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Native and exotic tree leaves litter contributions to soil organic matter formation in revegetation strategies

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ABSTRACT: The use of native and exotic species in the reforestation of degraded areas has been considered an important strategy to improve soil quality. However, there is still scarce information about which species are more efficient for soil organic matter (SOM) formation. This study aimed to evaluate the decomposition of leguminous and non-leguminous tree litter, its impact on light organic matter (LOM), particulate organic matter (POM), and mineral-associated organic matter (MAOM) dynamics, and consequently, SOM formation efficiency. Leaf litter from 16 native trees to the Atlantic Forest and a clonal Eucalyptus were added to the soil (incubation experiment) to evaluate the decomposition and contribution to the formation/degradation of SOM for 888 hours. The relative contents of δ_{13}C, N, P and C were assessed; the cumulative emission of C-CO$_2$, potentially mineralizable C (C$_0$), decomposition rate constant (k) and half-life time; calculation of the priming effect and physical fractionation, obtaining the LOM, POM and MAOM fractions. Cumulative emission of C-CO$_2$ increased, especially in the first 204 hours. Non-leguminous species *C. speciosa*, *S. saponaria* and *Trichilia* sp. showed faster decomposition and greater mineralization potential. *Lecythis* sp. showed the lowest k (0.0058), suggesting better degradability. *A. peregrina* was the only species with a negative priming effect and a greater contribution to the LOM fraction. *C. speciosa* made a greater contribution to the POM fraction. The highest efficiency of SOM formation was observed in eucalyptus residues. The leguminous species *A. peregrina*, *I. edulis*, *H. courbaril* and *P. gonoacantha* also showed high SOM formation efficiency, higher contribution in the MAOM fraction, slower mineralization and lower respiration rates. *I. edulis* showed the lowest respiration and decomposition rates and the greatest contribution to SOM formation efficiency. Litter quality has a significantt influence on decomposition dynamics and SOM formation. In this way, the data can help in the selection of tree species with suitable functional characteristics aimed at optimizing ecosystem services, especially in relation to soil quality and the carbon cycle in reforestation and recovery programs for degraded areas in the Atlantic Forest.

Keywords: Atlantic Forest, litter decomposition, CO$_2$ efflux, litter quality, soil organic matter.

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INTRODUCTION

While tropical forests provide a greater quality and quantity of ecosystem services compared to non-tropical forests, the rate at which they provide these services is decreasing rapidly (Alamgir et al., 2016). Anthropogenic and environmental factors have contributed to deforestation and declining ecosystem services (Malhi et al., 2008; Hu et al., 2017). Over 0.65 million km^2 of forests have been cleared in Brazil, and transformed into pasture or agricultural areas (Stabile et al., 2020).

In Brazil, the Atlantic Forest might be the most extreme example of how anthropogenic activities, deforestation and climate change have led to severe soil degradation. Before the European colonization of Brazil, the Atlantic Forest covered over 1.2 million km^2 (Adams et al., 2008), which is approximately twice the size of Texas, USA. Nowadays, only 12.5 % of the Atlantic Forest remains, existing in fragments along the coast and interior of Southeast Brazil (Guedes Pinto and Voivodic, 2021). Anthropogenic reasons contributing to the near-complete deforestation of the Atlantic Forest include the agriculture, pastureland, housing development, and mining required to sustain the 70 % of the Brazilian population currently living in this region (Souza et al., 2012).

Soil organic matter (SOM) is a vital environmental resource, due to the diverse ecosystem services it provides, but its vulnerability to land use change affects the SOM formation efficiency. Studies have demonstrated the importance of SOM in areas degraded by mining, due to its intrinsic relationship with the physical, chemical, and biological soil processes and properties (Mukhopadhyay et al., 2014; Boas et al., 2018). Therefore, understanding the processes of revegetation and regeneration in degraded native forests requires a clear understanding of how the decomposition of distinct leaf litterfalls from Atlantic Forest trees influences the dynamics of SOM formation efficiency.

Forest tree litterfalls are the main source of organic carbon (C) in soils of this environment (Menyailo et al., 2022). Their inputs are microbially decomposed and partially transformed in SOM, predominantly the mineral-associated organic matter (MAOM) fraction (Kleber et al., 2015). The MAOM (<53 μm) consists of fragments or molecules leached from plant material or transformed by soil microbiota, protected through association with soil minerals and aggregates (Lavallee et al., 2019) and is generally more stable than the particulate organic matter (POM) fraction (Cotrufo et al., 2015; Ridgeway et al., 2022). The POM fraction (>53 μm) is composed of partially decomposed labile plant materials and by-products of their decomposition (Canisares et al., 2023; Liao et al., 2023) and is generally more sensitive to land use (Silva et al., 2022).

Enhancing the efficiency of SOM formation from forest litterfall is crucial for sequestrating atmospheric C-CO_2 and sustaining soil fertility (Xu et al., 2022). However, the quality of plant materials supplied to the soil is of utmost importance in SOM formation. Thus, studying the decomposition and impact on the dynamic of SOM fractions of different native and exotic species litterfalls becomes essential due to the disparity of litterfall quality. Generally, leaf litterfalls of leguminous trees have a faster decomposition rate compared to non-leguminous leaf litterfalls, resulting in a higher contribution of organic matter (C, N and P) and a more significant influence on SOM formation (Cattanio et al., 2008). Due to the variable decomposition rates among different species, their contributions are also differentiated, contributing to SOM formation at different times and with distinct biochemical composition (Silva et al., 2022). They can contribute both with more labile compounds and with faster cycling, being more easily assimilated by microorganisms and mineralized by plants, and also with more stable and recalcitrant compounds, contributing to the formation of a more stable organic matter, with a longer permanence in the soil (Cotrufo et al., 2019; Lavallee et al., 2019; Zheng et al., 2021).

Due to its magnitude, the increment and maintaining SOM in the Atlantic Forest is an essential strategy with potential to address problems associated with climate change, food security, and biodiversity preservation on both local and global scales (Zanini et al., 2021). Although solutions exist, recovery of degraded areas is a challenge because of anthropogenic factors such as a poor political situation (Sivakumar, 2007), a lack of effective communication (Souza et al., 2010), a lack of research about SOM formation efficiency (Cotrufo et al., 2013), poverty and environmental factors such as climate change and biodiversity loss (Sivakumar, 2007). As a result of these challenges, many farmers, specifically in the Atlantic Forest region, have not been able to use innovations, such as using native trees to recover the soil or create sustainable agroforestry operations (Souza et al., 2012). Therefore, it is valuable to clarify, on both regional and global scale, the SOM formation efficiency of native Atlantic Forest trees.

Considering these interactions, our hypothesis was that litterfall from legume trees promotes a greater increase in MAOM-C than litterfall from non-legume trees used in reforestation strategies in Atlantic Forest areas. Our objectives were to evaluate the decomposition dynamics of litterfall from different forest species (leguminous and non-leguminous), their contributions to the POM-C and MAOM-C fractions, and SOM formation efficiency.

