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Seasonal dynamics of litterfall nutrients in a native Brazil nut stand in the Tapajós National Forest, Eastern Amazon

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ABSTRACT

This study quantified carbon (C), nitrogen (N), and sulfur (S) concentrations in the litterfall of a native Brazil nut (*Bertholletia excelsa*) stand in the Tapajós National Forest, Belterra (Pará, Brazil), across dry and wet seasons. Monthly collections were conducted from August 2015 to July 2016 within a permanent plot of the MapCast Project, using 12 circular litter traps (0.25 m² each) systematically distributed in the forest. Litterfall was separated into leaves, flowers and fruits, wood, and miscellaneous fractions. After drying and sorting, samples were analyzed for C, N, and S contents using an elemental analyzer (CHNS/O). Seasonal patterns in elemental composition were observed: higher N and S concentrations occurred during the wet season, particularly in the miscellaneous fraction, whereas C was more abundant in the dry season, especially in leaves. Nevertheless, differences between seasons were not statistically significant (t-test, $p \leq 0.05$). Significant correlations between nutrient contents and climatic variables (precipitation and temperature) were detected, emphasizing the responsiveness of litterfall to environmental variation. Overall, the results demonstrate that litterfall acts as a key reservoir and pathway for nutrient transfer in Brazil nut-dominated Amazonian forests, contributing to nutrient cycling and sustaining soil fertility. The persistence of litter on the soil surface plays an essential role in conserving edaphic fertility and supporting ecological stability. These findings provide valuable insights for forest management and conservation practices, while also advancing the understanding of biogeochemical processes that regulate the functioning and resilience of tropical ecosystems.

Keywords: cycling, fertility, forest.

Dinâmica sazonal dos nutrientes da serapilheira em um povoamento nativo de castanha-do-pará na Floresta Nacional do Tapajós, Amazônia Oriental

RESUMO

Este estudo quantificou as concentrações de carbono (C), nitrogênio (N) e enxofre (S) na serapilheira de um castanhal nativo situado na Floresta Nacional do Tapajós, em Belterra (PA), considerando os períodos seco e úmido. As coletas foram realizadas mensalmente entre agosto de 2015 e julho de 2016, em parcela permanente do Projeto MapCast, utilizando 12 coletores circulares (0,25 m² cada) dispostos sistematicamente na floresta. A serapilheira foi separada nas frações: folhas, flores e frutos, madeira e miscelânea. Após secagem e triagem, as amostras foram analisadas quanto aos teores de C, N e S em analisador elementar (CHNS/O). Observou-se variação sazonal nas concentrações dos elementos: maiores teores de N e S ocorreram no período úmido, principalmente na fração miscelânea, enquanto o C se destacou no período seco, especialmente nas folhas. Contudo, não houve diferenças estatísticas significativas (teste t, 5%) entre os períodos. Identificaram-se correlações significativas entre os teores de nutrientes e variáveis climáticas (precipitação e temperatura), evidenciando a sensibilidade da serapilheira às variações ambientais. Os resultados indicam que a serapilheira atua como reservatório e via de transferência de nutrientes em castanhais nativos amazônicos, sendo essencial à ciclagem de nutrientes e à manutenção da fertilidade destes solos. A manutenção desse material sobre a superfície do solo representa um mecanismo chave para a conservação da fertilidade edáfica e para a sustentabilidade ecológica desses ecossistemas florestais. Os resultados obtidos oferecem subsídios para ações de manejo e conservação, além de contribuírem para o entendimento da dinâmica biogeoquímica em florestas tropicais.

Palavras-chave: ciclagem, fertilidade, floresta.

1. INTRODUCTION

In tropical forest ecosystems, litter plays a fundamental role in maintaining soil fertility, acting as the main agent of nutrient cycling (Sayer and Tanner, 2010; Santos *et al.*, 2011; Giweta, 2020). This organic material accumulated on the soil surface comprises the litter-soil compartment, where essential processes such as organic matter decomposition, mineralization, and consequent nutrient release into the soil occur (Godinho *et al.*, 2014; Zhao *et al.*, 2025).

As plant residues decompose, their nutrients become available to plants, sustaining primary productivity and the ecological functioning of the system (Caldeira *et al.*, 2013; Santos *et al.*, 2022). Thus, soil quality is directly proportional to the quality of nutrients derived from the litter (Lima *et al.*, 2015). Composed of leaves, branches, reproductive structures, and other plant debris, the litter forms the uppermost layer of the forest soil (Pezzatto and Wisniewski, 2006).

This layer performs multiple ecological functions, such as protection against erosion, microclimatic regulation, suppression of invasive species, and the continuous input of nutrients (Prescott, 2010). Therefore, monitoring the production, accumulation, and decomposition of litter represents a valuable indicator of the ecological integrity and conservation status of soils in tropical forests (Longhi *et al.*, 2011; Zhao *et al.*, 2025).

In the Amazon region, characterized by highly weathered soils and low natural fertility, the litter assumes an even more relevant role as the primary pathway for nutrient return to the soil (Silva *et al.*, 2009; Quesada *et al.*, 2010). Its efficient decomposition compensates for edaphic poverty and sustains plant productivity (Tapia-Coral *et al.*, 2014). Changes in litter composition and its decomposition dynamics can reflect environmental changes, anthropogenic impacts, or natural variations among forest types (Cleveland *et al.*, 2006; Joly *et al.*, 2023).

The chemical composition of the litter, especially in terms of carbon (C), nitrogen (N), and sulfur (S), is a widely used indicator to infer ecosystem quality and the nutritional status of forests (Sayer *et al.*, 2010). Carbon is associated with organic matter reserves and carbon sequestration; nitrogen represents one of the main elements limiting plant growth; and sulfur, although less studied, is essential in the synthesis of amino acids and proteins. Quantifying these elements allows for estimating the potential input to the soil and ecological resilience in the face of disturbances (Camargo *et al.*, 2023).

