FOREST LITTER PRODUCTION VARIES WITH SEASON AND ELEVATION GRADIENT IN CHIAPAS, MEXICO †

[LA PRODUCCIÓN DE HOJARASCA FORESTAL VARÍA CON LA ESTACIÓN Y EL GRADIENTE DE ELEVACIÓN EN CHIAPAS MÉXICO]

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SUMMARY

Background. Forest litterfall is a fundamental process of ecosystem nutrient cycling, also, it is a source of energy for the development and propagation of wildfire. Understanding the temporal dynamics of litter production and storage is critical for sustainable management and conservation of forest ecosystems. **Objective.** To quantify the monthly production and storage of forest litter in an elevation gradient. **Methodology.** We selected forest sites at three elevations: 670, 775, and 1010 masl, corresponding to pine, oak, and tropical lowland forest ecosystems in Nambiyugua hill, Chiapas, Mexico. Sixteen sampling sites with a radius of 11.28 m were established for tree measurements, and 48 litter traps of 0.50 m^2 were installed to collect monthly litterfall for a year. To sample ground litter eight 30 by 30 cm^2 quadrats were used in each site. The fallen woody material was measured with the planar intersection method. Litter samples were oven-dried at 60 °C for 72 h and separated into leaves and other plant parts. One-way ANOVA was used to test the significant differences between forests. **Results.** The highest total loads of litter and fallen woody material were obtained in the pine forests of upper elevation with 29.01 t ha^{-1}. The highest litter production was obtained in January and April, with a mean of 1.34 ± 0.19 and 0.74 ± 0.13 t ha^{-1} respectively in pine forests. In the oak forest, the highest production occurred in March, with 1.08 ± 0.25 t ha^{-1}; while the lowland forest reached the highest production in January with 0.85 ± 0.26 t ha^{-1}, with a decreasing trend in June. **Implications.** Understanding the seasonal variability in litter production and forest fuel loads is crucial for forest productivity, carbon sequestration, and wildfire prevention **Conclusions.** The production of forest fuels was different among the ecosystems representing the elevation gradients. The highest monthly production of litter was registered during the January-May period for the pine and oak ecosystems but in November - January in tropical lowland forests.

Key words: Forest ecosystems; biomass storage; litter production; fallen woody material; pine forests; tropical forests

RESUMEN

Antecedentes. La producción de hojarasca forestal es un proceso fundamental en el ciclo de nutrientes de los ecosistemas, además, es una fuente de energía para el desarrollo y propagación de incendios forestales. Comprender la dinámica temporal de la producción y el almacenamiento de hojarasca es fundamental para la gestión sostenible y la conservación de los ecosistemas forestales. **Objetivo.** Cuantificar la producción y almacenamiento mensual de hojarasca forestal en un gradiente de elevación. **Metodología.** Seleccionamos sitios forestales en tres elevaciones: 670,

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775 y 1010 msnm, correspondientes a ecosistemas de bosques de pino, encino y tierras bajas tropicales en el cerro Nambiyugua, Chiapas, México. Se establecieron dieciséis sitios de muestreo con un radio de 11.28 m para mediciones de árboles y se instalaron 48 trampas de hojarasca de 0.50 m^2 para recolectar hojarasca mensual durante un año. Para muestrear la hojarasca del suelo se utilizaron ocho cuadrados de 30 por 30 cm^2 en cada sitio. El material leñoso caído se midió con el método de intersección plana. Las muestras de hojarasca se secaron en estufa a 60 °C durante 72 h y se separaron en hojas y otras partes de la planta. Se utilizó ANOVA unidireccional para probar las diferencias significativas entre bosques. **Resultados.** Las mayores cargas totales de hojarasca y material leñoso caído se obtuvieron en los pinares de mayor elevación con 29.01 t ha^{-1}. La mayor producción de hojarasca se obtuvo en enero y abril, con una media de 1.34 ± 0.19 y 0.74 ± 0.13 t ha^{-1} respectivamente en los pinares. En el bosque de encino la mayor producción se presentó en marzo, con 1.08 ± 0.25 t ha^{-1}; mientras que el bosque de tierras bajas alcanzó la mayor producción en enero con 0.85 ± 0.26 t ha^{-1}, con una tendencia decreciente en junio. **Implicaciones**. Comprender la variabilidad estacional en la producción de hojarasca y las cargas de combustible forestal es crucial para la productividad forestal, el secuestro de carbono y la prevención de incendios forestales. **Conclusiones.** La producción de combustibles forestales fue diferente entre los ecosistemas que representan los gradientes de elevación. La mayor producción mensual de hojarasca se registró durante el período enero-mayo para los ecosistemas de pino y encino, pero en noviembre-enero en los bosques tropicales de tierras bajas.

Palabras clave: Ecosistemas forestales; almacenamiento de biomasa; producción de hojarasca; material leñoso caído; bosques de pinos; bosques tropicales

INTRODUCTION

Forest litter is the fundamental component of the ecosystem, it is the source of energy for the development of fire, but also the means of nutrient cycling and soil fertility improvement (Arellano *et al*., 2017, Jaramillo *et al*., 2023). Forest litter is mostly composed of senescent leaves, dead branches and bark, flowers, fruits, and seeds. The production and decomposition are important processes of ecosystem functioning. This process transfers energy and nutrients from biomass to the soil. Litter production is also an important part of the net primary productivity (NPP) of ecosystems (López *et al*., 2013; Sánchez-Silva *et al*., 2022). The balance between production and decomposition determines the litter mass stock on the forest soil surface. The quantification of litterfall is important for understanding forest productivity, carbon dynamics, and the ability of forest ecosystems to recover from anthropogenic and natural disturbances (Aryal *et al*., 2015; Williams-Linera *et al*., 2021). Furthermore, understanding the seasonal variability of litter production and storage is crucial for forest fuel load management and the prevention of wildfires. Seasonal dynamics of litterfall can also be the basis for modeling forest ecosystem responses to climate change (Scheer *et al*., 2011; Sánchez-Silva *et al*., 2018).

