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REGULAR ARTICLE

Effects on nutrient cycling of conifer restoration in a degraded tropical montane forest

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Abstract
Background and aims Exotic coniferous species have been used widely in restoration efforts in tropical montane forests due to their tolerance to adverse conditions and rapid growth, with little consideration given to the potential ecological benefits provided by native tree species. The aim of this study was to elucidate differences in litterfall and nutrient flow between a montane oak forest (*Quercus humboldtii* Bonpl.) and exotic coniferous plantations of pine (*Pinus patula* Schltdl. & Cham.) and cypress (*Cupressus lusitanica* Mill.) in the Colombian Andes.
Methods Litter production, litter decomposition rate, and element composition of leaf litter were monitored during 3 years.
Results Litter production in the oak forest and pine plantation was similar, but considerably lower in the cypress plantation . Similar patterns were observed for nutrient concentrations in litterfall, with the exception of Ca which was three times higher in the cypress plantation. The annual decay rate of litter was faster in the montane oak forest than in either of the exotic coniferous plantations. The potential and net return of nutrients

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to the forest floor were significantly higher in oak forest than in the exotic coniferous plantations.

Conclusions Future restoration programs should consider new species that can emulate the nutrient flow of native broadleaf species instead of exotic species that tend to impoverish soil nutrient stocks in tropical montane forests.

Keywords Leaf litterfall · Nutrient flows · Montane tropical forests · Plantations · *Quercus humboldtii* · *Pinus patula* · *Cupressus lusitanica*

Introduction

The tropical Andes is one of the most important biodiversity hotspots due to its biological diversity and high levels of endemism, as well as the vital ecosystem goods and services that it provides (Gradstein et al. 2008; Myers et al. 2000; Olson and Dinerstein 1998; Stadtmuller 1987). Nevertheless, a large extent of tropical montane forest in South America has been converted to agricultural fields, cattle pastures, or urban areas (Armenteras et al. 2011; Etter et al. 2006). Despite efforts to reduce land-use change and to conserve remaining forests dominated by Andean oak or roble (*Quercus humboldtii* Bonpl.), these tropical montane forests now cover less than 10 % of their original area. Concomitant with this loss in forest cover, the provision of ecosystem services in high Andean ecosystems has also declined precipitously (Galindo et al. 2003; Gradstein et al. 2008; Young et al. 2011).

Deliberate planting of exotic tree species has been encouraged throughout the tropics (Evans and Turnbull 2004; ITTO 2009) to help mitigate soil degradation and erosion by modifying above- and below-ground microclimates and by increasing the activity of soil organisms (Boley et al. 2009; Cole et al. 2010; Fisher 1995). Reforestation in the Colombian Andes has been and continues to be performed using mainly exotic coniferous species (Acosta-Contreras 2004; Motta-Tello and Candelo-Cardenas 2003). Approximately 50 % and 17 % of the reforested area with exotic species have been planted with Mexican weeping pine (*Pinus patula*) and Mexican cypress (*Cupressus lusitanica*), respectively (DANE 2004). Land managers select these species principally because of their rapid growth and the ease with which they are propagated, as the lack of knowledge about the propagation and establishment of native tree species has impeded their use in reforestation efforts (Acosta-Contreras 2004; Aldana 2004).

The selection of tree species used in reforestation initiatives is a fundamental issue for maintaining or restoring ecosystem functions in tropical ecosystems, including those related to soil nutrient dynamics. Species composition strongly influences litter chemistry and decay rate (Zou et al. 1995), which in turn affects nutrient cycling and carbon accumulation in tropical forest ecosystems (Vitousek and Sanford 1986). In general, angiosperms have been found to produce greater amounts of faster decomposing leaf litter than gymnosperms in the tropics, due to lower leaf construction costs and less nitrogen allocated to tissues (Cornwell et al. 2008; Reich et al. 2007; Wang et al. 2008; Yang et al. 2004; Zhang et al. 2008).

Despite the apparent importance of species composition to nutrient dynamics, we have not found previous studies where the implications of species selection in reforestation efforts on nutrient dynamics have been addressed in tropical montane ecosystems. The objective of this study was to examine nutrient cycles in two exotic coniferous plantations of *Pinus patula* and *Cupressus lusitanica* and an adjacent natural forest dominated by *Quercus humboldtii* in the Colombian Andes. We hypothesised that leaf litter in two exotic coniferous plantations would decay more slowly and would not return the same amount of nutrients to the forest floor as the oak-dominated tropical montane forest.

