



Assessing the of carbon and nitrogen storage potential in *Khaya* spp. stands in Southeastern Brazil

Gabriel Soares Lopes Gomes¹ · Marcos Vinicius Winckler Caldeira¹ · Robert Gomes¹ · Victor Braga Rodrigues Duarte¹ · Dione Richer Momolli¹ · Tiago de Oliveira Godinho² · Sarah Ola Moreira³ · Paulo André Trazzi⁴ · Laio Silva Sobrinho⁵ · Angélica de Cássia Oliveira Carneiro⁶ · Mauro Valdir Schumacher⁷

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Abstract

The objective of this study was to assess the dynamics of carbon and nitrogen in soil, forest floor, and aboveground biomass in 9.5 years-old planted stands of three *Khaya* spp. (*K. grandifoliola*, *K. ivorensis*, and *K. senegalensis*). The study was conducted at the Reserva Natural Vale (RNV), Brazil. The stands were planted at 5 × 5 m spacing, distributed over rectangular plots of 1250 m². Soil bulk density at the evaluated depths, as well nitrogen contents, were similar among the species. However, *K. ivorensis* exhibited higher carbon concentration in the soil. In general, there were no differences in carbon and nitrogen content in soil between the three species; however, the values obtained are comparable to those of the reference area—Native Forest. The carbon stocks in the aboveground biomass for *K. grandifoliola*, *K. ivorensis*, and *K. senegalensis* averaged 37.97, 33.66 and 33.86 Mg ha⁻¹, respectively ($p \leq 0.05$). These values collectively represent about 28% of the total carbon stocks across the observed compartments. Notably, the nitrogen content within the aboveground biomass did not differ among these species. Therefore, African mahogany possesses a robust potential to store both carbon and nitrogen.

Keywords Soil fertility · Biogeochemical cycling · African mahogany · Land use and land cover · Litter · Aboveground biomass

✉ Gabriel Soares Lopes Gomes
gsoares.flo@gmail.com

¹ Universidade Federal do Espírito Santo, Jerônimo Monteiro, Espírito Santo, Brazil

² Vale S/A, Linhares, Espírito Santo, Brazil

³ Assistência Técnica e Extensão Rural, Instituto Capixaba de Pesquisa, Linhares, Espírito Santo, Brazil

⁴ Universidade Federal do Acre, Rio Branco, Acre, Brazil

⁵ Olds College of Agriculture & Technology, Olds, Alberta, Canada

⁶ Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil

⁷ Universidade Federal de Santa Maria, Santa Maria, Rio Grande do Sul, Brazil

Introduction

Agricultural activities occupy approximately 41% of Brazil's territory, encompassing around 351 million hectares (IBGE 2019). In contrast, concerns over rising deforestation rates, the opening of new areas, and increased in greenhouse gas (GHG) emissions are frequently debated topics concerning the sustainability of these ventures. Notably, these impacts often arise from inadequate agricultural and livestock management practices, such as shorter crop rotation cycles, excessive use of agricultural machinery, and degraded pastures (Soares et al. 2020; Sekaran et al. 2021).

Land-use change is among the primary drivers contributing to GHG emissions and the degradation of cultivated areas, as it alters nutrient cycling and the physicochemical properties of the soil (Thomaz et al. 2020; Haguénin and Meirelles 2022). Soil is regarded as the largest reservoir for carbon storage and other essential nutrients, such as nitrogen (Zhou et al. 2019; Thomaz et al. 2020). In forest ecosystems, the soil can be directly influenced by the physical and chemical characteristics of the constituent tree species. This interplay affects microbial activity, nutrient release, and the decomposition of woody material (Zheng et al. 2019; Chen et al. 2019; Romero et al. 2020).

Brazil has made voluntary commitments under the United Nations Framework Convention on Climate Change, aiming to expand areas of agroforestry systems as a strategy for sustainable production intensification (Brazil 2012). Furthermore, at the COP26 of the Climate Convention (2021), the country pledged to reduce emissions by 37% by 2025 and 43% by 2030, with aspirations of achieving carbon neutrality by 2050 (Wills et al. 2021; la Rovere et al. 2021). Within this context, forests play a crucial role in the global carbon cycle, such that the accumulation and preservation of forest carbon are imperative for limiting atmospheric emissions (Volkova et al. 2015).

Increasing the amount of organic carbon in the soil can improve its quality, serving as an indicator of sustainable land use practices and potentially helping to mitigate climate change (Wiesmeier et al. 2019). Understanding carbon and nitrogen balances and their fluxes within biomass compartments can assist in developing management techniques aimed at restoring degraded areas and increasing soil fertility (Chen and Chen 2019; Morais Júnior et al. 2020). Moreover, quantifying carbon content in planted species is essential to understand the potential of these forests to sequester this element. While the IPCC (2006) adopts generic metrics, citing conversion factors of 0.47 for biomass and 0.37 for litter, few species match these benchmarks, which may lead to biased estimates of carbon sequestration (Watzlawick et al. 2014).

Among the species gaining prominence is the African mahogany (*Khaya* genus). This species belongs to the Meliaceae family, popularly known as mahogany, encompassing around 600 species (Christenhusz and Byng 2016). Its selection is merited by economic return, adaptive traits, relative resistance to pests, and good productivity (Pierozan Junior et al. 2018; Ribeiro et al. 2018; Mukaila et al. 2021). In Brazil, plantations with the *Khaya* genus cover approximately 50,000 hectares and are distributed throughout Brazil's territory, with a predominant presence in the Southeast region of the country (Ferraz Filho et al. 2021).

Evaluating forest plantations for silvicultural responses and identifying species that contribute to carbon sequestration in the soil and plant-derived biomass to mitigate potential global warming effects are essential (Souza et al. 2023; Li et al. 2023). Therefore, the objective of this study was to assess the changes of carbon and nitrogen in the soil, in the forest floor, and in the aboveground biomass in stands of three species of *Khaya*. We

posited the following research questions: (1) Do *Khaya* spp. contribute with similar organic carbon and total nitrogen stock in the soil compared to native forests in the reference area? (2) Are there differences in the quantity and quality of forest floor among the species? (3) Are carbon and nitrogen storage in the aboveground biomass compartments consistent across the species?

Material and methods

Study area

The study area is located at the Reserva natural vale (RNV) in Sooretama, Espírito Santo state, Brazil. The regional climate is classified as Aw according to the Köppen classification, characterized by a wet summer and dry winter. The average air temperature is 23.5 °C, with an average annual precipitation of 1294 mm (Alvares et al. 2013). The region's topography is predominantly flat, with slopes ranging from 0 to 3%. The soil is identified as of the Acrisol type, featuring a moderate A horizon and a textural B horizon (FAO 2015).

Stand characteristics

The area occupied by the *Khaya* spp. stands was previously occupied by *Eucalyptus* spp. In the 1980s, there was a shift to monoculture leguminous species plantations, followed by a fallow period. The soil was prepared by harrowing and then fertilized in the hole with 200 g of simple superphosphate (Caldeira et al. 2020). The planting of *Khaya* spp. seedlings was conducted in 2013 using manually dug pits with dimensions of 30×30×30 cm. The base fertilization consisted of 150 g of yoorin thermophosphate and 15 g of FTE BR 12 per seedling. The containerized seedlings were seed-originated, sourced from different regions in Brazil, representing three species: *K. grandifoliola* (Belém, Pará state), *K. ivorensis* (Sooretama, Espírito Santos state) and *K. senegalensis* (Poranguatu, Goiás state). In the event of mortality, the seedlings were replanted within 30 days. Each species was established in three randomized blocks, set at an interspacing of 5×5 m apart and distributed in rectangular plots of 1,250 m². The effective study area within each plot was 750 m² (15×50 m) encircled by a simple border, resulting in 30 primary trees per replication (Fig. 1).

