Inoculation with a soil fungus accelerates decomposition of avocado cv. Hass leaf litter in three plantations in Colombia

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ABSTRACT

The objective of this study was to evaluate the effect of a fungal inoculation on the litter decomposition in three plantations of avocado (*Persea americana*) cv. Hass in Colombia at different altitudes (Támesis 1340 m, Jericó 1900 m, and Entrerríos 2420 m). These processes are key in the proper functioning of soil biogeochemical cycles. The litter was either uninoculated or inoculated with the fungus *Mortierella* sp., then transferred into litter bags and finally deposited in the field sites where remained for 430 days. Residual dry matter (RDM) and nutrient content was monitored overtime. Five regression models of litter decomposition were employed: single, double, and triple exponential models and two continuous models. Although, all models properly fitted the data variation, the double exponential was the most effective based on regression parameters (mean square error and Akaike index). In all three sites the rate of decomposition was higher when the litter was inoculated with the fungus. Thus, the RDM was significantly lower when the litter was inoculated with *Mortierella* sp. At day 430, the uninoculated RDM in Tamesis, Jerico, and Entrerrios was 0.48, 0.47, and 0.50, respectively; while the inoculated RDM was 0.47, 0.44, and 0.46, respectively. The rate of decomposition followed the decreasing sequence: Jericó > Támesis > Entrerríos. The nutrient release pattern was: K > Ca > Mg > N > P > Cu > Mn > Zn > Fe. While K was rapidly released, Ca, Mg, and N were slowly released; P, Cu, Mn, Zn, and Fe were immobilized during the decomposition process. However, fungal inoculation on the litter significantly reduced the magnitude of nutrient accumulation for P, Mg, S, Mn, and Zn. This effect was variable overtime and among sites. Litter N and P contents and the N:P ratio were good indicators of the decaying process.

KEYWORDS

Persea americana; litter bags; litter decomposition; nutrient cycling

1. Introduction

In the last decade, avocado (*Persea americana*) cv. Hass fruit production is a growing agroindustry in Colombia as an alternative to traditional crops. This crop has been receiving great attention due to the profit margins that this generates and promising export expectations (Bernal and Diaz 2014). Avocado cv. Hass has been introduced from California and Mexico to the highlands in Colombia where the moderate temperature (16–18 °C) favors its yield and fruit quality. This is a new crop in the country and little is known about its management. It has been noticed that it produces a lot of leaf litter (Tamayo 2016); however, the litter decomposition seems to be slow likely due to low temperatures and perhaps lack of microorganisms capable of accelerating the process. The litter decomposition is a key process in this system because soil fertility and soil's nutrient holding capacity is too low.

Litter decomposition is the set of physical and chemical processes by which this is reduced in its basic chemical constituents (Aert 1997). It is also the most important process of nutrient recycling in any ecosystem (Wang et al. 2008; Castellanos and Leon 2011), as by the decomposition of litter, nutrients become available to plants. This process regulates the amount and biochemical content of organic matter produced in an ecosystem (Aber and Melillo 1991) and is responsible for the formation of humic substances that contribute to soil quality/fertility (Berg and McClaugherty 2008; Versini et al. 2014). Litter decomposition is controlled by three main factors: climate, leaf litter quality, and abundance of degradative organisms (Swift et al. 1979; Lavelle et al. 1993; Coûteaux et al. 1995; Aerts 1997; Rocha-Loredo and Ramírez-Marcial 2009; Lorenzo and Rodríguez-Echeverría 2015).

The use of biofertilizers to promote plant growth and nutrient uptake is gaining attention because it is effective and environment friendly (Osorno and Osorio 2015). Among the functions of some biofertilizers are: nitrogen fixation, mineral dissolution (particularly phosphate compounds), plant root promotion, mycorrhizal association, and organic matter decomposition (Afanandor 2017). Unfortunately, little has been studied about the use of biofertilizers in tropical environments and lesser associated to litter decaying. The soil fungus *Mortierella* sp. has been used as a biofertilizer to promote plant growth and nutrient uptake given its ability to dissolve minerals (via organic acid production) and decompose organic matter (via cellulase and phosphatase enzymes) (Alvarez et al. 2013). In a recent study with this fungus some soil fertility parameters were enhanced when the avocado litter was inoculated with it (Tamayo and Osorio 2018).

The processes of leaf litter decomposition have been studied extensively in tropical and subtropical ecosystems (Heneghan et al. 1998; Pandey et al. 2007), semiarid (Tateno et al. 2007), temperate (Magill and Aber 2000; Cookson et al. 2007) and in Mediterranean conditions (Moro and Domingo 2000; Ribeiro et al. 2002). However, studies on rates of leaf litter decomposition and nutrient release in crops in tropical environments are less frequent are the studies in which microbial inoculation is directly involved. One of the main factors that control air and soil temperature is the altitude and since plantations of avocado cv. Hass have been established at different altitudes from 1300 to 2500 m (Bernal and Diaz 2014), this condition may affect the soil microbial activity and consequently the rate of litter decay. Therefore, we consider that this factor should be considered. Our hypothesis in this study is that the fungal inoculation of leaf litter accelerates its decomposition rate and increases nutrient release. Therefore, the aim of this study was to determine the effect of inoculation with the soil fungus *Mortierella* sp. on the decomposition of avocado cv. Hass leaf litter and nutrient release in three plantations with contrasting altitude in Colombia.

2. Materials and methods

2.1 Experimental sites

The study was conducted in three 5-yr-old plantations of avocado cv. Hass in Colombia with contrasting altitude. The trees were grafted on Antillean rootstocks grown in three production zones in the department of Antioquia, Colombia (Támesis, Jericó and Entrerríos) (Table 1). The distance among trees was 5 × 7 m (285 trees ha⁻¹). Automated meteorological stations (SpecWare 9 Pro®, Spectrum Technologies Inc., version 9.03 Build 0240) were established in these sites (Table 1). Soil fertility tests were performed in surface

Tab. 1 Description of the sites where leaf litter production was evaluated.

Site	Altitude (m)	Annual mean temperature (°C)	Annual rainfall (mm)	Annual mean air humidity (%)	Sunshine (h)	Ecological life zone*	USDA soil taxonomy (2014)**
Támesis	1350	23	1900	85	1726	PMF	Ultic Melanudand
Jericó	1900	18	2500	85	2430	PWF	Typic Hapludand
Entrerríos	2420	16	1900	83	1684	LMMF	Ultic Melanudand

* PMF: premontane moist forest; PWF: premontane wet forest, LMMF: lower montane moist forest (Holdrige, 1967)
** Soil profiles were described and classified by Professor Juan Carlos Loaiza, Universidad Nacional de Colombia

Tab. 2 Soil chemical properties in the three experimental sites.

Site	pH	SOM	Al	Ca	Mg	K	Na	P	S	Fe	Cu	Mn	Zn	B
		g kg^{-1}	cmol$_c$ kg^{-1}					mg kg^{-1}						
Támesis	4.8	284	2.4	1.2	0.6	0.25	0.05	8	7	58	2	5	20	0.2
Jericó	5.0	132	1.7	2.4	0.9	0.37	0.01	13	43	115	2	6	4	0.1
Entrerríos	5.4	258	1.6	3.4	4.8	0.76	0.16	20	43	177	16	49	7	2.1

Soil pH (water, 1 : 1); soil organic matter (SOM) content by Walkley and Black method; Al extracted by 1 M KCl; Ca, Mg, K, and Na extracted by 1 M ammonium acetate; P extracted by Bray II; S extracted by 0.008 M calcium phosphate; Fe, Mn, Cu, and Zn extracted by Olsen-EDTA; B extracted by hot water.

samples (0–20 cm) collected at random in the root area of 15 trees per site. These tests were carried out in the Soil Fertility Laboratory of the Universidad Nacional de Colombia at Medellín (Table 2). Details for the methods are available in the Soil Survey Staff (2014)

2.2 Leaf litter material

In each experimental site, some senescent leaves were collected at random from 5-year-old avocado trees cv. Hass and then a sample was oven-dried at 60 °C until reaching constant dry mass and analyzed for initial nutrient content in the Laboratory of Soil Chemistry Soil and Plant Tissue of CORPOICA. The methods are described in Westermann (1990).