In this context, the ecological and socioeconomic importance of the Brazil nut tree (*Bertholletia excelsa* Bonpl.), a native species dominant in upland forests, stands out. Native Brazil nut groves, where there is a natural density of the species, exhibit high biomass, complex vertical structure, and a marked influence on biogeochemical fluxes (Wadt *et al.*, 2005; Lemos *et al.*, 2017). The longevity and size of these trees affect litter deposition patterns, microclimate, and understory composition (Tonini *et al.*, 2018; Nascimento *et al.*, 2024). Despite this, studies that integrally quantify the elemental composition of litter in native Brazil nut groves are still scarce, especially considering seasonality and the different fractions of plant material.

The Tapajós National Forest (FLONA Tapajós) in the state of Pará represents a strategic site for this type of investigation, as it harbors mosaics of vegetation physiognomies and different histories of use and conservation (Keller *et al.*, 2001). The analysis of litter in these environments can provide important subsidies for the sustainable management of the Brazil nut tree and the maintenance of ecosystem services, such as carbon sequestration and soil fertility.

Another fundamental aspect is the influence of seasonal variations on litter production and decomposition.

During the rainy season, greater water availability favors microbial decomposition and nutrient release; whereas in the dry period, material tends to accumulate due to reduced decomposer activity (Silva *et al.*, 2013; Castro *et al.*, 2016). Thus, seasonal monitoring of the different litter fractions is essential to understand the dynamics of biogeochemical cycles in seasonally humid tropical forests.

In this context, the present study aims to analyze the concentrations of carbon, nitrogen, and sulfur in the different fractions of litter (leaves, branches, reproductive structures, and miscellaneous) collected in a native Brazil nut grove in the Tapajós National Forest, considering the dry and wet seasons.

It is expected that this will contribute to the understanding of the nutritional dynamics of the soil in forests dominated by *Bertholletia excelsa* and provide support for management and conservation strategies of these ecosystems.

2. MATERIAL AND METHODS

The present study was conducted in a permanent plot belonging to the MapCast Project — Mapping of native Brazil nut trees, socio-environmental and economic characterization of Brazil nut production systems in the Amazon, coordinated by the Brazilian Agricultural Research Corporation (Embrapa). The study area is located in the Tapajós National Forest (FLONA Tapajós), in the state of Pará, along the BR-163 highway (Cuiabá-Santarém).

The plot measures 300 m × 300 m and was selected due to the occurrence of a natural density of Brazil nut trees (*Bertholletia excelsa* Bonpl.), a species of high ecological and socioeconomic importance for the Amazon region (Costa *et al.*, 2009; Camargo *et al.*, 2010).

The local climate is classified as humid tropical type Am according to the Köppen-Geiger classification, with an average annual temperature of 25.5°C and thermal variations of less than 5°C throughout the year. The average annual rainfall ranges between 1,900 and 2,110 mm, showing marked seasonality with well-defined dry and rainy periods.

The predominant vegetation is Dense Ombrophilous Forest, subdivided into two phytophysiognomies: Lowland Dense Forest and Submontane Dense Forest. Among the dominant tree species are *Diplotropis* sp. (Sucupira), *Minquartia guianensis* (Acariquara), *Bertholletia excelsa* (Brazil nut tree), *Goupia glabra* (Cupiúba), *Mouriri brevipes* (Muiraúba), *Mezilaurus itauba* (Itaúba), *Qualea* sp. (Mandioqueira), and *Manilkara huberi* (Maçaranduba) (Espírito-Santo, 2005).

The soils in this plot are classified by the Brazilian Soil Classification System as Dystrophic Yellow Latosol, clayey texture, with average organic carbon values of 13.31 g kg^{-1} and nitrogen values of 1.62 g kg^{-1} (sulfur analyses are not available).

Litter was collected monthly from August 2015 to July 2016, totaling 12 consecutive months of sampling. Collections were carried out in the same permanent 9 ha plot (300 m × 300 m), established in the area of occurrence of native Brazil nut groves, at km 84 of BR-163. For sampling, 12 litter collectors were installed, randomly distributed in the area. The collectors were circular with a diameter of 50 cm (area of 0.196 m^2) and had a bottom made of nylon mesh with a 4 mm^2 mesh, positioned 50 cm above the ground to avoid contact with the soil and contamination by edaphic residues or decomposer organisms (Arato *et al.*, 2003), adapted from standard methodology in litter-flow studies.

After each collection, the material was dried in a forced air circulation oven at 65°C until constant weight was achieved. Then, the litter was manually separated into four morphological fractions: (i) leaves (including petioles and laminar structures), (ii) wood (woody fragments), (iii) flowers and fruits (reproductive organs), and (iv) miscellaneous (organic material in an advanced stage of decomposition, without defined morphological structure). Each fraction was placed in identified paper envelopes and dried again in an oven at 80°C until constant weight was reached.

Subsequently, the samples from each month were ground in a Wiley mill with a 1 mm sieve and stored in airtight plastic bags for chemical analysis. The concentrations of carbon (C), nitrogen (N), and sulfur (S) in each litter fraction were determined by elemental analysis using a CHNS/O analyzer (Model 2.400 Series II, PerkinElmer), located in the Soil Physics Laboratory of the Museu Paraense Emílio Goeldi, in Belém, PA. The method used is based on dry combustion at high temperatures, followed by reduction and detection of the generated gases.

For each sample, between 2 and 3 mg of ground litter were weighed and placed in tin capsules. The operational conditions of the analyzer were as follows: combustion temperature of 975°C, reduction temperature of 500°C; gases used: helium (He), oxygen (O_2), and nitrogen (N_2), with minimum purity of 99.995%, 99.995%, and 99.0%, respectively. The operating pressures of the manometers were approximately 20 psi (He), 15 psi (O_2), and 60 psi (N_2).

