Biogeochemistry **61:** 73-94, 2002.

Litter breakdown and mineralization in a central African rain forest dominated by ectomycorrhizal trees

G.B. CHUYONG[1,2,4], D.M. NEWBERY[1,3,*] and N.C. SONGWE[2]
*[1]Department of Biological and Molecular Sciences, University of Stirling, FK9 4LA Stirling, Scotland; [2]Institute of Agronomic Research, Forest Research Station, Kumba, PMB 29, Cameroon; [3]Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013 Berne, Switzerland; [4]Current address: Department of Life Sciences, University of Buea, P.O. Box 63, Buea, Cameroon; *Author for correspondence (e-mail: david.newbery@ips.unibe.ch; phone: 0041-31-631-8815; fax: -31-332-2059)*

Received 8 March 2001; accepted in revised form 24 September 2001

Key words: Caesalps, Central Africa, Decomposition, Ectomycorrhizas, Magnesium, Mineralization, Phosphorus release

Abstract. Based on litter mass and litterfall data, decomposition rates for leaves were found to be fast (k = 3.3) and the turnover times short (3.6 mo) on the low-nutrient sandy soils of Korup. Leaf litter of four ectomycorrhizal tree species (*Berlinia bracteosa, Didelotia africana, Microberlinia bisulcata* and *Tetraberlinia bifoliolata*) and of three non-ectomycorrhizal species (*Cola verticillata, Oubanguia alata* and *Strephonema pseudocola*) from Korup were left to decompose in 2-mm mesh bags on the forest floor in three plots of each of two forest types forest of low (LEM) and high (HEM) abundance of ectomycorrhizal (caesalp) trees. The litter of the ectomycorrhizal species decayed at a significantly slower rate than that of the non-ectomycorrhizal species, although the former were richer in P and N concentrations of the start. Disappearance rates of the litter layer showed a similar trend. Ectomycorrhizal species immobilized less N, but mineralized more P, than non-ectomycorrhizal species. Differences between species groups in K, Mg and Ca mineralization were negligible. Effect of forest type was clear only for Mg: mineralization of Mg was faster in the HEM than LEM plots, a pattern repeated across all species. This difference was attributed to a much more prolific fine root mat in the HEM than LEM forest. The relatively fast release of P from the litter of the ectomycorrhizal species suggests that the mat must allow an efficient uptake to maintain P in the forest ecosystem.

Introduction

Litter reaching the forest floor is subjected to a series of interrelated processes involving the breakdown, chemical transformation and subsequent release of the nutrients (Anderson and Swift 1983; Attiwill 1968; Jensen 1974; Lavelle et al. 1993; Swift et al. 1979). Many factors (both intrinsic and extrinsic) interact, in different ways at different locations and times to influence these processes and thus regulate nutrient availability. Various authors have classified the factors into three categories: (i) abiotic or physical factors, which include climate (Meentemeyer 1978; Singh and Gupta 1977), soil factors (Proctor et al. 1983; Tanner 1981; Vitousek et al. 1994); (ii) resource quality, defined by both the quantity and type of the structural and nutritional constituents of the litter (Fogel and Cromack 1977; Kuiters 1990; Melillo et al. 1982; Meentemeyer 1978; Swift et al. 1979; Upadhyay et al. 1989); and (iii) biotic factors (Anderson et al. 1983; Blair et al. 1992; Bunnell and Flanagan 1977; Seastedt 1984).

Tropical forests differ in their internal patterns of nutrient use. To maintain the high biomass, the species must have evolved strategies for ensuring the return of sufficient nutrients to satisfy their demands for production (Anderson and Swift 1983). In Korup National Park, established groves of large ectomycorrhizal legume trees are found growing on sandy, acidic and characteristically low-phosphorus soils (Gartlan et al. 1986; Newbery et al. 1988) with a phosphorus cycle enhanced by ectomycorrhizal symbiosis (Newbery et al. 1997). Chuyong et al. (2000) have shown higher concentration of phosphorus in leaf litter of ectomycorrhizal species than non-ectomycorrhizal species. Ectomycorrhizal species also exhibit relatively lower retranslocation of nitrogen and phosphorus than non-ectomycorrhizal species.

Janos (1983); Högberg (1986); Alexander (1989a) and Alexander (1989b) have reviewed the widespread occurrence of mycorrhizas in the tropical forests, and stressed the potential role of mycorrhizas in nutrient cycling. The majority of the tropical trees form vesicular-arbuscular mycorrhizas (VAM) but certain others form ectomycorrhizas (ECM). Both are reported to enhance nutrient uptake especially poorly mobile phosphates (Alexander 1989a; Brundrett 1991; Janos 1983) and nitrogen (Alexander 1989a). Very few field studies have been carried out to evaluate the role of mycorrhizas in nutrient cycling (Brundrett 1991; Fogel and Cromack 1980; Singer and Araujo-Aguiar 1986).

This paper focuses on the comparison of litter breakdown and mineralization within and outside of an ectomycorrhizal grove. The first part examines the temporal trends in litter accumulation on the forest floor and estimates the turnover time for the different litter fractions and the litter layer as a whole. As leaf litter constitutes approximately two thirds of total small litter input to the forest floor in Korup (Chuyong et al. 2000), the second part focuses on rates of mass loss and mineralization from decomposing leaf litter of selected ectomycorrhizal and non-ectomycorrhizal species. The selected species were representative of the dominant trees (in terms of basal area distributions) and they contribute significantly to leaf litter input to the forest floor (Chuyong 1994; Chuyong et al. 2000).

Materials and methods

Selection of sample plots

Two sets of half-plots (80 m × 40 m) were selected along transect ‘P’, one of the four transects of 80-m × 80-m plots in Korup National Park described by Gartlan et al. (1986) and Newbery et al. (1988). (Each plot consisted of four quarter-plots labelled A – D.) The first set were within the central half of the transect dominated by a high abundance of ectomycorrhizal caesalps, and the second set were from the eastern half with low abundance of these ectomycorrhizal trees. None of the half-plots on P was without any ectomycorrhizal trees. The three half-plots in each forest type were subsets of the five per forest type used in litter fall studies by Chuyong et al. (2000) and the nine per forest type used for the phosphorus dynamics study of Newbery et al. (1997). Full descriptions of these half-plots in terms of their floristic composition, root distributions and soils are given in Newbery et al. (1997).

The half-plots used were restricted to those on relatively flat ground which were freely draining, and had relatively low densities of herbs and woody undergrowth which would not hamper sampling at the forest floor. This selection was primarily to avoid litterbags being flooded in the wet season. Lateral displacement of litter on forest floor by either overland flow from heavy rains, or by gravitational movement, is higher on steep slopes. This may have led to an underestimation of litter on the forest floor up-slope and an overestimation downslope. The half-plots finally chosen were: LEM - 3AB, 7AD and 9BC; HEM - 15AD, 24BC and 25AD.

Litter layer on forest floor

Litter mass on the forest floor was sampled at monthly intervals from 14 February 1991 to 15 June 1992 from within twenty 0.4 -m × 0.4 -m quadrats randomly placed in each of two half-plots in LEM and HEM forest. (Half-plots 7AD and 24 BC were not used.) All litter within a quadrat was removed, including twigs and bark fractions $\leqslant 2$ cm diameter or along the longest axis (Proctor 1983). Larger woody fractions were sectioned and the portion $\leqslant 2$ cm diameter included in the sample. Samples from each quadrat were stored temporarily in separate sealable polythene bags labelled with the half-plot number. The sampling spots were centrally marked with 12-cm wooden pegs to avoid resampling them on later occasions. The 20 samples from each half-plot provided a direct comparison with litter fall input which used the same unit collecting area.

Samples were air-dried in the laboratory at the Forestry Research Station, Kumba, for a maximum of 1 wk to reduce the moisture content and to facilitate sorting. The air-dried samples were sorted in the following fractions: leaves, small wood and bark, reproductive parts, and mosses and lichens. Roots were discarded. The fractions were oven-dried at 85 °C for 48 h in separate paper envelopes. Each oven-dried sample was emptied into a nylon sieve with a mesh-size of 2 mm to remove dried soil particles and highly fragmented organic matter adhering to the litter fractions, then redried for 3 h and weighed.