MATERIALS AND METHODS

Soil and plant sampling and analysis

The soil used in the experiment was classified as Latossolo Vermelho Amarelo distrófico (Santos et al., 2018), corresponding to an Oxisol. Samples were collected from the 0.00–0.20 m layer at coordinates 20° 52’ 31.1” S, 42° 58’ 21.6” W, in Brazil. The soil had been cultivated with *Urochloa brizantha* (A.Rich.) for over 20 years, which allowed the construction of an isotopic abundance of ^{13}C different ($\delta^{13}C$: - 13.25; Table 1) from those found in leaf litter used in the experiment. Additionally, soil samples (0.01-0.05 m layer) were taken from the area with tree native and exotic species, which were sieved with a 2 mm sieve, organic materials were removed with the aid of tweezers and they were stored at -20 °C. These soil samples were used to prepare an inoculum with the native population of microorganisms to be inoculated in the soil used in the experiment.

Soil samples (20 g of dry soil inoculated with 1 % w:w of inoculant) were placed into glass pots (600 mL) with lids equipped for air sampling. Two control groups were created by leaving four glass pots empty and placing only soil in four glass pots.

$$LW = (\%C_{Lit} \times DWoS \times 0.01) \quad \text{Eq. 1}$$

in which: LW represents the weight of each different litter required for each pot in g; $\%C_{Lit}$ is the C content (%) of a particular litter; and Dw_oS is the dry weight (g) of the soil added to each pot.

Leaf litter and soil were gently mixed, and one only-soil and one blank pot were added. The humidity was adjusted for 80 % of the field capacity. Mature and undamaged leaf litter was harvested from each tree species in January 2017 (approximately 6 years old). Leaves (blades, petioles and leaflets) were cut with a guillotine, wrapped in aluminum foil, labeled, and stored in a cooler on ice until returned to the laboratory. Leaves were taken during the rainy season and did not need to be rinsed.

Leaf samples were frozen at -80 °C and dried for 72 h at -46 °C in a freeze-dryer using sublimation to avoid any tissue damage. Dried samples were sealed in plastic bags and stored at -20 °C to minimize unwanted metabolic changes. Leaves were homogenized with a 1 mm electric mill in minimal light to avoid photorespiration. The homogenized material was placed in vials and stored at -20 °C.

Table 1. Chemical and physical characterization of soil used in experiment

Soil characteristics	Values
C (%)(1)	2.23
δ^{13}C (‰)(1)	-13.25
N (%) (1)	0.19
P available (mg dm^{-3})(2)	3.60
K (mg dm^{-3})(2)	85.10
S (mg dm^{-3})(2)	2.50
Cu (mg dm^{-3})(2)	1.60
Fe (mg dm^{-3})(2)	197.00
Zn (mg dm^{-3})(2)	4.56
Mn (mg dm^{-3})(2)	87.50
B (mg dm^{-3})(2)	0.27
Coarse sand (200-2000 µm) (g kg^{-1})(3)	410.00
Fine sand (50-200 µm) (g kg^{-1})(3)	110.00
Silt (2-50 µm) (g kg^{-1})(3)	170.00
Clay (<2 µm) (g kg^{-1})(3)	310.00

(1) Isotopic Ratio Mass Spectrometer – IRMS. (2) Extraction and determination by Teixeira et al. (2017): N by the Kjeldahl method; P and K$^+$: extracted by Mehlich and determined by colorimetry and flame photometry, respectively; S: sulfur extracted with monocalcium phosphate in acetic acid and determined by photometry; B: boron extracted with hot water and determined by photometry; Fe, Zn, Mn and Cu: extracted by absorption atomic absorption spectrometry. (3) Coarse sand, fine sand, silt and clay: pipette and sieving method (Gee and Bauder, 1986).

Approximately 1.5 mg of homogenized of leaf litter was used for quantifying C, N and δ^{13}C by an Isotopic Ratio Mass Spectrometer - IRMS (ANCA GSL 20-20, Sercon, Crewe, UK). The material was also digested using HCl and HNO_3 and analyzed for P, K, Ca, Mg, S, Cu, Fe, Zn, Mn and B (Supplementary Material 1) contents using inductively coupled plasma optical emission spectrometry (ICP-OES) as outlined by Bettinelli et al. (2000).

Incubation experiment

Native tree leaf litter was collected in the municipality of São Sebastião da Vargem Alegre, State of Minas Gerais, Brazil (21° 4′ 13″ S, 42° 38′ 14″ W; 780 m elevation). The annual precipitation is generally between 1,000-1,200 mm, with a maximum annual temperature of 26.4 °C and a minimum of 14.8 °C. The area in which the tree leaf litter were collected was a post-mined bauxite mine in a long-term experimental with native and exotic species (Supplementary Material 2).

The experiment was installed in a randomized block design in an incubation room (temperature ~ 25 °C in dark), with four replicates, in which soil samples were placed together without and with 17 tree leaf litters. The 16 species in the mixed native forest and a clonal eucalyptus were divided into two groups: i) Legume: *Anadenanthera peregrina* (L.)[1], *Inga edulis* Mart.[1], *Piptadenia gonoacantha* (Mart.)[1], *Enterolobium contortisiliquum* (Vell.) Morong[1], *Apuleia leiocarpa* (Vogel) JF Macbr.[2], *Paubrasilia echinata* Lam. Gagnon[2] and *Hymenaea courbaril var.* stilbocarpa (Hayne) YT Lee & Langenh[2] and ii) Non-legume: *Pera glabrata* (Schott) Poepp. ex Baill.[1], *Ficus insipida* Willd[1], *Sapindus saponaria* L.[1], *Annona squamosa* L.[1], *Trichilia* sp.[2], *Cupania oblongifolia* Mart.[2], *Handroanthus chrysotrichus* (Mart. Ex A. DC.) Mattos[2], *Lecythis* sp.[2], *Ceiba speciosa* (A.St.-Hil., A.Juss. & Cambess.) Ravenna[2] and clonal *Eucalyptus*[3] (clone AEC144®).

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[1] The pioneers which are those species most effective at growing in new ecosystems.

[2] The non-pioneers that are most successful after an ecosystem has been developed by the pioneer species.

[3] An exotic and commercial hybrid cross between *Eucalyptus urophylla* and *Eucalyptus grandis*.

Gases analysis

The experiment lasted 888 h, with air samplings collected at 4, 12, 24, 36, 60, 84, 132, 156, 180, 204, 240, 276, 312, 360, 408, 468, 540, 612, 708 and 888 h (a total of 37 days). Two different 60 mL needle-head syringes penetrated into the lid of the pots to take 120 mL of air at each interval. Before extracting air from the pot, each of the syringes was pumped four times to ensure the air inside was mixed and representative of the air quality inside. Each block was sampled individually, and the air was refreshed outside after each interval. The syringes were stored in the same room as the pots. A prior laboratory analysis indicated they retained air quality for up to 14 days. After every sampling interval, the glass pots were rotated to avoid bias based on location in the room.

To determine C-CO_2 concentration and δ^{13}C-CO_2, both syringes were connected to a Cavity Ring Down Spectroscopy (CRDS) device (Picarro G 2121-i isotopic carbon-analyzer), and the 120 mL of air was passed through a hose connected to both syringes simultaneously. Once obtained the C-CO_2 concentration, the contribution of different litters and the soil to C-CO_2 emissions were calculated according to equation 2 (Stewart et al., 2009; Haddix et al., 2016).

$$f_{bf} = \left(\frac{\delta t - \delta s}{\delta r - \delta s}\right) \tag{Eq. 2}$$

in which: f_{bf} is the proportion of C that can be attributed to the litter in the given sample; δt is the δ^{13}C-CO_2 (‰) of the gas sample; δs is the δ^{13}C (‰) of the soil sample only control group; δr is the δ^{13}C (‰) of the original litter. To determine the weight of litter-derived C in each air sample, the f_{bt} value was multiplied by the total C weight of each sample.

