Nutrient Cycling in Ectomycorrhizal Legume-Dominated Forest in Korup National Park, Cameroon.

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by

George Bindeh Chuyong
B.Sc, M.Sc (Forestry) Ibadan

Department of Biological and Molecular Sciences
University of Stirling
Scotland.

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ABSTRACT

Patterns and rates of nutrient input to the forest floor in litterfall, throughfall and stemflow were investigated in plots of low and high abundance of ectomycorrhizal species. The aim of the study was to examine the comparative advantage of the ectomycorrhizal species in nutrient acquisition and cycling on nutrient-poor soils in Korup.

Litterfall was similar in both forests with annual estimates of 9.00 and 8.33 t ha^{-1} yr^{-1} for LEM and HEM forests respectively. Litterfall distribution followed a mono-modal pattern, with peaks in the dry season in both forests and the HEM forest showing stronger seasonality. The concentrations N, K and Ca in total litterfall were higher in the LEM forest while those of P and Mg were higher in the HEM forest. The bulk of nutrients in total litterfall was in leaf litter with the reproductive fractions having the highest concentrations of nutrients. Ectomycorrhizal species showed lesser internal redistribution of nutrients than non-ectomycorrhizal species which resulted in their higher leaf litter concentrations of nutrients.

Breakdown of litter was relatively faster in the LEM forest with an annual decomposition constant (K_L) of 3.21 compared to 2.43 for the HEM forest. The reproductive fractions had relatively higher annual decomposition constants of 8.20 and 4.27 in the LEM and HEM forests respectively compared to the other fractions. The overall element mobility in decomposing leaf litter was similar in both forests and in the following order: Mg > K > Ca > P > N. Mineralization of N, P and K in the decomposing leaf litter was similar in both forests and higher in the HEM forest for Mg and Ca.

Throughfall was 96.6% and 92.4%, and stemflow 1.5% and 2.2%, of gross rainfall in LEM and HEM forests respectively. Considerable amounts of Ca, Mg and P were brought to the forest canopy in gross rainfall (24-45% of total input through this route) with higher amounts of K and Ca leached from plant parts by the rainwater. The amounts of P, K and Ca in stemflow and throughfall were of the same magnitude in both forests with the enhancement of N slightly higher in the LEM forest and Mg in the HEM forest.

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Declaration

I declare that the thesis has been composed by myself and that it embodies the results of my own research. Where appropiate I have acknowleged the nature and extent of work carried out in collaboration with others included in the thesis.

G.B Chuyong.

TABLE OF CONTENTS

ABSTRACT

ACKNOWLEDGEMENTS

CHAPTER 1. GENERAL INTRODUCTION

1.1 Some perspectives on Nutrient cycling in tropical forests. 1

1.2 Rationale of study 5

1.3 Objectives of the study 6

CHAPTER 2. DESCRIPTION OF THE STUDY AREA

2.1 Forest status 7

2.2 Location 7

2.3 Climate 7

2.3.1 Rainfall 8

2.3.2 Temperature and humidity 8

2.3.3 Radiation 8

2.4.1 Relief and drainage 11

2.4.2 Geology and soils 11

2.4.2.1 Soil profiles 14

2.5 Vegetation 14

CHAPTER 3. LITTER PRODUCTION

3.1 INTRODUCTION 16

3.2. MATERIALS AND METHODS 19
3.2.1. Selection of sample plots 19
3.2.1.1 Floristic composition of the selected plots 21
3.2.2 Layout of litter traps 29
3.2.3 Litter collection and treatment 29
3.2.4 Data analysis 32
3.3 RESULTS 35
3.3.1 Annual Estimates of Litterfall 35
Total Litterfall 35
3.3.1.2 Litter Components 35
3.3.2 Temporal Pattern in Litterfall Distribution 36
3.3.2.1 Total Litterfall 36
3.3.2.2 Litter Components 44
3.3.3 Contribution by the various species to leaf litter 45
3.3.4 Relationships among total litterfall and various litterfall fractions . . 55
3.3.5 Climatic factors and Litterfall 55
3.4 DISCUSSION 59
3.4.1 Litter production 59
3.4.2. Seasonality of litter production 60
3.4.3 Leaf fall patterns in single tree species 62

CHAPTER 4. NUTRIENT CONCENTRATION AND ACCESSION IN LITTERFALL

4.1 INTRODUCTION 64

4.1 MATERIALS AND METHODS 66
4.2.1 Selection and preparation of samples 66
4.2.1.1 Litter samples. 66
4.2.1.2 Foliar samples 68
4.2.2 Chemical analysis 69
4.2.2.1 Preparation and digestion of samples 69

4.2.2.2 Elemental analysis 70
4.2.3 Data analysis 72

4.3 RESULTS 75
4.3.1 Mineral-element concentrations in litterfall 75
4.3.1.1 Mean elemental concentrations 75
4.3.1.2 Temporal variation in mineral element concentrations . . . 77
4.3.1.3 Mineral element concentration in leaf litter of selected species 84
4.3.2 Mineral element accession in litterfall 94
4.3.3. Foliar concentration and retranslocation 99

4.4 DISCUSSION 101
4.4.1 Mineral-element concentration in litterfall 101
4.4.2 Mineral element accession in litterfall 103
4.4.3 Nutrient retranslocation 111
4.4.4 Nutrient use efficiency 113

CHAPTER 5. BREAKDOWN AND MINERALIZATION OF LITTER

5.1 INTRODUCTION 114

5.2 MATERIALS AND METHODS 117
5.2.1 Selection of sample plots 117
5.2.2 Litter layer on forest floor 117
5.2.3 Leaf litter decomposition 118
5.2.3.1 Collection and treatment of leaf litter 119
5.2.3.2 Experimental layout and sampling 121
5.2.3.3 Chemical analysis 122
5.2.4 Data analysis 122
5.2.4.1 Litter layer on forest floor 122
5.2.4.2 Mass loss and mineralization of leaf litter confined in litterbags 123

5.3 RESULTS 127
5.3.1 Litter layer on forest floor 127
5.3.1.1 Variation in dry mass of the different litter fractions 127
5.3.1.2 Monthly and annual estimates of turn-over rates 129
5.3.1.3 Climatic factors and turn-over rates 136
5.3.2 Mass loss in leaf litter confined in litter litterbags 136
5.3.2.1 Initial chemical composition of the leaf litter 136
5.3.2.2 Comparison between species in both forest types 137
5.3.2.3 Mass loss and litter quality 159
5.3.3 Rates of mineralization 159
5.3.3.1 Temporal changes in nutrient concentration in decomposing leaf litter 159
5.3.3.2 Initial concentration and rates of mineralization 166
5.3.3.3 Element mobility 166

5.4 DISCUSSION 168
5.4.1 Forest floor litter layer and turn-over rates 168
5.4.2 Mass loss in leaf litter confined in litterbags 172
5.4.3 Rates of mineralization in leaf litter in both forest types 173

CHAPTER 6. NUTRIENT INPUT IN THROUGHFALL AND STEMFLOW

6.1 INTRODUCTION 177

6.2 Materials and methods 179
6.2.1 Sample plot selection and layout. 179
6.2.2 Collection preservation and storage of samples. 184
6.2.3 Chemical analysis 185
6.2.4 Data analysis 186

6.3 RESULTS 189
6.3.1 Gross rainfall 189
6.3.2 Throughfall 189

6.3.3 Stemflow 190
6.3.4 Nutrient concentration and fluxes 194

6.4 DISCUSSION 202
6.4.1 Nutrient fluxes in gross rainfall, throughfall and stemflow 202
6.4.2 Temporal and spatial variability in inputs 206

CHAPTER 7. GENERAL DISCUSSION AND CONCLUSSION

7.1 Nutrient input and availability. 208

7.2 Nutrient redistribution. 211

7.3 Conclusions 214

REFERENCES. 215
APPENDIX 1a 233
APPENDIX 1b 237
APPENDIX 2a 238
APPENDIX 2b 239

CHAPTER ONE

GENERAL INTRODUCTION

GENERAL INTRODUCTION

1.1 Some perspectives on nutrient cycling in tropical forests.

The functioning of the tropical forests like other ecosystems of the world is strongly dependent on the availability of nutrients for proper functioning and maintaining productivity. For self perpetuation of the forests, the available nutrients must be efficiently cycled between the abiotic and biotic components of the forest ecosystem (Coleman *et al.* 1983). Tropical forests are not entirely closed systems and exchange of nutrients (by gains and losses) with other ecosystems which constitutes intersystem cycles occurs (Bormann and Likens 1967, Likens *et al.* 1981). Within the tropical forest itself, there are movements of nutrients between the different pools which also constitute intrasystem cycles. The whole cycle can be considered complete only when the entire globe is considered as a single unit (Waring and Schlesinger 1986).

The general model of nutrient cycling involves series of inter-related feedback processes between the abiotic and biotic components of the ecosystem (Figure 1.1). These feedback processes have generally been classified into three sub-processes (Switzer and Nelson 1972, Proctor 1987, Attiwill and Adams 1993) which embrace:

(i) Input and output from the forests. Nutrients enter the forest ecosystem with rain and deposition of dust and aerosols, biological fixation by microorganisms in the phyllosphere (canopy) and rhizosphere in the soil and from weathering of the bedrock. Nutrients are lost from the forests in streamwater and in gaseous forms (resulting from denitrification and volatilization) to the atmosphere.

(ii) Transfer of nutrients between plant and soil. Nutrients are returned to the soil in litterfall, root turnover and death of the whole tree, throughfall and stemflow. The dead organic matter undergoes a series of complex transformations (decomposition) mediated by soil macro and microorganisms to release the nutrients therein. Nutrients are taken up from the soil by roots either through direct absorption from soil solution or mediated by mycorrhizas.

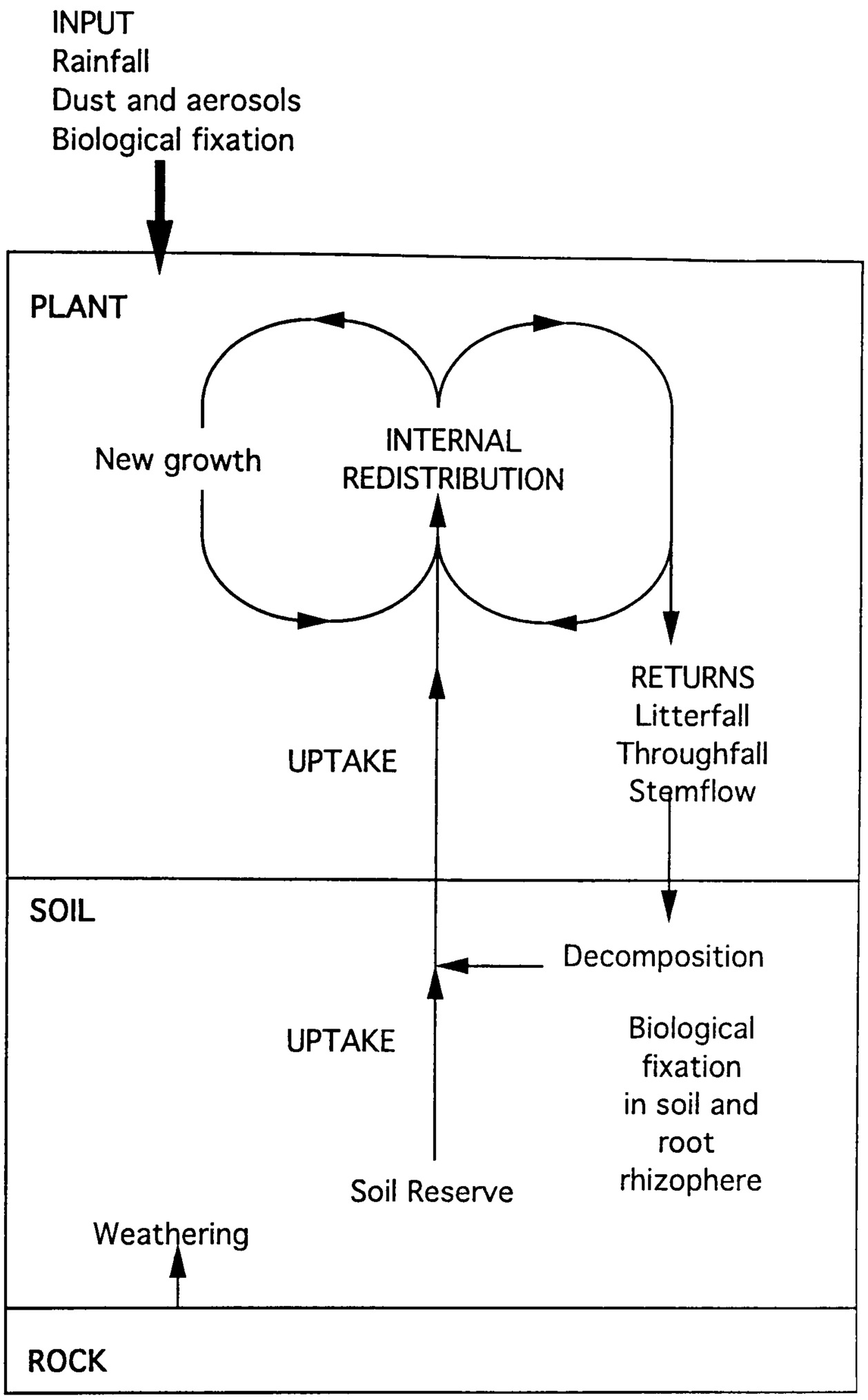


Figure 1.1: Schematic picture of the cycling of nutrients in a forest. (Adapted from Attiwill and Adams 1993).

(iii) Internal redistribution of mobile nutrients from storage sites or from senescing plant parts prior to their detachment from the plant to active sites of growth and synthesis.

Early studies on tropical forest functioning gave the impression of higher rates of ecosystem processes which include productivity, decomposition and nutrient cycling (Jenny *et al.* 1949, Laudelot and Meyer 1954, Nye 1961) compared to the temperate forests. These generalisations were reported to be representative of the tropical forests (Rodin and Bazilevich 1967). Furthermore, soils of the tropical forests are often described as being highly leached with low base saturation, low pH, high aluminium mobility and therefore generally infertile which notwithstanding, bears the bulk of nutrients in an apparent luxuriant vegetation above the very thin top soil layer (Whittaker 1975).

Reviews of recent studies of overall patterns of nutrient cycling in tropical forests (Proctor 1983b, 1987, Jordan 1986, Vitousek and Sanford 1986, Attiwill and Adams 1993) and of important sub-processes such as litterfall (Proctor 1984, Vitousek 1984), decomposition (Anderson and Swift 1983, Esser and Lieth 1989, Lavelle *et al.* 1993), litter and nutrient turnover on the forest floor (Vogt *et al.* 1986) and the hydrological framework (Bruijnzeel 1989, 1991) show that patterns of nutrient cycling in tropical forests are diverse. Sanchez (1976, 1989) has also shown that soils of the humid tropical regions are very variable, ranging from the youngest to about the oldest, from amongst the most fertile to the least fertile.

Patterns of nutrient cycling are dependent on the availability of the different nutrients in the soil (Jordan and Herrera 1981, Vitousek and Sanford 1986). The high variability in soil fertility of the humid tropical zone (Sanchez 1989) may also reflect highly diversified patterns of nutrient cycles in the forests above them.

Tropical forests on nutrient poor soils are known to have evolved several nutrient conservation mechanisms which enable them to conserve and efficiently recycle the available nutrients in the organic matter. Prominent amongst the proposed conservation mechanisms is the formation of the root mat (Stark and Spratt 1977, Jordan and Herrera 1981) which is thought to trap nutrients released from decomposing litter and other

sources of nutrient input to the forest floor and transport them into the plants. Direct absorption of nutrients which enter the root mat had been reported by Stark and Jordan (1978). Went and Stark (1968) also proposed direct nutrient transfer from litter to the roots via mycorrhiza. Other proposed strategies include the conservation of nutrients within the trees through efficient redistribution, morphological adaptations such as leaf arrangements to minimise leaching, canopy scavenging of nutrients from rain water and the production of sclerophyllous leaves high in secondary products which retards their decomposition and prevent the rapid of loss nutrients released through leaching. These strategies allows the trees to function properly irrespective of the nutrient limitations in the soil.

The role of mycorrhizas in forest nutrition studies has continued to increase as recent results are in favour of their direct role in the uptake of nitrogen and phosphorus which have often been considered as the limiting nutrients in tropical soils for plant nutrition (St John and Coleman 1983, Harley and Smith 1983, Fogel 1986, Högberg 1986). Much attention has been on vesicular-arbuscular mycorrhizas (VAM) and ectomycorrhizas (ECM) which are reported to be widely distributed in most tropical forests (Högberg 1986, Brundrett 1991). Ectomycorrhizas have also been reported to have a comparative advantage over vesicular-arbuscular mycorrhizas (VAM) because of their morphology (the Hartig net) which tends to increase the surface area and storage capacity of the host roots (Alexander 1989). Different hypotheses have been proposed to describe the functional role of mycorrhizas in nutrient uptake by the plants and how they affect plant growth.

The different tree species will have different nutrient requirements and cycles and with the high species diversity in tropical forests, the cycling of nutrients will be complex with much interactions expected. Plants with similar tolerance and strategies may tend to occupy the same ecological niche. Such associations may play an important role in determining their spatial distribution patterns.

1.2 Rationale of study.

One of the major ecological consequences of improper utilization of the forests (extensive logging, burning, etc.) is the loss of the surface organic matter which has taken long to develop. This surface organic matter plays a crucial role in stabilising soil fertility. The tropical forest is being lost at an alarming rate through timber exploitation, conversion to agricultural and other developmental activities. Proper ecological bases are required for sound forest policies on planning and management which will guarantee sustainable utilization with minimal effects to the environment. To reduce the impact on the existing tropical forests, management options have often been geared to encouraging the establishment of plantations, reforestation of degraded areas and to improving the process of regeneration in the existing exploited forests. For most of these projects, rapidly growing exotic species such as *Eucalyptus* spp., *Gmelina* spp. and *Tectona* spp. have often been introduced to these regions which in the short term alters the ecological processes. This has led to recommendations for the use of indigenous species which can easily adapt to local conditions. Little is often known of the indigenous species (lesser-known) which are not in the exploitable or marketable lists. These goals can be achieved by using the right species which can best suit a particular area or circumstance. Proper investigations on how evolutional processes have 'solved' the problems of survival in edaphically extreme conditions will provide clues on which species can best suit an area and how best to tackle issues on reforestation and regeneration programmes. Korup National Park is one of such sites which could provide such useful information on ecological processes and functioning typical of a natural tropical forest. From its history and location, the Park is classified as a refugium with a highly diverse flora and fauna which are considered to be adapted to the prevailing conditions through long-term competition and niche complementation.

In Korup extensive studies on the vegetation and soils have been carried out (Gartlan *et al.* 1986. Newbery *et al.* 1988) which showed distribution patterns strongly related to soil nutrient availability (particularly in phosphorus) and ectomycorrhizas. With the widespread assumptions about the important role played by the mycorrhizas in forest

nutrition, few studies have actually verified these findings in natural plant communities (Fogel 1986, Vogt *et al.* 1992). Field studies are therefore necessary to fully understand the importance of mycorrhizas in natural ecosystems and to increase our understanding of their interactions in the heterogenous natural system.

1.3 Objectives of the study

The main aim of this study was to assess the role of ectomycorrhizas in the cycling in nutrients in Korup and to evaluate the comparative advantage the ectomycorrhizal plants have over the non-ectomycorrhizal species in such an edaphically extreme condition. To achieve this goal the following sub-processes of nutrient cycling were fully examined in plots with low and high abundance of the ectomycorrhizal species:

(i) to quantify nutrient inputs to the forest floor in both forest types through litterfall, throughfall and stemflow;

(ii) to determine the rates of litter turnover on the forest floor in both forests;

(iii) to examine the rates of litter breakdown and mineralization of the major nutrient elements; and,

(iv) to estimate the rate of internal re-distribution of the major nutrients in species with and without the ectomycorrhizal association.

It is the hope that from these results the question of which nutrients are limiting growth in the Park will be determined as well as the existing nutrient conservation strategies of these species which allows them to thrive on such nutrient-poor soils.

Emphases were on the fluxes of nitrogen, phosphorus, potassium, magnesium and calcium which the major nutrient elements particularly essential for ecosystem functioning (Proctor 1987, Grubb 1989).

CHAPTER TWO

DESCRIPTION OF STUDY AREA

2.1 Forest status.

Korup was declared a Forest Reserve by order N° 25 of 14 October 1937 of the Government of West Cameroon. The Reserve was managed by the Forestry service of the successive Native Authorities of the Southern Province and later under the Kumba Western Council of Southern Cameroon, the Chief Conservator of Forests, Ministry of Natural Resources of Southern Cameroon and later by the Department of Forestry in the Ministry of Agriculture, Republic of Cameroon. The Reserve was finally declared a Forest National Park (the first in Cameroon) by decree N° 86/1283 of 30 October 1986 of the Government of Cameroon to conserve the very rich and natural ecosystem, foster scientific research and enhance tourism. The Park and its buffer area are currently under the management of the Korup National Park Project with supporting services from the Conservator of the Park. The Korup Project is envisaged to serve as a model of sustainable development through proper management of the Park and its buffer area for other countries to emulate.

2.2 Location

Korup National Park is located in the South West Province of Cameroon. The Park extends from 4°54′ to 5°28′ N and from 8°42′ to 9°16′ E. The Akpa Korup River forms part of the western boundary of the Park and the international boundary with Nigeria (Figure 2.1). The Ndian river which rises from the northern part and flows southwards, forms part of the south western boundary. The total area of the Park is approximately 123,000 ha with the southern portion west of Mundemba and extending northwards to Baro west of Nguti (Figure 2.1).

2.3 Climate

The climate of Ndian is characterized by a single short dry season of about three months from December to February and a corresponding long wet season of seven to nine months from March to November. The climatic data of the area were recorded at the Bulu

weather station (PAMOL, Ndian). This station is southeast and approximately 10 km away from the research plots and was thought to be representative of the area.

2.3.1 Rainfall

The mean annual rainfall for the period 1990-1993 was 5060 mm. This was lower than the mean annual rainfall of 5460 mm for the period 1968 to 1983 (Gartlan *et al.* 1986). That was however representative of the southern part of the Park and generally decreased to the north. Rainfall was recorded in all months with the highest amounts (630-1200 mm) in July and August which also had the highest number of rainy days (26-29 days). The mean monthly rainfall recorded for the period 1990-1993 is presented in Figure 2.2.

2.3.2 Temperature and humidity

The mean monthly temperature ranges between 24.0°C and 28.1°C with the maximum monthly record of 33.1°C in February and the minimum of 21.4°C in January. The absolute maximum temperature recorded during the study period (March 1990-June 1993) was 36°C in March 1992 and the absolute minimum temperature was 16°C in January 1992. The highest diurnal range in temperature is in the dry season as a result of the very low morning and night temperatures during the 'harmattan' period. The mean monthly minimum and maximum temperatures recorded for the period 1990 to 1993 are presented in Figure 2.2. The mean relative humidity of the area is estimated to range from 80% in the dry season to 90% in the wet season (Gartlan 1984).

2.3.3 Radiation

The amount of radiation recorded for Ndian ranged from 6 ml to 10.4 ml (units are volume (ml) of the condensate in the intergraded radiometer) with lower amounts recorded in the wet season as a result of thick cloud cover and in the later part of the dry season due the relatively high amount of dust particles in the atmosphere. Within the first month of the rainy season, these particles are washed down by the incident rain and result in high amounts of radiation being recorded in April and May.

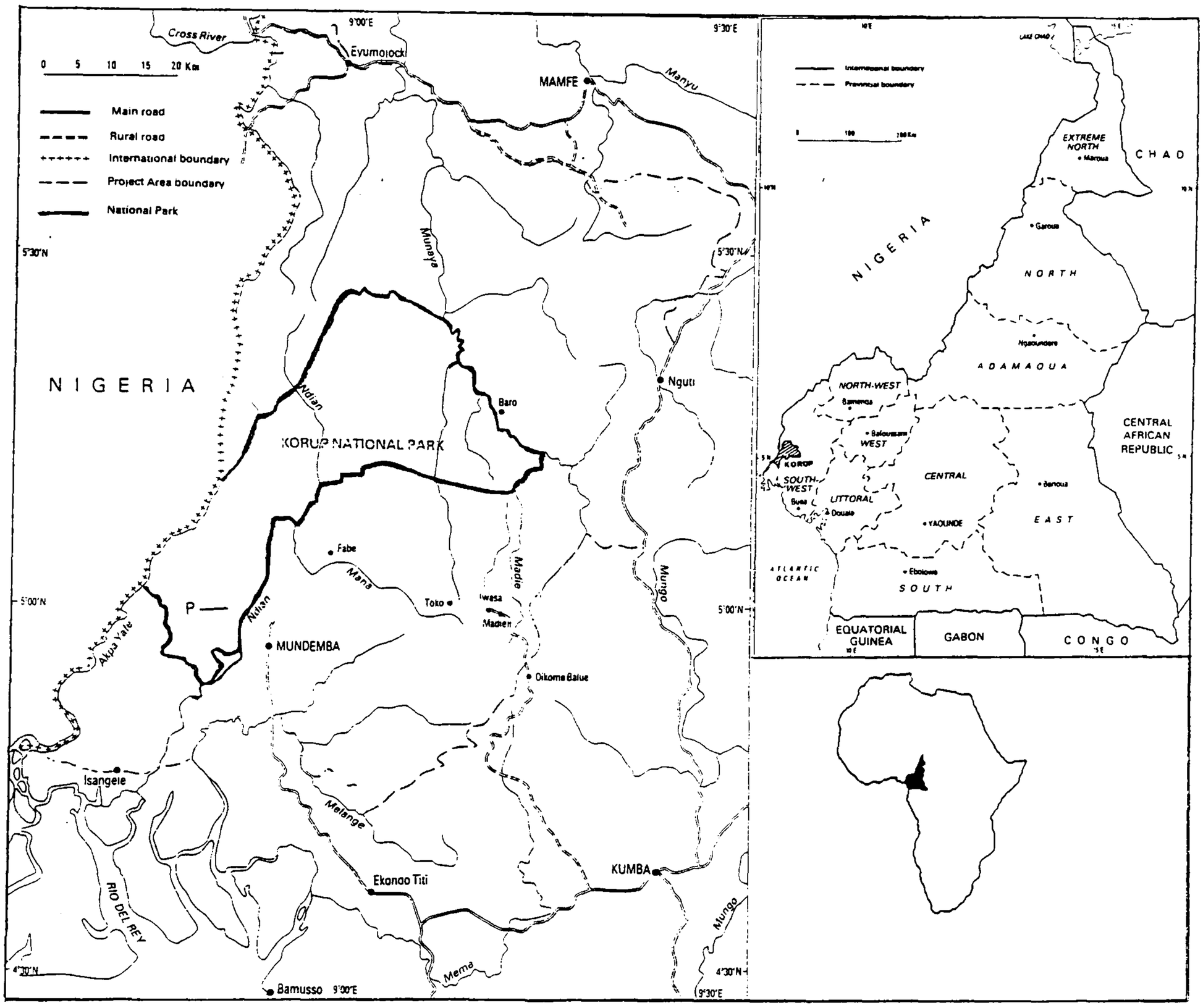


Figure 2.1: Location of study site (transect P) in Korup National Park, Cameroon and its position in Africa.

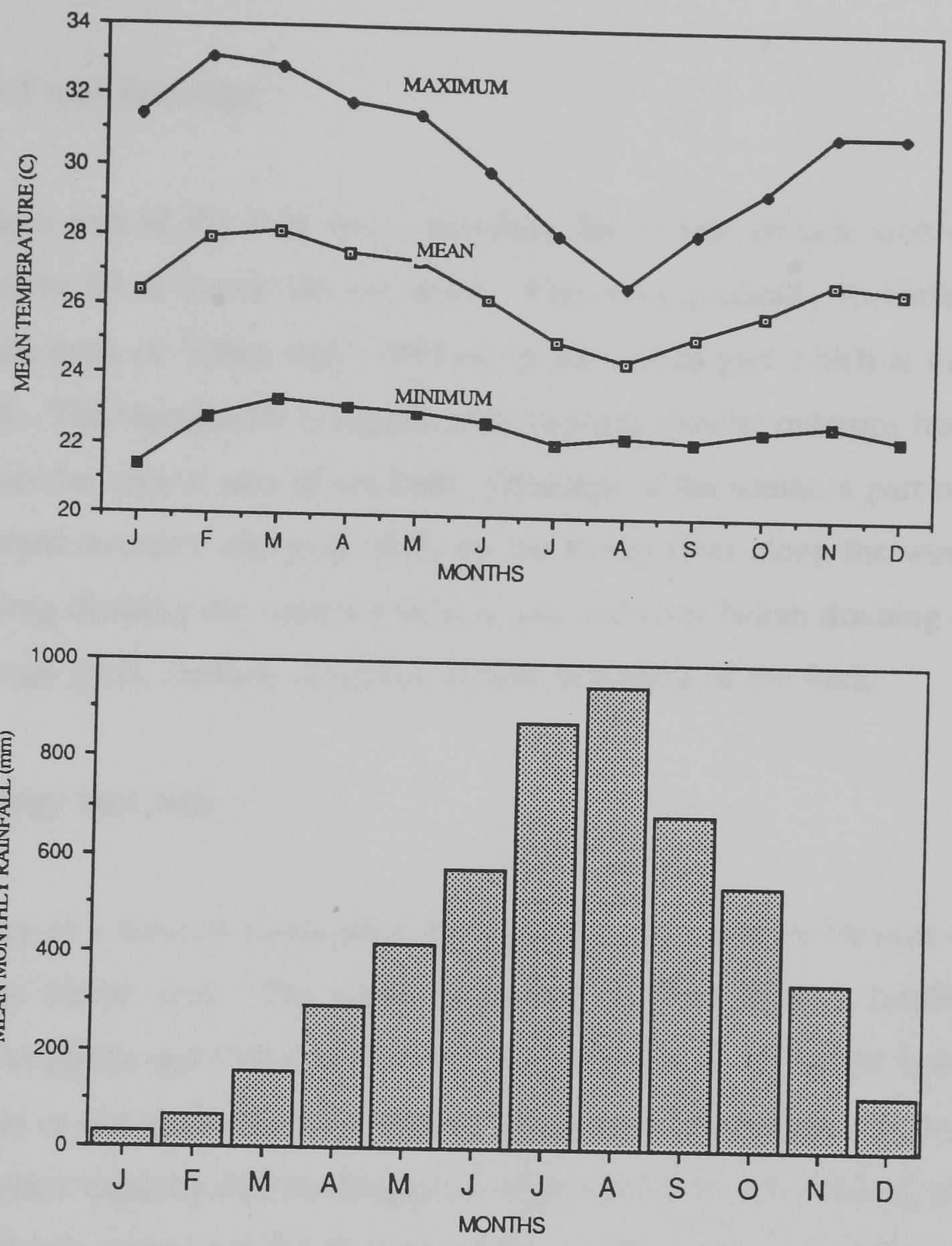


Figure 2.2: Mean monthly temperatures (maximum, mean and minimum) and rainfall for the period 1990-1993 for the Korup area. (Data from PAMOL weather station Bulu, Ndian).

2.4 Physical features.

2.4.1 Relief and drainage

The southern part of the Park has a generally flat to low altitude with an elevation of approximately 50 m above the sea level. This rises gradually towards the north and reaching the peak of Yuhan Hill (1079 m) in the central part which is the highest point of the Park. The topography is rugged with frequent granitic outcrops from the southern part towards the central area of the Park. Drainage of the southern part of the Park is in the southward direction and principally by the Korup river along the western boundary, the Akpasang draining the central southern part and river Ndian draining the central and south-western parts, flowing along the eastern boundary of the Park.

2.4.2 Geology and soils

The geology of a most of South West province was described by Dumort (1965) and this covered the Korup area. The southern part of the Park is on a bedding material of Precambrian gneiss and Cretaceous sedimentary sandstones. This old basement complex decomposes in situ into old sandy soils which are heavily leached as a result of their low water retention capacity and the frequently high rainfall in the southern part of the Park. Analysis of composite samples of cores of the top 10 cm of soils from the southern part of the Park showed that the soils are strongly acidic (low pH) and low in nutrients (Gartlan *et al.* 1986, Newbery *et al.* 1988). Results of a more recent analysis of soils from forest types of low and high abundance of ectomycorrhizal legumes (LEM and HEM) in Korup National Park by D.M.Newbery, I. J.Alexander and J.A.Rother (in preparation) are summarized in Table 2.1. This shows a trend of generally shallow organic layer which is consistently greater in the HEM forest. Soils of the HEM forest also have lower sand and higher clay contents than LEM forest (Table 2.1).

Table 2.1: Soil characteristics of three layers (L litter, O organic, and M mineral) in LEM and HEM forests, Korup National Park, Mundemba, Cameroon. (means±SE; n=9 replicate half-plots per forest type). (Data from Newbery D.M, Alexander I.J and Rother J.A unpublished)

Soil attributes	Layer	Forest type	
		LEM	HEM
Depth of layer (mm)	O	4.22±0.32	8.11±0.56
Bulk density (kg m^{-3})	O	5.17±0.22	6.70±0.51
	M	57.4±1.4	51.6±1.4
Moisture content (% dry weight)	L	168.0±5.9	183.1±3.7
	O	44.1±2.2	52.8±2.2
	M	18.4±0.6	20.8±0.9
Sand (%)	O	78.0±0.9	73.4±1.1
	M	81.4±0.9	77.1±1.0
Silt (%)	O	8.1±0.8	10.0±1.1
	M	6.6±0.5	8.7±1.0
Clay (%)	O	13.9±0.5	16.2±0.3
	M	12.0±0.2	14.2±0.3
pH	L	5.53±0.04	5.41±0.03
	O	4.59±0.06	4.19±0.03
	M	4.31±0.04	4.15±0.02
Carbon (%)	O	4.00±0.25	5.51±0.31
	M	1.58±0.03	1.88±0.08

Table 2.2: Descriptive characteristics of soil profiles from two soil pits along transect P in Korup National Park Mundemba. P1 is in LEM forest and P24 in HEM forest. (Data from Newbery D.M, Alexander I.J and Rother J.A. unpublished).

Plot	Horizon	Depth (cm)	Separation of horizons	Texture	Musell colour	Structure	Coarse material
P1	A	0-30	gradual	loamy sand	10YR3/3	weak (friable)	none
	B_1	30-70	distinct	sandy loam	7.5YR5/6	moderate (crumble)	none
	B_{2t}	70-150	distinct	sandy loam	7.5YR5/6	massive (aggregated)	small laterite and saprolyte
	B/C	150-210	none	sandy clay loam	7.5YR6/8	massive (aggregated)	small laterite and saprolyte
P24	A	0-12	gradual	sandy loam	10YR4/4	moderate (crumble)	none
	A/B	12-44	gradual	sandy loam	5YR5/6	massive (aggregated)	none
	B_t	44-136	gradual	sandy clay loam	3.75YR4/2	massive (aggregated)	small laterite and saprolyte
	B/C	136-210	none	sandy clay loam/ clay loam	10R4/8	massive (aggregated)	small laterite and saprolyte

2.4.2.1 Soil profiles

The general characteristics of the soil profile along transect P (which runs across LEM and HEM forests; as described by Newbery, Alexander and Rother in preparation) is that of predominantly sand with small clay components which increase with depth. The structure also showed corresponding trend from friable in the surface horizon to more aggregate below. A summary of the soil profile characteristics of two pits (P1 in LEM forest and P24 in HEM forest) along transect P are given in Table 2.2. Their results also show that the both forest types have a similar basement substrate except for trends in phosphorus from P19 westwards (middle of transect).

2.5 Vegetation

The vegetation of Korup National Park can be classified as lowland rainforest of the Guineo-Congolian type (White 1983). Korup together with the Rumpi Hills and Mount Cameroon form a major block of the Western Guinea-Congolean refuge area into which the rainforest was reduced during the Pleistocene (Gartlan 1974, Hamilton 1976, Endler 1982, Gartlan *et al.* 1986). As a lowland forest refuge Korup has a highly diverse flora and is richer in species than any other African rainforest for which comparable data are available (Gartlan 1986). A total of four hundred and eleven (411) different taxa were recognised in an enumeration of all trees ≥ 30 cm girth at breast height (gbh) in a sample area of 86.4 ha with a total of 75 to 101 taxa in the 0.64 ha (80 m × 80 m) sample plots (Gartlan *et al.* 1986).

The flora includes widely distributed species in genera common to other west and central African lowland forests. These includes *Anthonotha fragrans* (Bak.f.) Exell and Hillcoat, *Erythrophleum ivorense* A.Chev., *Xylopia aethiopica* (Dunal.) A.Rich. Some of the species occur only from Eastern Nigeria to the west across the Congo basin such as *Oubanguia alata* Bak.f., *Dichostemma glaucescens* Pierre, *Strobosiopsis tetrandra* Engl., *Afzelia bipindensis* Harms., and *Enatia chlorantha* Oliv. (Gartlan 1986). The flora of Korup also shows some affinities with that of South America. *Erismadelphus exsul*

Midbr. and *Sacoglottis gabonensis* (Baill.) Urb. which both occur in Korup are members of families poorly represented in Africa but with many more members in Latin America (Gartlan 1986).