2.3 Treatments

Samples of dried senescent leaves (10 g per sample) were either uninoculated or inoculated with the soil fungus *Mortierella* sp. This fungus was obtained from the microbial collection of the Laboratory of Ecology and Environmental Conservation of the Universidad Nacional de Colombia at Medellín. This fungus is capable of decompose organic materials via enzyme activity (e.g., cellulase and phosphatase) (Álvarez et al. 2013). To this purpose, the fungus was aseptically multiplied in yeast-mannitol-agar (YMA) medium for 5 days at 25 °C. After this time, spores and mycelia were suspended aseptically in sterile distilled water at a density of 10^7 colony forming units (CFU) per ml. Senescent leaves were inoculated by spraying them at a rate of 2.5 ml of fungal suspension per 10 g (dry base) of leaves. Uninoculated leaves were sprayed with 2.5 ml of sterile distilled water.

An aliquot of 10-g (dry base) of avocado leaves (either inoculated or uninoculated) were transferred into litter plastic bags (20 × 20 cm, mesh size 1 × 1 mm) to measure its decomposition based on the mass loss over time (Montagnini et al. 1991). The litter bag allows access of detritivores invertebrates to the inside of the bags, but minimizes fragmentation losses (Douce and Crossley 1982).

In each site (Jericó, Támesis, and Entrerríos), 50 bags (25 uninoculated and 25 inoculated) were randomly distributed on the soil surface around the trees and held by staples to prevent their lost by rodents or by runoff. Senescent leaves used in each site corresponded to the same site.

2.4 Variables

Five collections were made at 30, 90, 130, 330, and 430 days after treatment, covering this way a period of nearly 15 months. After each withdrawal, the bags were transported to the laboratory and the leaf litter contents were manually washed with distilled water to remove soil and roots adhered. Then, the residual leaf litter contained in the bags was dried at 60 °C, until reaching constant dry mass. Finally, samples were weighed (residual dry matter – RDM) and then grounded for analyzing elemental concentration. N content was measured by the Kjeldhal method. Samples were subjected to a closed digestion with nitric acid : hydrogen peroxide : water (5 : 1 : 2). Then, Ca, Mg, K, Fe, Mn, Cu, and Zn concentrations were measured with an atomic absorption spectrophotometer; P concentration was measured by the molybdate blue method with an visible-light spectrophotometer.

Residual contents of nutrients at each time were calculated by the product of the RDM × nutrient concentration divided by this product at the moment of inoculation (day 0). Pearson correlation coefficients were obtained to determine the relationship between RDM and some factors such as total rainfall and litter parameters (N, P, and N:P ratio).

Finally, the presence of *Mortierella* sp. In the litter samples was determined at the end of the study. Briefly, 1 g of litter sample from each bag was suspended in 9 ml of sterile distilled water to generate a 10^{-1} dilution, and then 10^{-2} and 10^{-3} serial dilutions were also obtained. From the last two dilutions, 100 μl were aseptically transferred into petri dishes containing YMA medium (Yeast-Mannitol-Agar). The medium contained two antibiotics [streptomycin sulfate 500 mg l^{-1} and tetracycline 0.1 mg l^{-1}] and two fungicides [benomyl 75 mg l^{-1} and cycloheximide 100 mg l^{-1}] based on the method developed by Osorio and Habte (2013).Then, Petri dishes were incubated at 28 °C for 48 h; after that, the number of fungal colonies was recorded.

2.5 Data analysis

Analyses of variance were performed to evaluate the effects of the inoculation, time and location on the variables. Changes of leaf litter RDM as a function of time were evaluated in each site with five regression models: single, double and triple exponential discontinuous models (Berg and McClaugherty, 2008) (D1,

D2, and D3, respectively) and two continuous models (C1 and C2, see results). The D1 model assumes a single compartment of all organic matter under a single constant of decomposition, k (Olson 1963). The D2 model is a derivation from the single exponential model, but it assumes that the leaf litter substrate has two compartments (labile and recalcitrant) and two decomposition constants (k_1 and k_2) (Bunnell and Tait 1974). The D3 model is based on the assumption that the substrate litter has three compartments (labile, metastable, and recalcitrant) with three different decomposition constants (k_1, k_2, and k_3) (Coûteaux et al. 1995). The models of continuous decomposition (C1 and C2) were proposed by Tarutis (1994) and Manzoni et al. (2012).

Using the D1 model, the time required to decompose 50 and 99% of the leaf litter were calculated as follows: $t_{0.5}$ = LN 0.5/k and $t_{0.99}$ = LN (1–0.99)/k. The time $t_{0.99}$ is used to provide an approximation of the time needed to clear almost all leaf litter, since the negative exponential model describes a curve that tends asymptotically to zero.

Similarly, the mean permanence time (Tp) was estimated as the inverse of k , this is Tp = 1/k (Olson 1963; Waring and Schlesinger1985; Songwe et al. 1995; Perez-Harguindeguy et al. 2013).

To find the model that fit the best, three indicators were employed: coefficient of determination (R^2), mean square error (MSE), and the Akaike Information Criterion (AIC). Models D1 and D2 and C1 were fit using SAS program (Statistical Analysis System, version 9.0), model C2 was fit using MATLAB (Mathworks, Natick, Massachusetts).

3. Results

3.1 Residual dry matter

The RDM was significantly affected by the factors site, time, inoculation and by the interaction site x time x inoculation (Table 3A). For instance, the initial loss of RDM at day 30 (RDM_{90}) was faster in Támesis (0.79–0.81) and Jericó (0.78–0.85) and slower in Entrerríos (0.89) (Fig. 1). This tendency was maintained until the end when RDM_{430} was 0.49 in Támesis, 0.42–0.48 in Jericó, and 0.46–0.51 in Entrerríos. In general, the values of RDM were lower when the leaf litter was inoculated than when was uninoculated (Fig.1). This effect was more significant in Támesis at day 90 (0.71 uninoculated vs. 0.63 inoculated), in Jericó at days 30 (0.85 uninoculated vs. 0.78 inoculated) and 430 (0.48 uninoculated vs. 0.42 inoculated), and in Entrerríos at day 430 (0.51 uninoculated vs. 0.46 inoculated).

Although all regression models exhibited highly significant P-values (<0.0001), the values of R^2 were consistently lower with the single exponential model (Table 4). In general, the double exponential model
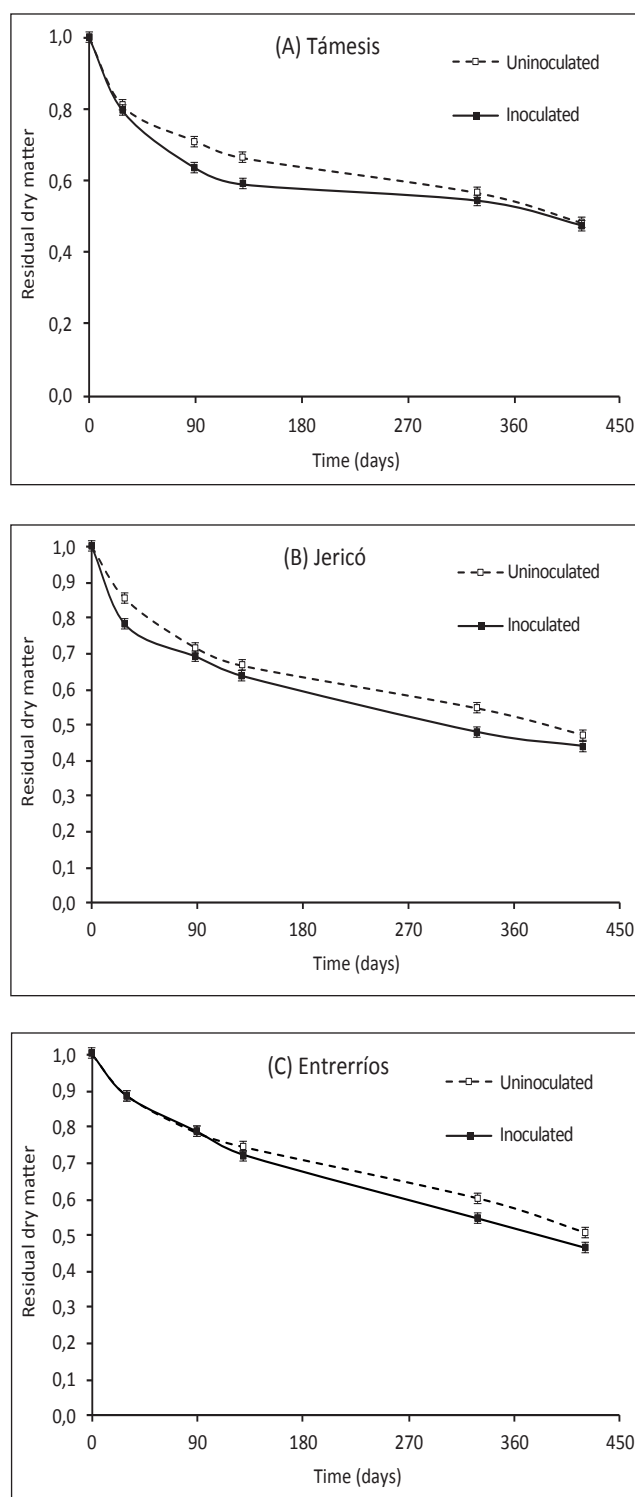