Two non-linear models and single exponential model (Jones, 1984; Bonde and Rosswall, 1987) were tested to fit the litter decomposition kinetics. However, the litter decomposition kinetics was fitted only with a single exponential model (Supplementary Material 3 and 4) using SigmaPlot statistical package (SigmaPlot 14.0), while the first-order model was chosen due to a better fit. The first-order kinetic model is expressed in equation 3.

$$C = C_0\left(1 - e^{-kt}\right) \tag{Eq. 3}$$

in which: C is the cumulative C-CO_2 evolution; C_0 is the potentially mineralizable C (mg g^{-1}); k is the decomposition rate constant (h^{-1}); t is the time of incubation (hours); and e is the natural constant. The regression procedure optimized parameter values C0 and k in the simulation models. However, the first-order exponential model provided a good fitting tool for litter decomposition.

Then, we calculated the total priming effect (PE) for each litter according to Kuzyakov (2006), using equation 4.

$$PE(\%) = \left[\left(C{-}CO_{2_{\text{Soil Trat}}} - C{-}CO_{2_{\text{Soil}}}\right) \Big/ C{-}CO_{2_{\text{Soil Control}}}\right] \times 100 \tag{Eq. 4}$$

in which: PE is the Priming effect (%); C-$CO_{2\ \text{Soil Trat}}$ is the total C-CO_2 soil-derived with different litter additions (mg g^{-1}); and C-$CO_{2\ \text{Soil Control}}$ is the total C-CO_2 soil-derived without litter addition (mg g^{-1}).

C and N in soil organic matter fractions

After being incubated for 888 h, the soil samples were submitted to physical fractionation, obtaining the light organic matter (LOM) and the heavy fraction (HF), according to Cambardella and Elliott (1992). Subsequently, the heavy fraction was further fractionated to obtain particulate organic matter (POM) and mineral-associated organic matter (MAOM), also following the methodology of Cambardella and Elliott (1992).

Three grams of post-incubated material were added to a solution of 1:1.6 water: sodium iodate in 30 mL tubes. The tubes were then agitated before being placed into a centrifuge at 20 °C and 1.300 rpm for 15 min. The LOM became separated, floated to the top, was extracted with a spatula, rinsed with deionized water, and the contents were placed into a pre-weighed plastic cup and stored in vials at room temperature.

The heavy fraction (HF) that remained in the tube was rinsed with deionized water and placed into a pre-weighed plastic cup. The LOM and HF samples were then placed in a furnace at 60 °C until dry and the quantified mass. The HF sample was then put in 30 mL of sodium hexametaphosphate (5 g L^{-1}) and shaken for 15 h in a reciprocal shaker at 120 rpm. The solution was then passed through a 53 µm sieve, which captured the POM. The POM was rinsed thoroughly with deionized water and poured into a preweighed plastic cup. As this happened, the MAOM fraction had passed through the sieve into a pre-weighed plastic cup. Both POM and MAOM samples were placed in a furnace at 60 °C until dry and reweighed. The contents were then stored in vials at room temperature.

In sequence, in the samples from the LOM, POM and MAOM fractions, were determined the C, N contents and $\delta^{13}C$ values using IRMS (20-20, SerCon Co., UK.) interfaced with an automatic N and C analyzer (ANCA-GSL, SerCon Co., UK). The $\delta^{13}C$ values to partition the litter-derived C for each of the fractions by calculating the f_{bt} value using the previously outlined equation 2. Due to the susceptibility of the fractionation process to human error, it was necessary to average the litter-derived C weight of the fractions and respiration in relation to the amount of litter-derived C added, using the following equation 5.

$$FracC_{XFinal} = \frac{FracC_1}{\left(FracC_1 + FracC_2 + FracC_3 + CR_{Lit/S}\right)} \times LCA \qquad \text{Eq. 5}$$

in which: $FracC_{XFinal}$ is the corrected weight of litter-derived C within a given fraction (mg); $Frac_X$ is the litter-derived C weight from each different fraction (mg); $CR_{Lit/S}$ is the cumulative weight of litter-derived C respired by a particular sample (mg) and *LCA* is the litter C added (mg). This equation ensured the sum of litter-derived C in the LOM, POM, MAOM fractions, and respiration was equal to the total amount of litter C added.

Using these corrected weights of litter-derived C in the POM and MAOM fractions allowed us to calculate the Soil Organic Matter Formation Efficiency (SOMFE) percentage as outlined by Cotrufo et al. (2015) (Equation 6).

$$SOMFE\% = \frac{FracC_F}{\left(LCA\text{-}C_{Fractions}\right)} \qquad \text{Eq. 6}$$

in which: *SOMFE%* is the % of decomposed litter C which became incorporated into a given fraction; $FracC_F$ is the corrected weight of litter-derived C within a given fraction (mg); LCA is the amount of litter C added to each pot (mg); and $C_{Fractions}$ is the weight of litter-derived C in MAOM and POM fraction (mg).

Statistical Analysis

Data normality was tested using a Shapiro-Wilk test ($p<0.05$), and the homogeneity of variances was tested using Levene test ($p<0.05$). A one-way ANOVA was applied to investigate the significant effects of organic matter addition in treatments with and without litter derived from leaf litter from legume and no-legume trees (native and exotic). The Skott-Knott Test was used to test significant differences between treatments ($p<0.05$). Principal components analysis (PCA) and Spearman correlation were also carried out, which are available in Supplemmentary Material 5. Statistical analyses were performed with SigmaPlot version 14.0 (Systat Software, San Jose, CA).

RESULTS

Mineralization kinetics of litter-derived C from native and exotic tree species and accumulated C in soil and initial stoichiometric characteristics of C, N and P

Table 2 presents the chemical characterization of the 17 residues evaluated. The highest nitrogen contents and the lowest C:N ratios were observed for *P. gonoacantha* (legume) and *A. squamosa* (non-legume), respectively. *Lecythis* sp. (non-legume) had the highest P content and C/P: 627 and N/P: 35 ratios. The clonal eucalyptus and the leguminous species *H. courbaril* showed elevated C:N ratios, with values of 32 and 26, respectively.

The soil exhibited the most intense C-CO_2 emission in the initial 204 hours of incubation, indicating substantial degradation of the native SOM. Treatments with non-legume residues (*C. speciosa*, *S. saponaria* and *Trichilia* sp.) resulted in a significantly higher increase in cumulative C-CO_2 emission than other residues (Figure 1a). In contrast, the treatments with legume residues (*I. edulis*, *P. gonoacantha*, *H. courbaril* and *A. peregrina*) showed slower C mineralization kinetics, resulting in lower C-CO_2 emission derived from these residues.