Also endemic to Korup are species such as *Hymenostegia bakeriana* Hutch. and Dalz., *Globulostylis talbotii* Wernham. and *Soyauxia talbotii* Bak.f.. Korup also appears to be a centre of diversity for several genera with *Cola* (Sterculiaceae) having about 25 species, *Diospyros* (Ebenaceae) at least 16 species and *Dorsteria* (Moraceae) with five species (D.Thomas quoted by Gartlan 1986). The flora of Korup is very poor in economically exploitable species. That notwithstanding, the eastern boundary of the southern part of the Park follows the Ndian river which renders it inaccessible for any logging operation.

More detailed studies on the floristic distribution of the species have been carried out in the southern part of the Park (see Gartlan *et al.* 1986, Newbery *et al.* 1988). These studies show comparatively high abundance of species in the sub-family Caesalpinioideae in terms of basal area and the Scytopetalaceae represented mainly by *Oubanguia alata* Bak.f. the most frequent species. The distribution of the species also show a major indirect floristic gradient correlated with increasing altitude, slope and soil phosphorus and potassium (Gartlan *et al.* 1986). The legumes are frequent in the lower part of the Park and tend to form groves dominated by *Microberlinia bisulcata,* A.Chev., *Tetraberlinia bifoliolata* (Harms.) Hauman and *T. moreliana* Aubr. (Newbery *et al.* 1988). Studies also show that these legumes are ectomycorrhizal and grow on soils which exhibit strong seasonal variation in available phosphorus (other soils outside the legume groves show similar variation) (Newbery *et al.* 1988).

A survey of the mycorrhizal status of the tree species in Korup showed that thirty-two of the species investigated formed only VA mycorrhizas, twenty-three formed ectomycorrhizas of which three, *Uapaca staudtii* Pax, *Afzelia pachyloba* Harms and *Gilbertiodendron dewevrei* (De Wild) J. Léonard also formed VA mycorrhizas (Newbery *et al.* 1988). Most of the ectomycorrhizal species were in the Leguminosae subfamily Caesalpinioidae, the only exception being *Uapaca staudtii* Pax in the family Euphorbiaceae (now Uapacaceae).

CHAPTER THREE

LITTER PRODUCTION

3.1 INTRODUCTION

Ecosystem functioning is strongly regulated by the fluxes of nutrients between the various pools (Odum 1970, DeAngelis 1980). Quantitative studies of litterfall continue to be an important aspect of forest ecology since litterfall is the major pathway for the transfer of organic matter and nutrients from the above ground vegetation to the soil (Nye 1961, Bray and Gorham 1964, Spain 1980, Proctor 1983a).

Because litter production is easier to measure than total net production, it has commonly been used as an index of the latter (Bray and Gorham 1964, Klinge 1978, Songwe *et al* 1988, Dantas and Phillipson 1989). This approach rests on the assumption of a steady state equilibrium, in which the rate of loss of nutrients from the vegetation is taken as a equivalent to the rate of uptake from the soil (Nye 1961, Minderman 1968, Morellato 1992).

Litterfall is also the principal source of energy for the saprobiota of the forest floor and soil. These organisms facilitate the breakdown of litter and nutrient release (Jensen 1974, Spain 1980, Coleman *et al.* 1983). The fallen amount and quality (or nature) of litter will have an important effect on the nature of soil organic matter formed and on the soil fertility (Coleman *et al* 1983). Rates of litterfall equally provide indices of seasonal phenomena relating to plant phenology. This increases the diversity and fluctuations in the abundance of many other biotic components of the forest community by modifying the microclimate (Kunkel-Westphal and Kunkel 1979, Lieberman 1982, Schaik 1986, Bullock and Solis-Magallanes 1990, Burghouts *et al.* 1994).

Attempts have been made to compare rates of nutrient cycling and ecosystem functioning at different sites and regions on the basis of their rates of litterfall. Important studies are those of Bray and Gorham (1964) at a global level, Brasell *et al.* (1980) for plantations of *Araucaria cunninghamii* and adjacent rainforest of NE Australia, Proctor *et al.* (1983b) for four lowland rainforests in Sarawak, Tanner (1980) for montane forest in Jamaica,

Veneklaas (1991) for two montane tropical rainforests in Columbia, and Morellato (1992) for a tropical semideciduous forest and a montane forest in Brasil.

Most of these quantitative studies on litterfall are diverse in approach and methodology rendering comparison between results of these different studies difficult. Proctor (1983a, 1984) has critically reviewed most of the litterfall studies carried out in tropical forests and has suggested methods which could be used as standards in further studies.

Litter production tends to follow a latitudinal trend with maximum production in the tropics to a minimum in the arctic zone (Bray and Gorham 1964, Spain 1980, Londale 1987). Within the tropics there are variations in litterfall: Typical examples include the altitudinal gradient from lowland forests to altitudinal montane forests (Heaney and Proctor 1989, Proctor *et al.* 1989), between primary to secondary forests (Dantas and Phillipson 1989, Burghouts *et al.* 1994) and between forests on hillslope and valley (different aspects) (Luizão and Schubart 1987, Martínez-Yrízar and Sarukhán 1990). These differences are due to local variations in topography, diverse species composition, age of the forest stand and prevailing microclimatic factors. Edaphic factors have been reported to have little influence or effect on litter production (Tanner 1980, Proctor 1983b, Scott *et al.* 1992).

Litterfall consists of different fractions which vary spatially and temporally in the amounts and concentrations of mineral nutrients. With the high species richness of most tropical forests, the different species shed their leaves at different times of the year as well as flowering over certain periods. This spatial and temporal heterogeneity in litterfall is likely to have a significant role in nutrient cycling processes. Few studies in the tropics have attempted to look at the contribution and pattern of litterfall of the different species. Litterfall, being one of the major routes of nutrient return to soil, may determine the timing of nutrient availability in the soil which controls many ecosystem processes.

This chapter focuses on the spatial and temporal distribution patterns in total litterfall, and the different litter fractions in plots with low abundance of ectomycorrhizal species (LEM)

and plots with high abundance of ectomycorrhizal species (HEM). Emphasis was also placed on individual species contributions to total leaf litter and the climatic factors which might influence the seasonality in litterfall.

3.2. MATERIALS AND METHODS

3.2.1. Selection of sample plots.

Due considerations were taken in selecting two sets of plots with low and high abundances of ectomycorrhizal species (in terms of % basal area) that were good representatives of the two forest types and guarantee sound statistical comparisons of these forest types. This was greatly facilitated by information from previous works carried out in this area. These included the enumeration data of Gartlan *et al.* (1986) on all living trees (≥ 30 cm gbh) in 135 0.64 ha plots, the subsequent survey of the mycorrhizal status of the trees and the spatial distribution patterns of ectomycorrhizal trees by Newbery *et al.* (1988), the detailed investigation of the floristic and edaphic relationships of the species in Korup by Newbery *et al.* (1988) and the dynamics of phosphorus cycling by Newbery, Alexander and Rother (in preparation).

For the original enumeration by Gartlan *et al.* (1986), four 5 km transect lines were established along an E-W compass bearing in the southern part of the Park. They were approximately 4 km apart and were designated from south to north as P, Q, R and S. Each transect consisted of thirty-four 80 m x 80 m sample plots separated by 70 m from each other (transect Q had 33 plots). Each sample plot was further divided into four 40 x 40 m sub-plots (A, B, C and D at the SE, SW, NW and NE corners respectively)for which floristic, topographic and edaphic variables were collected.

Newbery *et al.* (1988) found that 23 species in Korup formed ectomycorrhizas and of the four transects, P had a much greater percentage of the basal area contributed by these ectomycorrhizal species (28% for P compared to 3% for S). Transect P has the lowest elevation and was readily accessible all the year round rendering it feasible for a regular sampling programme and was chosen for the study. Furthermore, the major ectomycorrhizal species: *Microberlinia bisulcata, Tetraberlinia moreliana,* and *Tetraberlinia bifoliolata* occurred only on transect P relative to the other transects.
Along transect P the major ectomycorrhizal species were concentrated in three groves

within the central portion of the transect and contributed between 60-70 % of the plots' basal area (Newbery *et al.* 1988). These groves were dominated in both basal area and frequency by the three major ectomycorrhizal species named above. At both ends of the transect were outliers of some ectomycorrhizal species that contributed a lower percentage of the plots' basal area. These included *Anthonotha fragrans, Didelotia africana,* and *Berlinia bracteosa.* This distribution pattern of the ectomycorrhizal species justified the high and low categories of plot selection used. It was then logical for plots to be selected from within these groves and out of them to provide the two sets of plots for comparing the two forest types.

The whole plots (A, B, C and D quarter-plots) used by Gartlan *et al* (1986) were not sufficiently homogenous and had some sub-plots contributing strongly to within-plot variation, such as the presence of streams, rocky outcrops, steep slopes, and wide tree fall gaps. Newbery, Alexander and Rother (in preparation) in their studies on P cycling considered the quarter (sub) plots too small to be taken individually as they could be dominated by one large tree. In addition these plots also had large perimeter to area ratios for sampling purposes. The half-plot scale was chosen as the optimum plot unit for their study and the four possible combinations of adjacent pairs of quarter-plots (A+B, B+C, C+D and A+D) were carefully examined for all the plots on transect P. This was on the basis of edaphic factors, absences of large tree fall gaps, wetness (avoiding streams and swampy areas) and floristic heterogeneity with particular reference to ectomycorrhizal species which resulted in restricted random samples of both forest types. Eighteen half-plots were selected and examined by ordination analysis using nPCA on basal area and density as measures of abundances, for all the species in both category of plots. This was to determine the extent to which the low and high ectomycorrhizal half-plots differed in their floristic composition, the degree of clustering of these two categories of plots and the relative similarity of the adjacent pairs of sub-plots that constituted the half-plots. This showed strong separation of the two categories of half-plots, with much clustering within each of the categories. There was also less separation of the non-ectomycorrhizal species in both categories of half-plots.

For the purpose of the studies reported here, further examination was carried out to select ten half-plots from the eighteen previously used by Newbery, Alexander and Rother (in preparation). Based on earlier experiences in detailed litter studies by Songwe (1984, personal communication) and Songwe *et al.* (1988), it was estimated that no more than 10 half-plots could be measured adequately. The selected half-plots included five from the area with high abundances of ectomycorrhizal species and five from the area with low abundances of ectomycorrhizal species. For the low ectomycorrhizal plots half-plots, results showed that the three far end plots (P29, P32 and P34) at a generally lower elevation to the rest of the transect were similar in floristic composition to the near end plots (P3, P4, P7, P8 and P9). It was then logical not to select those half-plots at the far end of the transect. For the high ectomycorrhizal half-plots, P20-P23 differed quantitatively from the others and were excluded. P15 had a high within plot heterogeneity but was compensated for by being the plot with the highest basal area for *Microberlinia bisulcata.*

The ten half-plots finally selected were:

LEM; 3AB, 4BC, 7AD, 8BC, 9BC;

HEM; 15AD, 18CD, 19AB, 24BC, 25CD.

3.2.1.1 Floristic composition of the selected plots.

Both sets of half-plots had different floristic composition in terms of taxa (specifically the ectomycorrhizal species) and densities. The percentage contribution in basal area and density of the ectomycorrhizal species in relation to the rest of species in each of the selected plots are given in Table 3.1. There were a 5.0-fold and 3.5-fold difference between the two set of selected half-plots in the percentage contributions of the ectomycorrhizal species for mean basal area and density abundance respectively.

In all ten half-plots, a total of 148 species were recorded with 114 species represented in the LEM plots and 104 species in the HEM plots. They were all classified into forty-two families (sub-families for Leguminosae) and with six unknowns. A floristic comparison

of the first 40 species (ranked in descending order of basal area contribution) for both sets of half-plots is given in Table 3.2. These species contribute more than 90% and 70% to mean basal area and density respectively in both sets of half-plots. The major ectomycorrhizal species which dominated the groves: *Microberlinia bisulcata, Tetraberlinia moreliana,* and *Tetraberlinia bifoliolata* occurred only in the high ectomycorrhizal plots (with the exception of the single *Tetraberlinia bifoliolata* tree in plot 8C) as well as *Amanoa strobilacea.* Some other species, which included *Staudtia stipitata, Erismadelphus exsul, Strombosia scheffleri, Hypodaphnis zenkeri, Xylopia aethiopica, Crytogonone argentae* and *Xylopia philodora,* occurred only in the low ectomycorrhizal plots.

The percentage contribution of the first 16 families (ranked in decreasing order of mean basal area) to mean basal area of the selected low and high ectomycorrhizal plots are given in Table 3.3. The highest contribution was from the Caesalpinioideae (a sub-family of the Leguminosae) accounting for 61.6% and 17.1% of stand basal area for the HEM and LEM plots respectively. Not all of the caesalpinioids form ectomycorrhizas (see Table 3.2). The family Scytopetalaceae had the highest stand density with a higher abundance in the HEM plots. *Oubanguia alata,* which happens to be the commonest species in Korup, belongs to that family. Of the forty-two families recognised, the majority of the species were in the families (and sub-families); Caesalpinioideae (21), Euphorbiaceae (14), Annonaceae (13), Rubiaceae (11), Sterculiaceae (6) and Olacaceae (6). The number of species, basal area distribution and density of the different species in each family are presented in Table 3.3. Lianes and stranglers were however grouped in one category and were more abundant in the low ectomycorrhizal plots. The most frequent liane was a *Strychnos sp.*

Both basal area and density of the individual species were used to compute the degree of species diversity in both sets of half-plots. The low ectomycorrhizal plots showed higher H and D indices compared to the high ectomycorrhizal plots which were however not significantly different (Table 3.4).

Table 3.1 Basal area (BA) and density (D) of all, and of ectomycorrhizal species in each of the selected five half-plots with low abundance of ectomycorrhizal species (LEM) and 5 half-plots with high abundance of ectomycorrizal species (HEM) on transect P, and percentage contribution to these measures by ectomycorrhizal species, Korup National Park, Mundemba.

		BA (m^2 ha^{-1})			D (ha^{-1})		
Plot	Sub-plot	All species	EM	%EM	All species	EM	%EM
LEM							
3	AB	32.6	3.3	10.1	522	16	3.1
4	BC	34.3	3.9	11.4	447	16	3.6
7	AD	23.5	2.8	10.8	491	22	4.5
8	BC	31.4	3.4	12.1	528	16	3.0
9	BC	27.3	3.3	11.3	488	9	1.8
Mean		29.82	3.34	11.26	495	16	3.2
SE		±1.60	±0.14	±0.30	±12	±2	±0.36
HEM							
15	AD	40.8	24.6	60.3	406	34	8.4
18	CD	34.8	21.4	61.5	413	50	12.8
19	AB	38.7	26.2	67.7	350	50	14.3
24	BC	34.0	15.5	45.6	506	41	8.1
25	AD	30.3	15.8	52.1	425	53	12.5
Mean		35.72	20.7	57.44	420	46	11.1
SE		±1.50	±1.80	±3.16	±21	±3	±1.21

Table 3.2: Floristic comparison of five selected half-plots with low abundance of ectomycorrhizal species (LEM) and five half-plots with high abundance of ectomycorrhizal species (HEM) on transect P, classified into ectomycorrhizal and non-extomycorrhizal species and ranked in decending order to overall mean basal area (BA) abundance in the ten half-plots together with the corresponding frequencies (F) and densities (D) of the trees. * Full family names are given in Appendix 1.

		LEM			HEM			Mean
	Family*	F (n/5)	BA (m^2 ha^{-1})	D (ha^{-1})	F (n/5)	BA (m^2 ha^{-1})	D (ha^{-1})	BA (m^2 ha^{-1})
(a) Ectomycorrhizal species								
Microberlinia bisulcata	CAES	0	0.0	0.0	5	15.5	12.5	7.73
Tetraberlinia bifoliolata	CAES	1	0.18	0.6	5	2.25	7.5	1.22
Tetraberlinia moreliana	CAES	0	0.0	0.0	1	1.67	5.6	0.84
Berlinia bracteosa	CAES	3	1.05	3.1	5	0.18	0.6	0.61
Didelotia africana	CAES	1	0.42	2.5	3	0.52	3.8	0.47
Anthonotha fragrans	CAES	3	0.80	2.5	1	0.06	1.3	0.43
Anthonotha sp.	CAES	1	0.41	1.3	0	0.00	0.0	0.21
Uapaca staudtii	EUPH	2	0.24	2.5	2	0.08	1.9	0.16
others (9 species)			0.24	3.5		0.48	12.8	0.35
sub-total			3.34	16.0		20.7	46.0	12.0

	Family*	LEM			HEM			Mean
		F (n/5)	BA (m^2 ha^{-1})	D (ha^{-1})	F (n/5)	BA (m^2 ha^{-1})	D (ha^{-1})	BA (m^2 ha^{-1})
(b) Non-ectomycorrhizal species								
Oubanguia alata	SCYT	5	3.89	55.0	5	3.80	85.0	3.84
Strephonema pseudocola	COMB	5	1.58	10.0	4	0.87	8.1	1.22
Klaineanthus gaboniae	EUPH	5	1.76	23.7	5	0.38	11.9	1.07
Cola rostrata	STER	5	1.43	48.4	5	0.38	17.5	0.90
Hymenostegia afzelii	CAES	5	0.82	28.1	5	0.70	20.0	0.76
Erythrophleum ivorense	CAES	1	0.80	0.6	1	0.52	0.6	0.66
Diospyros gabunensis	EBEN	5	0.61	21.3	5	0.70	25.0	0.65
Strombosia glaucescens	OLAC	5	0.86	30.6	5	0.26	8.8	0.56
Cola verticillata	STER	3	0.67	3.1	4	0.43	3.8	0.55
Coula edulis	OLAC	5	0.46	5.0	4	0.55	4.4	0.51
Staudtia stipitata	MYRI	2	0.97	1.3	0	0.00	0.0	0.49
Dichostemma glaucescens	EUPH	5	0.59	26.3	5	0.34	16.2	0.47
Erismadelphus exsul	VOCH	3	0.89	3.1	0	0.00	0.0	0.45
Cola lateritia	STER	3	0.71	3.8	1	0.19	1.9	0.45
Baphia laurifolia	PAPI	5	0.47	6.3	4	0.32	4.4	0.39
Vitex sp.	VERB	2	0.28	1.3	1	0.45	0.6	0.37
Irvingia gabunensis	IXON	1	0.07	0.6	4	0.60	3.7	0.34
Vitex grandifolia	VERB	3	0.53	2.5	2	0.97	1.2	0.31

	Family*	LEM			HEM			Mean
		F (n/5)	BA (m^2 ha^{-1})	D (ha^{-1})	F (n/5)	BA (m^2 ha^{-1})	D (ha^{-1})	BA (m^2 ha^{-1})
Dacryodes edulis	BURS	2	0.53	1.9	1	0.52	0.6	0.29
Diospyros iturensis	EBEN	5	0.19	13.1	4	0.37	23.1	0.28
Strombosia scheffleri	OLAC	4	0.53	5.6	0	0.00	0.0	0.28
Diogoa zenkeri	OLAC	5	0.36	15.6	5	0.16	7.5	0.26
Strombosiopsis tetrandra	OLAC	3	0.37	3.8	2	0.12	1.3	0.24
Hypodaphnis zenkeri	LAUR	4	0.46	4.4	0	0.00	0.0	0.23
Fagara tessmannii	RUTA	2	0.38	1.9	1	0.06	0.6	0.22
Xylopia aethiopica	ANNO	2	0.41	1.2	0	0.00	0.0	0.21
Soyauxia gabunensis	MEDU	5	0.23	8.7	4	0.15	6.9	0.19
Scytopetalum klaineanum	SCYT	3	0.30	2.5	1	0.02	0.6	0.16
Amanoa strobilacea	EUPH	0	0.00	0.0	1	0.31	3.1	0.15
Crytogonone argentea	EUPH	2	0.31	1.9	0	0.00	0.0	0.15
Magnistipula glaberima	CHRY	2	0.04	1.3	4	0.25	5.6	0.14
Xylopia philodora	ANNO	1	0.29	0.6	0	0.00	0.0	0.14
Others (99 species)			1.43	130		1.49	106	1.46
Sub-total			26.3	465		14.9	368	20.6
Lianes, stranglers (≥30 cm gbh)			0.18	14.4		0.11	5.6	0.15
TOTAL (all species)			29.8	495		35.7	420	32.8

Table 3.3 Percentage contribution of basal area (BA), tree densities (D) and number of species of the first 16 families in five selected half-plots with low abundance of ectomycorrhizal species (LEM) and five half-plots with high abundance of ectomycorrhizal species (HEM) on transect P.Families are ranked in decending order of overall mean basal area (BA) abundance in the ten half-plots.

Families	LEM			HEM			ALL		
	No. of species	BA (%)	D (ha^{-1})	No. of species	BA (%)	D (ha^{-1})	No. of species	BA (%)	D (ha^{-1})
Caesalpinioideae (s)	12	17.1	46.9	16	61.6	71.7	21	41.4	59.4
Scytopetalaceae	3	14.1	59.4	3	10.7	86.3	3	12.3	72.8
Euphorbiaceae	13	10.6	65.7	9	3.8	38.8	14	6.9	52.2
Sterculiaceae	6	9.5	59.4	4	2.8	23.8	6	5.9	41.6
Olacaceae	6	8.7	61.3	4	3.1	21.9	6	5.6	41.6
Combretaceae	1	5.3	10.0	1	2.4	8.1	1	3.7	9.1
Ebenaceae	4	2.9	35.6	3	3.1	53.1	4	3.0	44.4
Annonaceae	12	4.3	21.3	8	0.9	16.1	13	2.4	18.8
Verbenaceae	2	2.7	3.8	3	1.6	2.5	3	2.1	3.1
Papilionoideae (s)	3	2.5	10.0	2	1.0	6.3	3	1.7	8.1
Myristicaceae	1	3.3	1.3	1	0.1	0.6	2	1.5	0.9
Vochysiaceae	1	3.0	3.1	0	0.0	0.0	1	1.4	1.6
Lauraceae	3	2.5	10.6	1	0.1	1.3	3	1.2	5.9
Ixonanthaceae	1	0.2	0.6	2	1.9	4.4	2	1.1	2.5
Rubiaceae	10	1.3	10.7	5	0.6	12.5	11	1.0	11.6
Burseraceae	1	1.8	1.9	1	0.1	0.6	1	0.9	1.3
Others (26 + 6 unknowns)	35	9.6	93.4	41	5.9	66.2	54	7.4	72.6
All lianes (≥30 cm gbh)	-	0.6	14.4	-	0.3	5.6	-	0.5	10.0
TOTAL	114	100	495	104	100	420	148	100	458

(s) = sub-family in Leguminosae.

Table 3.4 Species diversity indices for all species (≥30 cm gbh) in five selected half-plots with low abundance of ectomycorrhizal species (LEM) and five half-plots with high abundance of ectomycorrhizal species (HEM) on transect P using basal area (BA) and densities (D) of the individual species in the respective sets of half-plots as measures of abundance.

	LEM		HEM	
	BA (m^2 ha^{-1})	Density (ha^{-1})	BA (m^2 ha^{-1})	Density (ha^{-1})
Shannon-Wiener Diversity index (H)	3.820	3.771	2.632	3.641
Simpson's index (D)	0.962	0.983	0.796	0.939

3.2.2 Layout of litter traps.

Each half-plot was divided into 128 5m × 5m quadrats. With the aid of random numbers, twenty quadrats were selected and to each was allocated a litter trap. The litter traps were positioned closest to the centre of the quadrat as was practicable. These traps maintained the same position during the entire sampling period. The traps consisted of V-shaped galvanised mesh (40 cm × 40 cm × 30 cm deep) with a mesh-size of 1.5 mm, raised 40 cm above the forest floor by wooden legs (see Plate 1). Other traps were also use to replace those either damaged or removed. The substitute traps had square wooden frames with nylon mesh fitted at the bases. The frames were 40 cm × 40 cm and 10 cm deep and at the bases were fitted nylon mesh of 1.5 mm mesh-size. Seven traps were replaced during the entire study period. These were similarly raised 40 cm above the forest floor with wooden legs. The mesh-size was sufficient to allow free passage rain water during the rainy season while retaining the very fine litter fragments. The litter traps were raised above the forest floor in order to prevent contamination by rain-splashed litter and soil particles. This arrangement also deterred animal browsing.

3.2.3 Litter collection and treatment.

The litter traps were emptied twice every month, once between the 14th and 16th day of the month (depending on the number of days in that month) and once at the end of the each month. Litter from the twenty litter traps in each half-plot were bulked in the field. This frequent collection was to minimize the loss of litter by decomposition and to limit nutrient loss through leaching. On collection, the litter samples were taken without delay to the Forestry Research Station Kumba, where they were air-dried in a well ventilated room (room temperature of 27°C) on large plastic sheets for 3-5 days depending on their moisture content. This conserved the leaf shape and facilitated sorting into the various litter fractions.

The two sets of collection for each month was then bulked at sub-plot levels for sorting.

Plate 3.1: **V-shaped galvanised mesh trap for litter collection.**

The air-dried litter samples were sorted into the following categories (following Proctor 1983a):

1. Leaf components: consisting of whole leaves, leaflets and rachises of compound leaves, leaf petioles of digitate leaves, bracts and recognizable leaf fragments.
2. Small wood fractions: consisting of small branches and twigs (≤ 2.5 cm diameter) and bark fragments not greater than that size as well.
3. Reproductive components: flowers, fruits (all categories), seeds, pods and other recognizable flower parts.
4. Epiphytic mosses and lichens: Those attached to woody fragments or leaves in litter were separated.
5. Trash: consisting of non-recognizable fragments ≤ 2 mm in size.

The trash fraction was the most diverse and consisted of very fine plant fragments, insect frass, droppings and chaffs from canopy feeders. All wood fractions greater than 2.5 cm were discarded.

The leaf fraction was then sorted into the individual species as far as could be identified. More than 80% the amount (dry weight) of the leaves were identified to the various genera and species. The bulk of the unidentified leaf fraction consisted of leaves from lianes and climbers, as well as highly fragmented leaves. Leaves trapped in the tree canopy usually deteriorate before falling and as such they reach the litter trap without distinctive features for them to be properly identified.

After sorting, the various litter fractions were put into labelled paper envelopes and oven-dried at 85°C for 48 hrs to constant weight. These were then weighed separately and stored in plastic bags for later chemical analysis. The oven-dried weights of the various litterfall fractions for the ten half-plots from May 1990 to June 1992 are given in Appendix 2. The various species, their code numbers, family names and authorities are given in Appendix 1.

Twenty-six species which included; the six major ectomycorrhizal species: *Anthonotha*

fragrans, Berlinia bracteosa, Didelotia africana, Tetraberlinia bifoliolata, T. moreliana and *Microberlinia bisulcata*; six other large emergents an canopy top species: *Erismadelphus exsul, Erythrophleum ivorense, Staudtia stipitata, Strephonema pseudocola, Irvingia gabonensis* and *Vitex* sp.; eleven canopy species: *Cola rostrata, Cola verticillata, Coula edulis, Diospyros gabunensis, Diospyros iturensis, Dichostemma glaucescens, Klaineanthus gaboniae, Hypodaphnis zenkeri, Strombosia glaucescens, Hymenostegia afzelii* and *Oubanguia alata; Warneckea memecyloides* (an understorey species) and *Strychnos* sp. and *Ageleae* sp. (both lianes) were selected for detailed investigation on their spatial and temporal distribution patterns. These included the 16 most abundant species (in terms of basal area contribution in the plots) (Table 3.2), major contributors to total leaf litter (Table 3.9). The commonest understorey species and lianes were also included.

3.2.4 Data analysis

The layout was of a split-plot design with forest type (LEM and HEM) and sampling date (months) as the factors and the five replicate half-plots in each forest type as the experimental units. Litterfall records were obtained from the same plots at each sampling date over a period of twenty-six months resulting in repeated measures on this factor. Repeated measures of this nature are often correlated (Diggle and Donnelly 1989, Moser *et al.* 1990, Verbyla and Curtis 1992) and stronger between adjacent observations than between observations that are well separated (Gurevitch and Chester 1986, Gumpertz and Brownie 1993).

A univariate repeated measures analysis (Winer *et al.* 1991) was carried out to investigate the differences in litterfall patterns between the two forest types and how this varied for the sampling dates over time and their interactions which defined the shape of the mean profiles of litterfall patterns. Following this approach, the two sources of experimental variations are separated:

(1) plot to plot variations (between plots) for testing hypotheses on differences between the forest types as the plots are replicated in both forest types.

(2) variations amongst the sampling dates in the plots (within plots) for testing

hypotheses on collection dates and interactions between forest type and collection dates as the plots' measurements at each given date provided replicates for date to date variations.

The validity of these tests are based on the structure of the pooled variance-covariance matrix which is required to have a compound symmetry. This assumption may be violated as a result of the correlation amongst the repeated measurement errors. Under such conditions the univariate test is considered too robust and will require approximate corrections (Greenhouse and Geisser 1959). The Box's test equality of the covariance matrices could not be carried out as there were fewer observation units (plots) than time points thereby resulting in a singular estimate. The observations at the twenty-six time points were then split into 10 separate matrices, each consisting of five consecutive time points (1-4, 5-9, 10-14, 15-19, 20-25, 4-8, 9-13, 14-18, 19-23, 22-26). The Box's chi-squared test and F test of symmetry of the covariance matrices were carried out for each of the these pooled variance-covariance matrices. For each of these pooled matrices the Greenhouse-Geisser epsilon ε was estimated (Greenhouse and Geisser 1959) and the mean value for the ten separate matrices used to adjust the F-test degrees of freedom. These approximate corrections were carried out only on the within-plots tests as the between plots tests are unaffected by the structure of the variance-covariance matrices of the repeated measure factor.

Separate analysis were carried out for total litterfall, leaves, small wood, reproductive, mosses and lichen and trash fractions as well as on the log transformed data set of these litter fractions and total litterfall (small wood and mosses and lichen fractions were not normally distributed as seen from the plots of the residuals versus the fitted values). The REPMEAS procedure of GENSTAT 5 (Payne 1987) was use for the analysis of these repeated measures data. Furthermore two-sample-t testing for differences in litter production (total litterfall and all the litterfall fractions) between the two forest types were carried out on the individual half-plot values at each sampling date.

Inter-annual variability in litterfall for both LEM and HEM plots was investigated using

the Mann-Whitney U test in comparing year 1 (July 1990-June 1991) and year 2 (July 1991-June 1992) dry weight values for total litterfall and the various fractions, as well as the percentage contribution of the litter fractions to total litterfall.

Correlation analysis was carried out between the various litter fractions summed across the five replicate half-plots in each forest type to ascertain if common regulating factors were operating in these forests (Cuevas and Medina 1986). Correlation analysis was also carried out between total litterfall and the various fractions for LEM and HEM plots.

Principal component analysis (PCA) was carried out on the monthly leaf litter dry-weights of the selected twenty-six species recorded in LEM and HEM forests to investigate their associations in litterfall patterns. The first three principal axes of this multivariate analysis accounted for 64% of the total variation in litterfall patterns amongst these selected species. The co-ordinates for the individual species ordination were obtained by multiplying their respective scores of the first three principal axes from the PCA and the square root of the eigen-values of these principal axes (Ludwig and Reynolds 1988). The PCA was carried using the Multivariate procedure of MINITAB (Minitab Inc. 1989).

To investigate the effects of weather (climatic variables) on litterfall, the mean monthly rates of total litterfall and the fractions were separately correlated with the monthly averages of mean daily temperature and rainfall recorded during the sampling period. Since there may be a considerable time-lag between cause and effect, a time-lag correlation analysis was carried out between total litterfall, leaves, small wood, reproductive parts and mean daily temperature and rainfall (Lam and Dudgeon 1985; Martínez-Yrízar and Sarukhán 1990). This involved computing the linear correlation (r) between total litterfall, litter fractions and increasing lags of the climatic variables. If the variables are associated with a time-lag, then significant correlations will be found when the displacement (following the increased lags) of the climatic variables coincides with the time-lag under investigation (Martínez-Yrízar and Sarukhán 1990). This tends to look at the time lag between peaks in litterfall (total and fractions) and the maximum influence of the particular climatic variable.

3.3 RESULTS

3.3.1 Annual estimates of litterfall

3.3.1.1 Total litterfall

The annual rate of litterfall was estimated at 8.99 ± 0.48 and 8.33 ± 0.93 t ha^{-1} yr^{-1} for LEM and HEM plots respectively (Table 3.5.). There was no significant difference in total litterfall between LEM and HEM plots ($P>0.05$). Significant differences were however found in the log transformed dry weight values ($p<0.05$) (Table 3.6b). Differences between the sampling dates were highly significant ($p<0.001$) as well as the interaction between forest types and sampling dates ($P<0.001$). Significant differences were found between the forest types during the wet months (May - October) when individual plot values were compared at each sampling date (Table 3.7). The variation between years was not significant for LEM and HEM plots though there was an increase in litterfall in the second year by 14.2% and 21.7% for LEM and HEM plots respectively (Table 3.5).

3.3.1.2 Litter components

The annual estimates of the contribution of the different litter fractions are given in Table 3.5. Amongst the individual litter components, leaves constituted the largest fraction, contributing 62.90% and 61.59% of total litterfall for both LEM and HEM plots respectively (Table 3.5). The contribution of the other fractions were : 21.23% and 19.45% for small wood; 9.45% and 14.05% for the reproductive fraction; 0.11% and 0.60% for mosses and lichens; 6.22% and 4.44% for trash. Neither leaves nor small wood nor reproductive fractions differed significantly ($p < 0.05$) between LEM and HEM plots in both absolute and proportional contribution (% of total litterfall). Contributions of the leaf litter however were significantly higher in the LEM forests compared with the HEM forest following the logarithmic transformation (Table 3.6a). Significant differences were found between the two forest types in the contributions of moss and lichen and trash ($F=68.02$ and 5.95; $df=25,200$; $p< 0.001$ and 0.05; respectively). Contributions of all the fractions differed significantly in both forests for the different months ($p<0.001$).

Interactions between the forest types and sampling dates were also highly significant for all the litter fractions ($p<0.001$) with the exception of the mosses and lichen. When the individual plot values were compared at each sampling date, the contributions of the leaf fraction were significantly higher in the LEM forest during the wet months (similar trend with total litterfall) and the reproductive fraction during the dry months in the second year only for both LEM and HEM plots (Table 3.7).

There was an increase in all the litter components (except for mosses and lichens) in the second year (July 1991-June 1992) with the contribution of the reproductive fraction being almost two-fold that of the previous year (Table 3.5). This increase did not result in any significant difference between the years for LEM and HEM plots for both absolute and percentage contribution of the various fractions to total litterfall.

3.3.2 Temporal pattern in litterfall distribution

3.3.2.1 Total litterfall

The temporal patterns in total litterfall for the 26 months (May 1990-July 1992) for LEM and HEM plots is given in Fig.3.1. Litterfall was continuous, highly seasonal and exhibited a mono-modal pattern. Peaks were recorded between December and March (dry months) and the minima occurred between May and September (wet months). Two peaks were however recorded for the HEM plots during the second year (July 1991 - June 1992). The first peak occurred in December 1991 (coinciding with maximum leaf fall) and the second in March 1992 (coinciding with maximum flower fall and small twigs).

