

Decomposition of leaf litter of *Ochroma pyramidale* (Malvaceae)

La descomposición de la hojarasca de *Ochroma pyramidale* (Malvaceae)

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Abstract

The tree *Ochroma pyramidale* is used to recover jungle areas that have been cultivated. This native species generates a thick layer of leaf litter that remains for several years. The objectives of this study were: 1) to know how much leaf litter is produced, 2) to estimate how long it persists in the soil, and 3) to identify the role of soil fauna in its decomposition. Leaf litter production was estimated at 11 Mg/ha/year, while over the course of 13 years the biomass and depth of the leaf litter layer measured in three sites previously planted with *Ochroma* showed a decrease of over 60%. In a leaf litter decomposition experiment, 37% of biomass was lost in 180 days. Soil mesofauna reduced the concentration of cellulose in leaf litter, while lignin decreased due to the time of permanence of the leaf litter in the soil. The high C:N proportion of the leaves, together with high lignin concentrations, could explain the low levels of loss and accumulation of biomass.

Keywords: Soil fauna; litter chemistry; restoration; tropical rain forest; Mexico.

Resumen

El árbol *Ochroma pyramidale* se utiliza para recuperar áreas de selva que fueron cultivadas, ya que genera una gruesa capa de hojarasca que persiste por varios años. Los objetivos de este estudio fueron: 1) conocer cuánta hojarasca produce esta especie, 2) estimar cuánto tiempo persiste en el suelo e 3) identificar cuál es el papel de la fauna del suelo en su descomposición. Se estimó la producción de hojarasca en 11 Mg/ha/año; la medición de biomasa y profundidad de la capa de hojarasca en sitios previamente plantados con *Ochroma* mostró una disminución de 60% en 13 años. En el experimento de descomposición de la hojarasca se perdió el 37% de su biomasa en 180 días. La fauna del suelo disminuyó la concentración de celulosa, mientras la lignina disminuyó debido al tiempo de permanencia de la hojarasca en el suelo. La alta proporción C:N de las hojas y su elevada concentración de lignina explican la baja pérdida de biomasa y su acumulación.

Palabras clave: Fauna del suelo; química del litter; restauración; selva alta perenifolia; México.

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Introduction

In tropical ecosystems, pioneer tree species are of particular interest for ecological restoration due to their capacity to compete with aggressive colonization of herbaceous plants that demand light; thus, these trees catalyze forest succession (Lamb *et al.*, 2005). The Lacandon and Ch'ol Mayan indigenous groups of the tropical Lacandon Jungle of southern Mexico have long used certain tree species to promote natural regeneration of the high evergreen forest after it has been used for slash and burn agriculture. Specifically, they use the tree *Ochroma pyramidale* (Cav. Ex Lam.) Urb., Malvaceae, to accelerate recovery of degraded soil (Levy-Tacher & Golicher, 2004). This tree is native to the region, it is present in secondary vegetation, and the Mayan peasants intentionally plant it in their agricultural plots to regenerate soil as it requires minimal maintenance. It also used to counter invasion by bracken fern (*Pteridium aquilinum*) as it shades out and eventually kills the fern (Levy-Tacher *et al.*, 2015).

Ochroma pyramidale is a pioneer tree species with a short life cycle, and the density of its wood is the lowest of that produced on commercial plantations (0.17 g cm^{-3}). Its leaves have a rapid turnover rate and are the largest of all neotropical trees, generating a thick layer of leaf litter (Coley, 1983; Francis, 1991; Park & Cameron, 2008). The generation of this thick layer is likely the result of its high content of recalcitrant C (condensed tannins, lignin), negatively correlated with loss of litter mass (Hättenschwiler & Bracht, 2010). This species presents episodes of rapid growth, quickly reaching great heights and a large basal area (Aide *et al.*, 2001; Cusack & Montagnini, 2004; Denslow & Guzman, 2000; Finegan 1996; Park & Cameron, 2008; Saldarriaga *et al.*, 1988). The relatively open canopy of populations of *O. pyramidale* allows light to reach the understory, promoting establishment and growth of tree seedlings (Poorter, 1999; Whitmore, 1978).

The specific rate of production of the leaf litter of this species and those factors controlling its decomposition, such as its foliar chemistry and the activity of soil fauna, have not been quantified. Understanding these variables will in turn allow a better understanding of leaf litter accumulation.

This study had three objectives: 1) to quantify the rate of production of leaf litter; 2) to estimate how long the leaf litter layer persists in the soil and the depth layer in sites planted with *O. pyramidale* after three, eight, and 16 years; and 3) to estimate the effect of soil fauna on decomposition of this leaf litter and its chemical characteristics in an open site and in a plantation of *O. pyramidale* over the course of one year.

Despite the fact that *O. pyramidale* is a pioneer species (Pearson *et al.*, 2003), its leaf litter does not disappear within few months; rather, it is likely that the chemical composition of its leaf litter prevents it from rapidly being consumed by soil fauna, allowing it to accumulate in a thick layer.

Materials and methods

Site description

This study was carried out in Lacanha Chansayab, Chiapas, Mexico ($16^{\circ} 47' \text{ N}$; $91^{\circ} 09' \text{ W}$), which has an altitude of 350 m. a. s. l. Climate is warm-humid with a mean annual temperature of 24° C and a mean annual precipitation of 2814 mm (Servicio Meteorológico Nacional-Comisión Nacional del Agua [SMN-Conagua], 2022). Monthly distribution of rainfall and temperature during the study period are shown in Figure 1. The predominant soil is humic acrisol (World Reference Base, 2015). While the predominant vegetation was previously tropical evergreen forest, currently the area is a mosaic of patches of secondary forest, mature vegetation, grassland, and *milpas* (diversified maize fields) (personal observation).