It is evident that different species contributed significantly to respiration during incubation (Figure 1b). The non-legume group *Trichilia* sp., *C. speciosa,* and *S. saponaria* showed the highest mean values for emission (1.44, 1.78, and 1.70 mg g^{-1}, respectively). On

Table 2. Relative $\delta^{13}C$, N, P and C contents and their respective C:N, C:P and N:P ratios of different residues from leguminous and non-leguminous species

Groups	Species	$\delta^{13}C$	N	P	C	C:N	C:P	N:P
		‰	—— % ——					
Legume	*A. leiocarpa*	-30.18	2.71	0.11	45.46	17	433	26
	A. peregrina	-28.57	2.90	0.12	48.01	17	390	24
	E. contortisiliquum	-28.08	3.03	0.11	48.08	16	425	27
	H. courbaril	-28.75	1.83	0.11	48.24	26	427	16
	I. edulis	-29.53	3.26	0.16	45.46	14	291	21
	P. echinata	-29.69	2.44	0.13	46.69	19	371	19
	P. gonoacantha	-28.45	3.79	0.11	56.17	15	497	34
Non-legume	*A. squamosa*	-30.62	3.41	0.19	42.12	12	224	18
	C. oblongifolia	-28.13	3.15	0.16	56.67	18	350	19
	C. speciosa	-27.73	2.95	0.15	41.81	14	277	20
	Clonal *Eucalyptus*	-31.06	1.53	-	48.40	32	-	-
	F. insipida	-30.82	2.21	0.13	39.98	18	320	18
	H. chrysotrichus	-30.31	3.24	0.15	43.10	13	293	22
	Lecythis sp.	-27.28	2.49	0.07	45.14	18	627	35
	P. glabrata	-28.75	2.98	-	44.94	15	-	-
	S. saponaria	-30.44	3.16	0.22	45.03	14	205	14
	Trichilia sp.	-30.58	2.64	0.20	43.98	17	216	13

- values not detected.

the other hand, legume species *A. peregrina*, *I. edulis*, *H. courbaril* and *P. gonoacantha* presented the lowest mean emission values, with *I. edulis* notably registering 0.43 mg g^{-1}.

The potentially mineralizable C (C_0) ranged from 0.41 to 1.81 mg g^{-1} (Table 3). Higher C-CO_2 emissions from non-legume residues (*C. speciosa*, S. saponaria and *Trichilia* sp.) reflected in higher amounts of mineralized C: 1.81, 1.74, and 1.48 mg g^{-1}, respectively. Residues from *I. edulis* and *P. gonoacantha* resulted in the lowest C-CO_2 emissions, indicating lower mineralization of C from these residues (0.41 and 0.47 mg $g^{-1,}$ respectively). Eucalyptus residues showed an intermediate mineralization rate among the evaluated residues with C_0 of 0.71 mg g^{-1} (Table 3).

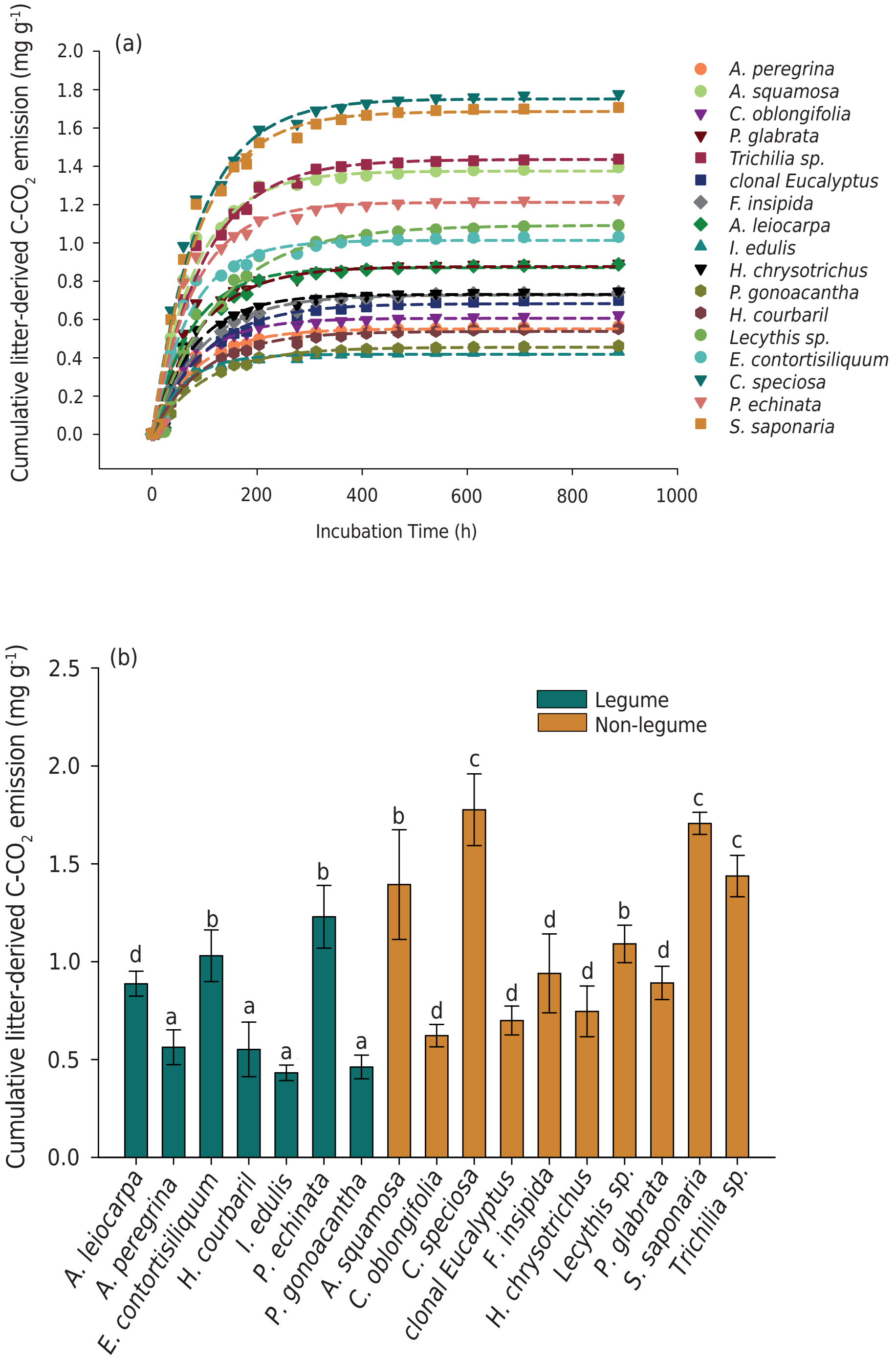

Figure 1. Cumulative litter-derived C-CO_2 emission during the 888 hours incubation period for 17 residues trees from Atlantic Forest with the soil. Mean separated by the same lowercase letters are not significantly different at $p<0.05$. Vertical bars denote standard error (n = 4).

I. edulis residue showed the highest decomposition constant rate (k) (0.0105 h^{-1}), with a half-life equivalent to 66 h (Table 3). Regarding the half-life of residues, the non-legume *Lecythis* sp. residue demonstrated greate recalcitrance, with a longer mean decomposition time (120 h). Apart from the treatment with *I. edulis* residues, *E. contortisiliquum* and *P. glabrata* showed shorter half-lives, 77.0 and 77.9 h, respectively.