This marked seasonal pattern was evident in the significant ($p<0.05$) difference between the mean monthly litterfall of the wet (April-November) and dry (December-March) seasons for LEM and HEM plots respectively (Table 3.5). Though the dry season was shorter compared with other tropical forests, 40% and 53% of total litterfall occur in the dry season for both LEM and HEM plots respectively. The strong seasonal effect was significant ($p<0.05$) in the first year for the LEM plots and in the second year for the HEM plots (Table 3.8). The temporal variability in litterfall was more pronounced for the

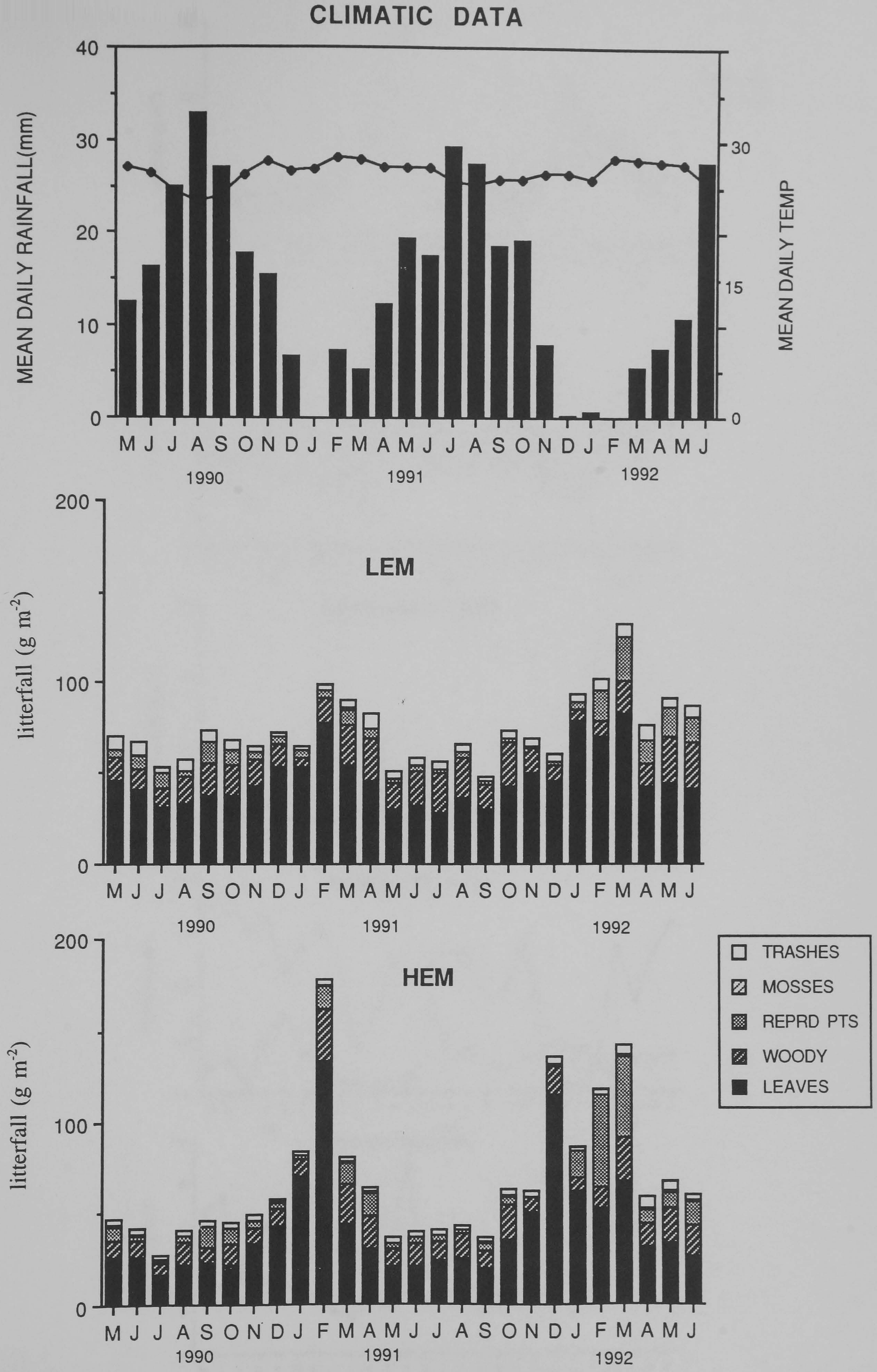


Figure 3.1: The temporal distribution pattern of litterfall collected from five replicate plots from May 1990 to June 1992 in LEM and HEM forests, Korup National Park, Cameroon. Monthly rainfall and temperature recorded during the study period are also presented.

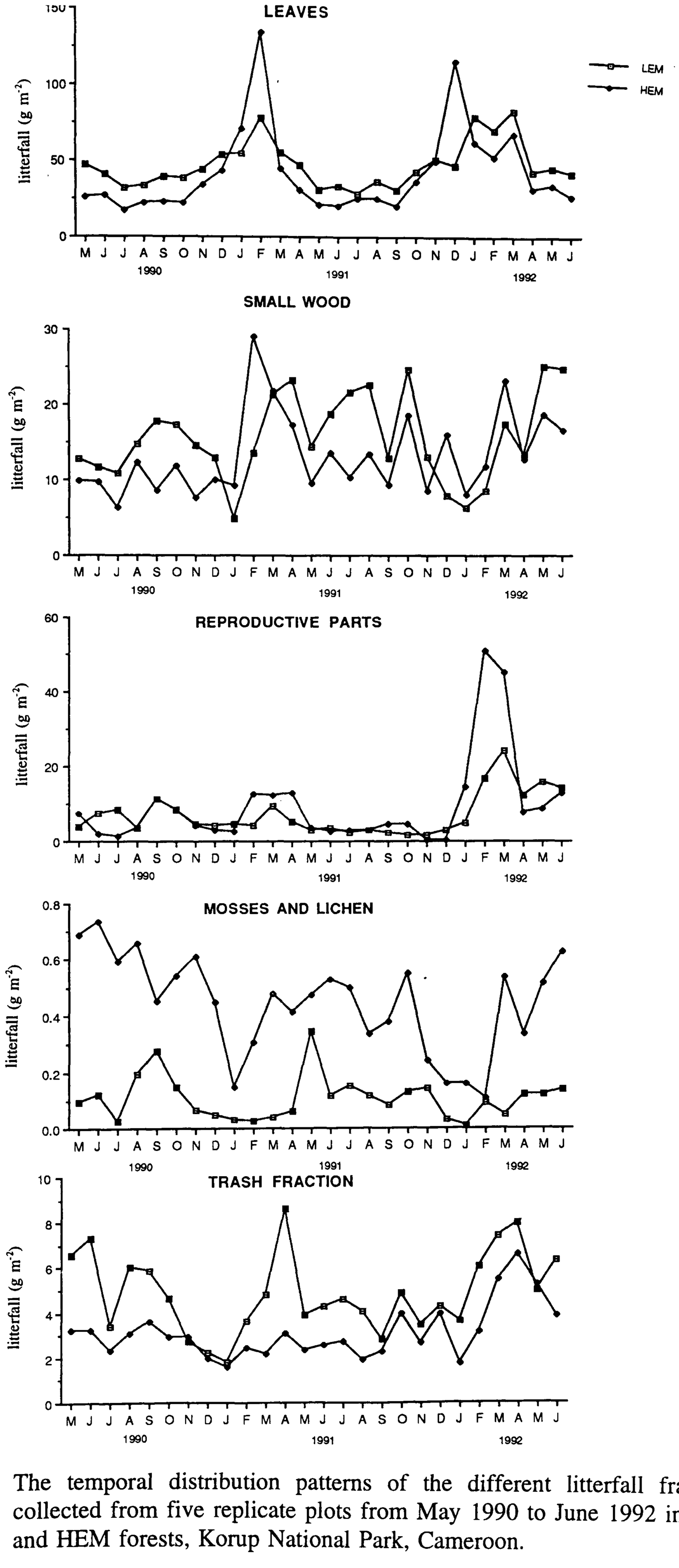


Figure 3.2: The temporal distribution patterns of the different litterfall fractions collected from five replicate plots from May 1990 to June 1992 in LEM and HEM forests, Korup National Park, Cameroon.

Table 3.5: Estimated annual litterfall (t ha^{-1} yr^{-1}) from 100 (0.4m x 0.4m) traps in both LEM and HEM forests, Korup National Park Mundemba, Cameroon.

	PERIOD					
	1990-1991		1991-1992		MEAN (1990-1992)	
Litter fraction	Dry weight	%(Range)	Dry weight	%(Range)	Dry weight	percentage
LEM						
Leaves	5.34	(52.2-82.9)	5.98	(48.1-84.3)	5.66±0.39	62.9
Small wood*	1.84	(7.35-31.5)	1.98	(6.77-37.8)	1.91±0.15	21.2
Reproductive parts+	0.694	(4.10-15.5)	1.01	(2.23-18.3)	0.854±0.14	9.45
Moss lichen	0.014	(0.03-0.66)	0.01	(0.01-0.26)	0.013±0.002	0.111
Trash	0.516	(2.70-10.5)	0.60	(3.86-10.4)	0.559±0.04	6.22
TOTAL	8.40		9.59		8.99±0.48	
HEM						
Leaves	4.807	(47.84-83.94)	5.45	(43.9-85.0)	5.13±0.72	61.6
Small wood*	1.565	(10.92-34.21)	1.68	(9.32-31.0)	1.62±0.14	19.5
Reproductive parts+	0.781	(3.12-24.30)	1.55	(0.25-43.1)	1.17±0.31	14.1
Moss lichen	0.057	(0.17-2.17)	0.045	(0.09-1.22)	0.051±0.004	0.600
Trash	0.307	(1.36-8.41)	0.432	(1.99-11.2)	0.370±0.03	4.44
TOTAL	7.516		9.15		8.33±0.93	

* < 2cm diameter, + flowers, fruit pods

Table 3.6a: Univariate analysis of the split-plot repeated measures model for leaf litter (and the log transformed values) collected over a period of twenty-six months in LEM and HEM forests, Korup National park, Mundemba, Cameroon.

1. LEAVES					Adj.P>F
SOURCE	df	MS	F	P>F	G-G
Between-plots					
Ecto	1	19760	3.23	0.110	
Residual	8	6122	2.65		
Within-plots					
Date	25	42785	18.54	<0.001	<0.001
Ecto * Date	25	11443	4.96	<0.001	<0.001
Residual	200	2308			
TOTAL	259				

Log(LEAVES)					Adj.P>F
SOURCE	df	MS	F	P>F	G-G
Between-plots					
Ecto	1	4.923	7.04	0.029	
Residual	8	0.699	12.43		
Within-plots					
Date	25	1.592	28.29	<0.001	<0.001
Ecto * Date	25	0.290	5.15	<0.001	<0.001
Residual	200	0.056			
TOTAL	259				

Note: Adj.P>F are probabilities associated with the Greenhouse-Geisser (G-G) adjusted F-test with ε=0.5283 for leaves; ε=0.5817 for log(leaves).
Ecto is the forest type (LEM and HEM).

Table 3.6b: Univariate analysis of the split-plot repeated measures model for total litterfall (and log transformed values) collected over a period of twenty-six months in LEM and HEM forests, Korup National Park, Mundemba, Cameroon.

TOTAL LITTERFALL					Adj.P>F
SOURCE	df	MS	F	P>F	G-G
Between-plots					
Ecto	1	31025	2.37	0.162	
Residual	8	13096	4.11		
Within-plots					
Date	25	69317	6.64	<0.001	<0.001
Ecto * Date	25	19096	8.89	<0.001	<0.001
Residual	200	3184			
TOTAL	259				
Log(TOTAL)					Adj.P>F
SOURCE	df	MS	F	P>F	G-G
Between-plots					
Ecto	1	2.673	6.64	0.033	
Residual	8	0.402	8.89		
Within-plots					
Date	25	1.097	24.25	<0.001	<0.001
Ecto * Date	25	0.260	5.76	<0.001	<0.001
Residual	200	0.045			
TOTAL	259				

Note: Adjusted P>F are probabilities associated with the Greenhouse-Geisser (G-G) adjusted F-test with ε=0.5293 for total litterfall; ε=0.5749 for log(total litterfall).
Ecto is the forest type (LEM and HEM).

Table 3.7 Level of significance of students t-test for differences in the different litter fractions and total litterfall and litterfall between the LEM and HEM forests at each sampling date ($n_1=n_2=5$) for LEM and HEM forests), Korup National Park, Mundemba.

	1990								1991												1992					
	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J
Leaves	*	*	**	*	*	**	NS	NS	NS	NS	NS	*	*	**	NS	**	**	NS	NS	*	NS	*	NS	NS	NS	*
Wood	NS	NS	*	NS	*	NS	*	NS	NS	NS	NS	NS	NS	NS	*	*	NS	NS	NS	*	NS	NS	NS	NS	NS	NS
Rep: parts	NS	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	*	*	NS	NS	NS	NS
Moss/ lichen	*	*	*	NS	NS	*	*	NS	*	*	*	**	NS	*	**	**	*	**	NS	*	*	NS	*	**	*	**
Trash	*	NS	NS	**	*	*	NS	NS	NS	NS	*	*	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Total	*	*	**	NS	*	**	NS	NS	NS	*	NS	*	*	*	NS	*	NS	NS	NS	*	NS	NS	NS	NS	NS	*

significant level: * = $p<0.05$, ** = $p<0.01$, NS = Not significant.

Table 3.8: Estimated mean litterfall (g m^{-2} $month^{-1}$) for dry (December-March) and wet (April-November) seasons for both LEM and HEM plots in Korup National Park, Mundemba, Cameroon. (values in parentheses are SE of mean, n=5).

Site	Year	Season	Leaves		Small wood		Reproductive parts		Mosses & lichen		Trash		Total	
LEM														
	1990-91	Dry	60.0	(5.9)*	13.2	(3.4)	5.49	(1.3)	0.05	(0.005)*	3.09	(0.70)	81.8	(7.9)*
		Wet	36.7	(2.1)	16.4	(1.3)	5.94	(1.1)	0.15	(0.039)	4.91	(0.67)	64.1	(3.8)
	1991-92	Dry	69.7	(8.1)*	10.1	(2.5)*	12.1	(5.1)	0.05	(0.02)*	5.31	(0.86)	97.2	(15.0)
		Wet	39.9	(2.6)	19.8	(2.0)	6.61	(2.2)	0.13	(0.01)	4.85	(0.58)	71.3	(5.1)
	1990-92	Dry	64.9	(5.0)**	11.6	(2.0)*	8.81	(2.7)	0.04	(0.009)***	4.20	(0.66)	89.5	(8.2)*
		Wet	38.3	(1.7)	18.1	(1.2)	6.27	(1.2)	0.14	(0.02)	4.88	(0.43)	67.7	(3.2)
HEM														
	1990-91	Dry	72.7	(2.1)	17.5	(4.8)	7.60	(2.8)	0.34	(0.07)	2.01	(0.18)	100	(26.0)
		Wet	23.7	(2.0)	10.8	(1.3)	5.96	(1.5)	0.54	(0.03)	2.83	(2.7)	43.8	(1.7)
	1991-92	Dry	74.3	(14.0)	14.8	(3.3)	27.7	(12.0)	0.24	(0.10)	3.55	(0.77)	120	(12.0)*
		Wet	31.0	(3.3)	13.6	(1.4)	5.51	(1.4)	0.44	(0.05)	3.62	(0.57)	54.1	(4.2)
	1990-92	Dry	73.5	(14.0)**	16.1	(2.7)	17.7	(6.9)	0.29	(0.06)*	2.78	(0.47)	110	(14.0)**
		Wet	27.4	(2.1)	12.2	(0.1)	5.73	(1.0)	0.49	(0.03)	3.23	(0.30)	49.0	(3.0)

* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$.

HEM plots with a ratio of minimum to maximum monthly litterfall of 1:6.5 compared to 1:2.7 for the LEM plots.

3.3.2.2 Litter Components

The temporal patterns exhibited by the various litterfall fractions for both LEM and HEM plots are presented in Figure 3.2. The different fractions showed varying patterns at both forests. The leaf fraction being the major litterfall constituent, followed the same pattern as total litterfall with marked seasonality. This resulted in more than two-thirds of annual litterfall being recorded in the dry months (December-March) (see Table 3.8). In the first year, peaks in leaf fall were recorded in February 1991 for both LEM and HEM plots whilst in the second year they occurred earlier in December for the HEM plots, and were prominent from January to March 1992 for the LEM plots. Much variation was exhibited in the small wood fractions in both forest types. Whilst the contribution of small wood was high in the wet season for the LEM plots, the reverse occurred for the HEM plots which had major peaks during the dry season and minor peaks during the wet season. For the reproductive fraction, two low peaks were recorded in September 1990 and March 1991 for LEM and HEM plots in the first year. In the second year there was a very pronounced peak in February to March 1992 as a result of profuse flowering of most of species. Moss and lichen fractions showed a significant ($p<0.05$) seasonal pattern with the highest amounts falling during the early part of the wet season in the LEM and HEM plots for both years (Table 3.8).

The trash fractions exhibited very variable patterns throughout the sampling period. They showed inconsistent peaks in the wet season for the LEM plots in June 1990, August/September 1990 and April 1991 in the first year, and March/April 1992 in the second year. For the HEM plots, this fraction was consistently low with similar fluctuations as the LEM plots but with a sudden rise from February 1992 to a peak in April 1992. The contribution (% of total litterfall) of the various litter fractions was fairly similar for the LEM and HEM plots at each sampling date (except for the reproductive fraction which showed a marked difference of about 20% in February 1992).

3.3.3 Contribution by the various species to leaf litter.

Leaf fall and percentage contribution to total leaf litter were estimated on an annual basis for the 26 selected species in both LEM and HEM plots (Table 3.9). These species contributed 56.3 and 77.8% of total leaf litter for both LEM and HEM plots respectively. The bulk of the leaf litter came from *Microberlinia bisulcata*, *Tetraberlinia bifoliolata*, and *Oubanguia alata* for the HEM plots. These species contributed approximately 54% of the total leaf fall in the HEM plots. *Oubanguia alata*, *Erythrophleum ivorense* and *Strephonema pseudocola* were the major contributors and accounted for about 20.5% of total leaf litter in the LEM plots. The six dominant ectomycorrhizal species as a whole contributed 53.9% to total leaf litter in the HEM plots compared to 6.3% in the LEM plots.

It was also noticed that some species which were not enumerated in the plots contributed to leaf litter. This must have been from trees outside the plots or from smaller trees below the girth limit of 30 cm which was the minimum girth size for the original enumeration (Gartlan *et al.* 1986). When these trees were classified on the basis of their crown position, the emergents and top canopy species (dominant) contributed more to leaf litter in spite of their relatively few numbers (Table 3.9). Some of the canopy species particularly *Oubanguia alata* and *Hymenostegia afzelii*, by virtue of their high abundance in both forests were also predominant in leaf fall in the LEM and HEM forests (Table 3.9). *Warneckea memecycloides* was the principal understorey species and contributed significantly to total leaf litter. *Strychnos* sp. which was the commonest liane identified also contributed substantial amounts to total leaf litter and was ranked amongst the first 10 major contributors at both sites (Table 3.9).

The various species however showed varying temporal distribution patterns at both sites. Most of the species showed strong seasonality in leaf fall with pronounced peaks during the dry months. The percentage contribution of each of the species to the monthly leaf litter and total leaf litter (sum over the whole sampling period for the respective species) are presented in Figure 3.3a - 3.3c. *Microberlinia bisulcata, Anthonotha fragrans* and *Berlinia bracteosa* which are all ectomycorrhizal as well as being amongst the top

canopy species were strongly deciduous and shed all their leaves at different times during the dry season (November-March). Their high abundance in the HEM forest accounted for the pronounced peak in leaf fall in that forest during the dry season. The two peaks exhibited by *Berlinia bracteosa* in early and late dry season were due to different timings in leaf fall for different individual trees.

Both *Tetraberlinia moreliana* and *T. bifoliolata* shed their leaves in short bursts in intervals of 3-4 months all round the year. *Didelotia africana, Erismadelphus exsul, Erythrophleum ivorense, Strephonema pseudocola, Vitex* sp. all top canopy species, had their leaf fall concentrated within the dry season. *Erythrophleum ivorense,* however, had an unusual leaf fall in September 1990 contributing significantly to that month's leaf fall for the HEM plots. *Strephonema pseudocola* showed different patterns for LEM and HEM plots with two peaks in early dry season and rainy season in the HEM plots (Figure 3.3c). *Staudtia stipitata* and *Irvingia gabonensis* on the contrary contributed more to leaf litter in the wet season despite pronounced dry season peaks in February 1991 for *Staudtia stipitata* and in February 1992 for *Irvingia gabonensis.*

The majority of the canopy species contributed higher proportions to the monthly leaf litter during the wet season than in the dry season. *Oubanguia alata* showed major peaks in June 1990, April 1991 (wet months) and *Coula edulis* also shed its leaves in short bursts in LEM plots at intervals of 2-3 months and showed major peaks in March-June for the HEM plots. *Dichostemma glaucescens, Klaineanthus gaboniae, Cola rostrata* and *Cola verticillata* all showed similar seasonal patterns with peaks in leaf fall in the late dry season and early rainy season. This was more prominent in the second year of sampling. Peaks in leaf fall for *Diospyros iturensis* appeared only in the wet season. *Warneckea memecyloides,* the understorey species, showed a different pattern in both LEM and HEM plots: leaf fall was high in the dry season and early rainy season for the LEM plots and was mostly constant in the HEM plots but with a sharp peak occurring in May 1992. This species however contributed highly to monthly leaf litter in the wet season. *Strychnos* sp. shed their leaves in short bursts with a greater part falling in the wet season (Figure 3.4b).

Ordination of the twenty-six species using the first two principal axes classified them into three distinct groups in relation to the litterfall patterns (Figure 3.3). The eigen-values, proportion and cumulative variability of the first five axes of the principal component analysis are presented in Table 3.10. Group one consisted of: *Didelotia africana, Diospyros gabunensis, Microberlinia bisulcata, Tetraberlinia bifoliolata* and *T. moreliana*; group two: *Anthonotha fragrans, Cola rostrata, Cola verticillata, Oubanguia alata, Hymenostegia afzelii* and *Diospyros iturensis*; Group three: *Berlinia bracteosa, Coula edulis, Dichostemma glaucescens, Erismadelphus exsul, Erythrophleum ivorense, Klaineanthus gaboniae, Staudtia stipitata, Strephonema pseudocola, Strychnos sp., Vitex sp., Warneckea memecyloides, Strombosia glaucescens* and *Hypodaphnis zenkeri.* Group one consist of species which were strongly seasonal, shedding the bulk of their leaves in the dry season and included the major ectomycorrhizal species (Figure 3.3a). Group two consisted of species that had either minor or major peaks in the wet season (Figure 3.3b). Group three consisted of species that shed their leaves at the later part of the dry season and early wet season (or the transitional period between the dry and wet seasons)(Figure 3.3c).

Table 3.10: Results of the first six principal axes of the principal component analysis on monthly leaf litter of twenty-six selected species in the LEM and HEM forests, Korup National Park, Mundemba, Cameroon. (Six species were however represented only in the HEM forests).

	Principal axes				
	PA1	PA2	PA3	PA4	PA5
Eigen-value	10.66	3.45	2.84	1.53	1.13
Proportion	0.40	0.13	0.11	0.06	0.04
Cumulative	0.40	0.53	0.64	0.62	0.66

Table 3.9: Annual estimates of individual species contribution to total leaf litter in LEM and HEM forests, Korup National Park, Mundemba. Classified in to a) Canopy top, b) canopy, c) Understorey species and d) lianes and climbers (superscript number indicates rank in percentage contribution to total leaf litter).

Species	Family*	n	LEM g/m2/yr	LEM %Total leaf litter	F	HEM g/m2/yr	HEM %Total leaf litter
a) Canopy top species							
Anthonotha fragrans	Caes	4	3.49	0.62	2	1.36	0.27
Berlinia bracteosa	Caes	5	14.3	2.54[9]	1	0.43	0.09
Didelotia africana	Caes	54	3.40	0.60	6	5.62	1.13[11]
Erismadelphus exsul	Voch	5	14.14	2.51[10]	0	0.01	0.002
Erythrophleum ivorense	Caes	2	38.9	6.91[2]	1	7.92	1.59[7]
Staudtia stipitata	Myri	2	15.8	2.81[6]	0	0.01	0.001
Strephonema pseudocola	Comb	16	30.0	5.49[3]	13	5.97	1.20[10]
Microberlinia bisulcata	Caes	0	0	0	20	188	37.8[1]
Tetraberlinia bifoliolata	Caes	2	14.0	2.49[11]	12	30.1	6.05[4]
Tetraberlinia moreliana	Caes	0	0	0	9	42.5	8.53[2]
Irvingia gabonensis	Ixon	1	0.47	0.08	6	11.2	2.24[6]
Vitex sp.	Verb	2	14.0	2.48[12]	1	2.03	0.41
b) Canopy species							
Cola rostrata	Ster	78	6.74	1.20	28	2.42	0.49
Cola verticillata	Ster	5	5.13	0.91	6	3.74	0.75
Coula edulis	Olac	8	7	1.24	7	3.64	0.73
Diospyros gabunensis	Eben	34	1.51	0.27	40	3.92	0.79[12]
Diospyros iturensis	Eben	5	3.01	0.54	9	3.74	0.75
Dichostemma glaucescens	Euph	42	5.93	1.05	26	2.83	0.57
Klaineanthus gaboniae	Euph	38	14.9	2.65[7]	19	3.52	0.71
Hypodaphnis zenkeri	Laur	7	8.29	1.47	0	1.35	0.27
Strombosia glaucescens	Olac	49	6.94	1.23	14	1.16	0.23
Hymenostegia afzelli	Caes	45	16.0	2.85[5]	32	11.9	2.39[5]
Oubanguia alata	Scyt	88	45.4	8.06[1]	136	38.8	7.81[3]
c) Under storey species							
Warneckea memecyloides	Mela	-	14.4	2.57[8]	-	7.02	1.42[9]
d) Lianas and climbers							
Strychnos sp.	Loga	-	29.2	5.19[4]	-	7.22	1.45[8]
Agelaea sp.	Conn	-	3.16	0.56	-	0.47	0.10

* full family names are given in appendix 1.
n= numbers of individuals in the selected plots.

Table 3.11: Correlation matrix for monthly mean litterfall fractions and total litterfall for LEM and HEM forests, Korup National Park, Mundemba, Cameroon. (n=26).

Litter fraction	Leaves	Small wood	Reproductive parts	Moss & Lichen	Trash	Total
LEM						
Small wood	-0.302					
Reproductive parts	0.422*	0.155	0.155			
Moss & lichen	-0.532**	0.296	0.296	-0.057		
Trash	0.056	0.336	0.336**	0.503**	0.188	
Total	0.852**	0.144	0.741**	-0.337	0.398*	
HEM						
Small wood	0.542**					
Reproductive parts	0.216	0.343				
Moss & lichen	-0.579**	-0.014	-0.229			
Trash	-0.003	0.324	0.301	0.192		
Total	0.921**	0.690**	0.555**	-0.514**	0.178	
Between Forest types	0.696**	0.442*	0.762**	0.297	0.659**	0.705**

* = $p<0.05$, ** = $p<0.01$

Table 3.12 Correlation coefficient between various litterfall fractions, total litterfall and some climatic variables for LEM and HEM forests in Korup National Park, Mundemba, Cameroon.

	Rainfall		Temperature	
Litter Fraction	LEM	HEM	LEM	HEM
Leaves	-0.733**	-0.653**	0.507**	0.404**
Small wood	0.518**	-0.222	-0.080	0.424**
Reproductive parts	-0.195	-0.369**	0.284	0.396*
Moss and lichen	0.579**	0.632**	-0.342	-0.244
Trash	0.109	-0.063	0.063	0.215
Total	-0.483**	-0.658**	0.479**	0.511**

* = $p<0.05$ ** = $p<0.01$

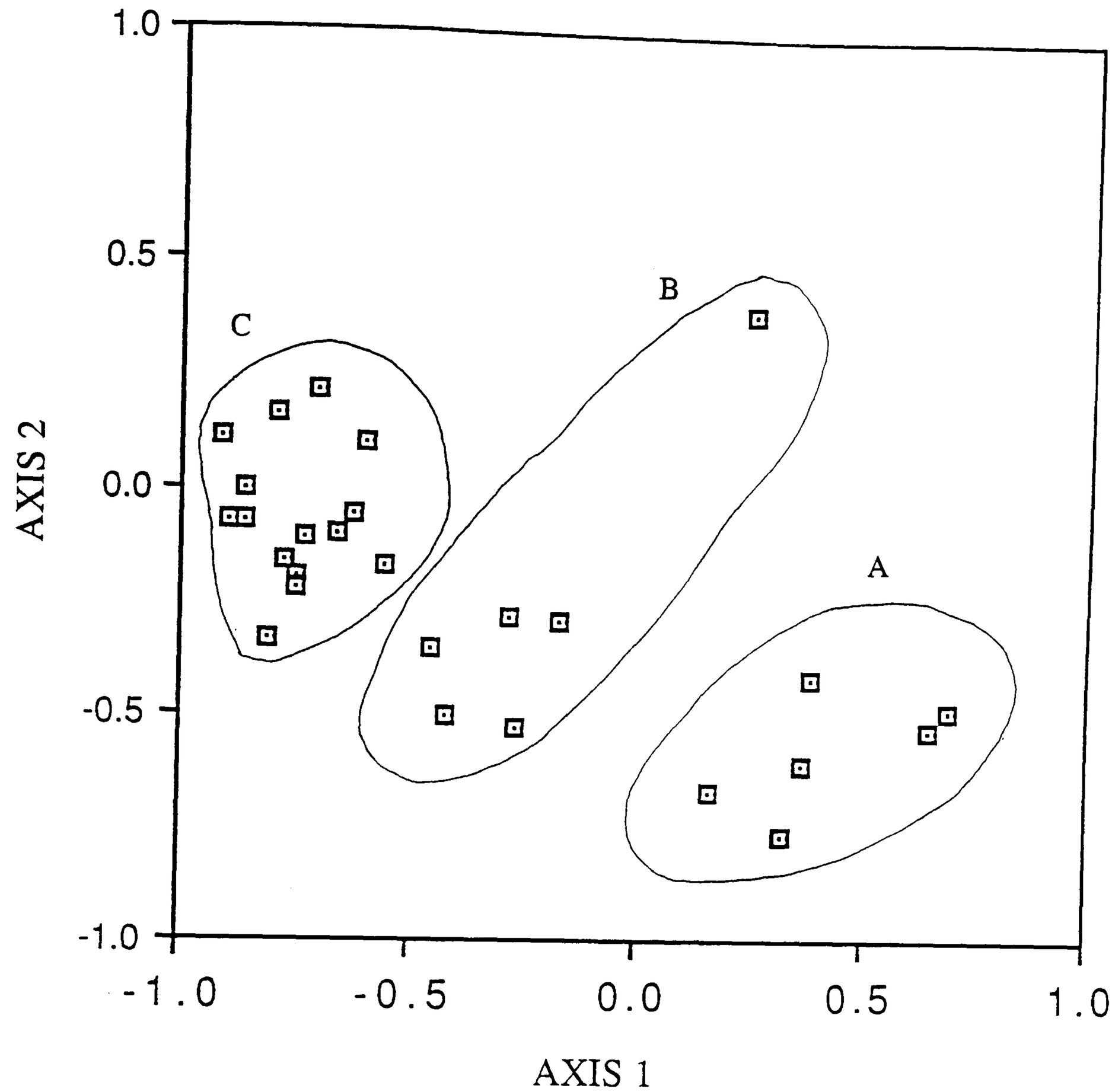
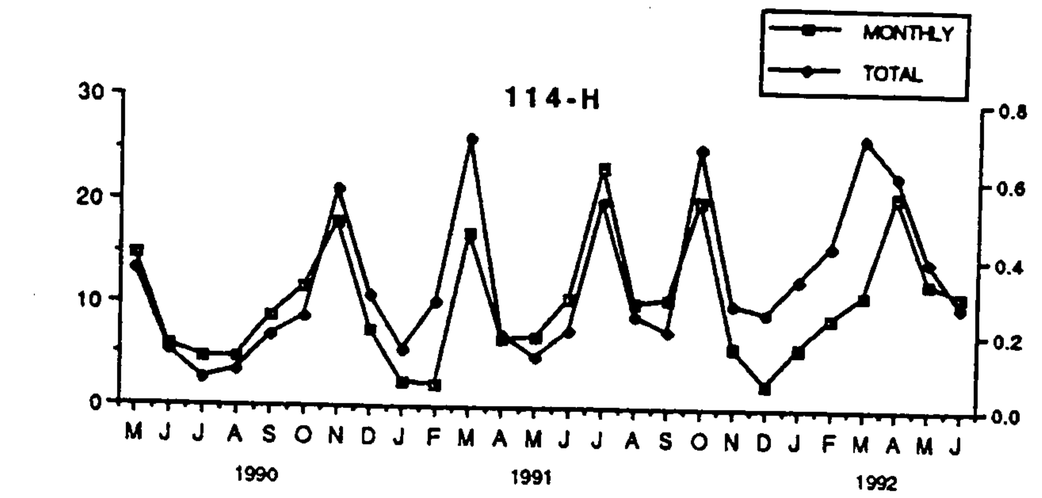
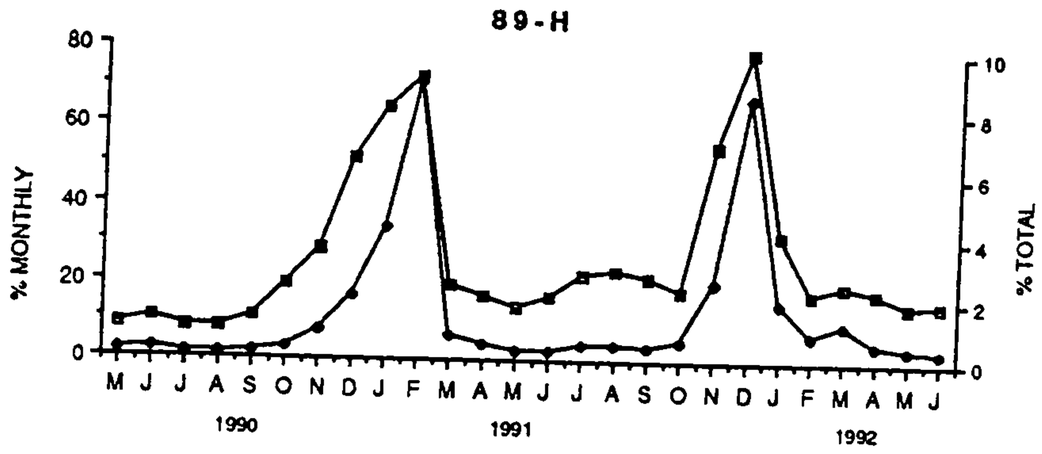
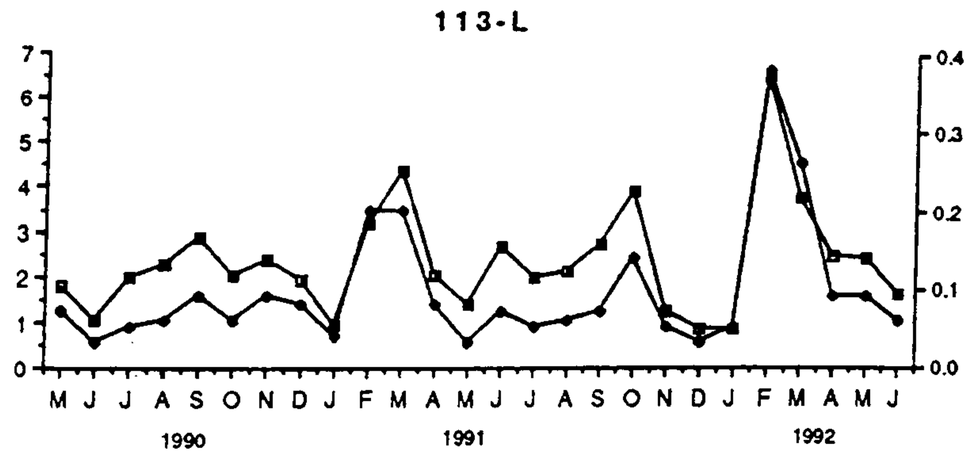


Figure 3.3: Ordination of monthly leaf litter input by the different species for a period of twenty-six months in LEM and HEM forests. *Didelotia africana, Microberlinia bisulcata, Didelotia africana* were classified into group A; *Anthonotha fragrans Cola rostrata, Cola verticillata, Oubanguia alata, Hymenostegia afzelii and Diospyros iturensis* in group B and *Berlinia bracteosa, Coula edulis, Dichostemma glaucescens, Warneckea memecyloides, Strephonema pseudocola, Staudtia stipitata, and Berlinia bracteosa* in group C.







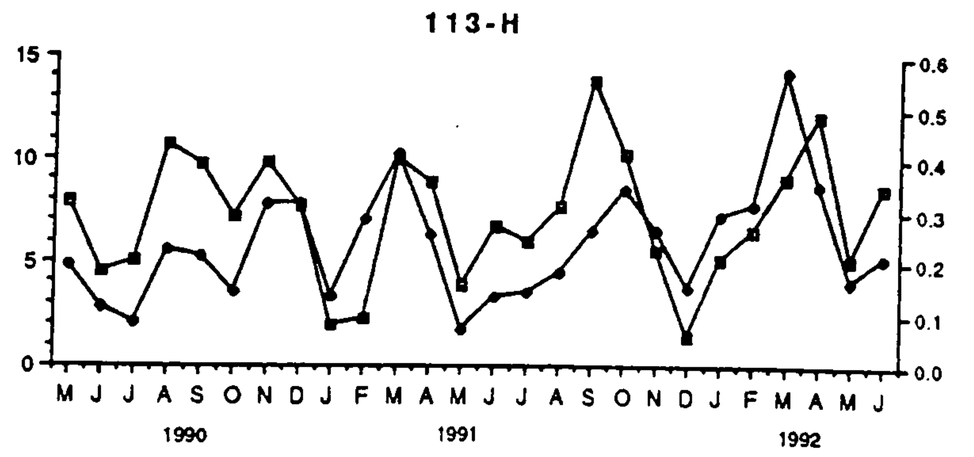


Figure 3.4a: Individual species contribution to leaf litter from group A species (as classified by the ordination of the monthly amounts of the different species). These species include *Tetraberlinia moreliana* (114), *Tetraberlinia bifoliolata* (113) and *Microberlinia bisulcata* (89). L=LEM and H=HEM, Y-axis is common to all the graphs.

