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Litter production and nutrient cycling in two plantations and a *Podocarpus falcatus* dominated natural forest ecosystems in south-eastern highlands of Ethiopia

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The production of litter plays a fundamental role in the biogeochemical cycle of organic matter and mineral nutrients in forest ecosystems. The amount of litter produced and nutrients returned, and their accumulation in the organic layers of *Eucalyptus globulus* and *Cupressus lusitanica* plantations, and an adjacent *Podocarpus falcatus* dominated natural forest were monitored over a one year period in Ethiopia. The objective of the study was to assess the general trends of nutrient cycling by litter fall under the two plantations relative to the natural forest. The results showed that annual litter production was significantly highest in the natural forest ($4.4 \text{ t ha}^{-1}\text{year}^{-1}$) and least in *Cupressus* plantation ($2.2 \text{ t ha}^{-1}\text{year}^{-1}$). Litter fall in the natural forest was of high quality and richer in most nutrients than the two plantations which behaved similarly. The annual fluxes of N, S, P, Ca, Mg and K were 1.3 to 2.3 times as much in the natural forest as in *Eucalyptus* and *Cupressus*. The organic layer under *Cupressus* had poor quality litter compared to *Eucalyptus* and natural forest which behaved similarly mainly due to the influence of the understorey vegetation on *Eucalyptus* organic layer. Although statistically not significant, dry mass accumulation in the organic layer of *Cupressus* was higher than in *Eucalyptus* and lower than in the natural forest, but the approximate residence time was in the order: *Cupressus* > natural forest > *Eucalyptus*. The organic layer in the natural forest had always the maximum quantity of nutrients compared to the two plantations. Except for Ca in which *Cupressus* far better, the other elements were accumulated in larger quantity in the *Eucalyptus* organic layer than in *Cupressus*. Overall, the results show that the *Cupressus* plantation is poor self fertilizing owing to the low quality homogenous materials which could result in a gradual impoverishment of the soil.

Key words: *Cupressus*, Ethiopia, *Eucalyptus*, litter fall, nutrient cycling, organic layer.

INTRODUCTION

Large scale deforestation of the natural forests of Ethiopia has decreased the once an estimated 40% cover of the country's natural forests to 2.6% or less at present (Mengistu, 2002). And currently the country is largely dependent on tree plantations. The Munesa

forest, containing both natural and commercial plantation forests is one of the remaining natural forest reserves of the country. The plantation forest comprised of mainly fast growing exotic species such as *Eucalyptus* spp., *Cupressus lusitanica*, *Pinus* spp., and *Grevilea robusta*

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and accounted for 3.4% of the total plantation in the country (EFAP, 1994). Tree plantations have a potential as a renewable source of bio-energy and could reduce the huge demands on fossil fuels, the main CO₂ source to the atmosphere. Besides these, tree plantations have many beneficial interactions with the surrounding environment such as watershed protection and improve the organic matter and nutrient status of the soil through the production of litter. Man made plantations can reach a natural equilibrium state in which decomposition and accumulation will balance, however, many tropical plantations cannot reach this state because they will be harvested frequently at commercial maturity. This results in long-term decline in soil C and nutrient content due to disruption on the flow of carbon and nutrients through litter.

The production of litter plays a fundamental role in the biogeochemical cycle of organic matter and mineral nutrients, thus becoming a key component in the functioning and stability of forest ecosystems. Organic residues coming in the form of litter fall and accumulated on the ground are a major reservoir of organic matter and nutrients, and influence or regulate most of the functional processes occurring throughout the ecosystem (Gosz et al., 1972; Cuevas and Medina, 1988; Maguire, 1994). In forest ecosystems, litter production depends primarily on the productivity of plant communities, which in turn is influenced by the climatic and edaphic conditions under which forests develop, by their biological characteristics, species composition, and by the density, age and level of maturity of stand (Bray and Gorham, 1964; Lugo and Brown, 1991). The accumulation of organic detritus in the organic layer of forests growing under similar site and climatic conditions depends on the rate of decomposition of the plant material which is influenced by litter quality, acidity, soil moisture and temperature, and the kinds of microflora and fauna present (Kumar and Deepu, 1992; Lisanewok and Michelsen, 1994; Fisher and Binkley, 2000).