Fig. 1 Residual dry matter (RDM) of leaf litter avocado cv. Hass uninoculated (□) and inoculated (■) with the fungus *Mortierella* sp. as a function of time in three sites of Colombia. Each value is the mean of five replicates. The bars indicate the standard error.

showed values of R^2 higher, MSE lower, and AIC lower than the other models. For this reason, this model can be considered the most effective to fit the data and represent satisfactorily the dynamics of mass loss of avocado leaf litter in all three sites.

3.2 Residual nutrient content

The residual nutrient contents were significantly affected by the single factors site and time, and by the interaction site x time (except for Fe) (Table 3A, 3B). On the other hand, the single effect of inoculation on Mn residual content was significant. Also, significant interactive effects of site x inoculation affected P and Zn residual contents; time x inoculation significantly affected Mg, S, and Zn residual contents. On the other hand, site x time x inoculation affected significantly P and Zn residual nutrient contents (Table 3A, 3B). The coefficients of variation (CV) were low for all macronutrients (<30%) and high for all micronutrients (30–60%).

The residual contents for all macronutrients, except P, showed a tendency to decrease over time (Table 5). According to the residual contents at day 430, the relative release of macronutrients followed the following pattern: K (0.02–0.03) > Mg (0.3–0.4) > Ca (0.3–0.53) > N (0.64–0.74) >> P (2.1–4.3).

It is worthy to mention that release of K was very rapid, at day 30 the residual K contents were only 0.18, 0.15, and 0.21 in Támesis, Jericó, and Entrerríos, respectively. This indicates that the relative release of K contained in the leaf litter of avocado was 82, 85, and 79% at the end of the first month of decomposition. The release continued during the period of observation, thus at day 430 this was between 97–98%. In the case of N, its release was slower and seemed to be irregular. In intermediate sampling dates (130–330 d) occurred an apparently stabilization phase because the values increased with respect to previous values.

In all three sites, the tendency for the residual P content was to increase overtime (Table 5A). At day 430, in Támesis, Jericó, and Entrerríos the values were 2.09, 4.33, and 2.69, respectively, which suggested an apparent process of P immobilization or even gain. This was detected from the initial stages of decomposition, for instance at day 30 the values already were 1.51, 2.55, and 2.48, respectively. However, this effect was lower in Támesis and Jericó when the litter was inoculated, particularly at the beginning of the decaying process (<90 d).

In the case of Mg, there was an accumulation over time, but this had a lower magnitude when the litter was inoculated, particularly after 130 d. There was also accumulation of sulfur in the litter over time, but this effect was lower when the litter was inoculated.

All microelements also exhibited significant increases in the residual content in the leaf litter of avocado (Table 5B). For instance, at day 430 the value for Fe-residual ranged 100–171, Zn 18–58, Mn 7–14, and Cu 1–6; significant differences were detected among sites. These results clearly suggest that there was a gain in the content of these micronutrients. In the case of Fe and Zn the increase was higher over time, while with Mn and Cu there were higher values in intermediate dates (90–330 d). The inoculation with the fungus changed the pattern of accumulation. For instance, the quantity of Mn accumulated was lower when the litter was inoculated; in the case of Zn, there were less accumulation at the beginning of the decomposition process (<90 d) in Tamesis and Entrerrios and along the process in Jerico.

Tab. 3A Significant *P*-values for Anova's tests of RDM and macronutrient contents.

Factor	Degree of fredom	RDM	N	P	K	Ca	Mg	S
Site (A)	2	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0261
Time (B)	5	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Inoculation (C)	1	<0.0001	NS	NS	NS	NS	NS	NS
AB	10	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
AC	2	NS	NS	0.0371	NS	NS	NS	NS
BC	5	NS	NS	NS	NS	NS	<0.0001	0.0010
ABC	10	0.0435	NS	0.0047	NS	NS	NS	NS
CV (%)		5.0	14.1	27.6	17.3	14.4	10.3	25.0

Tab. 3B Significant *P*-values for Anova's tests of micronutrient contents.

Factor	Fe	Mn	Zn	Cu
Site (A)	<0.0001	<0.0001	<0.0001	<0.0001
Time (B)	<0.0001	<0.0001	<0.0001	<0.0001
Inoculation (C)	NS	0.0084	NS	NS
AB	NS	<0.0001	0.0002	0.0003
AC	NS	NS	0.0005	NS
BC	NS	NS	0.0254	NS
ABC	NS	NS	0.0067	NS
CV (%)	56	30	55	60

Tab. 4 Regression models for RDM of leaf litter avocado cv. Hass uninoculated (−) and inoculated (+) with the fungus *Mortierella* sp. as a function of time in three sites of Colombia.

