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ARTICLE

Alterations in litter decomposition patterns in tropical montane forests of Colombia: a comparison of oak forests and coniferous plantations

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Abstract: Understanding the alterations in litter decay patterns that follow changes in land use in tropical montane forests is essential for comprehending carbon, energy, and nutrient dynamics in this understudied ecosystem. The main objective of this study was to determine the changes in organic matter, carbon return, and nutrient cycling when oak forests are replaced by coniferous plantations in tropical montane forests. Five litter decay models (single, double, and triple pool exponential, gamma p_k, log-uniform p_k) were used to fit litter mass loss data over time. Although all models properly fitted the data, the triple pool exponential model was chosen because all parameters (coefficient of determination (R^2), mean square of error (MSE), and Akaike information criterion (AIC)) were statistically the most adequate. Results indicated that litter of coniferous species decomposes more slowly than oak litter material, thus slowing the nutrient cycling. In this study, lignin content, C:N ratio, and N:P ratio were poor predictors of litter decomposition.

Résumé : Il est essentiel de connaître les modifications que subit la décomposition de la litière à la suite de changements dans l'utilisation du sol dans les forêts alpestres tropicales pour comprendre la dynamique du carbone, de l'énergie et des nutriments dans cet écosystème méconnu. L'objectif principal de cette étude était d'identifier les changements dans la matière organique, le bilan du carbone et le recyclage des nutriments lorsque les forêts de chêne sont remplacées par des plantations de conifères dans les forêts alpestres tropicales. Cinq modèles de décomposition de la litière (exponentiel à un, deux ou trois compartiments, gamma p_k, log-uniforme p_k) ont été utilisés pour modéliser les données de perte de masse de la litière en fonction du temps. Bien que tous les modèles permettent de modéliser correctement les données, le modèle exponentiel à trois compartiments a été choisi parce que tous les paramètres (R^2, EQM, AIC) étaient statistiquement les plus adéquats. Les résultats indiquent que la litière des espèces de conifère se décompose plus lentement que la litière de chêne, ce qui ralentit par conséquent le recyclage des nutriments. Dans le cadre de cette étude, la teneur en lignine, le rapport C:N et le rapport N:P étaient de mauvais prédicteurs de la décomposition de la litière.

Introduction

Plant litter production and decomposition are two important processes that provide soil organic matter and regulate nutrient cycling in forest ecosystems (Singh et al. 1999; Weltzin et al. 2005). Litter decomposition varies among species and sites as a result of litter chemical composition, climate conditions, and soil microbial activity (Gholz et al. 2000; Polyakova and Billor 2007; Wang et al. 2008). Differences in these factors control, to some extent, the structure and functioning of forest ecosystems (Hobbie 2000; Berg and McClaugherty 2008). Leaf litter decomposition has been widely recognized as a key process in the nutrient cycle of terrestrial ecosystems (Vitousek et al. 1994; Aerts and de Caluwe 1997; Aerts and Chapin 2000).

In Colombia, large areas of Andean montane forests have been destroyed for agricultural use (Etter et al. 2006) and for the establishment of commercial coniferous plantations. This has altered not only the high diversity and endemism found in these ecosystems (Gentry and Dodson 1987; Henderson et al. 1991), but also ecosystem processes such as nutrient cycling and hydrological regulation in watersheds (León et al. 2011). Consequently, many montane oak forest remnants (dominated by *Quercus humboldtii* Bonpl.) have been eliminated, threatening this plant species, which is currently classified as vulnerable according to the International Union for Conservation of Nature (IUCN) (Galindo et al. 2003; León et al. 2009). Designing management policies for both natural forests and established plantations requires adequate knowledge of diverse aspects of their functioning. The objective of this study was to compare one particular ecosystem process, litter decomposition, in these two kinds of forests. The results may provide scientific guidance to decision makers involved in the management of tropical highland ecosystems.