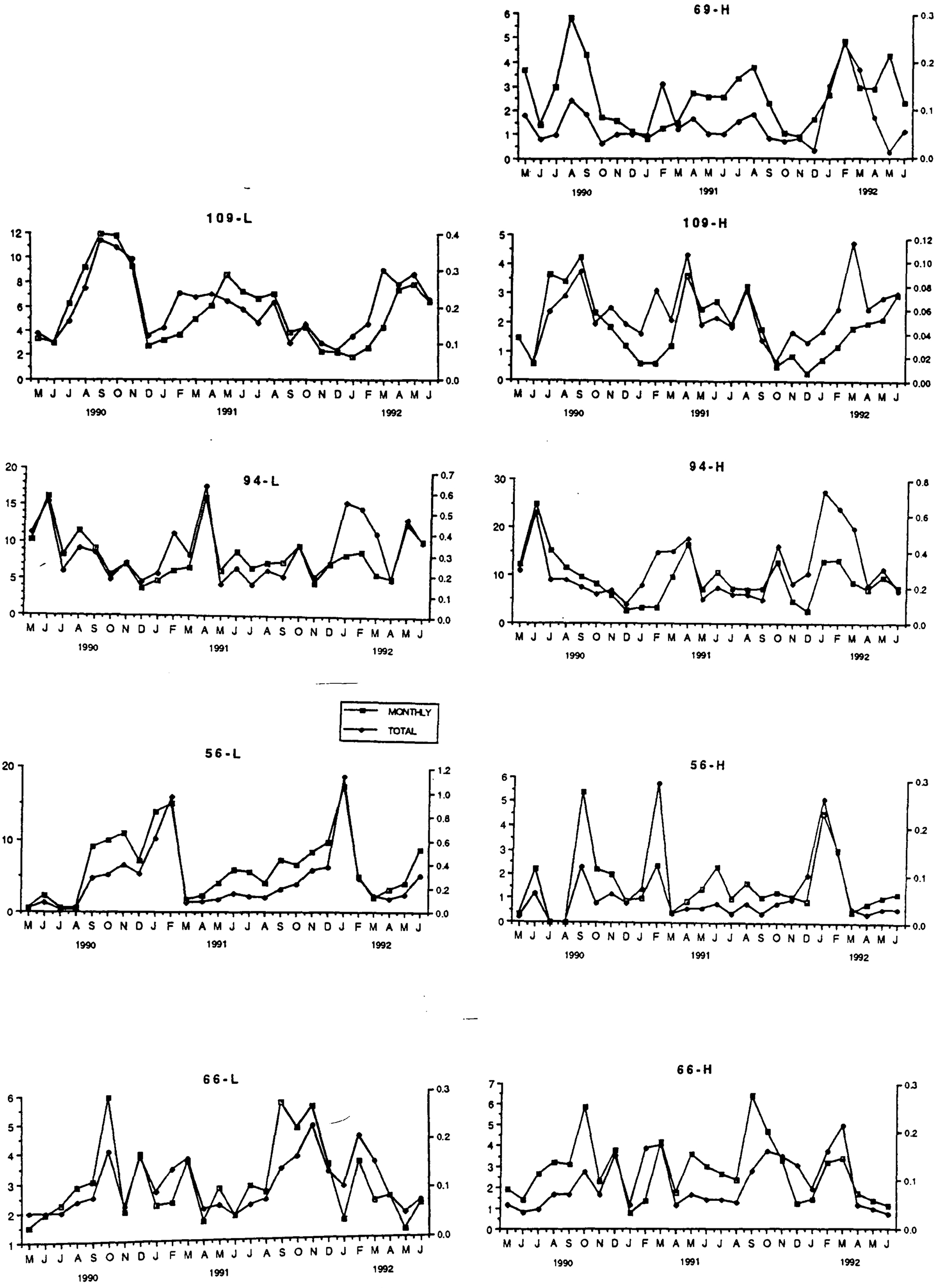


Figure 3.4b: Individual species contribution to leaf litter from group B species and C (as classified by the ordination of the monthly amounts of the different species). These species include *Hymenostegia afzelii* (66), *Erythrophleum ivorense* (56) *Oubanguia alata* (94) *Strychnos sp.* (109) and *Irvingia gabonensis* (69). L=LEM and H=HEM, Y-axis is common to all the graphs.

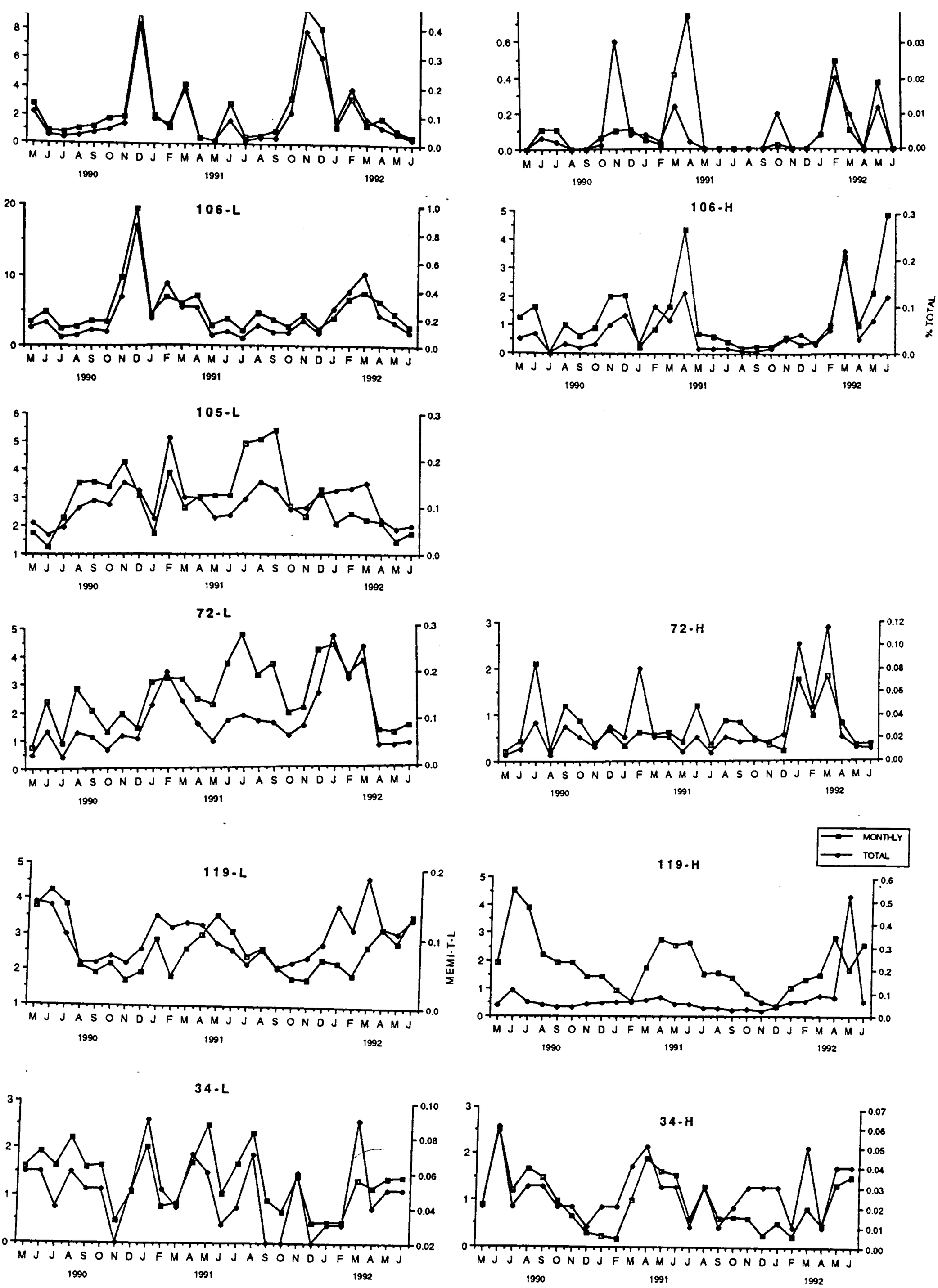


Figure 3.4c: Individual species contribution to leaf litter from group A species (as classified by the ordination of the monthly amounts of the different species). These species include *Coula edulis* (34), *Warneckea memecyloides* (119), *Strephonema pseudocola* (106), *Staudtia stipitata* (105), *Berlinia bracteosa* (19) and *Klaineanthus gaboniae* (72). L=LEM and H=HEM, Y-axis is common to all the graphs.

3.3.4 Relationships among total litterfall and various litterfall fractions

Correlation analysis between the LEM and HEM plots showed a positive and highly significant association between total litterfall, leaves, reproductive parts, trash ($p<0.01$, $n=26$) and wood fractions ($p<0.05$, $n=26$). The correlation matrices for total litterfall and litterfall fractions for the LEM and HEM forests are presented in Table 3.11. The magnitude and nature of association varied for the different fractions for LEM and HEM plots.

The leaf, reproductive and trash fractions were positively and significantly correlated with total litterfall for LEM plots ($p<0.01$, $p<0.05$ and $p<0.05$ respectively). For HEM plots, leaves, reproductive and small wood fractions were positively and significantly correlated to total litterfall ($p<0.05$). Moss and lichen were the only fractions negatively significantly correlated ($p<0.01$) to total litterfall for both LEM and HEM plots. The significant correlations amongst the various litterfall fractions were recorded for: leaves and reproductive parts; reproductive parts and trash; leaves and mosses and lichens for the LEM plots, leaves and small wood; leaves and moss and lichen for HEM plots.

3.3.5 Climatic factors and litterfall

Rainfall and temperature were the only climatic parameters investigated. Table 3.12 presents the correlation coefficients between these climatic variables, total litterfall and the various litter fractions summed across the five replicate half-plots in LEM and HEM plots. Total litterfall, leaf fractions, moss and lichen fractions were strongly and significantly ($p<0.01$) correlated with both mean monthly temperature and mean daily rainfall. These were positive for temperature and negative for rainfall. Small wood fractions were significantly and positively correlated with rainfall for the LEM plots and temperature for LEM plots. The reproductive fractions were also correlated negatively with rainfall and positively with temperature. This was however only significant for HEM plots ($p<0.05$, $n=26$).

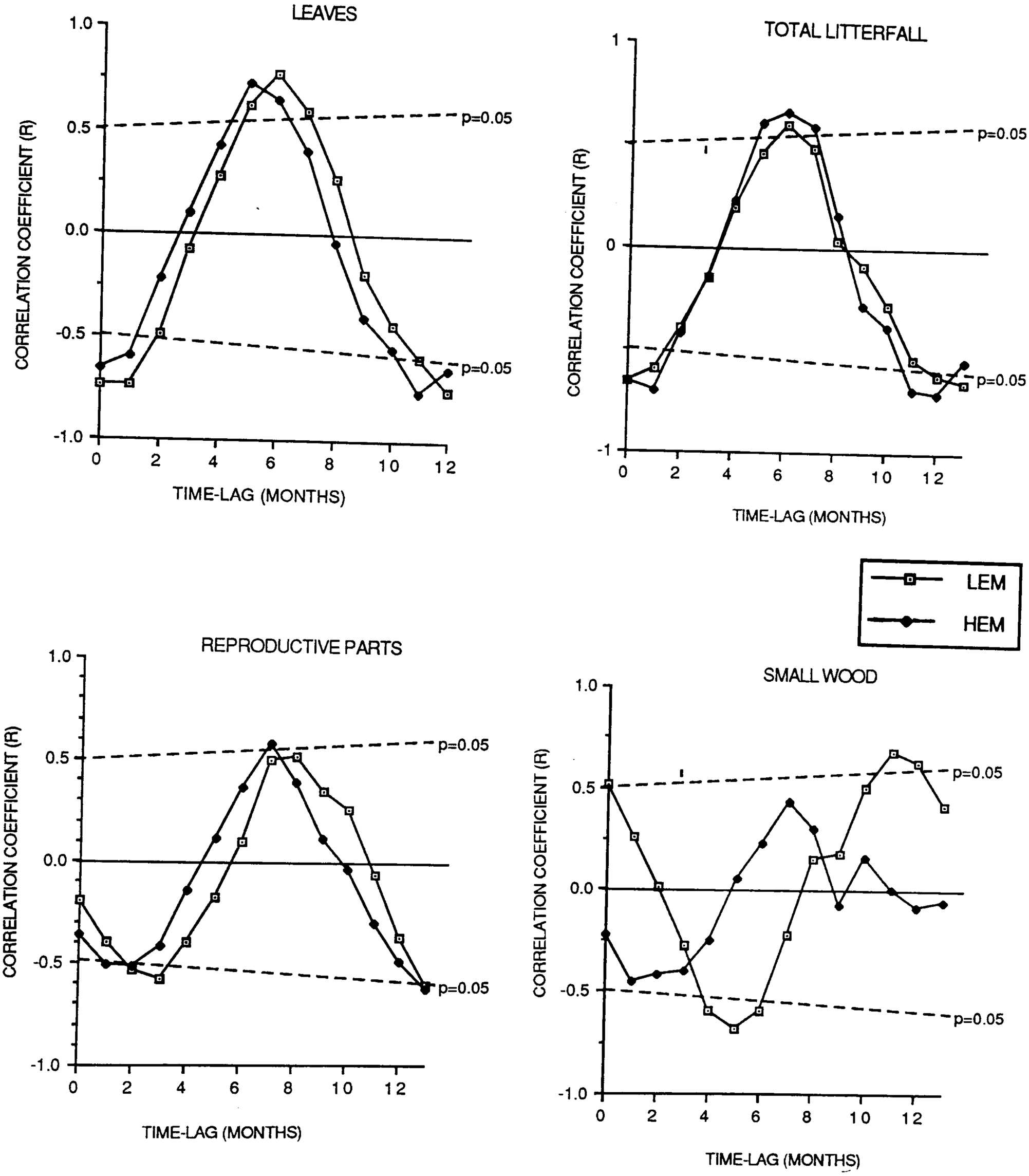


Figure 3.5: Correlation coefficients between monthly mean litterfall and rainfall recorded during the month of litter collection as well as those recorded in the previous months (lags) in LEM and HEM forests, Korup National Park, Cameroon.

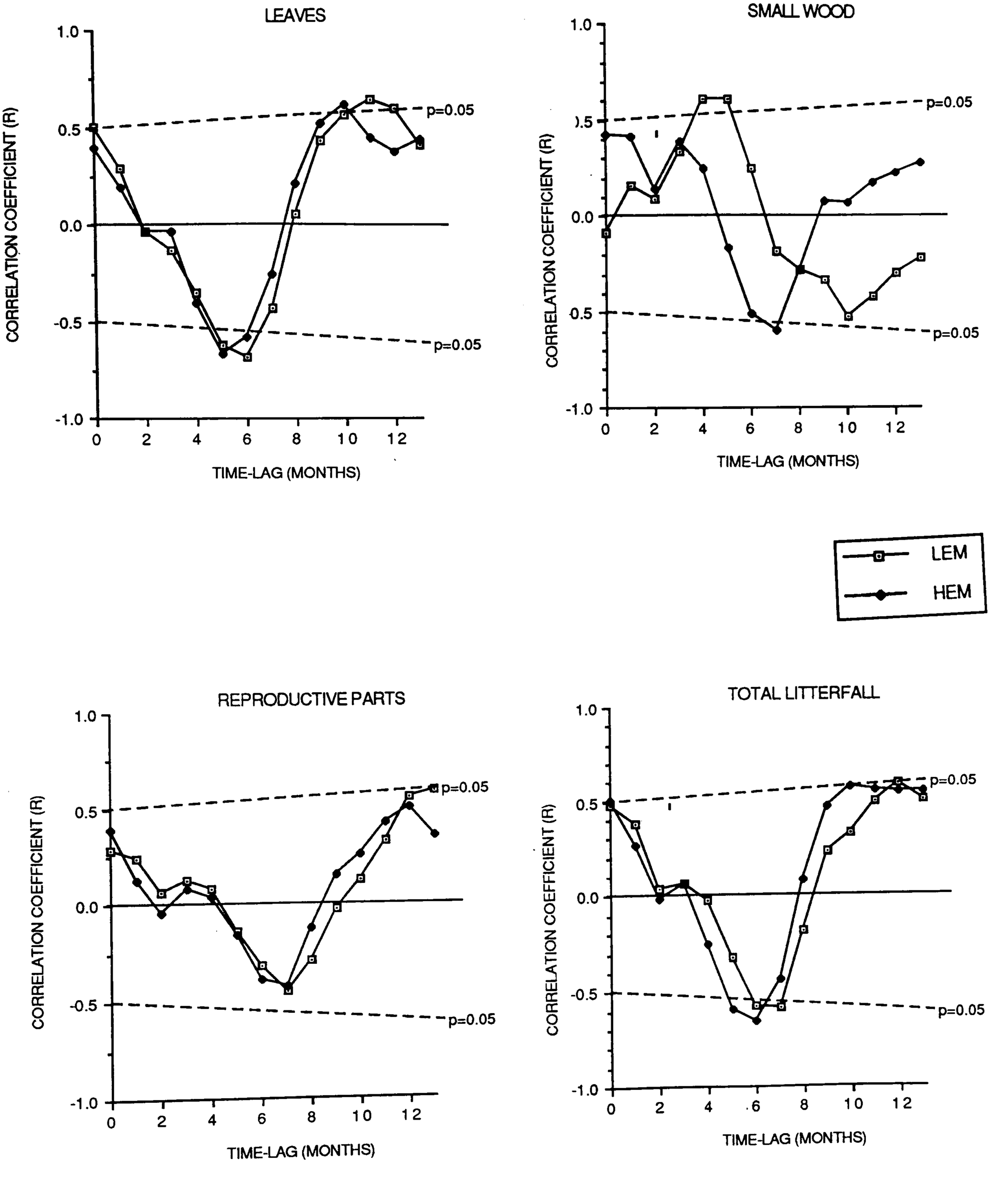


Figure 3.6: Correlation coefficients between monthly mean litterfall and temperature recorded during the month of litter collection as well as those recorded in the previous months (lags) in LEM and HEM forests, Korup National Park, Cameroon.

The response time of the various litterfall fractions and total litterfall to the effects of the climatic variables differed as well for LEM and HEM plots. There was a significant time-lag of 7 months for the LEM plots and 5-7 months for HEM plots between maximum rainfall and maximum total litterfall ($p<0.01$, $n=26$). A significant time lag of 6 months for LEM plots and 5-6 months for HEM plot was similarly recorded for the leaf fraction. The small wood fraction showed a zero time lag as well as a significant lag of 11-12 months for LEM plots ($P<0.5$). The 11-12 months lag coincided with the months of maximum rainfall of the preceding year indicating a possible significant time lag of 0-1 months (Figure 3.5)

A significant time-lag of 4-5 months was recorded between maximum mean monthly temperature and small wood fractions for the LEM plots ($p<0.05$). Since total litterfall and leaf fractions were significantly and positively correlated with mean monthly temperature at sampling date for both sites, a zero time-lag was recorded (Figure 3.6). The significant time-lag of 11-12 months for LEM plots and 10 months for HEM plots for both total litterfall and leaf fraction coincided with months of maximum mean temperature of the preceeding year. This indicated a possible significant time-lag of 0-2 months for both sites.

3.4 DISCUSSION

3.4.1 Litter production.

The annual litterfall estimates of 8.99 and 8.33 t ha^{-1} yr^{-1} for both LEM and HEM plots in Korup National Park fall within the published range of values recorded for other lowland rainforest (Proctor 1984). The lowest value reported for tropical Africa is 4.40 t ha^{-1} yr^{-1} for a moist evergreen forest in Auguedon, Ivory Coast, by Muller and Neilson (1965) (quoted by John 1973). This value as well as the 25.3 t ha^{-1} yr^{-1} for a tropical forest in Thailand (Ogawa *et al.* 1961) often reported as the highest record for tropical forests, were both estimated indirectly. This coupled with differences in methodology in other studies makes comparison plausible.

The litterfall estimates for Korup National Park are lower that the values recorded for Bakundu Forest Reserve by Songwe *et al.* (1988). The two sites are approximately 150 km apart. This could be due to local variations such as species composition, other microclimatic factors and the history of development since the Bakundu Reserve had been previously subjected to exploitation. Rai and Proctor (1986) recorded litterfall values of 3.44-4.18 t ha^{-1} yr^{-1} for lowland forest in Karnataka, India. This happens to be the lowest estimates for any lowland forest studied (Proctor 1987). The climate of Korup National Park is quite similar (rainfall amounts over 5000 mm) to that reported for Karnataka (Bannadpare site) by Rai and Proctor (1986), but much higher litterfall values were recorded for Korup. Jenny *et al.* (1949) recorded litterfall values of 8.5 t ha^{-1} yr^{-1} for a tropical forest in Columbia with an annual rainfall of 9100 mm, but their results were based on just one 1.0 m^{-2} litter trap.

Annual variation in litterfall was very low for both forest types in Korup National Park. The ratio of minimum to maximum annual values was 1:1.1 and 1:1.2 for both LEM and HEM plots respectively. These values are comparable to those recorded for other tropical forests with longer durations of litterfall studies. Spain (1980) found ratios not greater

than 1:1.3 for studies spanning 3 years; Brasell *et al.* (1980) had a ratio of 1:1.07 which was similar to that obtained by Songwe *et al.* (1988) for two years studies in Bakundu Forest Reserve, Cameroon. Martínez-Yrízar and Sarukhán (1990) had ratios of 1:1.14 and 1:1.2 for their valley and hill sites respectively in a tropical deciduous forest in Mexico studied over a five-year period. This then implies that annual returns of nutrients via litterfall will follow the same pattern with variations only in nutrient concentration. As such, it will be the seasonal patterns of litterfall that will have a crucial role in the temporal heterogeneity in soil nutrient status.

3.4.2. Seasonality of litter production.

Total litterfall and the various litter fractions were correlated for both sites (small wood fractions exempted). This suggested common regulating factors operating at both sites. Litterfall in Korup National Park was markly seasonal exhibiting a mono-modal pattern with very conspicuous peaks in the dry season. This appears to be a common phenomenon in most tropical forests where one or more peaks are recorded during this period of water stress. Peaks in litterfall have also been reported in the wet season in New Guinea (Edwards 1977); Trinidad (Conforth 1970); Australia (Brasell *et al.* 1980) and in Sarawak (Proctor *et al.* 1983). The only explanation put forward has been the influence of strong winds and storms at the onset and during the rainy season. Both plots showed similar response time for total litterfall to the effects of rainfall and temperature.

Since leaves are the major constituents of total litterfall in most tropical forest, the seasonal patterns of litterfall is often attributed to the seasonal variations of leaf shedding and the associated factors responsible for leaf senescence and abscission. The temporal patterning of leaf fall was different at both sites. The one month difference in the response time in leaf fall to moisture availability for the two sites indicates that the HEM plots are more prone water stress. Addicott (1982) emphasised the role of moisture availability in triggering the abscission processes. The response time of 5-6 months was longer than that reported by Martínez-Yrízar and Sarukhán (1990) for their Mexican sites. This implied that the soil moisture stress was not very acute in Korup.

The small wood fraction differed considerably at both sites. While small wood contribution was high in the dry season for the HEM plots, the reverse occurred in the LEM plots. It was observed that the twigs were shed during and shortly after leaf fall at the HEM site during the dry months. This was similar to cladoptosis described by Addicott (1982) in which the discrete leafy branchlet and leaflets are lost at once. This was evident in the fact that small wood showed a significant response time of 6-7 months to rainfall in the HEM plots. There was also a strong correlation between leaves and small wood for the HEM plots. The fall in small wood fractions have always been observed to be associated with rainfall patterns. This has been explained by the fact that the wood absorbs moisture and fall as a result of the increase in weight (Brasell *et al.* 1980, Songwe *et al.* 1988). The small wood fraction of LEM plots did follow that pattern and recorded a significant response time of 0-1 month for rainfall and 4-5 months for temperature. Because of the combined effects on small wood fall for HEM plots, no significant response time could be recorded to both rainfall and temperature.

The importance of epiphytic mosses and lichens in mineral cycling has been reported by Pike (1978), but this fraction has often been neglected in most studies. This fraction was more abundant in the wet season as a result of increased weight due to moisture absorption. Moreover, mosses and lichens often grow on branches and twigs which can all be dropped together. The reason for the relatively higher production of mosses and lichens in the HEM plots is not yet known but could be due to the broader crown size of the dominant trees in those plots.

The two peaks recorded for the reproductive fraction were due to the different reproductive phenology of the species. The first peak in the early wet season coincided with bud break and eventual flowering, while the second peak was during fruit fall shortly before the commencement of the dry season. This synchronised pattern has been reported as a survival strategy of the different species in competing for dispersers and pollinators (Janzen 1971, Kunkel-Westphal and Kunkel 1979). Herbivory was high during this period and was evident in the high records of insect frass in the trash fraction. Lam and Dudgeon (1985) observed an increase in organic debris during the months of May and

June and related the increase in herbivore activity to increase in temperature. In the present study, the proportion of trash was comparatively higher for the LEM plots, with peaks at the on set and end of the dry season indicating high levels of herbivore activity. which can be related to the palatability of the young leaves shortly after expansion. Other studies have related this to foliar nutrient and polyphenolic content, leaf age, and crown position in relation to incoming insolation (Newbery and de Foresta 1985, Besset 1991). Comparison of foliar samples from both sites will be required to ascertain differences.

The sudden rise in trash fraction in the second year for the HEM plots was due to the high proportion of fine pollen grains which could not be separated from the rest of the finer material.

3.4.3 Leaf fall patterns in single tree species

The present study buttresses the fact that high species diversity in the tropical forest results in big inter-specific differences in nutrient use and turnover. Patterns of leaf shedding varied between the different species and even amongst individuals of same species in both forests. This however indicated that environmental factors are not solely responsible for these varying patterns. All species investigated did show peaks in leaf fall though at varying times. A comparison with patterns of leaf shedding in some tree species in Bakundu Forest Reserve reported by Songwe *et al.* (1988) were similar despite the differences in microclimatic conditions (notably rainfall which was 1929 mm for Bakundu Forest Reserve and 5460 mm for Korup) and in soil nutrient status. A clear example was *Staudtia stipitata,* a top canopy species found in both forests shed most of its leaves in the wet season in both forests. This then implies that other internal factors which can be species-specific influence periodicity in leaf fall. Kunkel-Westphal and Kunkel (1979) arrived at the same conclusion for the tropical forest in Guatemala. They also attributed the diverse patterns in the legumes to the vastness of that family. The rhythms shown by the various species in Korup National Park were all strongly related to soil moisture regimes. Leaf fall was initiated 1-2 months earlier in the second year of the study due to the severe dry season that year.

Lianes also contribute to tropical forest diversity (Gentry and Dodson 1987, Hegarty 1991, Campbell and Newbery 1993) and are 'leafier' than trees thereby contributing significantly to leaf litter. Their contribution was comparatively high in Korup particularly in the LEM plots.

CHAPTER FOUR

NUTRIENT CONCENTRATION AND ACCESSION IN LITTERFALL

4.1 INTRODUCTION

The major route of transfer or return of nutrients from the trees to the forest floor is through litterfall. The quantity of the mineral elements returned is determined not only by the rate of litterfall but also by the concentrations of the respective mineral elements in the litter. The nutrients in litterfall constitutes a loss to the tree and will depend on the requirements of the individual tree species and how readily available these nutrients are to the tree species.

Nutrients which are not readily available to the trees or which are in short supply in the soil for uptake by the trees are efficiently retranslocated from the senescing leaves and other older plant parts to other perennial organs (Chapin 1980, Edwards 1982, Chapin *et al.* 1983, Veneklass 1991, Tripathi and Singh 1994). Litterfall in such situations will have low concentrations of the mineral elements which are in limited supply, thereby minimising their loss from the tree. The reverse happens when the mineral elements are in excess and in some cases are accumulated in the leaves (Tolsma *et al.* 1987, Medina *et al.* 1990). Mineral element circulation in litterfall has therefore been considered a reliable indicator of nutrient availability for the different sites (Vitousek 1982). Based on this, the ratios of litterfall dry mass/nutrients has often been used as the index in assessing how efficiently the different forests utilise the different mineral elements (Chapin 1980, Vitousek 1982, 1984, Cuevas and Medina 1986, Vitousek and Sanford 1986, Singh 1989).

Litterfall consist of different fractions with varying concentrations of the different mineral elements. Seasonal distribution in litterfall may determine the relative availability of the mineral elements in the soil. Gosz (1984) related the "manuring effect" to the timing of peak uptake by the trees, whereby the high nutrient levels in the flowers in litterfall at that time, cause not only their rapid breakdown but also an increased breakdown of the other materials. This also shows that the concentration of the mineral elements defines the quality of the various litterfall fractions and also determines their rates of decay and mineralization (Jensen 1974, Swift *et al.* 1979, Anderson and Swift 1983). The chemical indices for substrate quality often used, are the ratios of the concentrations of the different

elements including the various classes of organic compounds (Bossata and Staaf 1982, Mellilo *et al.* 1982, Upadhyay *et al.* 1989, Lavelle *et al.* 1993).

This chapter concentrates on the examination of comparative rates of nutrient fluxes in litterfall for both LEM and HEM plots in Korup National Park. Emphasis was placed on the following aspects:

1. How gross litterfall concentrations of N, P, K, Mg and Ca vary in time in the different litter fractions for LEM and HEM plots.
2. How the concentrations of N, P, K, Mg and Ca in leaf litter of selected top canopy, canopy and understorey species differ in both the wet and dry seasons.
3. In using the litterfall dry mass from chapter 3 and concentrations from (1) above, estimate the annual rates of accession of N, P, K, Mg and Ca in the various litterfall fractions (external cycling).
4. Estimate the degree of retranslocation (internal cycling) of N, P, K, Mg and Ca in leaves of selected species with and without the ectomycorrhizal association.
5. Evaluate the efficiency of nutrient-use based on litterfall dry mass/nutrient ratios and degree of retranslocation of the various mineral elements.

4.1 MATERIALS AND METHODS

4.2.1 Selection and preparation of samples

4.2.1.1 Litter samples.

The basic sets of samples consisted of monthly litter collections bulked for all traps in each of the ten half-plots selected for litterfall studies from May 1990 to June 1992 (chapter 3). The litter had been sorted into the various fractions and the leaf fractions sorted further into their constituent species. These were oven-dried, weighed and stored in polythene bags labelled with collection date, litter fraction (and species code for leaf fractions), and number of the half-plot (each pair of the quarter-plots that constituted the half-plot).

In July 1991 and 1992, the stored litter samples were separated, redried and ground for elemental analysis. The monthly litter collections for each half-plot were separated into two sets of samples: set A which consisted of the different litter fractions (leaves, small wood, reproductive, mosses and lichens and trash) and set B consisted of only leaf litter (of twenty-one selected species). The different litter fractions were stored separately for each half-plot and month. The leaf litter of the different species were also stored in separate polybags after sorting. To obtain samples for set A and B, each of the stored litter fractions for each half-plot and month was divided into two. In certain half-plots the reproductive, mosses and lichen and trash fractions were relatively small and were all classified for set A since these were not needed in set B. For the leaf fraction, leaf litter of the individual species were divided into two, one half was bulked for set A and the other for set B from which leaf litter of the selected twenty-one species were sorted out.

SET A

These samples were aimed at examining how the mineral elements in gross litter (all species combined) vary in time and in both low and high ectomycorrhizal plots (LEM and HEM plots respectively). The halved monthly leaf litter of all the different species was re-bulked to constitute the leaf fraction for each of the half-plots and collection dates. Samples of each of the litter fractions: leaves, small wood, reproductive parts, mosses and

lichens and trash; were separately re-dried in large paper envelopes in an oven at 60°C for 4 hours prior to milling. All the leaves were initially crushed in the envelope (manually, by rubbing the dried leaves against each other) and ground to a finer size in a Wiley electric mill fitted with a 0.5 mm mesh screen. Some were also milled in a coffee grinder. The small wood and reproductive fractions were initially crushed with a hammer before milling. The moss and lichen and trash fractions were milled directly.

The milled samples were thoroughly mixed with a spatula and subsampled as follows: For leaves, three random samples of approximately 2 g each were collected and separately placed in small sealable polythene bags, labelled as replicates 'a', 'b' and 'c'; for the other fractions, one sample of approximately 2 g was collected. Each bag was labelled with collection date (month and year), half-plot number and litter category. Some air-dried seeds of *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* were also ground for elemental analysis.

Set B.

These samples were sorted for the comparison of mineral element concentration of the twenty-one individual species in the wet and dry seasons of both years (May 1990-June 1992) in both LEM and HEM plots respectively. From the rainfall records for the months during which litter was collected, the typically wet months were from May to October and the typically dry months were from December to February. November and March/April were considered as the transitional months. Three consecutive sampling periods were chosen for each year: two wet periods from May to July as 'wet1' and August to October as 'wet2'; and December to February as the dry period (dry1). The bulking of leaf litter of the individual species during these periods provided substantial quantities for milling. The species selected for this studies included; six ectomycorrhizal species: *Anthonotha fragrans, Berlinia bracteosa, Didelotia africana, Microberlinia bisulcata, Tetraberlinia bifoliolata* and *T. moreliana*; ten other abundant species (in terms of basal area) were; *Cola rostrata, C. verticillata, Coula edulis, Diospyros gabunensis, D. iturensis, Dichostemma glaucescens, Hymenostegia afzelii, Klaineanthus gaboniae, Strephonema pseudocola, Strombosia glaucescens* and *Oubanguia alata.* Four other top canopy and canopy species contributing substantially to total leaf litter were also selected. These were; *Erythrophleum*

ivorense, Staudtia stipitata, Hypodaphnis zenkeri and Irvingia gabonensis. Warneckea memecyloides was the only understorey species which provided enough material for milling and analysis. Some of these species occurred only in either the LEM or in the HEM plots and furthermore, some of these species could only provide enough material in either the LEM or in the HEM plots.

Samples of individual species were bulked for each of the collection periods and half-plots into large paper envelopes, oven-dried at 60°C and milled. These were thoroughly mixed and subsamples of approximately 2 g collected and separately placed in small sealable polybags, labelled for collection periods/year and the species. The mill was thoroughly brushed after milling each sample to prevent contamination between samples.

4.2.1.2 Foliar samples

In December 1991, April 1992 and July 1992, fresh mature leaves were collected from well-illuminated positions at top of crowns of the following top canopy (emergents) and main canopy trees:

(1) Ectomycorrhizal species: *Anthonotha fragrans, Berlinia bracteosa, Didelotia africana, Microberlinia bisulcata and Tetraberlinia bifoliolata;* (2) Non ectomycorrhizal species: *Cola verticillata, Coula edulis, Klaineanthus gaboniae, Hymenostegia afzelii, Oubanguia alata and Strephonema pseudocola.* Three individuals of each of the these species were selected from the ten tagged for monthly phenological observation. The leaves were collected by a tree climber using a metal pruner mounted on a 7.5 m telescopic pole and were stored in polythene bags immediately after collection and were air-dried on plastic sheets at the camp. Young leaves were also collected from three of these species which flushed during these collection periods. These included: *Coula edulis, Hymenostegia afzelii* and *Strephonema pseudocola.* Because of constraints in the forest such as the impossibility to climb some of the very large trees, poor weather conditions in April and July 1992 (wet season), samples were collected from only two individuals each in December 1991 and one each in April and July 1992.

Freshly fallen leaf litter of these selected species was also collected by trapping onto four large plastic sheets (4m × 3m) placed under each of these selected trees during the periods

when fresh foliage was collected. The freshness of the leaf litter was determined by visual observation of the petiole (the abscission layer). These plastic sheets were left underneath the canopies the selected individuals and the freshly fallen leaf litter samples were collected every morning, midday and evening for the three days during which mature leaves were collected for each of the three sampling periods. The samples were air-dried on plastic sheets at the camp during the three days of collection.

The samples were taken to the Forestry Research Station Kumba and were immediately oven-dried at 85°C for 48 h and milled to fine size in a Wiley electric mill fitted with a 0.5 mm mesh screen. The milled samples were thoroughly mixed and subsamples of approximately 2 g were collected and stored in sealable polybags labelled for age (young, mature and senesced), collection date and species.

All milled samples were packed in well sealed bags to avoid any uptake of moisture that would encourage fungal growth, and sent to Stirling for chemical analysis.

4.2.2 Chemical analysis

The analyses were undertaken by M. White, research technician employed on the C.E.C grant for the project.

4.2.2.1 Preparation and digestion of samples

Preparation of sample solution for the analysis of individual elements was by acid digestion (wet ashing) and was carried out as follows:

1. Sample preparation: The milled samples were thoroughly mixed and subsamples of approximately 150 mg were put into small clean glass tubes (of known weights) and oven-dried at 70°C for 4 h. These were re-weighed and stored in a desiccator to avoid any re-absorption of moisture prior to digestion. Only replicates 'a' and 'b' of the milled leaf litter were digested for analysis. The trash samples were bulked for the five half-plots in both LEM and HEM forest types to provide monthly composite samples for each forest type. The moss and lichen samples were also bulked to provide annual composite samples for each forest type.

2. Mixed digestion reagent: This was prepared following the procedure described by Allen (1989), in which 350 ml of '100 volume' hydrogen peroxide was added to 0.42 g of

selenium powder and 14 g lithium sulphate. This was followed by 420 ml of concentrated sulphuric acid which was added slowly while cooling the mixture. The digest mixture was put in a Winchester bottle and stored just above 0°C when not in use.