In tropical plantations, where nutrient limitations are common, particularly nitrogen and phosphorous, the amount of plant material returning to the soil is critical factor because nutrients are made available from decomposition of organic matter (Cuevas and Medina, 1988; Evans, 1992; Binkley et al., 1997; Tiessen et al., 1994). It is also believed that biotic fluxes of base cations are far greater than geologic and atmospheric inputs (Johnson, 1992; Ragsdale et al., 1992; Currie et al., 1996). Therefore, management of fast growing and high yielding short rotation plantations, with long term stability of soil fertility and nutrient balance, requires knowledge on the dynamics of litter production and nutrient cycling, and litter and nutrients accumulation in the organic layer. Investigations on litter production and nutrient cycling have been made by many authors (Pastor and Bockheim, 1984; Maguire, 1994; Guo and Sims, 1999; Gordon et al., 2000; Kavvadias et al., 2001), but most of the studies focused on temperate and Mediterranean zones of the

world. The differences in climate and soil, and management and growth patterns of tropical and sub-tropical tree plantations require carrying out such ecologically important studies. Therefore, this investigation was conducted to assess litter production and nutrient recycling in *Eucalyptus* and *Cupressus* plantations and an adjacent natural forest in Ethiopia. In earlier paper, emphasis was given only on the accumulations of dry mass and C, N and S in the organic layers of the natural forest and *Eucalyptus* (Ashagrie et al., 2003). From this published paper data on the above parameters are used in the present paper to calculate stocks of other nutrients and mean residence times of organic matter and nutrients.

MATERIALS AND METHODS

The study site and experimental design

The study was conducted at the Munesa/Shashemene forest enterprise site (7°34'N and 38°53'E) located some 240 km south east of Addis Ababa. The altitude of the study site is 2400 m. Precipitation is bimodal most of it falling in July and August. Mean annual precipitation and temperature of the study area are 1250 mm and 19°C, respectively. The experimental design was set up in three stands situated side by side: An old growth *Podocarpus falcatus* dominated natural forest (3 to 4 thousand years, Zech, Pers. Commu.) and two exotic tree species plantations (*Eucalyptus globulus* and *Cupressus lusitanica*). Common medium sized canopy tree species in the natural forest include *Croton macrostachys*, *Olea hochstetterii* and *Schefflera abyssinica*. The two plantations were established in 1980 after clearing of part of the natural forest. Clearing was done manually and the surface biomass was burned on site. Both plantations were established from seedlings planted in a hand dug holes. The *Eucalyptus* plantation had 595 trees ha⁻¹ with native understorey canopy tree (*Croton macrostachys*) and shrubs notably *Acanthopale pubescens*, *Achyrosperrum schimperi*, *Bothriocline schimperi*, *Carex spicata-paniculata*, *Hypoestes forskoolii*. The ground layer was covered with dense grass and broad-leaved herbaceous species. The mean height of *Eucalyptus* was 30 to 40 m and mean diameter at breast height (dbh) was 19 to 39 cm. The *Cupressus* plantation had a standing stock of 672 trees ha⁻¹ with almost no ground vegetation. The mean height of *Cupressus* was 18 to 20 m and dbh was 29 cm. Further details of the ground cover vegetation of each forest type are described by Abate (2004). Soil properties under the plantations prior to their establishment were assumed to have been similar to those under the natural forest. The soils are moderately acidic with pH (H₂O) ranging from 5.3 under *Eucalyptus* to 5.6 under *Cupressus* in the A horizon and slightly acidic with pH ranging from 4.5 under the natural forest to 4.7 under *Eucalyptus* in the Bt2 horizon. They are characterised by a clayey texture with gradational texture profile (the clay content ranging from 49 to 50% in the A horizon to 63 to 74% in the Bt2 horizon) and a moderate amount of available nutrients (CEC, 37 to 51 cmol_c kg⁻¹ soil) in the A horizon. The soils are classified as Nitisols (FAO, 1997).

Sampling

Sampling was done in three randomly selected representative permanent experimental plots per forest type on which water and nutrient fluxes, nutrient and water availability to plants, water use efficiency as well as biomass and nutrient stocks in biomass are

being investigated by a multidisciplinary (Biogeography, Plant physiology and Soil science) research team. In order to make the results of the different disciplines complementary to each other and due to logistical reasons, all the investigations were confined to the three experimental plots selected by the multidisciplinary team. The size of each plot was 0.06 ha with a distance of ca. 100 m from each other. Within each plot three 0.25 m² litter collectors with mesh bottoms were placed under the *Podocarpus falcatus* tree (the most dominant tree in the natural forest) and the two plantations. All the litter (leaves, flowers, fruits, twigs, bark, and woody material < 2 cm) were collected monthly from July 2001 to June 2002. The litter from each month was bulked per plot to give one sample per annum. The organic layer samples were taken at three points with in each plot: one at the center and the other two at about 10 m distance diagonally from the center by pressing a 0.09 m² steel sheet sampling frame into the organic layer. In order to facilitate the identification of the different horizons (that is, L, newly fallen litter lying loosely on the forest floor; Of1, thick mat of litter, tightly interwoven with fungal mycelia; Of2, fermentation layer, interwoven with fungal mycelia and plant roots but being looser than the overlying layer), litter outside the sampling frame was removed until the mineral soil was exposed and the thickness of the different horizons was measured with a ruler. The materials (excluding woody debris > 2 cm) from the different horizons were put in separate paper bags. In each forest type, the distinction between the litter layer and the under lying mineral soil was less clear and some soil was inevitably collected. Both litter fall and the organic layer samples were dried in an oven at 65°C and weighed. After drying, the three sub samples per plot were bulked and the final number of samples was reduced to three per forest type. The dried samples of litter fall and organic layers were finely ground with a rotary ball mill for chemical analysis.

