$^{-1}$) | Juveniles (%) | DBH (cm) | References |
|---|---|---|---|---|
| Carajás, Pará, Brazil | 1.30 | - | 134.8 | Salomão 1991 |
| Marabá, Pará, Brazil | 4.20 | - | 131.4 | Salomão 1991 |
| Platô Almeida, Oriximiná, Pará, Brazil, | 1.49 | 1.2 | - | Salomão 2009 |
| Platô Aviso, Oriximiná Pará, Brazil | 0.005 | 71.4 | - | Salomão 2009 |
| Platô Bacaba, Oriximiná Pará, Brazil | 0.3 | - | - | Salomão 2009 |
| Platô Bela Cruz, Oriximiná Pará, Brazil | 0.023 | - | - | Salomão 2009 |
| Trombetas River, Pará, Brazil | 6.80 | 7.0 | 128.5 | Scoles and Gribel 2011 |
| Capanã Grande, Amazonas, Brazil | 12.50 | 18.0 | 73.1 | Scoles and Gribel 2011 |
| River Trombetas Region, Pará, Brazil | 6.80 | - | 128.4 | Scoles and Gribel 2012 |
| Oriximiná, Pará, Brazil | 2.00 | 4.6 | 159 | Scoles et al. 2016 |
| Caxiuanã Reserve, Pará, Brazil | 25.00 | 54.5 | 64.9 | Sousa et al. 2014 |
| North Bolivia | 1.70 | - | - | Stoian 2004 |
| Caracaraí-Itã, Roraima, Brazil | 13.50 | - | 82.7 | Tonini et al. 2014 |
| Caracaraí-Cujubim, Roraima, Brazil | 6.50 | - | 118.8 | Tonini et al. 2014 |
| São João da Baliza, Roraima, Brazil | 3.70 | - | 65.9 | Tonini et al. 2014 |
| São João Baliza, Roraima, Brazil | 3.70 | 35.3 | 65.9 | Tonini et al. 2008 |
| Caracaraí, Roraima, Brazil | 12.90 | 26.7 | 74.6 | Tonini et al. 2008 |
| Caracaraí-Itã, Roraima, Brazil | 13.00 | - | 81.8 | Tonini and Baldoni 2019 |
| Caracaraí-Cujubim, Roraima, Brazil | 6.00 | - | 112.6 | Tonini and Baldoni 2019 |
| Itaúba, Mato Grosso, Brazil | 15.00 | - | 59.9 | Tonini and Baldoni 2019 |
| Chico Mendes Reserve, Acre, Brazil | 1.35 | 25.5 | 86.1 | Wadt et al. 2005 |
| Cachoeira, Acre, Brazil | 2.50 | - | 93 | Wadt et al. 2008 |
| Pindamonhangaba, Acre, Brazil | 2.20 | - | 71.6 | Wadt et al. 2008 |
| Filipinas, Acre, Brazil | 1.50 | - | 70.9 | Wadt et al. 2008 |
| El Tigre Reserve, Beni, Bolivia | 3.00 | - | 107.5 | Zuidema and Boot 2002 |
| El Sena Reserve, Pando, Bolivia | 2.40 | - | 126.9 | Zuidema and Boot 2002 |