However, seasonal litterfall production differs with environmental variables, and ecosystem type (Becker *et al*., 2015; Ruiz *et al*., 2022). Different landforms create a gradient of forest ecosystems within the same region in many parts of the world. In Chiapas, located in southern Mexico, forest ecosystems on the upper, middle part, and lower parts of the hills are different within a short distance due to topographical variability (Aryal *et al*., 2022). Hence, we hypothesized that the production of forest litter and storage differ with such a gradient of elevation (Chen *et al*., 2023; Takeda and Takahashi, 2020; SoiBecker *et al*., 2015).

Globally, studies of litter production and forest fuel storage have been conducted (Scheer *et al*., 2011; Zhou *et al*., 2014). However, the dynamics of seasonal litterfall production and forest fuel storage, are not well known in the elevation gradient in regions like Chiapas, Mexico, located in causing poor decisions on forest management and conservation practices (Rodríguez *et al*., 2020). Ecosystem-specific studies on the seasonality of litter production and forest fuel load would help in better planning of wildfire prevention programs, ecosystem productivity, and carbon sequestration strategies. Therefore, the main objective of this study was to quantify the monthly production and storage of forest litterfall in an elevation gradient of the Nambiyugua hill in Chiapas, Mexico, corresponding to pine, oak and tropical lowland forest ecosystems.

MATERIALS AND METHODS

The research was carried out in three clusters considering an elevation gradient: 1) 670 masl (tropical lowland rainforest), 2) 775 masl (oak forest), and 3) 1010 masl (pine forest) of Nambiyugua hill in the municipality of Villaflores, Chiapas (Figure 1) in Mexico. The municipality of Villaflores is located on the border of the Central Depression and the Sierra Madre de Chiapas, with a predominantly mountainous terrain. The Nambiyugua hill is located northwest of the municipal capital of Villaflores. The geographic coordinates of the center of the hill are 16° 16" 45.78" N, 93° 19" 32.79" W (Cepeda *et al*., 2010). It has a maximum altitude of 1,520 masl and it is characterized by rugged terrain, with ravines and elevations. The differences in elevation created different micro-climatic conditions, which allowed the existence of different types of vegetation. The climate Af(m) constitutes a dry season and a rainy season, where the driest months receive about 5% of rain, winter months less than 18%; and the rest in summer months. (UNAM, 2007; CONANP, 2012). The predominant soil types are Leptosol, and Cambisol (INEGI, 2013). The predominant vegetation in the upper elevation is pine (*Pinus oocarpa* Shiede) with trees from 10 to 35 m heights, they can be found from 900 to 1100 masl. In the middle elevation (700-900 masl), oak (*Quercus peduncularis* Neé) trees are dominant but associated mainly with *Byrsonima crassifolia* (L.) Kunth, *Heliocarpus appendiculatus* Turcz. These trees are from 5 to 20 m tall. Tropical sub-deciduous trees are found in the low elevation range 300 - 700 masl. The main species in lowland forests are *Diphysa thurberi* (A.Gray) Rydb. ex Standl, *Bursera simaruba* (L.) Sarg, *Guazuma ulmifolia* Lam and *Poeppigia procera* C. Presl (Gómez-Pompa, 1965; Miranda, 2015; Gaona *et al*., 2015; INEGI, 2018). The exact age of the vegetation is unknown, but according to the history of the formation of the municipality of Villaflores, it dates back to 1875. Existing disturbances within Nambiyugua hill such as the extraction of bulrush (*Dioon merolae*) as an ornamental plant, extraction of firewood, and timber wood in the oak and lowland tropical forests are common. Likewise, forest fires have been linked to this site, the most important being in 1998 and 2019, when large-scale wildfires considerably affected the herbaceous, shrub, and tree vegetation (Fernández, 2022). By consulting residents, it is understood that the age of the pine and oak forests ranges from 40 to 50 years, while the lowland tropical forests from 25 to 35 years (CONANP, 2012).

Data Collection

Data collection was carried out using the method of the National Forest and Soil Inventory (INFyS) promoted in Mexico by the National Forestry Commission (CONAFOR). It consisted of establishing a Primary Sampling Unit (PSU) with a radius of 56.42 m for an area equivalent to one hectare. The clusters were integrated by four units equidistant from the center at each 45.14 m, they were constituted by four circular sampling sites or secondary sampling units with a radius of 11.28 m for an approximate area of 400 m^2, for each type of forest, a conglomerate was established, distributed by four sampling sites where: site 1 is the center, site 2 was placed at 0° azimuth, site 3 in a direction of 120° azimuth and site 4 was accommodated at 240° azimuth, these site distributions correspond to an inverted "Y" (INFyS, 2010). Monthly litterfall and storage in four sites in each forest type were measured.