Priming effects

The priming effect (PE) was positive for all litters applied, except for *A. peregrina* litter (Figure 2).

Soil organic matter fractions

In the LOM fraction, the contribution of C derived from the residue varied from 4.00 to 10.74 mg g^{-1} (Figure 3a). The POM fraction ranged from 1.08 to 3.70 mg g^{-1} for the residues (Figure 3b). Higher contributions of C and N in the MAOM fraction (Figure 3c and 3f), ranging from 14.20 to 17.11 mg g^{-1} and 1.36 to 1.93 mg g^{-1} respectively. The contribution of forest residues to MAOM ranged from 15.76 to 18.48 mg g^{-1} (Figure 3c).

There were significant differences ($p<0.05$) in the contribution of C in the LOM fraction. The leguminous forest species *A. peregrina* and *P. echinata* showed the highest contributions, while *C. speciosa* the lowest contribution derived from the residue (Figure 3a). The lowest levels of N-LOM derived from residue+soil (Figure 3d) for the species *C. oblongifolia*, clonal *Eucalyptus*, *H. courbaril*, *Lecythis* sp., *E. contortisiliquum*, *C. speciosa* and *S. saponaria*. As for the C derived from the residue in the POM fraction (Figure 3b), only the residue from the non-leguminous species *C. speciosa* made a greater contribution ($p<0.05$). No significant differences for the soil C-POM, residue-derived C-MAOM+soil and soil N-MAOM fractions from the contribution of the different species evaluated (Figures 3b, 3c and 3f).

Table 3. Estimated potentially mineralizable C (C_0), decomposition rate constant (k), half-life time ($t_{1/2}$), and coefficients of determination (R^2) from the 17 exotic and native tree residues using the first-order exponential model of cumulative litter-derived C-CO_2 emissions

Groups	Tree species	C_0	k	$t_{1/2}$	R^2
		mg g^{-1}	h^{-1}	h	
Legume	*A. leiocarpa*	0.91**	0.0077**	90.0	0.91
	A. peregrina	0.57**	0.0081**	85.6	0.80
	E. contortisiliquum	1.04**	0.0090**	77.0	0.81
	H. courbaril	0.56**	0.0071**	97.6	0.58
	I. edulis	0.41**	0.0105**	66.0	0.86
	P. echinata	1.25**	0.0084**	82.5	0.79
	P. gonoacantha	0.47**	0.0069**	101.0	0.85
Non-legume	*A. squamosa*	1.42**	0.0083**	83.5	0.66
	C. oblongifolia	0.63**	0.0084**	82.5	0.90
	C. speciosa	1.81**	0.0077**	90.0	0.86
	Clonal *Eucalyptus*	0.71**	0.0070**	99.0	0.88
	F. insipida	0.97**	0.0059**	118.0	0.70
	H. chrysotrichus	0.76**	0.0084**	82.5	0.71
	Lecythis sp.	1.14**	0.0058**	120.0	0.89
	P. glabrata	0.90**	0.0089**	77.9	0.90
	S. saponaria	1.74**	0.0078**	88.9	0.97
	Trichilia sp.	1.48**	0.0072**	96.3	0.92

** Significant difference ($p<0.01$). $C_m = C_L + C_R * [1 - \exp(-k * x)]$. The equation represents an Exponential Rise to Maximum (ERM) model with a single equation and three parameters.

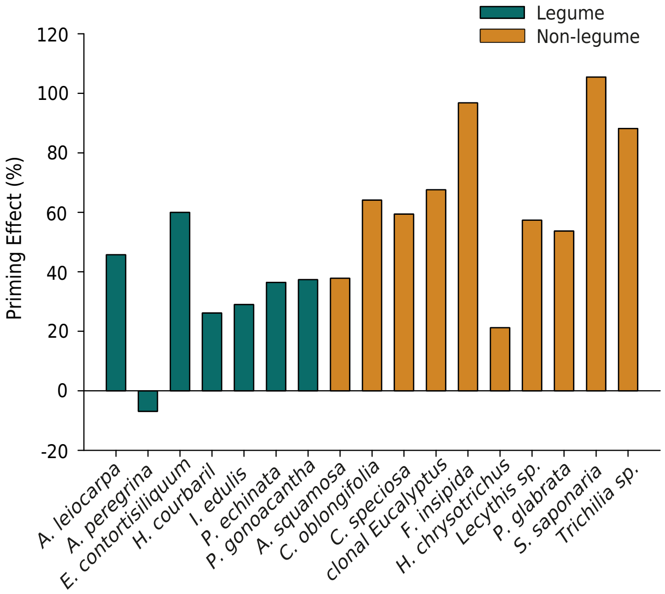

Figure 2. Cumulative priming effect (%) after 888 hours incubation period for 17 different residues of trees from Atlantic Forest with the soil.

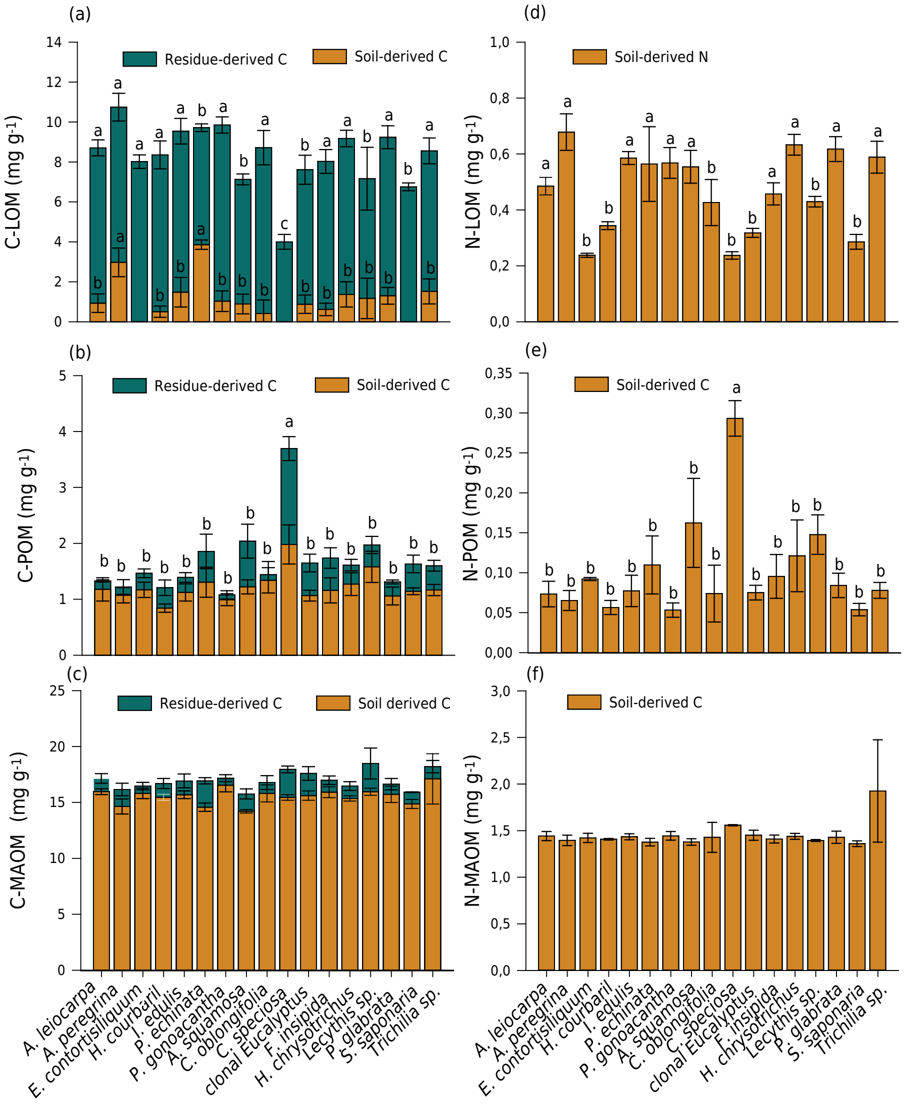

Figure 3. Residue derived-C, soil derived-C (a-c), and N (d-f) from organic matter fractions LOM, POM and MAOM after 888 hours incubation period for 17 different residues of trees from Atlantic Forest with the soil. Vertical bars denote standard error (n = 4).