Material and methods

Study area

The present study was conducted from May 2001 to July 2004 in the upper part of the Piedras Blancas Watershed (6° 18′ N; 75° 30′ W), which is located in province of Antioquia, Colombia. The elevation of the upper part of the watershed ranges between 2,200 and 2,600 m a.s.l. and covers an area of 4,187 ha. Mean annual precipitation in the watershed during the study period was 1,948 mm year^{-1}, mean annual air temperature was 14.9 °C, and the relative humidity often exceeds 80 % (data adapted from *Empresas Públicas de Medellín*).

The forest cover of the watershed is dominated by natural oak forest (1,346 ha) and plantations of *Cupressus lusitanica* (574 ha), hereon referred to as cypress, and *Pinus patula* (338 ha), hereon referred to as pine, and other land uses, such as cattle pastures and agricultural fields, which cover about 20 % of the area (Blandon 2008). The landscape is dominated by low hills that are covered by volcanic ash over amphibolite rock material (Tschinkel 1972). The soils were classified as *Fulvudands* and *Hapludands* (based on soil organic C and SOC content); both subgroups are within the *Andosol* unit (USDA Soil Taxonomy System) and are distinguished by their SOC content and lixiviation. Soil pH ranges between 4.7 and 5.1 (Table 1). These soils usually have a high soil organic matter (SOM) content, high cation exchange capacity (55–61 $cmol_c$ kg^{-1} at pH 7.0), are strongly desaturated, and have a high proportion of allophanes in the clay fraction, which results in a high P retention capacity (3–5 mg PO_4-P L^{-1}).

The most abundant species in the oak forest was *Q. humboldtii*, followed by *Alfaroa colombiana*, *Escallonia paniculata*, *Myrcia popayanensis*, *Nectandra* spp. and *Vismia* spp. (León et al. 2009). Two mono-specific plantations of Mexican weeping pine and Mexican cypress were established in 1965 without any management activities thereafter (Table 2).

Experimental design

Three experimental plots of 0.5 ha were randomly established at the midslope position in a montane oak forest and two adjacent mature exotic species plantations. Twenty circular litter traps (each 0.5 m^2) were placed in a systematic array within each plot. The traps were constructed of fine mesh cloth and suspended from galvanised wire frames at 1 m above ground level. This number of litter traps per area cover was considered acceptable for obtaining a mean standard error of less than 5 % (Proctor 1983). Litter collection in each plot was performed bi-weekly for 3 years. Upon retrieval, litter was transported in polyethylene bags to the laboratory, where it was air-dried and then oven-dried (65 °C) to constant mass. Litterfall from each plot was sorted into the following categories: (a) leaves of the dominant species (LD); (b) leaves of other species (LO); (c) woody material (WM), consisting of twigs <2 cm diameter, conifer cones, and small bark fragments; and (d) unclassified material (UM), which consisted mainly of unrecognizable organic residues, including very small fragments and some reproductive tissue. Dried samples were weighed to the nearest mg using an electronic balance. Subsequently, litterfall collected during 2-month periods in each plot was pooled for chemical analyses.

Decomposition of leaf litter originating from the dominant tree species in their respective stands was evaluated using the nylon net bag technique (Bocock and Gilbert 1957). Senescent leaves were collected in each site using nylon mesh screens. Thirty-six nylon-net bags (15×15 cm^2, 2 mm mesh) containing 25.00 g oven-dried (65 °C) of oak, pine, and cypress were prepared and deployed randomly in each plot on June 2001. Litter was allowed to decompose in the field for up to 789 days. In each plantation, three bags containing decaying litter were randomly retrieved at intervals of approximately 2 months. Upon retrieval, litterbags were air-dried, gently cleaned to remove mineral soil, oven-dried at 65 °C, and weighed. Residual dry matter (RDM) was estimated for each sampling date in kg DM ha^{-1} $year^{-1}$. Samples from each sampling date were pooled by species for chemical analysis (for more details regarding the decomposition experiment, see Loaiza-Usuga et al. 2013).

Samples from the litterfall and decomposition experiments were homogenized and ground for chemical analysis. For cation determination, samples were ashed at 550 °C, after which ash was dissolved in heated nitric acid, diluted, and analysed by atomic absorption spectrophotometry. Total P was determined colorimetrically. Total C, N, and S concentrations were determined with a LECO CNS-2000 automated dry combustion analyser.

