

Article

Variability in Fruit Production of *Carapa guianensis* Associated with Edaphoclimatic Factors in the Amazon

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Abstract

Carapa guianensis Aubl., widely distributed throughout the Amazon, is recognized for its ecological, economic, and social importance, and constitutes a key source of income for numerous extractive communities. However, fruit production exhibits marked spatial variation that may be influenced by soil properties and climatic factors. In this study, we assessed this variability using data from 21 studies conducted in the Brazilian Amazon, incorporating georeferenced information from each site on climate and soil characteristics. Environmental variables were evaluated using Random Forest models. Although the number of independent production estimates available in the literature is limited, average fruit productivity showed a broad range (0.34 to $34.6 \text{ kg} \cdot \text{tree}^{-1} \cdot \text{year}^{-1}$), with higher values in várzea forests ($16.5 \text{ kg} \cdot \text{tree}^{-1} \cdot \text{year}^{-1}$) and lower values in igapó forests ($2.5 \text{ kg} \cdot \text{tree}^{-1} \cdot \text{year}^{-1}$). The Random Forest model explained 42% of the variability in fruit production according to cross-validation, whereas the model fit using the full dataset showed a higher R^2 value (0.83). Soil organic carbon, mean annual temperature, and clay content were the most influential predictors. These findings demonstrate that fruit production is shaped by the interaction between edaphic and climatic conditions, which determine the species' productivity patterns and highlight the need to foster adaptive management strategies that ensure the sustainable use of andiroba across Amazonian ecosystems. Nevertheless, it is acknowledged that the number of available production estimates is limited and that methodological heterogeneity exists among the analyzed studies. Despite this, the results reveal consistent patterns of association between *Carapa guianensis* fruit production and edaphoclimatic gradients, highlighting the influence of climatic and soil-related variables at a regional scale.

Keywords: *Carapa guianensis*; Amazon; edaphoclimatic factors; fruit production; random forest; sustainable forest management



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1. Introduction

The Amazon region contains some of the most biodiverse ecosystems on the planet and is characterized by a remarkable variety of tree species [1–3] many of which hold significant ecological, economic, and social importance [4,5]. Among these is *Carapa guianensis* Aubl. (Meliaceae), commonly known as andiroba, a large tree widely distributed throughout the Amazon basin [6] and noted for its multiple uses [7]. Its seeds are primarily used for oil extraction [8], which has medicinal [9–12], cosmetic [13], and insecticidal properties [14], making it an important source of income for traditional Amazonian communities [15]. The species is also valued for timber [16,17] and possesses relevant cultural significance. Moreover, its presence plays a fundamental role in maintaining ecosystem services, including nutrient cycling and the provision of food resources for wildlife [18].

Fruit production in *C. guianensis* exhibits considerable temporal and spatial variability, likely influenced by different environmental factors [19] that can determine its annual yield [20]. Several studies have indicated that the productivity of tropical forest species is closely linked to edaphoclimatic conditions, including precipitation, temperature, and soil properties [21–23]. For *C. guianensis*, fluctuations in annual fruit production have been reported across various regions of the Amazon, suggesting a response to seasonal climatic variation and to extreme events such as prolonged droughts or atypical floods [24–26]. This variability is common among tropical tree species and may represent an adaptive strategy, although it also poses challenges for management aimed at the sustainable harvest of fruits. Despite the existence of long-term data records, analyses capable of identifying fruit production patterns associated with edaphoclimatic factors across the entire Amazon are still lacking.

Precipitation plays a fundamental role in the phenology and fruit production of Amazonian species [21,27]. Changes in hydrological patterns can directly affect processes such as flowering, pollination, and fruit development [28]. Various studies highlight that the alignment between phenological events and the availability of water and nutrients largely determines the reproductive success of tree species, leading to substantial interannual variability in fruiting [16,27,29,30]. In addition to precipitation, soil properties such as fertility, texture, effective depth, and nutrient availability also influence the vegetative and reproductive growth of tropical trees [31,32]. The interplay between climatic and edaphic conditions, together with intraspecific genetic variation, contributes to the heterogeneous productivity patterns observed across different regions of the Amazon.

An additional aspect for understanding productivity patterns is the diversity of environmental conditions found across the Amazon. The region is composed of a mosaic of ecosystems that differ widely in their flooding regimes, nutrient availability, and hydrological dynamics [33]. In várzea areas, which are periodically flooded, trees receive a constant supply of nutrient-rich sediments, which supports higher productivity [34,35]. In contrast, terra firme forests, where flooding does not occur, develop on nutrient-poor soils that restrict both growth and reproduction in many species [36]. Baixio environments, characterized by waterlogged soils and generally low fertility, present intermediate and highly variable conditions. On the other hand, igapó forests—flooded by acidic blackwater and with very limited nutrient availability—represent some of the most restrictive environments for fruit production [35,37,38]. In this context, assessing fruit production in *C. guianensis* across these distinct Amazonian environments is essential for understanding how environmental heterogeneity shapes the species' phenological and reproductive patterns.

The interaction between edaphic and climatic factors within each of these environments exerts a strong influence on the reproduction of *C. guianensis* [17,25]. In várzea forests, the annual deposition of sediments during flooding increases soil fertility [39], which can enhance vegetative growth and, consequently, fruit production. In contrast, in

terra firme forests, highly weathered and nutrient-poor soils impose nutritional limitations, making water availability and nutrient cycling critical elements for reproductive phenology. In *baixio* environments, prolonged soil saturation can reduce root aeration and limit fruit production, while in *igapó* forests, the low fertility associated with acidic blackwater [35,36] represents one of the most restrictive contexts for fruiting. These edaphoclimatic conditions, combined with interannual variability in precipitation and the occurrence of extreme climatic events, generate highly heterogeneous patterns of fruit production throughout the Amazon [40,41].

In this context, understanding the edaphic and climatic determinants of fruit production in *C. guianensis* is essential for the sustainable management of the species, particularly in initiatives focused on non-timber forest products and forest conservation. Beyond strengthening the scientific basis for community-based management, this knowledge can guide public policies and conservation strategies that reconcile local income generation with biodiversity preservation. However, quantitative studies that integrate environmental variables with actual fruit production remain scarce in the Amazonian literature, limiting the understanding of causal relationships and the ability to predict productivity under different conditions.

Therefore, this study seeks to fill this gap by analyzing the variability in fruit production of *C. guianensis* across different localities in the Amazon, relating it to climatic and edaphic factors using empirical data and statistical modeling. By providing scientific evidence on the environmental factors that determine productivity, this research aims to support the development of adaptive management strategies and strengthen sustainable value chains based on the use of andiroba.

2. Materials and Methods

2.1. Literature Review

A literature review was conducted covering scientific publications that reported quantitative data on fruit production of *Carapa guianensis* in the Amazon region between 2000 and 2024. Searches were performed in the Scopus, Web of Science, SciELO, and Google Scholar databases, using combinations of keywords in English, Spanish, and Portuguese (*Carapa guianensis*, fruit production, Amazon, seed yield, andiroba, phenology), linked with Boolean operators (AND/OR). Only studies that provided georeferenced data or allowed precise identification of the sampling site were included (Figure 1).