Breakdown and mineralization of leaf litter

Rates of weight loss and mineralization of leaf litter of selected ectomycorrhizal and non-ectomycorrhizal species in both LEM and HEM forest types were studied using the litterbag technique (Bocock and Gilbert 1957; Lunt 1933). Freshly fallen leaf litter of the following species was collected for these studies: (i) Ectomycorrhizal species: *Berlinia bracteosa* Benth., *Didelotia africana* Baill., *Microberlinia* *bisulcata* A. Chev., and *Tetraberlinia bifoliolata* (Harms) Hauman. (ii) Non-ectomycorrhizal species: *Cola verticillata* (Thonn) Stapf. ex A. Chev., *Oubanguia alata* Bak.f., and *Strephonema pseudocola* A. Chev. These species dominated leaf litter inputs in either or both forest types (Chuyong et al. 2000).

Three mature individuals of each of the selected species were chosen at random amongst the 10 individuals being observed monthly for phenology (Chuyong 1994). Freshly fallen leaves were trapped on large perforated plastic sheets (4 m × 3 m) raised 1.2 m above the forest floor on wooden posts. Collections were made daily, in the mornings and evenings from 8–16 January 1991 and were air-dried at the camp. Leaves and leaflets mined or partly eaten by herbivores were sorted and discarded.

All species had leathery leaves (sometimes glabrous) except *O. alata. M. bisulcata* was special because it had compound leaves of 10–15 pairs of leaflets, each 2–3 cm × 6–10 mm. The leaflets of *T. bifoliolata* were much larger, 5–10 cm × 4–6 cm. Rachises counted as part of the leaf, these being taken as approximately equivalent in mass to the midribs and petioles of the non-compound leaves.

For each species, 15 g of the air-dried leaves were enclosed in 20-cm × 20-cm, green nylon litterbags of 2-mm mesh. Two bags were randomly selected from each set as initial samples and their leaves oven-dried at 85 °C for 48 h and weighed to obtain the initial mass (X_0). These were then milled and stored in sealed plastic bags for later chemical analysis.

Six replicate quadrats (2.5 m × 2.5 m) were marked out, one centrally within each of the sub-(quarter-) plots 3B, 7D, 9B, 15A, 24C and 25D, avoiding sloping ground. All litter within the quadrats was removed to allow the litterbags direct contact with organic matter at the soil surface. The quadrats were then divided lengthwise with long wooden poles into seven contiguous subquadrats to which the different species were randomly allocated. This design aimed to minimize variations resulting from the possible local effects of different neighbouring tree species on the forest floor. Eight replicate litterbags of each species were laid in each quadrat on 15 July 1991. This resulted in a total of 336 bags being used.

One litterbag was retrieved at random from each subquadrat at monthly intervals until 15 March 1992 (three replicate samples of each species and forest type per sampling occasion). All overlain debris was removed and the litterbags put into separate polythene bags, and taken to the laboratory at the Forest Research Station at Kumba. The residual leaf litter in each litterbag was thoroughly cleaned by hand to remove all exogenous material including roots and soil particles and then separately oven-dried at 85 °C for 48 h. Samples were weighed after redrying for 3 h, and then milled through a 0.5-mm mesh screen (Wiley), and stored in well-sealed polythene bags for chemical analysis.

Rainfall per month of the trial was extracted from records of the Bulu meteorological station, 12 km SW from the site.

Chemical analysis

Two milligrams of the milled leaf litter samples were acid-digested and analysed for total N, P, K, Mg and Ca. Nitrogen and P in the samples were determined colorimetrically using the ammonia-salicylate method for N and phosphomolybdenum method for P. Concentrations of K, Mg and Ca were determined by atomic spectrophotometry. These analyses followed the same procedures as described in Chuyong et al. (2000).

Data analysis

Litter layer on forest floor

Litter data were used to predict decay constants and turnover times for the various fractions using the continuous input model for litter accumulation (Olson 1963). This model assumes a steady-state equilibrium where the mass of litter accumulated on the forest floor (X) at time (t) is the balance between the rate of litter fall as input and rate of decay or loss from the forest floor as output (Birk and Simpson 1980; Esser and Lieth 1989; Jenny et al. 1949; Olson 1963; UNESCO 1978). Since litter fall is strongly seasonal in both the LEM and HEM forests in Korup (Chuyong 1994), the monthly net decay (UNESCO 1978) was calculated for each fraction as follows:

$$\text{decay}_{t_{1-2}} = LFF_{t_1} + LF_{t_{1-2}} - LFF_{t_2}$$

where LFF = mass of litter (or fractions) on forest floor (g m^{-2}), LF = litter fall input (or fractions) (g m^{-2}), t_1 and t_2 are consecutive observations (1 mo apart in the present study), and t_{1-2} is the change between t_1 and t_2.

From each monthly decay estimate, a decomposition coefficient (k_L) was calculated as follows:

$$k_L = \frac{\text{decay}_{t_{1-2}}}{(LFF_{t_1} + LFF_{t_2})/2}$$

The monthly decomposition coefficients (k_L) from May 1991 to April 1992 were summed to obtain the decomposition constant on an annual basis (K_L). The inverse of K_L is the turnover time (in yr) for each of the litter fractions on the forest floor.

Correlation analysis was carried out between the monthly decomposition coefficients (k_L) of the various fractions and mean monthly temperature and rainfall recorded for those months. Pairwise comparisons using the t-test were used to determine significant differences in the monthly decomposition coefficients for each fraction between the two forest types.

Mass loss and mineralization of leaf litter in litterbags

Dry mass and elemental concentrations were expressed as proportions of the initial values. Species-specific models were fitted for each forest type to estimate the constants that describe mass loss of leaf litter over time (Ezcurra and Becerra 1987; Palm and Sanchez 1990; Taylor and Parkinson 1987; Van Vuuren et al. 1993; Wieder and Lang 1982). The following three widely recommended mathematical models were fitted to the data set:
(a) Linear model:

$$X_t/X_0 = -k_0 t$$

(b) Single-exponential model:

$$X_t/X_0 = e^{-k_1 t}$$

(c) Double-exponential model:

$$X_t/X_0 = Ae^{-k_2 t} + (1 - A)e^{-k_3 t}$$

where X_t/X_o is the proportion of the initial material remaining at time t, and k_0, k_1, k_2, and k_3 are decomposition constants; and A is the relatively labile portion of the initial material with (1–A) the relatively recalcitrant portion.

Both the linear and single exponential models (using the *ln*-transformation) were fitted by an ordinary least squares procedure using MINITAB (1989). The double-exponential model was fitted numerically using the Nelder-Mead simplex algorithm in MATLAB (1987). Coefficients of determination were found as: r^2 = (corrected total sum of squares – error sum of squares)/(corrected total sum of squares).

The models were validated by the significance of the regression analysis, and the magnitude of the deviation of the Y-axis intercept from 100%. The single-exponential model was the most appropriate and was thus used to estimate the half-life and turnover time of the leaf litter of the different species.

Given that the design was of a split-plot form with species (litter types) and sampling dates nested within half-plots of the two forest types (LEM and HEM plots), the effects of forest type were tested in the first stratum (between-plots factor) while species, sampling dates and all interactions were tested in the second stratum (within-plots factors) (Winer et al. 1991). As the same plots were repeatedly sampled over time, measurements were not independent of each other, and thus the Greenhouse-Geisser statistic was found to allow adjustment of the degrees of freedom in the second stratum (Payne 1993). When significance (P = 0.05) was found for the species factor, Tukey's studentized multiple comparison test was used to determine differences between species.

Table 1. Means (n = 2) of monthly litter mass (g m^{-2}) of litter fractions on the forest floor in half-plots with low (LEM) and high (HEM) abundances of ectomycorrhizal trees in Korup National Park (May 1991 – April 1992)

Forest type	Litter fractions				
	Leaves	Small wood	Reproductive parts	Mosses and lichens	Total
LEM	164.7	90.6	9.5	0.1	265
HEM	175.3	112.8	45.7	0.6	334

Results

Litter layer on forest floor

Leaf and small wood fractions had similar mean monthly masses of litter in both forests, but the reproductive and moss/lichen fractions were higher in the HEM than LEM forest (Table 1). Both forest types showed similar trends in total litter on the floor with high accumulation at the end of the dry season (February–March) (Chuyong et al. 2000). Minor accumulations were also recorded during periods of strong winds and heavy storms in the wet season (June–July).