Reference area

The reference site consists of a native forest, also within the bounds of the RNV. This site is characterized as a permanently preserved area in an advanced stage of regeneration, situated approximately 1.04 km northwest of the *Khaya* spp. stands. Depending on the hydrological regime, it is classified as either seasonal semideciduous or evergreen, with a pronounced water deficit (Saiter et al. 2017). Historically, in the 1960s, the area underwent intensive selective logging followed by a period of fallow. For comparative purposes, an additional plot encompassing 43.7 ha was delineated within the RNV.

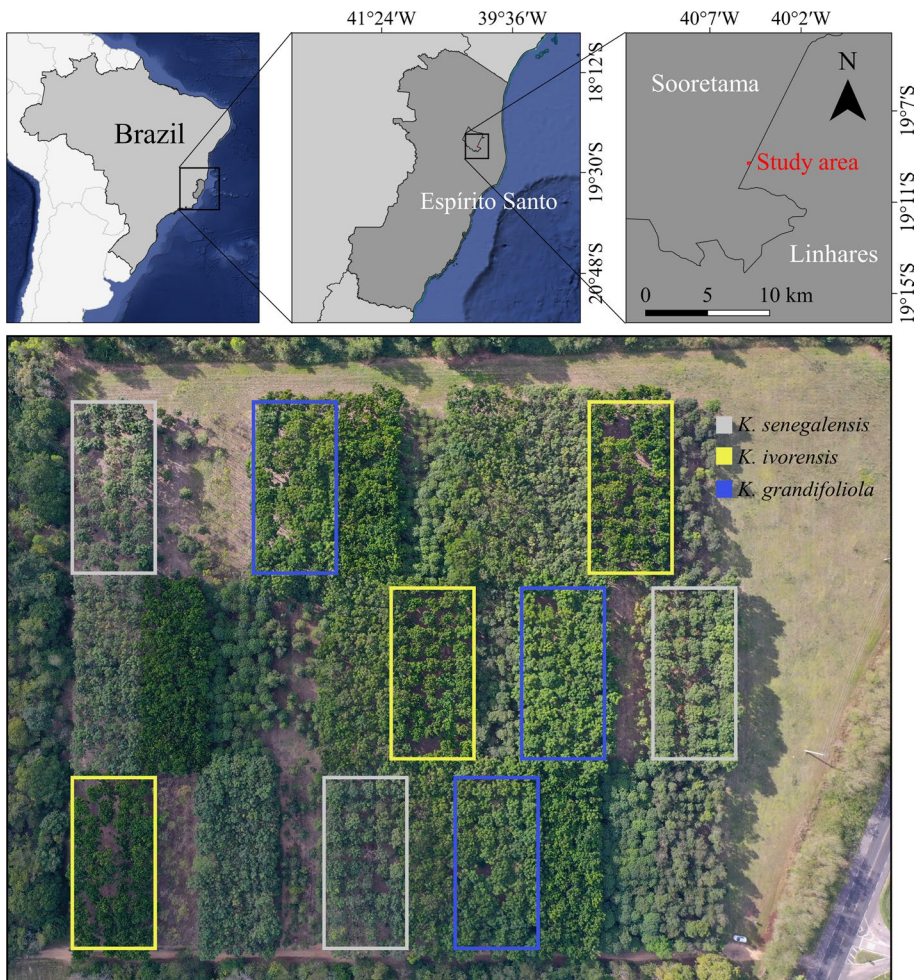


Fig. 1 Geographic distribution of *Khaya* spp. plots at age 9.5 years within the study site

Soils

Sample collection and chemical analysis

Soil samples, both disturbed and undisturbed, were collected from each plot 9.5 years post-planting for chemical characterization and quantification of organic carbon and total nitrogen contents (Table 1). Disturbed samples intended for nutrient availability analysis was collected at depths of 0–20 cm and 20–40 cm during June 2022. Analysis included the determination of phosphorus, potassium and sodium using Mehlich⁻¹ extractant; pH in a 1:2.5 water solution; H + Al using the SMP pH method; organic matter through oxidation with $\text{Na}_2\text{Cr}_2\text{O}_7 \cdot 2\text{H}_2\text{O} + \text{H}_2\text{SO}_4$ 10 mol L⁻¹; and calcium, magnesium and aluminum using a 1 mol L⁻¹ KCl extractant (Tedesco et al. 1995). Samples were collected using a Dutch auger, with 15 individual samples combined to form three composite samples for each depth within each plot, collected in a randomized manner.

Table 1 Soil chemical attributes at various depths within the experimental area in Sooretama, ES

Species	Depth cm	pH H ₂ O	P mg dcm ⁻³	K cmolc dm ⁻³	Ca cmolc dm ⁻³	Mg	Al	H+Al	SB	CEC	BS %	OM g kg ⁻¹
<i>K. grandifoliola</i>	0–20	5.91 ab	2.33	26.00	1.66 ab	0.51	0.00	2.19 ab	2.25 ab	4.44	50.57 b	24.4
<i>K. ivorensis</i>		5.76 b	2.33	23.67	1.33 b	0.43	0.00	2.22 a	1.84 b	4.06	45.17 b	22.4
<i>K. senegalensis</i>		6.07 a	2.67	26.11	2.29 a	0.60	0.00	1.73 b	2.97 a	4.71	62.15 a	26.1
<i>p</i> -value*		0.0458	0.3574	0.6982	0.0173	0.0533	0.7214	0.0362	0.0173	0.2957	0.0018	0.4322
<i>K. grandifoliola</i>	20–40	5.81	1.33	19.78	1.12	0.36	0.02	2.01	1.54	3.55	43.12 ab	19.3
<i>K. ivorensis</i>		5.74	1.33	16.78	1.02	0.30	0.01	1.91	1.37	3.28	41.44 b	16.7
<i>K. senegalensis</i>		6.00	1.44	19.00	1.40	0.42	0.00	1.67	1.88	3.55	52.48 a	18.6
<i>p</i> -value		0.0864	0.5606	0.3568	0.2452	0.1354	0.8564	0.2619	0.2015	0.7304	0.0428	0.3393
Reference area	0–20	5.37	2.33	40.00	0.67	0.33	0.23	3.20	1.12	4.32	26.00	29.0
	20–40	5.30	1.33	34.67	0.53	0.30	0.30	3.33	0.94	4.27	22.12	28.3

pH in water, contents of phosphorus (P), potassium (K⁺), calcium (Ca²⁺), magnesium (Mg²⁺), aluminum (Al³⁺), potential acidity (H+Al), sum of bases (SB), cation exchange capacity (CEC), base saturation (BS), and organic matter (OM) content

*Means followed by different letters indicate statistically significant difference by the Tukey test ($p \leq 0.05$)

Subsequently, these samples were stored in plastic containers and sent to the laboratory for analysis.

For the undisturbed samples, three trenches were dug in each plot to a depth of 40 cm, one at every 15 m section, totaling 27 trenches. Each trench was excavated within the core area of the plot, positioned transversely at 25% of the spacing from the planting rows. Sampling depths were established at intervals of 0–5, 5–10, 10–20, 20–30, and 30–40 cm. From these samples, soil bulk density (BD) and carbon and nitrogen analyses were also conducted.