Table 1 Chemical content of the soils (*A* horizon) in three forest types in the Piedras Blancas Watershed, Antioquia Province, Colombia

Forests	Soil classification	pH	C	N	C:N	P	Ca	Mg	K	Fe	Mn	Zn	Cu
			(mg g^{-1})			(mg L^{-1})				(mg kg^{-1})			
Oak	*Hapludands*	4.7	67.0	3.2	20.5	1.1	0.16	0.18	0.13	98.8	1.4	3.2	1.0
Pine	*Hapludands*	4.7	67.3	3.3	20.3	1.2	0.20	0.13	0.25	70.0	1.6	1.3	0.8
Cypress	*Fulvudans*	5.1	138	6.0	22.9	0.7	0.10	0.13	0.25	43.2	1.7	1.0	0.4

Table 2 General description of the three forest types studied in the *Piedras Blancas* watershed, Antioquia, Colombia

Forest	Age (years)	Stem density (N ha^{-1})	Mean canopy height (m)	Mean dbh (cm)	Stand basal area (m^2 ha^{-1})	Total biomass (Mg DM ha^{-1})	Altitude (m)
Oak	>48	614	10.3	15.9	17.3	166.4	2,480
Pine	48	439	19.7	23.1	41.7	328.1	2,460
Cypress	48	615	12.5	18.2	36.6	194.8	2,440

Only trees >10 cm DBH (diameter at breast height, 1.3 m) were measured

Results of RDM, C, and nutrients are presented graphically. Since these results are expressed in relative values (percentages), values can exceed 100 %, which implies biological retention. Absolute values of nutrients can increase due to natural contamination of samples from throughfall or, in the case of N, bacterial fixation. Mineralized nutrients were leached into the soil, with the exception of C, which was released into the atmosphere. Potential nutrient return (PNR) to the forest floor from each litter fraction was calculated by multiplying monthly mass values of each fraction by its corresponding nutrient concentrations. Monthly nutrient inputs were then added based on 12 monthly estimates. Net nutrient return (NNR) was calculated on the basis of the nutrients remaining in the tissues at the end of the 2-year-long decomposition experiment; i.e., nutrient return to soil is equal to PNR minus nutrients retained by the recalcitrant organic residues.

Data analysis

A simple model of exponential decay was employed to estimate decomposition rates (Jenny et al. 1949; Olson 1963):

$$X_t/X_0 = e^{-kt}$$

where X_0 is the initial dry mass, X_t is the dry mass at time *t*, and *k* is the decay constant.

To compare litter production between oak forest and the two exotic coniferous plantations, we used bootstrapping with 10,000 permutations to calculate the annual mean and estimate the standard error of the mean (Efron and Tibshirani 1993). Differences in litter production, potential, and net return of nutrients between oak forest and exotic coniferous plantations were assessed using a 95 % bootstrapped confidence interval test. All statistical analyses were performed using the packages MASS (Venables and Ripley 2002) and STATS in R (version 2.15.0; R Development Core Team, 2012).

Results

Litter production

Litterfall in the pine plantation (7.77 Mg DM ha^{-1} $year^{-1}$) and oak forest (7.48 Mg DM ha^{-1} $year^{-1}$) was similar, but was significantly lower in the cypress plantation (3.49 Mg DM ha^{-1} $year^{-1}$; $P<0.05$; Fig. 1, Table 3). The greatest amount of leaf litterfall for the dominant species (LD) occurred in the pine plantation (4.76 DM ha^{-1} $year^{-1}$). When the LO fraction was included, mean values of leaf production were highest for the oak forest (5.31 Mg DM ha^{-1} $year^{-1}$).

Leaf litter comprised 62 to 71 % of total annual litterfall in the oak forest and plantations. Non-leaf litterfall included woody material and unclassified material (reproductive material and miscellaneous tissues), which ranged from 29 to 38 % of total litterfall. No statistically significant relationship was found between litterfall and rainfall (r=0.08, −0.09 and 0.10 respectively for oak, pine and cypress. $P>0.05$). However, pine

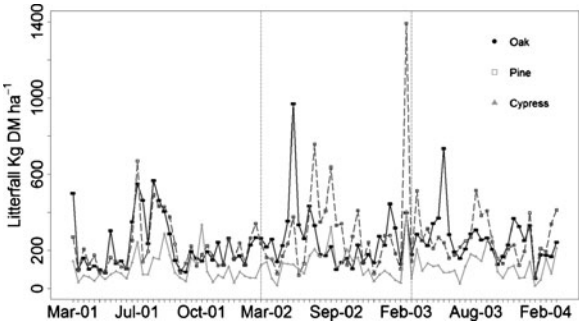


Fig. 1 Litterfall (kg ha^{-1}) in oak forest and pine and cypress plantations during the study period in *Piedras Blancas* watershed

Table 3 Annual litterfall fractions from the three forests studied at the Piedras Blancas Watershed

Forest	Leaves of dominant species		Leaves of other species		Woody material		Unclassified material		Total	
	(kg DM ha^{-1} year^{-1})									
Oak	2,915 (104.0)	a	2,401 (34.9)	c	1,069 (43.3)	b	1,110 (45.3)	NS	7,480 (47.9)	b
Pine	4,767 (70.6)	b	102 (2.9)	b	1,908 (146.0)	b	977 (35.9)		7,769 (227.0)	b
Cypress	2,459 (62.9)	a	7.9 (0.4)	a	310 (13.8)	a	720 (37.6)		3,497 (87.3)	a

Three year mean values and standard errors in parenthesis

Different letters indicate significant differences and NS indicates non-significant differences as determined by the bootstrap test ($P<0.05$)

and oak had higher literfall during June–September for the first 2 years of the study (Fig. 1).