Breakdown of litter on forest floor

Breakdown of total litter was significantly higher in the LEM than the HEM forest ($t = 2.10$, df = 10, $P < 0.05$) (Table 2). This was conversely reflected in the turnover times (Table 2). Mass loss was highest in the month of August for leaves, and for the total litter layer as a whole whilst it was highest in April for the small wood and reproductive-parts fractions in both forest types. However, net accumulation, indicated by the negative coefficients, was found in different months for the different fractions. Net accumulation of leaves occurred in January when litter input was dominated by leaves. A similar situation was seen for small wood and twigs with negative coefficients (k_L) in the period May to July and December to February. This also coincided with the months of increased input of small wood and twigs to the forest floor in both forest types. The monthly rates of disappearance (k_L) of total litter (i.e. all fractions) on the forest floor in both LEM and HEM forests are given in Figure 1. Breakdown of total litter on the forest floor was positively correlated with rainfall ($r = 0.55$ and 0.57 for LEM and HEM respectively, df = 14, $P < 0.05$).

Breakdown of leaf litter in litterbags

The effect of forest type on residual mass after 8 mo (expressed as percentage of initial oven-dried mass) of leaf litter of the selected species was not significant (Table 3; LEM 51.7%, HEM 45.3%) but the effect of species and date were both highly significant (Figure 2, Table 3). The significant interaction between species

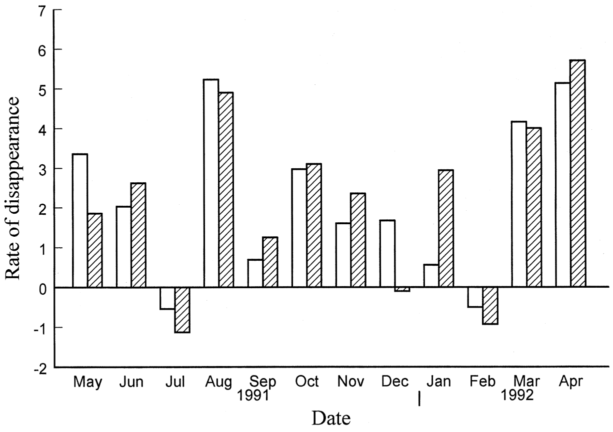


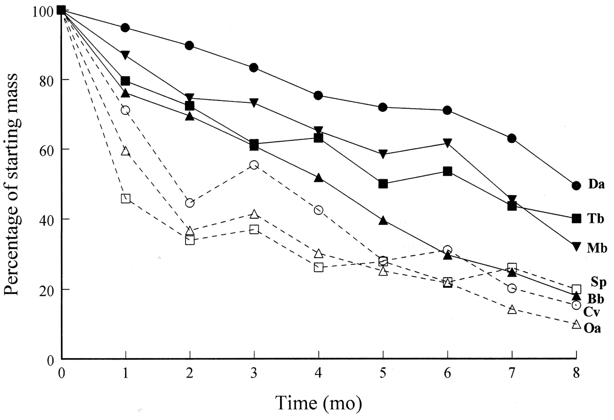
Figure 1. Rates of disappearance of leaf litter on the forest floor, calculated from leaf litter mass and litter fall, in half-plots with low (LEM) and high (HEM) abundances of ectomycorrhizal trees in Korup National Park (May 1991 – April 1992).

Table 2. Decay rates, decomposition constants (K_L) and turnover times for fractions of the litter layer on the forest floor in half-plots with low (LEM) and high (HEM) abundances of ectomycorrhizal trees in Korup National Park (May 1991 – April 1992).

Fraction	Forest type	Decay rate ($g\ m^{-2}\ d^{-1}$)	K_L	Turnover (mo)
Leaves	LEM	1.45	3.49	3.43
	HEM	1.30	3.13	3.83
Small wood	LEM	0.54	2.27	5.28
	HEM	0.40	1.21	9.92
Reproductive parts	LEM	0.16	8.20	1.46
	HEM	0.51	4.27	2.81
Total	LEM	2.33	3.21	3.74
	HEM	2.23	2.43	4.94

and forest type indicated that *B. bracteosa, C. verticillata, O. alata* and *S. pseudocola* had lower residual leaf weights in HEM than LEM forest but *D. africana, T. bifoliolata* and *M. bisulcata* differed very little between forest types. Other interactions were not significant ($P > 0.15$). From the species-specific decomposition constants (k_1) which describe the rates of mass loss, and the corresponding turnover times (Table 4), it was shown that *O. alata, C. verticillata* and *S. pseudocola* (all non-ectomycorrhizal species) were clearly differentiated from the other species by their rapid losses in mass within the first 2 mo in both forest types (Figure 2). This was followed by a relatively slower phase and at the end of the 8 mo only fractions of the petiole and midrib were left in the litterbags. Mass loss in leaf litter of *D. africana, T. bifoliolata, M. bisulcata* and *B. bracteosa* (all the ectomycorrhizal species) was significantly slower ($P < 0.001$) than those of the other

(a) Dry mass



(b) Rainfall

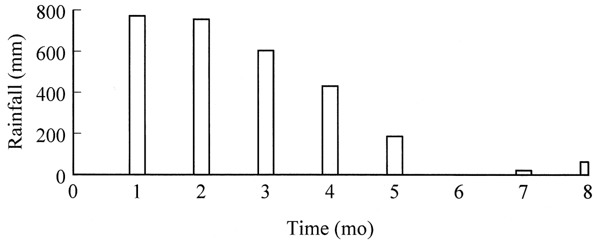


Figure 2. Percentage loss (a) in dry mass of leaf litter of seven species decomposing on the forest floor in Korup National Park over 8 mo (July 1991 to March 1992), averaged for forest types with low (LEM) and high (HEM) abundances of ectomycorrhizal trees, with (b) the rainfall during the time-course of the trial. Closed symbols and solid lines, ectomycorrhizal species; open symbols and dashed lines, non-ectomycorrhizal species. Abbreviations for species: Bb, *Berlinia bracteosa*; Cv, *Cola verticillata*; Da, *Didelotia africana*; Mb, *Microberlinia bisulcata*; Oa, *Oubanguia alata*; Sp, *Strephonema pseudocola*; Tb, *Tetraberlinia bifoliolata.*

three non-ectomycorrhizal species at 2 mo. After 8 mo the ectomycorrhizal species were still with higher relative mass than the non-ectomycorrhizal ones but with some overlap (*B. bracteosa* and *S. pseudocola*). Leaf litter of *B. bracteosa*, however, showed a different pattern from the other three ectomycorrhizal species with a relatively more rapid mass loss from the third month onwards.

After the initial relatively large weight loss, the subsequent rate of loss (months 2–8) did not differ between species. Re-analysis of variance with these seven dates showed an insignificant interaction between species and date (F = 0.85, unadj. df = 36, 189; P = 0.710). Adding species × date to a regression model of just species led to very little change (F = 0.45).

Table 3. Variance-ratio (F-) values for the effects of forest type (LEM vs HEM), species (n = 7) and date (months 1 – 8) for the percentage dry mass remaining and the concentrations of five nutrients relative to the start, of decomposing leaf litter in Korup National Park. The significance of F is based on an adjusted df for stratum b of the ANOVA (i.e. all terms except forest). F-values with superscript are significant ($P \leqslant 0.05$).