**DBH* Diameter at breast height measured at 1.3 m above ground level.

**Table 6** Fruit and seed production of Brazil nut trees in natural forests

| Local | DBH | Fruit production | Seed production | | References |
|---|---|---|---|---|---|
| | | (Fruit tree$^{-1}$) | (kg ha$^{-1}$) | (kg tree$^{-1}$) | |
| Pinkaiti Reserve, Pará, Brazil | - | 184.3 | - | - | Baider 2000 |
| RESEX Cajari, Amapá, Brazil – Capoeira | 57 | 9 | - | - | Guedes et al. 2014 |
| RESEX Cajari, Amapá, Brazil – Forest | 112 | 22 | - | - | Guedes et al. 2014 |
| Chico Mendes Reserve, Acre, Brazil | - | 65.5 | - | 9.7 | Kainer et al. 2006 |
| Chico Mendes Reserve, Acre, Brazil | - | 72.0 | - | 10.07 | Kainer et al. 2006 |
| Chico Mendes Reserve, Acre, Brazil | - | 66.2 | 12.5 | 9.3 | Kainer et al. 2007 |
| Alto Cajari—Forest, Amapá, Brazil | - | 165.0 | - | - | Neves et al. 2015 |
| Alto Cajaria—Capoeira, Amapá, Brazil | - | 62.0 | - | - | Neves et al. 2015 |
| Tahuamanu Reserve, Madre de Dios, Peru | - | - | 15.0 | 17.14 | Nunes et al. 2012 |
| Tambopata Reserve, Madre de Dios, Peru | - | - | 14.3 | 35.7 | Nunes et al. 2012 |
| Kayapó land, Pará, Brazil | - | 207.0 | - | | Ribeiro et al. 2014 |
| Madre de Dios, Peru | 125 | 218.5 | - | 39.4 | Rockwell et al. 2015 |
| Plato Almeida, Pará, Brazil | 122 | 29 | - | - | Salomão et al. 2006 |
| São João Baliza – Roraima | 65.9 | 24.8 | 32.7 | 4.3 | Tonini et al. 2008 |
| Caracaraí – Roraima | 74.6 | 18.6 | 8.48 | 3.8 | Tonini et al. 2008 |
| Caracaraí-Itã, Roraima, Brazil | 82.7 | - | 34.8 | - | Tonini et al. 2014 |
| Caracaraí-Cujubim, Roraima, Brazil | 118.8 | - | 116.18 | - | Tonini et al. 2014 |
| São João da Baliza, Roraima, Brazil | 65.9 | - | 16 | - | Tonini et al. 2014 |
| RESEX Chico Mendes, Acre, Brazil | 86.1 | - | - | 10.28 | Wadt et al. 2005 |
| Pindamonhangaba, Acre, Brazil | - | 86.5 | - | - | Wadt et al. 2008 |
| Filipinas, Acre, Brazil | - | 79.6 | - | - | Wadt et al. 2008 |
| Beni, Bolivia | 184 | - | - | - | Zuidema 2003 |
| Pando, Bolivia | 139 | - | - | - | Zuidema 2003 |

**DBH* Diameter at breast height measured at 1.3 m above ground level.

**Table 7** Brazil nut under different plantation systems within (Northern Brazil and Peru) and outside the Amazon region (Southeastern Brazil)