Site	Inoculation	Regression models	P-value	R2*	MSE	AIC
Támesis	−	$X_t/X_o = e^{-0.7627t}$	<0.0001	68.3	0.097	−136.9
	+	$X_t/X_o = e^{-0.8788t}$	<0.0001	49.8	0.129	−119.7
	−	$X_t/X_o = 0.226e^{-17.1301} + 0.774e^{-0.3861t}$	<0.0001	96.6	0.033	−200.1
	+	$X_t/X_o = 0.363e^{-9.913} + 0.637e^{-0.229t}$	<0.0001	95.9	0.039	−190.5
	−	$X_t/X_o = 0.226e^{-17.1265} + 0.431e^{-0.3861t} + 0.343e^{-0.3861t}$	<0.0001	96.6	0.033	−200.1
	+	$X_t/X_o = 0.280e^{-9.9421} + 0.637e^{-0.2293t} + 0.083e^{-9.9421t}$	<0.0001	95.9	0.039	−190.5
	−	$X_t/X_o = 0.059^{-0.780}/(0.059 + t)^{0.780}$	<0.0001	95.6	0.038	−119.9
	+	$X_t/X_o = 0.031^{-0.833}/(0.031 + t)^{0.833}$	<0.0001	95.3	0.041	−186.9
	−	$X_t/X_o = 29.082e^{-0.0063t} - 0.0063e^{-29.082t} [Ei(-29.082t) - Ei(-0.0063t)]0.1832t/29.076$	<0.0001	95.7	0.036	−193.9
	+	$X_t/X_o = 54.4878e^{-0.0059t} - 0.0063e^{-54.488t} [Ei(-54.488t) - Ei(-0.0059t)]0.3215t/54.172$	<0.0001	95.2	0.041	−187.0
Jericó	−	$X_t/X_o = e^{-0.781t}$	<0.0001	76.8	0.089	−142.0
	+	$X_t/X_o = e^{-0.913t}$	<0.0001	74.6	0.097	−136.9
	−	$X_t/X_o = 0.238e^{-9.4071} + 0.762e^{-0.3963t}$	<0.0001	94.6	0.045	−181.7
	+	$X_t/X_o = 0.221e^{-24.0382} + 0.779e^{-0.514t}$	<0.0001	97.6	0.031	−204.2
	−	$X_t/X_o = 0.238e^{-9.4438} + 0.423e^{-0.3965t} + 0.338e^{-0.3965t}$	<0.0001	94.6	0.045	−181.7
	+	$X_t/X_o = 0.169e^{-11.8918} + 0.335e^{-t} + 0.497e^{-1.3523t}$	<0.0001	97.8	0.029	−206.6
	−	$X_t/X_o = 0.119^{-0.701}/(0.119 + t)^{0.701}$	<0.0001	94.3	0.046	−180.1
	+	$X_t/X_o = 0.080^{-0.714}/(0.080 + t)^{0.714}$	<0.0001	96.3	0.038	−190.9
	−	$X_t/X_o = 16.072e^{-0,0167t} - 0.0167e^{-16.0722t} - [Ei(-16.072t) - Ei(-0.0167t)]0.0.25715t/16.072 - 00.167$	<0.0001	94.3	0.045	−181.0
	+	$X_t/X_o = 25.746e^{-0.0177t} - 0.0177e^{-25.7458t} - [Ei(-25.746t) - Ei(-0.0177t)]0.4570t/25.748$	<0.0001	96.5	0.037	−193.1
Entrerríos	−	$X_t/X_o = e^{-0.691t}$	<0.0001	87.2	0.062	−164.3
	+	$X_t/X_o = e^{-0.732t}$	<0.0001	93.8	0.047	−180.1
	−	$X_t/X_o = 0.124e^{-13.8325} + 0.876e^{-0.4532t}$	<0.0001	95.0	0.040	−188.1
	+	$X_t/X_o = 0.112e^{-13.4596} + 0.888e^{-0.558t}$	<0.0001	98.5	0.024	−219.6
	−	$X_t/X_o = 0.333e^{-0.4532} + 0.543e^{-0.4532t} + 0.124e^{-13.8637}$	<0.0001	95.0	0.040	−188.1
	+	$X_t/X_o = 0.112e^{-13.4199} + 0.555e^{-0.558t} + 0.333e^{-0.558t}$	<0.0001	98.5	0.024	−219.6
	−	$X_t/X_o = 0.301^{-0.599}/(0.301b + t)^{0.599}$	<0.0001	94.0	0.044	−182.9
	+	$X_t/X_o = 0.475^{-0.401}/(0.475 + t)^{0.401}$	<0.0001	98.1	0.027	−211.3
	−	$X_t/X_o = 7.1786e^{-0.0235t} - 0.0235e^{-7.1786t} - [Ei(-7.1786t) - Ei(-0.0235t)]0.1686971t/7.1551$	<0.0001	93.9	0.043	−183.6
	+	$X_t/X_o = 5.5686e^{-0.0579t} - 0.0579e^{-5.5686t} - [Ei(-5.569t) - Ei(-0.0579t)]0.32242t/5.569$	<0.0001	98.0	0.027	−211.8

*R^2: Coefficient of determination; MSE: Mean Square Error; AIC: Akaike Information Criterion (1974).

Tab. 5A Residual macronutrient contents in leaf litter of avocado cv. Hass as a function on the decomposition time in three sites of Colombia. Each value is the mean of five replicates; in parenthesis the standard error. Means followed by a common letters do not significantly differ (*P*-value ≤0.05) (vertical comparisons).

Time (days)	Támesis					Jericó					Entrerríos				
	N	P	K	Ca	Mg	N	P	K	Ca	Mg	N	P	K	Ca	Mg
0	1.00* (0.03) a	1.00 (0.01) k	1.00 (0.02) a	1.00 (0.04) a	1.00 (0.02) a	1.00 (0.03) a	1.00 (0.01) k	1.00 (0.02) a	1.00 (0.04) a	1.00 (0.02) a	1.00 (0.03) a	1.00 (0.01) k	1.00 (0.02) a	1.00 (0.04) a	1.00 (0.02) a
30	0.91 (0.03) ab	1.51 (0.01) j	0.18 (0.02) c	0.87 (0.04) b	0.60 (0.02) c	0.70 (0.03) def	2.55 (0.01) ef	0.15 (0.02) d	0.88 (0.04) b	0.41 (0.02) e	0.70 (0.03) def	2.48 (0.01) f	0.21 (0.02) b	0.93 (0.04) ab	0.70 (0.02) b
90	0.77 (0.03) cde	1.59 (0.01) ij	0.14 (0.02) d	0.67 (0.04) c	0.50 (0.02) d	0.76 (0.03) de	2.92 (0.01) d	0.09 (0.02) e	0.62 (0.04) c	0.37 (0.02) ef	0.71 (0.03) def	2.27 (0.01) g	0.12 (0.02) bc	0.80 (0.04) b	0.50 (0.02) d
130	0.80 (0.03) bcd	1.73 (0.01) i	0.10 (0.02) de	0.63 (0.04) c	0.40 (0.02) e	0.87 (0.03) g	3.82 (0.01) b	0.09 (0.02) ef	0.50 (0.04) d	0.35 (0.02) ef	0.73 (0.03) def	2.97 (0.01) d	0.13(0.02) bc	0.80 (0.04) b	0.40 (0.02) e
330	0.88 (0.03) b	1.91 (0.01) h	0.04 (0.02) ef	0.57 (0.04) cd	0.40 (0.02) e	0.58 (0.03) efg	3.55 (0.01) c	0.04 (0.02) fg	0.40 (0.04) e	0.30 (0.02) f	0.75 (0.03) de	2.95 (0.01) d	0.05 (0.02) ef	0.60 (0.04) c	0.40 (0.02) e
430	0.74 (0.03) def	2.09 (0.01) g	0.02 (0.02) fg	0.53 (0.04) d	0.40 (0.02) e	0.67 (0.03) a	4.33 (0.01) a	0.02 (0.02) g	0.30 (0.04) f	0.30 (0.02) f	0.64 (0.03) fg	2.69 (0.01) e	0.03 (0.02) fg	0.50 (0.04) d	0.30 (0.02) f

Tab. 5B Residual microelements contents in leaf litter of avocado cv. Hass as a function on the decomposition time in three sites of Colombia.

Time (days)	Támesis				Jericó				Entrerríos			
	Fe	Cu	Mn	Zn	Fe	Cu	Mn	Zn	Fe	Cu	Mn	Zn
0	1* f	1 f	1 g	1 e	1 f	1 f	1 g	1 e	1 f	1 cd	1 g	1 e
30	51 (14) de	15 (3.9) bc	11 (1.4) cd	13 (9.1) bc	51 (14) de	4 (3.9) ef	7 (1.4) f	16 (9.1) de	17 (14) f	14 (3.9) bc	12 (1.4) bcd	9 (9.1) de
90	80 (14) cd	17 (3.9) bc	11 (1.4) cd	15 (9.1) bc	67 (14) cd	6 (3.9) ef	8 (1.4) ef	15 (9.1) de	22 (14) ef	8 (3.9) cd	15 (1.4) ab	13 (9.1) de
130	81 (14) cd	17 (3.9) bc	10 (1.4) d	20 (9.1) b	135 (14) ab	6 (3.9) ef	8 (1.4) ef	33 (9.1) c	16 (14) ef	13 (3.9) bc	11 (1.4) ab	13 (9.1) de
330	126 (14) b	21 (3.9) ab	16 (1.4) a	50 (9.1) a	174 (14) a	5 (3.9) ef	8 (1.4) ef	41 (9.1) bc	105 (14) bc	24 (3.9) a	13 (1.4) abc	17 (9.1) de
430	138 (14) ab	5 (3.9) f	14 (1.4) ab	58 (9.1) a	171 (14) a	6 (3.9) f	7 (1.4) f	46 (9.1) abc	100 (14) bc	1 (3.9) cd	10 (1.4) de	18 (9.1) d

* Each value is the mean of five replicates; in parenthesis the standard error. Means followed by common letters do not significantly differ (*P*-value ≤ 0.05) (vertical comparisons).