Source	df	Dry mass	N	P	K	Mg	Ca
Forest[1]	1	0.3	2.8	0.1	0.1	5.5	4.3
Species[2]	6	65.1^{***}	51.3^{***}	121.0^{***}	50.4^{***}	48.6^{***}	11.3^{***}
Date	7	43.3^{***}	48.1^{***}	45.8^{***}	52.2^{***}	48.8^{***}	16.0^{***}
Species × forest	6	3.8^{*}	2.6	1.1	0.3	3.6	2.7
Species × date	42	1.0	2.3^{**}	1.8	2.0	0.9	1.3
Forest × date	7	1.5	6.3^{**}	3.2	8.9^{**}	5.3^{**}	3.6^{**}
Species × forest × date	42	0.4	1.2	0.7	0.6	0.6	0.4

1 Error df (stratum a) = 4

2 Error df (stratum b) = 216 (adjusted 99 – 142)

*, $P \leqslant 0.05$; **, $P \leqslant 0.01$; ***, $P \leqslant 0.001$

Table 4. Decomposition constants (k_1) derived from the single exponential model and turn-over times for leaf litter of seven species (in ectomycorrhizal and non-ectomycorrhizal groups) after 8 mo of decay in litterbags on the forest floor in Korup National Park. Species differed significantly in k_1 ($P \leqslant 0.05$) if they have no small letter in common. The difference in k_1 between groups is shown by the t-test.

Species	k_1	Turnover (mo)
Ectomycorrhizal		
Berlinia bracteosa	0.209 ab	4.78
Didelotia africana	0.081 c	12.34
Microberlinia bisulcata	0.119 bc	8.40
Tetraberlinia bifoliolata	0.106 bc	9.43
Mean	0.129	8.74
Non-ectomycorrhizal		
Cola verticillata	0.210 ab	4.76
Oubanguia alata	0.284 a	3.52
Strephonema pseudocola	0.220 a	4.55
Mean	0.238	4.28
t(df)	−3.01 (4)	
P	0.039	

Temporal changes in nutrient concentrations in decomposing leaf litter

Changes in concentration of elements, expressed as percentage of initial concentration in leaf litter (Appendix 1) are shown in Figures 3a–e with means after 8 mo shown in Table 5. The effect of forest type (LEM vs HEM) was highly insignificant for all the elements except for Mg which was marginally significant (P = 0.08). All five elements showed highly significant differences ($P < 0.001$) between species and dates, but the date × species interaction was insignificant for all elements apart from N (Table 3). Species and forest interactions were not significant except for Mg ($P < 0.02$; Figure 3d and Table 3). The percentage concentration of Mg remaining in the decomposing leaf litter was less in the HEM than LEM forest type overall. Forest × date interaction was significant for K, Mg and Ca, but not for N and P (Table 3).

Potassium showed the greatest change with *c*. 16–37% loss within the first month (Figure 3c). Magnesium and Ca showed a similar pattern of rapid loss but within 6 mo only (Figure 3d, e). Nitrogen and P were both immobilised though there was an initial loss of P within the first 2 mo (Figure 3a, b).

The ectomycorrhizal species as a group had generally lower rates of immobilization of P (Figure 3b, $P < 0.001$) and N (Figure 3a; $P < 0.01$) than non-ectomycorrhizal species; and slightly lower rates of mineralization for K (Figure 3c). Whilst *D. africana, B. bracteosa* and *T. bifoliolata* were clearly the lowest in relative concentrations of P and N (Figure 3a, b), *M. bisulcata* overlapped with *O. alata* (for N) and *C. verticillata* (for P) in the non-ectomycorrhizal group. For Mg and Ca there were no discernable differences (Figure 3d, e). Overall, there was 16.9% more immobilisation of N and 28.5% of P in the non-ectomycorrhizal species compared to the ectomycorrhizal species where there was net release of P (Figure 3a, b).

Only Mg showed significant differences with the rate of mineralization between forest types (Figure 4a), HEM forest decreasing faster than LEM forest in the first 6 mo. This forest-type effect was strongest for litter of *T. bifoliolata, C. verticillata* and *S. pseudocola* (Figure 4b).

Discussion

Forest floor litter layer and turnover rates

Litter input estimates for LEM and HEM forest types were shown in previous studies to be not significantly different (Chuyong et al. 2000; Newbery et al. 1997). Sampling the litter in this study showed significantly higher amounts of litter on the forest floor in the HEM compared to the LEM forest. This difference can be interpreted as a result of a comparatively lower turnover rate of forest floor litter in the HEM forest. A closer look at the different fractions of the litter layer showed greater amounts of the small wood (twigs) and woody pods in the HEM forest. This small wood input in the LEM forest consisted of mostly small twigs and branches, which were long dead and were often already in advanced stages of decomposition before they were dropped. Since they were already colonized by fungi, the process of decomposition would be expected to have advanced faster on the forest floor. In the HEM forest, a greater part of this small wood input was from the ‘physiological pruning’ of the large ectomycorrhizal legumes, this requiring a longer period to be colonized and thus decomposed by micro-organisms. A similar

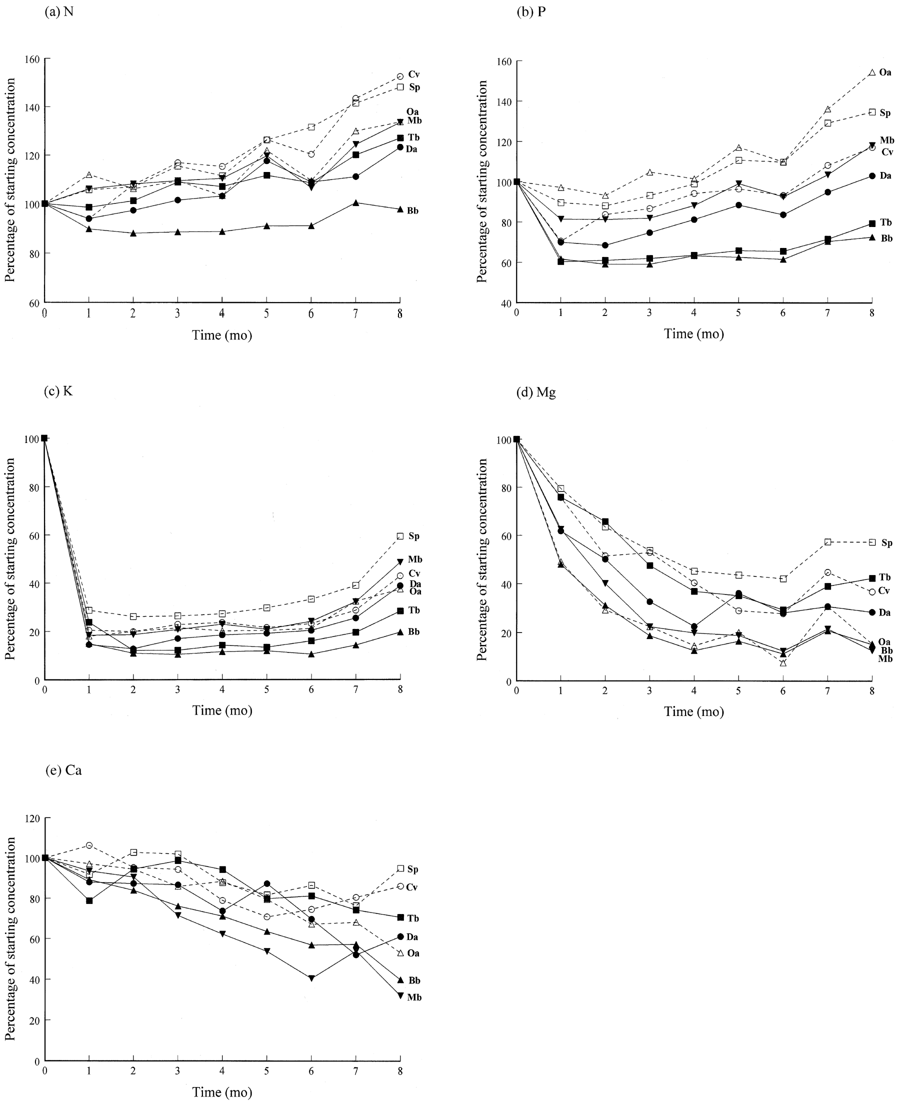
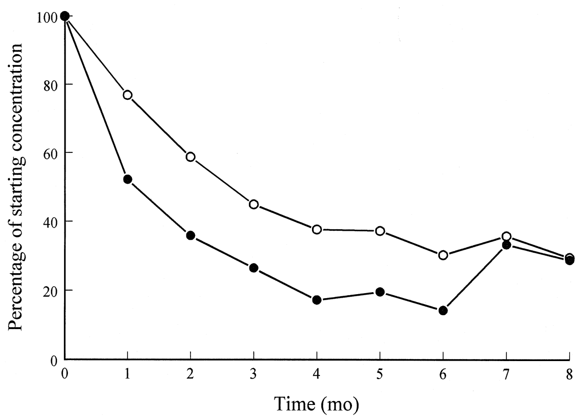
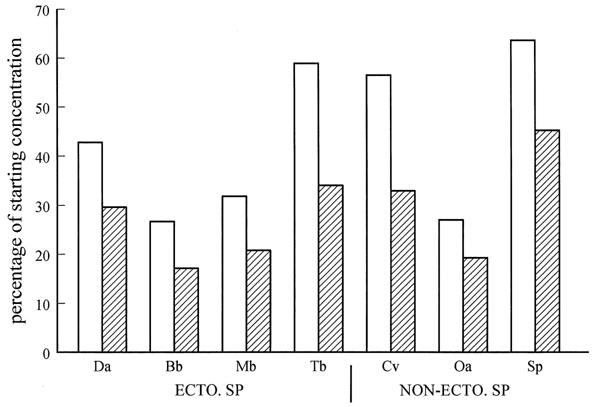


