



Species grouping and diameter growth of trees in the Eastern Amazon: Influence of environmental factors after reduced-impact logging

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ARTICLE INFO

Keywords:

Tree growth
Ecological groups
Soil
Climate
Forest management
CAFOGROM

ABSTRACT

Tree growth predictions still present a challenge to forestry scientists. Species richness, ecological behavior variations, and different climate and soil interactions make it difficult to predict and understand tree growth in managed forests. This study examined the relationship between soil, climate, and forest management parameters and tree growth, using data from more than 30 years of monitoring in the Brazilian Amazon. We evaluated all trees with DBH ≥ 20 cm in a database of 66,182 observations in 166 permanent plots, corresponding to 17,440 individuals and 642 species. We used the CAFOGROM growth model approach to analyze the dataset, and found 10 statistically distinct species groups in terms of tree diameter growth and maximal DBH for the species. Species classification based on ecological characteristics plays a crucial role in mitigating the impacts of treatment decisions and selective logging in forest management, making it possible to adopt appropriate practices and define logging intensities and cutting cycles compatible with conserving forest structure and species population. The model revealed variations in species growth resulting from the influence of factors including light, nutrients, and competition. Depending on the group, soil properties such as percentage of sand, silt, total carbon, presence of aluminum and phosphorus, and exchangeable bases or cation exchange capacity can accelerate or limit tree growth. However, no direct relationship has been found between specific soil and climate variables and an ecological group or tree size. Our study highlights distinct growth patterns among different species groups in response to reduced-impact logging and environmental variables. Effective forest management requires a nuanced approach, considering the varied growth responses of different species groups to ensure sustainable use and conservation of forest resources.

1. Introduction

Tropical forest management is an activity that stimulates local and regional development while also ensuring the legality and sustainability of wood production over time (Reis et al., 2016a; Reis et al., 2015; Sabogal et al., 2006). It is recognized as a means of conserving biodiversity (Gibson et al., 2011; Putz et al., 2012), carbon storage, and maintaining ecosystem services in tropical forests (Edwards et al.,

2014). However, it is still difficult to accurately predict timber volume recovery in tropical forests after logging and long-term sustainability of production (Piponiot et al., 2019, 2018). The high intensity of tree removal in tropical forests limits short-term supply of wood (Piponiot et al., 2019); this, coupled with the slow regeneration of commercially valuable species, limits production for a second cutting cycle (Reategui-Betancourt et al., 2023).

In a forest ecosystem where trees compete for light and space,

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mortality of large trees releases space for neighboring trees and stimulates the establishment of young individuals (Esquivel-Muelbert et al., 2020; Huth and Ditzer, 2000; Soamandaugh, 2017). The dynamics of tree species in tropical forests, particularly in the understory and canopy, are essential for understanding forest structure and function. Research indicates that these strata exhibit distinct ecological behaviors shaped by light availability and competition. For instance, Svenning (2000) demonstrated that understory plants thrive primarily in microsites with higher light exposure, emphasizing the importance of small canopy gaps in influencing plant distribution. Similarly, Montgomery and Chazdon (2001) examined how forest structure and canopy architecture affect light transmittance, revealing that variations in light availability significantly impact seedling regeneration across different forest types. Additionally, Alder and Silva (2000) found that mortality and growth rates differ between these layers due to the shaded environment of the understory. In logged areas, removing trees immediately reduces competition for resources, accelerating the growth of remaining individuals and recruiting new trees (Dwyer et al., 2010; Fargeon et al., 2016). This growth after canopy gaps are created by felling trees depends on site-specific factors such as inter-species competition (Dwyer et al., 2010), distribution of organic matter, nutrient cycling, and soil fertility (Lexerød, 2005; Yang and Huang, 2015).

Changes in the structure of the forest, for example by modifying the basal area and density of individuals through thinning, significantly impacts competition between individuals and directly influences growth of the remaining trees (Kuehne et al., 2015). Silvicultural interventions such as vine removal can also accelerate tree growth (Bezerra et al., 2018). Development in a managed forest is intrinsically linked to the species present and their remaining diameter distributions (Braz et al., 2012). The potential long-term reduction in growth in managed forests may indicate that thinning is needed as competition increases among young individuals recruited after logging (Costa et al., 2008).

Since parameters such as basal area, density of individuals, and tree size distribution are frequently altered by the type of management (Bezerra et al., 2018; Braz et al., 2012; Costa et al., 2008), logging intensities, cutting cycles, and silvicultural treatments must be adapted to achieve sustainable growth patterns. After logging, competition levels between remaining and regenerating individuals must be considered to maintain a resilient forest structure with the potential for management.

Several long-term experimental sites in the Amazon provide valuable insights into the impacts of forest management. For instance, the Tapajós National Forest has been monitored since the early 1980s, offering data on growth and yield in logged and unlogged areas (Silva et al., 1996). The Bionte project in the Central Amazon has examined forest responses to selective logging over a similar timeframe (Higuchi et al., 1997). In French Guiana, the Paracou experiment has provided insights into how juvenile tree recruitment responds to varying logging intensities (Hogan et al., 2018). These studies collectively enrich our understanding of forest dynamics and management practices.

Variations in climate across the Amazon basin make predicting species dynamics challenging (Clark et al., 2014; Esquivel-Muelbert et al., 2020), as each species employs distinct strategies to overcome growth limitations, acquire resources, and store biomass (Chao et al., 2008). While areas with higher rainfall, shorter dry seasons, and warmer temperatures are associated with increased tree growth rates, these patterns can vary significantly across different regions of the Amazon (Silva et al., 2002; Ferreira et al., 2020). It is crucial to acknowledge that regional differences in rainfall regimes, soil types, and other environmental factors play a role in tree growth dynamics (Toledo et al., 2011; Durgante et al., 2023). Moreover, climate models suggest an increasing risk of drought in tropical regions in the coming decades, potentially leading to reduced forest growth (Burban et al., 2016; Corlett, 2016; Sullivan et al., 2020).

Predictions for tree communities are also challenging in the forestry sector due to variability in mortality (temporal, regional, and local), as well as tree diameter distribution (McDowell et al., 2018) and edaphic

characteristics of the forest site. An interesting aspect to consider is the capacitance of trees, particularly how stem diameter variations (which are influenced by water storage) can affect predictions. New technologies like fine-scale point dendrometers have made it possible to measure these diameter fluctuations more precisely, but distinguishing whether these variations are due to water storage (capacitance) or actual growth (carbon storage—biomass gain) remains a challenge. This complexity underscores the scarcity of current knowledge about the relationship between the capacitance of different species and their growth abilities (Meinzer et al., 2003).