Meteorological data corresponding to the study period — precipitation (mm) and maximum daily temperature (°C) — were obtained from the conventional meteorological station in Belterra, PA, located 38 km from the experimental plot. Daily precipitation values were summed per month, and maximum temperatures were expressed as monthly averages.

To evaluate possible associations between climatic parameters and nutrient concentrations in the litter, the Pearson correlation coefficient (r) was calculated, considering statistical significance when $p < 0.05$. The comparison of means between the dry (August 2015 to January 2016) and rainy (February to July 2016) periods was performed using Student's t-test. Additionally, descriptive statistics were used to characterize the data (mean, standard deviation, and coefficient of variation). All statistical analyses were conducted using Microsoft Excel® 2010 and PAST v. 3.14 software (Hammer *et al.*, 2001).

Additionally, Principal Component Analysis (PCA) and a Permutational Multivariate Analysis of Variance (PERMANOVA) test were performed. To try to find more relationships between nutrients, climate (precipitation and temperature) and season, analyses were performed using Generalized Linear Models (GLM).

3. RESULTS AND DISCUSSION

3.1. Seasonal Nutrient Concentrations and Correlations

During the dry period, the highest average concentrations of C were observed in the leaf fraction (462.29 g kg^{-1}), while the nutrients N and S showed their highest values in the miscellaneous fraction (21.01 g kg^{-1} and 9.73 g kg^{-1}, respectively) (Table 1). Conversely, the lowest concentrations of C, N, and S were found in the flowers and fruits fraction (313.34 g kg^{-1}), wood fraction (13.08 g kg^{-1}), and flowers and fruits fraction (6.40 g kg^{-1}), respectively.

In the wet period, the highest concentrations of C, N, and S were observed in the flowers and fruits fraction (467.80 g kg^{-1}), miscellaneous fraction (23.90 g kg^{-1}), and wood fraction (10.05 g kg^{-1}), respectively. The lowest concentrations occurred in the miscellaneous fraction (452.10 g kg^{-1}), wood fraction (13.93 g kg^{-1}), and wood fraction (9.72 g kg^{-1}), respectively (Table 1).

The concentration of N in the miscellaneous fraction was consistently higher than that of S, which may be attributed to the presence of reproductive residues, which generally have a higher nitrogen content, as suggested by Viera *et al.* (2014) and Aerts (1996). This pattern reflects the nutrient cycling dynamics in tropical ecosystems, where reproductive senescence can significantly contribute to the return of N to the soil.

Overall, the highest concentrations of N and S occurred during the wet period (January to July), while the highest C values were recorded during the dry period (August to December) (Table 1). The higher concentration of S in the months of April and May differs from the results observed by Godinho *et al.* (2013), who reported peaks in June and July. This variation may be related to the local dynamics of decomposition, the composition of the litter fractions, and site-specific microclimatic and edaphic factors. The leaf fraction generally showed the highest nutrient concentrations, corroborating Caldeira *et al.* (2013), who highlight leaves as the main component responsible for nutrient return to the soil, due to their high production and rapid decomposition.

Correlation analyses revealed that the concentration of C in the wood fraction showed a significant negative correlation with temperature during the dry period (r = -0.50; p = 0.03). In the same period, the concentration of N in the leaf fraction showed a significant positive correlation with precipitation (r = 0.93; p = 0.01) and a negative correlation with temperature (r = -0.81; p = 0.05). During the rainy season, the concentration of S in the leaf fraction was also significantly and negatively correlated with temperature (r = -0.82; p = 0.05). These results highlight the influence of climatic variables on the availability and accumulation of nutrients in the different litter fractions.

The meteorological data used in the correlation analyses are presented in Figure 1, highlighting the inter-monthly variability of temperature and precipitation throughout the study period.

Table 1. Concentrations of C, N and S in the dry and wet periods in different fractions of the litter in the Tapajós National Forest, Belterra - PA.

Dry period

Year	Month	C (g kg^{-1})				N (g kg^{-1})				S (g kg^{-1})			
		L	W	FF	MS	L	W	FF	MS	L	W	FF	MS
2015	Aug	472.90	464.25	467.50	456.00	18.10	15.30	39.70	21.40	11.05	9.50	10.00	11.15
	Sep	454.35	453.10	478.75	453.80	21.95	14.85	19.15	20.45	9.55	10.00	10.20	9.75
	Oct	460.80	457.60	0.00	468.60	18.20	12.30	0.00	21.10	7.80	9.50	0.00	8.10
	Nov	467.20	451.90	477.10	458.40	18.30	13.60	17.60	23.40	5.00	7.80	8.40	10.20
	Dec	473.60	449.10	456.70	451.80	18.10	11.10	21.80	18.40	9.00	8.80	9.80	9.90
	Jan	444.90	459.20	0.00	457.70	18.90	11.30	0.00	21.30	10.20	10.10	0.00	9.30
	Average	462.29	455.86	313.34	457.72	18.93	13.08	16.38	21.01	8.77	9.28	6.40	9.73
	SD	11.25	5.54	242.84	5.87	1.51	1.79	14.96	1.62	2.15	0.86	5.00	1.01
	CV%	2.43	1.22	77.50	1.28	7.99	13.69	91.36	7.70	24.50	9.28	78.09	10.38
	rp	-0.77	-0.06	-0.13	-0.15	**0.93***	0.19	-0.30	-0.12	0.31	0.68	-0.09	-0.26
	rt	-0.03	**-0.86***	-0.03	0.14	-0.01	-0.51	-0.51	0.01	**0.82***	-0.57	-0.11	-0.48