Figure 3. Percentage change in concentrations of (a) nitrogen, (b) phosphorus, (c) potassium, (d) magnesium, and (e) calcium, with respect to the start, in leaf litter of seven species decomposing on the forest floor in Korup National Park over 8 mo (July 1991 to March 1992), averaged for forest types with low (LEM) and high (HEM) abundances of ectomycorrhizal trees. Symbols, lines and abbreviations for species are as given in Figure 2.

explanation could be put forward for differences in the reproductive-parts fraction. These large caesalp legumes which are predominant in the HEM forest, produce strong highly lignified pods which decompose very slowly on the forest floor and remain for many months.



(a) Mg: forest types



(b) Mg: species

Figure 4. Percentage change in concentrations of magnesium in the leaf litter of seven species decomposing on the forest floor in Korup National Park over 8 mo (July 1991 to February 1992) for (a) forest of low (LEM, open circles) and high (HEM, closed circles) abundances of ectomycorrhizal trees, averaging over seven species; and (b) the seven species in each forest type (LEM, open bar; HEM, hatched bar) averaged over time.

The high spatial and temporal variation in the litter layer in both forests is largely a function of variable litter input with the different fractions decomposing at different rates (Spain 1984; Vogt et al. 1986). The amounts and proportions of these different fractions are dependent on the phenological patterns of the different tree species (Chuyong et al. 2000), interacting with the prevailing conditions (Kunkel-Westphal and Kunkel 1979; Schaik and Mirmanto 1985). The highest accumulation of litter on the forest floor occurred in the dry season (December to February) in both forests. During this period the litter input exceeded the rate of breakdown and resulted in an accumulation of the litter layer on the forest floor. The rate of litter breakdown was significantly reduced during this period as a result of desiccation of the litter layer and limitation of decomposer activity. Light levels below the canopy increased in the dry season, particularly in the HEM forest where *M. bisulcata* sheds all of its leaves. Luizao and Schubart (1987) also reported lower mass loss in leaf samples from litterbags in the dry season (half-life of 218 days for leaf samples in the dry season in central Amazon compared to 32 days in the wet season). Different reasons have been put forward to explain the rapid breakdown of the accumulated litter with first months of the wet season. Swift et al. (1979); Gosz (1984) related this to the added supply of nutrients via canopy leaching, these having a priming effect on the decomposition of older organic material. Additional nutrients would also have been available from nutrient-rich flowers and insect frass in the litter during the early wet season in both forest types.

Turnover of leaf litter was similar in both forest types (LEM = 3.5 mo, HEM = 3.8 mo). Litterbag studies, however, showed that the leaf litter of the ectomycorrhizal species decomposed more slowly than that of the non-ectomycorrhizal species (Table 4). Breakdown of leaf litter has been reported to be generally inversely related to resource quality expressed as concentrations of phenolics, lignin and micro-nutrients (Aber and Melillo 1982; Kuiters 1990; Meentemeyer and Berg 1986; Tanner 1981; Upadhyay et al. 1989). However, in Korup related work has shown that total polyphenol concentration (expressed as quebracho tannin equivalents) was highly variable among leaf litter of the ectomycorrhizal (*B. bracteosa* 18.4, *M. bisulcata* 11.6 and *T. bifoliolata* 123.3 mg g^{-1}) and non-ectomycorrhizal (*O. alata* 14.7, and *S. pseudocola* 36.6 mg g^{-1}) species (L. Njampa, I.J. Alexander & G.B. Chuyong; unpubl. data). These values did not correspond at all with decomposition rates in the present study (Table 5) even though subsamples of the same 1991–92 litter collected and milled by Chuyong et al. (2000) was used, litter collected at the same time as the decomposition experiment here. *T. bifoliolata* and *M. bisulcata*, for example, had similar k_1-values but hugely different concentrations of polyphenols.

Estimates from the double-exponential model indicated some variability among species in the recalcitrant fraction (Chuyong 1994). This model did not, however, fit the data better than the single exponential one suggesting that the recalcitrant term was probably not so important. Lignin and polyphenols can be equated to a major part of this recalcitrant leaf fraction. Evidence from the literature is mixed. For four forest types in Sarawak, Anderson et al. (1983) found no relationship between polyphenol and lignin concentrations and decomposition rates; and Smith et al. (1998) found no relationships between mass loss and polyphenol, lignin or N concentrations in decomposing litter in Amazonian forest stands. However, comparing three woody legume species in an alley cropping system in Peru, Palm and Sanchez (1990) found that leaves of two of the species which had high polyphenol concentrations decomposed much slower than the third which had about one third the concentration. All three species, however, had high N concentrations (3.2–3.5%) and no N was immobilized over ca. 30 wks. These reports suggest that polyphenols

Table 5. Mean percentage concentrations of nutrients in decomposing a litter, relative to the start, of seven species (in ectomycorrhizal and nonectomycorrhizal groups) after 8 mo of decomposition in litterbags on the forest floor in Korup National Park. Species differ significantly in concentration ($P \leq 0.05$) if they have no small letters in common. Differences between groups are shown by the t-tests.

Species	N	P	K	Mg	Ca
Ectomycorrhizal					
Berlinia bracteosa	92.2 a	63.8 a	13.0 a	22.0 a	67.7 ab
Didelotia africana	106.9 ab	83.2 ab	20.8 ab	36.2 ab	74.6 ab
Microberlinia bisulcata	114.8 bc	93.3 bc	25.7 bc	26.3 ab	62.2 a
Tetraberlinia bifoliolata	110.4 bc	66.2 a	17.4 ab	46.5 c	84.0 bc
Mean	106.1	76.6	19.2	32.7	72.1
Non-ectomycorrhizal					
Cola verticillata	122.2 bc	94.2 bc	25.5 bc	44.7 ab	85.4 bc
Oubanguia alata	114.3 bc	115.0 cd	24.1 bc	23.2 a	76.8 bc
Strephonema pseudocola	123.0 c	106.7 d	33.5 c	54.4 c	89.6 c
Mean	119.8	105.3	27.7	40.8	83.9
t(df)	−2.44 (4)	−3.09 (4)	−2.13 (4)	−0.75 (3)	−1.96 (4)
P	0.071	0.037	0.10	0.51	0.12

can be limiting when N is abundant, but in Korup N was immobilized and it was probably P concentration that slowed the rates, with polyphenols taking a secondary role.

Ectomycorrhizal species had higher concentrations of N, P, K, Mg and Ca than non-ectomycorrhizal species, significantly so for N and P. As a consequence ectomycorrhizal species immobilized less N and mineralized more P than non-ectomycorrhizal species. Nevertheless, contrary to expectation the ectomycorrhizal group with higher initial concentrations of N and P decomposed the slowest. Khiewtam and Ramakrishnan (1993) also observed similar trends in *Engelhardtia spicata* that had a higher initial concentration of N but a lower decomposition rate than other species.

Gadgil and Gadgil (1971) attributed slower rates of decomposition by saprotrophs to the (competitive) effects of mycorrhizal fungi on the forest floor and in the surface soil layer. This is unlikely to be the cause of the slower breakdown of ectomycorrhizal species' leaf litter in Korup since the non-ectomycorrhizal species decomposed at even faster rates in the HEM than LEM forest.