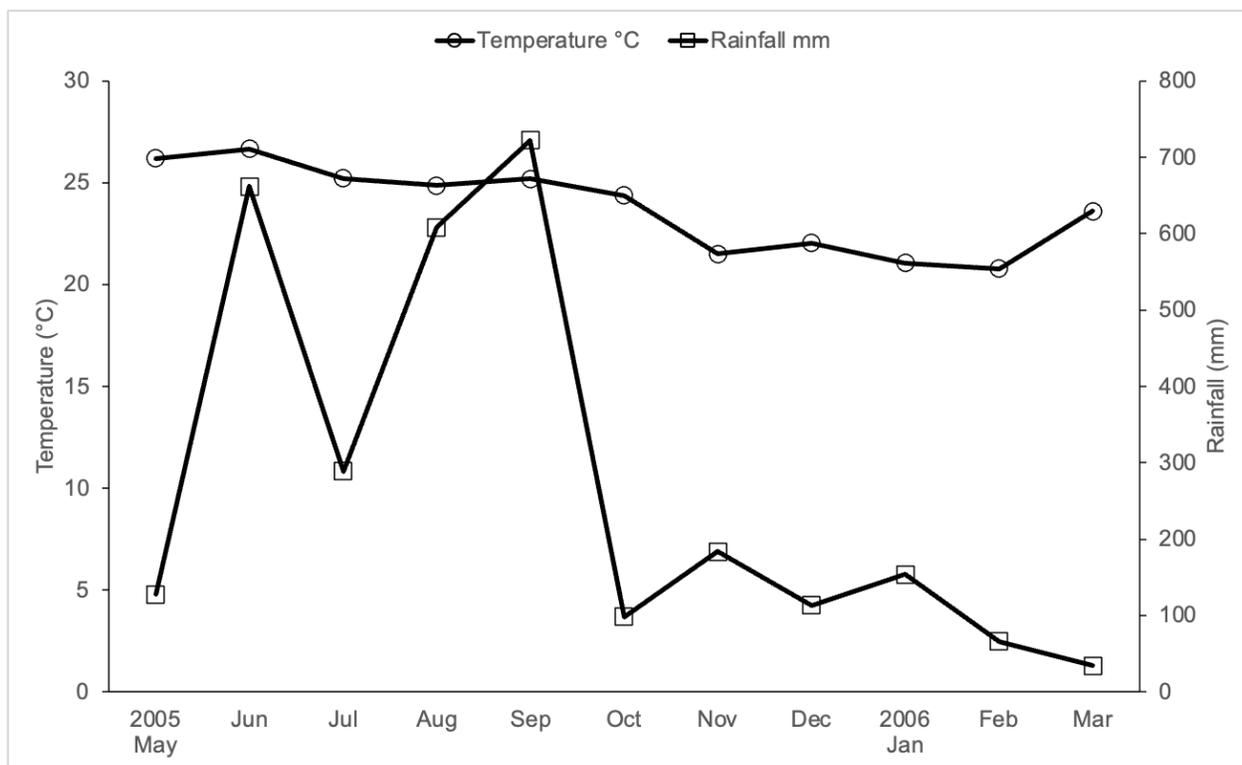


Figure 1. Ombrothermic diagram recorded 2005–2006 in Mexico’s Federal Electrical Commission’s Lacantun weather station, approximately 70 km from Lacanha Chansayab, Chiapas, Mexico.
Source: Author’s own elaboration.

The experimental site –which was last used for agriculture 35 years ago and later invaded by *Pteridium aquilinum*- was prepared for planting with *O. pyramidale* with the aim of controlling growth of ferns. The site included four 8 m x 8 m plots planted with *O. pyramidale* and four adjacent 8 m x 8 m control plots not planted with *O. pyramidale* (Levy-Tacher *et al.*, 2015). Additionally, we selected three sites sown with *O. pyramidale* in different years by local peasants (Figure 2).