For each selected record, the following information was extracted: total number of fruits or seeds per tree, forest type (*terra firme*, *várzea*, *baixio*, *restinga*, and *igapó*), geographic coordinates, and sampling year.

2.2. Acquisition of Fruit Production Data

The average fruit production per tree was obtained from data extracted from scientific articles. In some studies, the authors directly reported the mean annual production per individual ($\text{kg tree}^{-1} \text{ year}^{-1}$), and these values were used as originally presented. In cases where studies provided tables at the individual-tree level, the data were compiled and the mean annual production was calculated accordingly.

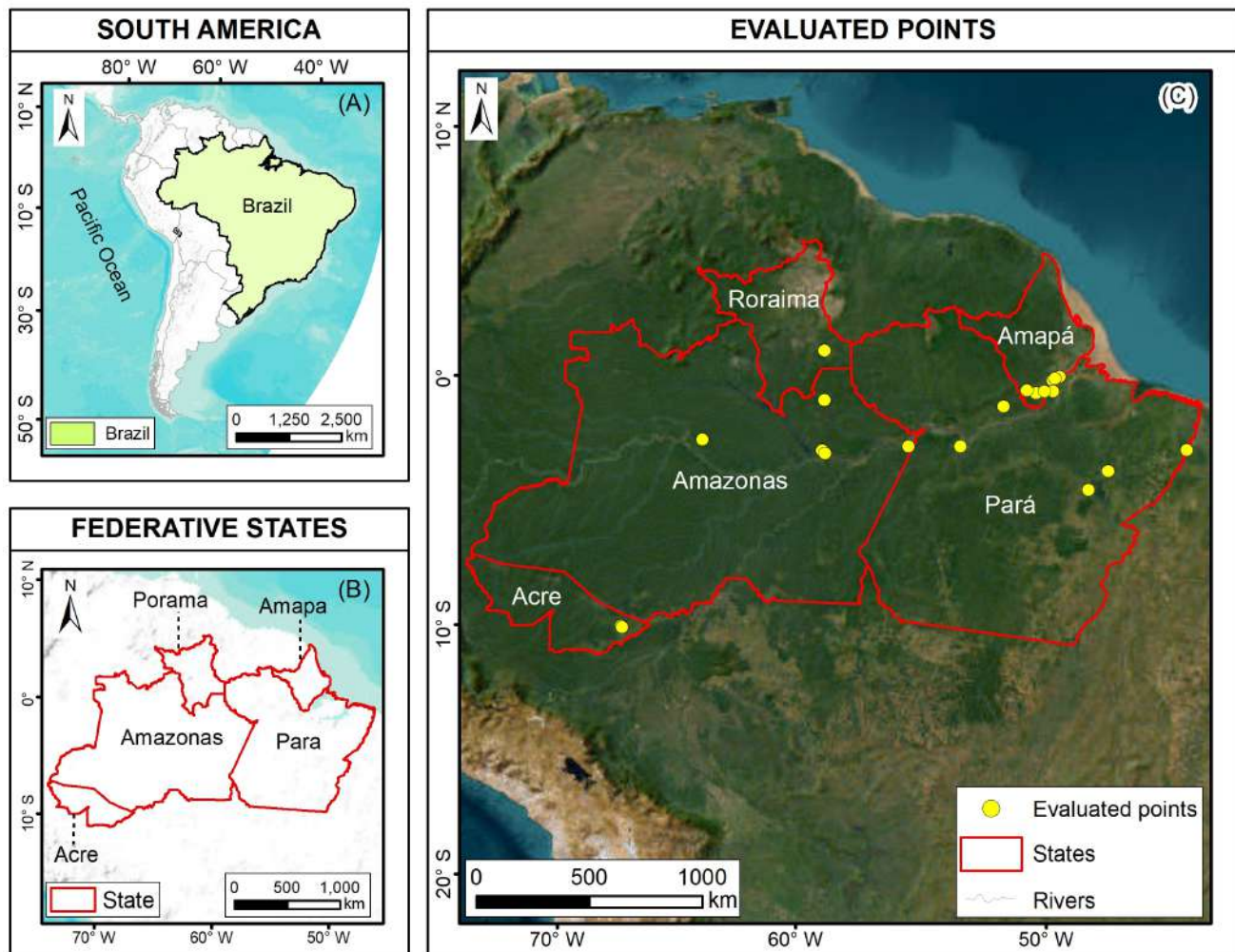


Figure 1. Map of the geographic distribution of studies on the fruit production of *Carapa guianensis* in the Brazilian Amazon. (A) Location of Brazil within the context of South America. (B) Brazilian States considered in the analyses. (C) Location study sites where studies recorded in the literature were conducted, covering different types of Amazonian ecosystems (terra firme, várzea, among others).

In studies where fruit production was reported as the number of fruits and/or the number of seeds per tree, seed-based production was converted to fruit-equivalent mass to ensure comparability among studies. When the total number of seeds was reported, mean seed production per tree was first calculated by dividing the total number of seeds by the number of sampled trees. Fruit-equivalent production was then estimated by multiplying the mean number of seeds per tree by an assumed mean fresh seed mass of 25 g per seed, based on published morphobotanical descriptions of *Carapa guianensis* [42]. Fruit-equivalent production (FP) was calculated as:

$$FP \text{ (kg} \cdot \text{tree}^{-1} \cdot \text{year}^{-1}) = (N_s \times 25) / 1000$$

where N_s is the mean number of seeds per tree and 25 represents the assumed mean fresh mass (g) of an individual seed. This standardization allowed harmonization of fruit production estimates across studies using heterogeneous reporting units.

The diameter at breast height (DBH) was considered for each site to evaluate the effect of tree size on mean fruit production whenever this information was available. Of the 21 sites in the database, 13 reported mean DBH values. DBH was not included in the Random Forest analyses in order to retain the full spatial coverage of the dataset.

and to avoid imputing missing dendrometric values, which could introduce bias into ecological inferences.

This methodological decision of partial exclusion aimed to balance spatial coverage by retaining all 21 sites in the general descriptive and predictive analyses, while ensuring rigor by controlling for a dendrometric covariate when appropriate.

The comparison between models fitted to the same dataset (model without DBH vs. model with DBH, both applied to the 13 available observations) was used to assess whether the inclusion of DBH significantly improved model performance, using an F-test (ANOVA for nested models). No DBH imputation procedures were applied to replace missing measurements in other sites in order to avoid introducing assumed dendrometric distributions that could bias ecological inferences.

2.3. Environmental Variables

To evaluate the variability in fruit production of *Carapa guianensis* associated with edaphoclimatic factors, the following variables were considered: (1) mean annual temperature ($^{\circ}\text{C} \times 10$); (2) temperature seasonality, expressed as standard deviation $\times 100$ ($^{\circ}\text{C} \times 10$); (3) precipitation seasonality ((standard deviation/mean) $\times 100$), in %; (4) annual precipitation, in millimeters; and (5) precipitation of the driest quarter, in millimeters. These variables were obtained from the WorldClim global climate database, version 2.1 (<https://www.worldclim.org/data/index.html>, accessed on 20 June 2025), derived from meteorological station records and representing climatic averages for the period 1950–2000 [43]. WorldClim provides high-resolution ($\sim 1 \text{ km}^2$) interpolated climate data widely used in ecological and biogeographical research.