Materials and methods

Site description

Field research was conducted over the course of 2 years at the Piedras Blancas watershed, a basin covering an area of 2876 ha (northwestern Antioquia Department, Colombia: 2490 m, 6°18″N, 75°30″W) (Fig. 1). The mean annual precipitation is 1948 mm/year, and the mean monthly air temperature is14.9 °C (Fig. 2). The landscape is dominated by low- to mid-slope hills covered by volcanic F1 F2

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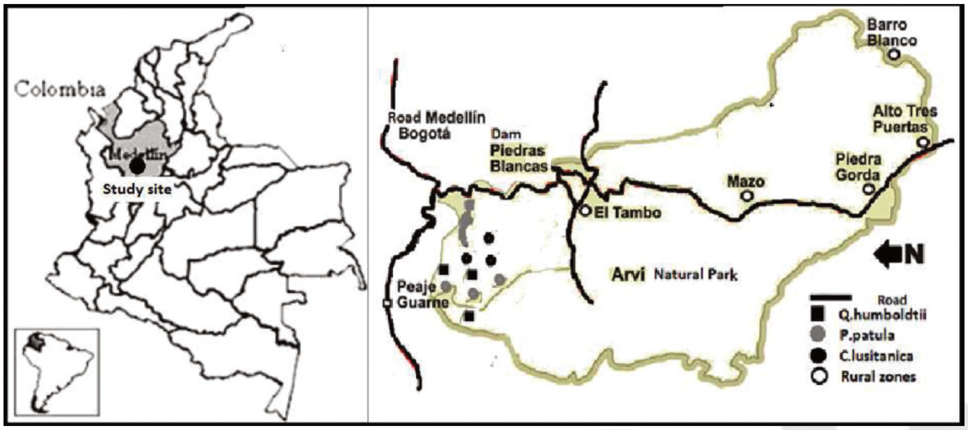
Fig. 1. Geographic location of the zone studied.



ash. The soils were classified as Fulvudands and Hapludands (U.S. Department of Agriculture 2010) (Table 1).

Three ecosystems were selected for this study. The first was a natural oak forest, the predominant Colombian montane forest type, which was dominated by *Quercus humboldtii* (36%) with a density of 614 trees/ha. The second two ecosystems were mature monoculture plantations of Mexican weeping pine (*Pinus patula* Schiede ex Schltdl. & Cham.) and Mexican cypress (*Callitropsis lusitanica* (Mill.) D.P. Little) established 43 years prior to the study without the use of silvicultural practices. Nine plots were randomly distributed in these three ecosystems. The spatial distribution of the plots appears in Fig. 1, and their major characteristics are summarized in Table 2. Before these plantations (~100 years), the soils were severely deforested and degraded by superficial gold mining and then converted to grassland for cattle (León 2007). More information about the study zone and experimental sites is available as Supplementary data (S1).[1]

Field study

Leaf litter decomposition was studied using the nylon net bag technique (Bocock et al. 1960). Senesced leaves were collected from the three sites with litter traps made of fine cloth. At each site, a total of 36 nylon-net bags (15 × 15 cm, 2 mm mesh) containing 25 g of oven-dried leaf litter from the three species (*Q. humboldtii*, *P. patula*, and *C. lusitanica*) were placed in their corresponding stand. Although the mesh size may have excluded some soil invertebrates, it prevented the loss of undecomposed fragments (Wieder and Lang 1982). Three bags containing decomposing litter were randomly retrieved at 56, 111, 175, 245, 308, 376, 456, 523, 614, 678, 719, and 789 days from each site and transported to the laboratory. The bags were opened and their litter materials were air dried, brushed gently to remove soil particles, oven-dried at 65 °C, and finally weighed. The residual dry matter (RDM) was estimated at each sampling date. Leaf litter placed in the litter bags was chemically analyzed at the beginning of the study. Total C, N, and S were analyzed using dry combustion. Leaf P concentrations were determined by the molybdate-blue method after dry combustion in a muffle furnace (500 °C, 3 h) (Habte and Osorio 2001). Neutral detergent fiber (NDF) and acid detergent fiber (ADF) were determined according to Goering and van Soest (1970). Hemicellulose was determined as the difference between NDF and ADF, while cellulose content was determined by subtracting acid detergent lignin (ADL) and ADF ash from ADF. Weather data were obtained from the meteorological station located at Corpoica's La Selva Experimental Station.