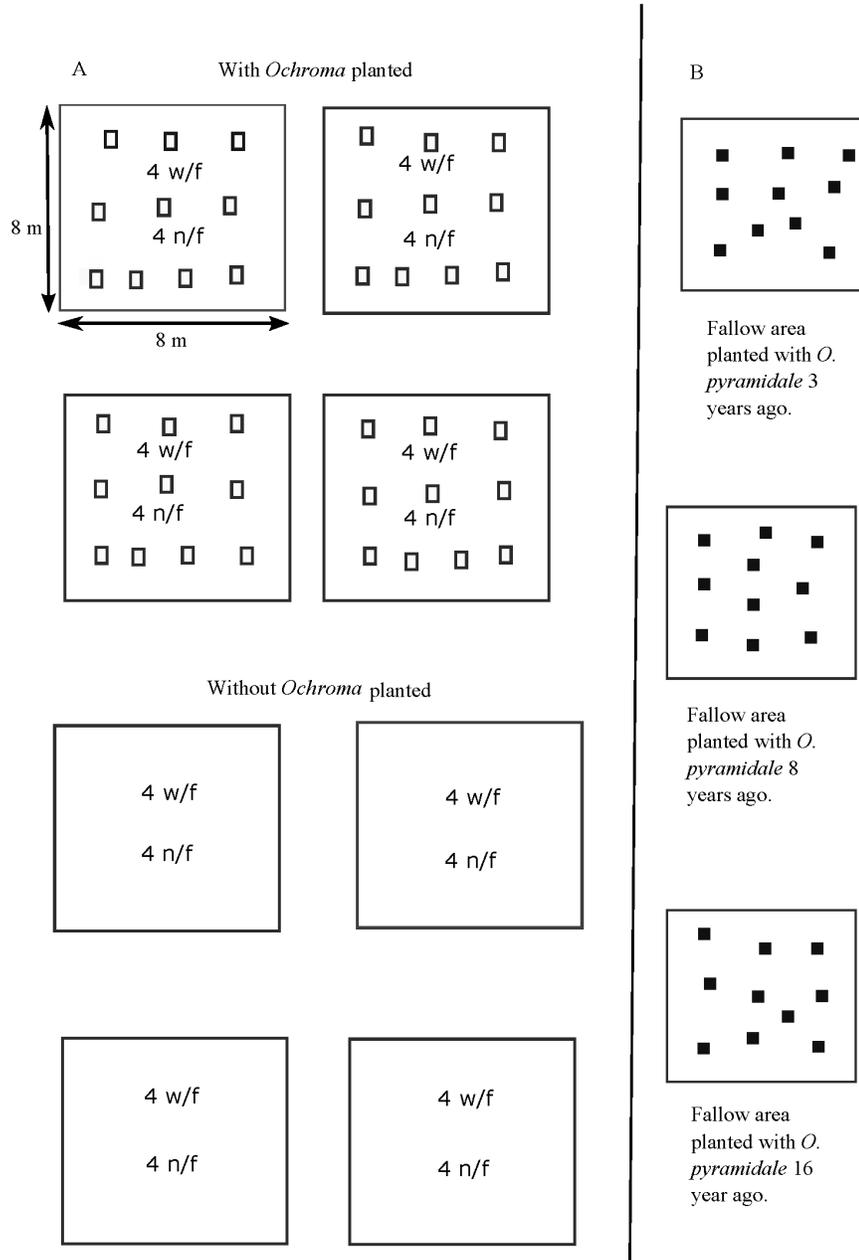


Figure 2. a) Schematic view of plots used to obtain net productivity of litter and to estimate decomposition of *O. pyramidale* leaf litter. Hollow squares = leaf litter traps; w/f nylon mesh bags which allow soil mesofauna to pass; n/f nylon mesh bags which do not allow soil mesofauna to pass. b) The three fallow areas were planted with *O. pyramidale* trees in different years. Solid squares = 1 m² areas from which accumulated leaf litter was collected and depth of leaf litter layer was measured. Illustration is not to scale.

Source: Author's own elaboration.

Production of leaf litter

a) Net productivity of leaf litter

Ten leaf litter traps measuring 1 m in height by 80 cm in diameter were placed at 10 points within each of the four 8 m x 8 m plots planted with *O. pyramidale* (Figure 2). In order to calculate the litter weight by month, the content of each trap was removed monthly and allowed to dry at ambient temperature until a constant weight was reached.

b) Biomass and depth of leaf litter layer in plots under recovery previously planted with *O. pyramidale*

Appart from the experimental plot described in section A, three fallow areas were selected –each one with three, eight, and 16 years of fallow-, which had previously been planted with *O. pyramidale* trees (Levy-Tacher & Golicher, 2004; Vleut *et al.*, 2013). In each of these plots, the accumulated leaf litter was collected from ten 1 m² randomly chosen areas (Figure 2). Leaf litter collected was dried at ambient temperature until a constant weight was obtained. Depth of the leaf litter layer was measured from the soil surface to the surface of the leaf litter with a measuring tape at 10 points within each 1 m², and then it was recorded.

c) Decomposition and chemical characteristics of leaf litter

To estimate decomposition of *O. pyramidale* leaf litter, a complete balanced factorial design with three factors was used: presence or absence of soil mesofauna, presence or absence of *O. pyramidale* plants, and four dates of collection of the bags with leaf litter over the course of one year. Nylon mesh bags measuring 20 cm x 20 cm with 3 mm openings (which allow soil mesofauna to pass) and others with openings < 1 mm (which do not allow soil mesofauna to pass) were used, previously placing 10 g in dry weight of leaf litter from recently fallen leaves of *O. pyramidale* trees. Four bags containing the treatment with soil mesofauna and four bags containing the treatment without soil mesofauna were located on the soil surface of each of the four plots (repetitions of the treatment) planted with *O. pyramidale* and on those without it (Figure 2). Every three months, one bag was removed from each repetition of each soil mesofauna treatment. In the laboratory, the leaf litter was carefully extracted so that none of it could be lost, then it was weighed fresh, and later it was dried at ambient temperature until reaching a constant weight. A total of 64 bags were used: 32 for the control and 32 for the treatment planted with *O. pyramidale*.

At the start of the experiment, the content of carbon (C), nitrogen (N), phosphorus (P), calcium (Ca), magnesium (Mg), cellulose, and lignin was determined for the leaf litter collected in the bags. For each date of harvesting, an analysis was carried out of the lignin, cellulose, and ADF content of the remaining leaf litter.

For the C and N analyses, a LECO-1000 autoanalyzer (LECO Corporation, Michigan US) was used. The concentration of lignin, cellulose, and ADF was obtained through incineration at 550 °C, acid digestion, and oxidation with potassium permanganate according to the Van Soest method.

Data on remaining leaf litter biomass and concentration of macromolecules was analyzed through an Anova factorial analysis, and Shapiro-Wilk and Bartlett tests were used to test the suppositions of normality and homocedasticity, respectively. In the case of data for lignin and cellulose, the arcsine transformation was used to comply with the suppositions of the model. For statistical analysis, we used the 4.1.1 version of the R software (R Core Team, 2021). A linear model was applied to calculate the constant (*k*) for the annual rate of decay of the remaining dry mass, using the following equation:

$$X_t = k \cdot t + X_0$$

where X_t is the remaining mass (g) at time t (days), X_0 is the initial leaf mass, and k is the decomposition rate constant (yr^{-1}) (Wider & Lang, 1982). To calculate the time it took for the leaf litter to decompose 50% and 99%, the following equations were used:

$$t(0.5) = -\ln(0.5)/k$$

$$t(0.99) = -\ln(1-0.99)/k$$

where t is time (years), and k is the decomposition rate constant (yr^{-1}) (Olson, 1963). All data are presented in their original scale of measurement.

Results

Net productivity of leaf litter and biomass and depth of leaf litter layer in plots under recovery

Data for productivity were obtained over 11 months, resulting in an average of 1.1 kg/m^2 (11 Mg/ha) in dry weight. Figure 3 shows the distribution of productivity throughout the year. The data for November and December are likely underestimated, as some leaf litter traps collapsed due to strong winds.