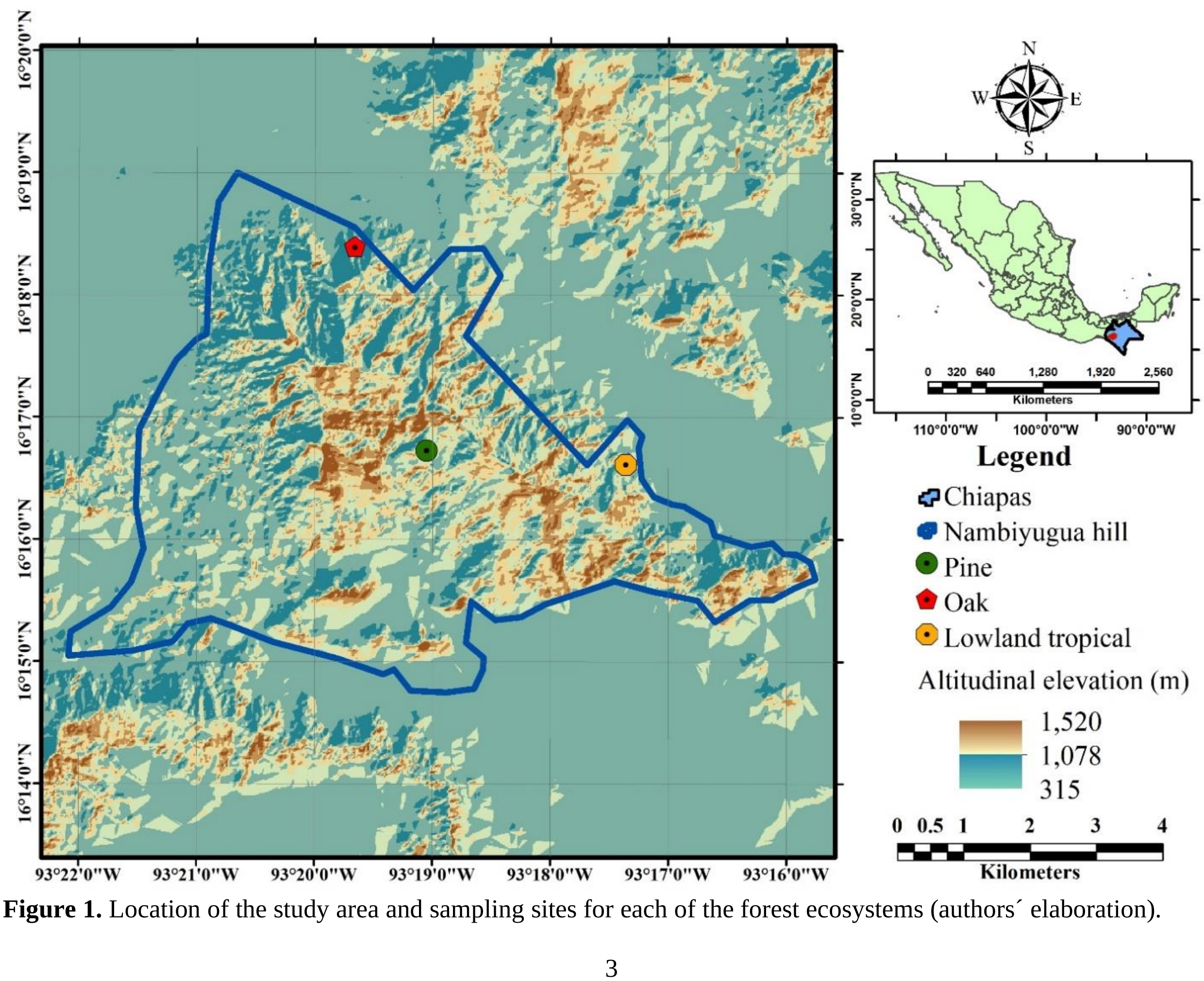


Figure 1. Location of the study area and sampling sites for each of the forest ecosystems (authors´ elaboration).

Tree biomass

Available allometric equations were used to calculate the aboveground biomass (AGB) of the trees, using diameter at breast height (DBH), total height, and wood density (Equations 1 and 2). Wood density data were obtained from published reports (Zanne *et al*., 2009; Ordoñez *et al*., 2015). For Pine and Oak ecosystems, species-specific allometric equations were used (Vargas-Larreta *et al*., 2017) and for the lowland tropical a general allometric equation (Cairns *et al*., 2003) was used (Equation 3) with correction for species-specific wood density (Urquiza-Haas e*t al*., 2007). It is noted that the equation 1 and 2 are additive equations developed for each component of the biomass.

Litterfall sampling

For seasonal sampling of litter production, a total of 48 circular litter traps of 0.50 m^2 were installed at a height of approximately 1 m from the ground. In each type of forest, 16 traps were installed, four traps per sampling site with a distribution of one trap per quadrant of each sampling site (Figure 2).

Each month, all the fallen materials in paper bags with their respective labels were collected for further processing. Subsequently, the samples were oven-dried at 60 °C for 72 hours to calculate the amount of moisture (Figure 3). Then they were separated by leaves, branches, flowers, fruits, and seeds. Each component was weighed separately to quantify the rate of litter accumulation over one year.

Pine Equation (1)

$$\mathrm{AGB} = 0.001753\mathrm{DBH}^{1.8261}H^{1.28397} + 0.02898\mathrm{DBH}^{2.08978} + 0.00948\mathrm{DBH}^{2.7493} + 0.04163\mathrm{DBH}^{1.93601}$$

$R^2 = 0.94$

Oak Equation (2)

$$\mathrm{AGB} = 0.01988\mathrm{DBH}^{2.28684}\mathrm{H}^{0.52175} + 0.05621\mathrm{DBH}^{2.0764} + 0.11276\mathrm{DBH}^{1.52164}\mathrm{H}^{0.53343} + 0.0377\mathrm{DBH}^{1.42193}\mathrm{H}^{0.70675}$$

$R^2 = 0.82$

Lowland tropical Equation (3)

$$\mathrm{AGB} = \left[\exp\left(-2.12605 + 0.868\ln\left(\mathrm{DBH}^2 H\right)\right)\right]\rho$$

$R^2 = 0.90$

Where:

AGB= Aboveground tree biomass (kg $ind.^{-1}$); DBH= Diameter at breast height (cm); H= Total tree height (m); ρ = Wood density of each individual (g cm^{-3}).

Figure 2. Installation of collection traps for falling plant structures.

Figure 3. Plant structures collected in an elevation gradient in three forest ecosystems. a) leaves and needles, b) branches, c) flowers, and d) seeds.

Ground litter stock sampling

Litter mass stock on the ground surface was sampled at eight points using quadrats of 30 by 30 cm^2 at each site. Undecomposed and decomposed litter was collected separately. For sample drying, paper bags containing the litter material were placed in an oven at 60°C for 72 hours and weighed to quantify the litter mass storage on the surface of the ground (INFyS, 2010). Dry matter storage was then calculated according to equation 4 (Honorio and Baker, 2010):

$$\mathrm{EV} = \left(\frac{PS\ (g)}{A\ (m^2)}\right) x100 \qquad \text{Equation (4)}$$

Where:
EV= Plant structure (t ha^{-1}); PS= Dry weight (g) and A= Sampling area (m^2)

Fallen woody material sampling

Fallen deadwood was measured according to the planar intersection methodology proposed by Van Wagner (1982) and Brown (1974). Fallen woody material was considered to be all twigs, branches, and trunks that were lying on the soil surface, separated from their source (not attached to the trunk), from 0 cm to 2 m in height. This material was measured in each of the study sites and along the four transects oriented towards each cardinal point considering its slope, measured from the center of the site to the outer endpoint. Smaller wood segments were counted while the larger wood pieces of 100 and 1000 hours of ignition were measured for their diameter (Table 1).