Bulk density, carbon and total nitrogen content

Soil BD was determined using the analytical method of the stainless-steel volumetric rings, specifically the TAI sampler (undeformed samples) with a volume of 100 cm³, following the guidelines recommended by Embrapa (Teixeira et al. 2017). Organic carbon analysis was performed by wet oxidation of organic matter using potassium dichromate (Walkley and Black 1934). Total nitrogen analysis was carried out using the Kjeldahl digestion method (Kjeldahl 1883), which involves titration with a sulfuric solution. Sampling of soil BD, organic carbon and total nitrogen was conducted during June 2022.

The content of organic carbon and total nitrogen in the soil for each sampled depth were calculated using Eq. (1) (Veldkamp 1994; Machado et al. 2003).

$$SOC(orTNS) = T \times BD \times \frac{t}{10} \quad (1)$$

where: *SOC* or *TNS* = content of organic carbon or total nitrogen in the soil at a specific depth, in Mg ha⁻¹; *T* = concentration of organic carbon or total nitrogen at a specific depth, in g kg⁻¹; *BD* = soil bulk density at the specific depth, determined as the average of the three replications, in g cm⁻³; and *t* = thickness of the specific soil depth, in cm.

Forest floor

Forest floor collection and processing

Sampling of the forest floor was conducted during June 2022, a period characterized by the lowest rainfall. To minimize edge effects, samples were taken from the interior of the plots. The forest floor encompasses all organic materials, including leaves, twigs, bark, and other miscellaneous debris in various stages of decomposition (unidentified materials fine vegetable tissue without specific dimensions). Thirty samples per plot were collected using a randomized approach, with the aid of a square template measuring 0.0625 m² in area (Santos et al. 2020a, b; Viera et al. 2022; Caló et al. 2022).

Carbon and nitrogen concentration and content in the forest floor

Organic carbon was determined through oxidation using potassium dichromate (Tedesco et al. 1995). Nitrogen was extracted via sulfuric acid digestion followed by titrimetric determination. Carbon and nitrogen stocks were estimated using the equation proposed by Cuevas and Medina (1986):

$$S_{FF} = [Nutrient] \times DML \quad (2)$$

where: S_{FF} : represents carbon or nitrogen content in the forest floor, measured in Mg ha^{-1} ; $[Nutrient]$: refers to carbon or nitrogen concentration in the forest floor, quantified in g kg^{-1} ; and DML: stands for the dry weight of the forest floor, in kg ha^{-1} .

Stand biomass

Dendrometric characteristics

At 9.5 years of age, a forest inventory was conducted. The diameter at breast height (dbh) at 1.30 m above the ground, total height (Ht), and merchantable height (Hc) of all the trees within effective study area were measured using a caliper and a Vertex hypsometer. Hc was considered up to the first branch bifurcation.

Following measurement, trees were grouped by diameter class to select the number of trees to be felled. A total of 12 trees per *Khaya* spp. species were assessed, representing the entire diameter range. The stem of each sample tree was measured at heights of 0.1, 0.5, 1.3, 2.0 m, and thereafter, at every 1.0 m, up to the merchantable height.

Aboveground biomass quantification

The biomass of each sampled tree was determined using the direct (destructive) method. After felling, each tree was segmented into: stem, bark, branches, and leaves (Ribeiro et al. 2011, 2015; Mishra et al. 2014). The components were weighed separately to obtain the fresh weight in the field.

For wood sampling (stem + bark), five discs of approximately 5.0 cm thickness were taken at the base, 25, 50, 75 and 100 of the merchantable height (Lafetá et al. 2021; Kulmann et al. 2022). Bark samples were extracted from the wood discs collected during sampling, constituting a composite sample from various sampled diameters.

For live branches, portions were taken from the lower, middle, and upper third of the crown with a diameter ≥ 1.0 cm. Leaves were sampled from the base, middle and upper crown portions (Dallagnol et al. 2011; Picard et al. 2012; Salvador et al. 2016).

Samples from all tree components were immediately weighed in the field to obtain the individual fresh biomass. The moisture content and the dry biomass weight of the compartments were determined from weighing the fresh samples, which were oven-dried using a forced air circulation at of 75 °C, until reaching a constant weight. Dry samples of stem with bark were weighed, and the compartments individualized as per Picard et al. (2012) (Eq. 3):

$$B_t = \frac{FW_c \times DW_s}{FW_s} \quad (3)$$

where: B_t : total dry biomass of a given compartment, in kg; FW_c : fresh weight of a given compartment, in kg; DW_s : dry weight of the samples, in kg; FW_s : fresh weight of the samples, in kg.

The stem bark biomass was calculated using the percentage of bark for each tree by species in this compartment (Salvador et al. 2016). Total biomass was calculated by summing the stembark, stemwood, branches and leaves components of each tree. Then extrapolated per hectare, based on the number of trees measured in the forest inventory plot.

Subsequently, regression models were adjusted to predict biomass based on dbh and H_c values. The models outlined below were the best fits for the stemwood, bark, leaves, branches, and aboveground biomass, selected based on the adjusted coefficient of determination (R^2_{adj}) and the residual standard error (S_{yx} %) (Table 2).

Carbon and nitrogen concentration and content

After drying, the samples were processed and stored for subsequent chemical analysis and determination of carbon and nitrogen content in the plant tissue (Tedesco et al. 1995; Miyazawa et al. 1999). The nutrient stock per hectare for each tree fraction was determined by multiplying the dry biomass per hectare of the respective compartments by the nutrient concentration in each corresponding fraction.

Statistical analysis

The experimental design used was randomized block design, with three treatments and three replications. The treatments consist of three *Khaya* spp. (*K. senegalensis*, *K.*

Table 2 Adjusted equations and their respective statistics for estimating the biomass of *Khaya* spp. trees, at 9.5 years old, in Sooretama, ES

Species	Equation	R^2_{adj}	S_{yx} %
<i>Stemwood</i>			
KG	$Y = -0.1692 + 0.0739dbh^2 + 0.0171(dbh^2H_c)$	0.968	9.5
KI	$Y = -56.5676 + 0.1234dbh^2 + 13.2225H_c$	0.961	7.3
KS	$Y = -3.35436 + 0.44785H_c + 0.08274dbh^2 + 0.01587(dbh^2H_c)$	0.965	9.9
<i>Bark</i>			
KG	$Y = 1.5418 + 0.1804H_c + 0.0294dbh^2 + 0.0011(dbh^2H_c)$	0.841	16.8
KI	$Y = -20.607 + 0.991dbh + 2.606H_c$	0.681	22.1
KS	$Y = 7.9288 - 0.0239dbh^2 + 0.0111(dbh^2H_c)$	0.774	14.2
<i>Leaves</i>			
KG	$Y = 28.5409 - 3.7886dbh + 0.1391dbh^2$	0.685	35.3
KI	$Y = -118.2059 + 10.9818dbh - 0.2127dbh^2$	0.396	23.2
KS	$Y = 37.46 - 3.743dbh + 0.0849dbh^2 + 0.0041(dbh^2H_c)$	0.439	36.9
<i>Branches</i>			
KG	$Y = -135.1929 + 14.7543dbh - 0.0175dbh^2H_c$	0.566	48.3
KI	$Y = 31.3925 + 0.3313dbh^2 - 0.0264(dbh^2H_c)$	0.311	25.2
KS	$Y = 128.8834 + 6.5241dbh - 30.8537H_c$	0.807	19.5
<i>Aboveground Biomass</i>			
KG	$Y = -164.9034 + 19.1161dbh$	0.814	24.3
KI	$Y = -109.034 + 14.588dbh + 3.603H_c$	0.681	16.4
KS	$Y = 517.66 - 87.845H_c - 0.515dbh^2 + 0.164(dbh^2H_c)$	0.861	11.3

where: *KG* = *Khaya grandifoliola*; *KI* = *Khaya ivorensis*; *KS* = *Khaya senegalensis*; R^2_{adj} = adjusted coefficient of determination; S_{yx} % = standard error of the estimate in percentage; Y = estimated biomass (kg tree^{-1}); dbh = diameter at 1.30 m above the ground (cm); H_c = merchantable height (m)

ivorensis, and *K. grandifoliola*). The data was tested for homogeneity of variance and normality of residuals using the Oneillmathews and Shapiro–Wilk tests, respectively, at a 5% probability level. Upon meeting the requirements, an analysis of variance (ANOVA) was performed. The means of the variables analyzed across the three species were compared using the Tukey test at 5% probability level, using the R environment, *ExpDes* package. Additionally, Dunnett's test was used to compare the variations in soil carbon and nitrogen between the *Khaya* spp. stands and the native forest.