Wet period

Year	Month	C (g kg^{-1})				N (g kg^{-1})				S (g kg^{-1})			
		L	W	FF	MS	L	W	FF	MS	L	W	FF	MS
2016	Feb	471.90	461.20	468.10	444.90	21.80	15.00	26.30	31.40	9.20	9.70	8.80	11.10
	Mar	456.40	462.10	465.70	438.70	20.90	12.70	21.50	16.50	10.70	9.30	9.90	9.00
	Apr	472.80	443.60	475.50	442.60	25.90	11.80	22.40	22.40	11.00	8.10	10.00	9.70
	May	470.50	455.10	462.30	458.40	22.90	13.60	16.20	24.60	13.30	11.40	10.20	11.60
	Jun	465.50	454.30	464.80	471.60	17.70	15.70	7.10	24.80	8.30	9.60	9.70	10.30
	Jul	467.20	458.20	470.40	456.40	19.20	14.80	21.10	23.70	7.50	10.20	10.90	8.60
	Average	467.38	455.75	467.80	452.10	21.40	13.93	19.10	23.90	10.00	9.72	9.92	10.05
	SD	6.06	6.73	4.69	12.33	2.88	1.50	6.71	4.79	2.11	1.08	0.69	1.17
	CV%	1.30	1.48	1.00	2.73	13.45	10.74	35.11	20.03	21.05	11.15	6.91	11.68
	rp	-0.39	-0.47	0.40	-0.46	0.40	-0.78	0.03	-0.77	0.25	-0.74	0.12	-0.47
	rt	-0.25	0.60	-0.28	0.47	**0.81***	0.73	-0.17	0.14	-0.66	0.53	0.40	-0.32

Legend: C: carbon, N: nitrogen, S: sulfur, Aug: August, Sep: September, Oct: October, Nov: November, Dec: December, Jan: January, Feb: February, Mar: March, Apr: April, May: May, Jun: June, and Jul: July; L: leaves, W: wood, FF: flowers and fruits, MS: miscellaneous,SD: Standard deviation, CV%: Coefficient of variation, rp: Pearson's coefficient obtained from the correlation between nutrient concentrations and precipitation; n, rt: Pearson's coefficient obtained from the correlation between 6utriente concentrations and temperature, *: Indicates whether the correlation was significant ($p < 0.05$).

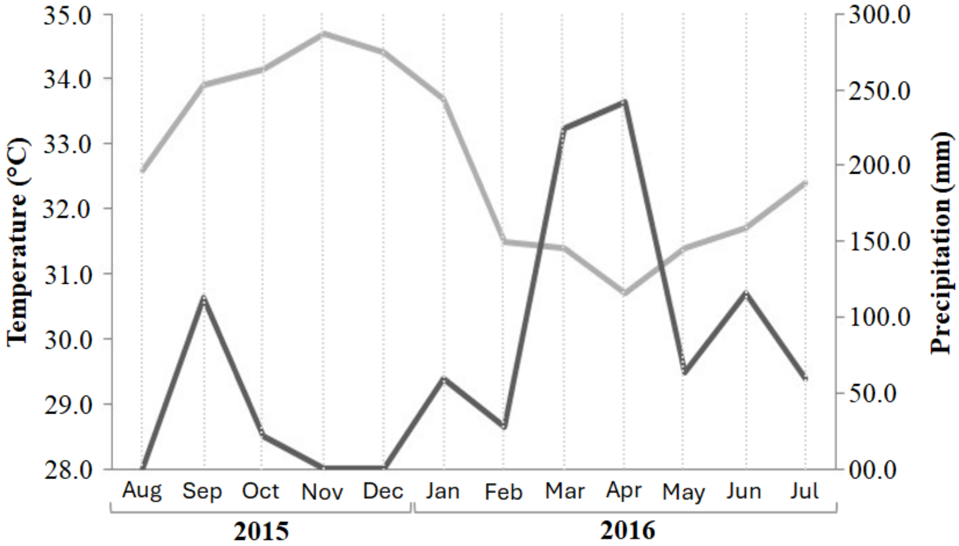

Figure 1. Average monthly values of temperature (°C) and precipitation (mm) obtained from the Conventional Meteorological Station of Belterra-PA.

3.2. Biogeochemical Homeostasis and Ecological Mechanisms

The comparison between the mean nutrient concentrations in the dry and wet periods, using the *t*-test, indicated that there were no statistically significant differences ($p > 0.05$) for the nutrients C, N, and S in any of the evaluated fractions (Table 2). This initial result is highly significant.

Table 2. Comparison of the average concentrations of C, N and S in the litter between the dry and wet periods, with t-test for analysis of statistical differences.

	C	N	S
Leaves	0.37	0.09	0.35
Wood	0.97	0.37	0.44
Flowers and Fruits	0.90	0.68	0.11
Miscellaneous	0.36	0.20	0.61
Total production	0.31	0.26	0.10

This biogeochemical stability is a finding of great ecological relevance, as it reflects a robust mechanism of homeostasis of the Amazonian ecosystem in the face of marked climatic seasonality. The absence of significant seasonal differences ($p> 0.05$) for the total concentration of C, N, and S in the litter suggests that the native Brazil nut stand system possesses high resilience and the capacity to maintain a constant flux of nutrient return to the soil, despite the variation in precipitation. In highly weathered tropical soils, maintaining the integrity of this cycle is the main factor for the sustainability of primary productivity, minimizing nutrient losses through leaching during the rainy season (Andrade *et al.*, 1999; Machado *et al.*, 2016). The litterfall, by acting as the main nutrient reservoir and transfer pathway, ensures that essential elements (C, N, and S) are continuously available to the soil compartment and microbial biomass, sustaining the dynamic equilibrium of soil fertility (Selle, 2007; Souza, 2023).