Table 1. Classification of fallen woody material.

Category	Diameter (cm)	Retardation time (hours)	Measurement on transect (m)
Fine	≤ 0.5	1	10 a 15
Regular	>0.5 to 2.5	10	10 a 15
Median	>2.5 to 7.5	100	0 a 15
Thick	>7.5	1000	0 a 15

Source: (INFyS, 2010; Xelhuantzi *et al*., 2011).

A diametric tape was used to measure the diameter of the fallen woody material and a caliper was used to measure them as per the retardation time (INFyS, 2010). The volume of dead wood was calculated by applying equation 5 and deadwood mass was calculated using wood densities according to the state of decomposition. Wood densities of 0.52 g cm^{-3}, 0.48 g cm^{-3}, 0.35 g cm^{-3}, and 0.23 g cm^{-3} were applied for fresh, dry, partially decomposed, and highly decomposed woody material (Reyes *et al*., 1992; Gutiérrez *et al*., 2010; Aryal *et al*., 2022).

$$V = \frac{\pi^2}{8L} \sum_{i=1}^{n} d_i^2$$

Equation (5)

Where:

V= Volume of dead wood (m^3 ha^{-1}); L= Length of sampling line (m) and di= Diameters of dead wood at the intersection (cm).

Data analysis

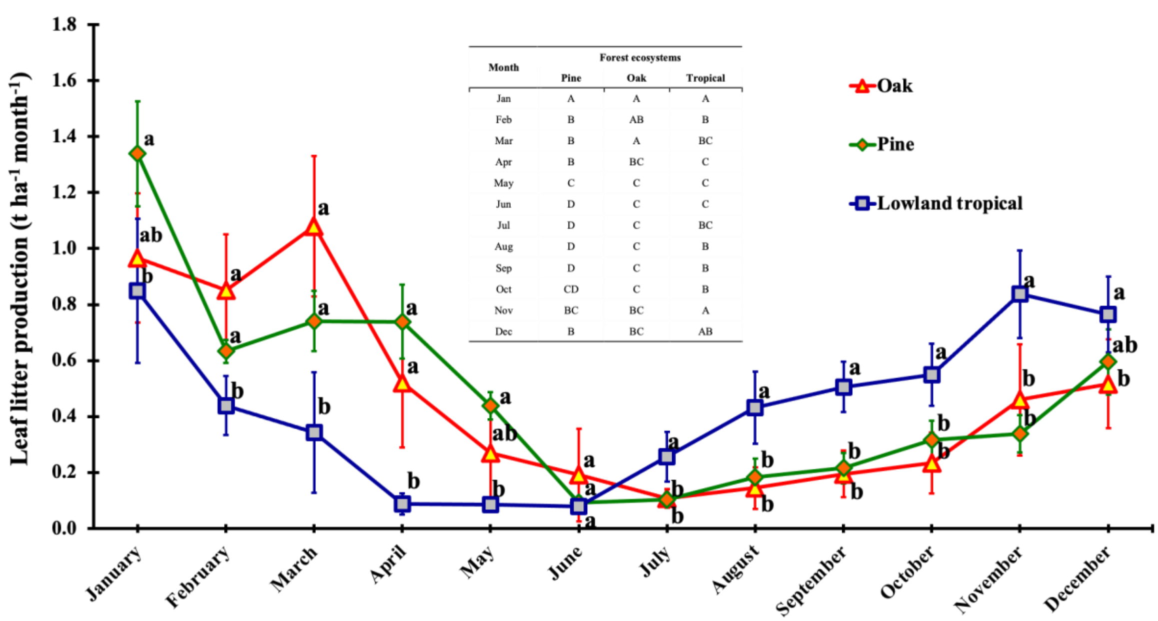
The information on litter production and the total sum (leaves, flowers, branches, and seeds) was analyzed using a one-way analysis of variance (ANOVA, $p<0.05$) to evaluate the significant differences between elevation gradients (vegetation type) by month. Likewise, significant differences between sampling months were evaluated using ANOVA in each forest ecosystem. Finally, Tukey's HSD test ($p<0.05$) was applied to verify mean comparisons. The normality of data was tested using the Shapiro-Wilk test. When not met with the assumptions of normality, the data were transformed only for the analysis purposes. Non-transformed means are presented in the results section. Furthermore, Pearson´s correlation and linear regression analyses were performed to test the association between tree AGB and litterfall. SPSS and R- packages were used to analyze the data (IBM Corporation, 2017; R Core Team, 2023).

RESULTS

Monthly litter production

Monthly leaf litter production showed significant differences between forest ecosystems, although this did not occur in the same months (Figure 4). Likewise, there were significant differences between collection months for each ecosystem. The highest leaf litter production occurred in January in the pine and lowland forest ecosystems. In the oak ecosystem, the highest production of leaf litter occurred in March, with 1.08 ± 0.25 t ha^{-1}, while the lowest amount was found in July with 0.11 ± 0.03 t ha^{-1}. For the case of the pine ecosystem, the highest leaf litter production was observed in January and April, with a mean of 1.34 ± 0.19 and 0.74 ± 0.13 t ha^{-1} respectively. The lowest amount was obtained in June with 0.09 ± 0.02 t ha^{-1}. After that, the production tends to increase from June to November 0.34 ± 0.07 t ha^{-1}. The lowland forest reached the highest production in January with 0.85 ± 0.26 t ha^{-1}, with a decreasing trend in June, in which an average of 0.08 ± 0.02 t ha^{-1} was obtained, but from June to November production tends to increase to 0.84 ± 0.16 t ha^{-1} (Figure 4).

A factorial ANOVA showed that there was a significant effect of both vegetation and sampling months on total litter production. A significant interaction between vegetation and month was found ($F = 5.4$, $p < 0.001$), indicating that monthly litterfall trends vary between forest types (Table 2).