The estimates of decomposition parameters for both LEM and HEM forest types are comparable to those reported for the other tropical forests (Anderson et al. 1983; Proctor et al. 1983), were in the lower (litter mass) and upper (turnover coefficients) parts of the ranges for other tropical forests. Results of the present study also confirm previous reports by Anderson et al. (1983) that decomposition rates in West African forests appear to be generally higher than those of the neotropics and those in SE Asia. The problems of standardizing size ranges of litter fractions (Proctor 1987) and intervals between sampling of the forest litter layer need to be considered when making comparisons with other studies (UNESCO 1978). In the present study, organic material < 2 mm was taken to be part of the soil organic matter. Because of the high seasonality in litter input monthly k_L values were found and these then summed to obtain the annual turnover coefficients (K_L, after Olson (1963)). These coefficients of turnover were only 6 and 16% higher, for the LEM and HEM forests respectively, than those based on annual inputs and mean litter mass.

Comparisons between ectomycorrhizal and non-ectomycorrhizal species is possibly confounded by phylogeny (Harvey and Pagel 1991), though this seems intractable because ectomycorrhizal status in Korup is so closely associated with one particular tribe within the Caesalpiniaceae, the Amherstieae (Alexander 1989b). The closest within-subfamily comparisons would be with arbuscular mycorrhizal species such as *Hymenostegia afzelii* (Oliv.) Harms in the tribe Detarieae and *Erythrophleum ivorense* A. Chev. in the tribe Caesalpineae. These and several other caesalps are relatively sparsely distributed on transect P in Korup (Newbery et al. 1988), although *E. ivorense* is more abundant on the richer soils of transect R (Gartlan et al. 1986).

Mineralization in the leaf litter in both forest types

The nutrient dynamics of decomposing leaf litter generally follows three sequential phases: an initial release mainly due to leaching, net accumulation by immobilisation, and net release by mineralization (Gosz et al. 1973; Staaf and Berg 1982; Swift et al. 1979; Upadhyay and Singh 1989; Yamashita and Takeda 1998). The five nutrient elements examined in the present study showed at least one of these phases for the leaf litter in both forest types. Overall, averaging the species studied, there was net accumulation of N, a near balance of immobilization and mineralization of P, but a net release of K, Mg and Ca in both forests. In the P-poor soils in Korup (Newbery et al. 1988, 1997) it appears that the balance between immobilization and mineralization of P is small and it is sensitive to species composition of the litter.

Accumulation of N in decomposing litter has been observed in most decomposition studies in temperate forests (Berg and Staaf 1981; Blair et al. 1992; Gosz et al. 1973; Van Vuuren et al. 1993) and in a few tropical forests (Cuevas and Medina 1988; Songwe 1984). In some tropical forests N was released at rates close to that of biomass loss (Bernhard-Reversat 1972; Swift et al. 1981) and in some cases conserved with very little or no addition (Anderson et al. 1983). Net accumulation of N in the present study is therefore not a contradiction. Several reasons have been advanced to account for this absolute increase in N mass in decomposing litter: N fixation (Wood 1974); absorption of atmospheric ammonia; contamination from insect frass, green litter and throughfall; microbial translocation and or immobilization (Gosz et al. 1973). Phosphorus was generally released or conserved with little or no addition from the decomposing litter as in most of the tropical studies reported (Anderson et al. 1983; Swift et al. 1981; Upadhyay and Singh 1989).

In the present study, net release of N occurred only in *B. bracteosa*, which had the highest initial concentration. Highest rates of immobilization were found in the litter samples of *C. verticillata* and *S. pseudocola*, which had the lowest initial concentrations of N (Appendix 1). A similar pattern was also seen for mineralization of P. This negative relationship indicated that the initial concentrations of different litter types were probably a more important regulating factor in N and P mineralization than local site characteristics. Most noticeably, net release of P occurred only in litter samples of the four ectomycorrhizal species, these having the relatively the highest initial concentrations. This indicates that the turnover of N and P should be relatively rapid in the HEM forest where these species contribute largely to the leaf litter input to the forest floor. Nutrient studies by Songwe et al. (1995) in Bakandu Forest Reserve, also in SW Cameroon (*c*. 80 km SE of Korup), a site with relatively nutrient-richer soils, showed that N was released from the decomposing leaf samples of *Celtis zenkeri* and *Cola lepidota* both having initial N concentrations of 1.73 and 1.40% respectively compared to 0.95% N for *Desbordesia glaucesens* which showed the highest initial N accumulation. These species were comparatively rich in P but showed net P accumulation (Songwe et al. 1995).

Mineralization of K was very rapid in all the species in both forests with more than 60% of its initial concentration released within 1 mo, on the forest floor. Potassium is a highly mobile and readily leached element (Parker 1983; Swift et al. 1981). Korup has one of the highest rainfall records for lowland tropical forests (c. 5300 mm yr^{-1}), and high precipitation enhances rapid release of K through leaching. The peak of rainfall in July-September is, however, after the main period of decomposition (April-June), at least for the strongly seasonal litter shedders like *M. bisulcata*.

Mineralization of Mg and Ca in the decomposing leaf litter proceeded independently of their initial concentrations. Cuevas and Medina (1988) in the tierra firme forest in the Amazon, observed a faster release of Mg, Ca and P from the litter when it was in contact with the fine root mat, and concluded that there must be a nutrient release mechanism mediated by these roots and/or their associated microorganisms. The numerous fine roots and hyphae that characterize the top organic layer of the soil in Korup (Newbery et al. 1988), invaded the litter bags, especially those set in the HEM forest.

Magnesium was the one element showing an appreciable difference in mineralization rates between forest types with HEM soils having a much faster rate. This strongly suggests that there is a sink for Mg, in the HEM organic layer, most likely caused by a greater requirement for Mg by ectomycorrhizal trees. Potassium and Ca showed a much weaker trend. Active fine root systems are known to be particularly Mg-demanding (Raspe 1997). The enhanced Mg mineralization in HEM forest was not species-specific, however. A further remarkable feature was the course of change in Mg concentration for HEM forest: after 6 mo the Mg immobilized back up to the LEM concentration level. This was at the start of the dry season (Figure 1) when the production of new fine roots and mycorrhizas probably slows down. A limitation of Mg might account for the slower decomposition rate in HEM than LEM. Since the litter in the HEM forest is made up very largely of ectomycorrhizal species their root activity may indirectly regulate the rate of mineralization of phosphorus. Fine roots need to be produced in advance of their function in taking up released P. But P release was not delayed in HEM forest although the ectomycorrhizal species mineralized P surprisingly fast in the first month (Figure 3b), by contrast to N (Figure 3a). This would imply a mechanism of direct access of ectomycorrhizal hyphae to organically bound P (Attiwill and Adams 1993; Herrera et al. 1978; Newbery et al. 1997), early in the decomposition process, to account for P release independent of saprotrophic activity. Newbery et al. (1997) have also suggested by their PACER hypothesis that climate effects on mast fruiting probably play an important role in moderating within-grove P cycles.

Finally, it is interesting that two of the three species for which mineralization of Mg was much faster in the HEM compared to LEM forest (*T. bifoliolata* and *S. pseudocola*) were the highest in polyphenol concentrations. (For the third species, *C. verticillata* no data on polyphenols are available.) This tentatively suggests that the differential effect of the HEM root mat on Mg release is possibly related to the amelioration of polyphenol inhibition. This is a promising area for investigation.

Conclusion

The relatively fast and early release of P from leaf litter of ectomycorrhizal species in Korup fits with the idea put forward in Chuyong et al. (2000) that the leaf litter of these species has a high concentration of P to enable a rapid recycling. But in an environment with high leaching, this return to the tree could not be effective without the fine root and hyphal mat immediately below the decomposing layer of fallen leaves. That Mg is released at an additional rate in forest with high abundance of ectomycorrhizal trees supports the notion that this thin top soil layer and its integral mat is very essential to the functioning of this ecosystem. It seems that Mg has a much larger role in the ecosystem in Korup than was hitherto suspected.