3. Digestion: The dried subsamples in (1) above were digested in 4.4 ml of the mixed digestion reagent in 'acid-washed' 75 mm digestion tubes mounted on a Tecam DG-1 block digestor. Each digestion run consisted of a batch of 40 samples. Two treatment blanks which were made up of 4.4 ml of the digestion mixture only, were included in each batch of samples digested. These served as the 'zero standard' for correcting the readings recorded for each for run.

Three reference materials of known chemical concentration were also included amongst the digestion batches. These included; a standard foliar material supplied by E.V.J. Tanner (Cambridge University) and was treated in the same manner as the other ground samples, 64 mg of phenacetin as the nitrogen standard (50 ppm N) and 25 mg of potassium orthophosphate as the phosphate standard (5.7 ppm P). The foliar control material had been previously analyzed by five other laboratories and therefore provided an important cross checks to other published values (Table 4.8). The N and P compounds were used to assess digestion recovery and instrument performance.

For each run, the digestion block was initially raised to 80°C for 30 minutes to allow full wetting of the organic material and reduce frothing and the temperature increased to 300-330°C which was maintained until the digest cleared usually after 6 hrs. The sample solution was allowed to cool and then filtered through Whatman filter paper (n° 44) into a 100 ml volumetric flask. The tube was washed out well to ensure all the digest solution was through the filter the filter paper and the latter rinsed to make up to 100 ml with deionized water, mixed and transferred into labelled plastic bottles for elemental analysis.

4.2.2.2 Elemental analysis

The sample solutions were analyzed for elemental concentrations in the same order as the batches were digested. Each sample solution was analyzed for total nitrogen and phosphorus, potassium, magnesium and calcium.

Nitrogen was determined by flow injection analysis and gas diffusion technique using a Tecator 5020 auto-analyzer and following the procedure given in Tecator's application notes ASN 50-03/84 (Tecator 1984). Following this procedure, each sample is injected into a carrier stream and mixed with sodium hydroxide. The joint stream passes over a PTFE membrane in a gas diffusion cell. The ammonia gas formed diffuses through the membrane into an indicator stream and the resulting colour change of the indicator is measured at 590 nm by the Tecator 5030 spectrophotometer. The detection range was 10-100 mg/l for nitrogen.

Phosphorus was also determined by flow injection analysis following the procedure given in Tecator's application notes ASN 60-02/83 (Tecator 1983). Each sample is injected into a carrier stream and merged with a second carrier to avoid matrix effects. The combined stream is then mixed with an acidic ammonium molybdate solution to form a heteropoly acid, which is reduced to molybdenum blue on addition of acidic stannous chloride in a second stream. The colour of the reduced heteropoly acid is measured at 650 nm by a Tecator 5030 spectrophotometer. The detection range was 0.25-5.0 mg/l for to phosphorus.

For nitrogen and phosphorus the first sample in each batch was re-measured at the end of each batch run to estimate the magnitude of the drift in that run and enable any correction for that drift.

The concentrations of calcium, potassium and magnesium in each of the samples were determined by flame spectroscopy using a Varian AA-575 atomic absorption spectrophotometer. Potassium was measured by flame emission using air-acetylene flame, while calcium and magnesium were measured by atomic absorption using a hotter nitrous oxide-acetylene flame (Grimshaw, Allen and Parkinson 1989).

All standards and reagent blanks used in calibrating the two instruments were prepared in 0.5M sulphuric acid to maintain acid levels the same as those in the sample solutions. Samples with concentrations above the detection limit of calibration were diluted with deionized water in 0.5M sulphuric acid (ten-fold) and rerun.

The readings for each batch of samples and (foliar and chemical) standards were corrected by subtracting from it, the mean value recorded for the treatment blanks in that batch. For each batch with a drift of more than 5%, corrections were also made by subtracting the drift factor from each reading which was related to the sample's rank order in the batch. The drift factor was estimated for each sample by the using the expression:

(Drift . rank order of sample)/40

4.2.3 Data analysis

After the corrections with values recorded for treatment blanks and for drift, the elemental concentrations expressed on a dry weight of material basis (mg g^{-1}) were calculated as follows:

Concentration (mg g^{-1}) = $c.v/(w.10^3)$

where, c = concentration in sample solution (ppm),
v = solution volume of diluted digest (ml),
w = dry weight of sample used (g).

The mean elemental concentrations of the various fractions were weighed by their respective proportions per unit weight of total litterfall to give the weighed mean concentrations in total litterfall.

The layout was of a split-plot design with forest type (LEM and HEM) and sampling date (months) as the factors and the five replicate half-plots in each forest as the experimental units. Two-factor nested analysis of variance (ANOVA) with the replicate half-plots nested in the forest types, was carried out to test for significant differences in mineral-element concentrations in the litter fractions between the months and forest types. Separate analyses were carried out for the five different mineral elements in leaves, small wood and reproductive fractions. No adjustments were made on the F-tests for within

plots variations for the correlated errors (repeated measures) as these were highly significant (similar adjustments for litterfall dry weights in Chapter 3 showed little changes due to the highly significant within-plot variations). Since the trash samples were bulked for each month across the five half-plots in both LEM and HEM forest types, the two-sample-t test was used to test for the significant differences in monthly elemental concentrations in the trash fractions between both forest types.

A three-way analysis of variance was carried out to test for the differences in mineral element concentrations in leaf litter of the selected species, seasons (wet and dry periods across the two years) and forest types. Differences in concentrations of samples of the individual species between the seasons and forest types (if that individual species occurred in the LEM and HEM forests) were further examined separately one and two-factor analysis of variance. All data were presented at Half-plot level and not tree level.

Mineral-element accessions in litterfall were computed for the various fraction for each forest type by multiplying the individual half-plots elemental concentrations values by their respective dry weights estimated on a per unit area basis (g m^2). These were summed across all fractions to give estimates of total mineral-element accession.

The percentages of nutrients retranslocated or accumulated prior to leaf fall in the selected ectomycorrhizal and non-ectomycorrhizal species were calculated from the leaf litter/ fresh leaf concentration expressed per unit dry weight and per unit weight of calcium in the leaf litter following the approaches of Vitousek and Sanford (1986), Scott *et al.* (1992) and Tripathi and Singh (1994). This was computed as follows:

$$\text{Retranslocation } (\%) = 100(1-(X/Y))$$

where, X=(nutrient concentration in leaf litter)/(Ca concentration in leaf litter)

Y=(nutrient concentration in mature leaves)/(Ca concentration in mature leaves)

In order to sum the proportions of the different nutrients retranslocated from leaf litter of

the different species across the three collection periods of the year, variations in the elemental concentration in the mature and senesced leaves between the sampling dates were investigated. This was by a three-factor analysis of variance (ANOVA) with the sampling periods, age of the leaves (mature and senescent leaves) and the different species as the factors.

4.3 RESULTS

4.3.1 Mineral-element concentrations in litterfall

4.3.1.1 Mean elemental concentrations

The mean concentrations of the five macronutrients (N, P, K, Mg and Ca), separately analyzed, differed in the various litterfall fractions for both LEM and HEM plots (Table 4.1). The mean concentrations of the mineral elements in litterfall were in the following order:

$$N > Ca > K > Mg > P,$$

for leaves, small wood, reproductive fractions mosses and lichen and total litterfall for both LEM and HEM plots. This was however different for the trash fraction with the mineral elements in the following order:

$$N > Ca > Mg > K > P.$$

The highest mean concentration of N recorded was in the trash fraction and the lowest in small wood fraction. These were consistently higher for the LEM plots for all the litter fractions (except for moss and lichen) with significant differences in small wood ($p<0.001$), reproductive parts ($p<0.05$), and trash fractions ($p<0.01$) compared to the HEM plots.

The mean concentrations of P were high in both reproductive parts and trash fractions and lowest in small wood fractions. Significant differences in P concentration was seen only in the leaf litter between the two forest types ($p<0.001$). The highest concentrations of K, Mg and Ca were found in the reproductive, leaves and small wood fractions respectively (Table 4.1). The lowest concentration of K was found in the trash fraction and Ca in the reproductive parts. Comparison between both forest types showed significant differences in the concentrations of K and Mg in leaf litter, small wood and reproductive parts ($p<0.001$) with higher concentrations in the HEM forest (with the exception of K in leaf litter which was higher in the LEM forest). This was also significantly higher in the LEM forest for Ca in leaf litter and trash fractions ($p<0.01$).

The overall weighed mean concentrations of N , K and Ca in total litterfall were higher for the LEM plots, while P and Mg were higher for the HEM plots (Table 4.1).

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4.3.1.2 Temporal variation in mineral element concentrations

The concentration of the different elements in the litterfall fractions fluctuated with time during the period of study from May 1990-June 1992 (Figures 4.1a-4.1e). All elements showed clear and significant seasonal trends which were prominent for K and Mg in all the fractions and total litterfall ($p<0.001$, but $p<0.05$ for Ca). The greatest fluctuation was seen in the concentration of K (coefficients of variation between 0.31-0.56 for all fractions, 0.32 and 0.42 for total litterfall for both LEM and HEM plots respectively). The lowest fluctuation was in N (coefficient of variation between 0.06-0.29 for all fractions, 0.06 and 0.07 for total litterfall for both LEM and HEM plots). The reproductive parts showed the highest fluctuation in all the elements while the leaf fraction showed the lowest.

The concentration of N was low in the dry season for leaves and small wood in the first and second year in both LEM and HEM forests. A similar trend was shown in the reproductive fractions in the LEM forest (Figure 4.1a). A rise in N concentration was recorded in all the fractions during the early part of the rainy season in the second year and was also expressed in the weighed concentration in total litter for both forest types (Figure 4.1a).

High concentrations of P were recorded in reproductive and trash fractions in the dry seasons of both years for both LEM and HEM plots. The small wood however differed in their P concentrations in both forest types. High concentrations were recorded in the dry season for the HEM plots and in the early and late wet season for the LEM plots (Figure 4.1b). The concentration of P in the leaf litter was relatively lower in the dry seasons for both LEM and HEM plots in the first year but only in the LEM plots in the second year. The weighted mean concentration followed a similar trend to the leaves because of the high proportion of leaves in total litterfall. There was a sharp rise in the concentration of P in total litterfall in February 1992 for the HEM plots. This was as a result of a much higher production of flowers in the HEM than LEM plots which had high concentrations of P. Small wood showed a slight upward trend in P concentration with no peaks in both LEM and HEM plots.

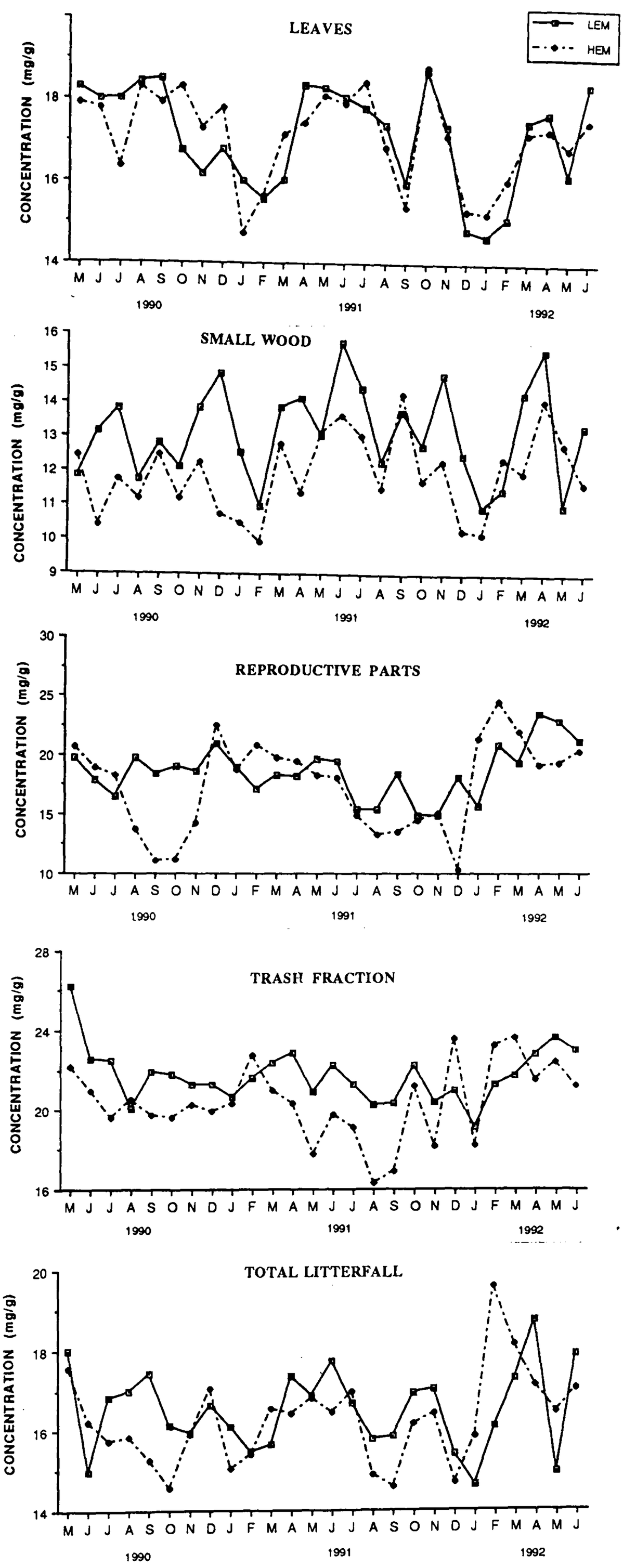


Figure 4.1a: Monthly mean concentrations of N (mg g^{-1}) in litterfall collected in five replicate plots in LEM and HEM forests in Korup National Park, Cameroon.

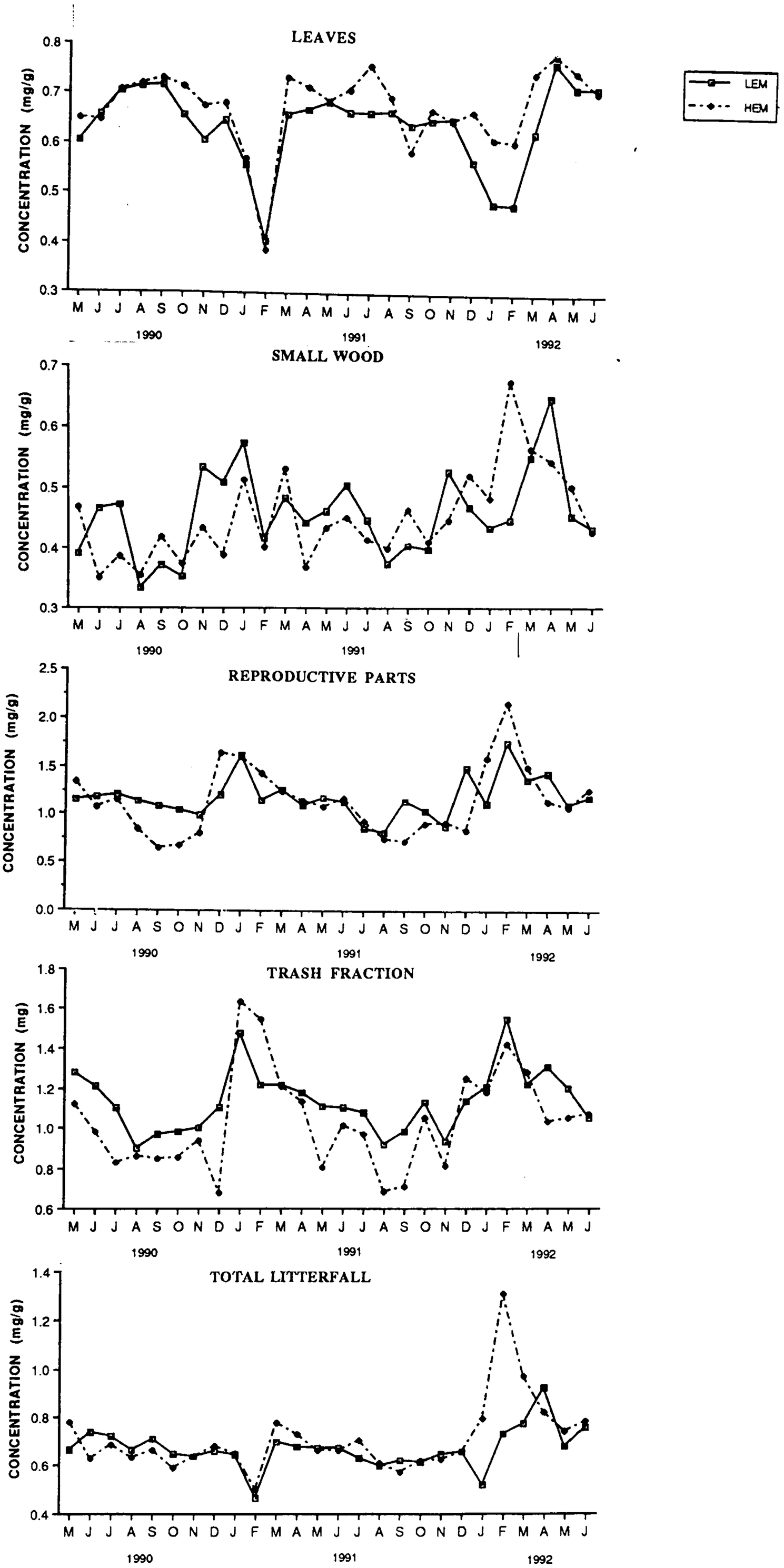


Figure 4.1b: Monthly mean concentrations of P (mg g^{-1}) in litterfall collected in five replicate plots in LEM and HEM forests in Korup National Park, Cameroon.

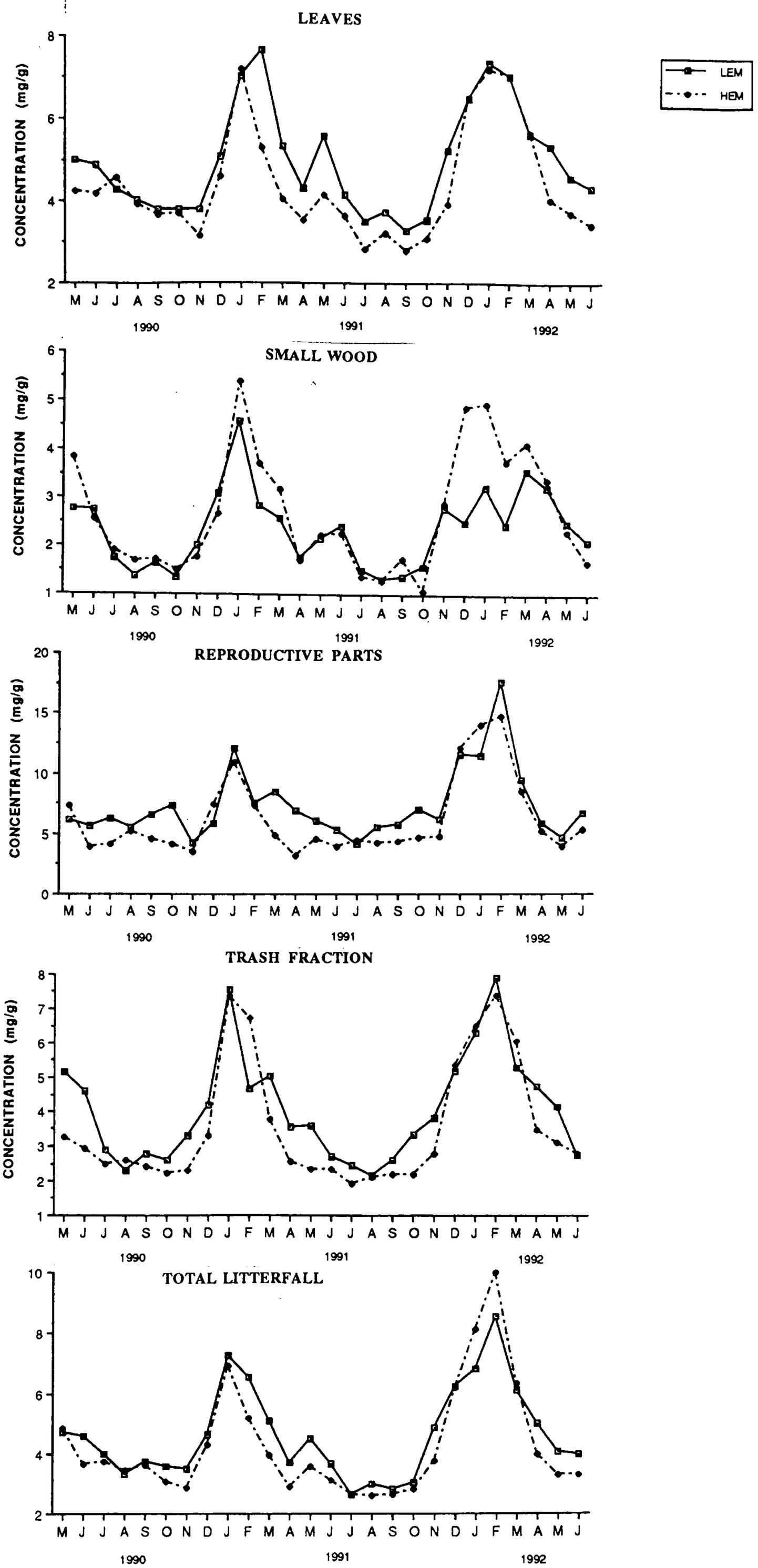


Figure 4.1c: Monthly mean concentrations of K (mg g^{-1}) in litterfall collected in five replicate plots in LEM and HEM forests, Korup National Park, Cameroon.

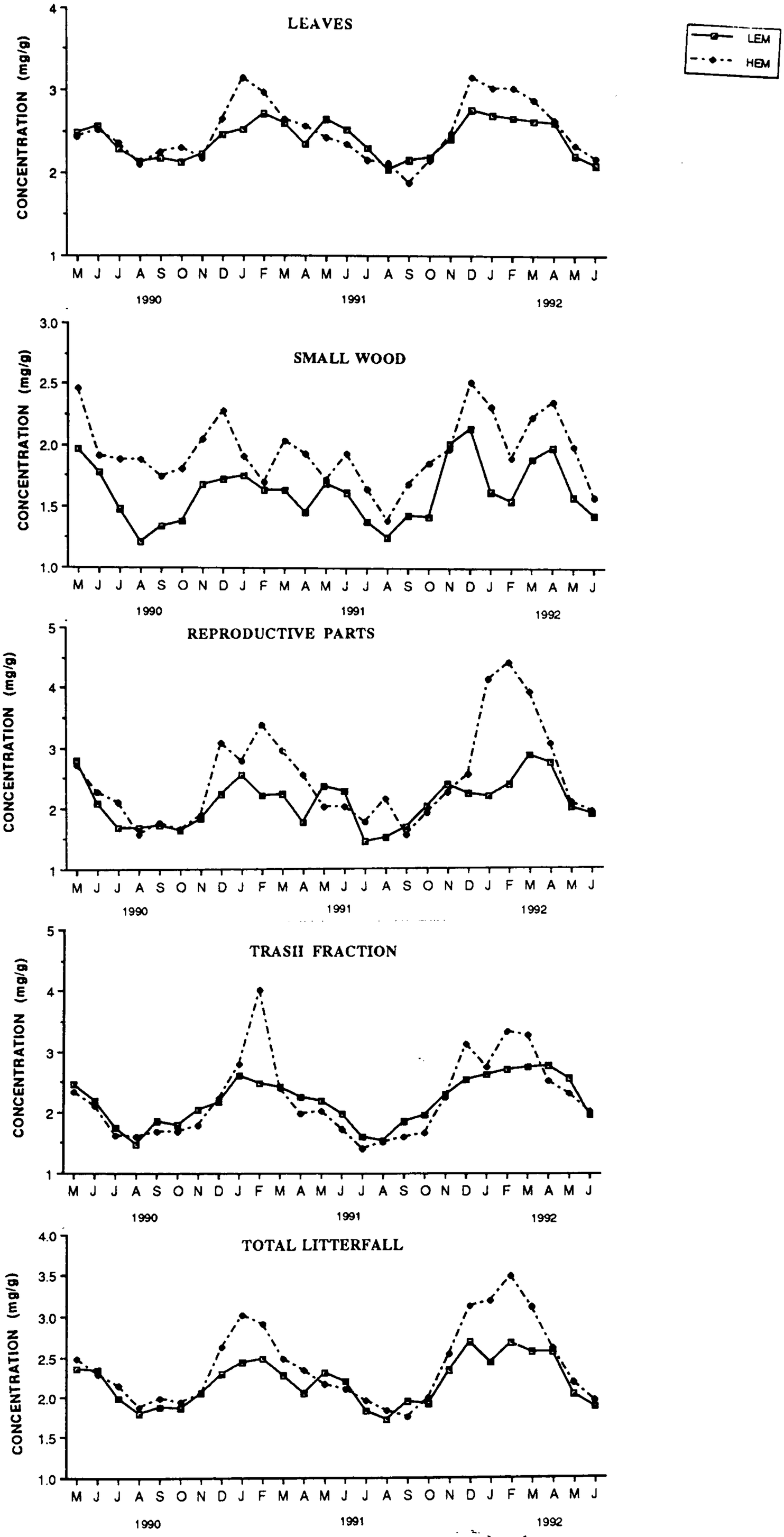


Figure 4.1d: Monthly mean concentrations of Mg (mg g^{-1}) in litterfall collected in five replicate plots in LEM and HEM forests, Korup National Park, Cameroon.

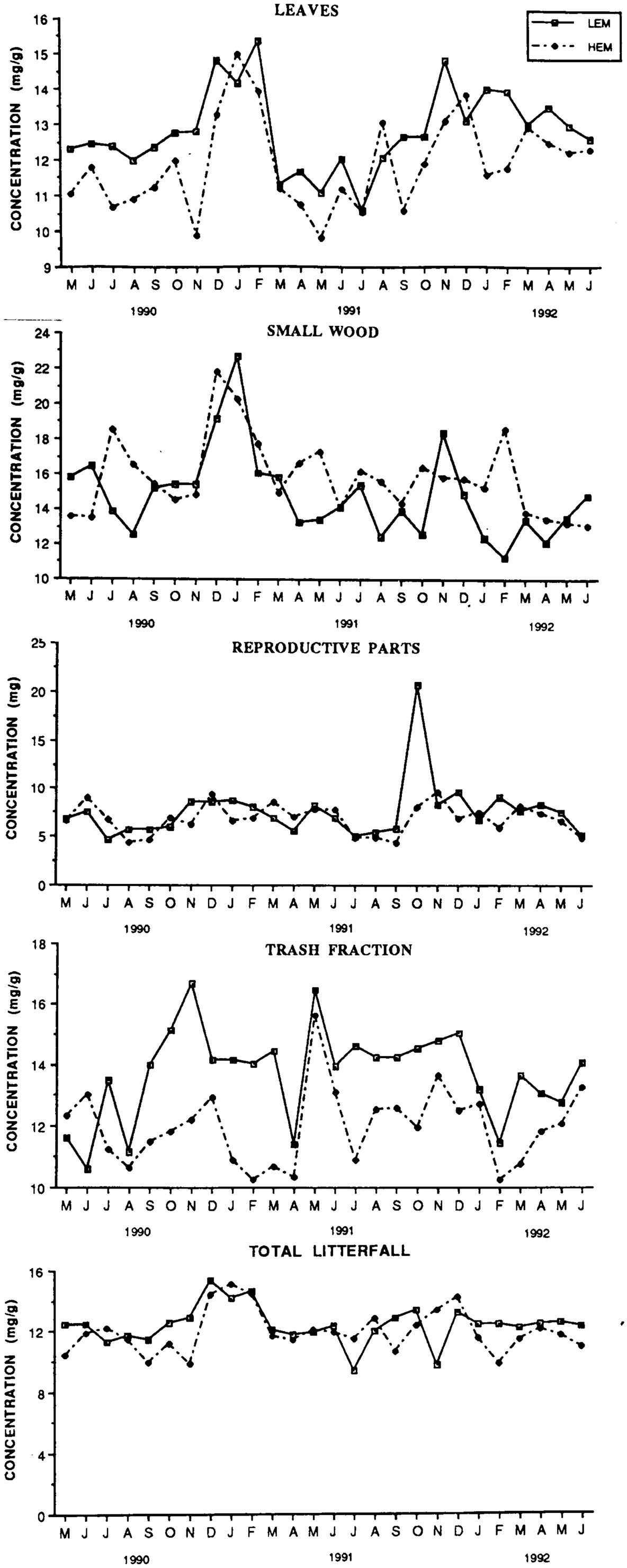


Figure 4.1e: Monthly mean concentrations of Ca (mg g^{-1}) in litterfall collected in five replicate plots in LEM and HEM forests, Korup National Park, Cameroon.

Table 4.1b: Correlation coefficients (rank) between the concentrations (mg g^{-1}) of the different mineral elements (means of replicate plots) in the different litter fractions and total litter (May 1990-June 1992) for LEM and HEM forests, Korup National Park, Mundemba, Cameroon. The superscripts indicates the level of significance of the correlation (n=26).

		LEM				HEM			
		N	P	K	Mg	N	P	K	Mg
Leaves	P	0.53^{2}				0.60^{2}			
	K	-0.33	-0.33			-0.27	-0.23		
	Mg	-0.21	-0.09	0.60^{2}		-0.19	-0.06	0.63^{3}	
	Ca	-0.35	-0.14	0.23	0.34	-0.23	-0.08	0.17	0.35
Small wood	P	0.55^{2}				0.56^{2}			
	K	-0.15	0.52^{2}			0.11	0.50^{1}		
	Mg	0.10	0.31	0.44^{1}		0.15	0.30	0.44^{1}	
	Ca	-0.17	-0.10	0.07	0.26	-0.14	-0.06	0.12	0.31
Repd parts	P	0.86^{3}				0.86^{3}			
	K	0.30	0.62^{2}			0.27	0.55^{2}		
	Mg	0.54^{2}	0.69^{3}	0.68^{3}		0.52^{2}	0.64^{3}	0.61^{2}	
	Ca	0.36	0.34	-0.01	0.39^{1}	0.36	0.32	0.05	0.49^{1}
Trash	P	0.58^{2}				0.96^{3}			
	K	0.34	0.85^{3}			0.80^{3}	0.91^{3}		
	Mg	0.46^{1}	0.76^{3}	0.86^{3}		0.92^{3}	0.96^{3}	0.93^{3}	
	Ca	-0.10	-0.23	-0.18	-0.20	0.94^{3}	0.89^{3}	0.71^{3}	0.84^{3}
Total litter	P	0.57^{2}				0.83^{3}			
	K	-0.26	-0.01			0.39^{1}	0.67^{3}		
	Mg	-0.10	0.15	0.86^{3}		0.39^{1}	0.57^{2}	0.92^{3}	
	Ca	-0.25	-0.21	0.34	0.32	-0.33	-0.42^{1}	0.10	0.31

Correlations between elemental concentrations and total litterfall for both forests

	N	P	K	Mg	Ca
LEM	-0.07	0.10	0.54^{2}	0.41^{1}	0.16
HEM	0.16	0.30	0.64^{3}	0.78^{3}	0.34

$1 = p \leq 0.05$, $2 = p \leq 0.01$, $3 = p \leq 0.001$.

Higher concentrations of K and Mg were recorded in all the fractions in the dry season for both LEM and HEM plots. The dry season peaks in Mg concentration were more pronounced in all litter fractions (especially in the reproductive fractions in the second year) in the HEM plots.

The mineral elements showed some specific associations in their concentrations in the various litter fractions and in total litterfall. They however, varied with the different mineral elements and litter fractions for both forest types (Table 4.1b). Strong and significant correlations were found between N and P, K and Mg in all the fractions (except for N and P in trash fractions, K and Mg in small wood for LEM plots) and total litterfall (r values between 0.60 and 0.88, $n=26$, $p<0.01$).

P and K were also positively and significantly correlated in small wood, reproductive and trash fractions in both forest types (Table 4.1b). Ca was positively and significantly correlated with all the other elements in the trash fraction in the HEM forest ($p\leq0.001$) and negatively in the LEM forest though not significant ($p>0.05$). There was a significant correlation between P and K, P and Mg in total litterfall for HEM plots ($r=0.67$ and 0.92 respectively, $n=26$, $p<0.01$). These relations were either negative or weak for the LEM plots and could be explained by the differences in proportion of the various litter fractions in total litterfall for both forest types.

4.3.1.3 Mineral element concentration in leaf litter of selected species

There was considerable variation between the twenty-two selected species in their leaf litter concentrations in N, P, K, Mg and Ca, in both wet and dry seasons and the two forest types (Table 4.2). The mean concentrations of N, P, K, and Mg (with the exception of Ca) for all the species were significantly different for both the wet and dry seasons ($p<0.001$ for N, K, and Mg; $p<0.01$ for P). The mean concentrations of N and P were higher during the wet season while those of Mg and K were higher during the dry season. Comparison between the forest types showed that concentrations of N, K, Mg and Ca (with the exception of P) differed significantly in the mean leaf litter concentrations of all the

selected species taken together ($p<0.001$ for K, Mg and Ca; $p<0.05$ for N).

High concentrations of N were found in *Hypodaphnis zenkeri, Erythrophleum ivorense, Microberlinia bisulcata, Hymenostegia afzelii* and *Warneckea memecyloides.* The concentrations of P and Mg were also high in *Berlinia bracteosa, Microberlinia bisulcata,* and *Didelotia africana* (all ectomycorrhizal species). The highest concentration of K was found in *Diospyros gabunensis* and the lowest in *Microberlinia bisulcata. Strephonema pseudocola* had the highest concentration of Ca and the lowest in N and P (Table 4.2). Among the selected species, *Microberlinia bisulcata* showed significant differences between the dry and wet seasons in N, P, K and Mg ($p<0.001$ for N and Mg; $p<0.01$ for P and $p<0.05$ for K) with higher concentrations of N and P in the wet season, K and Mg in the dry season (Table 4.2). Significant seasonal differences in N and Mg were found in *Hymenostegia afzelii, Strephonema pseudocola, Warneckea memecyloides* ($p<0.05$) and *Oubanguia alata* ($p<0.001$ and $p<0.05$ respectively). The concentration of P was significantly higher in the wet seasons in *Erythrophleum ivorense* and *Hymenostegia afzelii* ($p<0.05$), while that of K was significantly higher in dry season in *Berlinia bracteosa, Hypodaphnis zenkeri, Didelotia africana* and *Oubanguia alata* ($p<0.05$).

Coula edulis, Didelotia africana, Diospyros iturensis, Hymenostegia afzelii, Oubanguia alata, and *Warneckea memecyloides* showed significantly lower or higher Ca concentrations in the LEM forest compared to the HEM forests for the wet and dry seasons and *Erythrophleum ivorense* in the HEM forest ($p<0.05$). The concentrations were also significantly higher for: Mg in *Diospyros gabunensis* and *Tetraberlinia bifoliolata* in the HEM forest; K in *Diospyros gabunensis* and *Hymenostegia afzelii* in the LEM forest ($p<0.05$). Concentrations of P and N were significantly higher in the LEM forest for both seasons ($p<0.05$) and indifferent in *Warneckea memecyloides* and *Erythrophleum ivorense* respectively (Table 4.2).

The concentration of the mineral elements varied haphazardly for both top canopy and canopy species and no particular trend was seen in relation to crown position. The concentration of nutrients in *Warneckea memecyloides,* an understorey species was within the range recorded for the top and canopy species.

Table 4.2 Mean mineral-element concentration (mg g^{-1}) in leaves of selected species in leaf litter collected over 26 months and bulked for : 1) wet seasons and 2) dry seasons, in both LEM and HEM plots in Korup National Park, Mundemba, Cameroon. '-' indicates no leaf sample analysed.