Data from soil attributes, forest floor, and aboveground biomass were organized and summarized through descriptive data analysis, aiming to better understand the characteristics of the sampled area. All attributes were standardized by their respective means and standard deviations, generating new variables centered at zero with variances equal to 1 (Gotelli and Ellison 2011). Subsequently, the differences in characteristics between species were analyzed using Principal Component Analysis (PCA), which was performed in the R environment using the *prcomp* function from the *Stats* package (Martín-Sanz et al. 2021; Kulmann et al. 2022).

Results

Soil density and allocation of carbon and nitrogen

The *Khaya* spp. did not differ from each another regarding soil bulk density at the evaluated depths ($p > 0.05$). However, *K. grandifoliola* species had higher soil density than the reference area in the 5–10 cm and 30–40 cm layers, with values of 1.55 and 1.57 g cm⁻³, respectively ($p \leq 0.05$). Overall, soil bulk density increased with soil depth for both *Khaya* spp. and the reference areas (Fig. 2a).

Carbon and nitrogen concentration in the soil were not different across species ($p > 0.05$). Compared to the reference area (native forest) in the 20–30 cm layer, *K. grandifoliola* was 52% smaller in carbon and 65% in nitrogen concentration (Fig. 2b and 2d). A general decline in carbon and nitrogen concentration was noted with increasing soil depth (Fig. 2b and d). The C/N ratio in the *Khaya* spp. remained stable across the soil profile (Fig. 2c) and was consistent with that observed in the reference area, indicating no significant differences.

Across all evaluated depths, carbon and nitrogen content were not different across species ($p > 0.05$). On average, carbon content in the 0–10 cm layer ranged from 32.29 to 37.17 Mg ha⁻¹, while in the 10–20 cm layer, values ranged from 22.53 to 27.01 Mg ha⁻¹. For the deeper layers (20–30 cm), *K. grandifoliola* showed significant differences compared to the reference area, with values of 12.91 and 23.75 Mg ha⁻¹, respectively, indicating 54% less in soil carbon content ($p \leq 0.05$) (Fig. 3a). Considering the entire soil profile (0–40 cm), carbon content averaged 78.04, 91.39, and 87.05 Mg ha⁻¹ for *K. grandifoliola*, *K. ivorensis*, and *K. senegalensis*, respectively. These values represent 65, 70.2 and 69.6% of the total carbon stored among the analyzed compartments (Fig. 8). In comparison, the reference area showed a carbon stock of 103.93 Mg ha⁻¹ (soil profile 0–40 cm).

The average nitrogen content across the entire soil profile was 1.55 Mg ha⁻¹. In the 20–30 cm layer, a significant difference was observed for *K. grandifoliola* compared to the reference area, indicating a reduction of around 74% (Fig. 3b). Nitrogen content within the 0–40 cm profile ranged from 6.93, 8.31, 8.04 to 8.03 Mg ha⁻¹ for the species *K. grandifoliola*, *K. ivorensis*, *K. senegalensis* and the reference area, respectively. This represents an

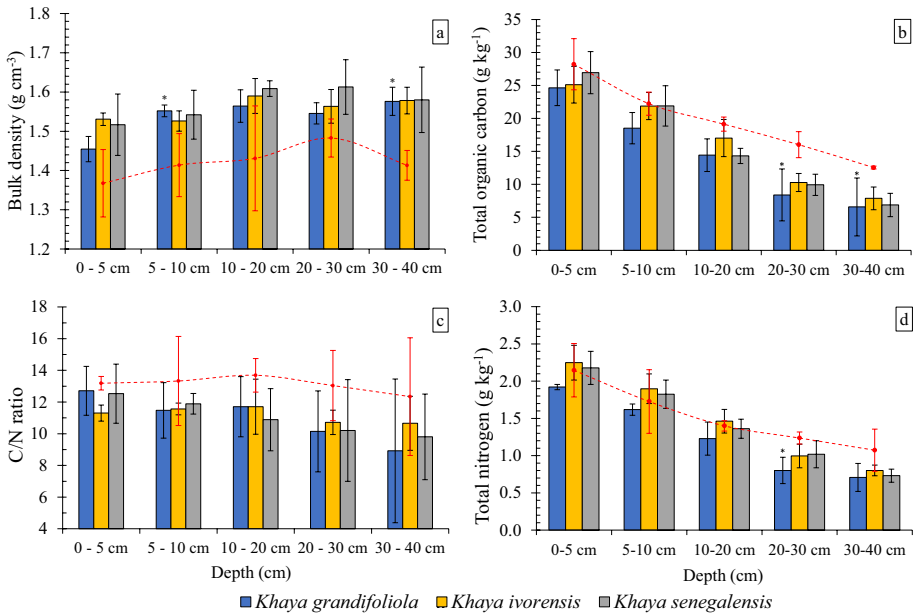


Fig. 2 Soil bulk density (a), total organic carbon concentration (b), C/N ratio (c), and total nitrogen concentration (d) at various depths for 9.5-year-old *Khaya* spp. stands. *Significant according to the Dunnett test $p \leq 0.05$, comparing African mahogany species with reference area (Seasonal Semideciduous or Evergreen Forest)

average soil nitrogen storage of approximately 93% when considering the compartments analyzed (Fig. 8).

Forest floor

There was no difference in forest floor biomass across the *Khaya* spp., averaging values of 9.47, 13.81, and 10.21 Mg ha⁻¹ for *K. grandifoliola*, *K. ivorensis*, and *K. senegalensis*, respectively ($p > 0.05$) (Fig. 4a). This same trend was observed for carbon concentration and, consequently, for carbon content in the forest floor ($p > 0.05$ for both) (Fig. 4b and e).

The carbon content in the forest floor averaged 3.91 Mg ha⁻¹ (*K. grandifoliola*), 5.05 Mg ha⁻¹ (*K. ivorensis*), and 4.11 Mg ha⁻¹ (*K. senegalensis*). Following the same sequence, this corresponds to a carbon content contribution of 3.3, 3.9 and 3.3%, considering all the analyzed compartments (Fig. 8).

Regarding the nitrogen concentration in the forest floor, *K. ivorensis* had the highest values, averaging 8.95 g kg⁻¹, followed by *K. senegalensis* with 8.14 g kg⁻¹ and *K. grandifoliola*, with 7.49 g kg⁻¹ ($p \leq 0.05$) (Fig. 4c). An inverse relationship to nitrogen concentration was found for the C/N ratio, where *K. grandifoliola* showed higher values than *K. ivorensis*, averaging 54.88 and 41.75, respectively ($p \leq 0.05$) (Fig. 4d).