Although fruit production records compiled in this study span publications from 2000 to 2024, the climatic predictors were derived from the WorldClim v2.1 climatologies (1950–2000), which represent long-term mean climatic conditions. These climatologies were used as proxies for baseline environmental conditions, as they are commonly applied in ecological analyses involving long-lived perennial tree species. Given the longevity and slow demographic responses of *Carapa guianensis*, fruit production patterns are assumed to be more strongly associated with long-term climatic regimes than with short-term interannual variability. In addition, the use of WorldClim ensured spatial consistency and comparability across study sites distributed throughout the Amazon basin. Nevertheless, this approach does not explicitly capture recent climatic anomalies or post-2000 climate trends, which is acknowledged as a methodological limitation.

Soil physicochemical variables were extracted using the specific geographic coordinates of each sampling point. The edaphic variables considered were: (1) organic carbon density ($\text{hg} \cdot \text{m}^{-3}$); (2) organic carbon stock ($\text{t} \cdot \text{ha}^{-1}$); (3) bulk density of the fine soil fraction ($\text{cg} \cdot \text{cm}^{-3}$); (4) clay content ($<0.002 \text{ mm}$) in the fine fraction ($\text{g} \cdot \text{kg}^{-1}$); (5) sand content ($>0.05/0.063 \text{ mm}$) in the fine fraction ($\text{g} \cdot \text{kg}^{-1}$); (6) silt content (≥ 0.002 and $\leq 0.05/0.063 \text{ mm}$) in the fine fraction ($\text{g} \cdot \text{kg}^{-1}$); (7) cation exchange capacity at pH 7 ($\text{mmol}(\text{c}) \cdot \text{kg}^{-1}$); (8) organic carbon content in the fine fraction ($\text{dg} \cdot \text{kg}^{-1}$); (9) total nitrogen (N) ($\text{cg} \cdot \text{kg}^{-1}$); and (10) soil pH in H_2O ($\text{pH} \times 10$).

These variables were obtained from the SoilGrids 250 m v2.0 database (<https://soilgrids.org>, accessed on 17 August 2025), which provides global predictions of soil properties at an average spatial resolution of 250 m using machine-learning models that generate interpolated estimates of edaphic variables [44]. The ten physicochemical parameters available on the platform were considered, calculated as the mean of three depth intervals (0–5, 5–15, and 15–30 cm), representing the topsoil layer (0–30 cm).

Data were extracted at the specific sampling points defined in the study, retaining the original column names, parameters, and corresponding units. All datasets were inspected

prior to analysis to identify missing values and potential outliers. No observations were excluded, as extreme values were interpreted as part of the natural environmental heterogeneity of Amazonian ecosystems. Prior to modeling, continuous environmental variables were standardized to ensure comparability among predictors and to avoid scale-related biases in the Random Forest analysis.

The data download was conducted in September 2025 using JavaScript scripts developed in Google Earth Engine, a geospatial analysis platform that enables processing of large environmental and satellite datasets at a global scale [45].

2.4. Random Forest

For the analysis of environmental and predictive data, the Random Forest (RF) algorithm was used. RF is an automated, decision tree-based method that combines multiple models to improve accuracy and reduce the risk of overfitting [46]. Its operation consists of generating numerous classification or regression trees, each built from random subsets of the training data and predictor variables. The model produces its final output by aggregating the predictions of all trees, using averaging in the case of regression or majority voting in the case of classification.

This method was selected due to its robustness in environmental studies, its ability to handle highly correlated predictors, and its strong performance even when nonlinear relationships exist between explanatory variables and the response variable. RF was used to determine the relative importance of bioclimatic and edaphic variables in explaining the observed variability in fruit production. Analyses were performed in R [47] using the *randomForest* package [48].

The dependent variable used was the mean fruit production of *C. guianensis* ($\text{kg tree}^{-1} \text{ year}^{-1}$). Predictor variables included soil characteristics such as bulk density (g cm^{-3}), cation exchange capacity (cmol (+) kg^{-1}), clay content (g kg^{-1}), nitrogen content (g kg^{-1}), pH, organic carbon density (kg m^{-3}), sand content (g kg^{-1}), silt content (g kg^{-1}), soil organic carbon (g kg^{-1}), soil organic carbon stock (Mg ha^{-1}), and total texture (clay + sand + silt). Climatic variables included annual precipitation (mm year^{-1}), precipitation of the driest quarter (mm), precipitation seasonality (CV, %), mean annual temperature ($^{\circ}\text{C}$), and temperature seasonality (standard deviation $\times 100$).

To examine relationships among predictors, a Pearson correlation matrix was constructed to identify significant associations and potential multicollinearity issues. Variables with high correlations ($r > 0.80$) were considered for exclusion from the model. The *mtry* parameter was set to 2, and the model was trained using five-fold cross-validation (5-fold CV). A total of 500 decision trees were generated to ensure stable predictions. Model performance was evaluated using three metrics: mean absolute error (MAE), root mean square error (RMSE), and coefficient of determination (R^2), calculated from the observed and predicted values during cross-validation.

The relative importance of the predictors was estimated using the “Mean Decrease in Accuracy” and “Mean Decrease in Gini” criteria, which allowed ranking the variables with the greatest influence. For those variables with the highest weight in the model, Partial Dependence Plots (PDPs) were generated to visualize their marginal effects on mean fruit production while keeping the remaining variables constant at their average values. Predictive performance was validated using a plot of observed versus predicted values, accompanied by the calculation of the adjusted R^2 .

Additional visualizations, such as scatterplots and stripcharts, were produced to compare fruit production across environmental variables and forest types. Multiple linear regression models were also fitted using subsets of predictor variables (soil texture, climatic factors, and soil chemical properties), and multicollinearity was evaluated using the

Variance Inflation Factor (VIF). Variables with $VIF > 2$ were iteratively removed until more parsimonious models were obtained.

All compiled data were organized and systematized into a database, and statistical analyses were conducted in R, version 4.5.0 [42].

3. Results

3.1. Study Coverage and Descriptive Statistics

The study included a total of 21 independent investigations conducted across different states of the Brazilian Amazon (Table 1). Most studies were concentrated in the states of Pará ($n = 7$), Amapá ($n = 5$), and Acre ($n = 4$), followed by Amazonas ($n = 2$), Roraima ($n = 2$), and Maranhão ($n = 1$) (Figure 2).

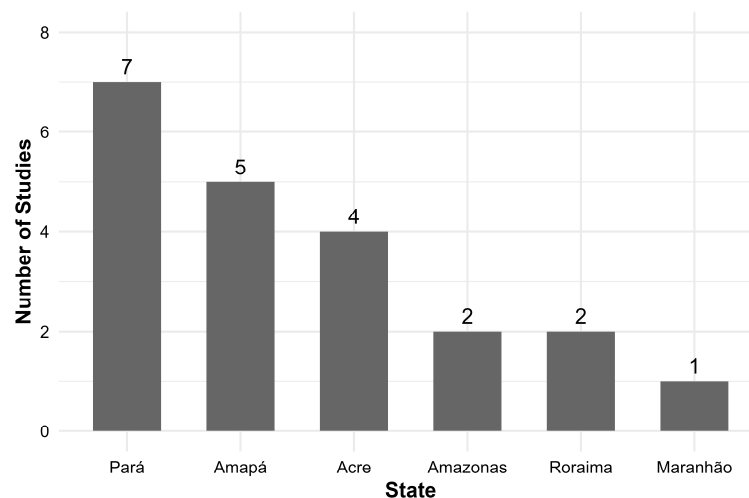


Figure 2. Number of studies on fruit production conducted in different states of the Brazilian Amazon.