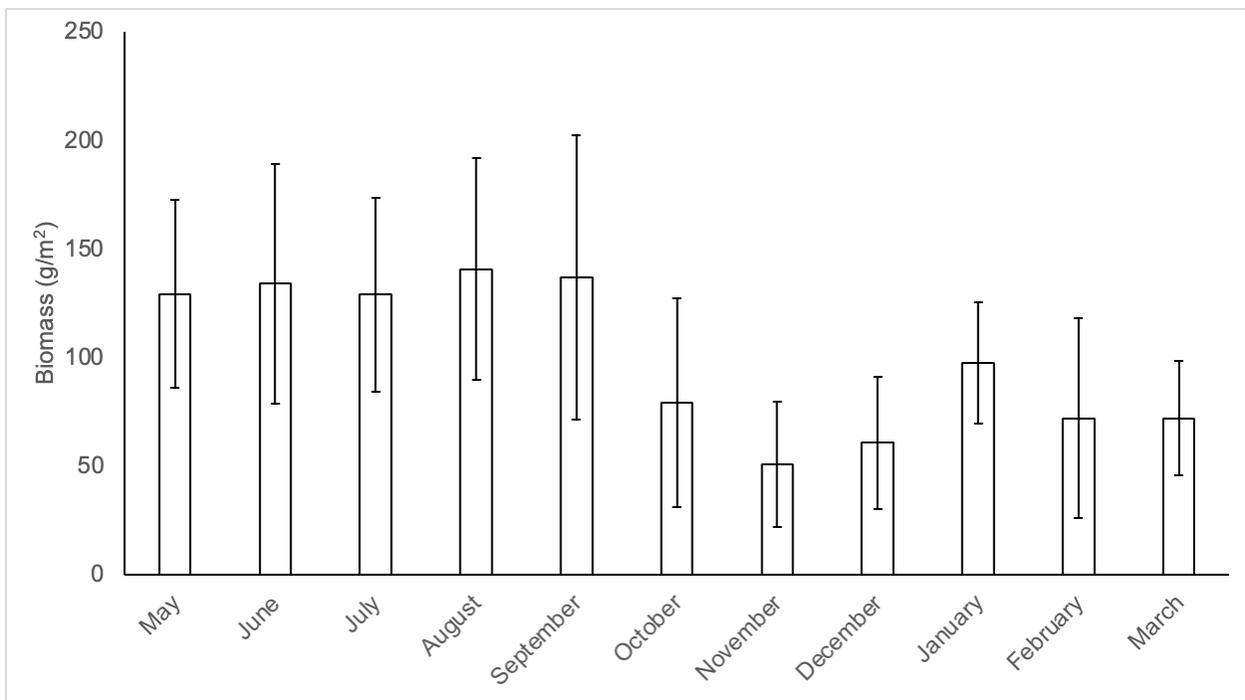


Figure 3. Production of *Ochroma pyramidale* leaf litter biomass during the study period. Bars represent mean of $n = 40$ traps per month ± 1 SD. Source: Author's own elaboration. Data obtained from the plots previously planted with *O. pyramidale* are shown in Table 1.

Table 1. Biomass of accumulated leaf litter and depth of leaf litter layer in sites planted with *Ochroma pyramidale* three, eight, and 16 years before collection. Values are the mean of $n = 10$ ($\pm 1SD$).

Age of fallow (years)	Accumulated biomass of leaf litter (Mg/ha)	Depth (cm)
3	6.2 (2.43)	22.5 (1.51)
8	16.3 (2.7)	16.1 (2.11)
16	6.5 (1.59)	9.4 (1.44)

Source: Author's own elaboration.

Decomposition and chemical characteristics of leaf litter

The results of the Anova factorial analysis did not indicate any interaction among the principal factors; time of permanence of leaf litter in the soil explained most of the variation ($F = 11.89$ with 3 and 58 degrees of freedom, $p < 0.001$), while soil mesofauna and presence/absence of *O. pyramidale* trees were not statistically significant. The greatest loss of biomass of *O. pyramidale* leaf litter occurred between the third and sixth month of the experiment; average loss was 37% and was almost constant after the first six months (Figure 4). The annual decay constant k value was 0.93 ($R^2 = 0.52$).