K. ivorensis showed higher nitrogen content in the forest floor when compared to the other species ($p \leq 0.05$). Values of 0.12 Mg ha⁻¹ were recorded for the *K. ivorensis*, whereas *K. grandifoliola* and *K. senegalensis* averaged 0.07 and 0.08 Mg ha⁻¹, respectively (Fig. 4f). Considering all compartments, *K. ivorensis* contributes 1.3% to the total nitrogen

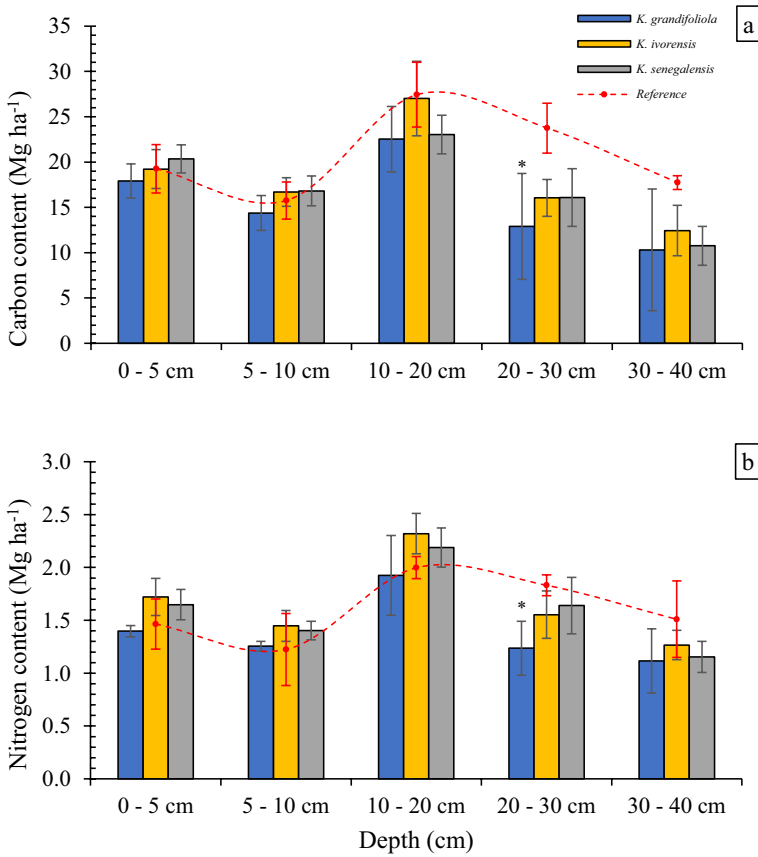


Fig. 3 Carbon (a) and nitrogen (b) content in the soil at various depths for 9.5-year-old *Khaya* spp. stands. *Significant according to the Dunnett test $p \leq 0.05$, comparing African mahogany species with reference area (Seasonal Semideciduous or Evergreen Forest)

stock. On the other hand, *K. grandifoliola* and *K. senegalensis* contributed 0.9% e 1%, respectively, of the overall nitrogen stock (Fig. 8).

Aboveground biomass

For the *Khaya* spp., the carbon concentration in bark, stemwood, and leaves were fairly consistent across species. Specifically, average carbon concentrations were measured at 400.99 g kg^{-1} for the bark, 433.80 g kg^{-1} for the wood, and 422.30 g kg^{-1} for the leaves (Fig. 5a, e, and i), and these differences were not statistically significant ($p > 0.05$ for all). However, when examining the branches, *K. grandifoliola* exhibited a carbon concentration of 414.54 g kg^{-1} , which was notably higher than the 361.62 g kg^{-1} observed in *K. ivorensis* ($p \leq 0.05$) (Fig. 5m). The pattern for nitrogen concentrations was analogous to that of carbon for most components. Specifically, there was no difference between the species for nitrogen concentrations in the bark, leaves, and branches ($p > 0.05$ for all) (Fig. 5b, j, and n). Yet, for the wood component, *K. senegalensis* stood out by having the highest nitrogen concentration in its stemwood compared to its counterparts ($p \leq 0.05$) (Fig. 5f).

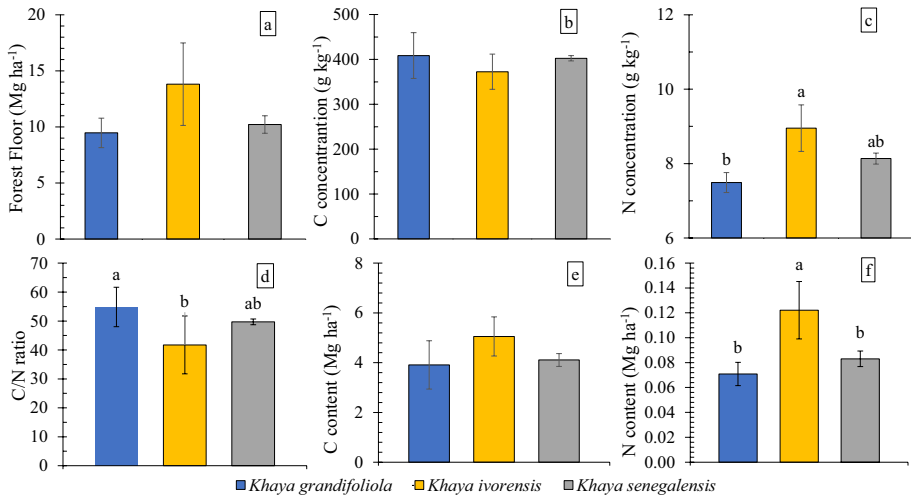


Fig. 4 Accumulated Forest floor (a), carbon concentration (b), total nitrogen concentration (c), C/N ratio (d), and carbon (e) and nitrogen (f) content for 9.5-year-old *Khaya* spp. stands

In the leaves, *K. ivorensis* outperformed the others in carbon and nitrogen content ($p \leq 0.05$ for both, Fig. 5k and l). This corresponded to 41.08% higher in carbon content and a 43% higher in nitrogen content compared to *K. grandifoliola*, and a greater of 69.26% in carbon and 72.73% in nitrogen when compared to *K. senegalensis*. Conversely, *K. ivorensis* had the lowest carbon and nitrogen content for the bark and branch compartments (Fig. 5c–d and o–p).

The species displayed distinct storage patterns across the compartments. However, it was consistently observed that the branches held the highest carbon and nitrogen content for all evaluated mahogany species. For *K. grandifoliola* and *K. senegalensis*, the carbon stock sequence was branches > stemwood > bark > leaves. In contrast, *K. ivorensis* demonstrated a sequence of branches > stemwood > leaves > bark. The nitrogen storage pattern of *K. grandifoliola* and *K. ivorensis* were similar, following the order of branches > leaves > bark > stemwood. Conversely, *K. senegalensis* showed a distinct sequence: branches > bark > stemwood > leaves.

The C/N ratios for the stemwood in *K. grandifoliola* and *K. ivorensis* were higher than those observed for *K. senegalensis*, with average values close to 310, 318 and 242, respectively ($p \leq 0.05$, Fig. 6). In contrast, the leaves showed an opposing trend, where *K. ivorensis* obtained an average C/N ratio of 27 ($p \leq 0.05$). The branches did not show any differences among the species, with C/N ratios ranging between 47 and 64 (Fig. 6).

K. grandifoliola and *K. senegalensis* had higher carbon concentration compared to *K. ivorensis* ($p \leq 0.05$, Fig. 8). The carbon content for *K. grandifoliola*, *K. ivorensis* and *K. senegalensis* was of 37.97, 33.66, and 33.86 Mg ha⁻¹, respectively, being greater in the *K. grandifoliola*, representing approximately 31.7% of the total content among the examined compartments ($p \leq 0.05$, Fig. 8).