Litter decomposition models

Five litter decomposition models (single (D1), double (D2), and triple (D3) pool exponential, gamma p_k, and log-uniform p_k) were tested to find the best fit for the data. Model D1 supposes a single compartment for all organic matter under a simple negative exponential model (Olson 1963). An essential condition for applying this equation is that the decomposition process runs at a set rate (Berg and McClaugherty 2008). The D2 model is a development of the single exponential model; it assumes that the litter substrate has two compartments (labile and recalcitrant) and two respective decomposition rates ($k1$ and $k2$) (Bunnel and Tait 1974; Hunt 1977). The D3 model is based on the assumption that the litter substrate has three main compartments (labile, metastable, and recalcitrant) with three different decomposition rates ($k1$, $k2$, and $k3$, respectively) (Coûteaux et al. 1998; Berg and McClaugherty 2008). The two continuous-quality models (C1 and C2) assume a distribution of decay rates in the organic matter sample (Tarutis 1994, Manzoni et al. 2012). These models are showed in Table 3.

To select the model with the best fit, we used each of the proposed models (D1, D2, D3, C1, and C2) with the available data sets using the NLIN procedure. The statistical indices used to evaluate the model's adequacy were coefficient of determination (R^2), mean square of error (MSE), and the Akaike information criterion (AIC). A comparison of RDM evolution among species in each sampling time was carried out using analysis of variance (ANOVA) and the Duncan multiple range test, with a significance level of ≤0.05 for both tests. All statistical analyses were performed using SAS software (version 9.2; SAS Institute, Inc., Cary, North Carolina).

The relationship between litter decomposition rate and weather variables was studied using the various models (Table 3). The decomposition rates estimated for a given point in time were evaluated from the derivative of each model at the respective times. For this purpose, the online application Wolphram Alpha (http://www.wolframalpha.com/) was used.

Results

Leaf litter mass loss

At the end of the study, the RDM of pine and cypress leaf litter was slightly greater than 0.5, whereas for oak, it was significantly ($P < 0.05$) less (RDM = 0.1) (Fig. 3). The leaf litter decomposed at a rapid rate during an initial decomposition stage that lasted around 175 days. At this time, RDM values for oak, pine, and cypress were 0.5, 0.7, and 0.78, respectively. After this time, pine

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2012-0438.

Fig. 2. Daily rainfall and mean temperature in the study period (La Selva Meteorological Station).

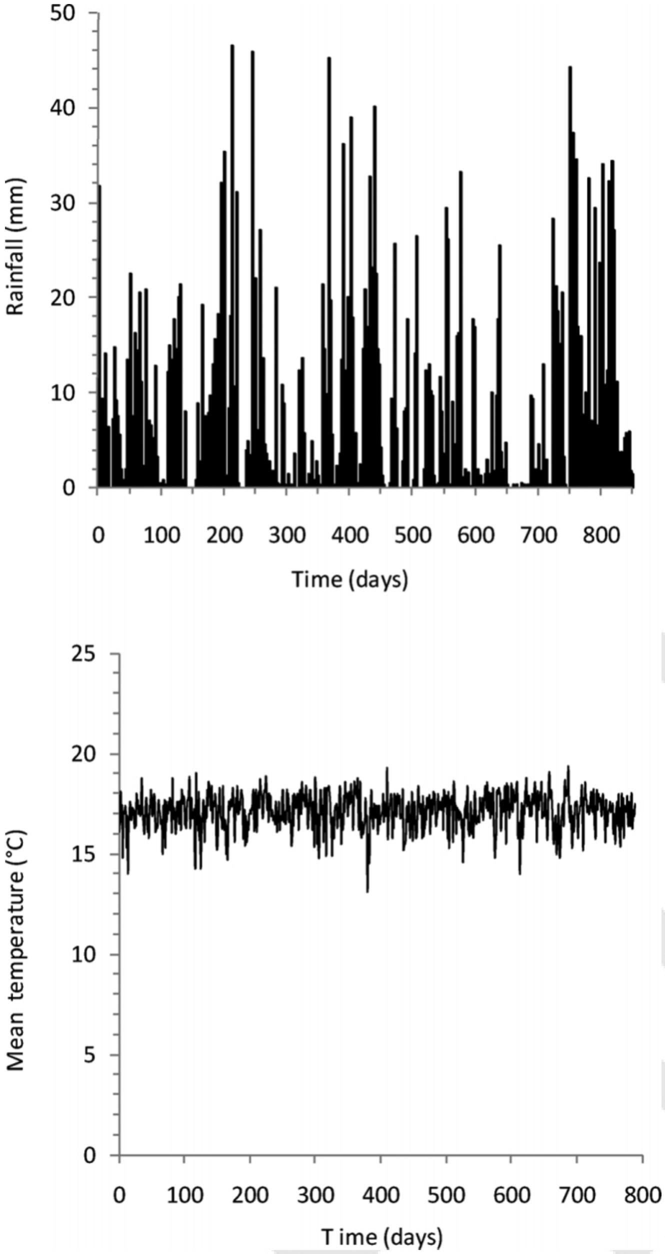


Table 1. Soil properties (0–30 cm depth) of the study sites in the Piedras Blancas watershed.