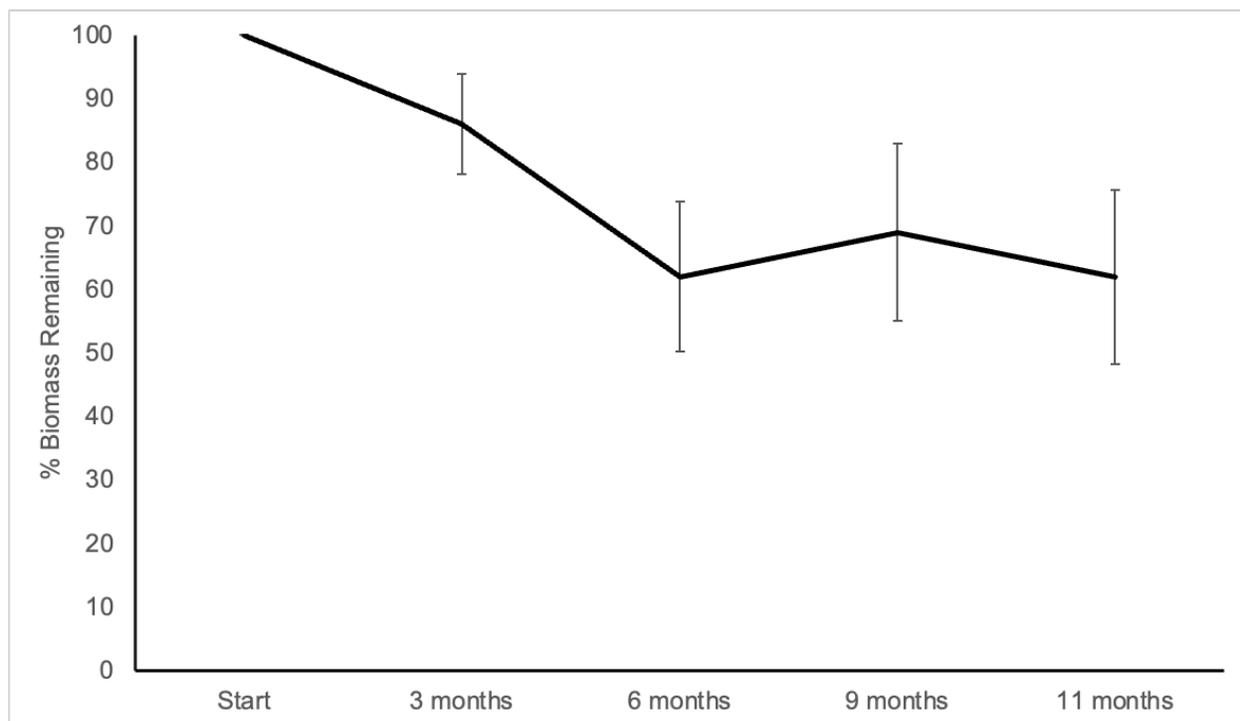


Figure 4. Loss of biomass in experiment of decomposition of *Ochroma pyramidale* leaf litter over 11 months. Values at each point are the mean of $n = 16 \pm 1$ SD.

Source: Author's own elaboration.

The initial chemical composition of *O. pyramidale* leaves was: C = 47.1%, N = 1.02%, P = 0.2103 mg/kg, K = 7515.45 mg/kg, Mg = 891.82 mg/kg, and Ca = 3068.29 mg/kg.

With respect to the macromolecules making up the leaf litter, the Anova test indicated that the average amount of cellulose in the bags that allowed soil mesofauna to pass was less (10.6%) than that of those that did not allow soil mesofauna to pass (12.3%; $F = 5.86$ with 1 and 58 degrees of freedom, $P = 0.018$). The mesofauna found principally belonged to Acari and Collembola, and to a lesser extent to Isoptera. Concentration of cellulose also varied according to the time in which the bags were withdrawn from the soil (Table 2). Concentrations of lignin and ADF were not altered by the presence of soil mesofauna, nor did they vary according to the site where they decomposed. Only the time in which the bags remained in the soil explained changes in concentrations (Table 2).

Table 2. Concentration of lignin, cellulose, and ADF, and the value of the lignin/cellulose ratio during the experiment of decomposition of *Ochroma pyramidale* leaf litter. Values are the mean of $n = 16$ ($\pm 1SD$) for each date. Different letters in the same row indicate statistically significant differences ($p < 0.01$).

Biomolecule %	Start ¹	3 months	6 months	9 months	11 months
Lignin	42.07	52.00(3.9)a	46.12(8.6)b	55.02(4.7)a	55.32(5.5)a
Cellulose	18.59	16.06(2.8)a	9.01(2.9)b	11.94(2.9)c	8.88(2.2)b
ADF	--	69.62(2.4)a	57.77(9.8)b	70.00(3.2)a	67.18(4.7)a
Lig/Cel	2.25	3.34(0.6)a	5.34(0.93) b	4.89(1.32)b	6.62(1.80)c

¹Initial data were not compared with the rest of the data.

Source: Author's own elaboration.

Discussion

Annual leaf litter productivity of *Ochroma pyramidale* ranges from 6 Mg/ha to 11 Mg/ha, which concurs with that found for other tropical species planted with the purpose of restoration (Goma-Tchimbakala & Bernhard-Reversat, 2006; Montagnini *et al.*, 1993).

The time it takes for the leaf litter produced to be reincorporated into the soil depends on its rate of decomposition; in this case, the constant k value (0.93) falls within the range reported for other tropical and temperate species with a slow decomposition rate and is correlated with a high C:N ratio and high lignin content (Zhang *et al.*, 2008). Table 3 compares the rate of leaf litter decomposition of the species studied with that of other tropical forest species. According to the calculations ($t_{(0.5)}$) and ($t_{(0.99)}$) of biomass loss, *O. pyramidale* will lose 50% of its leaf litter biomass in 270 days and will require approximately five years to lose 99% of its biomass. Due to its slow decomposition rate, *O. pyramidale* leaf litter tends to accumulate, forming a thick layer (Table 3), which requires many years to decompose.

Table 3. Comparison of biomass loss of leaf litter of different tropical tree species with that of *O. pyramidale*.

Tree species	Vegetation type	Time in which biomass was decomposed (days)	% decomposition of leaf litter biomass	C:N ratio	Successional stage	Reference
<i>Ficus yoponenis</i> Desv.	Tropical evergreen forest	100	< 200	17.5*	Pioneer	Álvarez-Sánchez & Becerra-Enríquez (1996)
<i>Poulsenia armata</i> (Miq.) Standl	Tropical evergreen forest	100	< 200	4-5**	Non- pioneer	Álvarez-Sánchez & Becerra-Enríquez (1996)
<i>Pithecellobium dulce</i> (Roxb) Benth	Tropical dry forest	67	183	18.6	Pioneer	Sánchez-Solis (2010)
<i>Ochroma pyramidale</i> (Cav. Ex Lam.) Urb.	Tropical evergreen forest	37	180	46.1	Pioneer	This study
<i>Manilkara zapota</i> (L.) P. Royen	Tropical semi-evergreen forest	23	190	80	Non- pioneer	Xuluc-Tolosa <i>et al.</i> (2003)

*Estimated from protein and cell wall values reported by Milton (1979)

**Data from Kattge *et al.* (2020)

Source: Author's own elaboration.