In general, growth variations are studied between groups of species, sizes, and ages (Aubry-Kientz et al., 2015; Bennett et al., 2015; Burban et al., 2016). Various models have been developed to better understand the dynamics of forest ecosystems and to generate and analyze management techniques (Botkin, 1993; Burkhardt and Tomé, 2012; Mendoza, 2006; Pretzsch, 2009). Predictions based on individual trees, empirical yield tables for different species, diameter classes, clearcuts, gap dynamics (ecophysiological), and landscape changes have already been studied. These models make it possible to test management strategies and apply silvicultural treatments in natural forests (Clutter et al., 1983; Pretzsch, 2009).

To sharpen the focus of this study, we posed the following research question: How do soil, climate, and logging parameters affect tree growth within different groups of species? Our main objectives were: a) to establish groups of species based on long-term data (over 30 years of monitoring), considering average tree growth and maximum diameter at breast height (DBH); b) to model the diameter growth of trees in different species groupings; and c) to understand the relationship between soil, climate, and logging parameters in tree growth.

2. Materials and methods

2.1. Description of the study area

We used data from five experimental areas monitored by Embrapa Eastern Amazon in the states of Pará and Amapá, Brazil: Jari, Km 114, Km 67, Moju, and Peteco (Fig. 1). The forest formation in the study areas is characterized as submontane dense ombrophile forest (IBGE - Instituto Brasileiro de Geografia e Estatística, 2012), with a regional climate classified as Köppen Am (tropical monsoon) (Alvares et al., 2013).

The Jari experimental area (0°54'19.97"S, 52°11'25.76"W) is located in forests pertaining to the Orsa Florestal company in the municipality of Vitória do Jari (AP); it totals 500 ha, with average altitude of 136 m. Average annual precipitation reaches 2234 mm, with a rainy period from December to May, and the average annual temperature is 25.8 °C. The soils are classified as dystrophic yellow oxisols (de Azevedo et al., 2011).

The Km 114 (3°17'19.79"S, 54°55'39.36"W) and Km 67 (2°53'0.90"S, 54°55'27.00"W) experimental sites are part of the Tapajós National Forest in the municipalities of Belterra and Aveiro (PA), with altitudes of 135 and 195 m above sea level, respectively. Average annual precipitation is 2100 mm: there is a rainy season from December to May, and from July to August total rainfall is less than 60 mm (Costa et al., 2002). The soils are classified as yellow oxisols and yellow argisols with a clayey texture (Rodrigues et al., 2003); average annual temperature is 26 °C (Oliveira et al., 2006).

The Moju site (2°8'14.00"S, 48°47'34.29"W) is located in Moju (PA) at an average altitude of 36 m, with a total area of 1050 ha. Annual rainfall is 2500 mm (Reis et al., 2016b), and average annual temperature is 26 °C. The soils are classified as dystrophic yellow latosols with different textures, with red-yellow argisols, gleisols, and plintisols also occurring.

The Peteco site (3°31'11.63"S, 48°47'26.19"W) is located in an area pertaining to CKBV Florestal Ltda., a company in the Keilla Group located in the municipality of Paragominas, PA. Average altitude is 115 m; average annual rainfall is 1800 mm and there is a well-defined

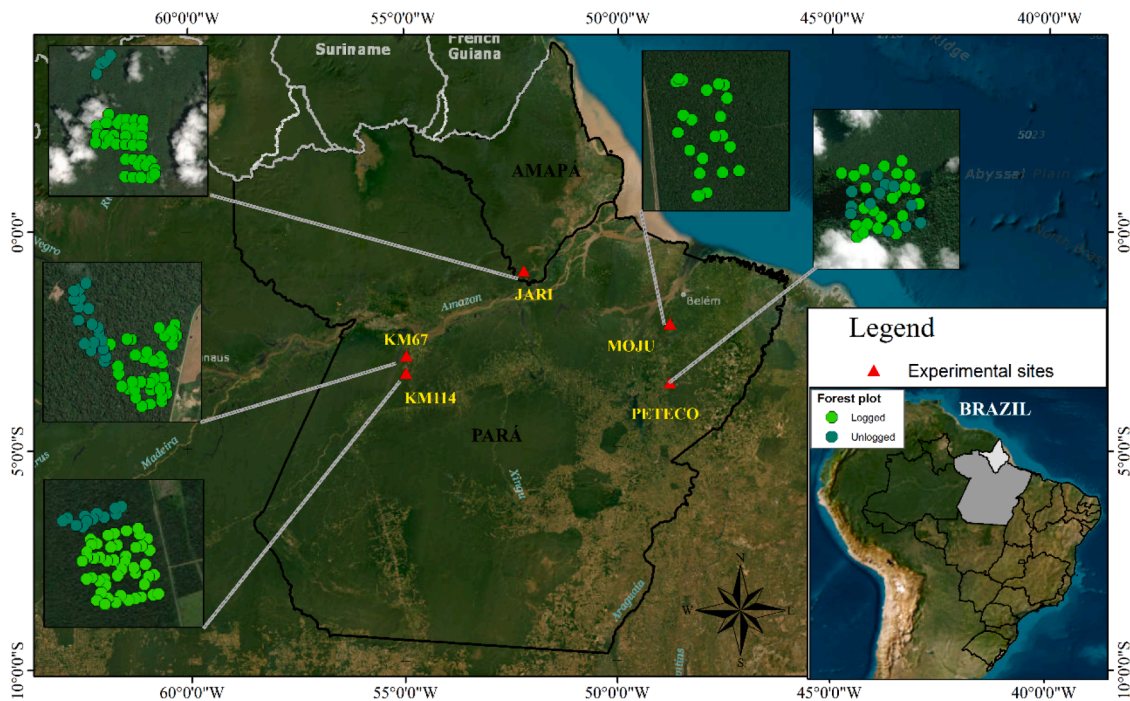


Fig. 1. Location of experimental area monitored by Embrapa Eastern Amazon in the states of Pará and Amapá, Brazil.

dry season from July to September. The average annual temperature is 26.3 °C and average relative humidity is 81 % (Alvares et al., 2013). The soils are classified as yellow oxisols, argisols, plintisols, geisols, and neosols.

The inventory periods after logging varied in each experimental area. The first measurement was carried out at the Jari site in 1984. It was logged in 1985, followed by monitoring in 1986, 1988, 1990, 1994, 1996, 2004 and 2011, spanning a total of 26 years of evaluation post-logging. At the Km 114 site, the first measurement was taken one year before logging in 1981; afterward, measurements were taken in 1983, 1987, 1989, 1995, 2003, 2008, and 2012 over a 30-year period. At the

Km 67 site, inventories were carried out after logging in 1981, 1982, 1983, 1985, 1987, 1992, 1997, 2007, 2012, and 2014, with a total of 33 years of monitoring. The Moju site was logged in 1997, and continuous measurements were taken at the site in 1998, 2004, 2010, and 2015, spanning 18 years of monitoring. Finally, at the Peteco site, the first measurement was carried out before logging in 2003. After logging, the area was measured in 2004, 2007, 2008, and 2011, a total of 8 years.