Month	Forest ecosystems		
	Pine	Oak	Tropical
Jan	A	A	A
Feb	B	AB	B
Mar	B	A	BC
Apr	B	BC	C
May	C	C	C
Jun	D	C	C
Jul	D	C	BC
Aug	D	C	B
Sep	D	C	B
Oct	CD	C	B
Nov	BC	BC	A
Dec	B	BC	AB

Figure 4. Monthly leaf litterfall production (t ha^{-1}) in three forest ecosystems of Nambiyugua hill, Villaflores, Chiapas. Error bars indicate the respective 95% confidence intervals. Uppercase letters in the table above indicate significant differences between collection months by ecosystem and lowercase letters indicate significant differences between ecosystem by month.

Table 2. Factorial ANOVA between total litter production as the dependent variable and forest type and month as the independent variable.

Effect	df	F-value	General effect of size	P-value
Forest type	2	6.52	0.024	0.002
Month of sampling	11	18.48	0.273	<0.001
Forest*Month	22	5.4	0.18	<0.001

The monthly productions of total forest fuels (leaves + branches + flowers + seeds) showed significant differences between collection months for each ecosystem ($F = 18.48$, $p < 0.001$), but this was not the case for all months (Table 3). Similarly, there was a significant difference between ecosystems ($F = 6.52$, $p = 0.002$) for some months but not for all months. Consistent with the behavior of leaf litter, the highest values were obtained in the pine and lowland forest ecosystem in January, while the highest production in the oak ecosystem was observed in March. The lowest values were found in July in the pine and oak ecosystems, while in the lowland forest, it was in June. The results of forest fuel fall indicated a significant variation among the three forest ecosystems studied. The highest total litterfall in the study ecosystems was observed in the dry season (Table 3).

Leaves contributed the most of the total annual litter production in all forest types, followed by the branches. We observed the significant differences between forest types only in the branch component, where pine forest had the highest branch fall followed by oak forest and the lowland tropical forests. The annual amount of flower, fruit, and seed fall was small and did not vary statistically among forest gradients (Table 4).

Ground litter load

The litter load was significantly different between the pine, oak, and lowland forest ecosystems, but there was no significant difference between oak and lowland forest (Tukey $p = 0.05$). In turn, the highest litter load was obtained by the pine forest with 12.51 ± 3.88 t ha^{-1} (Figure 5I). As for the decomposed litter, its storage varied significantly among ecosystems (Tukey $p = 0.05$). The highest load of it was found in the pine followed by oak and lowland tropical forest ecosystems (Figure 5II).

Table 3. Monthly production of total forest fuels (leaves + branches + flowers + seeds, t ha^{-1}) in three forest ecosystems of Cerro Nambiyugua, Villaflores, Chiapas (Mean ± 95% confidence interval). Capital letters indicate significant differences between ecosystems for each month and lowercase letters indicate significant differences between months of litterfall collection in each ecosystem (Tukey p<0.05).

Month	Forest ecosystems		
	Pine (1010 m amsl) (t ha^{-1})	Oak (775 m amsl) (t ha^{-1})	Lowland tropical (670 m amsl) (t ha^{-1})
January	$1.38 \pm 0.19^{A, a}$	$1.03 \pm 0.28^{A, a}$	$1.05 \pm 0.28^{A, a}$
February	$0.77 \pm 0.10^{A, b}$	$0.97 \pm 0.24^{A, a}$	$0.68 \pm 0.34^{A, ab}$
March	$0.85 \pm 0.12^{AB, b}$	$1.14 \pm 0.25^{A, a}$	$0.52 \pm 0.35^{B, b}$
April	$1.07 \pm 0.16^{A, ab}$	$0.72 \pm 0.29^{A, ab}$	$0.28 \pm 0.09^{B, bc}$
May	$1.0 5 \pm 0.13^{A, b}$	$0.58 \pm 0.41^{AB, ab}$	$0.17 \pm 0.04^{B, c}$
June	$0.35 \pm 0.17^{A, d}$	$0.37 \pm 0.20^{A, c}$	$0.14 \pm 0.04^{A, c}$
July	$0.26 \pm 0.07^{A, d}$	$0.21 \pm 0.10^{A, c}$	$0.32 \pm 0.09^{A, bc}$
August	$0.57 \pm 0.11^{A, c}$	$0.27 \pm 0.11^{B, c}$	$0.50 \pm 0.17^{AB, b}$
September	$0.36 \pm 0.08^{B, d}$	$0.31 \pm 0.12^{B, c}$	$0.57 \pm 0.10^{A, b}$
October	$0.54 \pm 0.10^{A, c}$	$0.33 \pm 0.14^{A, bc}$	$0.58 \pm 0.13^{A, b}$
November	$0.41 \pm 0.09^{B, cd}$	$0.53 \pm 0.26^{AB, bc}$	$0.92 \pm 0.17^{A, a}$
December	$0.72 \pm 0.21^{A, bc}$	$0.56 \pm 0.17^{A, b}$	$0.87 \pm 0.16^{A, ab}$

Table 4. Annual production of different litter components by forest type (average ± 95% confidence interval). The same letters followed by the numbers indicate no statistically significant difference between forest types.

Litter components	Annual production of litter components (t ha^{-1} yr^{-1})		
	Pine forest	Oak forest	Lowland Tropical forest
Branches	2.117 ±0.648[a]	1.172 ±0.648[ab]	1.098 ±0.648[b]
Flowers	0.512 ±0.357[a]	0.303 ±0.357[a]	0.327 ±0.357[a]
Fruits	0.004 ±0.107[a]	0.095 ±0.107[a]	0.006 ±0.107[a]
Seeds	0.075 ±0.077[a]	0.046 ±0.076[a]	0.127 ±0.076[a]
Leaves	5.605 ±0.830[a]	5.534 ±0.830[a]	5.228 ±0.830[a]