The number of sampled trees per study ranged from 6 to 352 individuals, with an average of 98.2 ± 83.6 trees (mean $\pm$ standard deviation). The diameter at breast height (DBH) averaged 37.95 ± 12.14 cm, with values ranging from 10.0 to 55.0 cm. Mean fruit production varied between $0.34 \text{ kg} \cdot \text{tree}^{-1} \cdot \text{year}^{-1}$ and $34.6 \text{ kg} \cdot \text{tree}^{-1} \cdot \text{year}^{-1}$, with an overall mean of $8.30 \pm 9.35 \text{ kg} \cdot \text{tree}^{-1} \cdot \text{year}^{-1}$.

3.2. Fruit Production Across Forest Types

When comparing forest types, the mean DBH was highest in Igapó forests (41.45 ± 5.59 cm), followed by Terra Firme forests (40.16 ± 9.02 cm), and lowest in Várzea forests (33.29 ± 16.39 cm). Regarding fruit production, Várzea forests exhibited the highest mean value ($16.55 \pm 11.87 \text{ kg} \cdot \text{tree}^{-1} \cdot \text{year}^{-1}$), followed by Terra Firme forests ($7.12 \pm 7.47 \text{ kg} \cdot \text{tree}^{-1} \cdot \text{year}^{-1}$), whereas Igapó forests showed the lowest production ($2.52 \pm 0.37 \text{ kg} \cdot \text{tree}^{-1} \cdot \text{year}^{-1}$). For Baixio and Restinga forests, only one study was available for each environment, with mean productions of 1.48 and $4.10 \text{ kg} \cdot \text{tree}^{-1} \cdot \text{year}^{-1}$, respectively (Figure 3).

Table 1. Geographic location, forest type, climatic conditions, and mean fruit production of *Carapa guianensis* reported in published studies across the Amazon Basin.

Author	State	Municipality	Study Area	Forest Type	Longitude (°)	Latitude (°)	Number of Trees	Mean DBH (cm)	Mean Fruit Production (kg Tree ⁻¹ Year ⁻¹)
[49]	Pará	Belterra	Floresta Nacional do Tapajós” (FLONA Tapajós)	Terra firme	−54.7500	−2.6667	192	41.5	10.29
[49]	Pará	Belterra	Floresta Nacional do Tapajós” (FLONA Tapajós)	Terra firme	−50.0000	−4.1667	137	41.3	9.67
[49]	Pará	Belterra	Floresta Nacional do Tapajós” (FLONA Tapajós)	Terra firme	−54.7500	−2.6667	86	37.4	8.17
[50]	Pará	Nova Esperança do Piriá	Aldeia de Tekohaw	Terra firme	−46.5570	−2.6265	46	39.4	1.2
[51]	Amazonas	Mara	Reserva de Desenvolvimento Sustentável Amanã	Igapó	−64.6400	−2.5283	42	45.4	2.7
[52]	Acre	Rio Branco	Reserva Florestal da Embrapa Acre	Baixio	−67.7411	−9.9747	26	NA	1.48
[52]	Acre	Rio Branco	Reserva Florestal da Embrapa Acre	Terra firme	−67.7411	−9.9747	23	NA	2.16
[53]	Pará	Breu Branco	Empresa Izabel medeiros do Brasil	Terra firme	49.3090	−3.4508	50	44.95	2.12
[54]	Acre	Rio Branco	Reserva Florestal da Embrapa Acre	Terra firme	−67.7411	−9.9747	118	25	1.6
[55]	Amapá	Mazagão	Escola Família Agrícola (EFA) do Carvão	Várzea	−51.3667	−0.1833	6	10	15.4
[56]	Amapá	Macapá	APA da Fazendinha	Várzea	−51.1283	−0.0529	30	44.4	34.6
[57]	Amapá	Mazagão	Reserva florestal da Empresa Brasileira de Pesquisa Agropecuária	Terra firme	−51.9667	−0.6667	34	38.1	4.9
[57]	Amapá	Mazagão	Reserva florestal da Empresa Brasileira de Pesquisa Agropecuária	Várzea	−51.9667	−0.6667	12	23.7	6.35
[16]	Acre	NA	Reserve of the Brazilian Agricultural Research Corporation (EMBRAPA)	Terra firme	−67.7053	−10.0244	168	37.5	1.77
[16]	Acre	NA	Reserve of the Brazilian Agricultural Research Corporation (EMBRAPA)	Igapó	−67.7053	−10.0244	184	37.5	2.33
[58]	Amazonas	Parintins	Comunidade N. S. do Rosário	Terra firme	−56.6935	−2.7107	15	NA	16.8
[59]	Amazonas	Manaus	Reserva Florestal Ducke	Terra firme	−59.9833	−2.9167	30	NA	9.31
[59]	Amazonas	Manaus	Reserva Florestal Ducke	Terra firme	−59.8833	−3.0167	30	NA	9.31
[60]	Roraima	Sao Joao da Baliza	Área de reserva legal de uma propriedade particular	Várzea	−59.9114	−0.9506	73	47.75	9.76
[25]	Acre	NA	Forest reserve of the Brazilian Agricultural Research Corporation (EMBRAPA)	Terra firme	−67.7053	−10.0244	352	32.5	2.06
[61]	Amapá	Laranjal do Jari	Reserva Extrativista Rio Cajari (RESEX) Cajari)	Terra firme	−52.3053	−0.5619	62	NA	1.84
[61]	Amapá	Mazagão	Estação Experimental da Embrapa	Várzea	−51.2889	−0.1150	16	NA	8.09
[62]	Amapá	Mazagão	Campo Experimental do Mazagão da Embrapa	Várzea	−51.2889	−0.1150	16	30	8.35
[63]	Pará	Almeirim	Cafezal/Paru	Terra firme	−53.1597	−1.1655	20	40.7	2.9
[26]	Roraima	São João da Baliza		Terra firme	−59.9114	−0.9506	121	20	29.99
[17]	Pará	Gurupá	Reserva de desenvolvimento Sustentavel (RDS) Itatupã-Baquiá	Terra firme	−51.3599	−0.5801	67	55	5.5
[17]	Pará	Gurupá	Reserva de desenvolvimento Sustentavel (RDS) Itatupã-Baquiá	Baixio	−51.3599	−0.5801	120	35	2.6
[17]	Pará	Gurupá	Reserva de desenvolvimento Sustentavel (RDS) Itatupã-Baquiá	Restinga	−51.3599	−0.5801	40	28	4.1
[19]	Pará	Gurupá	Reserva de desenvolvimento Sustentavel (RDS) Itatupã-Baquiá	Terra firme	−56.6935	−2.7107	21	55	11.47
[64]	Amapá	Porto Grande	Projeto de Assentamento Nova Canaã	Terra firme	−51.6725	−0.5867	26	NA	0.34

Notes: Coordinates are expressed in decimal degrees (WGS84). NA indicates information not reported in the original source. When the same author and year appear more than once, each entry corresponds to different study sites or forest types reported within the same publication.