The partitioning of litter-derived C showed differences among the residues (Figure 4). The amount of litter-derived C found in the LOM, POM and MAOM fractions ranged from 64.9 to 83.3 %; 1.02 to 7.6 %, and 6.5 to 16.6 %, respectively. The loss of C-CO_2 ranged from 5.6 to 20.1% (Figure 4). The leguminous species *P. gonoacantha* (83.3 %), *H. courbaril* (83.1%), *I. edulis* (82.6 %) and the non-leguminous species *H. chrysotrichus* (82.3 %) made the largest contributions to C partitioning in the LOM fraction. As for the POM fraction, the greatest contributions came from non-leguminous species: *Trichilia* sp. (7.6 %), *A. squamosa* (6.6 %), and *P. glabrata* (6.2 %). *A. squamosa* (non-leguminous), clonal *Eucalyptus* (non-leguminous) and *A. peregrina* (leguminous) had a MAOM formation potential of more than 15 %. Lower CO_2 fluxes in the legumes *A. peregrina*, *P. gonoacantha* and *I. edulis* and the non-legume *H. chrysotrichus*.

SOM formation efficiency

The efficiency of SOM formation (POM+MAOM; SOMFE) varied between 4.5 and 19.3 % between the different beds (Figure 5). The highest SOMFE was for the clonal *Eucalyptus* (19.3 %), followed by *I. edulis* (18.6 %) and *A. peregrina* (14.6 %), while the lowest was for *S. saponaria* (4.5 %).

DISCUSSION

Stoichiometric characteristics, decomposition, mineralization and respiration

Tree species found in the Atlantic Forest can impact litter decomposition dynamics due to the distinct qualities of their litter-forming residues. Leaves constitute more than 70 % of the litter composition that accumulates on the soil surface in tropical forests (Singh et al., 2021). Carbon enters the system mainly through litterfall and rhizodeposition, returning to the atmosphere as CO_2 through roots and microbial respiration (Díaz-Pinés et al., 2011). The quality and quantity of litter from different tree species influence the decomposition processes and C dynamics in forest soils (Ahmed et al., 2016; Liang et al., 2021). These processes are influenced by the physicochemical environment, the levels of C, N, P, K, Ca, lignin, cellulose and hemicellulose present in the plant material (Bohara et al., 2020; González et al., 2022; Tzec-Gamboa et al., 2023).

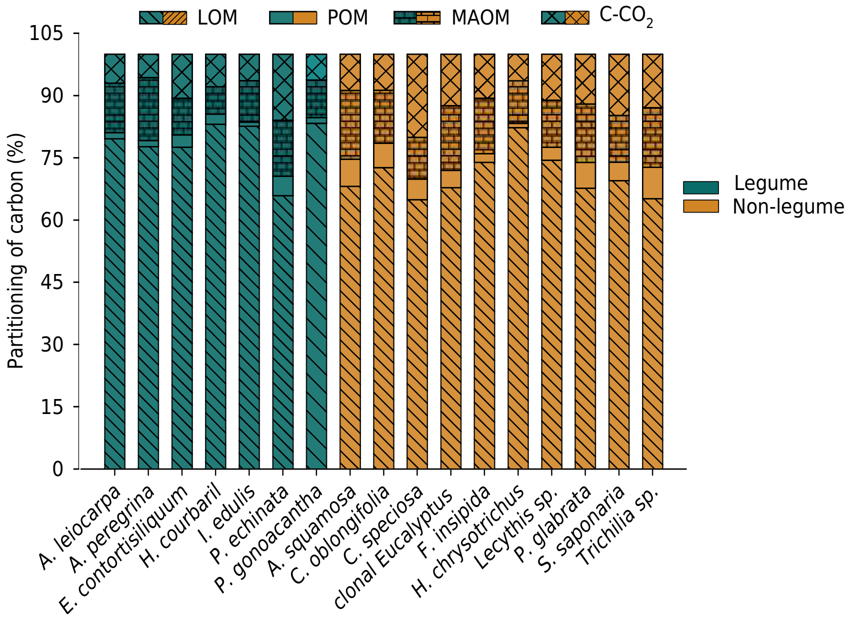

Figure 4. Partition of litter-derived C in the Light organic matter (LOM), Particulate Organic Matter (POM), Mineral associate organic matter (MAOM) fractions and C-CO_2 emissions after 888 hours incubation period for 17 different residues of trees from Atlantic Forest with the soil.

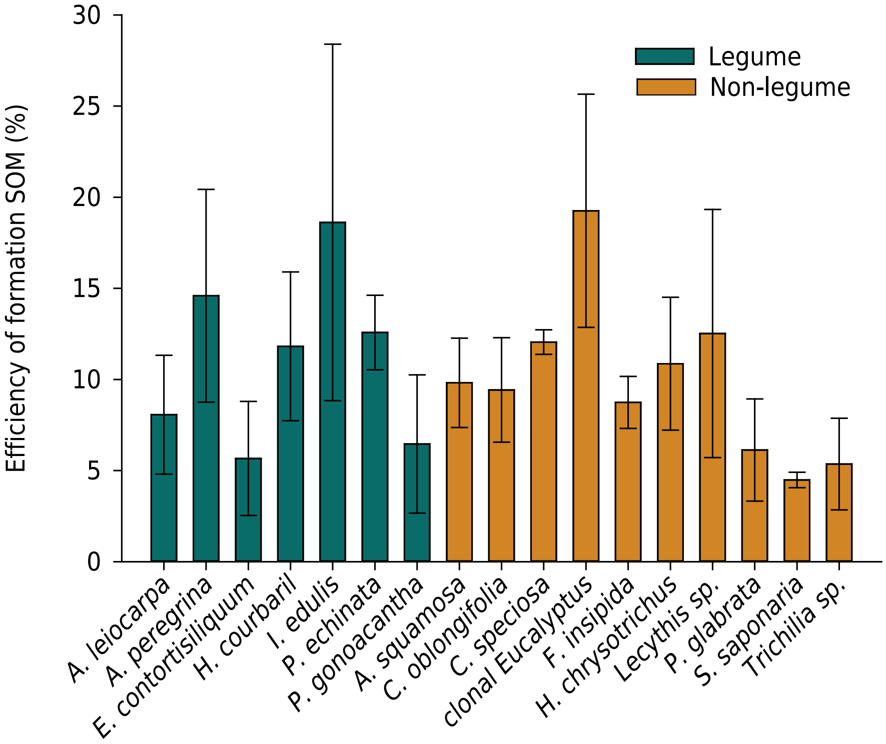

Figure 5. Soil organic matter formation efficiency (SOMFE) after 888 hours incubation period for 17 different residues of trees from Atlantic Forest with the soil. Vertical bars denote standard error (n = 4).