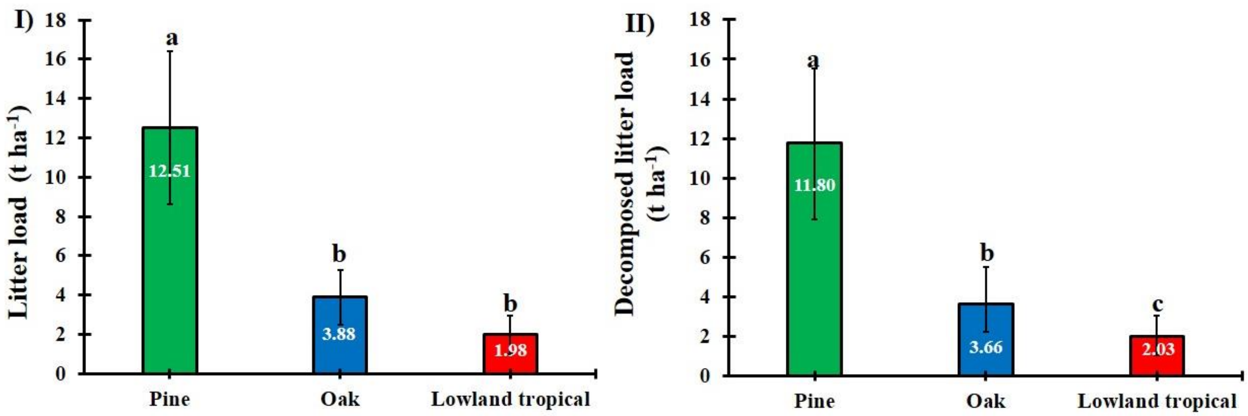


Figure 5. Leaf litter and mulch storage (t ha^{-1}) in three forest ecosystems of Nambiyugua, hill, Villaflores, Chiapas. I) Leaf litter; II) decomposed litter. Points with the same letter indicate that there was no significant difference between ecosystems (Tukey p = 0.05). Error bars indicate standard deviation.

Deadwood loads

There was a significant difference in fallen woody material of 1-hour ignition between pine and oak forests (Figure 6I). Numerically, the highest loads were found in pine forests and lowland forests. Significant differences were found only between the pine and oak ecosystems, with loads of 1.00 and 0.73 t ha^{-1} (Figure 6II). Likewise, the 100-hour deadwood (Figure 6III) was significantly different between the oak ecosystem and the lowland forest, with the highest accumulated load in the lowland forest at 2.71 t ha^{-1}. The downed woody materials from 1000 hours were not significantly different between forests. The highest loads were found in the pine ecosystem with 1.00 t ha^{-1}, followed by the lowland forest with 0.73 t ha^{-1} (Figure 6IV). In the sum of total storage of fallen woody material 1, 10, 100, and 1000 hours of retardation were not significantly different among the study ecosystems. The highest cumulative loads were obtained in the oak and lowland forest ecosystems (Figure 6V).

The total AGB of the trees was different between forest gradients, pine forests of the upper elevation had the highest AGB stock, and the tropical lowland forest had the lowest. The total annual litterfall also varied significantly between forests ($F = 3.82$, $p = 0.029$) with the order pine > oak > tropical lowland forests (Table 5).

We observed that there was a moderate positive correlation between AGB stock (t ha^{-1}) and annual litterfall (Pearson´s correlation coefficient, $r = 0.59$) which was statistically significant ($t = 2.2872$, df = 10, $p = 0.045$). However, the slope of the regression between litterfall and AGB was too small (0.0094) and not significantly different from zero at a 95% level of confidence ($t = 1.559$, $p = 0.15$). At the same time, the variance explained by the linear model between AGB and litterfall was small (20%), indicating that other variables explain more of the litterfall variance than the aboveground biomass stock (Figure 7).

DISCUSSION

Litterfall

Annual litter production, the monthly dynamics of litterfall, and the stock on the forest floor varied among forests at different elevations. The accumulation of litter stock is the function of production and decomposition but these processes are influenced by climate, soil type, plant species traits, and soil organisms that modulate litter fragmentation and decomposition processes (Jaramillo *et al*., 2023; Tan *et al*., 2020). The differences in this study can principally be attributed to the differences in tree species composition of each forest ecosystem (Rocha-Loredo and Ramírez-Marcial, 2009).