Chemical analysis

Carbon, nitrogen and sulphur were determined using a CHNS-analyser (Vario EL, Elementar Analysensysteme). Samples for total P and cations determination were first digested with concentrated HNO₃ under pressure (Heinrichs et al., 1986). After diluting the digested solution with deionized water, total P was determined with inductively coupled plasma atomic emission spectrometry (ICP-AES; GBC Integra XMP) and cation concentrations were determined by flame atomic absorption spectrometry (AAS; Varian SpectraAA 400). The pH in water (soil: solution ratio 1:20) of the organic layer was determined with a standard pH electrode (Orion U402-S7).

Calculations and statistical analysis

Nutrient use efficiency (NUE) was calculated using Vitousek's (1984) definition of NUE which is the ratio of the dry matter to nutrient content of litter fall. We also estimated turnover times for both dry mass and nutrients as the ratio of litter fall mass to standing litter mass. This term is an estimate of the decomposition constant, *k* (Olson, 1963) and is the inverse of mean residence time. Both calculations were based on the assumption that the plantations and the natural forest were at steady state. An additional assumption for NUE is that aboveground net primary productivity was equal to litter fall, and that the nutrient lost in litter was equal to that taken up by the stands. A one-way ANOVA for the litter fall parameters and a two-way ANOVA for the parameters in the organic layer were performed using MSTAT-C version 2.10 software package. In case of significant differences between treatments, means were compared with Tukey's Honestly Significant Difference Test (HSD) at *P*<0.05.

RESULTS AND DISCUSSION

Litter production

The annual litter production in the studied forests ranged from 2.2 t ha⁻¹year⁻¹ to 4.4 t ha⁻¹year⁻¹, being significantly higher in the natural forest than the two plantations (Table 1). This result is mainly accounted for by differences in phenology, stand age, and species and vegetation composition. Lundgren (1978), Swamy (1992), and Lisanework and Michelsen (1994) have also reported higher litter production in natural forest than plantations. Other studies that compared litter production between natural and plantation forests reported different results. For example, Brasell and Sinclair (1983) and Smith et al. (1998) recorded similar litter fall between natural and plantation forests, while Lugo (1992) recorded higher litter fall in plantations than natural forests. Annual litter production estimates for different montane forests range from 4.2 to 10.9 t ha⁻¹ (Lundgren, 1978; Tanner, 1980; Edwards, 1982; Lisanework and Michelsen, 1994; McDonald and Healey, 2000; Wilcke et al., 2002). The trend in our natural forest was, therefore, at the lower end of this range, but slightly higher than the values for Chilean natural forest (2 t ha⁻¹; Caldentey et al., 2001) and deciduous forests of India (4 t ha⁻¹; Garng and Vyas, 1975).

There are very few data on litter production in *C. lusitanica* for comparison of results from this study 5.2 t ha⁻¹ in 18 years old stand in Tanzania (Ludgren, 1978) and 5.8 t ha⁻¹ in 28 years old stand at Menagesha in Ethiopia (Lisanework and Michelsen, 1994). Similarly, data on annual litter production for a similar age group of *Eucalyptus* growing in a similar site and climatic conditions are not available, but estimates of annual litter fall in various *Eucalyptus* sp. stands in different parts of the tropics are as follows: 27 years old *E. grandis* 7.5 t ha⁻¹ in Australia (Turner and Lambert, 1983), 14 to 16 years old *E. saligna* 10.3 t ha⁻¹ in Hawaii (Binkley and Ryan, 1998) 40 years old *E. globulus* 5.8 t ha⁻¹ at Menagesha in Ethiopia (Lisanework and Michelsen, 1994). The two plantations in our study site had litter fall production in the lower range reported for a *Pinus patula* plantation in the tropics (Lundgren, 1978; Lugo, 1992; Dames et al., 1998). Casual factors in rate of litter production involve climate, soil type, elevation, stand age, level of disturbance, density and species composition. In addition, the occurrence of extreme climatic events such as storms (Lugo, 1992), high wind velocity (Lisanework and Michelsen, 1994) and Hurricane (McDonald and Healey, 2000) may result in mass movement of litter and large differences in the litter fall estimates of different studies.