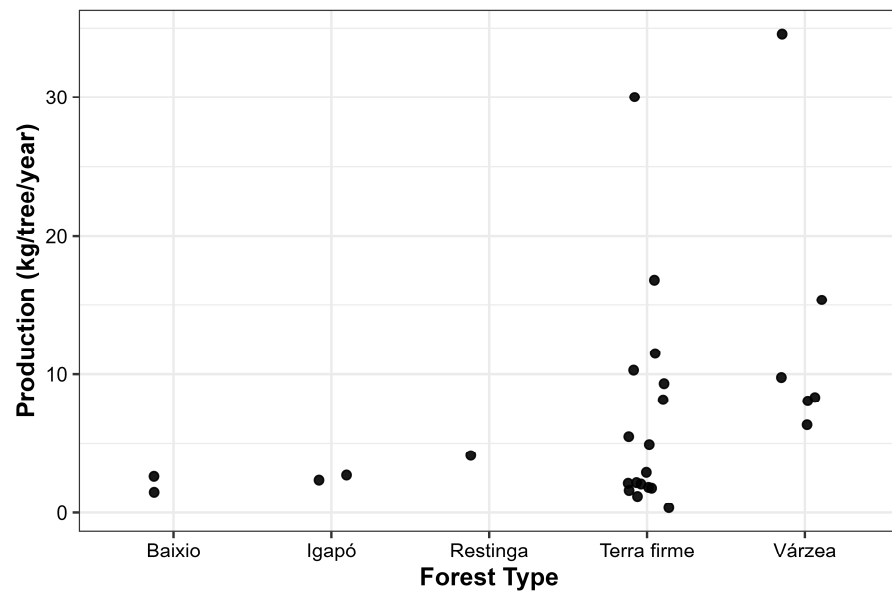


Figure 3. Variation in mean annual fruit production of *Carapa guianensis* ($\text{kg} \cdot \text{tree}^{-1} \cdot \text{year}^{-1}$) among forest types (Baixio, Igapó, Restinga, Terra firme, and Várzea) in the Amazon. Black dots indicate mean values of fruit production per tree.

3.3. Relationship Between Fruit Production and Environmental Variables

Higher production levels were concentrated in regions with annual precipitation between 2400 and 2800 mm, although with substantial variability (Figure 4a). This pattern suggests that fruit production is favored under humid conditions that ensure adequate water availability, while extremely low or excessive rainfall may impose physiological constraints on reproductive investment. Precipitation during the driest quarter did not show a defined trend; however, the highest production values were distributed between 200 and 300 mm (Figure 4b). This indicates that moderate water availability during the dry season may be sufficient to sustain fruit development, whereas more severe dry conditions could limit productivity. Regarding precipitation seasonality, trees tended to produce more when the coefficient of variation ranged between 40% and 50%, with reduced yields outside this interval (Figure 4c). This pattern suggests that fruit production is associated with relatively predictable seasonal rainfall regimes, while higher climatic variability may negatively affect reproductive processes. Mean annual temperature (Figure 4d) and temperature seasonality (Figure 4e) did not show clear relationships with fruit production; however, the highest fruiting values were concentrated at sites with lower thermal variability, indicating that more stable thermal conditions may favor reproductive performance.

Regarding soil properties, production was higher in sites with sand content between 30% and 50% (Figure 5), whereas values above 60% were associated with lower yields. This relationship likely reflects a balance between soil drainage and water retention, as excessively sandy soils may limit nutrient and moisture availability. In contrast, soils with silt contents ranging from 30% to 40% exhibited the highest production levels (Figure 5).

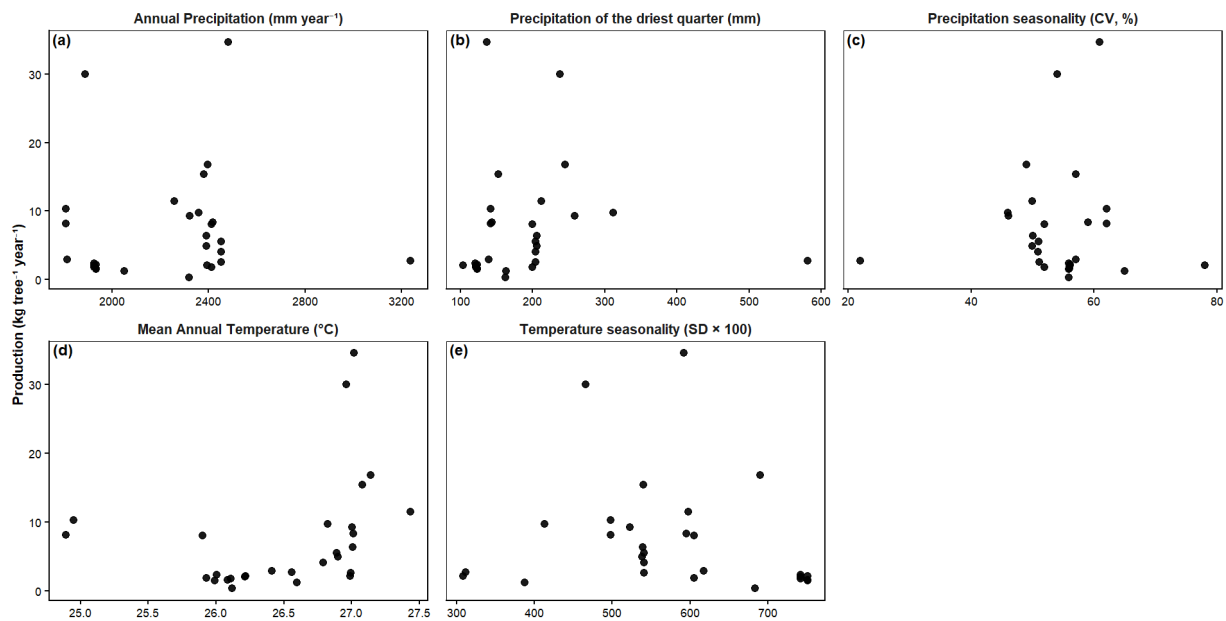


Figure 4. Relationship between fruit production of *Carapa guianensis* (kg tree⁻¹ year⁻¹) and climatic variables: (a) Annual Precipitation (mm year⁻¹), (b) Precipitation of the Driest Quarter (mm), (c) Precipitation Seasonality (CV, %), (d) Mean Annual Temperature (°C), and (e) Temperature Seasonality (SD × 100). Black dots represent mean annual fruit production per tree.