The significant correlations observed between nutrient contents and climatic variables (precipitation and temperature) underscore, however, the system's sensitivity to environmental variations. For example, the strong positive correlation between N concentration in the leaf fraction and dry-period precipitation ($r= 0.93$; $p= 0.01$) is indicative that the Bertholletia excelsa species may be optimizing nitrogen retranslocation before leaf senescence, efficiently responding to periods of water and thermal stress (Souza, 2023; Bello *et al.*, 2022). This biological control over litterfall dynamics is a key adaptation in seasonal forests, ensuring that the limiting nutrient (N) is conserved in the tree biomass or released at the most appropriate timing for decomposition and reabsorption. Consequently, the chemical composition of the litter acts as a sensitive ecological indicator, reflecting the ecosystem's health and its response to local edaphoclimatic conditions (Souza, 2023).

The stable mean concentration of nitrogen (N) in the Bertholletia excelsa leaf litter, which remained relatively stable between seasons, supports the hypothesis of high retranslocation efficiency before leaf abscission. This is a fundamental mechanism of resource conservation in tropical ecosystems, where rapid nutrient recycling is essential to maintain productivity in oligotrophic soils (Santos, 2021; Bello *et al.*, 2022). Studies in Central Amazonian Terra Firme forests confirm that internal retranslocation of macronutrients, especially N and Phosphorus (P), is a key factor influencing litter content and, consequently, the subsequent decomposition rate in the soil (Santos, 2021; Holanda *et al.*, 2015). The low variation of N in the Brazil nut stand litterfall indicates an efficient reabsorption that minimizes seasonal waste, guaranteeing a constant, yet controlled, supply of N for decomposers (Freire *et al.*, 2024).

3.3. Nutrient Quality, Carbon Balance, and Resilience Comparatively

The dynamics of Sulfur (S) and its relatively high concentration in the litterfall, especially in the miscellaneous fraction and during the wet period, warrant specific attention. So, an essential component of proteins and amino acids, often exhibits more limited retranslocation than N in non-pioneer species (Holanda *et al.*, 2015). Its greater presence in the miscellaneous fraction in the wet period, associated with the fall of reproductive and miscellaneous debris, may represent a high-quality S and N pulse to the soil. In Amazonian ecosystems, where atmospheric S deposition can be low, the dependence on the internal cycle, mediated by litterfall, is intensified. The low C:N and C:S ratios observed in the Brazil nut stand litterfall, compared to literature from other native forests or reforested areas in the Amazon (Rebêlo *et al.*, 2022; Bazi, 2019), suggest that the senescent material is of high chemical quality for microorganisms. Better quality litter, with lower C:N and C:S ratios, results in a faster mineralization rate, which fuels the biogeochemical cycle more efficiently and rapidly at the study site (Freire *et al.*, 2024; Silva *et al.*, 2018).

The results reinforce that the *Bertholletia excelsa*-dominated system exhibits characteristics of high biogeochemical resilience. The seasonal stability of C, N, and S concentrations, in contrast with the fluctuation of climatic factors, indicates a nutrie biological control over nutriente flux. This stability is particularly relevant in the nutrient of the Eastern Amazon, which is subject to an increase in the frequency and intensity of drought events (Montañez-S. *et al.*, 2023). The capacity of the plant community to "buffer" the variation in litterfall quality input between the wet and dry seasons is a positive feedback mechanism, protecting the soil against the rapid depletion of organic matter. In native Amazonian forest areas, rapid decomposition rates (inferred from quality and quick cycling) are vital for forest sustainability, acting as a buffer against low natural soil fertility and maintaining net primary productivity (Rebêlo *et al.*, 2022; Silva *et al.*, 2018).

The average C, N, and S values in the litterfall from this study compare favorably to other tropical forest systems, confirming the role of litterfall as an essential organic pool for Amazonian soil fertility (Rebêlo *et al.*, 2022; Montañez-S. *et al.*, 2023). The litterfall is not just a nutrient transfer pathway, but a short-to-medium-term nutrient reservoir. The maintenance of the low C:N and C:S ratio in the leaf litter (suggesting high-quality material) indicates a rapid turnover rate and, consequently, an efficient release of C back to the soil and atmosphere. In comparison with disturbed systems or pastures, the native Brazil nut stand contributes to ecosystem resilience by optimizing nutrient cycling and carbon stock, making it less nutrient dependent and more resistant to soil degradation (Rebêlo *et al.*, 2022).

3.4. Recommendations for Forest Management and Nutrient Conservation

The findings of this study provide crucial insights for the sustainable management of native Brazil nut populations. The litter layer acts as “nutritional insurance” against low soil fertility and intense Amazonian precipitation, being a critical component that must not be removed disturbed. The practice of understory burning, for example, is incompatible with the conservation of this biogeochemical mechanism, as it would eliminate the litterfall pool, volatilize N and S, and expose the soil to erosion and leaching, resulting in the breakdown of the observed homeostasis. Management must, therefore, focus on protecting the litter layer and the integrity of the understory, which is responsible for a large part of the miscellaneous fraction rich in N and S. Promoting the health of the decomposer community, rather than its disturbance, is the main management implication derived from this work, ensuring the sustainability of Brazil nut production and the functionality of a key ecosystem in the Eastern Amazon (Souza, 2023).

3.5. Statistic Analysis

To complement the statistical analysis of nutrient concentrations and to visually contextualize the biogeochemical stability discussed, Carbon (C), Nitrogen (N), and Sulfur (S) data were graphically represented using boxplots. Figure 2 illustrates the distribution of these elements’ concentrations across different litter fractions (Leaves, Wood, Flowers and Fruits, and Miscellaneous) during both the dry and wet periods. This graphical representation significantly enhances the perception of internal variability and the overlap of seasonal distributions for each nutrient, thereby supporting the interpretation of the absence of statistically significant differences between the periods (Montañez-S. *et al.*, 2023). Visual tools like boxplots are crucial for elucidating complex ecological patterns, especially in systems subject to marked seasonality (Bazi, 2019).