More than 20 % of the CO_2 emissions from the soil originate from microbial decomposition (Krishna and Mohan, 2017). The cumulative emission of C-CO_2 increased noticeably with incubation time (especially in the first 204 hours), followed by a stabilization of the curve. Previous studies suggest that this initial increase and subsequent decline in the curve reflect a decrease in the rate of C mineralization (Xu et al., 2011). Understanding C storage in the soil involves the processes of incorporation, transformation, and complete mineralization of residues (Cao et al., 2019). In addition, a slower decomposition process contributes to increased organic matter and nutrient availability in the soil (Isaac and Nair, 2005).

The addition of different leaf litter influenced the cumulative C-CO_2 derived from litter, indicating an early increase in C_0 with the addition of organic residue, suggesting that C_0 is dependent on the amount of residue input. Mineralization is extremely important for the accumulation of nutrients in the soil, indirectly impacting the establishment and development of cultivated species (Silva et al., 2021). The potential for C mineralization showed variation among different residues. Legume residues from the forest species *I. edulis*, *P. gonoacantha*, *H. courbaril* and *A. peregrina* showed slower mineralization (0.41, 0.47, 0.56 and 0.57 mg g^{-1}, respectively), resulting in lower C losses over the evaluated period. Forest soils release CO_2 through soil respiration, allowing C to be released from the soil reservoir into the atmosphere (Lee et al., 2023). The decomposition of leaf litter contributes between 5 and 45 % to soil respiration (Li et al., 2021).

The k values obtained in this study are in the range of 0.0058 to 0.0105. It is known that litter from forest species generally has k <1, and a lower k value indicates a slower decomposition of residues (Rawlik et al., 2022), which aligns with the results found. For example, *Lecythis* sp. (non-leguminous) had the lowest k values (0.0058) and P contents and the highest C:P and N:P ratios, thus suggesting better degradability.

Non-leguminous species, *C. speciosa* (C/N ratio:14), *S. saponaria* (C/N ratio:14), and *Trichilia* sp. (C/N ratio:17), showed faster decomposition and greater mineralization potential. Leppert et al. (2017) also observed higher decomposition rates for *S. saponaria*. Residues with high levels of more labile compounds are expected to demonstrate greater potential for mineralization and high CO_2 emissions due to the faster action of soil microbiota compared to more recalcitrant compounds (Uwamahoro et al., 2023). In addition, rapid decomposition and mineralization contributed to increased N availability in the soil (Martínez-García et al., 2021; Rawlik et al., 2022), considering the high initial N contents in the leaves of these species.

Among the indicators of litter quality, the N and P contents as well as the C:N, C:P, and N:P ratios, have allowed the assessment of decomposition rates and nutrient cycling (Gong et al., 2020; Li et al., 2022). The C:N, C:P and N:P ratios ranged from 12 to 32, 205 to 627 and 13 to 35, respectively. Previous studies have suggested that C:N and C:P ratios exceeding 25 and 900, respectively, along with N:P ratios below 16, have the potential to immobilize N and P (Arunachalam et al., 1998; Aerts and Chapin, 1999; Moore et al., 2006). Low C:N and C:P ratios lead to faster decomposition of the material (Bohara et al., 2020), and therefore, microorganisms consume these residues more quickly (Zhu et al., 2015), with the potential for greater release of these nutrients into the soil (Yue et al., 2021).

High decomposition rates in the initial days of incubation are expected due to the composition and nutrient concentration of the residues and the fact that they favor the rapid action of decomposing microorganisms (Awasthi et al., 2022; Siqueira et al., 2022). In a study on short-term decomposition, Aerts and Caluwe (1997) observed a strong correlation between initial decomposition in the first three months and litter quality in terms of initial P content. High levels of P in litter are advantageous for tropical forest soils with low P availability (Ge et al., 2013; Zhang et al., 2022). Therefore, species such as *S. saponaria* and *Trichilia* sp. can be beneficial in reforestation and recovery areas due to their potential to supply P. The high initial availability of N and P in residues is crucial for the activity of decomposer microorganisms, with their lability and solubility in water favoring accessibility and action (Zhang et al., 2018; Pereira et al., 2023).

Leguminous species *I. edulis* stood out from the others due to its lower respiration rates and reduced mineralization potential (Leblanc et al., 2006; Duarte et al., 2013) observed lower rates of decomposition and nutrient release in *Inga* sp. The decomposition rates of litter are highly specific to each species, as its chemical and stoichiometric characteristics determine the attractiveness of the residue to soil-decomposing microorganisms (Leppert et al., 2017). Thus, the slower decomposition and shorter half-life observed in *I. edulis* may be attributed to its unique chemical composition and morphological characteristics. Combining these characteristics can benefit reforestation by enhancing nutrient cycling and increasing N levels in the SOM (Palm and Sanchez, 1991; Leblanc et al., 2006).

Eucalyptus clonal had the highest C:N ratio (32), a half-life of 99 hours, intermediate decomposition, and the lowest initial N content (1.53 %). The C:N ratio is higher than that observed in the Atlantic Forest biome and subtropical regions, which generally range from 25 to 31 (Souza et al., 2016; Akoto et al., 2022; Chen et al., 2023). Thus, eucalyptus leaf litter decomposes more slowly, providing more permanent soil cover, due to its recalcitrant nature and high polyphenol content (Vargas and Hungria, 1997; Cizungu et al., 2014). In addition, the low nutrient availability in litter makes it less attractive to decomposing microorganisms (Patoine et al., 2020).

Priming effects

Non-additive interactions can result in an increased release of the soil-derived carbon as CO_2, $N\text{-}NH_4^+$ or $N\text{-}NO_3^-$, compared to soil mineralization without any additions. These interactions are summarized under the generic term “priming effects” (Kuzyakov et al., 2000). Priming effects are influenced by the quality and quantity of plant residue added to the soil (Shahbaz et al., 2017; Chen et al., 2022), the frequency of addition (Wu et al., 2020), the chemical and biochemical composition of the plants (Fanin et al., 2020) and the C:N ratio (Tian et al., 2023), leading to the occurrence of the priming effect (Kuzyakov et al., 2000).

Microorganisms can employ different mechanisms to mineralize and decompose plant residues in the soil (Su and Shangguan, 2023). These mechanisms can coexist in the same environment and vary over time (Fanin et al., 2020), directly influencing the priming effect (Yan et al., 2023). Positive priming effects for the leguminous (except for *A. peregrina*) and non-leguminous evaluated species, demonstrating the potential of their residues in relation to the decomposition and mineralization of C. Positive priming effect is explained by the co-metabolism hypothesis, involving an increase in microbial growth and activities (Kuzyakov et al., 2000). Greater availability of C and nutrients fosters greater microbial activity and, consequently, greater mineralization (Zhang et al., 2021).