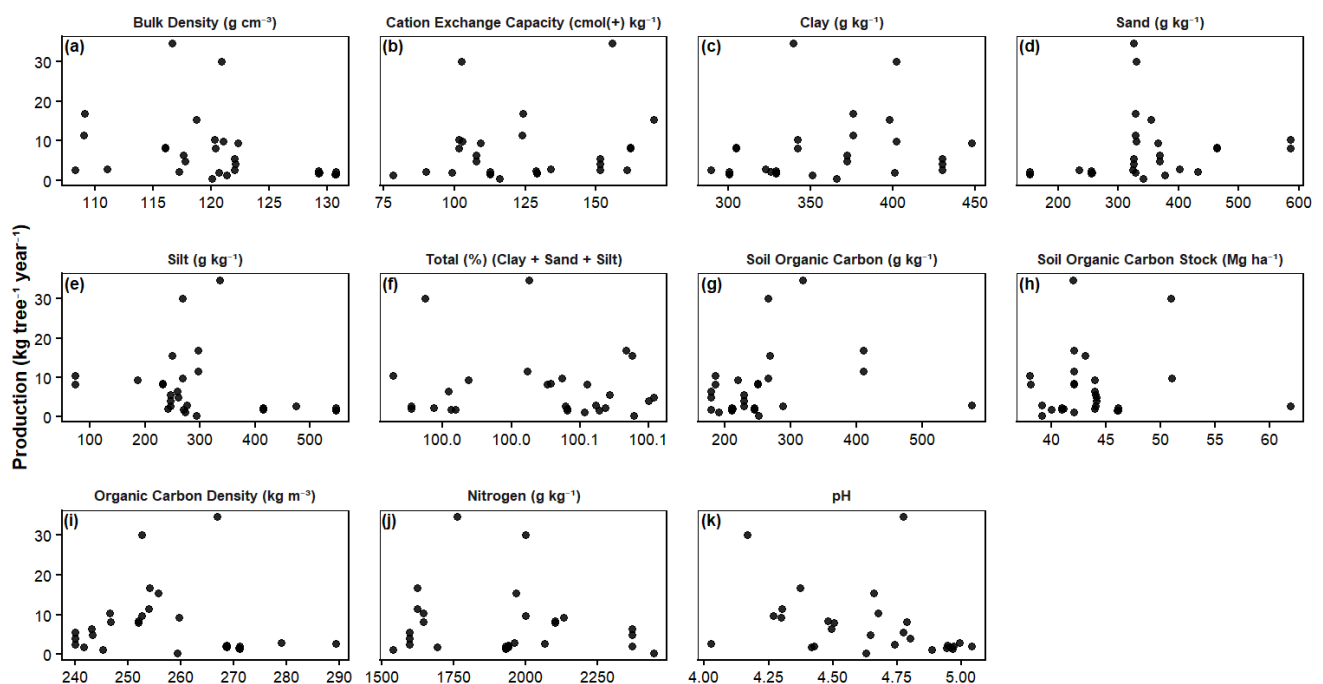


Figure 5. Relationship between fruit production of *Carapa guianensis* (kg tree⁻¹ year⁻¹) and edaphic variables: (a) Bulk Density (g·cm⁻³), (b) Cation Exchange Capacity (cmol(+)·kg⁻¹), (c) Clay (g·kg⁻¹), (d) Sand (g·kg⁻¹), (e) Silt (g·kg⁻¹), (f) Total (%) (Clay + Sand + Silt), (g) Soil Organic Carbon (g·kg⁻¹), (h) Soil Organic Carbon Stock (Mg·ha⁻¹), (i) Organic Carbon Density (kg·m⁻³), (j) Nitrogen (g·kg⁻¹), (k) pH.

3.4. Variable Importance and Model Performance

The analysis of variable importance in the Random Forest model revealed that the edaphoclimatic predictors contributing most to the variability in fruit production of *Carapa guianensis* were soil organic carbon content (%IncMSE = 5.77; IncNodePu-

rity = 215.46) (Figure 6j), followed by mean annual temperature (%IncMSE = 5.28; IncNodePurity = 182.26) (Figure 7e), annual precipitation (%IncMSE = 2.69; IncNodePurity = 156.83) (Figure 7c), and clay content (%IncMSE = 5.52; IncNodePurity = 79.25) (Figure 6c). These variables consistently ranked highest across both importance metrics, indicating a strong contribution to model performance and prediction accuracy.

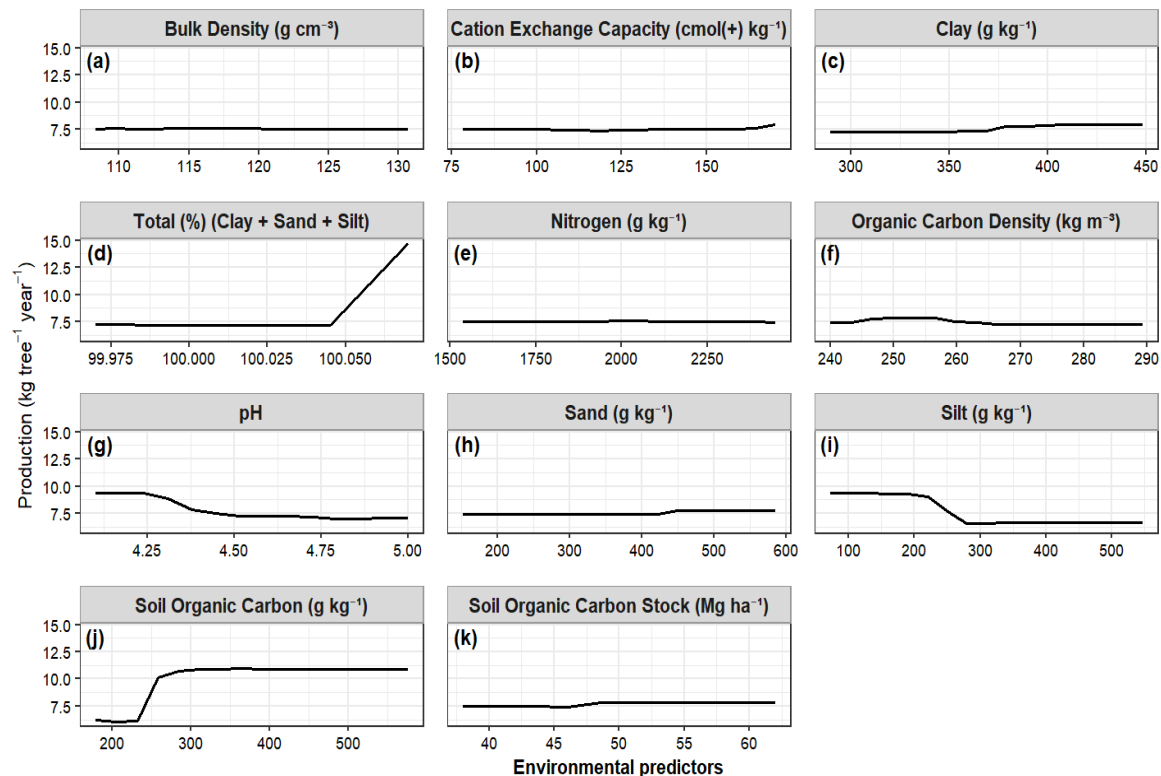


Figure 6. Partial Dependence Plots (PDP) of the edaphic predictors on the mean fruit production of *Carapa guianensis* ($\text{kg tree}^{-1} \text{ year}^{-1}$). Each panel shows the marginal effect of an individual predictor variable while the remaining variables are held constant at their average values. Black lines represent the model-predicted mean partial dependence of fruit production on each predictor. (a) Bulk density ($\text{g} \cdot \text{cm}^{-3}$), (b) Cation exchange capacity ($\text{cmol}(+) \cdot \text{kg}^{-1}$), (c) Clay ($\text{g} \cdot \text{kg}^{-1}$), (d) Total (%) (clay + sand + silt), (e) Nitrogen ($\text{g} \cdot \text{kg}^{-1}$), (f) Organic carbon density ($\text{kg} \cdot \text{m}^{-3}$), (g) pH, (h) Sand ($\text{g} \cdot \text{kg}^{-1}$), (i) Silt ($\text{g} \cdot \text{kg}^{-1}$), (j) Soil organic carbon ($\text{g} \cdot \text{kg}^{-1}$), (k) Soil organic carbon stock ($\text{Mg} \cdot \text{ha}^{-1}$).