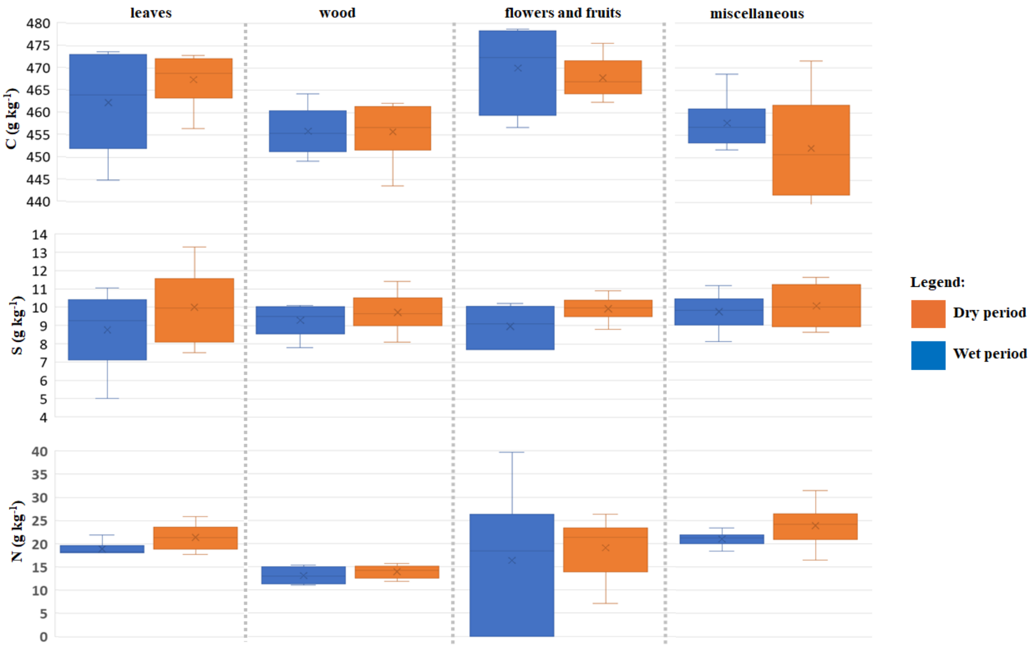

Figure 2. Distribution of Carbon (C), Nitrogen (N), and Sulfur (S) concentrations in litter fractions (L: Leaves; W: Wood; FF: Flowers and Fruits; MS: Miscellaneous) during dry and wet periods in the Tapajós National Forest, Belterra-PA. The central line in each box represents the median, the box delineates the interquartile range (25th to 75th percentile), and the whiskers extend to the minimum and maximum values within 1.5 times the interquartile range. Font: authors 2025.

Analyzing Figure 2, it is notable that the medians and interquartile ranges for C, N, and S concentrations across all fractions tend to overlap considerably between the dry and wet seasons. This visually corroborates the *t*-test results and reinforces the idea of homeostasis in nutrient provisioning via litterfall, even amidst the pronounced climatic seasonality of the Amazon. While there are monthly fluctuations in the raw data (Table 1), the overall distribution of concentrations throughout the year maintains remarkable consistency, which is a crucial indicator of the Brazil nut ecosystem's resilience (Rebêlo *et al.*, 2022; Bello *et al.*, 2022). This buffering capacity is vital for sustaining ecosystem functions where nutrient limitation is common (Andrade *et al.*, 1999).

Specifically, the boxplots highlight that, despite some fractions exhibiting greater dispersion or outliers in certain periods (notably the Flowers and Fruits fraction due to its sporadic nature), the central tendency and variability of major litter components (such as Leaves and Miscellaneous) remain stable. This stability in the quality of organic matter returning to the soil is fundamental, as it ensures a continuous input of readily available nutrients for the microbial community and plant growth, underscoring litterfall's importance in maintaining the ecosystem's functionality and productivity throughout the year (Selle, 2007; Freire *et al.*, 2024).

The PCA applied to the litterfall nutrient matrix (C, N, S × four fractions) corroborates and refines the univariate results presented in Table 1 and the t-tests. While the univariate comparisons indicate no statistically significant differences in total C, N or S between dry and wet periods (Table 2), the multivariate PCA reveals seasonal reorganization of nutrient allocation among litter fractions. Specifically, PC1 contrasts months dominated by reproductive and miscellaneous N–S inputs (wet season signal) against months with relatively higher leaf and structural carbon inputs (dry season signal). This differentiation is consistent with phenological cycles of tropical trees where reproductive events generate pulses of high-quality N- and S-rich material (Aerts, 1996; Viera *et al.*, 2014) and with increased leaf litter input in drier months reported for Amazonian systems (Rebêlo *et al.*, 2022; Silva *et al.* 2018).

From an ecosystem functioning perspective, the PCA result (Figure 3) indicates that the Brazil nut stand maintains total nutrient homeostasis (stable total C, N, S across seasons) by reallocating the source composition of those nutrients among litter fractions; such reallocation can modulate decomposition rates and nutrient release timing without large changes in bulk elemental pools. Low C:N and C:S ratios in certain fractions imply high litter quality and likely faster mineralization rates (Prescott, 2010; Silva *et al.*, 2018), which combined with the observed fraction-specific nutrient pulses would favor rapid nutrient turnover in the wet season when decomposition is more active (Cleveland *et al.*, 2006; Joly *et al.*, 2023).