Nutrient concentrations in litterfall

Consistent with expectations, N was the most abundant element in litterfall (Table 4). N content of the LD fraction in the oak forest and pine plantation was almost twice as high as that of the cypress plantation. S and Ca occurred in similar concentrations in each fraction and among the oak forest and plantations. Concentrations of P were almost equal for all fractions in the oak forest and plantations, except for the UM fraction. Concentrations of K were highest in all fractions of cypress, except for LO (Table 4).

Litter decomposition

RDM at the end of the incubation period (789 days) was higher ($P<0.05$) in the pine and cypress plantations than in the oak forest (50 vs. 10 %, respectively; Fig. 2). The initial period of decomposition was approximately 308 days in the oak forest and 111 and 175 days in the pine and cypress plantations, respectively. After this initial period of decomposition, pine and cypress litter reached a steady period of slow decomposition. Consequently, the annual decay rate (k) was significantly higher for oak, compared to cypress and pine ($P<0.05$). Over time, residual-C showed a pattern of decay similar to that of residual dry matter (Fig. 2).

Nitrogen dynamics differed between oak and the two exotic coniferous species. For both exotic coniferous species, there was an initial period of residual-N accumulation and a subsequent stabilisation by the end of the study. Final values for both conifer species were higher than 100 % (Fig. 3, left). In contrast, N in oak leaf litter decreased throughout the study, finally reaching a value of 20 %. Temporal dynamics of residual S were similar to those observed for N. At the end of the study, residual S for pine, cypress, and oak was 175, 100, and 35 % of initial values, respectively. Each species exhibited different dynamics for P release during leaf litter decay. Oak had an initial increase in residual P, followed by a drastic decrease until the end of the study 15 %, indicating net P release. Cypress also showed an initial increase in residual P and had a final value of 110 %, which was significantly higher than those of the other two species. For pine, residual P rapidly decreased until stabilizing at 50 %. Residual Ca and Mg both had an initial accumulation phase and then decreased to 10 % in oak litter, 100 % in pine litter, and 30 % in cypress litter for Ca and to 20 % in oak litter, 70 % in pine litter, and 40 % in cypress litter for Mg. Patterns of K also differed between oak and exotic coniferous species. For oak, residual K increased and then decreased, reaching a final value of 70 %. In contrast, conifer K concentrations continued to decrease with time, reaching a final value of 50 %. Considering element dynamics across all studied species, oak leaf litter showed the highest net release (between 94 and 98 %), followed by cypress (except for P) and pine (Fig. 3, right).

Potential nutrient return (PNR) and net nutrient return (NNR)

Since mineral element concentrations showed little temporal variation, the seasonal distribution of element return was similar to that found in litterfall. Potential nutrient return (PNR) through total litterfall varied significantly across the studied species ($P<0.05$; Table 5), with oak having the highest values, followed by pine and cypress. Leaves returned more nutrients to the forest

Table 4 Composition of litterfall fractions from three forests studied in the Piedras Blancas Watershed