There were no significant differences observed in the nitrogen concentration of the aboveground biomass compartment among the species ($p > 0.05$) (Fig. 8). In absolute terms, the total nitrogen content in the aboveground biomass were 0.55 Mg ha⁻¹ for *K. grandifoliola*, followed by *K. senegalensis* (0.53 Mg ha⁻¹) and *K. ivorensis* (0.45 Mg ha⁻¹).

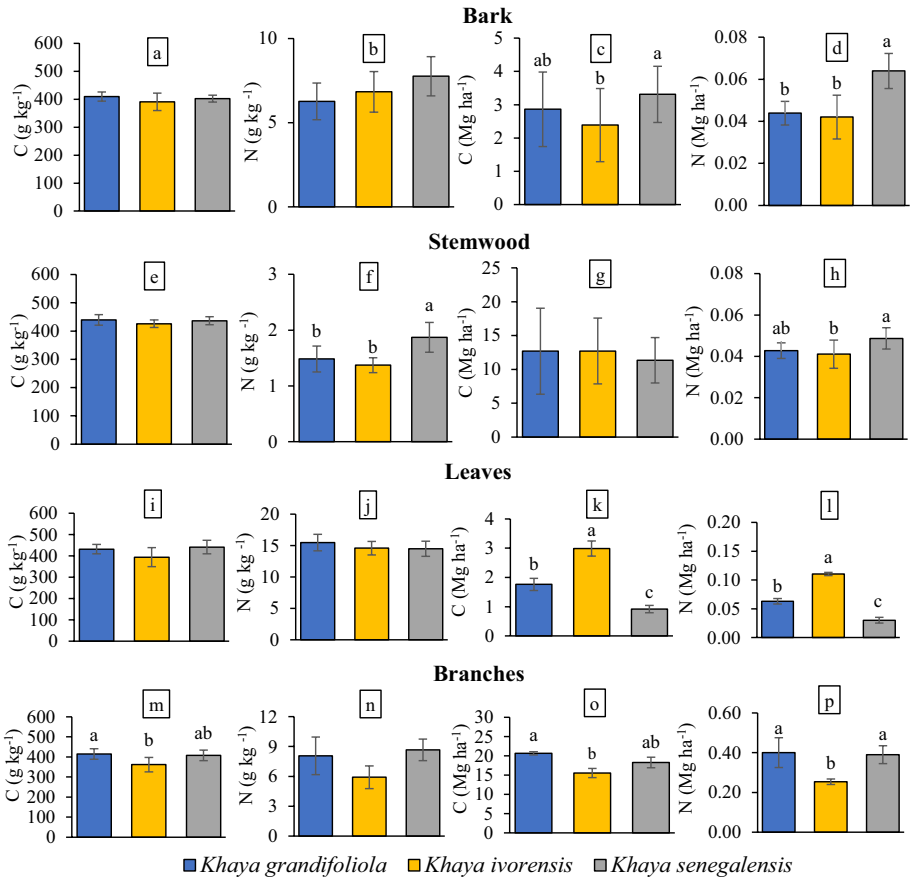


Fig. 5 Carbon and nitrogen concentration (g kg^{-1}) and content (Mg ha^{-1}) in various aboveground compartments of 9.5-year-old *Khaya* spp. stands

This represents an average contribution of only 6.2% of the total nitrogen stored in the stand (Fig. 8).

The first two components of the PCA accounted for 46.97% of the variance in the soil, forest floor, and aboveground biomass (Fig. 7). It was observed that *K. grandifoliola* and *K. senegalensis* had greater similarities, particularly when assessing carbon and nitrogen concentration and content in branches and leaves. On the other hand, *K. ivorensis* appeared to be more closely associated with higher nitrogen content in leaves, as well as in soil and forest floor.

Discussion

Soil response to *Khaya* spp. plantations

The species used in forest plantations can be one of the determinants impacting soil BD due to the distribution of roots and their relationship with soil porosity (Yu et al. 2018;

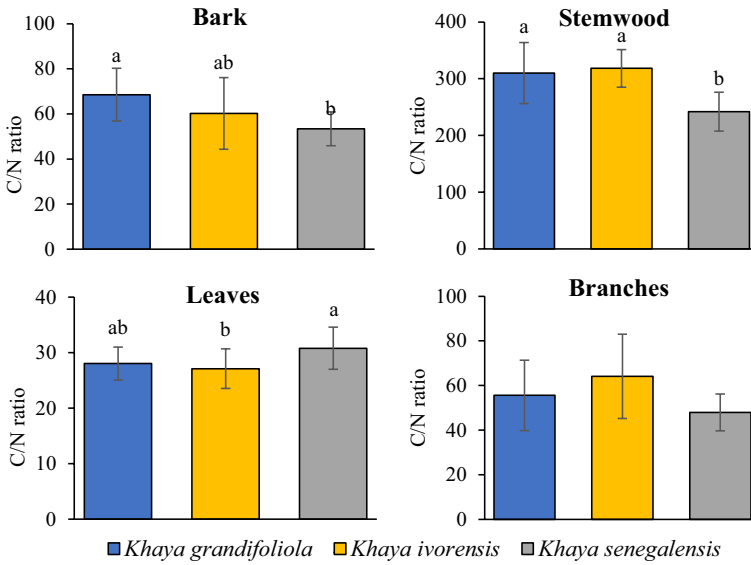


Fig. 6 C/N ratio in various aboveground compartments of 9.5-year-old *Khaya* spp. trees

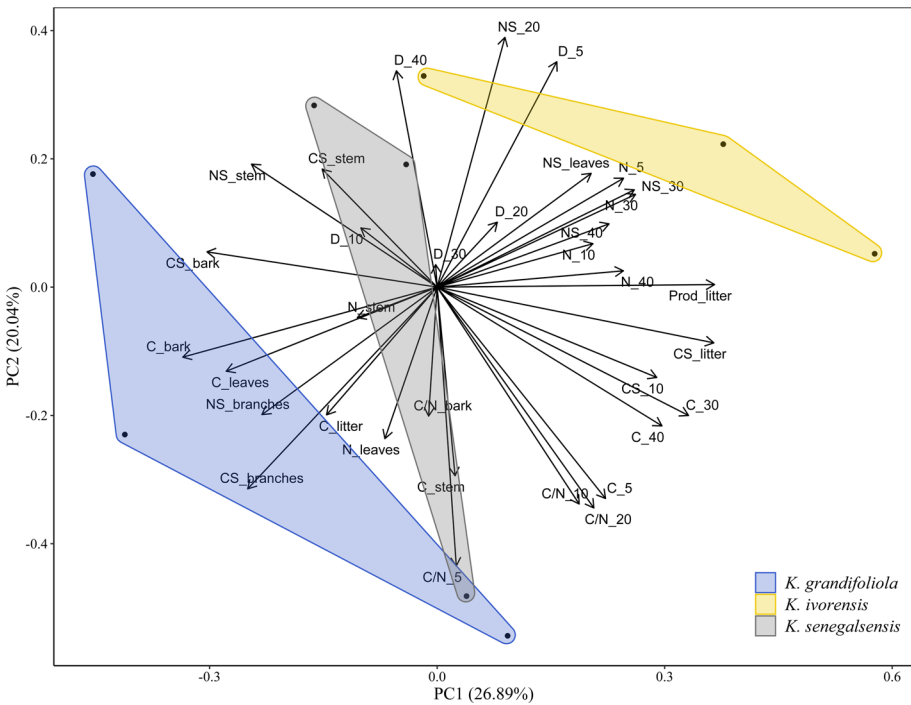


Fig. 7 Principal component analysis (PCA) of soil variables, forest floor, and aboveground biomass of 9.5-year-old *Khaya* spp. stands. Abbreviations for PCA parameters are provided in Appendix (Table S1)