The contrasting dynamics for some nutrients can be summarized in Table 6. In the case of litter K concentration, the final value (430 d = mean 0.04%) was lower than the initial value (mean 0.50%), a clear example of release. With N there was an immobilization because at the end of the study the N concentration in the leaf litter was higher (mean 2.22%) than the initial concentration (mean 1.42%). In the case of P, the initial mean concentration was 0.04 and at the end it was 0.28, meaning a net gain. The initial values of the N:P ratio were very high (24.1–46.3), higher than the optimal suggested of 10–11 (Léon 2007).

Site	N (%)	P (%)	K (%)	N: P
Initial values				
Támesis	1.69 (0.08)	0.07 (0.02)	0.44 (0.01)	24.1 (0.78)
Jericó	1.39 (0.08)	0.03 (0.02)	0.62 (0.01)	46.3 (0.78)
Entrerríos	1.19 (0.08)	0.03 (0.02)	0.45 (0.01)	39.7 (0.78)
Mean	1.42 (0.05)	0.04 (0.01)	0.50 (0.005)	36.7 (0.45)
Final values				
Támesis	2.62 (0.08)	0.30 (0.02)	0.05 (0.01)	9.9 (0.78)
Jericó	2.00 (0.08)	0.28 (0.02)	0.03 (0.01)	7.1 (0.78)
Entrerríos	1.56 (0.08)	0.17 (0.02)	0.05 (0.01)	9.7 (0.78)
Mean	2.06 (0.05)	0.28 (0.01)	0.04 (0.005)	9.0 (0.45)

Although the best regression model was the double exponential, the single exponential model offers some parameters of easy visualization of the contrasts detected in this study. For instance, in all three sites the decomposition rate (k) was higher when the leaf litter of avocado was inoculated (Támesis: 0.88 > 0.76; Jericó 0.91 > 0.78; Entrerríos 0.73 > 0.69). Consequently, the mean residence time of the leaf litter was lower when it was inoculated (1.09–1.36) than when was uninoculated (1.28–1.44). In the same way, the time needed for decomposing half of the litter ($t_{0.5}$) was also lesser in the inoculated leaf litter: in Támesis it was 10.9 months with uninoculated leaf litter and 9.5 months when inoculated; in Jericó, 10.7 months with uninoculated leaf litter and 9.1 months when inoculated; and in Enterríos, 12 months without inoculation and 11.4 months with inoculation.

4. Discussion

The results clearly support our hypothesis that the decomposition rate of avocado leaf litter can be increased with the inoculation of effective microorganisms. It was evident that in all three sites the mass loss in the RDM was higher when the leaf litter was inoculated with the fungus *Mortierella* sp. The uninoculated RDM in Tamesis, Jerico, and Entrerrios at day 330 were 0.57, 0.55, and 0.60, respectively; while the inoculated RDM was 0.54, 0.48, and 0.54, respectively. At day 430 the values of uninoculated RDM were 0.48, 0.47, 0.50, while the values for inoculated RDM were 0.47, 0.44, and 0.46, respectively. This indicates that the rate of decomposition was higher when the litter was inoculated with *Mortierella* sp. In a previous work, it was detected that this fungus is able to release cellulase and phosphatase enzymes (Álvarez et al. 2013).

The high rate of decomposition in the early stages of the process coincide with those reported by Berg (2000), Goma-Tchimbakala and Bernhard-Reversat (2006) for *Terminalia superba*, Castellanos and León (2011) in plantations of *Acacia mangium* and Florez et al. (2013) in *Azadirachta indica*. The general pattern for mass loss during this process comprises two phases: an initial phase with a fast decomposition of labile materials (e.g., sugars, some phenols, starches, and proteins) and a second phase that results in a gradual (slow) decomposition of recalcitrant elements (e.g., cellulose, hemicellulose, lignin, and tannins) (Arellano et al. 2004; Goma-Tchimbakala and Bernhard-Reversat, 2006; Weerakkody and Parkinson 2006a). This rate of litter decomposition can vary depending on different factors such as soil humidity, soil temperature, soil nutrient availability, plant species, plant age, and litter concentrations of N and P, C:N and N:P ratios, lignin, tannins, etc.). The litter quality characteristics determine in turn the microbial biomass and nutrient release (Attiwill and Adams 1993; Bubb et al. 1998; McGrath et al. 2000; Kumar and Agrawal, 2001; Villela Proctor, 2002; Singh et al. 2004; Weerakkody and Parkinson, 2006a; Liao et al. 2006; Huang et al. 2007; Castellanos and Leon 2010; Aragon et al. 2014).

The rate of decomposition (k) of leaf litter among sites followed a decreasing order: Jericó ≥ Támesis > Entrerríos. It is possible that these differences can be attributable to the environmental conditions of each site as microclimate, soil properties, and mainly the activity of soil biota (Swift et al. 1979; Attiwill and Adams 1993; Aerts and Chapin 2000; Leon 2007). According to the double exponential model for the three sites, a rapid degradation of labile materials occurred during the first 100 days, followed by a slower decomposition. These results differ from studies of Castellanos and León (2011), whose values of k indicate a more rapid degradation of the labile fractions. Differences in these decomposition rates suggest that affect the rate at which leaf litter nutrients become available for plant roots. Speed and efficiency with which the plant again uptake these nutrients depend on other soil process since them may be (i) leached out from the soil profile (e.g., NO_3^-, K^+), (ii) strongly adsorbed by soil clay and Fe-oxides (e.g., $H_2PO_4^-$, SO_4^{2-}) or (iii) absorbed by soil biota (Schlesinger 2000; Ribeiro et al. 2002).

Values of k from 0.69 to 0.91 obtained in this study are similar to those reported in avocado ($k = 0.90$) on the coast of Granada Spain by Rodríguez et al. (2011) and Pleguezuelo et al. (2011) and in several forest species of Sri Lanka by Weerakkody and Parkinson 2006b and in Andean forests of Colombia by Loaiza et al. (2013). The difference of k between Entrerríos (2420 m, 16 °C) and the other two sites, Jericó (1900 m, 18 °C) and Támesis (1350 m, 23 °C) may be associated with the differences in altitude and climate conditions. It has been demonstrated the importance of soil and climate in the regulation of leaf litter decomposition (Berg 2000; Martin et al. 1996;

Gholz et al. 2000; Barlow et al. 2007; Cornwell et al. 2008).

In many studies it has been determined that the quality of the leaf litter also influences the decomposition (Xuluc-Tolosa et al. 2003; Ngoran et al. 2006; Martinez-Yerízar et al. 2007; Prause and Fernández 2007; Castellanos and Léon 2011 Furey et al. 2014; Gaspar Santos et al. 2015). Among the indicators of litter quality are the litter content of N and P and the N:P ratio (Kainulainen and Holopainen 2002; Xuluc-Tolosa et al. 2003; Alhamd et al. 2004; Ngoran et al. 2006; Martinez-Yerízar et al. 2007; Prause and Fernández 2007; Castellanos and Léon 2011; Nouvellon et al. 2012 Pérez-Harguindeguy et al. 2013; Aragon et al. 2014; Furey et al. 2014). According to Budd et al. (1998) and Gallardo-Lancho (2000) the N and P concentrations showed a negative correlation with the residual dry matter (RDM) this indicates their participation in the leaf litter decomposition. It is important to highlight the limiting nature of P in these Andisols on the decay process and the low N supply from the soil humus. This could be corroborated by obtaining a significant inverse correlation between the decomposition constant (k) and the N:P ratio. This agrees with reports of some authors who claim that the N:P ratio exercises control over the decomposition (Flórez et al. 2013; Prescott 2005; Berg and Laskowski 1997). Aerts (1997) proposed the value 11.9 as critical in the leaf litter for the N:P ratio, which represents in tropical forests, some degree of shortage of P for decomposition organisms, as in the cells of fungi and bacteria such ratio is about 10–15. A low N:P ratio may be associated with larger populations of bacteria in the decomposition process (Güsewell and Gessner 2009).