Fraction	Forest	N		C:N		S		P		Ca		Mg		K		Lignin	Cellulose	Lignin:N
		(%)														(mg g^{-1})		
LD	Oak	9.6 (0.6)	b	45.5	a	0.8 (0.1)	NS	0.3 (0.0)	NS	0.4 (0.0)	a	0.9 (0.1)	b	0.8 (0.3)	b	175	402	23.6
	Pine	9.2 (0.7)	b	47.5	a	0.9 (0.1)		0.3 (0.0)		0.4 (0.1)	a	1.0 (0.1)	b	0.6 (0.1)	a	160	313	20.3
	Cypress	5.1 (0.2)	a	81.8	b	0.7 (0.1)		0.3 (0.0)		1.2 (0.2)	b	0.6 (0.0)	a	0.7 (0.2)	a	140	361	35.9
LO	Oak	10.0 (0.9)	b	42.9	b	1.1 (0.1)	b	0.3 (0.0)	NS	0.8 (0.1)	a	1.5 (0.2)	a	1.2 (0.3)	ab			
	Pine	13.1 (1.0)	c	31.5	a	1.0 (0.1)	a	0.4 (0.0)		0.8 (0.1)	a	1.8 (0.1)	a	1.0 (0.2)	a			
	Cypress[a]	5.3	a	75.6	c	1.3	c	0.3		1.7	b	1.9	b	1.5	b			
WM	Oak	7.2 (1.1)	b	58.2	a	0.7 (0.1)	NS	0.3 (0.0)	NS	0.8 (0.1)	b	1.1 (0.1)	b	0.7 (0.2)	b			
	Pine	4.2 (1.1)	a	102.0	b	0.6 (0.1)		0.3 (0.0)		0.4 (0.1)	a	0.5 (0.1)	a	0.4 (0.2)	a			
	Cypress	3.7 (0.5)	a	116.1	b	0.6 (0.1)		0.3 (0.0)		0.7 (0.1)	b	0.5 (0.1)	a	0.6 (0.1)	ab			
UM	Oak	16.3 (1.5)	c	25.7	a	1.3 (0.1)	b	0.4 (0.0)	NS	0.8 (0.2)	b	1.5 (0.2)	b	1.8 (0.4)	b			
	Pine	10.4 (0.6)	b	42.2	b	1.1 (0.2)	a	0.4 (0.0)		0.3 (0.1)	a	0.7 (0.1)	a	0.7 (0.2)	a			
	Cypress	6.4 (0.3)	a	68.7	c	0.8 (0.1)	a	0.4 (0.0)		1.0 (0.2)	b	0.9 (0.3)	a	0.7 (0.1)	a			

Standard errors are in parentheses

Means nutrient concentrations (each column) of the same litter fraction. Different letters indicate significant differences and NS indicates non-significant differences as determined by the bootstrap test ($P<0.05$)

LD leaves of the dominant species, *LO* leaves of other species, *WM* woody material, *UM* unclassified material

[a] The values corresponding to the standard error of the LO fraction in the Cypress plantation were not available

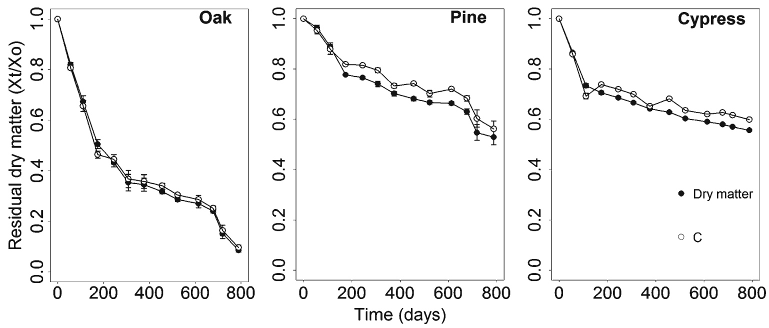


Fig 2 Residual dry matter and C from leaf litter for oak (*Quercus humboldtii*), pine (*Pinus patula*), and cypress (*Cupressus lusitanica*) species

floor compared to needles. The most abundant nutrient in the different fractions was N, with the exception of Ca in the cypress plantation. The total flow of P through the fine litterfall in the natural forest and plantations followed the same sequence. Despite low litterfall values in the cypress plantation, the return of Ca in this forest was very similar to that of the oak forest (Table 5).

For all elements analysed, the oak forest had the highest NNR ($P<0.05$; Table 6). Between the two coniferous species, pine had higher NNR for N, Mg, K, and P, whereas cypress had higher NNR for S and Ca (Table 6).

Discussion

Numerous studies have evaluated the amount and patterns of litterfall in native forests and plantations, but these have been conducted mainly in tropical lowland forests of South America. To our knowledge, nutrient cycling patterns have not been compared between native forest and exotic tree plantations located under similar climatic and edaphic conditions in tropical montane forest ecosystems.