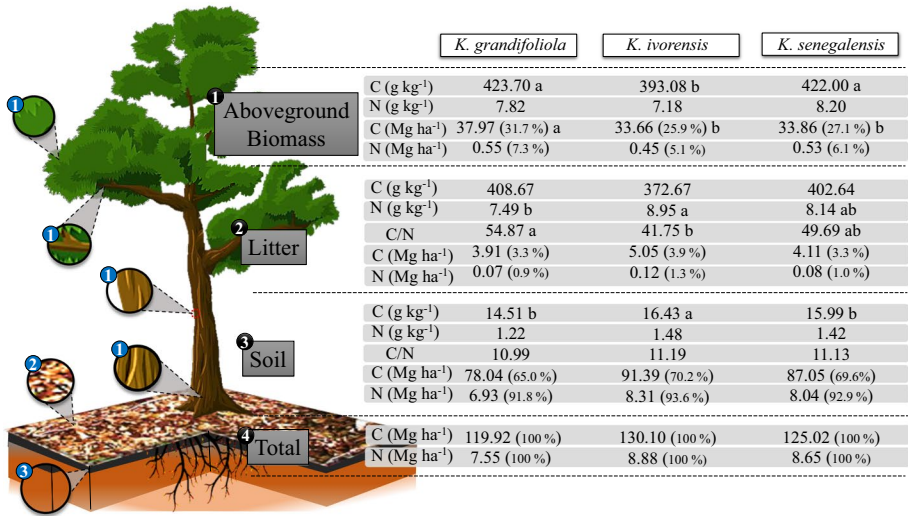


Fig. 8 Comparisons of means between aboveground compartments (bark + stemwood + leaves + branches), forest floor and soil (0–40 cm) as well as total content of 9.5 years-old *Khaya* spp. Stands

Huang et al. 2021). However, our results indicate that there was no significant difference in soil density among the examined *Khaya* spp. stands. Other factors can influence soil BD, such as topography, organic matter content, and soil texture. The differences noted when compared to the reference area are likely due to machine trafficking, management practices (Shrestha and Lal 2011; Korkanç 2014).

Carbon and nitrogen concentration showed an inverse relationship with soil BD. This pattern aligns with findings from studies on various tree species, such as those belonging to the genus *Pinus*, *Eucalyptus*, and the palm species *Elaeis guineensis* Jacq. (Butnor et al. 2017; Bieluczyk et al. 2020; Santos et al. 2020a, b; Rahman et al. 2021). Several intertwined factors may underlie this observation. Primarily, the uppermost soil strata is subject to an active renewal of fine roots (Lamb 1966; Lamprecht 1990; Santos et al. 2022), which are decomposed and enrich the soil with organic matter. This contribution of organic residues on the soil surface amplifies soil microbial activity, further promoting the formation of organic matter in the soil’s topmost layers (Kogel-Knabner 2017).

In quantitative terms, the soil C/N ratios observed in our study closely aligned with the values reported by Oliveira Filho et al. (2022) in northeastern Brazil, where they identified C/N ratios ranging from 8 to 12 across various vegetation types and edaphoclimatic characteristics. These findings are further corroborated by Wehr et al. (2020), who documented average C/N ratios fluctuating between 5.7 and 13.5 across different sites in Southeast Queensland, Australia. The broad variability in their results was attributed to the application of nitrogen fertilizers, the presence of leguminous species as well as differences of edaphoclimatic conditions, age and species types.

Factors such as the diversity of planted species, soil management practices, climatic variables, and clay content can influence soil carbon content (Paula et al. 2022). While the *Khaya* spp. did not influence our observed soil carbon content, our values were notably higher than those documented in studies on Atlantic Forest species by Assad et al. (2013), Dortzbach et al. (2015), and Santos et al. (2019). Specifically, these authors reported

carbon content of 72.3, 49.3, and ≤ 80 Mg ha⁻¹ for depth intervals of 0–30, 0–30, and 0–40 cm, respectively. Such disparity might be associated with our site's history, considering that leguminous species were previously planted in the area (Caldeira et al. 2020).

The higher soil carbon content in the reference can be attributed to the increased accumulation of litter and the rapid decomposition rate, facilitated by intense biological activity and the absence of anthropogenic disturbances (Leite et al. 2013; Petter et al. 2017). The disparities between the reference area and *K. grandifoliola* are mainly due to the species' lower carbon concentration (14.51 g kg⁻¹), which results in diminished carbon content in the deeper soil layers (Table 1 and Fig. 3a).

The same trend was observed for nitrogen content, with *K. grandifoliola* exhibiting the lowest levels in the 20–40 cm depth range. This may be related to the fact that soil nitrogen levels are strongly linked to carbon cycling. As a consequence, there is a decrease in nitrogen levels along the soil profile. This decrease can be explained by the lack of organic residue inputs and reduced microbial biomass activity in the subsurface soil layers (Costa Júnior et al. 2011; Bieluczyk et al. 2020).

Stand effects on forest floor

Nutrients stored in forest floor are essential for replenishing the soil, as they are a crucial part of the biogeochemical cycles within forest ecosystems (Han et al. 2012; Zhou et al. 2015). For both natural forests and plantations, forest floor acts as a temporary reserve of nutrients, which can be made available throughout the production cycle (Tesfay et al. 2020; Oyedeji et al. 2021). Consequently, forest productivity is directly influenced by both the quantity and quality of the litter produced (Michopoulos et al. 2019).

The forest floor values from the present study are comparable to, or exceed those from other plantations of exotic species. Pinto et al. (2016) reported a total forest floor accumulation of 12.7 Mg ha⁻¹ for *E. urophylla* at 7 years of age in the southwest of Bahia. In the same region, Barbosa et al. (2017) observed a production of 13.1 and 1.5 Mg ha⁻¹ for *E. urophylla* and *P. nitens* at 5–6-year-old stands, respectively.

Although there were no differences, *K. ivorensis* had higher values of forest floor biomass when compared to the other species (Fig. 4a). This might be related to the fact that the amount and decomposition rate of forest floor can be influenced by climate and ecological factors, such as tree size, foliar biomass, and C/P ratio (Kim et al. 2010; Negash and Starr 2013; Godinho et al. 2014). Moreover, *K. ivorensis* possesses a denser canopy structure with leaves, leading to a greater deposition and accumulation on the soil. This explains the higher forest floor biomass observed for this species assuming similar decomposition rate.

The carbon concentration of the forest floor from this study aligns with those obtained by Sanquetta et al. (2014a) for the Seasonal Semideciduous Forest (362.2 g kg⁻¹) and for the Araucaria Moist Forest (382.1 g kg⁻¹), both located in the state of Paraná, Brazil. Lee et al. (2020) found that conifers, deciduous species, and mixed forests in South Korea have carbon concentration of 447.8, 425.9, and 438.9 g kg⁻¹, respectively. Godinho et al. (2014) reported average carbon concentration of 505.8 g kg⁻¹ in Submontane Seasonal Semideciduous Forest, also situated in the state of Espírito Santo, Brazil. Despite differences in edaphoclimatic conditions and species diversity in the environments examined in these studies, it can be observed that African mahogany possesses carbon concentration in the forest floor similar to those reported for different types of native forests.

Regarding the carbon content in forest floor, the values observed are similar to those reported by Watzlawick et al. (2012), which showed at 3.06 Mg ha⁻¹ in the Montana Araucaria Moist Forest, and are higher than those reported by Almeida et al. (2010) for *Tectona grandis* plantations aged 5.5 years (2.68 Mg ha⁻¹). These differences between carbon content of *Khaya* spp. and other species could be attributed to the age of the plantation, which directly influences biomass production and canopy volume (Kooch and Bayranvand 2017). In addition, in tropical conditions such as Brazil, factors as high temperatures, availability of water in the soil and different types of foliage interfere with the decomposition rate of forest floor (Caldeira et al. 2019; Braga et al. 2022).