Acknowledgements

This research was funded by European Commission DGXII-G4 contract STD2*0246 UK (SMA) 1990–1994 to Stirling University (DMN) in cooperation with Institute de la Recherche Agronomique du Cameroun (IRA), and continued after August 1996 at University of Bern. The project was then based at Forest Research Station, Kumba, directed by NCS, now part of the Ekona Centre near Buea. We thank Dr J. Ayuk-Takem, Director of IRA (now IRAD) for facilitating the project, and the Ministries of Parks and Tourism (MINEF), and of Education, Science and Research (MESIRES) for permission to work in Korup. We thank E. Abeto for field assistance, M. White for undertaking the nutrient analyses, and two anonymous referees for their comments.

Appendix

Table A1. Mean initial concentrations (mg g^{-1} dry mass; n = 2 bulked samples) of freshly collected leaf litter of seven species (ectomycorrhizal and non-ectomycorrhizal) for decomposition studies in Korup National Park. Differences between groups are shown by the t-tests.

Species	N	P	K	Mg	Ca
Ectomycorrhizal					
Berlinia bracteosa	17.9	0.97	11.88	4.18	14.8
Didelotia africana	16.8	0.68	5.07	2.59	13.1
Microberlinia bisulcata	13.9	0.55	4.95	3.46	14.2
Tetraberlinia bifoliolata	15.3	0.95	6.43	1.81	5.5
Mean	16.0	0.788	7.08	3.01	11.9
Nonectomycorrhizal					
Cola verticillata	10.7	0.55	5.59	2.87	13.4
Oubanguia alata	12.9	0.49	6.37	2.66	8.2
Strephonema pseudocola	10.1	0.39	4.16	2.21	19.8
Mean	11.23	0.477	5.37	2.58	13.8
t(df)	−3.92(4)	−2.75(4)	−0.97(3)	−0.78(3)	−0.47(3)
P	0.017	0.052	0.40	0.49	0.67

References

Aber J.D. and Melillo J.M. 1982. Nitrogen immobilization in decaying hardwood leaf litter as a function of initial nitrogen and lignin content. Can. J. Bot. 60: 2263–2269.

Alexander I.J. 1983. The role of ectomycorrhizas in the nitrogen cycle. In: Lee J.A., McNeill S. and Rorison I.H. (eds), Nitrogen as an Ecological Factor. Blackwell Scientific Publications, Oxford, pp. 69–93.

Alexander I.J. 1989a. Mycorrhizas in tropical forests. In: Proctor J. (ed.), Mineral Nutrients in Tropical Forests and Savanna Ecosystems. Blackwell Scientific Publications, Oxford, pp. 169–188.

Alexander I.J. 1989b. Systematics and ecology of ectomycorrhizal legumes. Monograph of Systematic Botany, Missouri Bot. Gdn 29: 607–624.

Anderson J.M., Proctor J. and Vallack H.W. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. III. Decomposition processes and nutrient losses from leaf litter. J. Ecol. 71: 503–528.

Anderson J.M. and Swift M.J. 1983. Decomposition in tropical forests. In: Sutton S.L., Whitmore T.C. and Chadwick A.C. (eds), Tropical Rain Forest: Ecology and Management. Blackwell Scientific Publications, Oxford, pp. 287–309.

Attiwill P.M. 1968. The loss of elements from decomposing litter. Ecology 49: 142–145.

Attiwill P.M. and Adams M.A. 1993. Nutrient cycling in forests. New Phytol. 124: 561–582.

Berg B. and Staaf H. 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. In: Terrestrial Nitrogen Cycles: Ecosystem Strategies and Management Impacts. Ecol. Bull. (Stockholm) 33., pp. 163–178.

Bernhard-Reversat F. 1972. Decomposition de la litière de feuilles en forêt ombrophile de basse Côte d'lvoire. Oecol. Plant. 7: 279–300.

Bernhard-Reversat F. and Schwartz D. 1997. Change in lignin content during litter decomposition in tropical forest soils (Congo): comparison of exotic plantations and native stands. Compt. Rend. Acad. Sci., Paris: Sci. Terre Planètes 325: 427–432.

Birk E.M. and Simpson R.W. 1980. Steady state and the continuous input model of litter accumulation and decomposition in Australian *Eucalyptus* forests. Ecology 61: 481–485.

Blair J.M., Crossley D.A. and Callaham L.C. 1992. Effects of litter quality and microarthropods on N dynamics and retention of exogenous N in decomposing litter. Biol. Fert. Soils 12: 241–252.

Brundrett M. 1991. Mycorrhizas in natural ecosystems. Adv. Ecol. Res. 21: 171–313.

Bocock K.L. and Gilbert O.J.W. 1957. The disappearance of leaf litter under different woodland conditions. Plant Soil 9: 179–185.

Bunnell F. and Flanagan P.W. 1977. Microbial respiration and substrate weight loss II. A model of the influences of chemical composition. Soil Biol. & Biochem. 4: 41–47.

Chuyong G.B. 1994. Nutrient cycling in ectomycorrhizal legume-dominated forest in Korup National Park, Cameroon. PhD Dissertation, Stirling University, UK.

Chuyong G.B., Newbery D.M. and Songwe N.C. 2000. Litter nutrient concentrations and retranslocation in ectomycorrhizal and non-ectomycorrhizal rain forest trees in Central Africa. New Phytol. 148: 493–510.

Cuevas E. and Medina E. 1988. Nutrient dynamics within Amazonian forests. II. Fine root growth, nutrient availability and leaf litter decomposition. Oecologia 76: 222–235.

Esser G. and Lieth H. 1989. Decomposition in tropical rain forests compared with other parts of the world. In: Leith H. and Werger M.J.A. (eds), Ecosystems of the World 14B. Tropical Rain Forest: Biogeography and Ecological Studies. Elsevier, Amsterdam, pp. 571–580.

Ezcurra E. and Becerra J. 1987. Experimental decomposition of litter from the Tamaulipan Cloud Forest: a comparison of four simple methods. Biotropica 19: 290–296.

Fogel R. and Cromack K.L. 1977. Mycorrhizae and nutrient cycling in natural forest ecosystems. New Phytol. 86: 199–212.

Fogel R. and Cromack K.L. 1980. Effect of habitat and substrate quality on Douglas fir litter decomposition in Western Oregon. Can. J. Bot. 55: 1632–1640.

Gadgil R.L. and Gadgil P.D. 1971. Mycorrhiza and litter decomposition. Nature 233: 133.

Gartlan J.S., Newbery D.M., Thomas D.W. and Waterman P.G. 1986. The influence of topography and soil phosphorus on the vegetation of Korup Forest Reserve, Cameroon. Vegetatio 65: 131–148.

Gosz J.R. 1984. Biological factors influencing nutrient supply in forests soils. In: Bowen G.D. and Nambiar E.K.S. (eds), Nutrition of Plantation Forests. Academic Press, London, pp. 119–146.

Gosz J.R., Likens G.E. and Bormann F.H. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest New Hampshire. Ecol. Monogr. 47: 173–191.

Harvey P.H. and Pagel M.D. 1991. The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford, UK.

Herrera R., Medina T., Stark N. and Jordan C.F. 1978. Direct phosphorus transfer from leaf litter to roots. Naturwissenchaften 65: 208.

Hilton G. 1987. Nutrient cycling in tropical rainforests: implication for management and sustained yield. Forest Ecol. Manag. 22: 297–300.

Högberg P. 1986. Soil nutrient availability, root symbioses and tree species composition in tropical Africa: a review. J. Trop. Ecol. 2: 359–372.

Janos D.P. 1983. Tropical mycorrhizas, nutrient cycles, and plant growth. In: Sutton S.L., Whitmore T.C. and Chadwick A.C. (eds), Tropical Rain Forest: Ecology and Management. Blackwell Scientific Publications, Oxford, pp. 327–345.

Jenny H., Gesse S. and Bingham F.T. 1949. Comparative study of decomposition of organic matter in temperate and tropical regions. Soil Sci. 68: 419–432.

Jensen V. 1974. Decomposition of angiosperm tree leaf litter. In: Dickinson C.H. and Puch G.J.F. (eds), Biology of Plant Litter Decomposition. Academic Press, London, pp. 69–104.

Jordan C.F. and Escalante G. 1980. Root productivity in an Amazonian rainforest. Ecology 61: 14–18.