Soil property	Method*	*Q. humboltii*	*P. patula*	*C. lusitanica*
pH	1:2 (soil:water)	4.7	4.7	5.1
S (g/kg)	0.008 mol/L CaH_2PO_4	0.5	0.4	0.6
C (g/kg)	Walkley and Black	67.0	67.3	138
N (g/kg)	Kjedahl	3.2	3.3	6.0
C:N ratio	—	20.5	20.3	22.9
Ca (cmol(+)/kg)	1 mol/L ammonium acetate	0.16	0.20	0.10
Mg (cmol(+)/kg)	1 mol/L ammonium acetate	0.18	0.13	0.13
K (cmol(+)/kg)	1 mol/L ammonium acetate	0.13	0.25	0.25
P (mg/kg)	Bray II	1.1	1.2	0.7
Fe (mg/kg)	Olsen EDTA	98.8	70.0	43.2
Mn (mgkg)	Olsen EDTA	1.4	1.6	1.7
Zn (mg/kg)	Olsen EDTA	3.2	1.3	1.0
Cu (mg/kg)	Olsen EDTA	1.0	0.8	0.4

*Soil Survey Laboratory methods manual (U.S. Department of Agriculture 2004).

Table 2. Structural characteristics for oak forest and coniferous plantations at the Piedras Blancas watershed.

Forest	*Q. humboldtii*	*P. patula*	*C. lusitanica*
Age (years)	60	43	43
Sd (no./ha)	614	439	615
Mch (m)	10.3	19.7	12.5
Mean dbh (cm)	15.9	23.1	18.2
Sba (m^2/ha)	17.3	41.7	36.6
Total biomass (Mg/ha)	166.4	328.1	194.8
Soil parent material	Volcanic ashes	Volcanic ashes	Volcanic ashes
Soil classification	Typic Hapludands	Typic Hapludands	Typic Fulvudans
Soil thickness	>150 cm	>150 cm	>150 cm
Life zone ecology*	LMMF	LMMF	LMMF
Altitude (m)	2480	2460	2440
Old land use	Forest	Grassland	Grassland

Note: Sd, stand density for trees with dbh >10 cm; Mch, mean canopy height; dbh, diameter at breast height; Sba, stand basal area for all trees with dbh >10 cm; LMMF, lower montane moist forest.

*Holdridge (1967).

Table 3. Initial composition (mg/g) of the oak, pine, and cypress leaf litter substrates used in the decomposition experiment.

Species	C	N	C:N	S	P	Lignin	Cellulose	Lignin:N
Oak	431a	7.4a	58.4a	0.5a	0.2a	175	402	23.6
Pine	419a	7.9a	53.0a	0.5a	0.4a	160	313	20.3
Cypress	431a	3.9b	111.9b	0.4a	0.2a	140	361	35.9

Note: Values in the same column with different letters are statistically different (Duncan's test, $P < 0.05$).