All sites except for Moju have control plots of unlogged forest that were measured at the same intervals; the other exception is Km 67, where the control plots were established in 2008 and measured in 2012 and 2014 (Fig. 2).

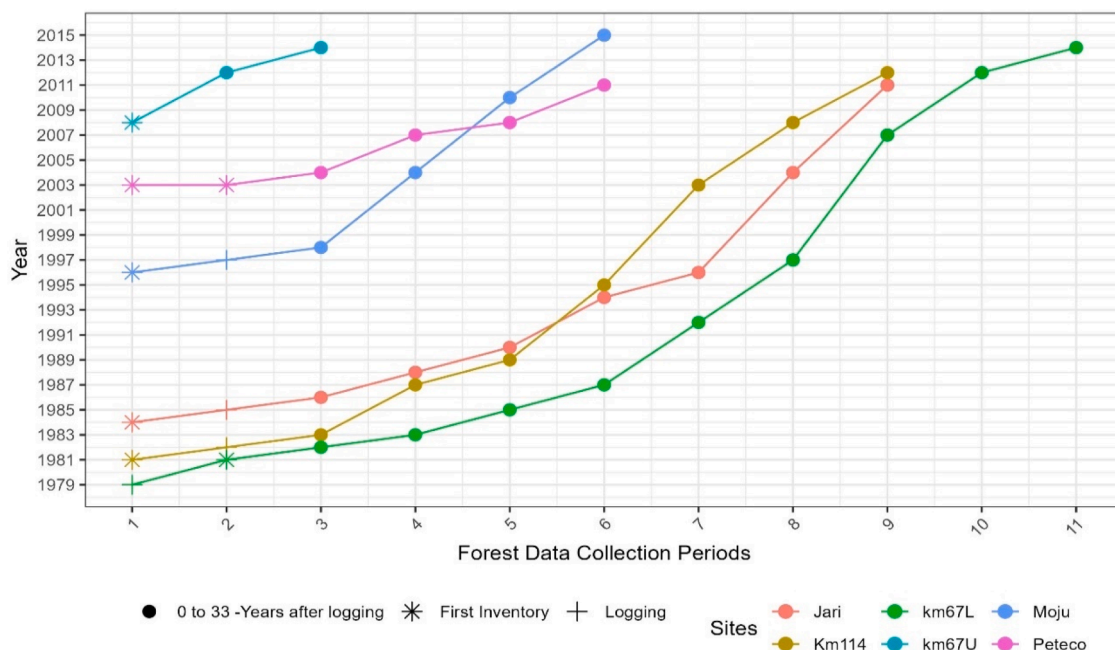


Fig. 2. Inventory and logging years at the areas monitored by Embrapa Eastern Amazon.

2.2. Statistical analysis

2.2.1. Data

We analyzed 166 permanent plots (Table 1) and all trees with DBH ≥ 20 cm. To analyze tree growth in logged forests, we evaluated 66,182 observations (trees x measurement) corresponding to 17,440 individuals of 642 species. The species were classified into three ecological groups: pioneers (P), light-demanding non-pioneers (LD), and shade-tolerant non-pioneers (ST), following classifications in previous studies (Alder et al., 2002; Carvalho, 1992; Swaine and Whitmore, 1988; Whitmore, 1989a; Whitmore, 1989b). In total, we evaluated 56 pioneer species, 225 light-demanding species, 287 shade-tolerant species, and 74 species classified as indeterminate (In). The evaluated forests have an average DBH of 35.3 cm and an average height of 21.30 m (Fig. S1). Additionally, some trees or individuals in the study area exhibit DBH values greater than 80 cm and heights exceeding 35 m, highlighting the presence of large, mature individuals within the forest.

2.2.2. Species grouping

We aggregated the species using a CAFOGROM approach (Alder, 2011; Alder et al., 2012, 2002), which considers two parameters for each species: average tree growth and maximal DBH. Tree growth for the species was calculated using the average obtained from all measurement periods after logging (Formula 1). The maximal DBH used is the one that represents the diameter of the tree located in the 95th percentile of diameter distribution of the entire population for each species, including plots in logged areas (46 permanent plots) and non-logged forests. This DBH represents the typical diameter of dominant, mature trees, and is a statistical indicator of the species maximum potential size. It is associated with the possible growth potential of all trees in the species population. This type of grouping, based on structural parameters and forest dynamics processes, is recommended for modeling exploited tropical forests (Gourlet-Fleury et al., 2005). We did not utilize the highest DBH for each species recorded in the inventories to avoid including relict trees or outliers.

$$PAId_i = \frac{1}{n} \sum_{j=1}^n (DBH_{ij} - DBH_{i0}) \quad (1)$$

Where: PAId represents the periodic annual increment in diameter (cm year⁻¹) for trees of species *i*; DBH_{ij} is the diameter at breast height (DBH) of the tree in period *j* for species *i*; DBH_{i0} is the diameter at breast height in the initial period for species *i*; *n* is the total number of measurement periods after logging.

The clusters were made using the k-means method with an unsupervised learning algorithm to partition the species into *k* groups, minimizing the sum of squares of the clusters. K-means groups are established based on the mean centroid, where each species belongs to the closest possible group to a given group. We used the *kmeans* function from the *stats* package in the R program (Core, 2021).

We used a non-parametric multivariate test (PERMANOVA) to evaluate the quality of the proposed grouping by comparing group distributions. The null hypothesis means that the centroids of all groups are the same; in this way, rejection of the null hypothesis means at least one pair of groups will have significantly different centroids. We used

Table 1

Size and numbers of plots in experimental areas monitored by Embrapa Eastern Amazon.

| Site | Number of plots | | Plot size |
|--------|-----------------|-------------|-----------------------|
| | Logged | Unlogged | |
| Jari | 36 (36 ha) | 4 (4 ha) | 1 ha (100 m x 100 m) |
| Km 114 | 48 (12 ha) | 12 (3 ha) | 0.25 ha (50 m x 50 m) |
| Km 67 | 36 (9 ha) | 18 (4.5 ha) | 0.25 ha (50 m x 50 m) |
| Moju | 22 (11 ha) | | 0.5 ha (50 m x 100 m) |
| Peteco | 24 (6 ha) | 12 (3 ha) | 0.25 ha (50 m x 50 m) |

the *adonis* function from the “vegan” package using the Euclidean distance method with 999 permutations (Oksanen et al., 2019). Finally, the optimal number of groups was tested with Bonferroni post-hoc analyses, with each group pair evaluated iteratively. We used the *pairwise.adonis* function from the “vegan” package. All analyses were performed using R software version 4.1.2 (Core, 2021).

2.2.3. Explanatory variables

We tested a set of 10 variables to evaluate the relationship between tree growth, logging practices, climate, and soil (Table 2).