SPECIES	SEASON	Mineral element concentration (mg g^{-1})									
		N		P		K		Mg		Ca	
		LEM	HEM	LEM	HEM	LEM	HEM	LEM	HEM	LEM	HEM
A.Top Canopy Species											
Anthonotha fragrans	1	17.7	-	0.76	-	4.80	-	2.29	-	10.4	-
	2	17.0	-	0.77	-	5.29	-	2.20	-	10.0	-
Berlinia bracteosa	1	19.0	-	0.89	-	5.92	-	3.70	-	13.5	-
	2	16.4	-	0.87	-	8.53	-	3.87	-	14.3	-
Didelotia africana	1	18.7	20.5	0.77	0.88	3.14	2.94	1.87	2.03	14.8	8.21
	2	19.0	19.4	0.88	0.85	4.54	3.32	2.25	2.13	14.2	8.51
Erythrophleum ivorense	1	24.6	21.4	0.64	0.59	4.00	3.55	1.28	2.19	3.99	5.74
	2	22.0	20.4	0.47	0.54	3.48	3.48	1.60	2.26	3.99	6.01
Irvingia gabonensis	1	-	15.1	-	0.67	-	4.72	-	2.00	-	9.60
	2	-	13.5	-	0.64	-	5.63	-	2.19	-	11.0

SPECIES	SEASON	Mineral element concentration (mg g^{-1})									
		N		P		K		Mg		Ca	
		LEM	HEM	LEM	HEM	LEM	HEM	LEM	HEM	LEM	HEM
Staudtia stipitata	1	15.2	-	0.55	-	3.02	-	2.05	-	10.6	-
	2	13.8	-	0.55	-	3.35	-	2.13	-	11.6	-
Strephonema pseudocola	1	11.9	11.5	0.48	0.46	3.37	3.32	2.07	2.03	17.5	16.9
	2	10.2	9.44	0.47	0.39	3.83	2.91	2.13	1.88	17.9	18.3
Microberlinia bisulcata	1	-	21.4	-	0.90	-	2.84	-	2.42	-	12.0
	2	-	17.5	-	0.75	-	3.56	-	3.21	-	13.4
Tetraberlinia bifoliolata	1	16.1	15.8	0.63	0.65	3.19	3.22	1.89	1.93	7.34	7.15
	2	14.8	15.5	0.62	0.67	3.95	3.69	1.71	2.26	6.37	6.93
Tetraberlinia moreliana	1	-	19.0	-	0.90	-	5.92	-	3.70	-	13.5
	2	-	16.4	-	0.87	-	8.53	-	3.87	-	14.3
B. Canopy Species											
Cola rostrata	1	14.7	14.3	0.69	0.68	5.62	5.14	2.31	2.18	9.34	8.31
	2	13.4	13.3	0.67	0.62	6.13	4.13	2.45	2.42	8.48	8.79

SPECIES	SEASON	Mineral element concentration (mg g^{-1})									
		N		P		K		Mg		Ca	
		LEM	HEM	LEM	HEM	LEM	HEM	LEM	HEM	LEM	HEM
Cola verticillata	1	13.6	13.2	0.66	0.62	4.31	4.94	2.76	2.66	16.8	11.3
	2	11.2	12.3	0.62	0.58	4.46	4.56	2.84	3.32	16.3	14.0
Coula edulis	1	15.4	13.3	0.61	0.57	3.60	3.54	1.45	1.56	7.20	5.79
	2	13.7	13.6	0.62	0.55	4.18	3.86	1.41	1.52	6.26	4.30
Diospyros gabunensis	1	18.6	17.6	0.63	0.64	8.01	5.54	2.80	3.73	15.1	16.6
	2	17.4	15.0	0.66	0.55	10.15	6.56	3.09	4.37	14.1	18.0
Diospyros iturensis	1	16.8	15.7	0.55	0.54	4.09	3.91	2.19	2.23	15.5	12.1
	2	15.5	15.0	0.57	0.64	5.77	5.01	2.19	2.38	13.7	10.0
Dichostemma glaucescens	1	15.9	-	0.50	-	3.75	-	2.12	-	9.90	-
	2	14.3	-	0.46	-	4.10	-	2.07	-	8.72	-
Hymenostegia afzelii	1	20.7	20.2	0.70	0.71	4.45	3.83	2.26	2.19	11.8	10.1
	2	19.0	18.5	0.66	0.67	4.61	3.98	2.42	2.56	12.8	9.44
Hypodaphnis zenkeri	1	22.9	-	0.69	-	5.65	-	1.78	-	9.70	-
	2	24.2	-	0.72	-	7.98	-	1.98	-	10.3	-

SPECIES	SEASON	Mineral element concentration (mg g^{-1})									
		N		P		K		Mg		Ca	
		LEM	HEM	LEM	HEM	LEM	HEM	LEM	HEM	LEM	HEM
Klaineanthus gaboniae	1	17.2	15.7	0.63	0.57	3.77	3.43	2.75	2.93	11.8	12.4
	2	15.2	14.5	0.55	0.51	4.66	3.66	2.83	2.88	10.8	12.1
Oubanguia alata	1	15.8	15.0	0.56	0.54	4.43	3.80	2.15	2.15	9.53	8.28
	2	13.8	13.8	0.52	0.51	4.97	4.69	2.18	2.56	9.25	7.92
Strombosia glaucescens	1	20.2	-	0.66	-	4.83	-	1.89	-	7.88	-
	2	17.4	-	0.58	-	5.45	-	1.72	-	6.84	-
C. Understorey Species											
Warneckea memecyloides	1	19.2	19.4	0.67	0.71	4.02	3.54	2.00	1.96	12.7	10.4
	2	17.4	17.6	0.64	0.73	4.85	4.69	1.94	2.12	13.0	11.5

Table 4.3 Estimated quantities (kg ha^{-1} yr^{-1}) of mineral elements returned annually to the forest floor in the various litterfall fractions for both LEM and HEM plots in Korup National Park, Mundemba, Cameroon.

Litter fraction	Forest type	Litterfall (t ha^{-1} yr^{-1})	Mineral nutrients accession (kg ha^{-1} yr^{-1})				
			N	P	K	Mg	Ca
Leaves	LEM	5.66	96.9	3.61	27.9	13.6	68.1
	HEM	5.13	87.7	3.47	22.3	12.8	57.4
Small wood	LEM	1.91	25.1	0.87	4.51	3.09	28.2
	HEM	1.62	19.3	0.74	4.39	3.16	25.7
Reproductive parts	LEM	0.854	15.9	1.01	6.11	1.78	6.37
	HEM	1.17	20.6	1.34	7.06	2.88	7.94
Moss & Lichen	LEM	0.013	0.22	0.01	0.07	0.03	0.12
	HEM	0.051	0.89	0.05	0.26	0.13	0.57
Trash	LEM	0.559	12.2	0.63	0.87	1.22	7.67
	HEM	0.370	7.54	0.38	0.66	0.82	4.41
Total	LEM	8.99	150	6.13	39.5	19.7	111
	HEM	8.33	136	5.89	34.7	19.7	96.0

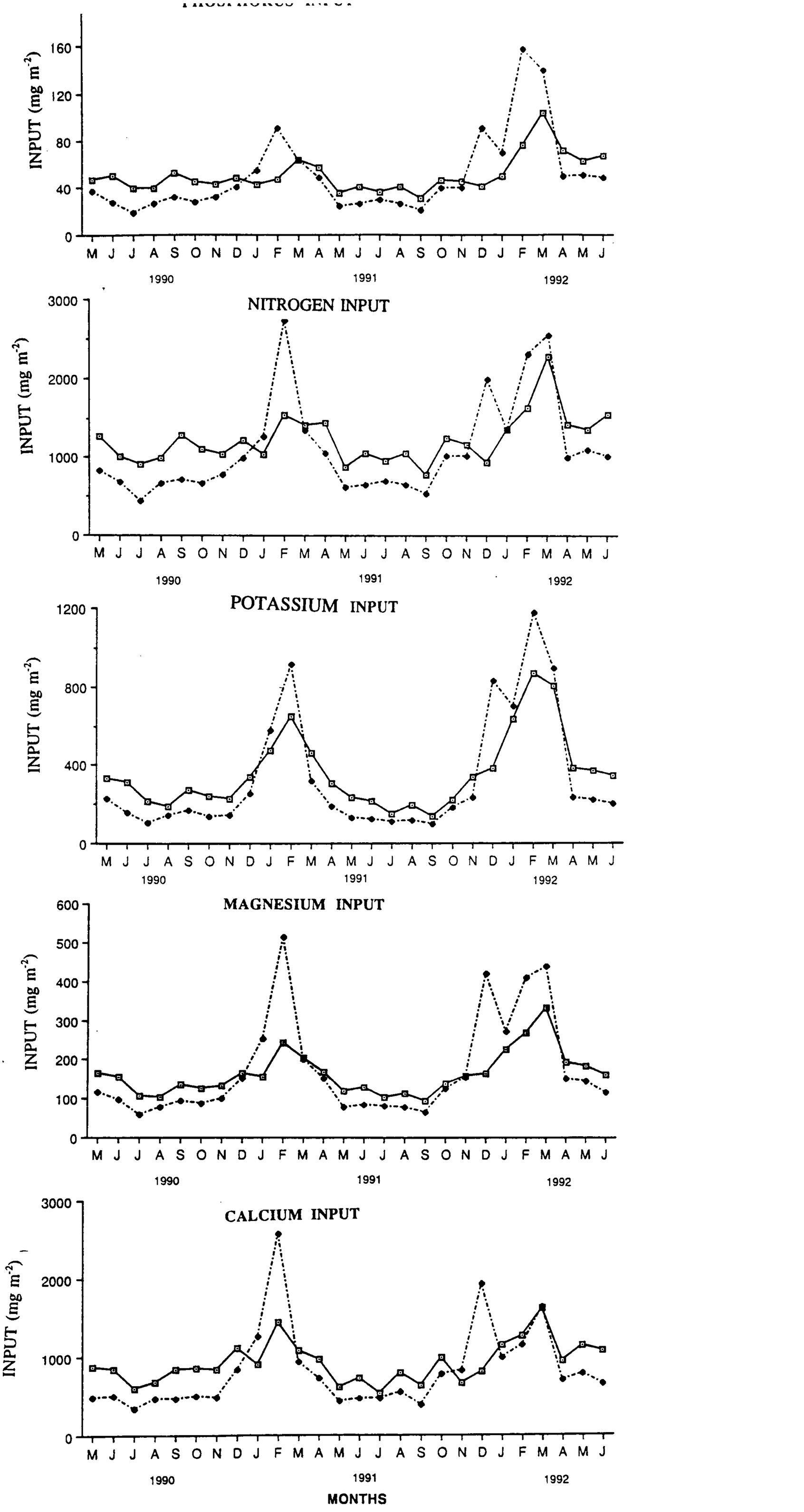


Figure 4.2: Monthly input of N, P, K, Mg and Ca (mg m^{-2}) in total litterfall collected in five replicate plots in LEM and HEM forests, Korup National Park, Cameroon.

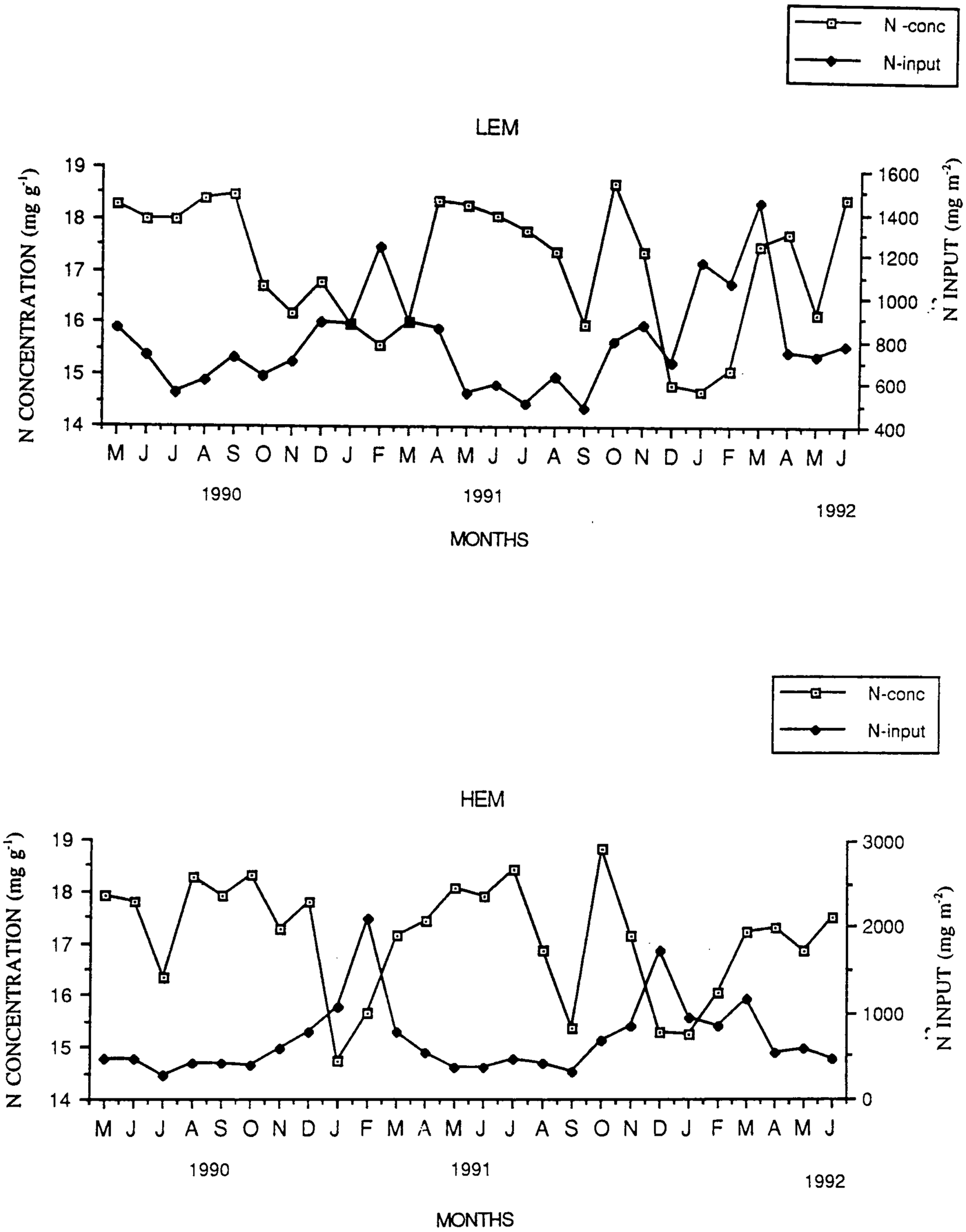


Figure 4.3: Monthly mean concentration (mg g^{-1}) and input of N (mg m^{-2}) in leaf litter collected in five replicate plots in LEM and HEM forests, Korup National Park, Cameroon.

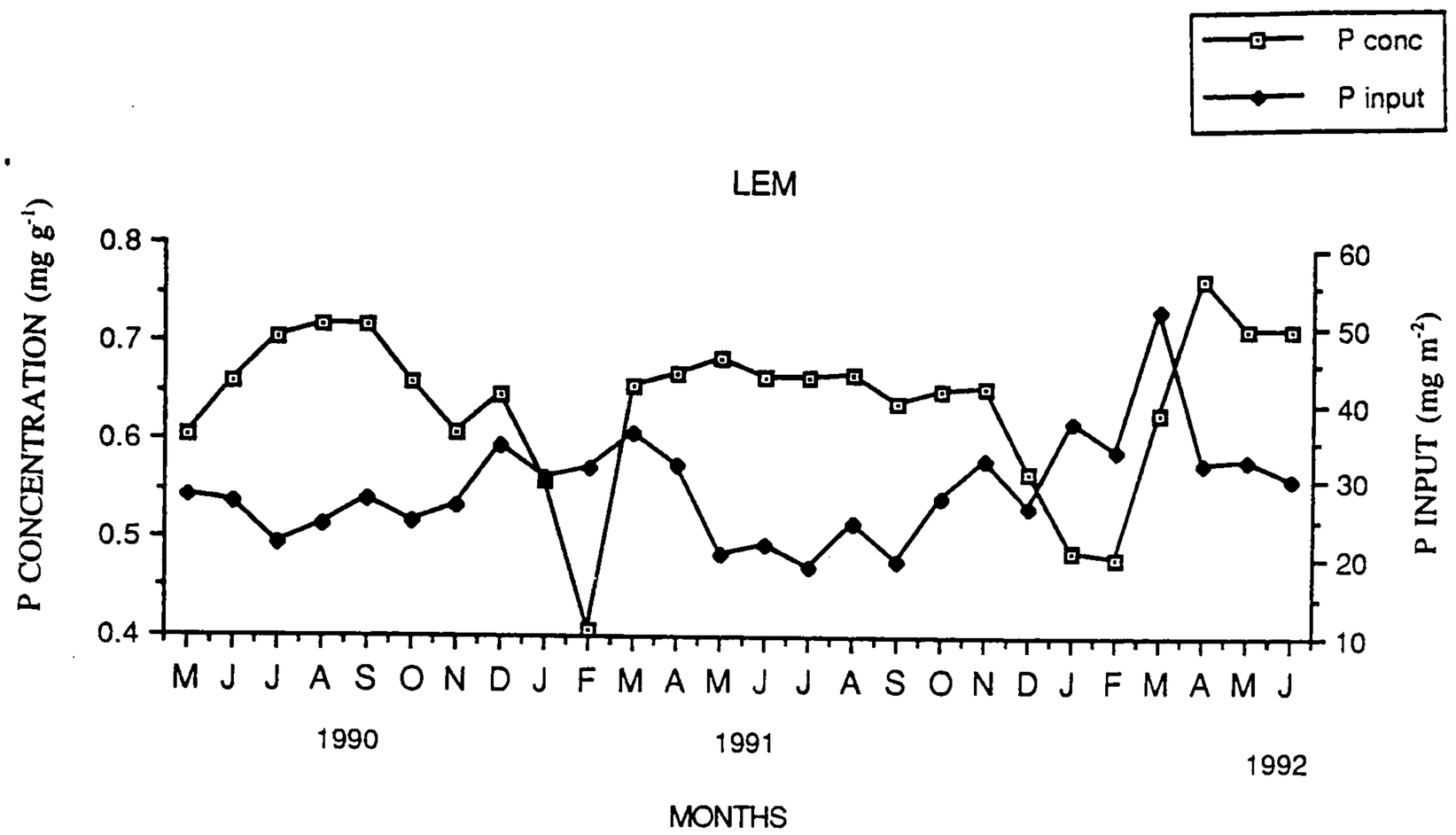


Figure 4.4: Monthly mean concentration (mg g^{-1}) and input of P (mg m^{-2}) in leaf litter collected in five replicate plots in LEM and HEM forests, Korup National Park, Cameroon.

4.3.2 Mineral element accession in litterfall

The estimated mean quantities of N, P, K, Mg and Ca returned to the forest floor annually in the various litter fractions for both forest types are given in Table 4.3. Rates of accession of N, P, K, and Ca in total litterfall were higher for LEM plots while Mg was similar for both LEM and HEM plots. The high returns of Mg in the HEM plots resulted from the higher proportion of reproductive parts which had high concentrations of Mg, as well as the significantly high concentration of this element in leaf litter. The highest returns of mineral elements to the forest floor were through leaf litter (Table 3.9).

Trends in monthly accession of the different elements in both forest types are presented in Figure 4.2. These followed similar patterns with total litterfall in all the mineral elements. Peaks in accession in all the elements were between January and March (dry months) for both LEM and HEM plots. These were prominently higher for the HEM plots during the dry season and lower during the rest of months. The two peaks recorded in the second year for the HEM plots coincided with those in litterfall (the first in December 1991 for leaves and the second in February 1992 for reproductive parts). These contributed to the higher returns of P and Mg during that same period as a result of the high concentration of these elements in those fractions.

In comparing the monthly mean concentrations and rates of accession of the mineral elements, a consistent pattern was seen in N and P for leaf litter in both LEM and HEM plots. In the dry seasons during which peaks in leaf fall were recorded, as well as the rate of accession of the elements in them, the concentrations of N and P were comparatively lower and this situation was reversed during the wet seasons (Figures 4.3 and 4.4). These were indications of comparatively higher rates of withdrawal or reallocation of N and P from the leaves prior to leaf fall in the dry season.

Table 4.4a Mean mineral element concentration (mg g^{-1}) in 1) fresh mature leaves from top crown position and 2) freshly fallen leaf litter of five ectomycorrhizal species collected in December 1991, April 1992 and July 1992, in Korup National Park, Mundemba, Cameroon. The percentage of leaf litter/ fresh leaf concentration is calculated for : 3) element concentration per unit mass; and 4) element concentration per unit calcium. The percentage of nutrients retranslocated is given in (5). Values for mature and leaf litter are means ±SE (n=3).

Species		N	P	K	Mg	Ca
Anthonotha fragrans	1	19.2±1.7	1.36±0.16	8.39±1.19	2.44±0.23	5.96±1.69
	2	17.3±0.77	0.84±0.06	7.03±0.74	2.43±0.16	7.29±1.25
	3	90	62	84	99	122
	4	74	51	68	82	100
	5	26	49	32	18	-
Berlinia bracteosa	1	22.0±1.26	1.57±0.13	17.44±0.23	4.94±0.08	16.6±1.33
	2	18.9±1.14	1.40±0.36	12.02±4.48	3.86±0.24	16.0±4.42
	3	86	89	69	78	96
	4	89	93	72	81	100
	5	11	7.0	28	19	-
Didelotia africana	1	19.7±1.08	1.20±0.05	6.55±0.74	2.39±0.11	7.46±1.86
	2	18.5±0.39	0.92±0.08	4.85±0.26	2.26±0.14	9.98±0.35
	3	94	77	74	95	134
	4	70	57	55	71	100
	5	30	43	45	29	-
Microberlinia bisulcata	1	22.3±0.76	1.18±0.11	5.91±0.10	3.77±0.35	13.2±1.99
	2	20.6±1.93	0.93±0.10	4.52±0.10	3.26±0.43	14.5±3.46
	3	92	78	76	86	110
	4	84	71	69	79	100
	5	16.1	29	31	21	-
Tetraberlinia bifoliolata	1	17.6±0.39	1.02±0.14	4.23±0.60	1.41±0.05	5.82±0.49
	2	15.3±0.67	0.74±0.16	2.20±0.80	1.62±0.12	5.12±0.26
	3	87	73	52	115	88
	4	99	83	59	131	100
	5	1.0	17	41	-31	-
Ectomycorhizal spp.	1	20.2±0.67	1.27±0.07	8.51±0.90	3.00±0.34	9.80±1.35
	2	18.1±0.68	0.97±0.10	6.12±1.27	2.69±0.25	10.6±1.58
	3	90	76	72	90	108
	4	83	71	67	83	100
	5	17	29	33	17	-

Table 4.4b Mean mineral element concentration (mg g^{-1}) in 1) fresh mature leaves from top crown position and 2) freshly fallen leaf litter of six non-ectomycorrhizal species collected in December 1991, April 1992 and July 1992, in Korup National Park, Mundemba, Cameroon. The percentage of leaf litter/ fresh leaf concentration is calculated for : 3) element concentration per unit mass; and 4) element concentration per unit calcium. The percentage of nutrients retranslocated is given in (5). Values for mature and leaf litter are means ±SE (n=3).

Species		N	P	K	Mg	Ca
Cola verticillata	1	19.1±0.74	1.12±0.13	9.28±0.90	3.83±0.12	10.4±1.07
	2	13.1±0.41	0.71±0.08	6.81±0.64	3.38±0.12	9.28±1.19
	3	68	63	73	88	90
	4	76	71	82	98	100
	5	24	29	18	2.0	-
Coula edulis	1	17.8±0.52	1.00±0.07	5.90±1.19	1.13±0.07	3.12±0.46
	2	14.1±1.12	0.58±0.06	3.66±0.44	1.37±0.13	3.52±0.45
	3	79	58	62	121	113
	4	70	51	55	107	100
	5	30	49	45	-7.3	-
Hymenostegia afzelii	1	28.9±1.41	1.59±0.22	8.94±0.87	2.13±0.24	6.21±1.98
	2	20.1±1.23	0.89±0.13	5.57±0.43	2.47±0.10	10.1±5.21
	3	70	56	62	116	162
	4	43	34	38	71	100
	5	57	66	62	29	-
Klaineanthus gaboniae	1	22.6±1.42	1.00±0.02	7.43±0.83	3.14±0.23	9.01±0.29
	2	15.5±0.93	0.60±0.05	5.67±1.10	3.71±0.14	10.7±1.94
	3	69	60	76	118	118
	4	58	51	65	100	100
	5	42	49	35	0.0	-
Oubanguia alata	1	20.2±1.47	1.20±0.11	12.2±1.22	2.96±0.14	6.66±0.1
	2	14.3±0.51	0.63±0.04	6.60±0.26	2.55±0.34	7.04±1.11
	3	71	53	54	86	106
	4	67	50	51	81	100
	5	33	50	49	19	-

Species		N	P	K	Mg	Ca
Strephonema pseudocola	1	12.0±0.89	0.81±0.12	7.58±1.64	2.08±0.29	9.26±3.02
	2	10.8±0.39	0.48±0.06	4.63±0.58	2.01±0.24	15.1±1.72
	3	90	59	61	96	163
	4	55	36	37	59	100
	5	45	64	63	41	-
Non-ectomycorrhizal spps. (6)	1	20.1±1.30	1.12±0.07	8.55±0.63	2.55±0.22	7.44±0.80
	2	14.6±0.75	0.65±0.04	5.49±0.35	2.58±0.20	9.28±1.03
	3	73	58	64	101	125
	4	58	46	51	81	100
	5	42	54	49	19	-

Table 4.4c: Mean mineral elemental concentration (mg g^{-1} of oven dried-weight) in 1) fresh young leaves and 2) fresh mature leaves from top crown position of three species collected in December 1991 and April 1992, in Korup National Park, Mundemba, Cameroon. (Mean±SE, n=2 for young leaves, n=3 for mature leaves).

Species	Age of leaf	Mineral element concentration (mg g^{-1})				
		N	P	K	Mg	Ca
Coula edulis	1	24.5±4.04	2.18±0.52	8.89±1.61	1.58±0.36	2.65±0.53
	2	17.8±0.52	1.00±0.07	5.90±1.19	1.13±0.07	3.12±0.46
Hymenostegia afzelii	1	52.4±0.31	5.50±0.29	23.4±2.99	2.78±0.06	2.41±0.66
	2	28.9±1.41	1.59±0.22	8.94±0.87	2.13±0.24	6.21±1.98
Strephonema pseudocola	1	12.9±1.41	1.10±0.09	12.1±1.95	2.09±0.01	7.83±2.73
	2	11.9±0.89	0.81±0.12	7.58±1.64	2.08±0.29	9.26±3.02

4.3.3. Foliar concentration and retranslocation

The concentrations of N, P and K were lower in the freshly fallen leaf litter than in the freshly collected mature leaves of the selected species. The concentrations of Mg and Ca were generally higher in the leaf litter but fluctuated in some species (Tables 4.4a and 4.4b). These differences were however significant for N, P, and K ($p<0.01$). The nonsignificant difference between the collection periods indicated that the sampling procedure adopted was consistent and eliminated variations which could have been introduced, due to fluctuations in nutrient levels within the crown and differences in the 'physiological age' of the leaves (in relation to time of bud breaking and leaf expansion to maturity).

In comparing the concentrations of the mineral elements in the young leaves (for those species that flushed during the collection periods), mature and freshly fallen leaves, it was noticed that substantial proportions of N, P and K were withdrawn from the leaves prior to leaf fall. Mg and Ca were rather accumulated as their concentrations were higher in the abscised leaves. The concentrations of N, P and K in the very young leaves (at flush) were more than double those in the mature leaves. Mean concentrations of N, P, K, Mg and Ca in young and mature leaves of *Coula edulis*, *Hymenostegia afzelii* and *Strephonema pseudocola* are presented in Table 4.4c. This showed that withdrawal of N and P may start once the leaves are fully expanded and proceeds as the leaf grows older until the formation of abscission layer. Alternatively, the fall in leaf concentrations may be due to dilution by carbohydrates in growth.

The proportion of the elements either retranslocated or accumulated prior to leaf fall are shown in Tables 4.4a and 4.4b. These were expressed per unit mass of the leaves and per unit Ca in the abscised leaves. Estimates based on per unit mass has been reported to be inaccurate due to changes in weight caused by differential withdrawal or accumulation of materials into the leaves prior to abscission (Ostman and Weaver 1982, Boerner 1984, Vitousek and Sanford 1986). In overcoming the problem, Vitousek and Sanford (1986) estimated retranslocation of N and P by using the ratios of these elements to that of Ca in leaf litter. This was on the assumption that Ca is relatively immobile once in plant tissues.

The highest proportions of N and P retranslocated were in *Hymenostegia afzelii* and the lowest in *Tetraberlinia bifoliolata* and *Berlinia bracteosa* for N and P respectively (Tables 4.4a and 4.4b).

The proportions of N, P and K retranslocated were comparatively higher for the non-ectomycorrhizal species relative to the ectomycorrhizal species (Tables 4.4a and 4.4b). The proportions of N and P retranslocated from leaves of the non-ectomycorrhizal species were approximately two-fold those of the ectomycorrhizal species. The proportion of K retranslocated may probably have been over-estimated since corrections for losses through leaching prior to leaf fall was not included in the estimation procedure. K has a high ionic mobility and is easily leached from the canopy.

4.4 DISCUSSION

4.4.1 Mineral-element concentration in litterfall

The elemental analysis revealed considerable variation in the mean concentrations of N, P, K, Mg and Ca in the litter fractions for both forest types. The overall weighted mean concentrations of N, K and Ca were higher in the LEM forest and P and Mg were higher in the HEM forest. The variability in total mineral element concentrations in both forest types can be explained by the differences in concentrations and relative proportions of the different litter fractions in total litterfall. The leaf litter which contributed approximately 60% to total litterfall (Table 3.9) in both forest types accounted most to weighed concentrations of these elements in total litterfall. The significant differences in the concentrations of P, K, Mg and Ca in leaf litter between both LEM and HEM forest types (Table 4.1), were also reflected in the mean concentrations of these mineral elements in total litterfall. Small wood fractions are dropped from the canopy in a highly decomposed state with high concentrations of Ca but very low concentrations K and Mg which are easily leached (Edwards 1982). This situation was however different for the bulk of woody twigs that fell in the HEM forest. These were abscised together with the leaflets in the dry season and had higher concentrations of nutrients than those in the LEM forest.

The reproductive fraction consisted of flowers, seeds, fruits and pods, which are all of different structural composition with varying mineral element concentrations. The HEM forest is dominated by legumes which produce pods while the LEM forest is dominated by other types of fruits such as drupes. Owing to high allocation of nutrients to the reproductive parts, particularly fruits (Ernst and Tolsma 1989), these organs tend to be sinks for nutrients and this results in their having high concentrations of mineral elements in litterfall. Seeds of *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* were the only reproductive components analyzed separately (Table 4.5). Both showed high concentrations of N, P, K and Mg, with low concentrations of Ca. High concentrations of mineral elements in the reproductive fraction have also been reported for other tropical forests (Proctor *et al.* 1983, Veneklaas 1991, Scott *et al.* 1992)

Mosses and lichens though contributing very little to total litterfall had high concentrations

of nutrients. Lichens have the ability to fix N and mosses the ability to absorb nutrients from both the atmosphere and precipitation (Lang *et al.* 1976, Pike 1978, Jordan and Herera 1981).

The high mineral element concentrations in the trash fraction are more difficult to interpret because of its diverse composition. The frass, insect parts and faeces of canopy feeders are good sources of N, P and Ca. In the present study, fine pollen grains which could not easily be sorted were included in the trash these possibly could have contributed to the high concentrations of the mineral elements in that fraction.

Brasell *et al.* (1980) found no seasonal variation in mineral element concentrations in total litterfall of tropical forest. Cornforth (1970) also observed very little in leaf litter concentration for tropical forest in Trinidad. In the present study, clear seasonal variations were shown in the mineral element concentrations in all litter fractions and in total litterfall. Temporal variations in the overall weighted concentrations in total litterfall were not only a reflection of variations in litterfall composition (proportions of the different fractions). Leaching in the wet season as well as other physiological feedback mechanisms occurring in the plants may alter the concentrations of the various mineral elements in litterfall in relation to their availability either in soil or reserves within the tree. The fall in the concentrations of N and P in leaf litter in the dry season was a result of considerable retranslocation of these elements to other active sites in the plants prior to leaf abscission (Grubb 1977, Chabot and Hicks 1982, Chapin *et al* 1983). The sharp rise in the concentrations of N, P, K and Mg in total litterfall in the dry season of the second year of study from December 1991 to February 1992 can be attributed to the profuse flowering which occurred during that period and which contributed more than 50% of the total litterfall for the HEM plots.

K is known to have a high ionic mobility (Bernhard-Reversat 1975, Parker 1983, Forti and Moreira-Norderman 1991). The low concentration of this element in the wet season could be as a result leaching either from the forest canopy or while in the litter trap. The concentration of Mg was consistently higher in the HEM forest in all the fractions and total litterfall particularly in the dry season. In looking at the concentration of this element in leaf litter of the different species, *Microberlinia bisulcata* and *Tetraberlinia bifoliolata*

were among the species with the highest concentration of Mg in both dry and wet seasons. Both species are predominantly in the HEM forests and shed most of their leaves during the dry season. The high concentration of Mg in the dry season also shows that the cycling of Mg is predominantly in litterfall especially in the HEM forest. Ca however showed very little variation with time which reflects its relatively low mobility in plants.

Mineral element concentrations of leaf litter and total litterfall from a range of tropical forest are summarized in Table 4.7. Comparison could only be made on leaf litter and total litterfall concentrations due to variations in defining the various litter fractions in most studies. The concentrations of N, P, K, Mg and Ca in both leaf and total litterfall for LEM and HEM forest types were within the range reported for other African tropical forests. The concentrations of P, K, Mg and Ca were higher for the Bakundu forest with the concentrations of P and K more than twofold that recorded in the present study. These high values may have been a result of the addition of the trash fraction to leaf litter fraction. The concentrations of P and Ca recorded in the present study were higher than those reported for the Amazon forest and the tropical forest in Sarawak. Higher concentrations of P and Mg were recorded for the tropical forest in Australia and India (Karnataka).

4.4.2 Mineral element accession in litterfall

The present study showed that the annual rates of returns of N, K and Ca in litterfall were higher in the LEM forest compared to the HEM forest type. The differences in rates of accession of P and Mg was however marginal between both forest types with the accession of P slightly higher in the LEM forest and Mg in the HEM forest. This result is a clear indication of a strong interaction between the quantity and quality (defined by mineral element concentration) of litterfall in determining rates of mineral element accession (Brasell *et al.* 1980). The concentrations of N, K and Ca were higher in all litterfall fractions in the LEM forest and Mg in the HEM forest. That of P was higher only in the leaf fractions in the HEM forest. These variations in concentrations coupled with the slight differences in rates of litterfall (various fractions) accounted for the differences between the forest types.

In considering the quantity of litterfall, emphasis is placed on the relative proportions of the litter fractions in total litterfall. The high inter-annual variations in rates of accessions of N, P, K and Mg particularly in the HEM forest was a result of the considerable increase in the reproductive fraction from profuse flowering in the second year (July 1991-June 1992). Masting is a common phenomena in some tropical forests and usually requires different nutrient budgets (Schaik 1986).

Rates of accession of all the mineral elements were strongly seasonal in both forest types with peaks in the dry season. The dominant litterfall periods for both forest types were in the dry season apparently because of leaf fall. Other fractions such as the reproductive and, notably, the small wood ones for the HEM forest, contributed significantly to total litterfall during this period. With the strong seasonality in the HEM forest, the mean accession of all the mineral elements were higher in this forest type compared to the LEM forest. The reverse however occurred in the wet season with the accession of these mineral elements rather higher in the LEM forest and lower in the HEM forest. The mean rates of litterfall were 89.5 and 110.4 g m^{-2} $month^{-1}$ in the dry season; 67.7 and 49.0 g m^{-2} $month^{-1}$ in the wet season for both LEM and HEM plots respectively. Coupled with the higher mineral element concentrations in total litterfall for the HEM forest, the rates of accession were exceptionally higher in the dry season and relatively lower in the wet season compared to the LEM forest (Figure 4.2).

These spatio-temporal differences in patterns of mineral element accession between both forest types accounted for similar variations in the availability of the mineral elements in the top soil. This shows a relationship between mineral element accession and soil nutrient concentrations. Newbery *et al.* (1988) reported differences in dry and wet season trends in the concentrations of extractable P in the top soil in both forest types in Korup. They recorded extractable P concentrations of 2.8 and 3.8 μg g^{-1} in the wet season; 12.3 and 7.9 μg g^{-1} in the dry season, within and without the ectomycorrhizal groves. In the present study, the mean rates of accession of total P was 57.9 and 86.9 mg g^{-1} $month^{-1}$ during the dry season; 46.2 and 33.1 mg g^{-1} $month^{-1}$ during the wet season for both HEM and LEM forest respectively. P inputs however did not follow the opposite trends observed in extractable P when the LEM and HEM forests were compared.

Table 4.5: Mean concentration (mg g^{-1} of air-dried weight) of mineral elements in seeds *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* collected from Korup National Park, Mundemba, Cameroon (mean±SE, n=3).

	Mineral element concentration (mg g^{-1})				
	N	P	K	Mg	Ca
Microberlinia bisulcata	13.8±0.07	2.09±0.02	6.41±0.04	2.22±0.01	3.50±0.09
Tetraberlinia bifoliolata	10.9±0.21	1.70±0.04	6.15±0.10	1.16±0.03	1.43±0.11

Table 4.6: Indices of nutrient use efficiency in both LEM and HEM forest types in Korup National Park, Mundemba, Cameroon.

		Mineral element				
	Forest type	N	P	K	Mg	Ca
Dry Mass/Nutrient Ratio	LEM	60	1468	228	457	81
	HEM	61	1415	240	423	87
Retranslocation (%)#	*EMS	17	29	33	17	0
	*NEMS	42	54	49	19	0

* EMS = Ectomycorrhizal species (n=5)
* NEMS= Non-ectomycorrhizal species (n=6)
# From Table 4.4.