| Region | Plantation system | Age | Spacing | Height | DBH | MAI | | Survival | References |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | DBH | Height | | |
| | | (years) | (m) | (m) | (cm) | (cm ano$^{-1}$) | (m ano$^{-1}$) | (%) | |
| Lavras, MG, Brazil | Agroforestry | 16 | 3 × 3 | 12 | 17.4 | | | 83.5 | Caetano 2012 |
| Manaus, AM, Brazil | Agroforestry | 12 | 12 × 12 | 20.9 | 38 | 3.16 | 1.74 | 78 | Costa et al. 2009 |
| Manaus, AM, Brazil | RAD monoculture | 8 | 2.5 × 1.5 | 11.47 | 9.57 | 1.20 | 1.43 | - | Costa et al. 2015 |
| West Amazon, AC, Brazil | Enrichment | 5 | 5 × 5 | 2.85 | 1.51 | | 0.53 | 10 | d'Oliveira 2000 |
| Manaus, AM, Brazil | Monoculture | 10 | 3 × 3 | | | | | | Fernandes Alencar 1993 |
| Nova Califórnia, RO, Brazil | Agroforestry | 16.5 | 10 × 4 | 19.9 | 36.1 | 1.39 | 1.5 | 69.4 | Condé et al. 2013 |
| Cantá, RR, Brazil | Mixed | 10 | - | 14 | 26 | - | - | 98.6 | Ferreira and Tonini 2009 |
| Madre de Dios, Peru | Silvopastures | 3 | 10 × 10 | 4.1 | 4.8 | | | 98.1 | Frank and Cruz 1995 |
| Madre de Dios, Peru | Silvopastures | 2 | 15 × 15 | 2.1 | 2 | | | 97.5 | Frank and Cruz 1996 |
| Porto Velho, RO, Brazil | Agroforestry | 25 | - | 20.6 | 41 | - | - | - | Locatelli et al. 2013 |
| Nova Mamoré, RO, Brazil | Monoculture | 35 | - | 23.9 | 44 | - | - | - | Locatelli et al. 2013 |
| Machadinho do Oeste, RO, Brazil | Monoculture | 28 | 12 × 12 | 28.3 | 60.09 | | | 86 | Locatelli et al. 2015 |
| Machadinho do Oeste, RO, Brazil | Mixed | 28 | 12 × 12 | 28.6 | 59.75 | | | 80 | Locatelli et al. 2015 |
| El Tigre, Bolivia—Close canopy | Enrichment | ~ 3 | 10 × 10 | 0.68 | | | | 86.5 | Peña-Claros et al. 2002 |
| El Tigre, Bolivia—Open canopy | Enrichment | ~ 3 | 10 × 10 | 3.86 | | | | 98.4 | Peña-Claros et al. 2002 |
| Oriximiná, PA, Brazil | RAD | 19 | - | 14.7 | 19.4 | 1.02 | 0.77 | | Salomão et al. 2006 |
| Manaus, AM, Brazil | Agroforestry | | ~ 10 × 10 | 5.4 | 8.4 | | | | Schroth et al. 1999 |
| Manaus, AM, Brazil | Agroforestry | 7 | 10.5 × 10.5 | | 20.6 | 3.0 | | 97 | Schroth et al. 2015 |
| Manacapuru, AM, Brazil | Agroforestry | 10 | - | - | - | 3.1 | 1.6 | - | Soares et al. 2004 |
| Manacapuru, AM, Brazil | Enrichment | 10 | - | - | - | 1.8 | 1.3 | - | Soares et al. 2005 |
| Saracá-Taquera, PA, Brazil | RAD mixed | 30 | 10 × 50 | 15.3 | 19 | 0.96 | 0.78 | | Tonini et al. 2008 |
| Machadinho do Oeste, RO, Brazil | Mixed | 10 | 12 × 12 | 12.95 | 21 | 3.2 | 2.23 | 89.63 | Vieira et al. 1998 |
| Machadinho do Oeste, RO, Brazil | Monoculture | 10 | 12 × 12 | 12.25 | 22 | 3.1 | 2.13 | 95.38 | Vieira et al. 1999 |
| Belterra, PA, Brazil | Monoculture | 6.5 | 3 × 3 | 7.5 | 12 | 1.8 | 1.2 | 66.7 | Yared et al. 1988 |
| Manaus, AM, Brazil | Monoculture | 40 | 10 × 10 | 23.9 | 69 | - | - | - | Yared et al. 1993 |
| Porto Velho, RO, Brazil | Monoculture | 30 | - | 22 | 40 | - | - | - | Yared et al. 1993 |
| Macapá, AP, Brazil | Monoculture | 30 | 10 × 10 | 20.4 | 45 | - | - | - | Yared et al. 1993 |
| Tomé-Açu, PA, Brazil | Monoculture | 49 | 20 × 20 | 20.6 | 80 | - | - | - | Yared et al. 1993 |
| Cláudia, MT, Brazil | Monoculture | - | - | - | - | - | - | - | Baldoni et al. 2019 |
| Santa Carmem, MT, Brazil | Monoculture | - | - | - | - | - | - | - | Baldoni et al. 2019 |
| São José do Rio Claro, MT, Brazil | Monoculture | - | - | - | - | - | - | - | Baldoni et al. 2019 |
| Rosário Oeste, MT, Brazil | Monoculture | - | - | - | - | - | - | - | Baldoni et al. 2019 |
| Sinop, MT, Brazil | Monoculture | - | - | - | - | - | - | - | Baldoni et al. 2019 |
| Terra Nova do Norte, MT, Brazil | Monoculture | - | - | - | - | - | - | - | Baldoni et al. 2019 |
| Nova Bandeirantes, MT, Brazil | Monoculture | - | - | - | - | - | - | - | Baldoni et al. 2019 |
| Alta Floresta, MT, Brazil | Monoculture | - | - | - | - | - | - | - | Baldoni et al. 2019 |
| Juína, MT, Brazil | Monoculture | - | - | - | - | - | - | - | Baldoni et al. 2019 |
| Paranaíta, MT, Brazil | Monoculture | - | - | - | - | - | - | - | Baldoni et al. 2019 |

**DBH* Diameter at breast height measured at 1.30 m above ground level.

**Acknowledgements** The authors are grateful to the National Institute for Amazonian Research (MCTI-INPA), the Amazonas State Research Support Foundation (FAPEAM), the Coordination for the Improvement of Higher Education Personnel (CAPES – Brazil- Finance Code 001), and the National Council for Scientific and Technological Development (CNPq, Brazil) for their financial support for the research. Many thanks to Empresa Agropecuária Aruanã S.A. for its support and cooperation. J.F.C Gonçalves, F.A. Lobo, M. V. Ramos, Hector H. F. Koolen, and P. Mazzafera thank (CNPq-Brazil) for PQ research fellowships.

## Declarations

**Conflict of Interest** The authors declare that they have no conflicts of interest.

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