Soil data were collected through surveys at the experimental sites, available in the Embrapa Eastern Amazon database (summary data Table S1 and S2). Climate data related to precipitation and temperature were obtained from data processed in CRU-TS 4.03 (Harris et al., 2014) reduced (Fick and Hijmans, 2017) in WorldClim 2.1. To extract the number of rainy months (Mc) and dry months (Ms), we carried out a temporal analysis of precipitation for each site in the 36-year interval (1981–2017), considering those with precipitation above the 85th percentile as Mc and those with precipitation below the 15th percentile as Ms. Finally, the total number of months obtained for each site was divided into the measurement period between inventories (Fig. S2).

We considered average values of the Oceanic Niño Index (ONI) to categorize strong and very strong La Niña events, using the SE and VSE indices for the former and SI for the latter (<https://ggweather.com/enso/oni.htm>). We counted the total number of months each event occurred and subsequently divided this value equally for the measurement period between inventories (Fig. S1).

2.2.4. Tree growth model

The CAFOGROM model uses quadratic regression (Formula 2) to predict the growth of trees in the Amazon Forest (Alder and Silva, 2000). This model was adjusted for each group of species.

$$PAId = \alpha + \beta_1 \cdot d + \beta_2 \cdot d^2 \quad (2)$$

Where: PAId is the periodic annual increment in diameter (cm year⁻¹); *d* is the DBH (cm) α , and β_i are the regression coefficients, estimated for each specific species group.

After adjusting the model, all explanatory variables related to logging, climate, and soil were added (Formula 2). The relationship was evaluated using generalized linear models with the “glm” function from the *stats* package (Team et al., 2018). This model consists of a flexible generalization of a simple linear regression based on ordinary least squares, which allows the response variable to have error distributions other than the normal distribution (Nelder and Wedderburn, 1972).

Table 2

Explanatory variables related to logging, climate, and soil.

| Variable | |
|--|--|
| Logging intensity (volume) | LI (m ³ ha ⁻¹) |
| Number of trees removed | TR (Trees.ha ⁻¹) |
| Managed basal area (BA) | MBA (m ² ha ⁻¹) |
| Total reduction in basal area (cut + impact) after logging | RBA (m ² ha ⁻¹) |
| Time after logging | Time (Years) |
| Sand | Sand (g kg ⁻¹) |
| Silt | Silt (g kg ⁻¹) |
| Clay | Clay (g kg ⁻¹) |
| Total carbon | TC (g kg ⁻¹) |
| Aluminum | Al (cmolc/dm ³) |
| Extractable phosphorus (Bray) | Ep_Bray (mg/dm ³) |
| Total exchangeable bases | TEB (cmolc/dm ³) |
| Cation exchange capacity | CEC (cmolc kg ⁻¹) |
| Rainy months | Rm (N° months) |
| Dry months | Dm (N° months) |
| Strong El Niño/La Niña events | El Niño/La Niña (Months/periods) |
| Minimum temperature | MinT (°C) |
| Maximum temperature | MaxT (°C) |

$$PAId = \alpha + \beta_1.d + \beta_2.d^2 + \beta_3.Silt + \dots \beta_n.Tmax \tag{3}$$

An iterative variable selection process was carried out, eliminating and adding different variables until achieving the greatest parsimony through an adjustment complexity trade-off (indicated by the lowest Akaike information criterion value, AIC). The AIC estimates the relative quality of a model based on the likelihood function and the number of parameters. To do so, we used the “stepwise” function in the RcmdrMisc package (Fox et al., 2022). All analyses were performed using R software version 4.02.3 (Core, 2021).

3. Results

3.1. Species groups

A total of 10 groups were formed using the k-means method (Fig. 3A). The clustering was significant (Pr(>F)= 0.001), and the pairs of species groups were statistically different from each other according to the Bonferroni post-hoc test (p.value=0.001, p.adjusted 0.045) (Table S3).

The extremes of the classification can be represented by two groups: group 6, containing large species (average DBHmax=140.47 cm) with higher median periodic increase (0.68 cm.year⁻¹), and group 4, containing smaller species (average DBHmax=27.55 cm) with very low periodic increase (0.12 cm.year⁻¹) (Fig. 3B).

Pioneer species were predominantly clustered around groups 3 and 9 (Fig. 4, Table 3). Light-demanding species were separated according to tree growth and size (groups 1, 6, 7, and 8). Tolerant species were predominantly separated according to size (2, 4, 5, 9, and 10). Some groups showed significant mixing of species from different ecological groups (2 and 9). Groups 3 and 9 also regrouped species with other ecological behaviors. Light-demanding species were found in groups of trees with the highest tree growth and max DBH values, while pioneer species were found in groups of smaller trees with high and low growth; shade-tolerant species were located in the medium and low growth groups (Fig. 4).

3.2. Modeling diameter growth

Based on the CAFOGROM model, we obtained the coefficients for all species groups (Table 3). The models created for the different groups of species indicate different growth for most groups. Groups 4, 5, and 10, containing predominantly low-growth species, are generally dominated

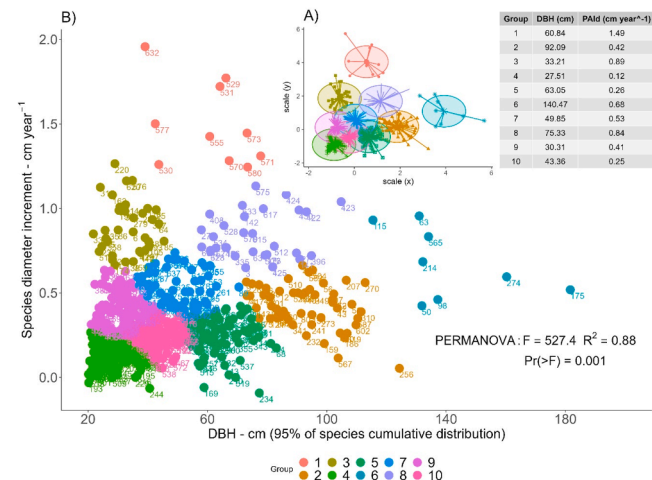


Fig. 3. A) Species grouping using the k-means method. B) Relationship between average tree growth of the species and DBHmax. DBH: average DBHmax of the species in the group; PAId: average diametric periodic increment of the species in the group. Each colored number represents one species.