In general, litter decomposition is driven by climate, quality of litter and substrate, and soil fauna (Aerts 1997; Frouz *et al.*, 2015); and when the litter is in the late decomposition stages, the lignin concentration has more influence on decomposition (Berg, 2000; Hättenschwiler & Bracht, 2010). Decomposition of biomass per unit of time is frequently greater in leaf litter with a high nutrient availability but is reduced with an increase in lignin or polyphenols (Preston *et al.*, 2000; Trofymow *et al.*, 2002), as would be the case of the species studied. *O. pyramidale* has an initial C:N ratio of 46.17, which indicates that its leaf litter has a slow rate of decomposition; leaf litter with a C:N ratio less than 20 is expected to have a rapid rate of decomposition (Cadish & Giller, 1997). Considering this, and the conceptual model of transformation of litter into the soil organic matter proposed by Gunina & Kuzyakov (2022), the leaf litter of *O. pyramidale* may initially be used by microbes as an energy source (most likely during the first six months of decomposition) and later may serve as an energy deposit to be used by other microbial communities which consume nutrients stored in the soil organic matter.

Due to the C:N ratio (46.17) and the initial N content (1.02) of *O. pyramidale*, its leaves are slow to decompose, which could also be the case of other tropical pioneer tree species such as *Cecropia obtusifolia* Bertol (C:N = 37.7 and N = 1.0) (Wieder *et al.*, 2009), as well as of secondary tree species; the leaves of secondary species also have greater concentrations of C and lignin, and less N than those of primary species, hence, decomposing more slowly (Vasconcelos & Laurance, 2005). It is likely that the chemical composition of *O. pyramidale* leaf litter prevents it from being consumed by degrading soil mesofauna, and possibly most of its decomposition is carried out by specialized groups of microorganisms such as fungi, which degrade lignin (Krishna & Mohan, 2017). Reduction in the percentage of cellulose (Table 2) may be partially attributed to the action of soil fauna as well as to the high level of solubility in water of cellulose as compared to lignin. In biomes dominated by herbs and grasses, soil fauna may consume up to 50% of the litter. However, in biomes dominated by trees, which produce litter with a high C:N ratio and a higher lignin content, the consumption rate decreases (Hedéneč *et al.*, 2020). As previously indicated, fungi could be a significant group of microorganisms decomposing *O. pyramidale* litter. Meanwhile, for other species with a high C:N rate, such as *Quercus petraea* (Matt.) Liebl., fungi are responsible for 35% of loss of litter dry mass (Steffen *et al.*, 2007), and they have been reported as principal drivers of lignocellulose degradation (Wang *et al.*, 2020).

The characteristics of *O. pyramidale* leaf litter and the results of the present decomposition experiment indicate that soil mesofauna do not alter loss of biomass, that they reduce the concentration of cellulose, and that they do not modify the concentration of other macromolecules of leaf litter. It is likely that abiotic factors (physical weathering) also play a role in decomposition of *Ochroma* leaf litter, as has been shown in the decomposition process of other species in different environments (Montaña *et al.*, 1988). *O. pyramidale* leaf litter likely remains for over two years before being completely integrated into the soil, which contributed to explaining the biomass and thickness of the leaf litter layer (Table 1) in sites planted with this species in different years. These results complement those of other studies (Diemont *et al.*, 2006; Douterlungne *et al.*, 2010; Levy-Tacher & Golicher, 2004; Vleut *et al.*, 2013) in which the *O. pyramidale* leaf litter layer was identified to be a selective physical barrier which allows for establishment of seeds of some species and prevents establishment of others. The large size of *O. pyramidale* leaves (13 cm × 13 cm to 35 cm × 35 cm), as well as its rapid growth, high rate of leaf turnover, and the chemical composition of its leaves as reported here, contribute to forming a thick layer of leaf litter, which may remain for over 10 years. This may impede the seeds of early succession plant species from reaching the soil surface, in turn impeding their colonization (Sayer 2006; Vázquez-Yanes & Orozco-Segovia, 1992). Late succession tree species have larger seeds with sufficient reserves to emerge and survive under conditions of little luminosity and, therefore, a thick layer of leaf litter -such as that observed and analyzed in the present study- could favor development of such species (Seiwa & Kikuzawa, 1996). Thus, species for which the chemical composition of their leaf litter result in slow decomposition, which are planted by peasants with the purpose of recovering soil fertility, could also facilitate succession.

Conclusions

After one year of decomposition, initial biomass of leaf litter of *Ochroma pyramidale* is reduced on average by 37%. This species' low annual decay constant k value (0.93) -in conjunction with its high C:N ratio (46.17), low initial N concentration (1.02 %), high lignin content (42 %), and low rate of activity of mesofauna- explain their slow decomposition, which could explain the persistence of a deep layer of litter in plots planted with this species after five or more years. The chemistry of the leaf litter of *O. pyramidale*, which is unlike that generally expected for pioneer species, contributes to the formation of a thick layer of leaf litter and may indirectly facilitate germination of late succession tree species.

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Conflicts of interest

The authors declare they have no conflicts of interest.