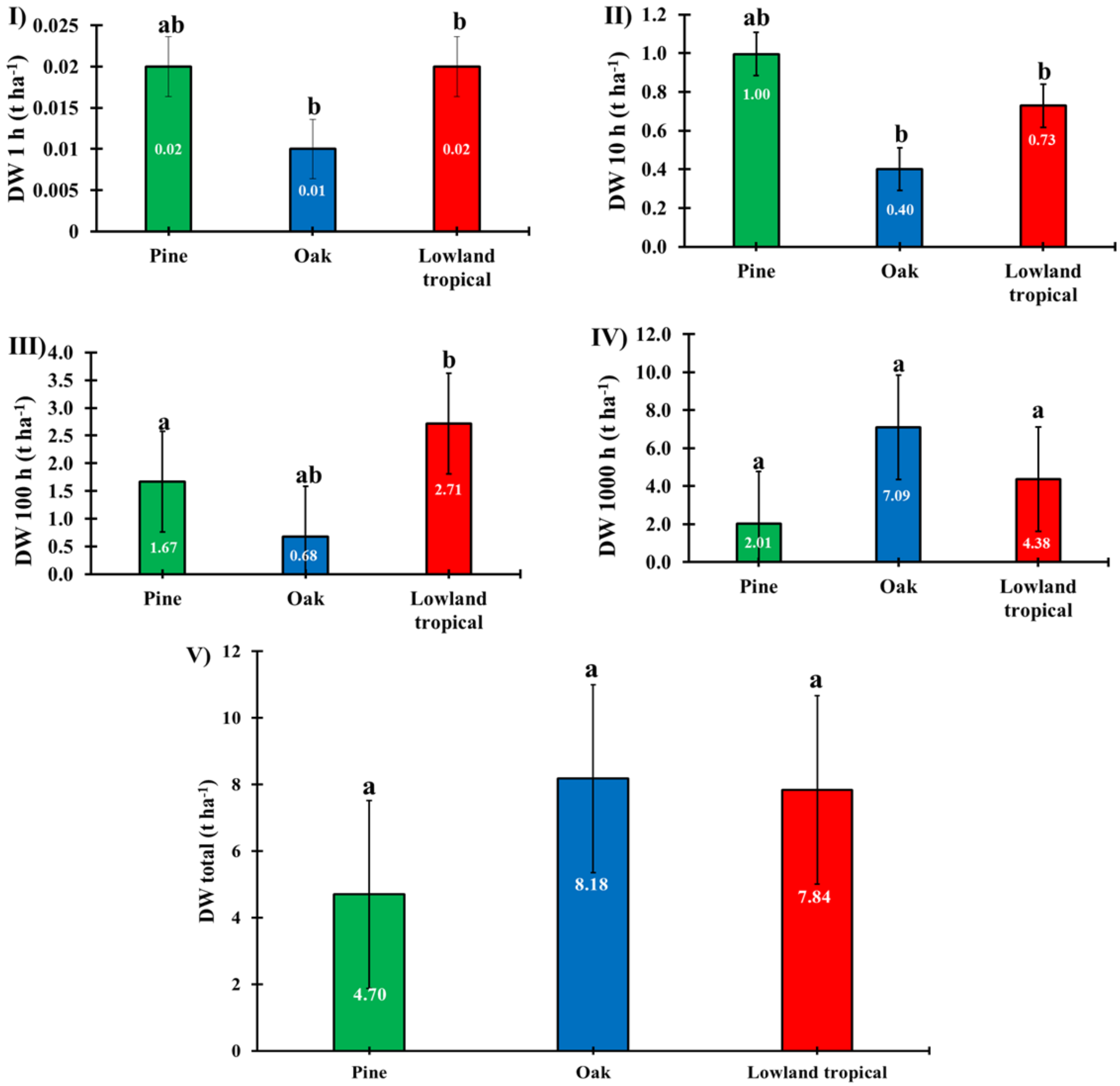


Figure 6. Storage of fallen woody material (t ha^{-1}) in three forest ecosystems of Nambiyugua hill, Villaflores, Chiapas. I) 1 h, II) 10 h, III) 100 h, IV) 1000 h (hour of retardation) deadwood loads, and V) total storage of fallen deadwood. Points with the same letter indicate that there was no significant difference between ecosystems (Tukey p = 0.05). Error bars indicate standard deviation.

Table 5. Tree biomass stocks and annual litterfall among forest types at elevation gradient in Chiapas, Mexico. Different letters followed by mean indicate statistically significant differences between forests.

Forests	AGB (t ha^{-1})		Litterfall (t ha^{-1} yr^{-1})	
	Mean	**95%CI**	**Mean**	**95%CI**
Pine	71.31^{a}	3.48	8.35^{a}	0.794
Oak	56.88^{ab}	33.84	7.07^{ab}	1.360
Lowland Tropical	14.94^{b}	8.33	6.29^{b}	0.762
Average across forests	47.71	31.85	7.24	1.092

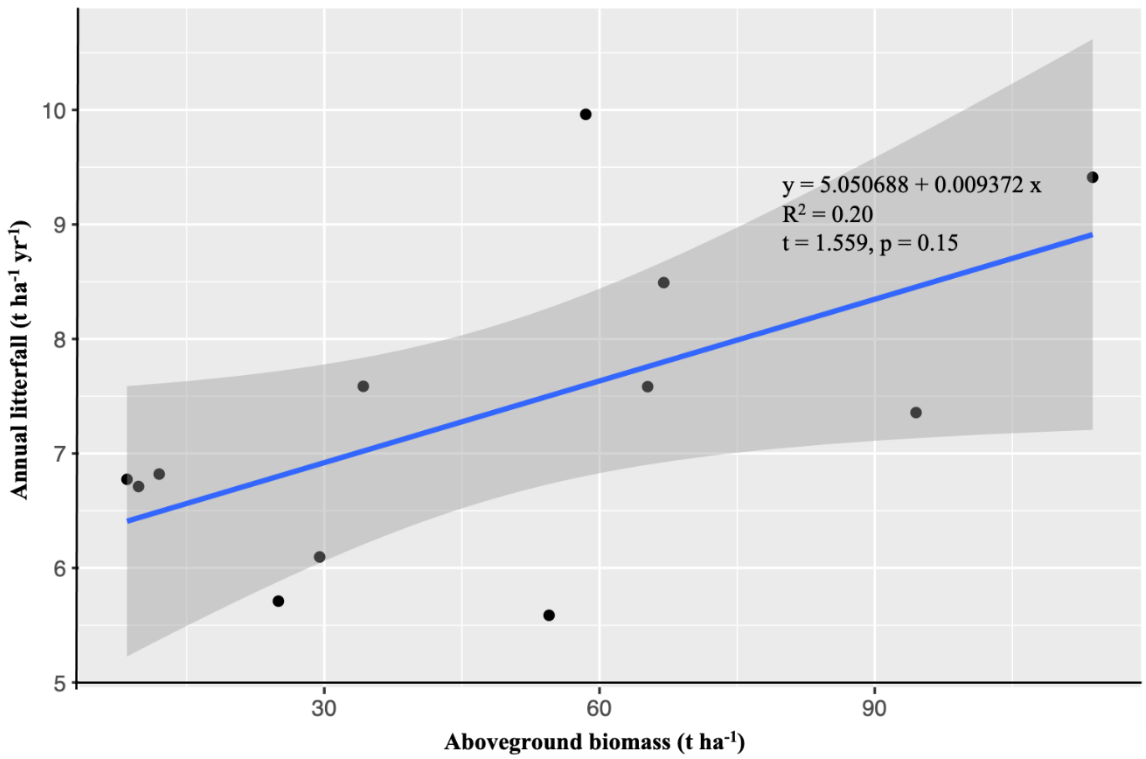


Figure 7: Linear relationship between annual litter production and tree aboveground biomass stock.