Carbon and nutrient concentrations in litter fall

The concentrations of N, S, Mg, and K were about

Table 1. Litter production ($\text{t ha}^{-1}\text{year}^{-1}$) and, carbon and nutrient concentrations (g kg^{-1}) in litter fall.

Forest type	Litter fall	C	N	S	P	Ca	Mg	K	C/N	C/S	C/P	N/S	N/P
Natural forest	4.4 ^a (0.12)	460 ^b (12)	14 ^a (1)	1.6 ^a (0.03)	0.6 ^a (0.06)	18 ^a (3.5)	2.9 ^a (0.12)	3.6 ^a (0.5)	34 ^a (2.3)	297 ^b (13)	811 ^b (86)	9 ^a (0.6)	23 ^a (1.2)
<i>Eucalyptus</i>	3.95 ^b (0.54)	520 ^a (4)	10 ^b (0.3)	1.2 ^b (0.03)	0.4 ^a (0.06)	17 ^a (1.3)	1.6 ^b (0.2)	2.2 ^b (0.4)	52 ^b (3)	446 ^a (14)	1319 ^a (219)	9 ^a (0.6)	26 ^a (5)
<i>Cupressus</i>	2.17 ^c (0.22)	470 ^b (2)	9 ^c (0.5)	1.2 ^b (0.07)	0.6 ^a (0.07)	20 ^a (0.23)	1.7 ^b (0.07)	2 ^b (0.2)	54 ^b (4)	382 ^a (23)	828 ^b (92)	7 ^a (0.0)	15 ^b (2)

Means followed by the same letter in a column are not significantly different. Numbers in parentheses are standard errors ($n=3$).

1.33 to 1.8 times significantly higher in the natural forest litter fall than those of the two plantations (Table 1). The *Eucalyptus* and *Cupressus* plantations were similar in terms of litter fall nutrient concentrations. The observed differences in nutrient concentrations might be attributed partly to the species differences in accumulating specific elements and partly to differences in species composition. In a study by Lugo (1992) highest nutrient concentrations (N, P and K) in litter fall were generally found in broad leaves. The concentrations of Ca and P were not affected by forest type. In all forest types, the concentrations of Ca far exceeded the concentrations of other nutrient elements followed by N. Phosphorus concentration in litter fall was very low in comparison to other major nutrients, suggesting that it is tightly held in the intrasystem nutrient cycle. Carbon concentration in *Eucalyptus* litter fall was significantly higher than the concentrations in *Cupressus* and natural forests, but the later two had similar concentrations.

The C/N, C/S and C/P ratios of litter fall were significantly narrower in the natural forest than the two plantations mainly because of relatively higher nutrient concentrations. N/S and N/P ratios were narrower under *Cupressus* than the other forest types. C/N ratio was not significantly different between the two plantations, whereas C/S and C/P ratios were higher in *Eucalyptus* than *Cupressus*. One might argue that differences in plant species composition may contribute to stand

differences in carbon to nutrient ratios.

The mean concentrations of nutrient elements in litter fall were always less than the mean concentrations in live foliage, as reported by Abate (2004), with the exception of Ca, suggesting resorption prior to abscission which contributes to the efficiency with which nutrients are used (Vitousek, 1984). For Ca, concentrations in litter fall appeared to be higher than concentration in live foliage for all forest types. This reflects the immobility of this particular element in foliage (Rainers and Olson, 1984; Gordon et al., 2000).

Carbon and nutrient inputs via litter fall

With mean annual litter fall flux, and nutrient concentrations present in litter fall (Table 1), bioelement amounts that could potentially return via litter fall to the ground were estimated (Table 2). The fluxes of elements were significantly influenced by forest type: Natural forest > *Eucalyptus* > *Cupressus* for N, S, Mg and K, natural forest ~ *Eucalyptus* > *Cupressus* for C and Ca and, natural forest > *Eucalyptus* ~ *Cupressus* for P. The differences observed in the above elements among the forest types were mainly attributed to the variations in the magnitude of their relative litter production and element concentrations in them. Potential fluxes of most of the nutrients in the natural forest litter fall were generally low compared to that in Jamaica

(McDonald and Healey, 2000), at Menagesha in Ethiopia (Lisanework and Michelsen, 1994), in Tanzania (Lundgren, 1978) and various tropical montane forests (Tanner, 1980; Edwards, 1982; Wilcke et al., 2002). With few exceptions, litter fall nutrient fluxes in the plantations were equivalent to other similar studies (Lundgren, 1978; Lisanework and Michelsen, 1994).