References

- Aerts, R. (1997). Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos*, 79, 439–449. <https://doi.org/10.2307/3546886>
- Aide, T. M., Zimmerman, J. K., Pascarella, J. B., Rivera, L., & Marcano-Vega, H. (2001). Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. *Restoration Ecology*, 8(4), 328–338. <http://dx.doi.org/10.1046/j.1526-100x.2000.80048.x>
- Álvarez-Sánchez, J., & Becerra-Enríquez, R. (1996). Leaf decomposition in a Mexican tropical rain forest. *Biotropica*, 28(4), 657–667. <http://dx.doi.org/10.2307/2389052>
- Berg, B. (2000). Litter decomposition and organic matter turnover in northern forest soils. *Forest Ecology and Management*, 133(1-2), 13–22. [http://dx.doi.org/10.1016/S0378-1127\(99\)00294-7](http://dx.doi.org/10.1016/S0378-1127(99)00294-7)
- Cadish, G., & Giller, K.E. (1997). *Driven by nature. Plant litter quality and decomposition*. CAB International.
- Coley, P. D. (1983). Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs*, 53(2), 209–233. <http://dx.doi.org/10.2307/1942495>
- Cusack, D., & Montagnini, F. (2004). The role of native species plantations in recovery of understory woody diversity in degraded pasturelands of Costa Rica. *Forest Ecology and Management*, 188(1-2), 1–15. [http://dx.doi.org/10.1016/S0378-1127\(03\)00302-5](http://dx.doi.org/10.1016/S0378-1127(03)00302-5)
- Denslow, J. S., & Guzman, S. (2000). Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. *Journal of Vegetation Science*, 11(2), 201–212. <http://dx.doi.org/10.2307/3236800>
- Diemont, S. A. W., Martin, J. F., Levy-Tacher, S. I., Nigh, R. B., Ramirez, P., & Golicher, J. D. (2006). Lacandon Maya forest management: restoration of soil fertility using native tree species. *Ecological Engineering*, 28(3), 205–212. <http://dx.doi.org/10.1016/j.ecoleng.2005.10.012>
- Douterlungne, D., Levy-Tacher, S. I., Golicher, D. J., & Román, F. (2010). Applying indigenous knowledge to the restoration of degraded tropical rain forest clearings dominated by bracken fern. *Restoration Ecology*, 18(3), 322–329. <http://dx.doi.org/10.1111/j.1526-100X.2008.00459.x>
- Finegan, B. (1996). Pattern and process in neotropical secondary rainforests: the first 100 years of succession. *Trends in Ecology and Evolution*, 11(3), 119–124. [https://doi.org/10.1016/0169-5347\(96\)81090-1](https://doi.org/10.1016/0169-5347(96)81090-1)
- Francis, J. K. (1991). *Ochroma pyramidale* Cav.: Balsa, Bombacaceae, Bombax Family.
- Institute of Tropical Forestry, USDA.
- Frouz, J., Roubíckova, A., Hedenec, P., & Tajovský, K. (2015). Do soil fauna really hasten litter decomposition? A meta-analysis of enclosure studies. *European Journal of Soil Biology*, 68, 18–24. <http://dx.doi.org/10.1016/j.ejsobi.2015.03.002>
- Goma-Tchimbakala, J., & Bernhard-Reversat, F. (2006). Comparison of litter dynamics in three plantations of an indigenous timber-tree species (*Terminalia superba*) and a natural tropical forest in Mayombe, Congo. *Forest Ecology and Management*, 229(1-3), 304–313. <https://doi.org/10.1016/j.foreco.2006.04.009>
- Gunina, A., & Kuzyakov, Y. (2022). From energy to (soil organic) matter. *Global Change Biology*, 28(7), 2169–2182. <http://dx.doi.org/10.1111/gcb.16071>
- Hättenschwiler, S., & Bracht, H. (2010). Carbon quality rather than stoichiometry controls litter decomposition in a tropical rain forest. *Journal of Ecology*, 98(4), 754–763. <http://dx.doi.org/10.1111/j.1365-2745.2010.01671.x>
- Heděnc, P., J. J. Jiménez, J. Moradi, X. Domene, D. Hackenberger, S. Barot, A. Frossard, L. Oktaba, J. Filser, P. Kindlmann & Frouz, J. (2020). Global distribution of soil fauna functional groups and their estimated litter consumption across biomes. *Scientific Reports*, 12, 17362. <https://doi.org/10.1038/s41598-022-21563-z>
- Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Colin, I., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar, C., Aleixo, I., Ali, H., Amiaud, B.,... & Wirth, C. (2020). TRY plant trait database - enhanced coverage and open access. *Global Change Biology*, 26(1), 119–188. <https://doi.org/10.1111/gcb.14904>
- Krishna, M. P., & Mohan, M. (2017). Litter decomposition in forest ecosystems: a review. *Energy, Ecology and Environment*, 2(4), 236–249. <http://dx.doi.org/10.1007/s40974-017-0064-9>