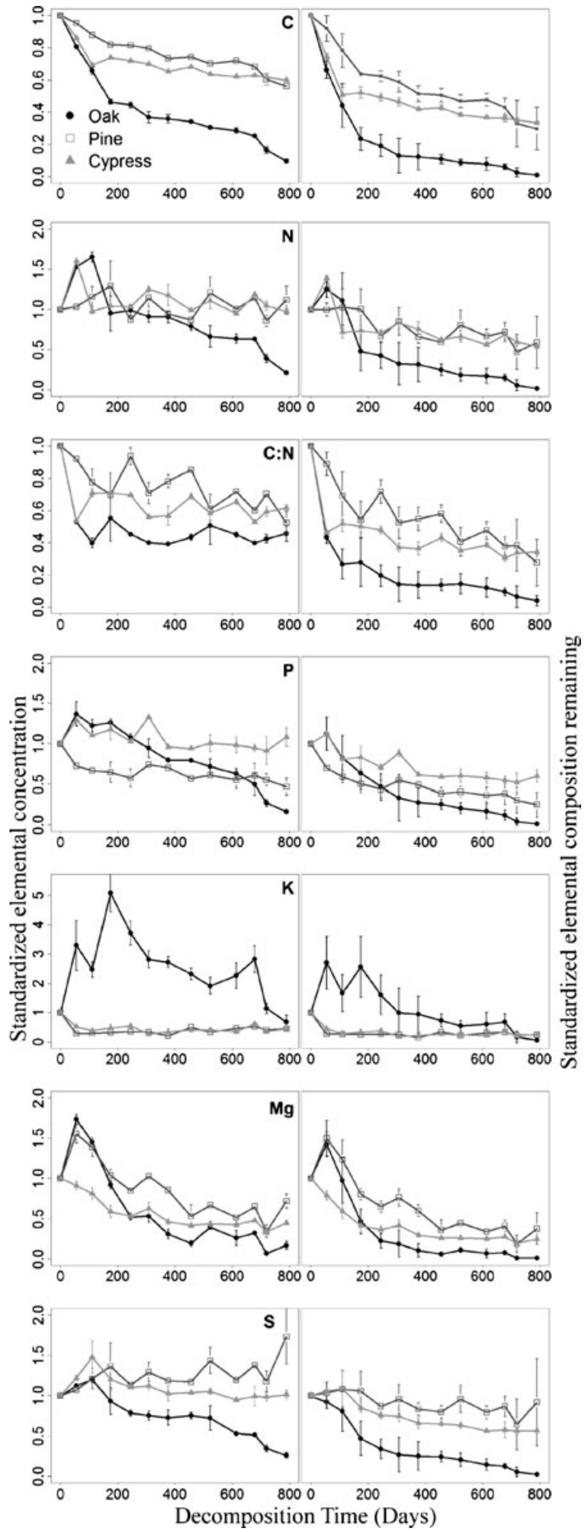
In the present study, despite having acidic soils with low nutrient availability in both the oak forest and the pine plantation, mean total litterfall production in both forest types were comparable and similar to values that have been reported for tropical forests, ranging from 3.0 to 14.4 Mg DM ha^{-1} $year^{-1}$ (Baraloto et al. 2010; Chave et al. 2010; Cuevas and Lugo 1998; McDonald and Healey 2000; Medina and Cuevas 1989; Priess et al. 1999; Proctor 1983; Sundarapandian and Swamy 1999; Yang et al. 2005). In contrast, the cypress plantation had significantly lower litterfall relative to the oak forest and pine plantation, as well as other studies (Celentano et al. 2011; Lisanework and Michelsen 1994; McDonald and Healey 2000; Priess et al. 1999). These differences could be due to local soil conditions or species composition (Sundarapandian and Swamy 1999; Yang et al. 2004) as factors such as climate and stand age were constant across forest types. While it has been reported that natural forests have higher litterfall than plantations (Pandey et al. 2007; Xu and Hirata 2002; Yang et al. 2005), the observed similarities in litter production between the oak forest and the pine plantation could be related to climate or species-specific functional traits that could affect nutrient dynamics like leaf lifespan (Cornwell et al. 2008; Reich et al. 2007).

With respect to the different fractions that constitute total litterfall, litterfall in the oak forest and the cypress plantation was divided similarly between leaf litterfall (LD+LO, 71 %) and branches and unclassified material (29 %), while in the pine plantation the proportion of LD+LO was lower (63 %), but higher for unclassified material and branches (37 %). This is comparable to the range recorded for tropical forests in Brazil, Malaysia, and Venezuela (Haase 1999).

While seasonal variation in litterfall have been reported in tropical forests (Sundarapandian and Swamy 1999), our results showed minimal seasonal variation in litterfall. For the oak forest and pine plantation, peaks in litter production occurred between June and September in the first 2 years of the study, corresponding to the middle of the dry season, while in the third year the biggest peak in pine litterfall was in March. These peaks may be associated with physiological leaf senescence due to droughts (Yang et al. 2004). There were no noticeable peaks in litterfall in either the oak forest or the cypress plantation in the third year.

Previous studies in tropical montane forests have demonstrated that N limits tree growth in these ecosystems (Benner et al. 2011; Fisher et al. 2012; Tanner et al. 1998). In certain volcanic soils, N limitation could be further exacerbated as bio-availability of P can also be quite low (Nanzyo et al. 1993). Consequently, tropical montane forests could limit growth through N or P