Table 4.7: Mineral-element concentrations and accession rates in leaf and total litterfall of some tropical forests in Africa, South America, Asia and Australia.

LOCATION	LITTER FRACTION	LITTER FALL	CONCENTRATION (% dry wt)					ACCESSION (kg ha^{-1})					REFERENCES
		(t ha^{-1}yr^{-1})	N	P	K	Mg	Ca	N	P	K	Mg	Ca	
AFRICA													
ZAIRE YANGAMBI	TOTAL	12.4	1.8	0.056	0.39	0.43	0.85	223.2	6.94	48.4	53.3	105.3	a
GHANA KADE	LEAF	7.0	2.1	0.087	1.00	0.54	2.02	147.0	6.1	70.0	37.8	140.0	b
	TOTAL	10.54	1.9	0.069	0.65	.43	1.99	199.5	7.3	68.4	45.2	209.0	b
COTE D'IVOIRE													
BANCO PLATEAU	LEAF	8.7	1.5	0.069	0.22	0.46	0.56	130.5	6.0	19.0	40.0	48.7	c
	TOTAL	12.6	1.3	0.063	0.22	0.40	0.48	163.8	7.9	27.7	50.4	60.5	
BANCO VALLEY	LEAF	7.9	1.8	0.160	0.91	0.41	0.95	142.2	12.6	71.9	32.4	75.1	
	TOTAL	9.5	1.7	0.14	0.85	0.37	0.90	161.5	13.3	80.8	35.2	85.2	
YAPO PLATEAU	LEAF	6.4	1.4	0.05	0.28	0.29	1.32	89.6	3.2	17.9	18.6	84.5	c
	TOTAL	8.8	1.3	0.048	0.30	0.26	1.20	114.4	4.2	26.4	22.9	105.6	
YAPO VALLEY	LEAF	5.9	1.4	0.053	0.49	0.32	1.36	82.6	3.13	28.9	18.9	80.2	
	TOTAL	8.0	1.3	0.054	0.47	0.27	1.30	104.0	4.32	37.6	21.6	104.6	
CAMEROON													
BAKUNDU RESERVE	LEAF	8.7	1.42	0.13	1.09	0.45	2.09	123.5	11.6	93.9	39.2	181.8	d
	TOTAL	13.6	1.3	0.16	1.21	0.36	1.78	176.8	22.9	164.6	40.8	242.1	
KORUP NAT. PARK													
LEM FOREST	LEAF	5.66	1.71	0.064	0.49	0.24	1.29	96.9	3.6	27.9	13.6	68.1	e
	TOTAL	8.99	1.67	0.068	0.44	0.22	1.23	150.3	6.1	39.5	19.7	110.5	
HEM FOREST	LEAF	5.13	1.71	0.068	0.43	0.25	1.19	87.7	3.5	22.3	12.8	57.5	
	TOTAL	8.33	1.63	0.072	0.42	0.24	1.15	136.0	5.9	34.7	19.7	96.0	

LOCATION	LITTER FRACTION	LITTER FALL	CONCENTRATION (% dry wt)					ACCESSION (kg ha^{-1})					REFERENCES
		(t ha^{-1}yr^{-1})	N	P	K	Mg	Ca	N	P	K	Mg	Ca	
SOUTH AMERICA													
BRAZIL													
MARACA	LEAF	6.30	1.26	0.058	0.47	0.27	0.74	79.1	3.6	29.4	16.8	46.4	f
	TOTAL	9.28	1.24	0.064	0.51	0.25	0.72	118.0	6.7	48.5	63.7	23.8	
MANAUS PLATEAU	LEAF	5.42	1.8	0.02	0.15	0.18	0.38	97.6	1.1	8.1	9.8	20.6	g
	TOTAL	8.25	1.8	0.04	0.18	0.17	0.44	151.0	3.1	15.0	13.8	36.7	
MANAUS VALLEY	LEAF	4.69	1.40	0.03	0.3	0.21	0.77	65.7	1.41	14.1	9.8	36.1	
	TOTAL	7.44	1.46	0.05	0.3	0.19	0.78	109.0	3.7	22.2	14.0	58.2	
ASIA													
SARAWAK (GUNUNG MULU)													
ALLUVIAL FOREST	LEAF	6.6	0.90	0.027	0.26	0.20	2.4	59.0	1.8	17.0	13.0	16.0	h
	TOTAL	11.5	0.97	0.036	0.23	2.5	0.17	111.0	4.1	26.1	20.1	286.0	
DIPTEROCARP FOREST	LEAF	5.4	0.95	0.011	0.45	0.11	0.15	51.0	0.56	24.0	5.8	8.1	
	TOTAL	8.8	0.92	0.014	0.38	0.15	0.10	81.0	1.20	33.0	8.9	13.0	
HEATH FOREST	LEAF	5.6	0.57	0.014	0.23	0.16	0.89	32.0	0.80	13.0	8.7	50.0	
	TOTAL	9.2	0.60	0.017	0.20	0.90	0.13	55.0	1.60	18.0	12.0	83.0	
CALCAREOUS FOREST	LEAF	7.3	1.20	0.038	0.16	0.33	3.10	84.0	2.7	11.0	25.0	230.0	
	TOTAL	12.0	1.20	0.038	0.13	3.1	0.28	140.0	4.5	16.0	33.0	370.0	

LOCATION	LITTER FRACTION	LITTER FALL	CONCENTRATION (% dry wt)					ACCESSION (kg ha^{-1})					REFERENCES
		(t $ha^{-1}yr^{-1}$)	N	P	K	Mg	Ca	N	P	K	Mg	Ca	
INDIA (KARNATAKA)													
AGUMBE	TOTAL	4.2	1.53	0.32	0.27	0.45	1.12	67.3	15.7	14.2	19.6	49.9	i
BANNADPARE	TOTAL	4.1	1.13	0.026	0.19	0.87	1.14	44.5	1.10	8.3	34.9	46.3	
KAGNERI	TOTAL	4.0	0.76	0.043	0.41	0.90	1.15	25.2	1.2	15.1	31.6	39.8	
SOUTH BHARA	TOTAL	3.4	1.04	0.24	0.15	0.32	0.70	38.6	9.5	5.6	11.3	27.0	
AUSTRALIA													
ATHERTON TABLELAND1	TOTAL	9.05	1.5	0.14	0.73	0.31	2.5	134.7	12.0	66.0	21.6	225.7	j
ATHERTON TABLELAND2	TOTAL	9.87	1.2	0.10	0.49	0.32	1.5	124.0	10.3	51.4	33.7	158.5	

(a) Laudelout and Meyer (1954) (b) Nye (1961) (c) Bernhard (1970) (d) Songwe (1984) (e) present study (f) Scott *et al.* (1992) (g) Luizão (1989) (h) Proctor *et al.* (1983) (i) Rai and Proctor (1986) (j) Brasell *et al.* (1980).

Table 4.8: Mean concentrations of different nutrient elements in the standard foliar samples provided by E.V.J. Tanner (Cambridge University UK). (Results from the other Laboratories and references cited were provided together with standard foliar samples).

Nutrient element	Reference					
	J.Thompson Stirling Univ. (mg g^{-1})	S.Ross Bristol Univ. (mg g^{-1})	Camus USA (mg g^{-1})	E.Tanner Cambridge Univ. (mg g^{-1})	ITE (Merlewood) (mg g^{-1})	Present study (mg g^{-1})
N	10.7	9.18	8.82	11.1	10.6	10.6
P	0.49	0.30	0.52	0.46	0.53	0.51
K	3.30	2.76	3.37	3.27	-	3.35
Na	0.04	0.12	0.24	-	-	-
Mg	2.81	2.19	2.86	-	-	2.59
Ca	4.77	2.72	4.77	-	-	5.78

'-' indicates no data available (not analysed for that particular element).

The annual rates of accession of N, P, K, Mg and Ca in litterfall for both LEM and HEM forests were within the lower range of estimates recorded for tropical forests of Africa (Table 4.7). The rates of accession of P, K, Mg and Ca recorded for Bakundu Forest Reserve by Songwe (1984), were more or less two-fold the estimates for both LEM and HEM forests. Comparison with other tropical forests showed that N accession in Korup was within the range reported for the Terra Firme forest in the Amazon (Luizăo 1989, Scott *et al.* 1992); the alluvial and calcareous forests in Sarawak (Proctor *et al.* 1983) and tropical forest of Australia (Brasell *et al.* 1980). Variations in rates of accession of P, K, Mg and Ca were relatively high between the different sites. However, the rates of return could be considered low for Mg, moderate for P, K, and N and high for Ca compared to the other tropical forests.

4.4.3 Nutrient retranslocation

The lower concentrations of N, P, K and Mg in leaf litter of the selected species compared to their respective mature leaves, reflects redistribution of this mineral elements to other active sites in the plants. This minimizes nutrient loss through litterfall and allows the plants to use the same nutrients to build new plant parts (Fife and Nambiar 1982, Foulds 1993). The degree of retranslocation is dependent on the availability of these elements to the plants. The trees can either meet their requirements from available nutrients pools in the soil or sinks within the plants (Chapin 1980, Staaf 1982, Gray 1983, Chapin *et al.* 1986, Ernst and Tolsma 1989).

Nutrient concentrations of upper crown samples have been reported to be correlated with factors such as tree height, site index, and soil nutrient concentration (van den Driesshe 1974). This justified the collection of samples consistently from the upper crown position. The three collection periods span the whole year, thereby reducing bias from the seasonal variation that has been reported in foliage of some trees (van den Driesshe 1974, Fife and Nambiar 1982, Songwe 1984). The soils in Korup are generally poor in nutrients, particularly in P (Gartlan *et al.* 1986, Newbery *et al.* 1988) and it is expected that the rates of nutrient redistribution will be generally high. This occurred only in the non-ectomycorrhizal species. The low rate of withdrawal of N, P, K, and Mg from senescent

leaves of ectomycorrhizal species may reflect a low requirement for these nutrients which can readily be met by uptake from the soil. Another interpretation is that the ectomycorrhizal association gives these species, comparative advantages to better exploit the available nutrient pools in soil or facilitates rapid uptake of nutrients from soil by the extensive network of mycelial strands (Coleman *et al.* 1983, Högberg 1986, Alexander 1989). All the other species are known to have VAM associations, with the exception of *Strephonema pseudocola* (Newbery *et al.* 1988). *Hymenostegia afzelii* belongs to the same family of ectomycorrhizal legumes and showed the highest rates of retranslocation of N and P which may disprove of any suggestion that low rates of nutrient distribution in these legumes is specific to that family. Most of the ectomycorrhizal legumes are strongly seasonal in their leaf fall patterns (with the exception of *Tetraberlinia moreliana*) shedding more than 60% of their litter in the dry season (Figure 3.5). Considering the high amounts of leaf litter produced during the short dry period, redistribution from the leaves could be significantly high just before the dry season and/or during the dry season, compared to the other months during which litterfall was comparatively very low.

The rates of retranslocation estimated for these species may however not be a true indication of the actual redistribution of the mineral elements particularly K and Mg, due to leaching from the leaves while still in the canopy (Parker 1983). The approach whereby the nutrient:Ca ratios in mature and leaf litter is used in computing the relative rates of retranslocation of the mineral elements, compensates for the weight loss during leaf senescence (Vitousek and Sanford 1986). This is based on the relative immobility of Ca in the leaves. The differences in the concentration of Ca in mature leaves and leaf litter varied among the different species and there were also slight redistributions and accumulations (Tables 4.4a and 4.4b). Net accumulation of Ca in leaves during senescence has been reported in other studies (Peace *et al.* 1981, Staaf 1982, Medina *et al.* 1990, Foulds 1993) which renders the approach reliable to use.

The relatively lower rates of retranslocation in the ectomycorrhizal species must have accounted for the higher mineral element concentrations found in the leaf litter for the HEM forest. Leaf litter comprised 62.9 and 61.6 % of total litterfall in the LEM and HEM forests respectively, with peaks in leaf fall occurring in the dry season. Looking at the

temporal variations in mineral element concentrations leaf litter, there was a considerable drop in the concentrations of N and P in the dry season as well. This shows considerable redistribution of these elements before the onset of the growth season which commences with the first rains at the end of the dry season. This internal cycling may lead the nutrient elements to be readily available to the plant during the growth period which commences with the first rains in March.

4.4.4 Nutrient use efficiency

In using the litterfall dry mass:nutrient ratios as indicators of within stand nutrient-use efficiency (Chapin 1980, Vitousek 1982, 1984), both LEM and HEM forests showed no significant differences in their nutrient economies (Table 4.7). The LEM forest was slightly more efficient in the utilisation of P (104%) and Mg (108%) and lower for K (95%) and Ca (91%) compared to the HEM forest. Higher ratios implies more within-stand efficient nutrient economies producing litter with low concentrations of the mineral elements.

The shortcoming of this approach is that nutrients leached from the litter while still in the forest canopy or in the litter trap, are not included in the computations (Grubb 1989). Estimates of mineral concentrations in throughfall may not necessarily reflect leaching because of possible inclusion of mineral elements of entirely exogenous sources (Lewis 1981, Edwards 1982, Parker 1983, Lovett and Lindberg 1984). In the present study, leaching was however minimised by the short interval between collections. The greater proportion of litterfall was in the dry season during which leaching is considerably low. Vitousek (1984), in evaluating within-stand nutrient-use efficiencies for 62 tropical forests found that those stands with the most efficient within-stand economies had ratios of >130 and >3000 for N and P respectively. Based on these limits, both LEM and HEM forest are comparatively less efficient in their economies and comparable to forest stands on moderately fertile soils (Vitousek and Sanford 1986). This supports the fact that the Korup forests must have evolved other strategies allowing the trees to survive independently of the soil as the major nutrient source. Further examination of processes at the soil level will be needed to further explain these mechanisms.

CHAPTER 5

BREAKDOWN AND MINERALIZATION OF LITTER

5.1 INTRODUCTION

The nutrients in litter reaching the forest floor are made available for uptake again by the plants through the process of decomposition. Decomposition describes a series of inter-related processes involving the breakdown of litter (also referred to as humification by Lavelle *et al.* 1993) and the subsequent chemical transformation and release (mineralization) of the nutrients therein (Attiwill 1968, Jensen 1974, Swift *et al.* 1979, Anderson and Swift 1983, Golley 1983). Decomposition has emerged as a very important component of ecosystem processes as it regulates nutrient availability and determines the nature of the soil organic matter formed (Sanchez 1976, Swift *et al.* 1981, Coleman *et al.* 1983, Parton *et al.* 1987, Lavelle *et al.* 1993). The soil organic matter maintains soil fertility by improving soil aeration and the cation exchange capacity (Coleman *et al.* 1983).

The rate of decomposition of litter is governed by many driving forces (both intrinsic and extrinsic) which interact diversely at different locations and time. Various authors have classified these regulating factors into one of the following three categories: (i) abiotic or physical factors which include climate (Jenny *et al.* 1949, Singh and Gupta 1977, Meetemeyer 1978) soil and elevation (Vitousek *et al.* 1994); (ii) resource quality defined by both the quantity and quality of the structural and nutritional constituents of the litter (Minderman 1968, Fogel and Cromack 1977, Meetemeyer 1978, Swift *et al.* 1979, Bosatta and Staaf 1982, Mellillo *et al.* 1982, Upadhyay *et al.* 1989); (iii) the biotic factor which encompasses the role played by macro and micro organisms (Jensen 1974, Bunnell *et al.* 1977, Anderson *et al.* 1983, Anderson and Ineson 1983, Seastedt 1984, Blair *et al.* 1992). The influences of these factors are organised hierarchically depending on the location and time.

It has frequently been reported in the literature that litter breakdown proceeds very rapidly in the moist tropical environment due to the prevalence of very favourable conditions for microbial activity throughout the year (Jenny *et al.* 1949, Jordan 1985, Deshmukh 1986, Hilton 1987). These favourable conditions encourage the rapid breakdown and incorporation of organic matter derived from the litter. Anderson *et al.* (1983) considered

the physical conditions in tropical rainforest to be generally favourable for the decomposer activity and concentrated their studies on the role of the biotic factor and resource quality of the litter. However, considerable differences in rates of decomposition have been reported within the tropics (Anderson and Swift 1983) indicating the importance of other local specific factors such as species composition which may account for variations in the microclimate on the forest floor in different locations.

The widespread occurrences of mycorrhizas in the tropical forests have been reviewed by Janos (1983), Högberg (1986) and Alexander (1989a, 1989b). They all 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 the ions such as phosphates (Janos 1983, Alexander 1989a, Brundrett 1991) and nitrates (Alexander 1989a). Most of the results reported on the role played by these mycorrhizas in enhancing nutrient uptake are obtained from experiments on cultured mycelia of the causal fungi in the laboratory and very few field studies have been carried out to evaluate these findings (Fogel 1980, Fitter 1986, Brundrett 1991, Mullen and Schmidt 1993). Ectomycorrhizal mycelia have been found in association with decomposing surface organic matter some in tropical forests (Singer and Araujo 1979, 1986, Newbery *et al.* 1988). This association has encouraged the idea that ectomycorrhizas play a role in breakdown and mineralization of the decomposing litter fractions (Alexander 1983, 1989).

Studies of decomposition of litter in forests have been dominated by the role of nitrogen and phosphorus as limiting factors in growth and development. Attiwill and Adams (1993) in their review on nutrient cycling in forests focused mainly on the mineralization of N and P which are thought to be limiting in tropical soils (Jordan and Herrera 1981, Vitousek 1984). Not much attention been given to the other elements which may equally be limiting or complexing the availability of the other elements (Keltejens and Tan 1993).

The difference between litter input and rates of breakdown results in the formation of a litter layer on the forest floor. This pattern of litter accumulation on the forest floor reflects the general rate of decomposition or the turnover time on the forest floor. This

relationship has widely been used to estimate rates of decomposition in the various biomes. The widely used decomposition annual constant (K) of Olson (1963) developed from this relationship was initially developed by Jenny *et al.* (1949). Other approaches that provide comparative measures of decomposition rates are: the estimation of carbon dioxide evolving from soil respiration (Anderson *et al.* 1983, Khiewtam and Ramakrishnan 1993); direct measure of mass loss from the litter on the forest which are either confined in litterbags (Lunt 1933, Bocock and Gilbert 1957) or tethered with strings (Swift *et al.* 1979, Tanner 1981, Vitousek *et al.* 1994). Each of these approaches has its own merits and demerits and their usage depends on the objective of the study.

This chapter focuses on the comparison of the temporal trends in litter accumulation on the forest floor in LEM and HEM forests. The estimated changes in mass of the different fractions of the litter layer were used to calculate the rates of decomposition on the forest floor and the turnover time for these litter fractions and the litter layer as a whole in both forests. Leaf litter constitutes approximately two thirds of total litter input to the forest floor. The second part looks at rates of mass loss and mineralization of N, P, K, Mg and Ca from decomposing leaf litter of *Cola verticillata*, *Oubanguia alata*, *Strephonema pseudocola* (three non-ectomycorrhizal species); *Berlinia bracteosa*, *Tetraberlinia bifoliolata*, *Didelotia africana* and *Microberlinia bisulcata* (four ectomycorrhizal species) on the forest floor in LEM and HEM forests. These leaves were confined in litterbags and monitored over a period of eight months. These selected species are representative of the dominant species (in terms of basal area distribution) and contribute most to leaf litter input to the forest floor in both LEM and HEM forests respectively.

5.2 MATERIALS AND METHODS

5.2.1 Selection of sample plots.

The ten half-plots selected for litterfall studies (section 3.2.1) were further examined on the basis of plot slope and the thickness of the undergrowth to select six half-plots (three in each forest type) within which studies on rates of decomposition would be carried out. The aim was to select relatively flat plots which were free draining and with relatively less undergrowth (herb layer) which would not hamper sampling from the forest floor. The rationale was to avoid the litterbags being flooded in the wet season. Lateral displacement of litter on forest floor by either overland flow from torrential rains or by gravitational movement is higher along steep slopes. This may lead to an under-estimation of litter on the forest floor upslope and an over-estimation downslope.

The selection was restricted to those half-plots within which litterfall studies were in progress as the monthly litterfall estimates constituted an input to the mass balance model (Jenny *et al.* 1949, Olson 1963) used in determining mass loss of litter layer on the forest floor.

Plot 4BC and 8BC were highly undulating and had high densities of undergrowth species. Plots 18CD and 19AB had relatively steep slopes with plot 19AB also having a thick forest floor vegetation (herb layer). The half-plots finally chosen were:

LEM plots: 3AB, 7AD, and 9BC.

HEM plots: 15AD, 24BC, and 25AD.

For sampling the forest floor litter layer, plots 7AD and 24BC were not used. The aim was to reduce the number of samples since there was very limited time available for sorting all the litter collected at each sampling occasion.

5.2.2 Litter layer on forest floor.

Samples of litter on the forest floor were collected at monthly intervals from within twenty quadrats randomly sited within each of the selected half-plots from 14 February

1991 to 15 June 1992. On each sampling occasion, a 0.4 × 0.4 m wooden quadrat (same collecting area as the litter traps) was located at random within each of the selected half-plots. All litter within the quadrat was removed, including twigs and bark fractions ≤ 2 cm in diameter or along its longest axis (Proctor 1983b). Larger woody fractions were sectioned and the portion ≤ 2 cm in diameter included in the sample. Samples from each quadrat were stored separately in sealable polybags labelled with the plot number. The sampling spots were marked with 12 cm wooden pegs at their centres to avoid resampling on later occasions. The twenty quadrats from each selected plot allowed direct comparisons with litterfall input estimates (same collecting area).

The samples were air-dried in the laboratory at the Forestry Research Station, Kumba for a maximum duration of one week 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 as no data were available or collected on their contributions to total litter input to the forest floor. The fractions were put in separate paper envelopes and oven-dried at 85°C for 48 hours. 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 adhered to the litter fractions, redried for 3 hrs and weighed.

Soil temperature at 20 mm below the litter layer were recorded during the day at three hours interval at the science camp and in plot 25AD alternatively between June 1991 and October 1991 (wet months), December 1991-January 1992 (dry months) and in May 1992. Readings were taken during field work in the middle and end of the month for the months specified.

5.2.3 Leaf litter decomposition.

Rates of weight loss and mineralization of leaf litter in both LEM and HEM forest types were studied using the litterbag technique (Lunt 1933, Bocock and Gilbert 1957). Freshly fallen leaf litter of the following species were collected for these studies:

(i) ectomycorrhizal species: *Berlinia bracteosa, Didelotia africana, Microberlinia*

bisulcata and *Tetraberlinia bifoliolata.*

(ii) non-ectomycorrhizal species: *Cola verticillata, Oubanguia alata* and *Strephonema pseudocola.*

These species dominated leaf litter inputs in both forest types (Table 3.9).

5.2.3.1 Collection and treatment of leaf litter

Three mature individuals of each of the selected species were chosen amongst the ten individuals for which monthly phenological observations were being recorded each month for the collection of their freshly fallen leaves. These leaves were trapped on large perforated plastic sheets (4 m × 3 m) raised 1.2 m above the forest floor with wooden pegs. Two of such sheets were placed underneath the canopy of each of the fourteen selected trees. Collection was daily in the mornings and evenings from 8 January 1991 to 16 January 1991 during which the leaves were air-dried at the camp. Substantial quantities of the air-dried leaves were taken to Kumba and further air-dried in a well ventilated room for one week. Leaves and leaflets mined or partly eaten by herbivores were sorted and discarded. The leaves differed in their shapes, sizes and texture and the major morphological features of leaves of each selected species given are below:

(1) *Berlinia bracteosa:* compound leaves with 4-6 pairs of leaflets, oblanceolate in shape with the terminal pair largest 10-18 cm long and 3.5-7.0 cm wide and decreasing in size to the lowest pair. Leaflets are glabrous with the nerves forming a close network visible underneath; stout and wrinkled stalk 4-6 mm long with a thick common stalk 9-20 cm long.

(2) *Didelotia africana:* compound leaves with one pair of leaflets which are elliptic and asymmetrical, 7-10 cm long and 4-6 cm wide, thick and leathery in texture and borne on a short common stalk 3-5 mm long. This species has three main lateral nerves all originating from the base of the leaflets and looping inwards.

(3) *Tetraberlinia bifoliolata:* compound leaves with one pair of leaflets which are elliptic, asymmetrical and acuminate, 5-10 cm long and 4-6 cm wide, thick and leathery with the midrib looping inwards. The common stalk is 3-5 mm long.

(4) *Microberlinia bisulcata:* microphyllous leaves with 10-15 pairs of leaflets which are

strictly opposite, 6-10 mm broad and 2-3 cm long, elongated and notched at the apex, asymmetrical at the base and the margin at one side reaching the winged rachis. The leaflets are thick and leathery with the lateral nerves forming a prominent network underneath.

(5) *Cola verticillata:* simple leaves, entire, 10-25 cm long and 3.5-9 cm wide, elliptic-lanceolate or obovate, obtuse at base and abruptly narrowly acuminate at the apex. The leaves are thick and glabrous with 6-8 lateral nerves, the lowest arising close to the base and running parallel to the margin, with the petiole 1.5-8 cm long.

(6) *Oubanguia alata:* simple and entire leaves, 10-25 cm long and 5-9 cm wide, subovate, acuminate and rounded at the base, thin and glabrous with 6-8 pairs of lateral nerves at a wide angle from the midrib and looped well away from the margin; short petiole about 6 mm long.

(7) *Strephonema pseudocola:* simple and entire leaves, 7-10 cm wide and 9-14 cm long, broadly elliptic to ovate, acuminate at apex and cuneate at base. The leaves are thick and glabrous with very prominent lateral nerves underneath; stout petiole 9-12 mm long.

Two sets of decomposition experiments were carried out in both forest types with two different types of litterbags. The same batch of air-dried leaves were used for both experiments. The coarse litterbags were 25 cm × 25 cm in size and made from black plastic netting with a mesh-size 5 mm on both sides. The fine mesh litterbags were 20 cm × 20 cm in size and made from green nylon mosquito netting with mesh-size of 2 mm on both sides. For each decomposition experiment, three hundred and fifty litterbags were prepared and fifty allocated to each species. For each species, 15 g of the air-dried leaves (or leaflets and rachises) were enclosed in each litterbag and the edges sewn with nylon thread. To each litterbag was attached a small tag bearing the species code and plot number. Two bags were randomly selected from each set of species as the initial samples and the leaves therein were oven-dried at 85°C for 48 hours and weighed to obtain the initial oven-dried mass (X_0). These were then milled and stored in sealed plastic bags labelled with species codes for chemical analysis.

Leaves confined in the coarse litterbags were laid out on the forest floor on 14 February 1991. The microphyllous leaflets of *Microberlinia bisulcata* were small enough to pass

through the mesh of the coarse litterbags and were exempted in the first experiment. The second experiment was laid out on the forest floor on 15 July 1991 using the fine litterbags and involving all of the selected species. Each decomposition experiment lasted for a duration of eight months.

5.2.3.2 Experimental layout and sampling.

One of each pair of the selected quarter-plots was selected at random for the first decomposition experiment and the other for the second experiment. Six replicate blocks (2.5 m × 2.5 m) were laid out in plots 3A, 7A, 9C, 15D, 24B and 25B for the first experiment and in plots 3B, 7D, 9B, 15A, 24C and 25D for the second experiment. All litter within the blocks was removed to allow the litterbags to have direct contact with surface soil organic matter. The blocks were then divided with long wooden poles into seven adjacent sub-plots (six in the first experiment) in to which were randomly allocated the different species. This design was aimed at eliminating variations resulting from the micro-effects of the different tree species on the forest floor. Eight litterbags of each species were laid in each block giving a total of forty-eight litterbags for each experiment.

One litterbag was retrieved at random from each sub-plot in each replicate block at monthly intervals. This provided three replicate samples of each species and forest type. All overlying debris were removed and the litterbags put into separate polybags and taken to the laboratory at the Forest Research Station Kumba. The leaves remaining in the litterbags were thoroughly cleaned by hand to remove all exogenous material including roots, and soil particles. The cleaned residual samples were oven-dried at 85°C for 48 hours in separate paper envelopes and passed over a sieve with mesh-size of 2 mm to separate soil particles and highly fragmented organic matter adhered to the leaves when wet. These were redried at 85°C for 3 hours, weighed and milled in a Wiley electric mill with a 0.5 mm mesh screen. Each milled sample was sealed in a small polybag labelled with the species name, plot number and date of collection. These were all packed in a well sealed polybag and sent to University of Stirling for chemical analysis.

5.2.3.3 Chemical analysis.

The chemical analysis was carried out in the Department of Biological and Molecular Sciences, University of Stirling, by M. White. The samples were acid digested and analyzed for total N and P, K, Mg and Ca. Total N and P in the samples were determined colorimetrically using the ammonia-salicylate method for N and phospho-molybdenum method for P. K, Mg and Ca were determined by atomic emission and absorption spectrophotometry. These analyses followed the same procedures described in section 4.2.2 (chapter 4).

5.2.4 Data analysis

5.2.4.1 Litter layer on forest floor.

The over-dried mass of the various fractions of the litter layer on the forest floor were expressed per unit area basis (g m^{-2}) for analysis. The continuous input model of litter accumulation (Olson 1963) was used to estimate net decay rate and turnover time for the various fractions. This model assumes a steady state equilibrium where the mass of litter accumulated on the forest floor (X) at anytime (t) represents the balance between the rate of litterfall as input and rate of decay or loss from the forest floor (Jenny et al. 1949, Olson 1963, UNESCO 1978, Birk and Simpson 1980, Esser and Lieth 1989). Since litterfall is strongly seasonal in both the LEM and HEM forests in Korup (Chapter 3), the monthly net decay (UNESCO 1978) was calculated for each fraction as follows:

$$decay_{t_{1-2}} = ((LFF_{t_1} + LF_{t_{1-2}}) - LFF_{t_2})$$

Where: LFF=mass of litter (or fractions) on forest floor (g m^{-2}),

LF=litterfall input (or fractions) (g m^{-2}),

t_1 and t_2 are consecutive observations (one month apart in the present study).

$t_{1\text{-}2}$ is the change between t_1 and t_2.

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

$$k_1 = \frac{decay}{0.5\,(LFF_{t_1} + LFF_{t_2})}$$

The monthly decomposition coefficients (k_l) from May 1991 to April 1992 were summed to obtain the annual estimate of the decomposition constant (K). The inverse of this constant (K) is the turnover time (in years) 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 students' t test was also carried out to investigate significant differences in the monthly decomposition coefficients for each fraction between the two forest types.

5.2.4.2 Mass loss and mineralization of leaf litter confined in litterbags.

Since the initial oven-dried mass and elemental concentration varied between leaf litter of the different species, the values obtained each sampling date (different periods) were expressed as proportions of the initial estimates of the respective species. This allowed for direct comparison between the different species and forest types.

Species-specific models were fitted to the data set of each species in each forest type to estimate constants that describe mass loss and mineralization of the leaf litter over time (Hunt 1977, Wieder and Lang 1982, Ezcurra and Becerra 1987, Taylor and Parkinson 1987, Palm and Sanchez 1990, Van Vuuren *et al.* 1993). The three widely recommended mathematical models fitted to the data include:

a. Linear model:

$$\frac{X_t}{X_0} = -kt$$

b. Single exponential model:

$$\frac{X_t}{X_0} = e^{-k_1 t}$$

c. Double exponential model:

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

where X_t/X_0 is the proportion of the initial material remaining at time t,

k, k_1, k_2 and k_3 are decomposition constants,

A is the relatively labile proportion of the initial material and (1-A) the relatively recalcitrant portion in the initial material.

All three models were initially fitted to the mean residual mass (% of initial mass) of the leaf samples obtained at each sampling date. This was a preliminary analysis to select the most appropriate of these three models to use in the analysis. A summary of the regression parameters are presented in Table 5.9a. Following the evaluation of these models the best fit was from the single exponential model (see Table 5.9a) which was then used in the subsequent analysis of rates of mass loss in the decomposing leaf samples. This incorporated all the data obtained at each sampling date for all replicates. The linear and single exponential models were fitted to the concentrations of the N, P, K, Mg and Ca (% initial concentration) in the residual mass obtained at each sampling date as the elements showed more diverse patterns. The initial oven-dried mass and concentration of N, P, K, Mg and Ca of the samples were included in the data set and it was assumed that each species in each forest type had three replicates at time zero.

Both the linear and single exponential models were fitted by ordinary least squares procedure (natural log transformation was carried out for the single exponential model) using MINITAB (Minitab Inc. 1989). The double exponential model was fitted numerically using MATLAB (Mathwork Inc. 1987). This program uses the Nelder-Mead simplex algorithm to estimate the three parameters of the non-linear function which minimizes the total residual error function:

$$\Sigma(X_t - X_p)^2$$

Where X_t is the residual mass of the litter at time t and X_p the predicted residual mass using the model for time t.

The coefficient of determination (R^2) were calculated following the approach of Wieder *et al.* (1983) where:

$$R^2 = \frac{\text{corrected total sum of squares - error sum of squares}}{\text{corrected total sum of squares}}$$

The models were validated by the significance of the regression analysis, R^2 and the magnitude of the deviation of the Y-axis intercept from 100%.

The students' t testing was carried out on the species-specific k values to determine significant differences in rates of mass loss and mineralization of N, P, K, Mg and Ca in leaf litter of the different species in both LEM and HEM forests (Zar 1984). One-way analysis of covariance (ANCOVA) was carried out on the log transformed data set (natural log transformation) for the different sampling dates to determine significant differences in the overall rates of mass loss and mineralization in both forest types (Zar 1984, Mead *et al.* 1993). For each forest type, one-way analysis of covariance (ANCOVA) was carried out to determine if the species differed in both mass loss and mineralization following the different incubation periods on the forest floor. When significant differences ($p<0.05$) were recorded, the Tukey's studentized multiple comparison test was carried out between the species-specific k values to test for significance among the species in the different forest types (Zar 1984). Because replication was sometimes uneven, analysis of covariance (ANCOVA) was carried out using the GLM procedure (Minitab Inc. 1989) with the sampling dates as the covariates for comparisons between forest types and between the different species in each forest

type. Uneven replication resulted from missing litterbags (two in plot 24C for the second experiment) and from very small amounts of residual leaf material which could not be milled for chemical analysis.

The species were scored according to their groupings from the Tukey's multiple comparison test in each forest type for all the five elements. The scores ranged from seven for the highest group (a) and one for the lowest classified (d). The overall scores were used to determine the order of mineralization in the selected species in each forest type.

Correlation analysis was carried out between the species-specific mass loss constants (k) and their respective initial concentrations of N, N:P and N:Ca ratios. This was to investigate the effects of substrate quality on rates of decomposition.

5.3 RESULTS

5.3.1 Litter layer on forest floor.

5.3.1.1 Variation in dry mass of the different litter fractions.

Trends in the monthly oven-dried mass of the various litter fractions on the forest floor collected from February 1991 to June 1992 in both the LEM and HEM forests are presented in Figure 5.1. Both forest types showed similar trends in total litter on the floor with high accumulation recorded in February 1991 and between February 1992 -April 1992. Minor accumulations were also recorded in July 1991 and June 1992 in both forests. The amount of litter on the forest floor summed for each plot was higher in the HEM compared to the LEM forest during the entire period of sampling. This difference was however not significant ($t=1.77$, $df=14$, $p>0.05$). In comparing the mass of the various fractions recorded, a highly significant difference was observed in the reproductive fractions between the LEM and HEM forests ($t=8.44$, $df=14$, $p<0.001$). No significant differences were observed between LEM and HEM forests in the amount of leaf, small wood and moss and lichen fractions on the forest floor. The mean annual estimates of the mass of the various fractions on the forest floor recorded in both forests from May 1991 to April 1992 are presented in Table 5.1. The accumulation of the reproductive fraction in the HEM forest was five-fold that of the LEM forest. This is evident in the highly significant difference recorded between both forest types.

Table 5.1: Mean annual estimates of mass (g m^{-2}) of the various fractions of litter on the forest floor in LEM and HEM forest, Korup National Park, Mundemba. (May 1991-April 1992, means±SE, n=2).