Different theories explain negative and positive effects, including preferential substrate use, co-metabolism, and mineralization of microbial N (Qiu et al., 2022). More labile residues with a low C:N ratio are expected to induce a negative priming effect (Liu et al., 2017; Zhu et al., 2021). The negative effect observed for *A. peregrina* can be partly explained by the theory of preferential substrate use, given its more labile biochemical composition and a high concentration of N (Valente et al., 2023). In this way, soil microorganisms tend to preferentially use this base material for their nutritional supply (due to its low energy cost) rather than using the soil's native C, leading to the occurrence of the negative priming effect (Kuzyakov, 2006). Another important point is the small size of *A. peregrina* leaflets, which can facilitate the decomposition process by soil microorganisms (Valente et al., 2021, 2023).

Soil organic matter fractions and formation efficiency

The litter of *A. peregrina* (leguminous plant) contributed significantly to C stocks in the LOM fraction, both in terms of C derived from residues and the soil. In addition, figure 4 shows how this fraction contributed more than 60 % to the partitioning of C derived from the litter. The LOM is of paramount importance for soil quality, given its ability to be easily decomposed by microorganisms and provide nutrients for plants (Li et al., 2022). Changes over a short period are expected in the more labile fractions of SOM, such as the light fraction (Loss et al., 2012), which can be associated with LOM in this case. The LOM fraction consists of fresh plant materials, root exudates and plant-derived polymers that lack protection from aggregates, leading to rapid cycling given their high lability (Haynes, 2000; Zhu et al., 2020).

Residues of *C. speciosa* (non-legume) showed different behavior in relation to LOM and POM, with a greater contribution of C and N to the latter. The greater persistence of C and N from this species in the POM can be explained by intrinsic characteristics of the species, such as low C:N ratio, high rates of mineralization and CO_2 efflux, as well as enhanced physical protection within aggregates (Cotrufo et al., 2019). Tree species with high N contents in their residues are able to enrich the soil N reservoirs through their litter (Osborne et al., 2021), as the action of decomposing microorganisms is not constrained by the availability of this element (Cotrufo et al., 2013).

Leaf litter contribution to the soil is important for increasing SOM, but the SOM formation efficiency (SOMFE) depends on the degree of residue decomposition (Núñez et al., 2022). The species that showed the highest SOMFE included the eucalyptus clone, a result similar to that observed by Almeida et al. (2018); followed by the leguminous species *I. edulis* and *A. peregrina*. We suggest grouping species based on litter respiration and the most labile materials, contributing to POM and MAOM formation.

The process of forming SOM from litter involves material decomposition with subsequent assimilation of C by soil microorganisms and microbial necromass (combined dead microbial products and residues), which is stabilized through physical or chemical protection (Cotrufo et al., 2015; Liang et al., 2017; Wei et al., 2021). These processes are influenced by biochemical composition (Almeida et al., 2018); nutrient supply at adequate levels (Almeida et al., 2021); residue input and lability (Liang et al., 2017; Prescott and Vesterdal, 2021); C:N ratio (Eastman et al., 2022) and suitable conditions for microbial activity, especially temperature and humidity (Silva et al., 2022). Enhancing SOMFE is crucial for maintaining fertility, soil physical characteristics and C sequestration (Xu et al., 2022). However, it is important to note that high SOMFE does not necessarily guarantee the absence of C loss from the incorporated plant residue (Cotrufo et al., 2015; Angst et al., 2021).

Leguminous species *I. edulis*, *A. peregrina*, *H. courbaril* and *P. gonoacantha* showed the greatest efficiencies and contributions to the formation of MAOM. Plant residues with a low C:N ratio are decomposed more efficiently by soil microorganisms, thereby contributing to the formation of MAOM (Eastman et al., 2022; Cotrufo et al., 2022), either through direct association with minerals or after being metabolized by microorganisms (Liang et al., 2017; Fulton-Smith and Cotrufo, 2019). Formation of MAOM is more efficient at the early stages of the decomposition process, due to the higher presence of labile (low C:N ratio) and soluble compounds (Cotrufo et al., 2013, 2022; Fulton-Smith and Cotrufo, 2019; Lavallee et al., 2019). Thus, the more labile and soluble compounds found in leguminous species allow for more efficient decomposition and greater allocation in the MAOM and POM fraction.

Among the leguminous species, only *H. courbaril* had a high C:N ratio (26), characterizing its residues as recalcitrant, leading to increased persistence in the soil and greater resistance to decomposition. Siqueira et al. (2022) also found a high C:N ratio for this species, suggesting that its decomposition is constrained by N, even with nutrient concentrations surpassing critical levels. In addition, *H. courbaril* residues facilitated greater formation and accumulation of MAOM. Recalcitrant residues with a high C:N ratio tend to be more persistent in the soil, contributing to the formation of the MAOM fraction (Córdova et al., 2018; Zheng et al., 2021), due to the favoring of a certain group of microorganisms, such as bacteria (Soares and Rousk, 2019).

The choice of forest species for reforestation is based on the quantity and quality of litter, biomass production, and nutrient input (Wang et al., 2023). The contribution and maintenance of C in the SOM are of fundamental importance for soil fertility and climate change mitigation (Angst et al., 2021). Thus, the leguminous species *I. edulis*, *A. peregrina*, *H. courbaril* and *P. gonoacantha* and the clonal Eucalyptus (non-leguminous) demonstrate significant potential for reforestation programs given their contributions to the input of C and SOMFE, as well as their rapid growth, good wood production and potential for medicine use (Lorenzi, 2002; Oliveira et al., 2017; Marinho et al., 2021; Siqueira et al., 2022).

Planting of both native tree species is considered efficient in soil recovery within mining areas, exhibiting CO_2 emissions comparable to those found under native vegetation (Valente et al., 2021). Native species such as *A. peregrina* (legume), *C. speciosa* (non-legume), *E. contortisiliquum* (legume) and *P. gonoacantha* (legume) share desirable characteristics with eucalyptus, including rapid growth and ground cover, high litter production and leaf senescence during the dry season (Valente et al., 2021, 2023) in addition the potential to enhance the soil C and N stocks (Valente et al., 2019, 2022, 2023).

CONCLUSIONS

This study supports our hypothesis that the quality of the litter from different Atlantic Forest tree species has a significant influence on decomposition dynamics and the formation of soil organic matter. Leguminous species *A. peregrina*, *I. edulis*, *H. courbaril* and *P. gonoacantha* showed greater potential for improving soil quality, with slower decomposition and greater efficiency in forming soil organic matter, mineral-associated organic matter and particulate organic matter fractions.

The efficiency of soil organic matter formation varies substantially between the species studied. Among them, some legumes and clonal Eucalyptus stood out as the most promising options, showing their potential to promote an increase in soil quality. The results obtained reinforce the importance of selecting tree species with suitable functional characteristics in forest restoration projects. This study highlights the crucial role of the functional diversity of species in optimizing ecosystem services, especially with regard to soil quality and the carbon cycle.

SUPPLEMENTARY MATERIALS

Supplementary data to this article can be found online at https://www.rbcsjournal.org/wp-content/uploads/articles_xml/1806-9657-rbcs-49-e0240211/1806-9657-rbcs-49-e0240211-suppl01.pdf

DATA AVAILABILITY

The data will be provided upon request.

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