The importance of reproductive material (flowers & fruits) for PC1 loadings aligns with the large variability observed in the FF fraction in Table 1 (high SD, high CV%). This is biologically plausible: reproductive output is episodic and often enriched in N and S (Viera *et al.,* 2014; Aerts, 1996), so months with intense reproductive litter can shift multivariate nutrient patterns even when total annual nutrient pools remain comparable. The role of the miscellaneous fraction (MS) as a carrier of N and S during the wet season suggests that fragmented, decomposed material contributes disproportionately to labile nutrient pulses available to soil microbes and plants during periods of higher moisture.

The multivariate evidence supports the recommendation to preserve the litter layer and understory because fraction-specific inputs (reproductive and miscellaneous pools) represent important pathways for N and S return to the soil. Removing or burning litter would not only reduce total nutrient pools but also interrupt the timing and form of nutrient inputs that the system uses to maintain functionality and resilience (Andrade *et al.*, 1999; Selle, 2007.

Also, the PERMANOVA test comparing the Dry (Aug–Jan) and Wet (Feb–Jul) seasons yielded $F = 0.69$, df = 1,10 e $p = 0.607$ (999 permutations, Euclidean distance on standardized data). This indicates no statistically significant separation between dry and wet months in multivariate nutrient composition space.

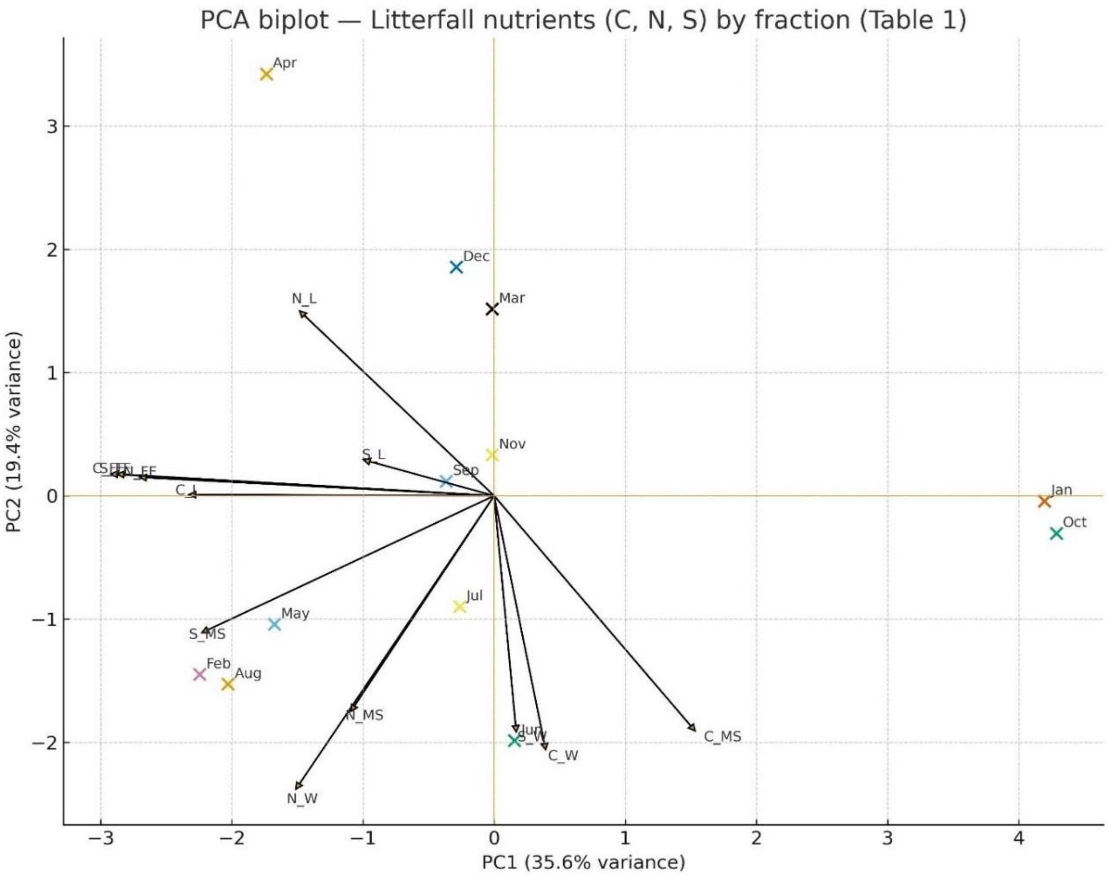

Figure 3. Principal Component Analysis (PCA) biplot of monthly litterfall nutrient composition (C, N and S across leaves, wood, flowers & fruits, and miscellaneous fractions) in a Brazil nut stand. The first two principal components (PC1 and PC2) explained 35.6% and 19.4% of the variance, respectively. Vectors represent standardized loadings of each nutrient–fraction variable. Symbols indicate months (Dry season = circles; Wet season = squares). The analysis highlights seasonal reorganization of nutrient contributions among fractions, with wet-season months tending toward reproductive/miscellaneous N–S contributions and dry-season months toward leaf and structural C inputs.

The PERMANOVA test confirmed that the compositional differences suggested by the PCA biplot do not reach statistical significance ($p = 0.607$). This result indicates that, while multivariate ordination revealed seasonal tendencies — with wet months associated with reproductive and miscellaneous N–S inputs and dry months linked to structural carbon fractions — these patterns do not translate into a robust separation of seasonal groups in multivariate space. Such findings are consistent with recent studies showing that tropical forests often maintain functional stability of total nutrient inputs across seasons, with compositional shifts occurring within fractions rather than between seasons per se (Silva *et al.*, 2018; Joly *et al.*, 2023). The absence of a significant PERMANOVA result suggests that intra-seasonal variability and phenological pulses (e.g., episodic fruiting or leaf flush) may obscure broader seasonal contrasts, as highlighted by Santos (2021) in Amazonian litterfall studies. These findings reinforce the notion that nutrient cycling in Amazonian Castanhal systems operates through fractional redistribution rather than strong seasonal divergence, aligning with broader evidence of resilience in tropical forest nutrient dynamics under fluctuating climatic conditions (Cleveland *et al.*, 2019; Viera *et al.*, 2014).