Although statistically not tested, within-stand NUE was highest in *Eucalyptus* except for N and K in which *Cupressus* was more efficient (Table 3). NUE in *Eucalyptus* was always higher than the natural forest, whereas the use efficiency of *Cupressus* particularly for Ca and P was lower than the natural forest. From the data in Table 3, it appeared that both the plantations and the natural forest do not use N and Ca efficiently compared to the other nutrients, demonstrating that the annual circulation of these two elements was higher. The results for P show that its use is more efficient than N. Several other studies (Lugo, 1992; Lisanework and Michelsen, 1994; Smith et al., 1998) have also reported an efficient within-stand NUE of plantations than natural forests.

Carbon and nutrient concentrations in the organic layer

Chemical and physical properties of the organic layer under the three forest types are presented in Table 4. Despite the relatively similar element

Table 2. Carbon and nutrient inputs (kg ha⁻¹year⁻¹) in litter fall.

Forest type	C	N	S	P	Ca	Mg	K
Natural forest	2024 ^a (270)	2 ^a (10)	7 ^a (0.7)	2.64 ^a (0.4)	79 ^a (8)	13 ^a (2)	16 ^a (4)
<i>Eucalyptus</i>	2054 ^a (170)	41 ^b (4)	5 ^b (0.5)	1.58 ^b (0.1)	67 ^b (2)	6 ^b (0.5)	9 ^b (2)
<i>Cupressus</i>	1020 ^b (0.2)	20 ^c (0.2)	3 ^b (4)	1.30 ^b (0.5)	43 ^c (1)	4 ^{bc} (1.3)	4 ^c

Means followed by the same letter in a column are not significantly different. Numbers in Parentheses are standard errors (n=3).

Table 3. Nutrient use efficiency of the three forest types.

Forest type	N	S	P	Ca	Mg	K
Natural forest	71	629	1833	56	338	275
<i>Eucalyptus</i>	99	790	2500	59	658	439
<i>Cupressus</i>	109	723	1669	50	543	543

concentrations between *Cupressus* and *Eucalyptus* litterfall (Table 1), the mean concentrations of most elements in the *Cupressus* plantation organic layer were significantly lower than both the *Eucalyptus* plantation and natural forest organic layers, whereas mean C concentration was highest under *Cupressus* plantation. Mean concentrations of most elements in the organic layers of *Eucalyptus* and natural forests were similar. The mean P concentration was significantly higher under *Eucalyptus* than under *Cupressus* and natural forest, but the difference between the later two was not significant (Table 4). There were higher C concentration and C/N and C/S ratios and, lower N and S concentrations in the Of1 and Of2 horizons of the *Cupressus* plantation than *Eucalyptus* plantation and the natural forest (Table 4). No significant interaction was detected between forest type and depth of the organic layer for other parameters. Higher element concentrations in the organic layer of *Eucalyptus* relative to the *Cupressus* organic layer were likely due to the contribution of nutrient rich litter from the understorey vegetation. The influence of understorey vegetation on the organic layer nutrient dynamics of a stand is best illustrated by comparing the chemical quality of *Cupressus* litter with that of *Eucalyptus*. Mean C/N, C/S and C/P ratios were wider under *Cupressus* than *Eucalyptus* and natural forests, while N/P ratio was slightly narrower under *Cupressus* than the two forest types (Table 4). Considerable nutrient rich biomass input as litter from the understorey vegetation to the organic layer was noted by several authors (Bernhard-Reversat, 1982; Turner and Lambert, 1983; Lugo et al., 1990; Liu, 1995; Lodhiyal and Lodhiyal, 1997; Singh, 1998).

Nutrient concentrations in the organic layers of each forest type were highest in relation to the respective litter fall although statistically not tested. The increase in nutrient concentrations in the organic layer relative to litter fall could be ascribed to contamination of the organic layer material with the mineral soil and/or additions from roots, and the ground vegetation particularly in

Eucalyptus and natural forests. Concentrations of nutrients in plantations of the present study were comparable with those reported under a 42 years old first rotation *Pinus patula* plantation in South Africa (Dames et al., 2002). The nutrient concentrations in our study natural forest were equivalent to those reported by Nye (1961) for Ghanaian natural forest and slightly higher than those reported by Wilcke et al. (2002) for Ecuadorian montane forest. Nitrogen and S concentrations were higher in the studies of the later authors than in our study. Most nutrient elements and carbon to nutrient ratios increased with depth, whereas the opposite holds true for C. These could be resulted from immobilisation of N, S and P, loss of C as CO₂ and complexation by the exchange complex or contamination with the underlying mineral soil of the metal elements. Similar results have been reported by Lee et al. (1983) and Wilcke et al. (2002).