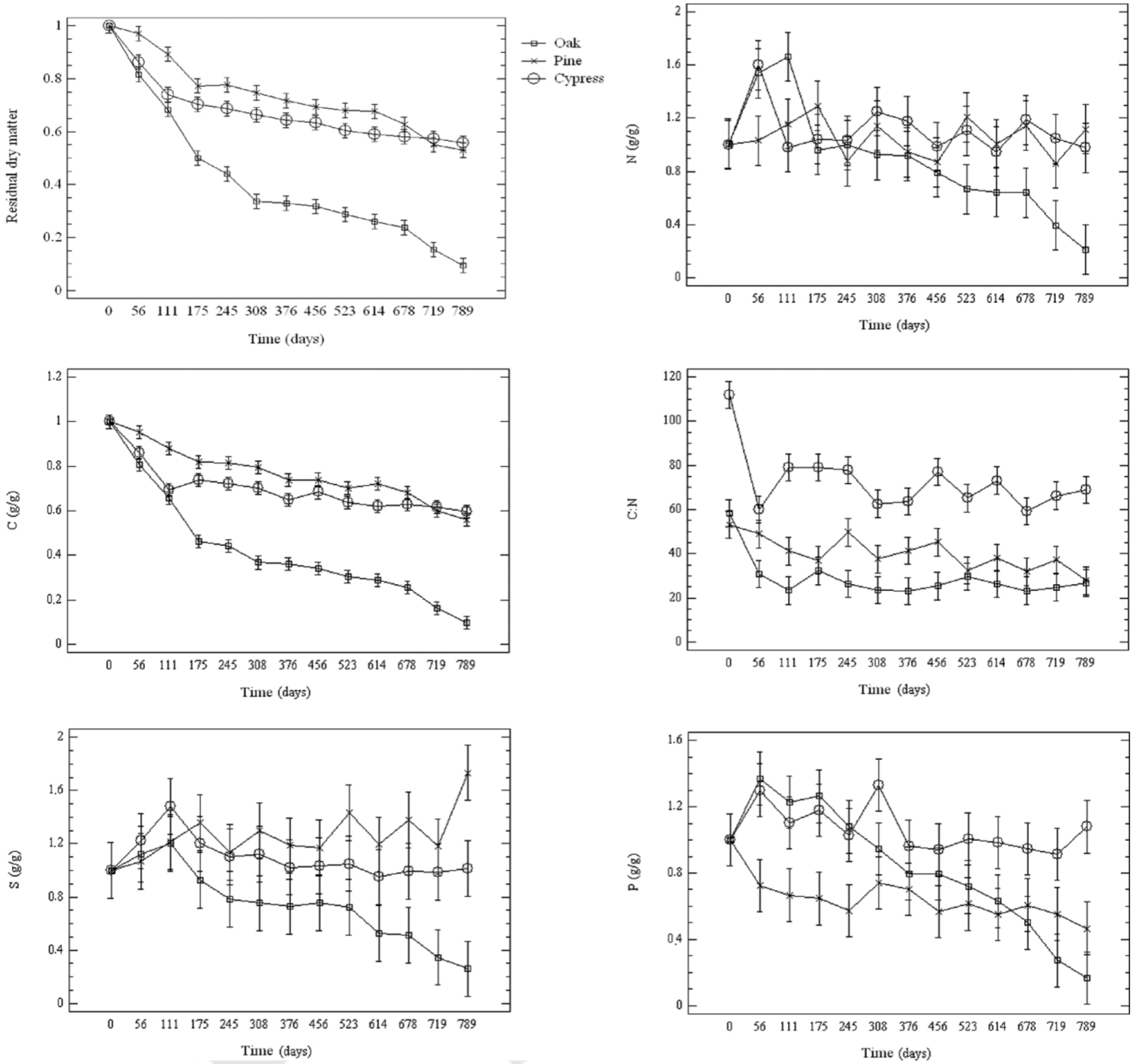
and cypress leaf litter reached a stabilization stage characterized by a very slow rate of decomposition. In contrast, oak leaf litter continued decaying for about 1 year (t = 376 days) at which point its RDM was 0.34.

Although all models properly fit the data and can be used to satisfactorily explain the dynamics of litter decay, the triple pool exponential model was the most effective because all parameters (R^2, MSE, and AIC) were statistically most adequate across the three species (Table 4). Statistical analysis revealed that there was no a direct relationship between weather conditions and the litter decomposition rate.

Leaf litter nutrient release

Over time, residual C showed a similar pattern to that of RDM (Fig. 3). At the end of this study, the residual C for oak was 0.1, which was significantly lower ($P < 0.05$) than for pine and cypress, both of which were around 0.6. For all three species, there was an initial increase in residual N (Fig. 3). Residual-N peak values were reached at 56, 111, and 175 days for cypress, oak, and pine, respectively. We detected two patterns in the N dynamics of these ecosystems. For coniferous species, the change in residual-N levels occurred in three phases: (*i*) an initial phase of N accumulation or element gain, (*ii*) a subsequent N leaching that depended on the plant species, and (*iii*) a third phase of N stabilization (immobilization), which is consistent with the triple compartment model used for the RDM. Final values for both coniferous species were significantly higher than 1.0–1.1. On the other hand, with the oak leaf litter, there was no stabilization phase, and N losses contin-

Fig. 3. Residual dry matter (X_t/X_0) from leaf litter and residual nutrient (C, N, C:N, S, P) contents remaining in the leaf litter of oak (*Quercus humboldtii*), pine (*Pinus patula*), and cypress (*Callitropsis lusitanica*). Values are means (n = 3), and bars indicate 95% confidence limits. RDM and residual nutrient contents are expressed in terms of the relative quantity at any given time with respect to the initial content placed in the litter mesh bags. Raw data are available as Supplemental material.[1]



ued over time reaching a final residual-N value of 0.2. This means that during the study period, N from oak leaf litter was mineralized, whereas N from both coniferous species was immobilized.