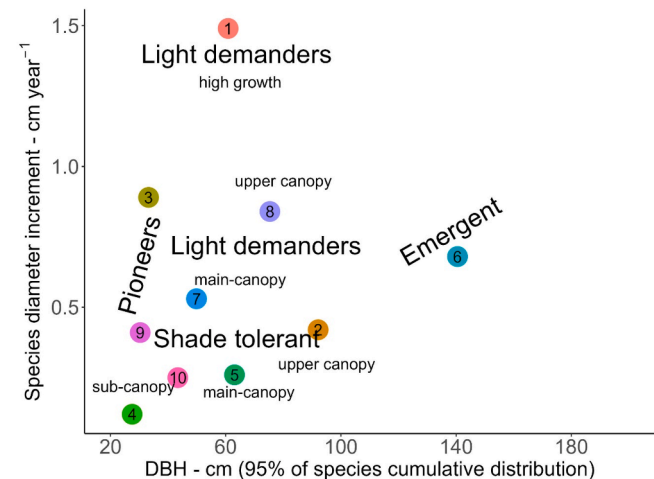


Fig. 4. Group of species with main ecological behaviors. DBHmax: DBH; tree growth: PAId. Figure is based on our results but was adapted from Alder and Silva (Alder and Silva, 2000).

by shade-tolerant tree species (Table 3 and Table S4).

In group 1, light-demanding species represent 97 % of the trees, with an average growth rate of $1.55 \pm 0.26 \text{ cm year}^{-1}$, with *Tachigali chrysophylla* (44 %) and *Tachigali glauca* (27 %) the most abundant species. Group 2 is mostly formed of shade-tolerant species, with average growth of $0.44 \pm 0.15 \text{ cm year}^{-1}$. The species with the most observations are *Manilkara elata* (15 %), *Pouteria oppositifolia* (8 %), and *Couratari stellata* (5 %). An exception in this group is *Goupia glabra*, a pioneer species which contributes 10 % of the abundance. Trees in group 3 are mainly pioneer and light-demanding species, with growth of $0.85 \pm 0.19 \text{ cm year}^{-1}$. The species with the highest percentage of individuals are *Cecropia sciadophylla* (54 %, pioneer) and *Bixa arborea* (34 %, light-demanding) (Table 3 and Fig. 5).

Group 4 concentrates trees in shade-tolerant species with average growth of $0.13 \pm 0.08 \text{ cm year}^{-1}$. The species with the highest participation are *Rinorea guianensis* (38 %), *Anaxagorea dolichocarpa* (6 %), and *Myrcia splendens* (3 %). In group 5 shade-tolerant species also predominate, with average growth of $0.27 \pm 0.12 \text{ cm year}^{-1}$. The most frequently observed species in this group are *Geissospermum sericeum* (12 %), *Pouteria* sp. (10 %), and *Minquartia guianensis* (5 %) (Table 3 and Fig. 5).

Group 6 is represented exclusively by light-demanding tree species with an average growth rate of $0.72 \pm 0.23 \text{ cm year}^{-1}$. The species *Swartzia polyphylla* (24 %), *Erismia uncinatum* (23 %), and *Bertholletia excelsa* (19 %) predominate in this group. Group 7 is also dominated by light-demanding species, with growth of $0.53 \pm 0.12 \text{ cm year}^{-1}$. The main species in this group are *Inga* sp. (16 %), *Virola michelii* (11 %), and *Jacaranda copaia* (10 %). In group 8, light-demanding species also predominate, with growth averaging $0.85 \pm 0.17 \text{ cm year}^{-1}$ and *Inga alba* (23 %), *Tachigali tinctoria* (14 %), and *Tachigali myrmecophila* (10 %) account for the greatest participation (Table 3 and Fig. 5).

Group 9 has a mixture of shade-tolerant and pioneer tree species with growth of $0.41 \pm 0.10 \text{ cm year}^{-1}$. The most common species are *Protium apiculatum* (19 %, shade tolerant), *Cecropia distachya* (13 %, pioneer), and *Drypetes variabilis* (7 %, indeterminate ecological group). Finally, group 10 is dominated by trees in shade-tolerant species, with a growth rate of $0.25 \pm 0.07 \text{ cm year}^{-1}$. The species with the highest number of individuals are *Eschweilera coriacea* (14 %), *Lecythis idatimon* (7 %), and *Eschweilera grandiflora* (6 %) (Table 3 and Fig. 5).

3.3. Variables that influence tree growth

Logging practices, climate, and soil variables were combined from the defined groups to evaluate their relationships with tree growth in the

Table 3
Tree growth coefficients for the CAFOGROM model.

| Group | No. | PAId | A | β 1 | β 2 | P | LD | ST | In |
|-------|-------|-------------|------------|-----------|-----------|------|-------|------|-------|
| 1 | 974 | 1.55 ± 0.26 | −1.132795 | 0.107263 | −0.001048 | 3 % | 97 % | 0 % | 0 % |
| 2 | 8165 | 0.44 ± 0.15 | 3.13E−01 | 5.50E−03 | −4.46E−05 | 17 % | 33 % | 50 % | 0.4 % |
| 3 | 2787 | 0.85 ± 0.19 | −0.376715 | 0.0628794 | −0.00074 | 49 % | 48 % | 2 % | 1 % |
| 4 | 5632 | 0.13 ± 0.08 | −0.706279 | 0.059339 | −0.001013 | 2 % | 4 % | 91 % | 4 % |
| 5 | 18692 | 0.27 ± 0.12 | −8.21E−02 | 1.86E−02 | −2.32E−04 | 3 % | 18 % | 60 % | 18 % |
| 6 | 338 | 0.72 ± 0.23 | −7.78E−03 | 2.09E−02 | −1.31E−04 | 0 % | 100 % | 0 % | 0 % |
| 7 | 7927 | 0.53 ± 0.12 | 0.1985859 | 0.0165695 | −0.000199 | 13 % | 63 % | 24 % | 0 % |
| 8 | 2444 | 0.85 ± 0.17 | 0.3740525 | 0.0197882 | −0.000157 | 3 % | 94 % | 1 % | 2 % |
| 9 | 3329 | 0.41 ± 0.10 | −0.1575317 | 0.0345172 | −0.000503 | 27 % | 16 % | 42 % | 14 % |
| 10 | 15894 | 0.25 ± 0.07 | −2.90E−01 | 2.91E−02 | −3.77E−04 | 2 % | 22 % | 72 % | 4 % |

No.: number of observations; PAId: tree growth (cm year^{−1}); P: pioneers; LD: light demanders; ST: shade tolerant; In: indeterminate.

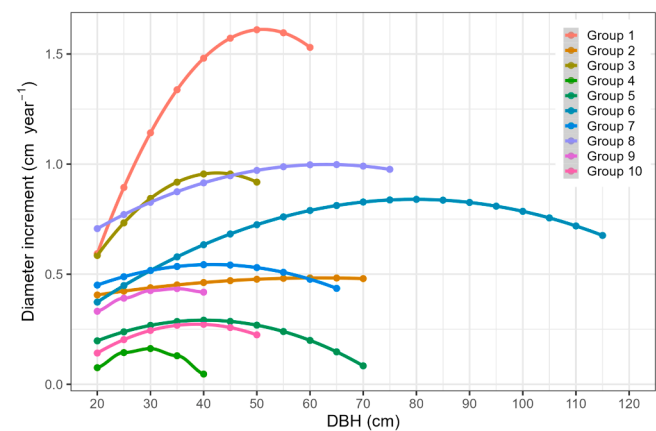


Fig. 5. Adjustment of tree growth for all species groups provided by the CAFOGROM model.

species groups (Table 4).