In a study carried out by Castellanos and Léon (2011), in *Acacia mangium* plantations established on degraded soils in Colombia, litter N and P contents and the C:N and N:P ratios were good predictors of the process. This could be corroborated by obtaining a significant inverse correlation between the decay constant (k) and the N:P ratio (r = 0.72, 0.76 and 0.75 for Támesis, Jericó and Entrerríos, respectively). The locality of slower litter decomposition was Entrerríos, followed by Támesis and Jericó.

In spite of the significant effect of inoculation on the RDM dynamic there were no significant differences with this on the litter residual nutrient contents. In other words, the data did not support that the inoculation can accelerate the release of nutrient from avocado litter. This may be due to the interference of other factors such as the microbial colonization of leaf litter during the observation time. It is worth to mention that in the same experimental sites, Tamayo and Osorio (2018) found that the soil below the inoculated litter had higher concentration of some nutrients (P, K, Ca, Mg, B) than the soil below the uninoculated litter, which suggested a more active nutrient release due to the enzymatic activity of *Mortierella* sp.

In other studies in the coffee region of Colombia, Cardona and Sadeghian (2005) evaluated the litter supply (leaves, stems, flowers, fruits and other plant organs) and associated nutrient release in coffee plantations to sun exposure and with shading. These authors concluded that in shade coffee plantations, there is a significant contribution of organic material equivalent to 11 t ha^{-1}, which contributes to the formation of stable soil organic matter and to supply nutrient into the soils (N, P, K, Ca, Mg, Fe, Mn, Zn).

Data in the present research showed variable dynamics of the litter residual nutrient contents during the decay process. Thus, nutrient release, immobilization, and gain in the litter occurred simultaneously or sequentially. For instance, there was a very rapid net release of K, while the N release was initially rapid (0–30 d), then there was a stabilization phase in intermediate dates (30–330), and finally a slow release (330–430 d), as reported by Schlesinger (1991). By contrast, there was apparently gain of P during the period of observation. This apparently gain of P occur in despite of an increase in the surface soil P availability (0–5 cm, upper A Horizon) reported by Tamayo and Osorio (2018) in the same avocado plantations. This contradiction can be explained by a possible translocation of P by fungi and insects that colonize litter and the abundant presence of fungal mycelium that occur, as reported by several authors (Melillo et al. 1982; Koenig and Cochran 1994; Musovoto et al. 2000).

The general pattern of nutrient release was: K > Ca > Mg > N > P. The rapid release of K has been widely reported due to their mobile nature as a result of not being occluded to the organic structures in leaf tissue, but being in free form, which is easily washed and/or removed (Tukey 1970; Parker 1983). Thus, Villela and Proctor (2002) in tropical forests of Pará (Brazil) found K losses of 70%, in leaves of *Ecclinusa guianensis*. Similar trends were reported by Ngoran et al. (2006) for A. *mangium*, with losses of this element higher than 80% and Castellanos and León (2011) of 70%. K was the element with the higher rate of release in all locations, reaching at the end of the study almost entirely on the initial content (96%), resulting from their mobile nature (Parker 1983).

The release of Ca was of 47%, this was higher than that of N (26%) and P (0%). These results are similar to those reported by Liao et al. (2006) in humid forests of Taiwan, where the Ca showed higher mobility during the decomposition process, exceeding the general release trends that show N and P, in the tropical forests. Pleguezuelo et al. (2011) in Spain found a net N release from litter avocado after 159 d, while in this study the release was detected as earlier as 30 d, but it was then immobilized , contrary to the reported by other authors as Hasegawa and Takeda (1996) and Enoki and Hawaguchi (2000).

On the other hand, during the litter decomposition process micronutrients (Fe, Mn, Cu, and Zn) were

immovilized (Table 5B). This had been also reported by León (2007) studying the litter decomposition of *Pinus patula* and *Cupresus lusitanica* in Andean forest of Colombia. The reason for this immobilization seems to be associated with the ability of organic matter to form complex with cations of these elements, leaving them in unavailable forms (Stevenson and Cole 1999).

5. Conclusions

The RDM was significantly lower when the litter was inoculated with the fungus *Mortierella* sp. It means the fungal inoculation accelerated the rate of decomposition; however, the effect was affected by the site and time after inoculation. Thus, the inoculation effect was significant in Támesis at day 90 (0.71 uninoculated vs. 0.63 inoculated), in Jericó at days 30 (0.85 uninoculated vs. 0.78 inoculated) and 430 (0.48 uninoculated vs. 0.42 inoculated), and in Entrerríos at day 430 (0.51 uninoculated vs. 0.46 inoculated).

The rate of decomposition followed the decreasing sequence: Jericó > Támesis > Entrerríos. The nutrient release pattern was: K > Ca > Mg > N > P > Cu > Mn > Zn > Fe. While K was rapidly released, Ca, Mg, and N were slowly released; P, Cu, Mn, Zn, and Fe were immobilized during the decomposition process. However, the fungal inoculation on the litter significantly reduced the magnitude of nutrient accumulation for P, Mg, S, Mn, and Zn. This effect was variable overtime and among sites.

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References

Akaike, H. (1974): A new look at the statistical model identification. IEEE Transactions on Automatic Control 19(6), 716–723, https://doi.org/10.1109/TAC.1974.1100705.

Aber, J. D., Melillo, J. M. (1991): Terrestrial Ecosystems. 2nd Ed. Academic Press, San Diego, California.

Aerts, R. (1997): Climate. Leaf litter chemistry and leaf litter decomposition in terrestial ecosystems: a triangular relationship. Oikos 79, 439–449, https://doi.org/10.2307/3546886.

Afanador, L. N. (2017): Biofertilizers: concepts, benefits and its application in Colombia. Ingeciencia 2(1), 65–76.

Alhamd, L., Arakaki S., Hagihara, A. (2004): Decomposition of leaf litter of four tree species in a subtropical evergreen broad-leaved forest, Okinawa Island. Forest Ecology and Management 202, 1–11, https://doi.org/10.1016/j.foreco.2004.02.062.

Álvarez, C. L., Osorio, N. W., Marin, M. (2013): Molecular identification of microorganisms associated to the rhizosphere of vanilla plants in Colombia. Acta Biologica Colombiana 18, 293–306, https://doi.org/10.15446/abc.

Aragón, R., Montti, L., Ayup, M., Fernandez, R. (2014): Exotic species as modifers of ecosystem processes: litter decomposition in native and invaded secondary forests of NW Argentina. Acta Oecologica 54, 21–28, https://doi.org/10.1016/j.actao.2013.03.007.

Arellano, R., Paolini, J., Vásquez, V., Mora, E. (2004): Producción y descomposición de hojarasca en tres agroecosistemas de café en el estado de Trujillo, Venezuela. Revista Forestal Venezuela 48, 7–14.

Attiwill, P. M., Adams, M. A. (1993): Tansley Review No. 50. Nutrient cycling in forests. New Phytologist 124, 561–582, https://doi.org/10.1111/j.1469-8137.1993.tb03847.x.

Barlow, J., Gardner, T. A., Ferreira, L. V., Peres, C. A. (2007): Litter fall and decomposition in primary, secondary and plantation forests in the Brazilian Amazon. Forest Ecology and Management 247, 91–97, https://doi.org/10.1016/j.foreco.2007.04.017.

Berg, B., Laskowski, R. (1997): Changes in nutrient concentrations and nutrient release in decomposing needle litter in monocultural systems of Pinus contorta and Pinus sylvestris: a comparison and synthesis. Scandinavian Journal of Forest Research 12, 113–121, https://doi.org/10.1080/02827589709355392.

Berg, B., McClaugherty, C. (2008): Plant litter: Decomposition, humus formation, carbon sequestration. 2nd Ed. Springer, Berlin, Heidelberg.

Berg, B. (2000): Litter decomposition and organic matter turnover in northern forest soils. Forest Ecology and Management 133, 13–22, https://doi.org /10.1016/S0378-1127(99)00294.

Bubb, K. A., Xu, Z. H., Simpson, J. A., Safigna, P. G. (1998): Some nutrient dynamics associated with litterfall and litter decomposition in hoop pine plantations of southeast Queensland, Australia. Forest Ecology and Management 110, 343–352, https://doi.org/10.1016/S0378-1127(98)00295-3.