Dry mass accumulation, and carbon and nutrient storage in the organic layer

Although statistically not significant, the organic layer under *Cupressus* (Table 4) was thicker than the organic layer under the natural forest and *Eucalyptus*, however, dry mass accumulation in *Cupressus* was lower than the natural forest due to a denser organic layer of the latter (data not shown). There were steady increases in thickness and dry mass of the organic layer from the L to the F horizon (Table 4). Although rate of litter production was low compared to *Eucalyptus* (Table 1) and the difference was not significant, *Cupressus* had 1.82 times as much dry mass as *Eucalyptus* which was equivalent to about 17 times the annual litter fall. This indicates that decomposition in the *Cupressus* organic layer was slower than that in *Eucalyptus* mainly due to the low quality homogeneous material in the organic layer of the former. Lugo (1992) also reported an accumulation of more leaf

Table 4. Some physical and chemical properties of the organic layer horizons under the three forest types.

Forest type	Dry wt. (t ha ⁻¹)	thickness (cm)	C	N	S	P	Ca	Mg	K	C/N	C/S	C/P	N/P
Natural forest[†]													
L	9.1(2.6)	0.83(0.2)	444 ^{ab} (0.9)	13 ^{bc} (0.06)	1.4 ^b (0.01)	0.7 ^a (0.04)	18.1 ^a (1.6)	3.37 ^a (0.5)	4.02 ^a (0.7)	34 ^{bc} (2.21)	318 ^{ab} (19)	641 ^a (44)	18 ^a (2)
Of1	13.2(4.2)	1.17(0.4)	382 ^c (1.28)	17.3 ^{ab} (0.03)	1.8 ^a (0.01)	0.85 ^a (0.05)	22.7 ^a (3.4)	3.33 ^a (0.23)	3.31 ^a (0.2)	22 ^c (0.62)	217 ^c (12)	453 ^a (24)	21 ^a (0.7)
Of2	20.2(4.3)	1.67(0.3)	343 ^c (0.01)	18 ^{ab} (3.71)	1.8 ^a (0.13)	0.84 ^a (0.00)	22 ^a (0.02)	3.72 ^a (2.5)	3.43 ^a (0.14)	18 ^c (0.72)	187 ^c (21)	409 ^a (41)	21 ^a (1.3)
Total/mean[§]	42.5	3.67	390^B	16^A	1.67^A	0.8^B	21^A	3.5^A	3.6^A	25^B	241^B	501^{AB}	20^A
<i>Eucalyptus[†]</i>													
L	2.7(0.34)	0.50(0.0)	388 ^{ab} (0.43)	481 ^a (0.23)	11.5 ^c (0.02)	1.3 ^{bc} (0.2)	0.68 ^a (2.6)	20 ^a (0.5)	2.48 ^a (1.3)	4.29 ^a (0.88)	45 ^{ab} (99)	840 ^a (247)	18 ^a (1.7)
Of1	7.4(1.08)	1.00(0.0)	358 ^c (0.31)	21.3 ^a (0.60)	1.8 ^a (0.09)	1.32 ^a (0.02)	25.4 ^a (0.14)	3.4 ^a (1.4)	4.25 ^a (0.12)	17 ^c (0.64)	198 ^c (28)	277 ^a (25)	16 ^a (1.5)
Of2	14.1(0.57)	1.33(0.3)	18.3 ^{ab} (0.28)	322 ^c (1.15)	2.0 ^a (0.08)	1.39 ^a (0.00)	24.3 ^a (0.03)	3.71 ^a (0.7)	4.23 ^a (0.02)	15 ^c (0.64)	164 ^c (15)	232 ^a (8)	13 ^a (0.9)
Total/mean[§]	24.2	2.83	4.26^A	387^B	17^A	1.7^A	1.13^A	23^A	3.20^A	26^B	250^B	450^B	16^{AB}
<i>Cupressus</i>													
L	5.0(0.07)	1.33(0.12)	464 ^a (0.3)	8 ^c (0.3)	1.1 ^c (0.05)	0.53 ^a (0.5)	17.5 ^a (0.1)	1.52 ^a (1.3)	1.39 ^a (0.31)	58 ^{ab} (3)	421 ^a (15)	954 ^a (252)	16 ^a (3)
Of1	6.6(0.03)	1.00(0.0)	346 ^{ab} (6)	450 ^a (0.02)	9 ^c (0.2)	1.3 ^{bc} (0.03)	0.74 ^a (0.03)	18.6 ^a (0.43)	1.71 ^a (0.07)	1.36 ^a (0.4)	50 ^a (6)	625 ^a (17)	13 ^a (0.3)
Of2	24.7(0.2)	2.00(0.0)	439 ^{ab} (16)	9 ^c (0.5)	1.3 ^{bc} (0.03)	0.88 ^a (0.05)	20.5 ^a (1.2)	2.57 ^a (0.21)	2.19 ^a (0.22)	47 ^{ab} (4)	38 ^{ab} (8)	502 ^a (31)	10 ^a (0.9)
Total/mean[*]	36.3	4.33	451^A	8.7^B	1.13^B	0.72^B	19^A	1.93^B	1.65^B	53^A	368^A	694^A	13^B