Khiewtam R.S. and Ramakrishnan P.S. 1993. Litter and fine root dynamics of a relict sacred grove forest at Cherapungi in northeastern India. Forest Ecol. Manage. 60: 327–344.

Kuiters A.T. 1990. Role of phenolic substances from decomposing forest litter in plant-soil interactions. Acta Bot. Neerl. 39: 329–348.

Kunkel-Westphal I. and Kunkel P. 1979. Litterfall in a Guatemalian primary forest, with details of leaf-shedding by some common tree species. J. Ecol. 67: 665–686.

Lavelle P., Blanchart E., Martin E., Martin S., Spain A., Toutain F. et al. 1993. A hierarchical model for decomposition in terrestrial ecosystems: application to soil of the humid tropics. Biotropica 25: 130–150.

Lunt H.A. 1933. Effects of weathering upon composition of hardwood leaves. J. For. 31: 43–45.

Luizao F.J. and Schubart H.O.R. 1987. Litter production and decomposition in a tierra firme forest of Central Amazonia. Experientia 43: 259–265.

MATLAB 1987. Mathworks Reference Manual. Mathworks Inc.

Meentemeyer V. 1978. Macroclimate and lignin control of litter decomposition rates. Ecology 59: 465–472.

Meentemeyer V. and Berg B. 1986. Regional variation in rate of mass loss of *Pinus sylvestris* needle litter in Swedish pine forests as influenced by climate and litter quality. Scand. J. Forest Res. 1: 167–180.

Melillo J.M., Aber J.D. and Muratore J.F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63: 621–626.

MINITAB 1989. Reference Manual. Release 7. MINITAB Inc. Penn State University, PA, USA.

Newbery D.M., Alexander I.J., Thomas D.W. and Gartlan J.S. 1988. Ectomycorrhizal rainforest legumes and soil phosphorus in Korup National Park, Cameroon. New Phytol. 109: 433–450.

Newbery D.M., Alexander I.J. and Rother J.A. 1997. Phosphorus dynamics in a lowland African rain forest: the influence of ectomycorrhizal trees. Ecol. Monogr. 67: 367–407.

Olson J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44: 322–331.

Palm C.A. and Sanchez P.A. 1990. Decomposition and nutrient release patterns of the leaves of three tropical legumes. Biotropica 22: 330–338.

Parker G.G. 1983. Throughfall and stemflow in the forest nutrient cycle. Adv. Ecol. Res. 13: 57–133.

Payne R.W.and the Genstat Committee 1993. Genstat 5.3 Reference Manual. Clarendon Press, Oxford.

Proctor J. 1983. Tropical forest litterfall 1. Problems of data comparison. In: Sutton S.L., Whitmore T.C. and Chadwick A.C. (eds), Tropical Rainforest: Ecology and Management. Blackwell Scientific Publications, Oxford, pp. 267–373.

Proctor J., Anderson J.M., Fodgen S.C.L. and Vallack H.W. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. II. Litterfall, litter standing crop and preliminary observations on herbivory. J. Ecol. 71: 261–283.

Proctor J. 1987. Nutrient cycling in primary and old secondary rainforests. Appl. Geogr. 7: 135–152.

Raspe S. 1997. Fine-root development. In: Hüttl R.F. and Schaaf W. (eds), Magnesium Deficiency in Forest Ecosystems. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 309–332.

Schaik C.P.V. and Mirmanto E. 1985. Spatial variation in the structure and litterfall of a Sumatran rainforest. Biotropica 17: 196–205.

Seastedt T.R. 1984. The role of microarthropods in decomposition and mineralization process. Ann. Rev. Entomol. 29: 25–46.

Singh J.S. and Gupta S.R. 1977. Plant decomposition and soil respiration in terrestrial ecosystems. Bot. Rev. 43: 449–528.

Singer R. and Araujo-Aguiar I. 1986. Litter decomposition and ectomycorrhizal *Basidiomycetes* in an igapo forest. Plant Syst. & Evol. 153: 107–117.

Smith C.K., Gholz H.L. and de Assis Oliveira F. 1998. Fine litter chemistry, early-stage decay, and nitrogen dynamics under plantations and primary forest in lowland Amazonia. Soil Biol. & Biochem. 30: 2159–2169.

Songwe N.C. 1984. Litter production and decomposition in a tropical rainforest, Southern Bakundu Forest Reserve, Cameroon. PhD Dissertation, University of Ibadan, Nigeria.

Songwe N.C., Fasehun F.E. and Okali D.U.U. 1995. Litter decomposition and nutrient release in a tropical rainforest, Southern Bakundu Forest Reserve, Cameroon. J. Trop. Ecol. 11: 333–350.

Spain A.V. 1984. Litterfall and standing crop of litter in three tropical Australian rainforests. J. Ecol. 72: 947–961.

Staaf H. and Berg B. 1982. Accumulation and release of plant nutrients in decomposing Scots pine needle litter. II. Long-term decomposition in a Scots pine forest. Can. J. Bot. 60: 1561–1568.

Stark N. and Jordan C.F. 1978. Nutrient retention by the root mat of an Amazonian rain forest. Ecology 59: 434–437.

Swift M.J. and Anderson J.M. 1989. Decomposition. In: Lieth H. and Werger M.J.A. (eds), Tropical Rain Forest Ecosystems: Biogeographical and Ecological Studies. Ecosystems of the World 14B. Elsevier, Amsterdam, pp. 547–569.

Swift M.J., Heal O.W. and Anderson J.M. 1979. Decomposition in Terrestrial Ecosystems. Blackwell Scientific Publications, Oxford.

Swift M.J., Russell-Smith A. and Perfect T.J. 1981. Decomposition and mineral-nutrient dynamics of plant litter in a regenerating bush-fallow in sub-humid tropical Nigeria. J. Ecol. 69: 981–995.

Tanner E.V.J. 1981. The decomposition of leaf litter in Jamaican montane rain forests. J. Ecol. 69: 263–275.

Taylor B.R. and Parkinson D. 1987. Aspen and pine leaf litter decomposition in laboratory microorganisms. 1. Linear versus exponential models of decay. Can. J. Bot. 66: 1960–1965.

UNESCO 1978. Decomposition and biogeochemical cycles. In: Tropical Forest Ecosystems. UNESCO/UNEP/FAO, Paris, pp. 270–285.

Upadhyay V.P. and Singh J.S. 1989. Patterns of nutrient immobilisation and release in decomposing forest litter in central Himalaya, India. J. Ecol. 77: 127–146.

Upadhyay V.P., Singh J.S. and Meentemeyer V. 1989. Dynamics and weight loss of leaf litter in central Himalayan forests: abiotic versus litter quality influences. J. Ecol. 77: 147–161.

Van Vuuren M.M.I., Berendse F. and De Visser W. 1993. Species and site differences in the decomposition of litter and roots from wet heathlands. Can. J. Bot. 71: 167–173.

Vitousek P.M., Turner D.R., Parton W.J. and Sanford R.L. 1994. Litter decomposition on the Mauna Loa environmental matrix, Hawaii: patterns, mechanisms, and models. Ecology 75: 418–429.

Vogt K.A., Grier C.G. and Vogt D.J. 1986. Production, turnover and nutrient dynamics of above and below ground detritus of world forests. Adv. Ecol. Res. 15: 303–377.

Vogt K.A., Publicover D.A. and Vogt D.J. 1991. A critique of the role of ectomycorrhizas in forest ecology. Agric. Ecosyst. & Environ. 35: 171–190.

Wieder R.K. and Lang G. 1982. A critique of the analytical methods used in examining decomposition data obtained from litterbags. Ecology 63: 1636–1642.

Winer B.J., Brown D.R. and Michels K.M. 1991. Statistical Principles in Experimental Design. 3rd edn. McGraw-Hill, New York.

Wood T.G. 1974. Field investigations on the decomposition of leaves of *Eucalyptus delsatensis* in relation to environmental factors. Pedobiologia 14: 343–371.

Yamashita T. and Takeda H. 1998. Decomposition and nutrient dynamics of leaf litter in litter bags of two mesh sizes set in two dipterocarp forest sites in Peninsular Malaysia. Pedobiologia 42: 11–21.