- Lamb, D., Erskine, P. D., & Parrotta, J. A. (2005). Restoration of degraded tropical forest landscapes. *Science*, 310(5754), 1628–1632. <http://dx.doi.org/10.1126/science.1111773>
- Levy-Tacher, S. I., & Golicher, D. J. (2004). How predictive is traditional ecological knowledge? The case of the Lacandon Maya fallow enrichment system. *Interciencia*, 29(9), 496-503. http://ve.scielo.org/scielo.php?pid=S0378-18442004000900005&script=sci_arttext&tlng=en
- Levy-Tacher, S. I., Vleut, I., Román-Dañobeytia, F., & Aronson, J. (2015). Natural regeneration after long-term bracken fern control with balsa (*Ochroma pyramidale*) in the neotropics. *Forest*, 6(6), 2163-2177. <http://dx.doi.org/10.3390/f6062163>
- Milton, K. (1979). Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *The American Naturalist*, 114(3), 362-378. <https://www.journals.uchicago.edu/doi/abs/10.1086/283485>
- Montagnini, F., Ramstad, K., & Sancho, F. (1993). Litterfall, litter decomposition and the use of mulch of four indigenous tree species in the Atlantic lowlands of Costa Rica. *Agroforestry Systems*, 23, 39-61. <https://doi.org/10.1007/BF00704850>
- Montaña, C., Ezcurra, E., Carrillo, A., & Delhoume, J. P. (1988). The decomposition of litter in grasslands of northern Mexico: a comparison between arid and non-arid environments. *Journal of Arid Environments*, 14(1), 55-60. [https://doi.org/10.1016/S0140-1963\(18\)31096-6](https://doi.org/10.1016/S0140-1963(18)31096-6)
- Olson, J. S. (1963). Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*, 44(2), 322-331. <https://doi.org/10.2307/1932179>
- Park, A., & Cameron, J. L. (2008). The influence of canopy traits on throughfall and stemflow in five tropical trees growing in a Panamanian plantation. *Forest Ecology and Management*, 255(5-6), 1915–1925. <http://dx.doi.org/10.1016/j.foreco.2007.12.025>
- Pearson, T. R. H., Burslem, D. F. R. P., Goeriz, R. E., & Dalling, J.W. (2003). Regeneration niche partitioning in neotropical pioneers: effects of gap size, seasonal drought and herbivory on growth and survival. *Oecologia*, 137, 456–465. <http://dx.doi.org/10.1007/s00442-003-1361-x>
- Poorter, L. (1999). Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology*, 13(3), 396–410. <http://dx.doi.org/10.1046/j.1365-2435.1999.00332.x>
- Preston, C. M., Trofymow, J. A., & the Canadian Intersite Decomposition Experiment Working Group. (2000). Variability in litter quality and its relationship to litter decay in Canadian forests. *Canadian Journal of Botany*, 78, 1269–1287. <http://dx.doi.org/10.1139/b00-101>
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Saldarriaga, J. G., West, D. C., Tharp, M. L., & Uhl, C. (1988). Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. *Journal of Ecology*, 76(4), 938–958. <http://dx.doi.org/10.2307/2260625>
- Sánchez-Solis, I. (2010). *Producción de hojarasca y descomposición de materia orgánica de cuatro especies arbóreas de Selva baja Caducifolia en una plantación de Zacatepec, Morelos* [Undergraduate thesis in Biology]. School of Sciences, National Autonomous University of Mexico.
- Sayer, E. J. (2006). Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological Reviews*, 81(1), 1–31. <http://dx.doi.org/10.1017/S1464793105006846>
- Seiwa, K., & Kikuzawa, K. (1996). Importance of seed size for the establishment of seedlings of five deciduous broad-leaved tree species. *Vegetatio*, 123, 532–538. <http://dx.doi.org/10.1007/BF00044887>
- Servicio Meteorológico Nacional-Comisión Nacional del Agua (SMN-Conagua). (2022). *Normales climatológicas por estado. Chiapas. Periodo 1981–2010*. Gobierno de México. <https://smn.conagua.gob.mx/es/informacion-climatologica-por-estado?estado=chis>
- Steffen, K. T., Cajthaml, T., Snajdr, J., & Baldrian, P. (2007). Differential degradation of oak (*Quercus petraea*) leaf litter by litter-decomposing basidiomycetes. *Research in Microbiology*, 158(5), 447-455. <https://doi.org/10.1016/j.resmic.2007.04.002>

- Trofymow, J. A., Moore, T. R., Titus, B., Prescott, C., Morrison, I., Siltanen, M., Smith, S., Fyles, J., Wein, R., Camiré, C., Duschene, L., Kozak, L., Kranabetter, M., & Visser, S. (2002). Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. *Canadian Journal of Forest Research*, 32, 789–804. <http://dx.doi.org/10.1139/x01-117>
- Vasconcelos, H. L., & Laurance, W. F. (2005). Influence of habitat, litter type, and soil invertebrates on leaf-litter decomposition in a fragmented Amazonian landscape. *Oecologia*, 144, 456–462. <http://dx.doi.org/10.1007/s00442-005-0117-1>
- Vázquez-Yanes, C., & Orozco-Segovia, A. (1992). Effects of litter from a tropical rainforest on tree seed germination and establishment under controlled conditions. *Tree Physiology*, 11(4), 391–400. <http://dx.doi.org/10.1093/treephys/11.4.391>
- Vleut, I., Levy-Tacher, S. I., de Boer, W. F., Galindo-González, J., & Ramírez-Marcial, N. (2013). Can a fast growing early successional tree (*Ochroma pyramidale*, Malvaceae) accelerate forest succession?. *Journal of Tropical Ecology*, 29(2), 173–180. <http://dx.doi.org/10.1017/S0266467413000126>
- Wang, W., Zhang, Q., Sun, X., Chen, D., Insam, H., Koide, R. T., & Zhang, S. (2020). Effects of mixed-species litter on bacterial and fungal lignocellulose degradation functions during litter decomposition. *Soil Biology and Biochemistry*, 141, 107690. <https://doi.org/10.1016/j.soilbio.2019.107690>
- Whitmore, T. C. (1978). Gaps in the forest canopy. In B. P. Tomlinson & M. H. Zimmermann (eds.), *Tropical trees as living systems* (pp. 639–656). Cambridge University Press.
- Wider, R. K., & Lang, G. E. (1982). A critique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology*, 63(6), 1636–1642. <https://doi.org/10.2307/1940104>
- Wieder, W. R., Cleveland, C. C., & Townsend, A. R. (2009). Controls over leaf litter decomposition in wet tropical forests. *Ecology*, 90(12) 3333–3341. <http://dx.doi.org/10.1890/08-2294.1>
- World Reference Base. (2015). *Base referencial mundial del recurso suelo 2014, Actualización 2015. Sistema internacional de clasificación de suelos para la nomenclatura de suelos y la creación de leyendas de mapas de suelos. Informes sobre recursos mundiales de suelos 106*. FAO. <https://www.fao.org/3/i3794es/i3794es.pdf>
- Xuluc-Tolosa, F. J., Vester, H. F. M., Ramírez-Marcial, N., Castellanos-Albores, J., & Lawrence, D. (2003). Leaf litter decomposition of tree species in three successional phases of tropical dry secondary forest in Campeche, Mexico. *Forest Ecology and Management*, 174(1-3), 401–412. [https://doi.org/10.1016/S0378-1127\(02\)00059-2](https://doi.org/10.1016/S0378-1127(02)00059-2)
- Zhang, D., Hui, D., Luo, Y., & Zhou, G. (2008). Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *Journal of Plant Ecology*, 1(2), 85–93. <https://doi.org/10.1093/jpe/rtn002>