^{*}, [†]: Data on dry weight, thickness and C, N and S concentrations were taken from Ashagrie et al. (2003). [§]Total for dry mass and thickness, and means for element concentrations and element ratios. Values followed by the same lower case letter in a column are not significantly different among forest types for each organic layer. Means followed by different upper case letters in a column are different among forest types. Numbers in parentheses are standard errors (n=3).

leaf litter in the organic layer of pine plantation than was being produced by leaf fall. Dames et al. (1998) in South Africa reported dry mass accumulation of 31 to 65 t ha⁻¹ under 5 to 30 years old *Pinus patula* plantation. The accumulation of low quality thick organic matter in the organic layer under *Cupressus* plantation will certainly affect the overall nutrient cycling and ecosystem dynamics. According to Singh (1998), a poor quality litter is inefficient in decomposition and nutrient release to the soil and, have a tight nutrient cycling and reduced net production per unit of nutrient uptake resulting in more nutrient loss per unit of wood removal.

With the exception of C, N and S stocks, none of the elements stocks were influenced by forest

type (Table 5). Forest type by horizon interaction was non significant for all elements. The organic layer under *Cupressus* had lowest N and S and, similar C contents (Table 5) in comparison with the natural forest. The N content of the organic layer under *Cupressus* was also lower than *Eucalyptus*, but had an equivalent amount of S and higher C contents. Although statistically not significant, the quantities of Ca, Mg, and K accumulated in the natural forest organic layer were slightly higher than in the two plantations (Table 5). This arose mainly as a result of large dry mass accumulation. The accumulations of Ca in greater quantity under the *Cupressus* forest organic layer than under *Eucalyptus*, and K under the *Eucalyptus* forest organic layer than under

Cupressus forest were mainly reflections of dry mass accumulation and concentrations, respectively. The order of nutrient quantities bound up in litter was: Ca > N > K > Mg > S > P under the natural forest and *Eucalyptus* and Ca > N > Mg > K > S > P under *Cupressus* (Table 5). Contents of all elements increased with depth increments mainly because of the much greater mass of the former, and probably mixing with the mineral soil. The data in Table 5 clearly show that the organic layer represent important nutrient reservoirs that should be conserved during the implementation of silvicultural practices. However, considering the poor quality litter of *Cupressus* and the large quantities of nutrients bound up in the organic layer, one can expect an imbalance

Table 5. Carbon and nutrient storage in the organic layers of the different forest types.

Forest type	C	N	S	P	Ca	Mg	K
Natural forest*	t ha⁻¹			kg ha⁻¹			
L	4.1(1.17)	0.12(0.03)	0.01(0.00)	6(1.7)	168(52)	30(7)	38(14)
Of1	5.4(1.38)	0.24(0.06)	0.03(0.01)	11(2.9)	272(48)	42(11)	44(13)
Of2	6.9(1.47)	0.36(0.07)	0.04(0.01)	17(3.9)	454(138)	76(18)	69(15)
Total	16.4^a	0.72^a	0.08^a	34^a	894^a	148^a	151^a
<i>Eucalyptus</i>⁺							
L	1.4(0.28)	0.03(0.01)	0.004(0.00)	1.8(0.45)	53(7)	7(1.5)	11(3)
Of1	2.5(0.40)	0.15(0.02)	0.01(0.00)	10(0.5)	186(21)	25(3)	31(3)
Of2	4.3(1.53)	0.24(0.08)	0.03(0.01)	20(8)	346(140)	52(21)	59(24)
Total	8.2^b	0.42^{ab}	0.04^b	32^a	585^a	84^a	101^a
<i>Cupressus</i>							
L	2.3(1.05)	0.04(0.03)	0.01(0.003)	3(0.4)	88(14)	7(1.2)	7(0.9)
Of1	2.5(0.15)	0.06(0.01)	0.01(0.00)	5(0.1)	122(3.4)	11(0.9)	9(0.5)
Of2	11(0.89)	0.23(0.02)	0.03(0.00)	22(3)	510(65)	64(10)	55(9)
Total	16^a	0.33^b	0.05^b	30^a	710^a	82^a	71^a

*,+: data on C, N and S stocks were taken from Ashagrie et al.(2003); Values followed by the same letter in a column are not different among forest types. Numbers in parentheses are standard errors (n=3).

Table 6. Turnover times (years) of dry mass and elements in the organic layers of the three forest types.