The soil characteristics that most influenced growth in most species groups were total carbon content (TC), cation exchange capacity (CEC), and aluminum levels; TC had a positive influence on groups 1, 5, and 9 (mainly light-demanding species) and a negative effect on groups 2, 6, 8, and 10 (predominantly shade-tolerant species). Sand and silt content were positively associated with growth of species in group 2, generally shade-tolerant trees.

In groups 3, 4, 8, and 10 CEC contributed to growth without a clear distinction between ecological groups, but these categories contain intermediate-sized trees with maximum DBH ranging from 40 to 75 cm. Finally, positive correlations were observed for aluminum in groups 1 and 7 (light-demanding species) and groups 4 and 10 (shade-tolerant species) (Table 4).

With regard to climate, a significant positive correlation was seen between the number of rainy months (Rm) and increased growth, especially in groups 4, 5, 7, 8, and 10, which include light-demanding and shade-tolerant species. On the other hand, the most intense El Niño events were negatively associated with diameter increase of trees in groups 2, 3, 7, 9, and 10. Severe La Niña events also had a negatively impact on growth of trees in groups 1, 2, 4, 5, 7, and 10, predominantly shade-tolerant species. Furthermore, the quantity of dry months (Dm) reduced the growth of species in group 5, mainly shade-tolerant species.

High temperatures (MaxT) also negatively affected the growth of species in groups 2, 3, 5, and 9 (Table 4). Group 5 and 2, mainly composed of shade-tolerant species, proved most sensitive to climate variables.

The time after logging was negatively associated with tree growth in most groups, regardless of their ecological behavior. Logging intensity had the opposite effect and positive influenced tree growth, mainly in shade-tolerant groups (5, 9, and 10) (Table 4).

4. Discussion

4.1. Species grouping in forest growth models

Because of the significant diversity of tropical ecosystems, species grouping is fundamental for developing forest growth models (Alder et al., 2012; Alder and Silva, 2000; Gourlet-Fleury et al., 2005). Various classification methods have been tested by the scientific community, ranging from the simplest empirical approaches to more complex efforts based on morphological and ecological attributes (Vanclay, 1991, 1989; Vanclay et al., 1997). The CAFOGROM model, which uses only two parameters (maximum species diameter and periodic tree growth), has been shown to be a good strategy for grouping species (Alder and Silva, 2000).

Few forest species are sufficiently represented in growth models. In the present study, we used data from experimental areas with a monitoring period spanning up to 33 years and formed ten statistically different species groups. The first version of the CAFOGROM model, which used a 12-year interval for its observations and analyses, established 54 species groups. According to the authors of the first version, the large number of groups can make this classification difficult to understand and very sensitive to changes in data limitations (Alder and Silva, 2000).

Our results highlight the importance of grouping species with similar growth patterns to optimize forest management practices. This grouping allows for the development of more effective and sustainable management strategies by tailoring harvesting practices to the specific needs of each species group (Brienen and Zuidema, 2006). By understanding how different species grow and behave, we can plan management cycles that ensure proper recovery of species between harvests, avoiding over-exploitation of slow-growing species and promoting their regeneration (Castro et al., 2021; Reategui-Betancourt et al., 2023). Additionally, identifying which species groups contain commercially valuable species and which can be managed sustainably is crucial for maintaining forest productivity (Piponiot et al., 2018). Not all species groups can be

Table 4

Results of generalized linear models for diametric growth of species groups, highlighting variables with 5 % significance ($p < 0.05$), as indicated by the lowest Akaike information criterion (AIC) value.

| Variable | Species group | | | | | | | | | |
|--|---------------|----------|-----------|-----------|----------|----------|----------|----------|-----------|----------|
| | G1 | G2 | G3 | G4 | G5 | G6 | G7 | G8 | G9 | G10 |
| Intercept | −2.4E−01 | 2.5E−01 | −1.4E+ 00 | −2.6E−01 | 6.3E−01 | 3.2E−01 | −1.6E−01 | −5.4E−01 | −1.5E+ 00 | −9.3E−02 |
| DBH | 6.0E−02 | 7.9E−03 | 7.8E−02 | 1.8E−02 | 6.0E−03 | 1.6E−02 | 1.5E−02 | 2.7E−02 | 1.4E−02 | 6.4E−03 |
| DBH ² | −4.4E−04 | −5.8E−05 | −9.6E−04 | −2.4E−04 | −4.7E−05 | −9.3E−05 | −1.3E−04 | −1.9E−04 | −2.6E−05 | 2.5E−05 |
| Logging intensity | | | | | 4.6E−04 | | | | 2.3E−03 | 3.3E−04 |
| Number of trees removed | | | | | | | | | −7.4E−03 | |
| Managed basal area (BA) | | | | | | | | | | 7.5E−03 |
| Total reduction in basal area (cut + impact) after logging | | −5.5E−02 | | | | | | | | |
| Time after logging | | −3.9E−03 | −2.9E−02 | −1.3E−03 | −2.8E−03 | | −2.3E−03 | −5.1E−03 | −1.1E−02 | −3.8E−03 |
| Sand | | 3.0E−04 | | | | | | | | |
| Silt | | −2.3E−03 | | | | | | | | |
| Clay | | | | | | | | | | |
| Total carbon | 3.1E−02 | 2.1E−02 | | | 4.5E−03 | −5.1E−02 | | −2.4E−02 | 1.8E−02 | −1.4E−02 |
| Aluminum | 8.6E−01 | | | −1.3E−03 | | | 2.2E−01 | | | −1.8E−01 |
| Extractable phosphorus (Bray) | | | | | | | | | 4.3E−02 | 2.5E−02 |
| Total exchangeable bases | | | | −3.9E−02 | | | 4.9E−02 | | | −1.5E−01 |
| Cation exchange capacity | | | 9.3E−02 | 1.8E−02 | | | | 1.3E−01 | | 8.6E−02 |
| Rainy months | | 2.9E−02 | | 3.4E−02 | 2.4E−02 | | 3.9E−02 | 1.1E−01 | | 3.3E−02 |
| Dry months | | | | | −1.0E−02 | | 2.8E−02 | | | 1.7E−02 |
| Strong La Niña events | −4.0E−02 | −9.6E−03 | | −4.1E−03 | −4.2E−03 | | −1.1E−02 | | | −6.5E−03 |
| Strong El Niño events | | −1.0E−02 | −3.5E−02 | | | | −2.3E−02 | | −1.6E−02 | −7.1E−03 |
| Minimum temperature | | | | | | | | | 2.8E−01 | |
| Maximum temperature | | −1.4E−01 | −3.1E−01 | | −9.9E−02 | | | | −1.5E−01 | |
| AIC | 2.5E+ 03 | 8.8E+ 03 | 4.6E+ 03 | −3.7E+ 03 | 4.8E+ 03 | 8.3E+ 02 | 9.7E+ 03 | 5.3E+ 03 | 2.9E+ 03 | 4.2E+ 03 |

managed sustainably without careful planning, however, since inadequate exploitation can lead to rarity or economic extinction of valuable species (Richardson and Peres, 2016). For this reason, grouping species by their growth characteristics provides a more adaptive and efficient approach to ensuring sustainability and continuity in forest production in the Amazon.