Bunnel, F. Y., Tait, D. E. (1974): Mathematical simulation models of decomposition soil organisms and decomposition in Tundra. In: Soil organisms and decomposition in tundra. Ed. A. J. Holding, S. F. Heal, J. Maclean, P. W. Flanagan. Tundra Biome Steering Conmmittee, Stockholm, 207–225.

Cardona, C., Sadeghian, K. S. (2005): Aporte de material orgánico y nutrientes en cafetales al sol y bajo sombrío de guamo. Avances Técnicos Cenicafé 334, 1–8.

Castellanos, J., León, J. D. (2010): Caída de hojarasca y dinámica de nutrientes en plantaciones de Acacia mangium (Mimosaceae) de Antioquia Colombia. Acta biológica Colombiana 15(2), 289–308.

Castellanos, J., León, J. D. (2011): Descomposición de hojarasca y liberación de nutrientes en plantaciones de Acacia mangium (Mimosaceae) establecidas en suelos degradados de Colombia. Revista de Biologia Tropical 59(1), 113–128.

Cookson, W. R., Osman, M., Marschner, P., Abaye, D. A., Clarck, I., Murphy, D. V., Stockdale, E. A., Watson, C. A.

(2007): Controls on soil nitrogen cycling and microbial community composition across land use and incubation temperature. Soil Biology and Biochemistry 39, 744–756, https://doi.org/10.1016/j.soilbio.2006.09.022.

Cornwell, W. K., Cornelissen, J. H., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison S. D., Van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T. V., Díaz, S., Garnier, E., Gurvich, D. E., Kazakou, E., Klein, J. A., Read, J., Reich, P. B., Soudzilovskaia, N. A., Vaieretti, M. V., Westoby, M. (2008): Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11(10), 1065–1071, https://doi.org/10.1111/j.1461-0248.2008.01219.x.

Coûteaux, M. M., Bottner, P., Berg, B. (1995): Litter decomposition climate and litter qualitym. Trends in Ecology Evolution 10, 63–66, https://doi.org/10.1016/S0169-5347(00)88978-8.

Enoki, T., Hawaguchi, H.(2000): Initial nitrogen and topographic moisture effects on the decomposition of pine needles. Ecological Research 15, 425–434, https://doi.org/10.1046/j.1440-1703.2000.00363.x.

Furey, C., Tecco, P. A., Perez-Harguindeguy, N., Giorgis, M. A., Grossi, M. (2014): The importance of native and exotic plant identity and dominance on decomposition patterns in mountain woodlands of central Argentina. Acta Oecologica 54, 13–20, https://doi.org/10.1016/j.actao.2012.12.005.

Gallardo-Lancho, J. F. (2000): Biogeochemistry of Mediterranean forest ecosystems, a case study. In: Soil Biochemtry 10. Ed. J. M. Bollag, G. Stotzky. Marcel Dekker, New York, EEUU, 423–460.

Gaspar-Santos, E. S., González-Espinosa, M., Ramírez-Marcial, N., Álvarez-Solís, J. D. (2015): Acumulación y descomposición de hojarasca en bosques secundarios del sur de la Sierra Madre de Chiapas, México. Bosque (Valdivia) 36(3), 467–480, https://doi.org/10.4067/S0717-92002015000300013.

Gholz, H. L., Wedin, D. A., Smitherman, S. M., Harmon, M. E., Parton, W. J. (2000): Long-term dynamics of pine and hardwood litter in contrasting envi- ronments: toward a global model of decomposition. Global Change Biology 6, 751–765, https://doi.org/10.4067/S0717-92002015000300013.

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, 304–313, https://doi.org/10.1016/j.foreco.2006.04.009.

Güsewell, S., Gessner, M. O. (2009): N:P ratios influence litter decomposition and colonization by fungi and bacteria in microcosms. Funtional Ecology 23, 211–219, https://doi.org/10.1111/j.1365-2435.2008.01478.x.

Hasegawa, M., Takeda, H. (1996): Carbon and nutrient dynamics in decomposing pineneedle litter in relation to fungal and fauna labundances. Pedobiologia 40, 171–184.

Heneghan, L., Coleman, D. C., Zou, X., Crossley, Jr D. A., Haines, B. L. (1998): Soil microarthropod community structure and litter decomposition dynamics: a study of tropical and temperate sites.

Applied Soil Ecology 9, 33-38, https://doi.org/10.1016/S0929-1393(98)00050-X.

Holdridge, L. R. (1967): Life zone ecology. Tropical Science Center, San Jose, Costa Rica.

Huang, J., Wang, X., Yan, E. (2007): Leaf nutrient concentration. Nutrient resorption and litter decomposition in an evergreen broad-leaved forest in eastern China. Forest Ecology and Management 239, 150–158, https://doi.org/10.1016/j.foreco.2006.11.019.

Kumar, R., Agrawal, M. (2001): Litterfall litter decomposition and nutrient release in five exotic plant species planted on coal mine spoils. Pedobiologia 45, 298–312, https://doi.org/10.1078/0031-4056-00088.

Lavelle, P., Blanchart, E., Martin, A., Spain, A., Toutain, F., Barois, I., Schaefer, R. (1993): A hierarchical model for decomposition in terrestial ecosystems: application to soil of the humid tropics. Biotropica 25, 130–150, https://doi.org/10.2307/2389178.

León, J. D. (2007): Contribución al conocimiento del ciclo de nutrientes en bosques montanos naturales de Quercus humboldtii y reforestados (Pinus patula y Cupresus lusitanica) de la Región de Piedras Blancas, Antioquia (Colombia). Tesis Doctoral, Universidad de Salamanca, Espa-a.

Liao, J. H., Wang, H. H., Tsai, C. H., Hseu, Z. Y. (2006): Litter production. Decomposition and nutrient return of uplifted Coral Reef tropical forest. Forest Ecology and Management 235, 4–185, https://doi.org/10.1016/j.foreco.2006.08.010.

Loaiza-Usuga, J. C., León-Peláez, J. D., González-Hernández, M. I., Gallardo-Lancho, J. F., Osorio-Vega, W., Correa-Londo-o, G. (2013): Alterations in litter decomposition patterns in tropical montane forests of Colombia: a comparison of oak forests and coniferous. Canadian Journal of Forest Research 3, 528–533, https://doi.org/10.1139/cjfr-2012-0438.

Lorenzo, P., Rodríguez-Echeverría, S. (2015): Soil changes mediated by invasive Australian acacias. Ecosistemas 24(1), 59–66, https://doi.org/10.7818/ECOS.2015.24-1.10.

Magill, A. H., Aber, J. D. (2000): Dissolved organic carbon and nitrogen relationships in forest litter as affected by nitrogen deposition. Soil Biology Biochemistry 32, 603–613, https://doi.org/10.1016/S0038-0717(99)00187-X.

Manzoni, S., Pieiro, G., Jackson, R. B., Jobbágy, E. G., Kim, J. H., Porporato, A. (2012): Analytical models of soil and litter decomposition: solutions for mass loss and time-dependent decay rates. Soil Biology Biochemistry 50, 66–76, https://doi.org/10.1016/j.soilbio.2012.02.029.

Mcgrath, A. D., Comerford, N. B., Duryea, M. L. (2000). Litter dynamics and monthly fluctuations in soil phosphorus availability in an Amazonian agroforest. Forest Ecology and Management 131, 167–181.

Melillo, J. M., Aber, J. D., Muratore, J. F. (1982): Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63, 621–626, https://doi.org/10.2307/1936780.

Montagnini, F., Sancho, F., Ramstad, K., Stijhoorn, E. (1991): Multipurpose trees for soil restoration in humid lowlands of Costa Rica. In: Research on multipurpose trees in Asia. Ed. D. A. Taylor, K.G. Dicken. Winrock Int. Inst. For Agricultural Developmente. Bangkok, 41–58.

Moro, M. J., Domingo, F. (2000): Litter decomposition in four woody spcies in a Mediterranean climate: weight loss. N and P dynamics. Annals Bot-London 86, 1065–1071, https://doi.org/10.1006/anbo.2000.1269.