Residual-S dynamics showed similar behaviour to that observed for residual N. At the end of this study, residual-S values were significantly different for pine, cypress, and oak (1.75, 1.00, and 0.35, respectively) (Fig. 3). These results indicate that pine leaf litter gained S, cypress remained constant, and only oak showed a net S release.

In contrast to N and S dynamics, each species exhibited varying P release dynamics during the leaf litter decay process (Fig. 3). For instance, oak showed an initial increase of residual P until day 56, at which point its value was 1.3, followed by a drastic decrease until the end of the study when it reached 0.15, indicating a net P release (mineralization). Cypress also showed an initial increase in residual P, but this remained stable and reached a final value of 1.1, which was significantly higher than the final values for the other two species. The residual P of pine leaf litter did not initially increase as it did with the other species. Rather, it showed a rapid decrease until day 245 (Fig. 3) and then remained between 0.5 and 0.6 until the end of the study. Thus leaf litter P release showed the following decreasing order: oak > pine > cypress.

Discussion

There were significant differences in leaf litter decomposition among the three species. Leaf litter of coniferous species decomposed more slowly than that of oak, which is consistent with the findings of Edwards (1977) and Cornwell et al. (2008), who reported that angiosperm litter decomposes faster than gymnosperm litter. This is likely due to the biochemistry of the litter. There were no relationships found between RDM, weather conditions, and soil moisture (Udic soil moisture regime, unpublished data). Although the importance of both weather and soil moisture

Table 4. Litter decomposition models for residual dry matter of three forestry species in tropical montane forests of Colombia.

		Q. humboldtii					*P. patula*					*C. lusitanica*				
Models	Par.	EV	*N*	R^2	MSE	AIC	EV	*N*	R^2	MSE	AIC	EV	*N*	R^2	MSE	AIC
$X_t/X_0 = e^{-kt}$ (D1)	*k*	1.04	39	93.5	1.65	42	0.29	39	97.6	1.01	4	0.36	39	92.2	1.81	49
$X_t/X_0 = Ae^{-k1t} + (1 - A)e^{-k2t}$ (D2)	k_1	3.28	39	97.1	1.14	16	3.13	39	98.3	0.88	−4	5.75	39	99.8	0.26	−100
	k_2	0.61					0.21					0.12				
	A	0.39					0.11					0.28				
$X_t/X_0 = Ae^{-k1t} + Be^{-k2t} + Ce^{-k3t}$ (D3)	k_1	3.28	39	97.1	1.13	14	0.18	39	98.3	0.87	−6	5.75	39	99.8	0.25	−102
	k_2	0.61					0.18					0.12				
	k_3	0.61					2.10					0.12				
	A	0.39					0.31					0.28				
	B	0.44					0.53					0.58				
	C	0.17					0.16					0.14				
$X_t/X_0 = b^{a-1}(b + t)^{1-a}$ (C1)	*a*	1.47	39	96.9	1.16	17	0.54	39	98.2	0.89	−4	0.16	39	99.8	0.31	−86
	b	0.92					1.21					0.06				
$X_t/X_0 = be^{-at} - ae^{-bt} - [\mathrm{Ei}(-bt) - \mathrm{Ei}(-at)]abt/b - a$ (C2)	*a*	0.26	39	97.0	1.12	12	0.02	39	91.6	0.87	−8	0.0008	39	98.6	0.30	−91
	b	5.07					2.16					22.39				

Note: Par., parameters; *k*, daily decomposition rate; *a* and *b*, shape parameters; *A*, litter labile fraction; *B*, litter metastable fraction; *C*, litter recalcitrant fraction; EV, estimated value of the parameter; *N*, total number of litter bags; R^2, determination coefficient; MSE, mean squared error; AIC, Akaike information criterion.

in regulating litter decay has been demonstrated both within (Berg et al. 1990; Martín et al. 1996) and across (Gholz et al. 2000) sites, our results are consistent with Cornwell et al. (2008), who found that species has a more significant impact on litter decay than the weather.