Fig 3 *Left*: residual dry matter and changes of concentrations of N, S, Ca, Mg, K, and P in leaf litters of oak (*Quercus humboldtii*), pine (*Pinus patula*), and cypress (*Cupressus lusitanica*) over a 789-day period. They are standardized as percentage (referred to 100 % of the initial amount). *Right*: Standarised values of N, S, Ca, Mg, K, and P remaining in the in leaf litters of oak (*Q. humboldtii*), pine (*P. patula*), and cypress (*C. lusitanica*) over a 789 day



supply, or both, since these nutrients are usually in close balance (Davidson and Howarth 2007). The different nutrient concentrations in litterfall, especially N and P concentrations in oak leaf litterfall, were slightly lower than values reported for tropical montane forests (Herbohn and Congdon 1998; Medina and Cuevas 1989; Medina et al. 1981; Proctor et al. 1989; Veneklaas 1991; Vera et al. 1999). N and P concentrations in conifers were consistent with values reported for leaf litterfall in other studies of tropical conifer plantations, whereas Ca, Mg and K contents in conifers were lower than concentrations reported for tropical conifer plantations (Edwards 1982; Fassbender and Grimm 1981; Herbohn and Congdon 1998; Veneklaas 1991; Vitousek et al. 1995; Vitousek and Sanford 1986). The lower N and P concentrations in leaf litter, along with the considerable amounts of litter production, suggest that oak forests are apparently better adapted to the local oligotrophic conditions despite the highly acidic pH and low exchangeable cation content of these andic soils.

In the cypress plantation, in spite of high soil C and N contents, the mineralization rate of organic residues (k=0.29 year^{-1}) in these soils was extremely low, which resulted in a low nutrient return. The higher concentration of Ca found in the leaf litter of the coniferous plantations, especially cypress (Table 4), could be due to the frequently observed increase in Ca that occurs as leaves age and lignify in coniferous plants (Lundgren 1978). The low concentrations of Mg found in the cypress plantation is likely attributable to its low availability, as the soils of the study site are of volcanic origin and are strongly acidic (Fassbender and Grimm 1981; Vitousek et al. 1995).

Potential nutrient return (PNR) and net nutrient return (NNR) were higher in the oak forest than in both exotic coniferous plantations for most of the studied elements (Tables 5 and 6). Nutrient release by litter decomposition is determined by the interaction between litter quality and decomposers (mainly microbial activity), in conjunction with interactions with climatic and soil conditions (Makkonen et al. 2012). Several leaf and litter traits related to litter quality also can affect decomposition and nutrient and carbon cycling (Bakker et al. 2011;

Table 5 Mean annual potential return of macro-nutrients to the forest floor by different litter fractions in the three forest types studied in the *Piedras Blancas* Watershed

	Forest	C		N		S		P		Ca		Mg		K	
		(kg ha^{-1} year^{-1})													
LD	Oak	1,274 (49.3)	a	28.6 (1.1)	b	2.6 (0.1)	a	0.8 (0.0)	a	9.7 (0.2)	a	2.7 (0.1)	b	3.3 (0.1)	NS
	Pine	2,042 (29.8)	b	43.1 (0.6)	c	4.0 (0.1)	b	1.7 (0.0)	b	17.9 (0.3)	b	4.3 (0.1)	c	3.5 (0.1)	
	Cypress	1,082 (22.7)	a	13.1 (0.3)	a	2.0 (0.1)	a	0.8 (0.0)	a	26.0 (0.5)	c	1.4 (0.0)	a	1.7 (0.1)	
LO	Oak	1,015 (14.6)	b	23.7 (0.4)	b	2.7 (0.0)	b	0.8 (0.0)	b	18.2 (0.5)	b	3.6 (0.1)	b	3.3 (0.1)	b
	Pine	41.6 (0.6)	a	1.3 (0.0)	a	0.1 (0.0)	a	0.0 (0.0)	a	0.9 (0.0)	a	0.2 (0.0)	a	0.1 (0.0)	a
	Cypress	3.1 (0.1)	a	0.1 (0.0)	a	0.0 (0.0)	a	0.0 (0.0)	a	0.1 (0.0)	a	0.0 (0.0)	a	0.0 (0.0)	a
WM	Oak	430 (10.6)	a	8.2 (0.4)	b	0.7 (0.0)	ab	0.3 (0.0)	a	7.8 (0.3)	b	1.2 (0.0)	b	0.9 (0.0)	a
	Pine	793 (47.7)	b	8.2 (0.5)	b	1.1 (0.1)	b	0.7 (0.0)	b	5.6 (0.3)	b	0.8 (0.0)	b	0.8 (0.0)	a
	Cypress	128 (4.8)	a	1.2 (0.1)	a	0.2 (0.0)	a	0.1 (0.0)	a	1.8 (0.1)	a	0.2 (0.0)	a	0.2 (0.0)	b
UM	Oak	460 (9.5)	NS	17.9 (0.5)	c	1.5 (0.0)	b	0.5 (0.0)	b	8.8 (0.3)	b	1.5 (0.0)	b	2.4 (0.1)	b
	Pine	426 (19.6)		10.4 (0.5)	b	1.0 (0.1)	b	0.4 (0.0)	ab	2.9 (0.1)	a	0.7 (0.0)	a	0.8 (0.0)	a
	Cypress	300 (10.0)		4.4 (0.1)	a	0.5 (0.0)	a	0.3 (0.0)	a	7.0 (0.2)	b	0.3 (0.0)	a	0.6 (0.0)	a
Total	Oak	3,199 (6.5)	b	77.4 (0.2)	c	7.1 (0.0)	b	2.3 (0.0)	b	44.5 (0.0)	c	9.0 (0.0)	c	7.9 (0.0)	c
	Pine	3,363 (8.2)	b	63.1 (0.1)	b	6.6 (0.0)	b	2.4 (0.0)	b	27.3 (0.0)	a	6.6 (0.0)	b	4.3 (0.0)	b
	Cypress	1,468 (3.3)	a	18.0 (0.0)	a	2.5 (0.0)	a	1.1 (0.0)	a	39.6 (0.0)	b	2.3 (0.0)	a	2.4 (0.0)	a