Musovoto, C., Campbell, B. M., Kirchmann, H. (2000): Decomposition and nutrient release from mango and miombo woodland litter in Zimbabwe. Soil Biology and Biochemistry 32, 1111–1119, https://doi.org/10.1016/S0038-0717(00)00023-7.

Ngoran, A., Zakra, N., Ballo, K., Kouamé, C., Zapata, F., Hofman, G., van Cleemput, O. (2006): Litter decomposition of Acacia auriculiformis Cunn. Ex Benth. and Acacia mangium Willd. under coconut trees on quaternary sandy soils in ivory Coast. Biology and Fertility of Soils 43, 102–106, https://doi.org/10.1007/s00374-005-0065-2.

Nouvellon, Y., Epron, D., Marsden, C., Kinana, A., Maire, C., Deleporte, P., Saint-André, L., Bouillet, J. P., Laclau, J. P. (2012): Age-related changes in litter inputs explain annual trends in soil C0$_2$ effluxes over a full Eucalyptus rotation after afforestation of a tropical savannah. Biogeochemistry-US 111, 515–533, https://doi.org/10.1007/s10533-011-9685-9.

Olson, J. S. (1963): Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44, 322–331, https://doi.org/10.2307/1932179.

Osorio, N. W., Habte, M. (2013): Synergistic effect of a phosphate solubilizing fungus and an arbuscular mycorrhizal fungus on leucaena seedlings in an oxisol fertilized with rock phosphate. Botany 91, 274–281, https://doi.org/10.1139/cjb-2012-0226.

Osorio, N. W., Osorno, L. (2015): Biofertilization with mycorrhizal fungi and phosphate solubilizing microorganisms enhance effectiveness of phosphate fertilizers in tropical soils. In: Fertilizer Technology, 2, Synthesis. Ed. J. N. Govil. Studium Press LLC (Houston, USA. New Delhi, India), 298–326.

Pandey, R. R., Sharma, G., Tripathi, S. K., Singh, A. K. (2007): Litterfall: Litter decomposition and nutrient dynamics in a subtropical oak forest and managed plantation in northeastern India. Forest Ecology and Management. 249, 96–104, https://doi.org/10.1016/j.foreco.2006.12.013.

Parker, G. G. (1983): Through fall and stem flow in the forest nutrient cycle. Advances in Ecological Research 13, 57–133, https://doi.org/10.1016/S0065-2504(08)60108-7.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, Veneklaas, J. E., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vosf, A. C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J. G., Thompson, K., Morgan, H. D., Ter Steege, H., van der Heijden, M. G. A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M. V., Conti, G., Staver, A. C., Aquino, S., Cornelissen, J. (2013): New handbook for standardized measurement of plant functional traits worldwide. Australian Journal of Botany 61, 167–234, https://doi.org/10.1071/BT12225.

Pleguezuelo, R., Zuazo, D. V., Fernández, M. J., Tarifa, F. D. (2011): Descomposición de hojarasca y reciclado del nitrógeno de frutales tropicales y subtropicales en terrazas de cultivo en la costa de granada (SE Espa-a). Comunicate Scientiae 2(1), 42–48.

Prause, J., Fernández, C. (2007): Litter decomposition and lignin/cellulose and lignin/total nitrogen rates of leaves in four species of the Argentine Subtropical forest. Agrochimica 51, 294–300.

Prescott, C. E. (2005): Decomposition and mineralization of nutrients from Litter and Humus. In: Nutrient acquisition by plants an ecological perspective. Ed. H. Bassiri Rad, 15–41, https://doi.org/10.1007/3-540-27675-0_2.

Ribeiro, C., Madeira, M., Araújo, M. C. (2002): Decomposition and nutrient release from leaf litter of Eucalyptus globulus grown under different water and nutrient regimes. Forest Ecology and Management 171, 31–41, https://doi.org/10.1016/S0378-1127(02)00459-0.

Rocha-Loredo, A. G., Ramírez-Marcial, N. (2009): Producción y descomposición de hojarasca en diferentes condiciones sucesionales del bosque de pino-encino en Chiapas, México. Boletín de la Sociedad Botánica de México 84, 1–12.

Schlesinger, W. H. (1991): Biogeochemistry: An analysis of global change. Academic, New York, EEUU.

Schlesinger, W. H. (2000): Biogeoquímica: un análisis global. Ariel Ciencia, Barcelona, Espa-a.

Singh, R., Kumar, R., Agrawal, M. (2004): Litter decomposition and nutrient release in relation to atmospheric deposition of S and N in a dry tropical region. Pedobiologia 48, 305–311, https://doi.org/10.1016/j.pedobi.2004.03.003.

Soil Survey Staff. Keys to soil taxonomy. (2014): USDA-Natural Resources Conservation Services. 12th Ed. Washington, DC.

Soil Survey Staff. Soil survey field and laboratory methods manual (2014): USDA-Natural Resources Conservation Services. Washington, DC.

Songwe, N. C., Okali, D. V. V., Fasehum, F. E. (1995): Litter decomposition and nutrient release in a tropical rainforest, Southern Bakkundu Forest Reserve, Cameroon. Journal of Tropical Ecology 11, 333–350, https://doi.org/10.1017/S0266467400008816.

Stevenson, F. J., Cole, A. M. (1999): Cycles of soil. Carbon, nitrogen, phosphorus, sulfur, and micronutrients. 2nd Ed. New York, John Wiley and Sons.

Swift, M. J., Heal, O. W., Anderson, J. M. (1979): Decomposition in terrestrial ecosystems. Blackwell Scientific, Oxford, UK.

Tamayo, A., Osorio, N. W. (2018): Soil fertility improvement by litter decomposition and inoculation with the fungus Motierella sp. in avocado plantations of Colombia. Communications in Soil Science and Plant Analysis 49, 139–147, https://doi.org/10.1080/00103624.2017.1417420.

Tarutis, W. J. (1994): A mean-variance approach for describing organic matter decomposition. Journal of Theoretical Biology, 168, 13–18, https://doi.org/10.1006/jtbi.1994.1083.

Tateno, R., Tokuchi, N., Yamanaka, N., Du, S., Otsuki, K., Shimamura, T., Xue, Z., Wang, S., Hou, Q. (2007): Comparison of litterfal production and leaf litter decomposition between an exotic black locust plantation and an indigenous oak forest near Yan'an on the Loess Plateau, China. Forest Ecology and Management 241, 84–90, https://doi.org/10.1016/j.foreco.2006.12.026.

Versini, A., Zeller, B., Derrien, D., Mazoumbou, J. C., Mareschal, L., Saint-André, L., Ranger, J., Laclau, J. P. (2014): The role of harvest residues to sustain tree growth and soil nitrogen stocks in a tropical Eucalyptus plantation. Plant and Soil 346, 245–260, https://doi.org/10.1007/s11104-013-1963-y.

Villela, D. M., Proctor, J. (2002): Leaf litter decomposition and monodominance in the Peltogyne forest of Maracá Island, Brazil. Biotropica 34, 334–347.

Wang, Q., Wang, S., Huang, Y. (2008): Comparisons of litterfall litter decomposition and nutrient return in a monoculture Cunninghamia lanceolata and a mixed stand in southern China. Forest Ecology and Management 255, 1210–1218, https://doi.org/10.1016/j.foreco.2007.10.026.

Waring, E. H., Schlesinger, W. H. (1985): Forest ecosystems. Academic Press. Orlando. USA.

Weerakkody, J., Parkinson, D. (2006a): Input. Accumulation and turnover of organic matter nitrogen and phosphorus in surface organic layers of an upper montane rainforest in Sri Lanka. Pedobiologia 50, 377–383, https://doi.org/10.1016/j.pedobi.2006.06.006.

Weerakkody, J., Parkinson, D. (2006b): Leaf litter decomposition in an upper montane rainforest in Sri Lanka. Pedobiologia, 50, 387–395, https://doi.org/10.1016/j.pedobi.2006.07.002.

Westerman, R. L. (1990): Soil testing and plant analysis. 3rd Ed. Soil Science Society of America.

Xuluc-Tolosa, F. J., Vestera, 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, México. Forest Ecology and Management 174, 401–412, https://doi.org/10.1016/S0378-1127(02)00059§2.