The labile fraction decay coefficient was higher in oak (0.39) than in pine (0.32) and cypress (0.28) (Table 4). Conversely, oak litter had lower metastable fraction (0.44) than pine (0.52) and cypress (0.58). The half life was 0.7, 2.0, and 2.4 years for oak, cypress, and pine litter, respectively.

The annual *k* values for our coniferous species found using Olson's model were close to 0.3, similar to other *k* constants in temperate regions (Aerts 1997; Martín et al. 1996; Palma et al. 2002). The *k* value for oak (1.02) was within the range found for the leaf litter of nine forest species (0.2–9.6) in montane rain forests of Sri Lanka (Weerakkody and Parkinson 2006).

It has been suggested (Berg 2000; Alhamd et al. 2004) that nutrient concentration in leaf litter may control its decomposition rate during the early stages of the process (Edwards 1977). Several studies have reported mass losses positively correlated to litter N concentrations (Cotrufo et al. 1995; Alhamd et al. 2004; Kainulainen and Holopainen 2002).In contrast with these earlier findings, pine had the highest N concentration at the beginning of the present study, but the lowest mass loss (Table 3). Oak leaf litter exhibited very similar N concentrations to those of pine and had the highest rates of mass loss. Ribeiro et al. (2002) found the highest mass losses during the early stages of the decomposition process of leaves with low N concentration. It is clear that factors others than litter N concentration play a key role in litter decay (Prescott 2005; Berg and McClaugherty 2008).

The C:N ratio has been suggested as a good predictor of leaf litter decay; when it is below 35, litter decays and N release is stimulated (Singh et al. 1999; Sundarapandian and Swamy 1999; Arunachalam and Singh 2002). However, our results suggest that this parameter was not a good predictor of oak leaf litter decomposition. In spite of the high initial C:N ratio in oak litter (58), the litter exhibited rapid decay. Again, the differential quantity of labile and recalcitrant compounds (C quality) among litter could explain these differences (Hobbie 2000). In fact, the proportions of labile compounds estimated from the double exponential model (Table 4) for oak, cypress, and pine were 0.38, 0.27, and 0.11, respectively (Table 4).

Mean values of the N:P ratio in leaf litter at the beginning of this study were 37.0, 19.8, and 19.5 for oak, pine, and cypress, respectively. These N:P ratio values suggest a P deficiency in all three samples, with the most severe deficiency seen in oak. The low levels of N and P coincide with the values reported by Edwards (1977) in the Eastern Highlands of New Guinea. However, this contradicts the higher decay rate found for oak. Clearly, the N:P ratio was not a good predictor of litter decay and P release. We believe that the P level in oak is enough to promote the activity of decomposers and subsequently litter decays. Although across species the best predictors of litter decay are usually N, P, and lignin, this did not occur in the current study. It is likely that other factors such as secondary compounds (e.g., fatty acids, diterpene acids, tannins, and phenols) impaired the decomposition rate (Berg and McClaugherty 2008).

Based on the annual leaf litter production of oak forests and cypress and pine plantations reported by León et al. (2011) (5313, 2460, and 4866 kg·ha^{-1}·year^{-1}, respectively) and considering Olson's single constant (*k*) (1.04, 0.35, and 0.29, respectively), organic matter return to the soil from the leaf litter represents 3435, 726, and 1225 kg·ha^{-1} ·year^{-1}, respectively.

Conclusions

The oak leaf litter showed higher rates of decomposition than the leaf litter of both coniferous species. In this study, lignin, N and P content, and C:N and N:P ratios were poor indicators of litter decays and nutrient release. Results suggest that coniferous litter decomposition slows as a consequence of certain other features of the tissue's secondary chemistry. In the Andean mountain range of Colombia, volcanic ash soils (Andisols), soil microclimate (Udic soil moisture regimes), and weather conditions appear to have less effect on litter decomposition than the species type and the proportion of labile and recalcitrant compounds. These results are consistent with the results of Cornwell et al. (2008), who found that gymnosperms leaf litter decomposes more slowly than that of angiosperms. In these ecosystems, P deficiency in all leaf litter species was associated with high weathering of parental material (volcanic ashes).

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