4.2. Species ecology and tree growth

An interesting finding from this study is the clustering of pioneer and shade-tolerant species (Fig. 4). Although these groups are empirically classified with different ecologies, their population structures and tree dynamics growth after logging are quite similar in our dataset, which was detected by the CAFOGROM model that placed species with different empirical ecological classification in the same group. The ecological groups identified in this study were extensively analyzed in previous studies (Alder et al., 2002; Alder and Silva, 2000), and cover a range of species categories: fast-growing emerging, small species with slow growth, light-demanding species, shade-tolerant species, and pioneers. These groups display variations in growth rates, as depicted in Figs. 3 and 4. For example, group 3 contains pioneer species and small trees generally represented by some species of *Cecropia*. This was also observed by Alder and Silva (Alder and Silva, 2000), who described them as species with a relatively short life, high mortality, and typical habit of extreme pioneering.

Species considered opportunistic, for example, were generally regrouped in groups of light-demanding species, such as the species *Inga alba* and *Tachigali chrysophylla*. The emerging species were regrouped in groups 2 and 6, which reach diameters exceeding 100 cm. Among the emerging species *Manilkara elata* and *Swartzia polyphylla* predominate, species of significant commercial interest because of their dense and durable wood (Reategui-Betancourt et al., 2023).

Maximum tree growth was generally observed in groups formed mainly of pioneer and light-demanding species. Studies indicate that the highest growth rates in pristine forests occur in emerging and pioneer groups (Manokaran and Kochummen, 1987). However, the greatest diameter growth in logged forests is often observed in groups of pioneers and light demanders, especially in the first years after logging (Costa et al., 2008; Silva et al., 1996, 1995). Pioneer species (whether small or

long-lived) presented maximum average growth rates between 1.5 and 1.1 cm year^{−1}, respectively. In groups of emerging species, growth varies from 0.6 to 0.7 cm year^{−1} (Alder et al., 2002; Carvalho, 1992).

The different dynamics of trees in the understory (species with small maximum DBH) and the canopy (high maximum DBH) play a crucial role in the configuration and functioning of tropical forests. These two groups represent different strata within the forest ecosystem and exhibit distinct behaviors related to ecology, growth, competition, and survival. Small trees grow in shade and under competition from larger trees, which can significantly influence their growth patterns and survival strategies (Svenning, 2000). Dominant trees can grow quickly, rising above others as they form the upper canopy of the forest and directly access sunlight, enhancing their reproductive success (Montgomery and Chazdon, 2001). In this study, we observed that the canopy comprises light-demanding and shade-tolerant species in general, with diameters exceeding 80 cm. Notably, small and generally shade-tolerant trees with a maximum diameter of 30–40 cm and medium-sized light-demanding trees with a maximum diameter of 50–70 cm exhibited low growth rates, likely due to the shaded environments and competitive pressures they face. Alder and Silva (2000) highlighted that growth rates differ between the understory and canopy due to the shaded conditions present in the understory.

In broad terms, tree growth increases up to a certain DBH and then stagnates, which recurs when clearings are opened. This growth is related to the ecology of the species, adaptation to low light, and external competitive factors. Competition processes, for example, determine the establishment and survival of individuals and tree growth (Lexnerød, 2005; Xiang et al., 2016; Yang and Huang, 2015). In logged forests, growth tends to change soon after thinning, mainly accelerating the growth of sub-canopy trees (Dwyer et al., 2010; Fargeon et al., 2016).

Each group demonstrated distinct growth patterns depending on their adaptation to different light conditions, which has significant consequences for forest dynamics. These results highlight the complex interaction between species-specific characteristics and environmental factors, emphasizing the need to consider these interactions in conservation and forest management strategies. Furthermore, awareness of the intrinsic diversity of growth behavior in some species with significant potential for adaptation (“plastic” species) is also important, as changes/

adaptations in morphological, physiological, or behavioral characteristics can permit adaptation to specific conditions (Weiner, 2004). Plasticity is valuable for species survival and establishment, especially as climate change and other disturbances are becoming more frequent and unpredictable. However, plasticity is not the only adaptation strategy, and species survival also depends on other factors such as genetic diversity, dispersal, and migration capacity (Schwinning and Weiner, 1998).

Exploring growth patterns in the Amazon region is crucial for understanding forest dynamics and improving management practices. Tools such as dendrometers make it possible to collect precise long-term data on tree development. Pumijumnong et al. (2023) highlight that while dendrometers provide valuable insights into growth rates and species performance, their findings should be complemented by destructive methods such as ring dating and stable isotope analysis for a more holistic understanding of cambial growth and wood formation. Research by Bräuning et al. (2009) illustrates how factors like moisture availability and climatic conditions influence cambial activity in species such as *Cedrela montana*, revealing important seasonal growth patterns. Dünisch et al. (2003) emphasize the value of dendrometers for long-term monitoring and advancing our understanding of forest ecology. Furthermore, studies by da Costa et al. (2010) and Jiménez et al. (2020) utilize dendrometry to analyze growth dynamics in various soil contexts and under drought conditions, underscoring the need to integrate multiple methodological approaches to gain a more complete understanding of the complex interactions within Amazonian ecosystems.

4.3. Environmental factors and their influence on tree growth

Parameters related to logging, such as reduction in total basal area and time after tree removal, negatively influenced tree growth for most species groups. Logging intensity (in terms of volume harvested) was positively correlated with growth in groups of medium-sized trees (diameters 20–70 cm) dominated by shade-tolerant species. Shortly after selective logging, these species increase their growth as light is more available, but this effect is temporary (Costa et al., 2008). Studies have shown that within the first 10 years, managed forests can maintain characteristics similar to unlogged forests (Oliveira et al., 2019; Reategui-Betancourt et al., 2024). As tree growth begins to stabilize, additional silvicultural treatments such as further thinning, enrichment planting, or liana removal may become necessary (Costa et al., 2008), but these activities must be conducted in accordance with the ecology of the species in question. The proliferation of vines after logging may also hinder the growth of remaining trees, making proper management essential to ensure their growth (Bezerra et al., 2018).