Standard errors in parentheses

Different letters indicate significant differences and NS indicates non-significant differences as determined by bootstrap test ($P<0.05$)

LD leaves of the dominant species, *LO* leaves of other species, *WM* woody material, *UM* unclassified material

Makkonen et al. 2012). For example, the C:N ratio has been suggested as a good predictor for leaf litter decay rates (Taylor et al. 1989). In the current study, the lowest C:N ratios were found in most fractions of the oak forest, which suggests faster decomposition of organic residues and, hence, a faster return of nutrients in these forests (Jordan 1985; Vitousek and Sanford 1986).

Nutrient return is strongly related to litter concentrations of structural compounds (such as lignin and to the lignin:N ratio; Currie et al. 2009). Lignin concentrations and the lignin:N of leaf litter from the three forests studied indicated that lignin concentration in the LD was higher in the oak forest than in the two exotic coniferous plantations (Table 4). Thus, the lignin:N ratio of the leaf litter would be expected to be positively correlated with both mass loss and decomposition (Makkonen et al. 2012), However, our results did not follow our expectations, as oak had higher lignin:N than

Table 6 Potential nutrient return (PNR) and net nutrient return (NNR) via leaf litter after two years of decomposition from the three forests studied in the Piedras Blancas Watershed

Fraction	Forest	C		N		S		P		Ca		Mg		K	
		(kg ha^{-1} year^{-1})													
PNR leaf litter	Oak	2,290	b	51.7	c	5.0	b	1.6	b	27.9	b	6.2	c	5.2	c
	Pine	2,114	b	45.0	b	4.4	b	1.5	b	19.0	a	4.9	b	3.0	b
	Cypress	1,021	a	12.5	a	1.7	a	0.7	a	26.1	b	1.5	a	1.7	a
NNR leaf litter	Oak	2,271	c	50.9	c	4.8	b	1.6	b	27.6	b	6.1	c	4.9	c
	Pine	1,486	b	18.4	b	0.4	a	1.1	b	8.9	a	3.1	b	2.3	b
	Cypress	682	a	5.7	a	0.8	a	0.3	a	21.2	b	1.1	a	1.3	a

Different letters indicate significant differences based on the bootstrap test ($P<0.05$)

both exotic coniferous species, yet faster decomposition. Our results indicate that oak had a 'home-field' advantage, as decomposer communities were apparently better adapted to degrading native leaf litter more efficiently than that of the two exotic tree species (Freschet et al. 2012; Montagnini 2005).

Pine and cypress, the tree species most commonly used in ecological restoration and reforestation plans in the Andean area of Colombia did not cycle nutrients back to the soil as quickly as the native oak forest in the present study. Consequently, our results provide evidence that areas reforested with these two exotic species could eventually suffer from greater depletion of nutrients in the soil relative to natural forests or, perhaps, areas reforested with native broadleaf tree species. Forest restoration in these areas should focus on using species that facilitate nutrient turnover rates similar to those of the native oak forest. The higher nutrient return and decay rates of oak species suggest that that these species may be more promising than exotic coniferous species for ecological restoration in tropical montane forests.

Conclusions

Annual litterfall and nutrient return estimates in Colombian tropical montane forests suggested that oak forest returned significantly greater quantities of nutrients to the soil surface than plantations of pine and cypress for most macro-nutrients. Oak litterfall had a higher rate of decay and nutrient release compared to the exotic conifer species that were analyzed, indicating that this forest type has better nutrient conservation mechanisms that permit for a more efficient use of these elements than exotic species plantations. Therefore, native broadleaved tree species should be considered in these areas for forest restoration in order to avoid soil nutrient impoverishment.

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