In addition, soil pH and silt content also showed considerable influence in the model, with IncNodePurity values of 95.67 and 94.57, respectively (Figure 6g,i). Although their %IncMSE values were lower than those of the top-ranked predictors, their node purity values indicate a relevant role in partitioning the response variable within the decision trees.

In contrast, cation exchange capacity and total nitrogen (N) exhibited relatively low influence, with %IncMSE values below 2.1 (Figure 6b,e). These variables contributed marginally to explaining variability in fruit production within the model, suggesting a limited predictive role compared to the dominant climatic and soil texture variables.

The Random Forest model applied to mean fruit production of *C. guianensis* explained 42% of the observed variability in yield according to cross-validation ($\text{RMSE} = 7.79 \text{ kg} \cdot \text{tree}^{-1}$; $\text{MAE} = 5.25 \text{ kg} \cdot \text{tree}^{-1}$). When all observations were used for model training, the comparison between observed and predicted values (Figure 8) indicated a strong in-sample fit ($R^2 = 0.83$).

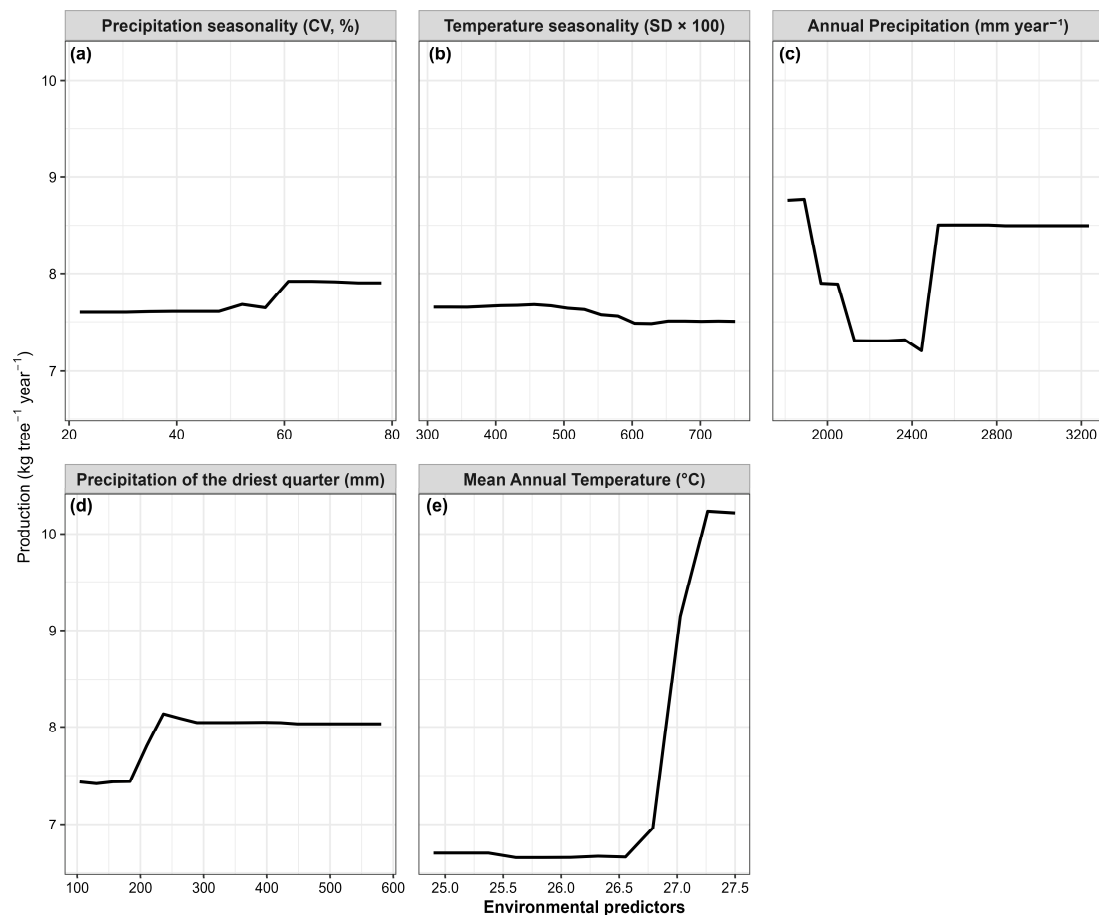


Figure 7. Partial Dependence Plots (PDP) of climatic predictors on the mean fruit production of *Carapa guianensis* ($\text{kg tree}^{-1} \text{yr}^{-1}$). Each panel shows the marginal effect of an individual predictor variable while the other variables are held constant at their mean values. Black lines represent the model-predicted mean partial dependence of fruit production on each predictor. (a) Precipitation seasonality (CV, %), (b) Temperature seasonality ($\text{SD} \times 100$), (c) Annual precipitation (mm year^{-1}), (d) Precipitation of the driest quarter (mm), (e) Mean annual temperature ($^{\circ}\text{C}$).

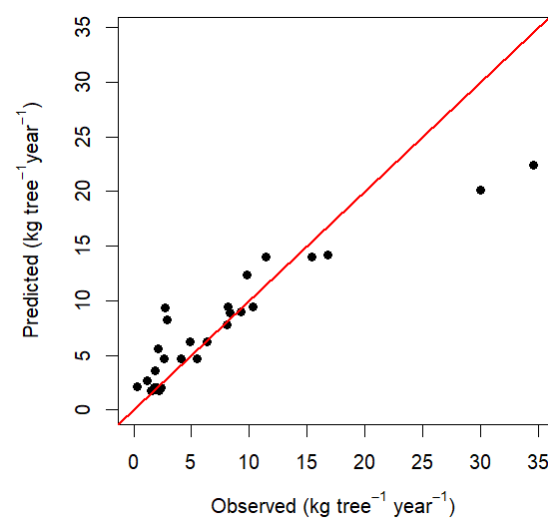


Figure 8. Observed versus predicted values of mean fruit production of *Carapa guianensis* ($\text{kg tree}^{-1} \text{year}^{-1}$), obtained using the Random Forest model. Black dots represent mean annual fruit production per tree. The red line represents the 1:1 relationship between observed and predicted values, used as a reference to assess model performance.

According to the relative importance of the predictors, soil organic carbon content was the most influential variable, reaching a standardized importance value of 100 in both metrics. It was followed by mean annual temperature (91.05), clay content (95.38), and annual precipitation (64.13).