Soil properties such as total carbon, exchangeable bases, and aluminum levels affected the growth of species groups, positively as well as negatively (Table 4). These factors influence the development and health of trees, although the complexity of interactions in the forest ecosystem makes it impossible to identify direct relationships with ecological groups or the size of the trees in question (Quesada et al., 2012; Schoenholtz et al., 2000). Clay content, high levels of organic carbon, high concentrations of exchangeable bases such as calcium, magnesium, potassium, and sodium, and high cation exchange capacity tend to make soils more fertile, providing more nutrients for tree development (Sayer and Banin, 2016; Soong et al., 2020).

Variations in forest production are mainly related to soil phosphorus status (Quesada et al., 2010, 2012). Aluminum ions in high concentrations are considered phytotoxic (Laurance et al., 1999; Sanchez, 2019), reducing tree growth (Quesada et al., 2009). Yet we found a positive correlation between aluminum and growth in groups comprising light-demanding species. It is likely that these species have Al resistance mechanisms linked to internal detoxification in order to maintain growth by exclusion or complexation of Al to stop it from entering through the roots (Kochian et al., 2015).

Our results indicate that tree growth in response to drought is

strongly dependent on soil conditions, a facet of forest productivity that is still underexplored and holds great potential for improving predictions of future growth in tropical trees in the face of projected climate change. Individuals growing in fertile soils experienced a drastic reduction in growth rates as drought intensity increased, while in less fertile sites growth rates remained slow but showed a smaller decrease as drought intensified (Durgante et al., 2023).

More frequent severe droughts contribute to imbalance in the dynamics of tropical forests (Bennett et al., 2015; Coomes et al., 2003; Esquivel-Muelbert et al., 2020). There is a precise relationship between tree growth and precipitation (Schöngart et al., 2006; Stahle et al., 2020), and drought, high temperatures, and storms influence forest development and tree mortality (Aleixo et al., 2019). Severe El Niño-related droughts mainly impact understory growth dynamics in tropical forests (Browne et al., 2021). In this study, the growth of dominant trees in logged forests had a positive relationship with the frequency of rainy months and a negative correlation with strong La Niña, El Niño, and maximum temperature events. These variables were seen to be very important for tree growth in light-demanding and shade-tolerant species (Table 4). The number of dry months (Ms) positively influenced growth of pioneer species and small trees of shade-tolerant species.

4.4. Long-term forest management studies

Comparison with other long-term forest management experiments conducted in the Amazon provides additional context for our findings. For instance, the Tapajós National Forest was logged between 1979 and 1982 and has been studied extensively, revealing insights into growth and yield dynamics similar to our observations here (Silva et al., 1996). Similarly, the Bionte project conducted in the Central Amazon from 1987 to 1993 examined growth and increment in managed tropical forests, providing comparative data on the impacts of various logging intensities (Higuchi et al., 1997). And the Paracou experiment in French Guiana, which was logged between 1986 and 1987, investigated juvenile tree responses to different logging intensities and offers valuable information on forest recovery (Hogan et al., 2018).

Comparing our results with these studies highlights both commonalities and differences in growth patterns and recovery dynamics. Like the studies in Tapajós and Bionte, our findings show that pioneer and light-demanding species exhibit increased growth rates following logging. However, our study also provides unique insights into species-specific behaviors and the influence of local soil conditions. These comparisons emphasize the importance of integrating findings from various long-term experiments to enhance forest management strategies and improve sustainability in tropical regions.

In terms of applications for our findings, they bear important implications within the context of forest management decision-making, underscoring the need for continuous monitoring of permanent plots to better understand the long-term impacts of logging and other disturbances on forest ecosystems. Monitoring these plots allows a more nuanced understanding of how different species and soil conditions interact with logging activities and climate variations, in turn informing more adaptive and sustainable forest management practices.

This study highlights the importance of integrating detailed observations from long-term experiments to refine management strategies. For example, the observed differences in growth responses between species in fertile versus less fertile soils could guide the development of targeted silvicultural interventions that account for soil variability. Moreover, recognizing the temporary nature of increased growth following logging emphasizes the need for ongoing monitoring to detect and address any emerging issues, such as the proliferation of invasive species or changes in forest structure that could affect long-term recovery.

5. Conclusions

Our study highlights distinct growth patterns among different species groups in response to reduced-impact logging and environmental variables. By applying the CAFOGROM model, we identified ten species groups with varying growth behaviors influenced by soil, climate, and logging practices.

The analysis revealed that tree growth and responses to environmental factors differ significantly across these groups. For example, pioneer species and light-demanding trees exhibited higher growth rates post-logging, reflecting their rapid establishment and adaptation to increased light availability. In contrast, shade-tolerant species showed slower growth, consistent with their adaptations to lower light conditions and slower recovery rates after disturbance.

The modeling strategy adopted here detected the heterogeneity of species growth in different dominance situations. This distinct growth among trees in the ten species groups was influenced by soil factors, climate, and logging practices. Soil factors such as the percentage of sand, silt, total carbon, aluminum, and total exchangeable bases have positive and negative effects on tree growth in logged forests, although no direct relationship was established with a particular ecological group or tree size. It is important to highlight that these influences are not always linear and may be affected by additional factors.

Future research should focus on refining species classification and growth modeling to enhance the applicability of these findings in forest management. Incorporating additional variables, such as wood density and canopy position, could provide more precise insights into species-specific responses and improve management practices. Continuous monitoring and long-term data analysis will be crucial to understand growth patterns and adapt forest management strategies to evolving environmental conditions and climate change.

Effective forest management requires a nuanced approach that considers the varied growth responses of different species groups to ensure sustainable use and conservation of forest resources. Models like CAFOGROM offer valuable tools for predicting future growth and guiding management decisions, but ongoing research and adaptation are necessary to address emerging challenges in forest ecosystems.

CRediT authorship contribution statement

Lucas José Mazzei de Freitas: Writing – review & editing, Validation, Supervision, Methodology, Formal analysis, Conceptualization. **Jorge Luis Reategui-Betancourt:** Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Guido Briceño:** Writing – review & editing. **Rodrigo Geroni Mendes Nascimento:** Writing – review & editing. **Axa Emanuele S. Figueiredo:** Writing – review & editing. **Denis Alder:** Writing – review & editing. **Alba Valéria Rezende:** Writing – review & editing, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by Embrapa Eastern Amazon, which provided data and funding (SEG 10.20.03.005.00.00; SEG 03.12.00.030.00.00). The Brazilian Coordination for the Improvement of Higher Education Personnel (CAPES) provided Ph.D. scholarship funding.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2024.122465](https://doi.org/10.1016/j.foreco.2024.122465).

Data availability

Data will be made available on request.

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