The concentration and content of forest floor can be influenced by factors such as age, climatic variables, and inherent characteristics of the species, including the lignin content and the mobility of the bioelements they contain (Siqueira et al. 2014; Godinho et al. 2014; Ma et al. 2018; Caldeira et al. 2020). Given that soil conditions, climate, and litter production are similar, the differences in nitrogen concentration and content may be linked to the quality of the deposited residues (Barbosa et al. 2017).

Nitrogen is characterized by its mobility within the plant (Taiz et al. 2017). The high N value in the leaves and litter of *K. ivorensis* could be associated with the fact that this species has a less efficient biogeochemical cycle compared to the other species (Jara et al. 2009; Viera and Shumacher 2009). Although its nitrogen content is high, it demonstrates a lower retranslocation rate to new leaves, resulting in its accumulation in older leaves and, consequently, in the forest floor (Jaramillo-Botero et al. 2009). Dinesha et al. (2023) stated that the nitrogen retranslocation rate in the leaves and rachises of *S. macrophylla* amounts to 90.34 and 77.65%, respectively. Another factor supporting this hypothesis is the high C/N ratios. With values exceeding 30, as in our study, Stevenson (1986) suggests that the immobilization rate becomes greater than mineralization, reducing the nitrogen availability in the soil and promoting its accumulation in the litter.

Differences in carbon and nitrogen allocation in aboveground biomass

Carbon concentration in plant-derived biomass tends to vary based on factors such as age (Azevedo et al. 2018), forest species (Watzlawick et al. 2014), and the specific compartment analyzed, rarely exceeding 50% (Dallagnol et al. 2011). In *E. urograndis* plantations at 5.5 years of age in southeastern Brazil, Ribeiro et al. (2015) found average carbon concentration of 44.6% in wood with bark, 43.0% in branches, and 46.1% in leaves. Similarly, Sanquetta et al. (2014b) reported average carbon concentration ranging from 45.28 to 46.09% for bark, 43.77 to 44.34% for wood, 47.79 to 48.34% for leaves, and 44.40 to 48.28% for branches when studying *Acacia mearsii* De Wild aged between 1 and 7 years.

The carbon concentration found in the present study showed lower values compared to other studies, but such differences likely stem from variations in species, site quality, or environmental conditions. Results ranged between 39 and 44% for all compartments, illustrating they fall within the generic range for estimating biomass carbon (Souza et al. 2020). Furthermore, carbon allocation in trees is influenced by factors such as nutrient availability, water, light, CO₂, age, root system, growing season length and even genetic composition, complicating the establishment of assessment standards (Ericsson et al. 1996; Pereira Júnior et al. 2016; Rodríguez-Soalleiro et al. 2018; Rocha et al. 2020), demonstrating the importance of studies like this for establishing standards for the species studied.

Although there were no differences for some compartments, it was noted that leaves have the highest nitrogen concentration across all *Khaya* spp. This is due to nitrogen's

involvement in most organic compound metabolism and its inherent mobility, concentrating in organs with high photosynthetic activity (Malavolta et al. 1997). A similar trend was observed by Viera et al. (2013), noting nitrogen concentration of 36.58 g kg⁻¹ for leaves, 7.15 g kg⁻¹ for branches, 6.41 g kg⁻¹ for bark, and 6.10 g kg⁻¹ for wood in a stand of *E. urograndis* intercropped with corn. In contrast, the *Acacia mearnsii* and corn intercrop registered 41.09, 14.63, 15.33, and 6.52 g kg⁻¹ for leaves, branches, bark, and wood, respectively.

The observed differences in wood nitrogen concentration likely relate to nutrient bioavailability in the soil. Organic matter mineralization might have supplied adequate nitrogen to meet the nutritional requirements of *K. senegalensis*, storing any surplus nutrient in the stem (Souza et al. 2010). Among the *Khaya* spp., *K. senegalensis* is the least demanding regarding soil conditions and can be found in both deep, well-drained soils and rocky, shallow terrains (Lamprecht 1990; Pinheiro et al. 2011).

In general, the higher carbon and nitrogen content in branches relate to the dominance in biomass production of this compartment across all studied *Khaya* spp. This behavior aligns with expectations, as *Khaya* spp. possess a dense and rounded canopy, comprising thick and cylindrical branches (Pinheiro et al. 2011; Opuni-Frimpong et al. 2016).

Conversely, leaves displayed the lowest carbon content. *K. ivorensis* showed the highest carbon and nitrogen content in the leaf compartment. This is primarily attributed to the biomass produced, which was 46.17 and 72.43% larger than to *K. grandifoliola* and *K. senegalensis*, respectively. Viera and Rodríguez-Soalleiro (2019) found a similar trend, observing average aboveground biomass carbon content for *E. urophylla* plantations at 118.48 Mg ha⁻¹, allocating 103.4 Mg ha⁻¹ to wood, 8.6 Mg ha⁻¹ to bark, 4.5 Mg ha⁻¹ to branches, and 2.0 Mg ha⁻¹ to leaves. Ribeiro et al. (2015) also noted that leaves contributed the least among the compartments (1.91 Mg ha⁻¹), followed by branches (4.45 Mg ha⁻¹), bark (5.09 Mg ha⁻¹), and wood (52.12 Mg ha⁻¹) when evaluating *E. urograndis* clones at 5.5 years.

The findings from this study suggests that the removal of branches and leaves from *Khaya* spp. stands can enhance carbon and nitrogen export. Therefore, it is recommended to implement practices of canopy pruning and chipping of vegetative material, ensuring its retention in the cultivation areas. Such practices are commonly applied to other forest species, such as eucalyptus (Witschoreck and Schumacher 2015; Schumacher et al. 2019) and pine (Garret et al. 2021; Kulmann et al. 2021).

Conclusion

African Mahogany species have carbon and nitrogen storage potential comparable to that of native Brazilian forests, contributing to mitigate the effects of global warming and providing an alternative economic return.

The forest floor is chemically different between the *Khaya* spp., although it does not differ in quantity. Our results suggest that the *K. ivorensis* stand is chemically different from the other species in terms of nitrogen, nutritionally increasing soil concentrations and favoring the decomposition and release of this nutrient in the 5 cm layer.

The aboveground biomass, especially the branches, has a greater capacity for storing C and N. The concentration and content of carbon in the bark and branches were most closely associated with *K. grandifoliola*, while the nitrogen content in the leaves highlighted to *K. ivorensis*. Moreover, *K. senegalensis* has the lowest C content and the highest N content

in commercial wood. Therefore, the maintenance of harvest residues is recommended in *Khaya* stands, especially for *K. ivorensis* due to the potential nitrogen content in the biomass leaves, which translates into forests floor and soil fertility.

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Author contributions GSLG: Conceptualization, data curation, formal analysis, methodology, writing—original draft, writing—review and editing. MVWC: Supervision, funding acquisition, data curation, writing—original draft preparation. RG: Writing—review and editing, validation, data curation. VBRD: Software, formal analysis, data curation. DRM: Writing—original draft preparation, validation. TOG: Funding acquisition, writing—reviewing and editing. SOM.: Writing—review and editing. LSS: Writing—review and editing. PAT: Writing—review and editing. ACOC: Writing—review and editing. MVS: Writing—review and editing.

Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no financial or other competing conflicts of interest.

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