Other predictors with notable contributions included soil bulk density (77.67), surface-layer organic carbon (73.99), and silt content (56.77). In contrast, variables such as cation exchange capacity and total nitrogen (N) showed very low importance, with values close to zero.

4. Discussion

The observed variability in fruit production of *C. guianensis* reflects the strong influence of edaphoclimatic conditions on the species' ecological and physiological processes. The observed productivity range (0.34 to 34.6 kg·tree⁻¹·year⁻¹) illustrates the spatial heterogeneity typical of Amazonian ecosystems, where soil gradients, topography, and hydrological regimes shape the productive dynamics of forest populations. Similar patterns have also been reported for other species of high ecological and economic value in the Amazon, in which phenotypic plasticity and the capacity to adapt to local conditions are key determinants [65,66]. These findings are consistent with reports by Klimas et al. [25] and Tonini et al. [26], who highlight that the phenotypic plasticity of *C. guianensis* is a critical factor underlying its broad ecological distribution.

4.1. Influence of Climatic Factors and Forest Type

The differences observed among forest types, with várzea forests showing the highest mean fruit production (16.55 ± 11.87 kg·tree⁻¹·year⁻¹), followed by terra firme and igapó, indicate that the hydrological and edaphic conditions characteristic of each environment exert a decisive influence on the fruiting of *C. guianensis*. Várzea environments, with more fertile soils and periodic nutrient inputs from seasonal flooding, provide particularly favorable conditions for fruit production, consistent with previous studies highlighting higher fruiting in alluvial habitats [33,67]. In contrast, igapó forests, subjected to prolonged flooding and poorer soils, exhibited the lowest fruit production. This may be attributed to physiological constraints on fruiting under more restrictive conditions, as noted by Wittmann et al. [68].

The importance of annual precipitation and mean annual temperature in the Random Forest model supports the hypothesis that *C. guianensis* productivity is strongly influenced by water availability and thermal stability. The concentration of the highest fruit production values in regions receiving between 2400 and 2800 mm of annual precipitation suggests the existence of an optimal moisture range, beyond which productivity tends to decline. In this regard, studies on Amazonian tree species indicate that excessive rainfall can negatively affect production by interfering with pollination or causing drainage problems [69]. Similarly, lower thermal variability associated with higher yields suggests that *C. guianensis* may benefit from more stable temperature regimes, which would favor the synchronization of phenological events and a more efficient allocation of resources for fruit production [24,25].

Temperature also showed a non-linear relationship with fruit production, with higher yields observed in sites where the annual thermal amplitude is lower. This thermal stability may favor key physiological processes, such as the formation of reproductive buds and the accumulation of reserves in the wood, as noted by Klimas et al. [25] for tropical species with similar phenological cycles. The interaction between mean annual temperature (MAT) and annual precipitation (AP), identified by the Random Forest model, suggests that the species' productivity responds to the synergy between both climatic factors rather than to the independent effect of each one.

4.2. Importance of Edaphic Factors

Regarding soil properties, the prominent influence of soil organic carbon (SOC) as the main predictor (%IncMSE = 5.77; IncNodePurity = 215.46) highlights the important role of organic matter in fruit productivity. Soils with higher SOC levels typically exhibit better physical structure, greater water retention capacity, and higher nutrient availability, which promotes fruit filling and maturation [70]. This finding aligns with studies linking high organic carbon content with soil quality and productivity in Amazonian systems [71].

Soil texture, particularly the clay and silt fractions, was also identified as an important set of predictors. The values obtained for clay fraction (95.38) and silt fraction (56.77) suggest that medium-textured soils, with a balance of water retention and aeration, are more conducive to fruit production in *C. guianensis*. In contrast, sand contents above 60% were associated with lower yields, likely due to reduced moisture and nutrient retention. This relationship between texture and productivity is consistent with studies analyzing aggregate stability and organic matter dynamics in Amazonian soils [72].

4.3. Model Performance and Methodological Considerations

The Random Forest model explained 42% of the observed variability in fruit production according to cross-validation, indicating a moderate predictive capacity consistent with the complexity of Amazonian ecological systems. The higher coefficient of determination obtained for the training dataset ($R^2 = 0.83$) reflects a strong in-sample fit but should be interpreted cautiously given the relatively small sample size ($n \approx 21$). The RMSE ($7.79 \text{ kg} \cdot \text{tree}^{-1}$) and MAE ($5.25 \text{ kg} \cdot \text{tree}^{-1}$) values further characterize model performance under cross-validation. Together, these results suggest that part of the unexplained variability may be associated with unconsidered biotic factors, such as genetic differences, pollination processes, herbivory, or intraspecific competition. Previous studies [25,69] have highlighted the importance of genetic variability within populations and pollinator connectivity in shaping the productivity of *C. guianensis*.

Although each study was treated as an independent observational unit, the number of sampled trees varied substantially among studies, and some forest types were represented by a single record. Because sample size and measures of variability were not consistently reported across the literature, weighted analyses based on the number of sampled trees were not feasible. Consequently, all records were assigned equal analytical weight, and results associated with forest types with low representation should be interpreted with caution.

4.4. Implications for Management, Conservation, and Climate

The results obtained provide important insights for the sustainable management of *C. guianensis*, a key species with ecological and socioeconomic significance in the Amazon. The identification of soils with high organic carbon content and balanced texture as the most favorable for fruit production allows for the prioritization of areas for management and conservation. Furthermore, under a climate change scenario marked by increasing temperatures and alterations in precipitation patterns, the fruit productivity of *C. guianensis* could be compromised, affecting its availability as a natural resource and its importance for traditional communities.

Incorporating these findings into genetic conservation and forest management strategies can help maintain productive and resilient populations. The inclusion of *C. guianensis* in agroforestry systems or restoration programs in várzea areas can take advantage of its fruiting potential in fertile alluvial soils. In contrast, in more restrictive areas (e.g., igapó), the implementation of specific management practices could help mitigate the effects of hydrological stress and low soil fertility.

Beyond the individual effects of environmental variables, the interaction between soil properties and water availability emerges as a central mechanism regulating the fruit productivity of *Carapa guianensis*. Soils with higher organic carbon content and intermediate texture exhibit greater water-retention capacity and nutrient availability, which can buffer the effects of climatic variability. Under scenarios of extreme drought, environments with higher hydrological regulation capacity such as várzea forests or areas with well-structured soils may become critical for sustaining fruit production. In this context, these environments acquire strategic importance for both productive management and conservation, as they function as refugia that stabilize yields under increasing climatic stress.

5. Conclusions

Fruit production of *C. guianensis* in the Amazon exhibits marked variation that is primarily influenced by edaphic and climatic factors, particularly soil organic carbon content, clay percentage, and mean annual temperature. Várzea environments showed the highest productivity, indicating that soils with moderate fertility and fewer hydrological constraints favor better reproductive performance of the species. These results highlight the importance of considering edaphoclimatic variables when defining potential areas for the management and conservation of *C. guianensis*, especially in the context of climate change and increasing pressures on Amazonian ecosystems. Future studies are recommended to integrate genetic and phenological aspects to better understand the interaction between environmental variability and the physiological responses of this species. This approach will help strengthen strategies for forest management and restoration in the region.

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