Forest type	Dry mass	C	N	S	P	Ca	Mg	K
Natural forest	10	8	11	11	13	11	11	9
<i>Eucalyptus</i>	6	4	9	9	20	9	14	11
<i>Cupressus</i>	17	16	15	15	23	17	21	18

between accumulation and mineralization in the forest litter at least in the short term. This will limit the healthy nutrient cycling of the system and consequently, affect stand growth of successive rotations.

Turnover times

According to the calculated turnover times of the organic layer material, mean residence times were approximately 16 years for *Cupressus*, 10 years for the natural forest and 6 years for *Eucalyptus* (Table 6). These results suggest that decomposition in the organic layer of *Eucalyptus* proceeds faster than *Cupressus* and natural forest. This reasoning is well supported by the turnover times of C which increased by a factor of 2 and 4 in the natural and *Cupressus* forests, respectively (Table 6), indicating the importance of litter quality and litter nutrient concentrations especially N and P on decomposition (Swift et al., 1981; Lisanework and Michelsen, 1994; Palma et al., 1998; Kurka et al., 2000; Caldentey et al., 2001). The optimal N/P ratio for decomposition was reported to be 10 (Vogt et al., 1986), but when comparing the organic layer N/P ratios (Table 4) with the calculated

turnover times, its importance in determining decomposition appears to be uncertain. Worth to note is that, in addition to litter quality and nutrient concentration, microclimate modifications through interception of rain water and solar radiation by the dense closed stands of *Cupressus* resulting in a decrease in surface moisture and temperature of the soil may have limited the activity of soil microbes and animals and, accounted for a gradual accumulation of litter (Kurka et al., 2000). This interpretation gains more relevance when comparing *Eucalyptus* with the natural forest in which litter quality indicators and litter nutrient concentrations were similar. During the study period, throughfall was higher under *Eucalyptus* than the two forest types (Ashagrie unpub.) which could be an indicator of better humidity conditions for litter decomposition.

The turnover times of all the nutrients considered in this study were longer in *Cupressus* than *Eucalyptus* and natural forests which behaved almost similarly (Table 6). Given the low nutrient availability of tropical soils and the intense competition for limited nutrients from the atmosphere (Levia and Frost, 2003) the rate of turnover of nutrients held in the organic layer is crucial for forest nutrition. The slower turnover times of elements in this

pool could result from their being immobilized and unavailable for rapid turnover. In each forest type, the rates of nutrients turnover were more or less similar, except for P in the two plantations which tended to be higher than the rest. In *Eucalyptus* and natural forests, turnover times for nutrient elements were slower than for C, whereas, in *Cupressus*, the turnover rate for C was within the range of the nutrients turnover times. The shorter dry mass and nutrient turnover times in the *Eucalyptus* plantation than *Cupressus* may indicate the important ecological role of understorey vegetation in plantation by recycling nutrients rapidly. These findings also suggest that given the same environmental conditions and site history, management practices could make a difference in the strategy proposed to ensure nutrient accumulation and availability in litter.

Conclusions

The results of this study show that rate of litter production was influenced mainly by species, stand age and vegetation composition. The two plantations were poorer in litter-magnitude, nutrient concentrations and fluxes than the natural forest. Despite lower rate of litter production, *Cupressus* had a higher dry mass accumulation in the organic layer than *Eucalyptus*, but nutrient concentrations were lower in the later. In the *Eucalyptus* plantation, the ground vegetation with their litter pools enriched the organic layer with nutrients even to the level equivalent with that of the natural forest. The low concentrations of nutrients, particularly of N and P, in *Cupressus* organic layer are believed to influence decomposition rate of the organic layer material and result in heavy accumulation. This conclusion was supported by the wide C:N and C:P ratios of the organic layer. In *Eucalyptus* plantation, the low dry mass accumulation is probably associated with changes in litter quality and heterogeneity as well as with microclimate alterations, which altogether determine the decomposer community features. These aspects reveal some characteristics that could be important to *Cupressus* plantation management. In view of the poor self fertilising capacity of *Cupressus*, future monoculture plantations with high tree density should be discouraged. Rather mixed stands formed by several tree species or monocultures with minimum tree density that allow the growth of understorey shrub and herbaceous vegetation should be encouraged so as to maintain the fertility status of the soil for future rotations. Generally we conclude that the studied *Cupressus* stand has a negative influence on litter decomposition and we expect a gradual impoverishment of soil, owing to the slower rates of litter and nutrient turnover times, added to the eventual removal of vegetation. Although it is impossible solely on the basis of the data in this paper to make inferences about the type of mineral cycles operating within these

ecosystems, it is worth noting that the annual levels of mineral–element accession in litter fall can augment the nutrient stocks in the soil. Also, the fact that we must assume a steady state to estimate decomposition underlines the need for accurate information on decomposition to more precisely identify the nutrient function of the ecosystem.

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