The density of trees per hectare was 381 ± 87 in the oak forest while that of the pine forest was 268 ± 87 trees ha^{-1}. The average height of the trees was 10.71 ± 4.95 m in pine, 9.25 ± 4.18 m in oak, and 8.47 ± 3.08 m in lowland tropical forests. Furthermore, the mean crown diameter was 5.09 ± 1.84 m in pine, 6.53 ± 3.11 m in oak, and 4.76 ± 1.38 m in lowland forests. In addition to stand structural properties, AGB stock can also play an important role in total annual litter production. For example, pine forests of the upper elevation which had a larger AGB pool showed a higher litterfall followed by oak and the tropical lowland forests. We also showed that there was a positive correlation between AGB stock and litter production. Human disturbance such as selective extraction of woody materials was more common in the lowland tropical forests resulting in a smaller AGB pool and consequently lower litter production. Furthermore, faster decomposition of broadleaf litter in the lowland tropical forest compared to oak and pine leaf litter can explain the small litter load on the forest floor of this ecosystem (Sánchez-Silva *et al*., 2018). In contrast, leaf litter decomposition is slower in pine forests because of leaf traits and lower temperatures at upper elevations (Ostertag *et al*., 2022).

Regarding the seasonal pattern of litterfall, the lowest litterfall was recorded during the rainy months of the year (June- September) for in pine and oak forests but during April – June in lowland tropical forests. Different from pine and oak forests, the highest litterfall peak in lowland tropical forests was recorded in the November – January period. The differences in tree phenological properties explain this variation in the monthly dynamics of litterfall. Forests in upper elevations such as pine forests are evergreen, in which, leaf senescence and cone droppings occur mostly during the late winter period (González-Rodríguez *et al*., 2019). New leaf sprouting and flowering occur during the dry season and leaf senescence and fruit droppings start at the end of the rainy season in lowland tropical forests (Jaramillo *et al*., 2023). This difference in the monthly dynamics of litterfall between forest ecosystems at different elevations has a profound implication in forest fuel load management planning for the prevention of wildfire and the post-fire recovery resilience of the ecosystems (Agne *et al*., 2022).

Results showed that monthly litter production in the pine-oak ecosystem is higher in comparison to those reported by López-Hernández *et al*. (2022) in the pine-oak forest in Nuevo León, Mexico, who found values of 0.55 t ha^{-1} per month. These values coincide with litterfall from January to April, which is the period when litter production is higher. The highest litter production in the ecosystems studied was certainly in the dry season, which coincides with Martínez-Alonso *et al*. (2007) and López-Hernández *et al*. (2022), who mentioned that the increase in temperature, periods of drought, and leaf physiology intervene in the seasonality of litter production in forest ecosystems.

From a more general perspective, the values found for monthly litterfall production in our ecosystems coincide with those reported by Rocha-Loredo and Ramírez-Marcial (2009) in oak, pine, pine-oak, and pine-oak-olive oak ecosystems in plots under forest restoration in Chiapas, Mexico, who found higher production in the January-April period with a range of 0.60 to 1.5 t ha^{-1} per month. In semi-evergreen tropical rainforests, Aryal *et al*. (2015) and Sánchez-Silva *et al*. (2018) reported monthly litterfall production highest values during February and March in the first year of study and during March to May in the second. The pattern of litterfall production in the first year of that study is similar to the results obtained in the oak ecosystem in this study but the production peaks do not coincide with the other forest ecosystems (Sánchez-Silva *et al*., 2018). This demonstrates the need to study litterfall production over the long term and explore the links between soil organisms, litter decomposition, and ground litter stocks.

Forest fuel storage

The results of litter and deadwood load on the ground surface are approximated for similar ecosystems in Mexico. In Coahuila, Puebla, Baja California Sur, Jalisco, Yucatan, Quintana Roo, Xelhuantzi *et al*. (2011), found loads from 2.5 to 6 t ha^{-1} in the fermentation layer, litterfall from 1.5 to 4 t ha^{-1}, 1 h deadwood from 0.01 to 0.08 t ha^{-1}, 10 h from 0.05 to 1.09 t ha^{-1}, 100 h from 0.3 to 1.02 t ha^{-1} and 1000 h from 0.00 to 0. 12 t ha^{-1} in temperate forests, medium and high forest. These values coincide with the oak and lowland tropical forest ecosystem results in the present study, but not with the pine ecosystem where higher values were found.

Likewise, Chávez *et al*. (2016) reported total fuel loads of 119.20 t ha^{-1} in the conifer ecosystem and 92.49 t ha^{-1} in the oak ecosystem in Jalisco, Mexico while in the present study values of 29.01 t ha^{-1} in pine and 15.72 t ha^{-1} in oak were found, possibly due to the occasional forest fire such as of 2019 causing the amount of fuel load to decrease. The results found for litter load in oak and lowland forest in the present study coincides with Cruz *et al*. (2018), who report loads of 2.94 to 4.70 t ha^{-1} in the temperate forest of Mixteca Alta, Oaxaca, Mexico, but the values are relatively low with the data found in the pine forest of the present study. Instead, deadwood results in this study were low in comparison to those reported by Cruz *et al*. (2018) who reported total loads of 41.89 to 45.54 t ha^{-1}.

CONCLUSIONS

The production of forest litter was different among the ecosystems representing the elevation gradients. Concerning monthly variation, the highest production of total litter was recorded in the January-April period for pine and oak ecosystems while in lowland tropical forests higher production was observed in November – January. Tree biomass stocks and annual litter productivity were higher in the pine forests corresponding to the upper elevation followed by the oak and lowland tropical forests at the middle to lower elevations. The monthly dynamics of litterfall and forest fuel storage could be useful for landscape management activities (prescribed burning, extraction, and/or transformation of forest fuels). These results can be useful in nutrient recycling and assessment of forest productivity variation. Our results on the differences in the monthly dynamics of litterfall in an elevation gradient also provide important insights into forest fuel load management and planning wildfire prevention activities.

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Compliance with ethical standards. Due to the nature of this work, this research does not require approval from an ethical committee.

Data availability. Data can be available from the corresponding author upon request.

Author contribution statement (CRediT). **R. Ruiz-Corzo -**conceptualization, methodology, project administration, investigation; writing original draft, and visualization. **D. R. Aryal -** conceptualization, methodology, project administration, investigation; writing original draft, and visualization. **A. Venegas-Sandoval -** writing, review, editing, validation, and supervision. **E. Díaz-Nigenda -** writing, review, editing, validation, and supervision. **C. Velazquez-Sanabria -** writing, review, editing, validation, and supervision.

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