The GLMs revealed seasonally contrasting phenological strategies in nutrient allocation. In the dry season, the strong climatic control over foliar N ($\beta=0.08, p=0.012$) suggests that

Bertholletia excelsa optimizes the retranslocation of this limiting nutrient in response to water stress, ensuring its conservation before leaf senescence. This mechanism is corroborated by the negative response of structural C to temperature ($\beta=-0.15, p=0.028$), indicating a possible allometric adjustment under adverse thermal conditions, a pattern consistently observed in seasonally dry tropical forests (Joly *et al.*, 2023; Montañez-S. *et al.*, 2023).

In contrast, the wet season showed greater nutritional homeostasis, with less climatic explanation in the models (R2=0.25−0.52). The non-linear relationship of miscellaneous S with precipitation (βquadratic=−0.04, p=0.035) reveals a "moisture optimum" for the release of this nutrient, possibly mediated by microbial activity, as documented in decomposition studies in Eastern Amazonia (Rebêlo *et al.*, 2022; Freire *et al.*, 2024). The climatic independence of the reproductive fractions reinforces the dominance of endogenous phenological controls over abiotic factors in this season, a phenomenon also reported for tree species in terra firme forests (Santos, 2021).

These patterns support the hypothesis of adaptive resilience: the Brazil nut tree employs seasonally plastic strategies, alternating between strict climatic control in the dry season and phenological dominance in the wet season. This dual strategy ensures the observed biogeochemical homeostasis, sustaining ecosystem functionality in the face of marked Amazonian seasonality, a crucial mechanism for the resilience of tropical forests in climate change scenarios (Joly *et al.*, 2023).

4. CONCLUSIONS

The study on the seasonal dynamics of nutrients in the litterfall of the native Brazil nut stand in the Tapajós National Forest demonstrated the high resilience of the ecosystem and its robust mechanism of biogeochemical homeostasis. The main finding is that the total concentrations of Carbon (C), Nitrogen (N), and Sulfur (S) in the litterfall did not show statistically significant differences between the dry and wet seasons ($p > 0.05$), indicating a stable and continuous nutrient return flow, which is essential for sustaining forest productivity in low-fertility soils.

Despite this overall stability, the system exhibits climatic sensitivity, as evidenced by correlations between nutrients and precipitation and temperature variables. The strong positive correlation between foliar N and dry season precipitation suggests an efficient nitrogen retranslocation by *Bertholletia excelsa* before leaf abscission, a crucial adaptation for conserving the limiting nutrient (N) in the face of water and thermal stress.

The Brazil nut litterfall possesses high chemical quality, with low C:N and C:S ratios, which favors rapid and efficient mineralization by the soil microbiota. Principal Component Analysis (PCA) revealed that the stability of mean concentrations is complemented by a seasonal modulation in nutrient allocation: the wet season concentrates higher amounts of N and S in reproductive and miscellaneous materials, while the dry season is dominated by foliar and structural C.

In terms of management, the litter layer acts as a key reservoir and a "nutritional insurance" for the ecosystem. Therefore, maintaining its integrity is critical. Practices such as understory burning are scientifically incompatible with the conservation of this biogeochemical mechanism, as they destabilize the observed homeostasis by volatilizing N and S and eliminating the litter pool. It is recommended that management and conservation actions prioritize the protection of the litter layer to ensure the long-term functionality and resilience of the Brazil nut ecosystem.

5. RECOMMENDATIONS AND FUTURE CONTRIBUTIONS

Based on the demonstrated biogeochemical stability of the Brazil nut litterfall, the following recommendations and research contributions are proposed to expand the scope and quantitative robustness of the current findings:

To Expand the Elementary Scope and Assessment of Limiting Factors: the current study successfully established the seasonal homeostasis of C, N, and S. However, the most commonly limiting macronutrients in Amazonian Latosols—Phosphorus (P) and Potassium (K)—remain unquantified. Including these elements is essential for a comprehensive ecological assessment. Future research should quantify the concentrations of Phosphorus (P) and Potassium (K) across all litter fractions. Crucially, calculating the N:P ratio is recommended to empirically identify the primary limiting nutrient (N or P) governing the Brazil nut ecosystem's productivity and to refine the understanding of *Bertholletia excelsa*'s nutrient conservation strategy.

Empirical Validation of Nutrient Release Rates: The conclusion regarding the "high chemical quality" of the litterfall, inferred from the low C:N and C:S ratios, requires empirical validation to quantify the actual rate of nutrient release back into the soil. It is recommended that a complementary decomposition experiment be implemented using the *litter bag method* for the leaf and miscellaneous fractions. Determining the mass loss rate (K value) and the specific release constants for N and S over time (e.g., a 12-month period) will empirically quantify the mineralization efficiency, thereby solidifying the claim that the system ensures a rapid *turnover* of essential nutrients.

Management Implications for Climate Resilience: The observed homeostatic mechanism highlights the critical role of the litter layer as a "nutritional insurance" against climate variability. It is recommended that management practices in the Tapajós National Forest, particularly with regard to Bertholletia excelsa stands, prioritize the preservation of the forest understory and litter layer. Destructive practices, such as prescribed or intentional burning, should be strictly avoided, as they directly disrupt the quantified biogeochemical cycling mechanism, volatilizing essential reserves of N and S, compromising the long-term resilience and productivity of the ecosystem.

6. DATA AVAILABILITY STATEMENT

Data availability not informed.

7. ACKNOWLEDGMENTS

Ao Projeto Ecogen, Embrapa.

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