Forest type	Litter fractions				
	Leaves	Small wood	Reprod. fraction	Moss & lichen	Total
LEM	164±21.7	90.6±6.4	9.5±1.6	0.14±0.01	265±20.5
HEM	175±23.6	113±6.1	45.7±4.5	0.61±0.01	334±25.4

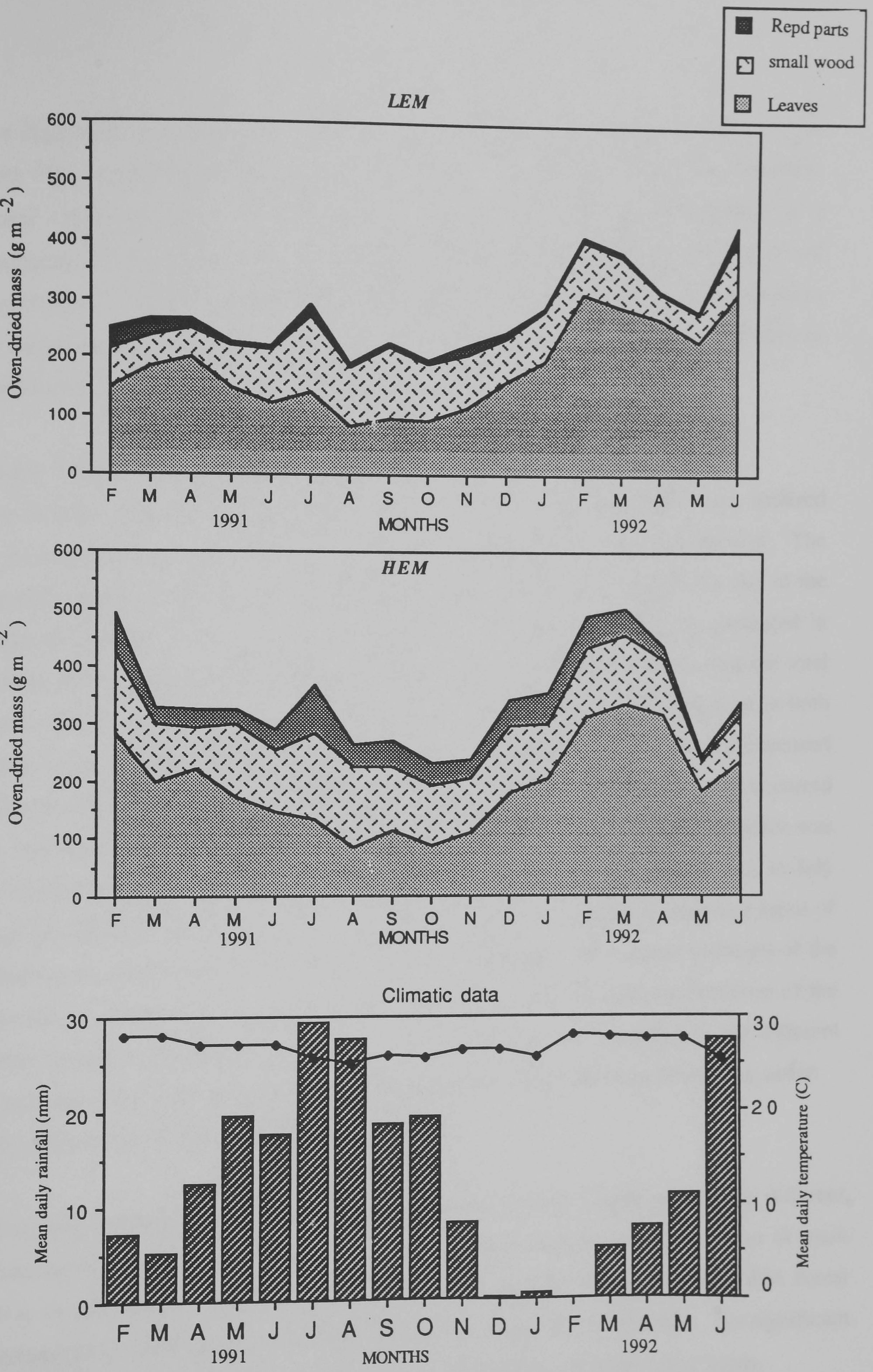


Figure 5.1: The temporal variations in mass (g m^{-2}) of the forest floor litter layer collected from randomly located quadrats in LEM and HEM forests, Korup National Park, Cameroon. Monthly rainfall and temperature recorded during the study period are also presented. The values indicate dry weights of the different fractions obtained at the end of the month.

Very high spatial and temporal variations were observed in all the litter fractions on the forest floor in both forest types. The coefficients of variation between the quadrats (spatial variation) ranged from a minimum value of 27% in the leaf fraction to a maximum of 353% and 137% in the reproductive fractions in both LEM and HEM forests respectively. Variation between the sampling dates (temporal variation) was highest in the reproductive and leaf fractions in both LEM and HEM forests respectively (coefficients of variation of 56% and 45% respectively).

5.3.1.2 Monthly and annual estimates of turn-over rates

The different fractions of the litter layer on the forest floor in both forest types differed in their rates of decomposition (net mass loss) for the different months of the year. The monthly decay estimates and the corresponding coefficients of decomposition (k_l) of the different fractions from May 1991 to April 1992 in both forest types are presented in Tables 5.2-5.5. Mass loss was highest in the months of August for leaves and the total litter layer as a whole and in April for the small wood and reproductive fractions in both forest types. However net accumulation indicated by negative coefficients was witnessed during different months for the different fractions. Net accumulation of leaves occurred in January during which litter input was dominated by leaf litter. A similar situation was witnessed for small wood and twigs with negative coefficients (k_l) between 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 overall estimates of the annual decomposition constant (K_L) and turn-over time for the different fractions of the litter layer are summarized in Table 5.6. This indicated that mass loss in the different fractions of the litter layer in both forest types was in the following decreasing order:

Reproductive > leaves > small wood and twigs.

Pair-wise comparisons between the monthly decomposition coefficients of the different fractions of the litter layer in both forest types showed significantly higher rates of mass loss in reproductive fractions and the total litter layer as a whole in the LEM forest compared to HEM forest ($t=1.83$ and 2.10 respectively, $df=10$, $p>0.05$). No significant differences were seen in leaves and small wood fractions in both forest types.

Table 5.2: Monthly estimates of decomposition coefficients (k_l) and the annual decomposition constant (K_L) for leaf litter on forest floor (May 1991-April 1992) using the continuous input model of litter accumulation. FFL_1 is the mass of leaf litter (g m^{-2}) on the forest floor at time t_1, $LF_{1,2}$ is leaffall (g m^{-2}) between time t_1 and t_2. (means ± SE, n=12).

MONTH	LEM				HEM			
	FFL_1	$LF_{1,2}$	decay	k_l	FFL_1	$LF_{1,2}$	decay	k_l
MAY 1991	202	35.6	87.1	0.49	222	28.1	77.8	0.39
JUNE	151	29.8	56.7	0.41	172	22.1	48.7	0.31
JULY	124	31.3	12.2	0.09	146	25.1	37.2	0.27
AUGUST	143	31.6	91.6	0.81	133	26.6	75.2	0.69
SEPTEMBER	83.1	32.2	18.7	0.21	85.2	25.1	-3.85	-0.04
OCTOBER	96.6	37.0	39.3	0.41	114	33.8	59.9	0.59
NOVEMBER	94.3	49.5	28.1	0.27	88.1	56.0	31.5	0.31
DECEMBER	115	55.1	9.84	0.07	112	83.5	17.2	0.12
JANUARY 1992	161	83.2	45.5	0.25	179	81.1	53.0	0.28
FEBRUARY	199	91.1	-26.5	-0.10	207	63.0	-42.2	-0.16
MARCH	316	71.1	96.2	0.32	312	68.2	45.1	0.14
APRIL	291	54.7	72.5	0.26	335	54.5	74.9	0.23
TOTAL	1977	602	531	3.5	2107	567	474	3.1
MEAN	165± 21.7		44.3± 10.9		175± 23.6		39.5± 10.3	
	K_L=3.5				K_L=3.1			

Table 5.3: Monthly estimates of decomposition coefficients (k_l) and the annual decomposition constant (K_L) for smallwood (≤2 cm in diameter) on the forest floor (May 1991-April 1992) using the continuous input model of litter accumulation. FFL_1 is the mass of small wood fraction (g m^{-2}) on forest floor at time t_1, $LF_{1,2}$ is the smallwood input (g m^{-2}) between time t_1 and t_2. (mean±SE, n=12).

MONTH	LEM				HEM			
	FFL_1	$LF_{1,2}$	decay	k_l	FFL_1	$LF_{1,2}$	decay	k_l
MAY 1991	46.2	20.7	-1.38	-0.02	71.4	15.5	-39.31	-0.40
JUNE	68.3	18.1	-3.15	-0.04	126	12.9	31.19	0.27
JULY	89.6	18.6	-20.3	-0.19	108	14.0	-27.89	-0.22
AUGUST	129.5	21.6	50.6	0.44	150	13.4	23.82	0.16
SEPTEMBER	100	18.8	-3.59	-0.03	139	10.2	37.70	0.30
OCTOBER	123	19.2	46.1	0.42	111	13.7	21.94	0.20
NOVEMBER	96.1	22.0	25.1	0.27	103	14.4	25.43	0.26
DECEMBER	93.0	14.9	32.4	0.38	92.7	12.0	-11.71	-0.11
JANUARY 1992	75.6	8.39	-3.62	-0.04	116	11.0	34.60	0.33
FEBRUARY	87.6	7.07	5.15	0.06	92.9	12.3	-15.70	-0.15
MARCH	89.5	12.4	13.2	0.15	120	22.5	23.22	0.19
APRIL	88.6	15.2	58.5	0.87	120	19.6	41.68	0.38
TOTAL	1087	198	198	2.27	1353	171	144.97	1.21
MEAN	90.6± 9.39		16.6± 7.35		112± 6.16		12.08± 8.03	
	K_L= 2.27				K_L= 1.21			

Table 5.3: Monthly estimates of decomposition coefficients (k_l) and the annual decomposition constant (K_L) for smallwood (≤2 cm in diameter) on the forest floor (May 1991-April 1992) using the continuous input model of litter accumulation. FFL_1 is the mass of small wood fraction (g m^{-2}) on forest floor at time t_1, $LF_{1,2}$ is the smallwood input (g m^{-2}) between time t_1 and t_2. (mean±SE, n=12).

MONTH	LEM				HEM			
	FFL_1	$LF_{1,2}$	decay	k_l	FFL_1	$LF_{1,2}$	decay	k_l
MAY 1991	46.2	20.7	-1.38	-0.02	71.4	15.5	-39.31	-0.40
JUNE	68.3	18.1	-3.15	-0.04	126	12.9	31.19	0.27
JULY	89.6	18.6	-20.3	-0.19	108	14.0	-27.89	-0.22
AUGUST	129.5	21.6	50.6	0.44	150	13.4	23.82	0.16
SEPTEMBER	100	18.8	-3.59	-0.03	139	10.2	37.70	0.30
OCTOBER	123	19.2	46.1	0.42	111	13.7	21.94	0.20
NOVEMBER	96.1	22.0	25.1	0.27	103	14.4	25.43	0.26
DECEMBER	93.0	14.9	32.4	0.38	92.7	12.0	-11.71	-0.11
JANUARY 1992	75.6	8.39	-3.62	-0.04	116	11.0	34.60	0.33
FEBRUARY	87.6	7.07	5.15	0.06	92.9	12.3	-15.70	-0.15
MARCH	89.5	12.4	13.2	0.15	120	22.5	23.22	0.19
APRIL	88.6	15.2	58.5	0.87	120	19.6	41.68	0.38
TOTAL	1087	198	198	2.27	1353	171	144.97	1.21
MEAN	90.6± 9.39		16.6± 7.35		112± 6.16		12.08± 8.03	
	K_L= 2.27				K_L= 1.21			

Table 5.4: Monthly estimates of decomposition coefficients (k_l) and the annual decomposition constant (K_L) for reproductive fractions on the forest floor (May 1991-April 1992) using the continuous input model of litter accumulation. FFL_1 is the mass of reproductive fractions (g m^{-2}) on forest floor at time t_2, $LF_{1,2}$ is the mass of reproductive fraction in litterfall (g m^{-2}) between time t_1 and t_2. (mean±SE, n=12).

MONTH	LEM				HEM			
	FFL_1	$LF_{1,2}$	decay	k_l	FFL_1	$LF_{1,2}$	decay	k_l
MAY 1991	17.7	2.92	12.8	1.01	34.0	6.94	14.0	0.46
JUNE	7.80	1.19	3.79	0.55	27.0	3.99	-4.47	-0.14
JULY	6.00	2.23	-11.8	-0.91	35.4	3.37	-46.0	-0.76
AUGUST	20.1	3.04	16.6	1.44	85.3	3.78	50.8	0.82
SEPTEMBER	6.48	2.85	2.52	0.38	38.3	7.04	0.68	0.02
OCTOBER	6.81	2.14	3.04	0.48	44.7	11.95	15.3	0.36
NOVEMBER	5.91	1.07	-8.44	-0.79	41.3	1.93	9.91	0.26
DECEMBER	15.4	1.21	5.76	0.44	33.4	0.54	-13.8	-0.34
JANUARY 1992	10.9	2.15	9.99	1.44	47.7	7.72	-0.24	-0.01
FEBRUARY	3.03	6.71	2.91	0.59	55.7	28.56	27.1	0.48
MARCH	6.83	13.6	13.3	1.91	57.2	61.12	70.2	1.33
APRIL	7.09	11.9	8.3	1.66	48.1	20.72	62.6	1.79
TOTAL	114	51.8	58.8	8.20	548	158.08	186	4.27
MEAN	9.50±1.55		4.90±2.43		45.7±4.46		15.5±9.59	
	K_L=8.20				K_L=4.27			

Table 5.5: Monthly estimates of decomposition coefficients (k_l) and the annual decomposition constant (K_L) of litter layer on the forest floor (May 1991-April 1992) using the continuous input model of litter accumulation. FFL_1 is the mass of the litter layer (g m^{-2}) on forest floor at time t_1, $LF_{1,2}$ is the total input of litterfall (g m^{-2}) between time t_1 and t_2. (mean±SE, n=12).

MONTH	LEM				HEM			
	FFL_1	$LF_{1,2}$	decay	k_l	FFL_1	$LF_{1,2}$	decay	k_l
MAY 1991	266	65.2	104	0.42	328	55.0	57.3	0.18
JUNE	227	53.6	60.9	0.27	326	42.3	78.7	0.26
JULY	220	57.0	-16.1	-0.06	290	45.8	-34.0	-0.10
AUGUST	293	60.1	162	0.67	369	46.4	152	0.48
SEPTEMBER	190	57.0	20.7	0.10	263	45.4	37.6	0.14
OCTOBER	226	61.9	92.0	0.44	271	58.4	96.0	0.38
NOVEMBER	196	76.2	48.1	0.23	233	76.8	70.8	0.30
DECEMBER	224	74.7	51.7	0.22	239	100	-3.04	-0.01
JANUARY 1992	247	97.3	55.4	0.21	343	104	91.1	0.26
FEBRUARY	289	109.3	-14.0	-0.04	356	108	-26.9	-0.06
MARCH	413	103.3	129	0.32	490	138	124	0.25
APRIL	387	88.5	154	0.43	504	104	171	0.36
TOTAL	3179	904	849	3.21	4012	923	815	2.43
MEAN	264.9± 20.46		70.74± 17.14		334.4± 25.39		67.9± 19.03	
	K_L= 3.21				K_L= 2.43			

Table 5.6: Estimates of the annual decomposition constants (K_L) and turn-over time (years) for the various fractions of the litter layer on the forest floor in Korup National Park, Mundemba. (May 1991-April 1992).

Fractions	Forest type	decay ($g\ m^{-2}\ yr^{-1}$)	K_L	Turn-over time (yr)
Leaves	LEM	531	3.5	0.29
	HEM	474	3.1	0.32
Small wood and twigs	LEM	199	2.3	0.44
	HEM	145	1.2	0.83
Reproductive fractions	LEM	58.8	8.2	0.12
	HEM	186	4.3	0.23
TOTAL	LEM	849	3.2	0.31
	HEM	815	2.4	0.41

Table 5.7: Correlation coefficients between the climatic variables and the monthly decomposition coefficients (k_1) of the various fractions of the litter layer in Korup National Park, Mundemba. (n=16, and an asterisk indicates significance at $p<0.05$).

		Climatic variables	
Fractions	Forest type	Rainfall	Temperature
Leaves	LEM	0.55*	-0.41
	HEM	0.57*	-0.57*
Small wood and twigs	LEM	-0.19	0.12
	HEM	-0.17	-0.13
Reproductive fractions	LEM	-0.28	0.31
	HEM	-0.21	0.50*
TOTAL	LEM	0.24	-0.17
	HEM	0.17	-0.22

5.3.1.3 Climatic factors and turn-over rates

Correlation analysis between mean monthly rainfall and temperature and the decomposition coefficients of the different fractions of the litter layer indicated both positive and negative influences of these factors on rates of mass loss (Table 5.7). The mean monthly rainfall was positively correlated with the coefficients of the leaf fractions and the total litter layer as a whole and negatively correlated with small wood and reproductive fractions. The correlation between the rainfall and the coefficients of decomposition of the litter fractions was significant for the leaf fractions only in both forest types ($p<0.05$).

The mean monthly temperature was negatively and significantly correlated with decomposition coefficients of the reproductive fractions in HEM forest ($p<0.05$). This was also significantly and negatively correlated with leaf litter in HEM forest ($p<0.05$).

5.3.2 Mass loss in leaf litter confined in litter litterbags

5.3.2.1 Initial chemical composition of the leaf litter

The freshly collected leaf litter of the selected species differed in their initial elemental concentrations (Table 5.8). N concentration ranged from 10.07 to 18.02 mg g^{-1}; P from 0.38 to 1.03 mg g^{-1}; K from 3.45 to 12.00 mg g^{-1}; Mg from 1.63 to 4.36 mg g^{-1} and Ca from 5.35 to 20.29 mg g^{-1}. The highest concentration of N was in *Didelotia africana;* P, K and Mg in *Berlinia bracteosa. Strephonema pseudocola* had highest concentration of Ca and the lowest in N, P, and K. *Tetraberlinia bifoliolata* had the lowest concentration of Mg and Ca. The concentrations of N and P were relatively higher in leaf litter of the ectomycorrhizal species compared to the non-ectomycorrhizal species (Table 5.8). No clear distinction was seen between these two group of species for K, Mg and Ca.

Table 5.8: Mean initial nutrient concentration (mg g^{-1} of oven-dried weight) of freshly collected leaf litter of selected tree species (four ectomycorrhizal and three non-ectomycorrhizal species) for decomposition studies on the forest floor in Korup National Park, Mundemba. (Values in mg g^{-1} oven-dried weight ± SE, n=2). Asterisks indicate the ectomycorrhizal species.

Species	N	P	K	Mg	Ca
Cola verticillata	10.7±0.03	0.55±0.01	5.59±0.01	2.87±0.16	13.4±0.85
Oubanguia alata	12.9±0.73	0.49±0.02	6.37±0.06	2.66±0.16	8.20±0.32
Strephonema pseudocola	10.1±0.04	0.39±0.02	4.16±0.70	2.21±0.16	19.8±0.51
*Berlinia bracteosa**	17.9±0.13	0.97±0.03	11.9±0.10	4.18±0.15	14.8±0.82
*Didelotia africana**	16.8±0.16	0.68±0.01	5.07±0.26	2.59±0.14	13.1±0.39
*Tetraberlinia bifoliolata**	15.3±0.41	0.95±0.09	6.43±0.13	1.81±0.14	5.53±0.14
*Microberlinia bisulcata**	13.9±0.05	0.55±0.01	4.95±0.04	3.46±0.11	14.2±0.12

Significant correlations existed between some of these elements across all the species, particularly for N and P, N and K, P and K, K and Mg ($r = 0.75, 0.73, 0.73$ and 0.71; $df = 5$, $p<0.05$). Ca was however negatively correlated with N and P while K positively with Mg, though none was significant.

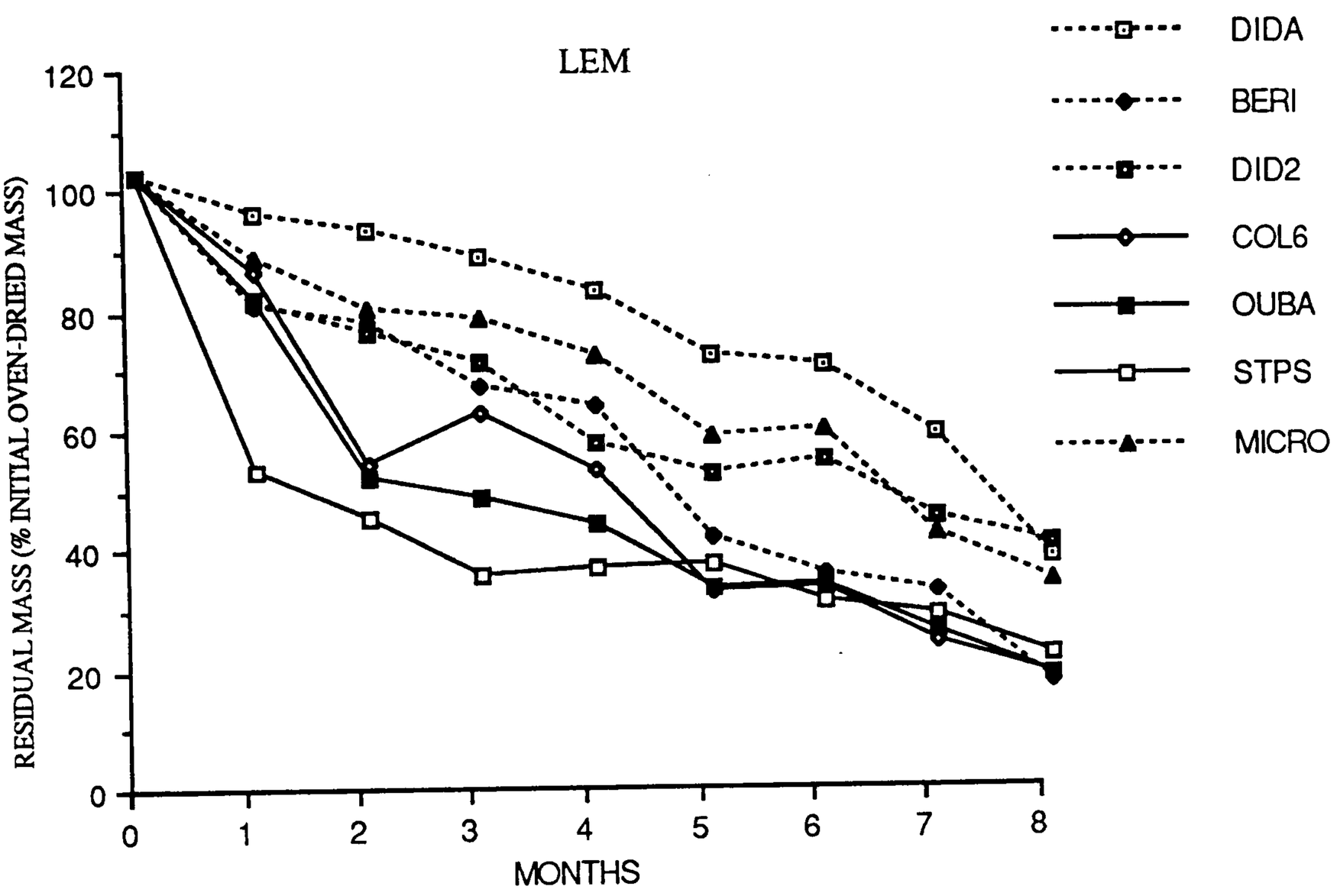
5.3.2.2 Comparison between species in both forest types

Rates of mass loss in leaf litter of the selected species in the first decomposition experiment with coarse mesh litterbags (mesh size of 5 mm) followed no clear pattern. Within the first month on the forest floor all replicate litterbags in plots 9C and 24B in the LEM and HEM forests respectively, had only the petioles and some persistent midribs of the leaf samples left. In the other plots, leaf samples of *Berlinia bracteosa, Strephonema pseudocola, Oubanguia alata* and *Cola verticillata* were similarly affected.

Due to the rapid loss of leaf samples from the litterbags in the first experiment, results on rates of mass loss focused mainly on the second decomposition experiment with the fine mesh litterbags.

Trends in the mean residual mass (expressed as per cent of initial oven-dried mass) of the leaf samples in the fine litterbags retrieved at different sampling dates from the forest floor in both forest types are presented in Figure 5.2. The leaf samples of *Oubanguia alata, Cola verticillata* and *Strephonema pseudocola* (all non-ectomycorrhizal species) were clearly differentiated by their rapid initial mass loss within the first two months on the forest floor in both forest types. This was followed by a relatively slower phase and at the end of the eighth month only fractions of the petiole and midrib were left in the litterbags. Mass loss in *Didelotia africana, Tetraberlinia bifoliolata* and *Microberlinia bisulcata* (all ectomycorrhizal species)was relatively slower. Leaf samples of *Berlinia bracteosa* showed an exceptional pattern from the rest of the other ectomycorrhizal species with a relatively rapid mass loss from the fourth month on the forest floor in both LEM and HEM forests.

Results of the analysis of covariance (that is comparison of regression slopes) revealed a marginal difference between the common slopes describing mass loss in forest types with faster rates in the HEM forest ($F=3.69$, $df = 1,171$, $p=0.056$). Differences were highly significant for the separate slopes for the different species within each forest type ($F=36.17$ and 8.67, $df = 6,175$ and $6,173$, $p<0.001$ for LEM and HEM forests respectively). The separate regressions on the per cent residual mass of the leaf samples of the seven species against time (months) using the single exponential model were significant for all the species in both forests ($p<0.001$, except $p=0.05$ for *Strephonema pseudocola* in HEM forest). The species-specific decomposition constants (k) which described rate of mass loss with time and their respective intercepts which represent the initial masses (at time zero) are presented in Table 5.9b. The decomposition constants (k) ranged from 0.111 for *Didelotia africana* to 0.243 for *Oubanguia alata* in the LEM forest and 0.056 for *Didelotia africana* to 0.43 for *Strephonema pseudocola* in the HEM forest. The species were ranked in the following order of increasing rates of mass loss in the LEM forest: *Didelotia africana, Tetraberlinia bifoliolata, Microberlinia bisulcata, Berlinia*



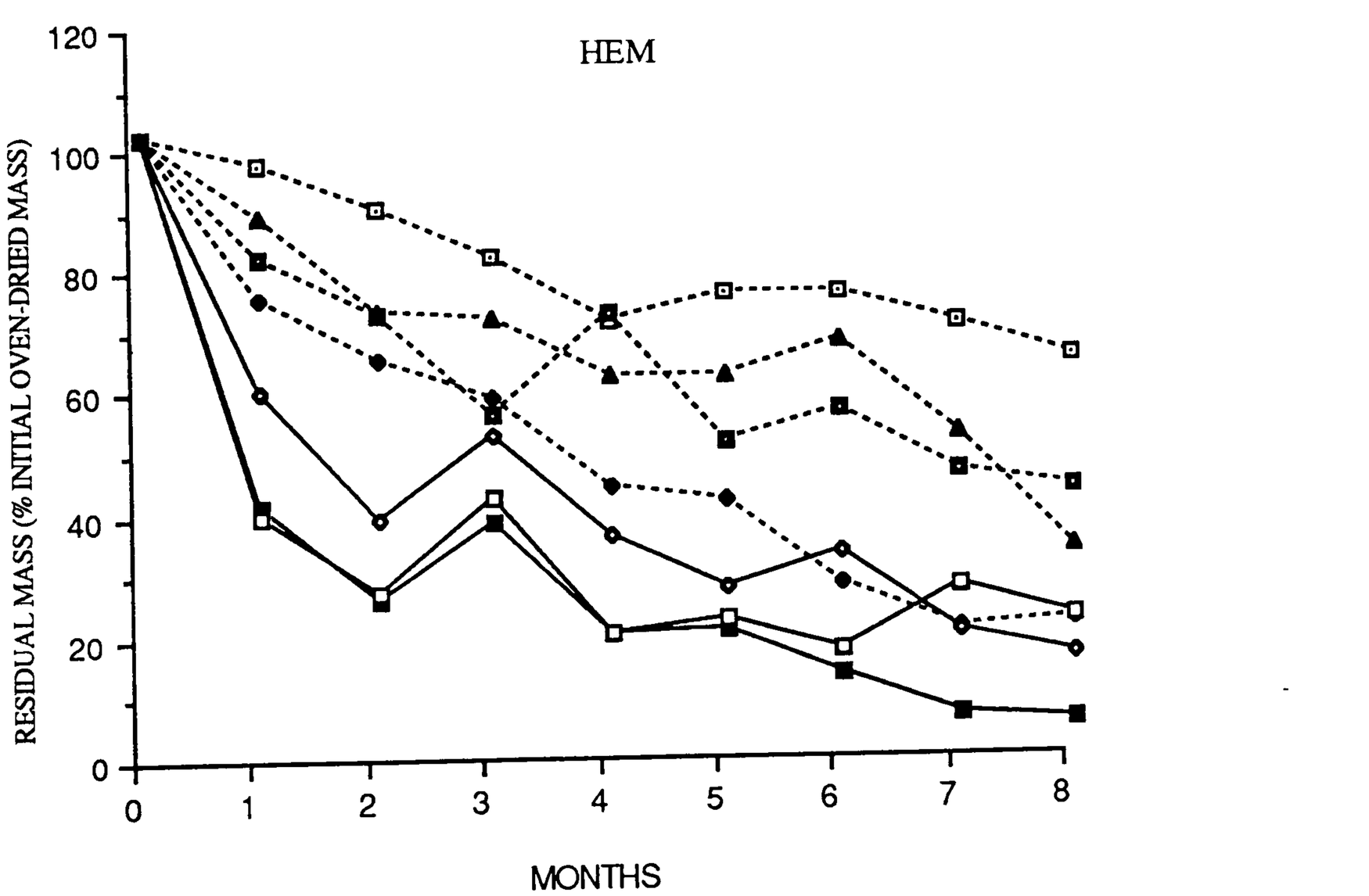


Figure 5.2: Mean residual mass (% initial oven-dried mass) of leaf litter in fine mesh litterbags placed on forest floor after different periods, averaged over the three plots (n=3) in LEM and HEM forests, Korup National Park, Cameroon.

Table 5.9a: Comparison of regressions of mass loss (%) on time (months) for leaf litter decomposed in over eight months in fine litterbags on the forest floor in LEM and HEM forests in Korup National Park, Mundemba, Cameroon. A (labile fraction) from the double exponential model was expressed as percentages.

		Linear model			Single exponential model			Double exponetial model			
SPECIES	Forest type	Intercept	k	R^2	Intercept	k_1	R^2	A (%)	k_2	k_3	R^2
Cola verticillata	LEM	83.1	8.90	87.6	101.1	0.216	94.6	68.0	2.60	0.21	85.7
	HEM	74.2	8.29	75.5	79.0	0.204	86.9		2.60	0.16	90.6
Oubanguia alata	LEM	83.8	9.23	87.1	91.5	0.203	95.3	40.0	0.48	0.09	92.7
	HEM	63.9	8.86	67.4	78.3	0.364	89.1		0.74	0.16	77.3
Didelotia africana	LEM	105.1	7.16	92.3	111.8	0.106	80.1	27.0	0.19	0.07	87.6
	HEM	87.5	2.89	44.8	97.5	0.056	88.1		0.19	0.01	94.4
Berlinia bracteosa	LEM	95.1	9.88	97.2	111.2	0.207	91.0	74.0	0.17	0.04	89.1
	HEM	87.3	9.59	94.0	99.4	0.211	96.7		0.28	0.17	94.0
Tetraberlinia bifoliolata	LEM	90.3	6.95	92.9	93.3	0.111	96.1	26.0	0.44	0.07	94.9
	HEM	87.9	6.26	81.2	89.3	0.100	82.6		1.34	0.08	90.9
Microberlinia bisulcata	LEM	98.0	7.88	97.0	105.6	0.130	91.3	45.0	0.11	0.13	91.9
	HEM	93.1	6.71	86.8	97.5	0.108	79.6		0.37	0.07	89.4

(*Strephonema pseudocola* not included as it was not used in fitting the double exponential model).

Table 5.9b: Regression analysis on mass loss(%) with time (months) for leaf litter of selected tree species (4 ectomycorrhizal and 3 non-ectomycorrhizal species) incubated on the forest floor in fine mesh litterbags for eight months (15 July 1991-14 March 1992) in both LEM and HEM forests, Korup National Park, Mundemba. Comparison between forest types was by student's t test.

			REGRESSION STATISTICS (SINGLE EXPONENTIAL DECAY MODEL)					COMPARISON BETWEEN FOREST TYPES		
SPECIES	FOREST TYPE	SAMPLE SIZE	INTERCEPT	SLOPE	F-RATIO	p-LEVEL	R^2	t	df	p-level
Cola verticillata	LEM HEM	27 27	4.62 4.44	-0.243 -0.301	39.88 15.08	<0.001 <0.001	61.5 37.6	0.67	50	NS
Oubanguia alata	LEM HEM	27 27	4.51 4.26	-0.227 -0.430	27.09 26.75	<0.001 <0.001	52.0 51.7	2.16	50	<0.05
Strephonema pseudocola	LEM HEM	27 24	4.14 3.47	-0.242 -0.209	8.79 4.14	<0.01 0.05	26.0 16.0	0.26	47	NS
*Berlinia bracteosa**	LEM HEM	26 27	4.72 4.54	-0.215 -0.230	64.02 28.53	<0.001 <0.001	72.7 53.3	0.29	49	NS
*Didelotia africana**	LEM HEM	27 27	4.72 4.58	-0.111 -0.056	51.56 28.83	<0.001 <0.001	67.3 53.6	2.96	50	<0.01
*Tetraberlinia bifoliolata**	LEM HEM	27 27	4.50 4.43	-0.118 -0.104	16.52 7.67	<0.001 <0.001	39.8 23.5	0.30	50	NS
*Microberlinia bisulcata**	LEM HEM	27 27	4.67 4.59	-0.135 -0.113	74.74 45.26	<0.001 <0.001	74.9 64.4	0.52	50	NS

* Ectomycorrhizal species.

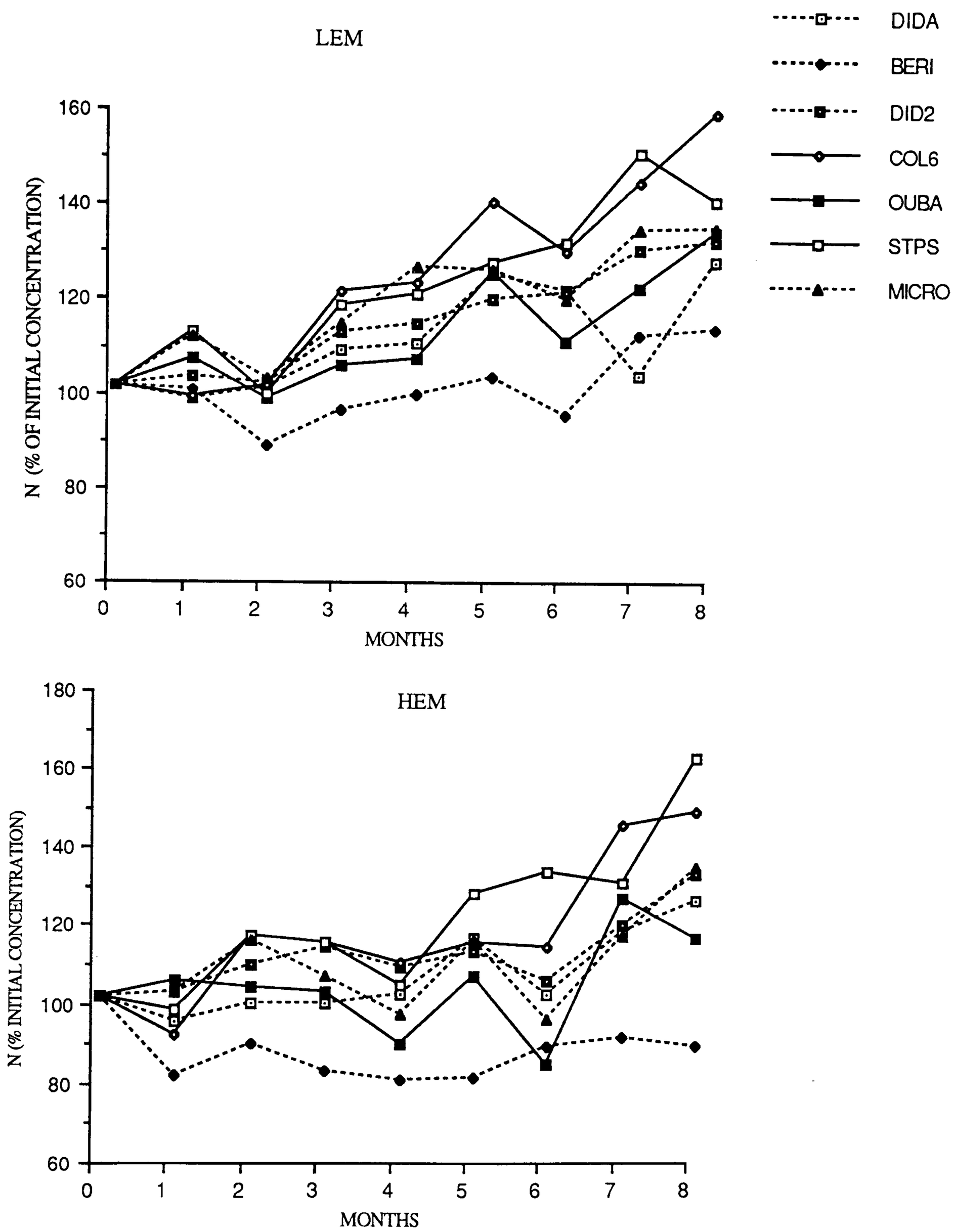


Figure 5.3: Mean nitrogen concentration (% initial concentration) in residual mass of leaf litter in litterbags placed on forest floor after different periods, averaged over the three plots (n=3) in LEM and HEM forests, Korup National Park, Cameroon.

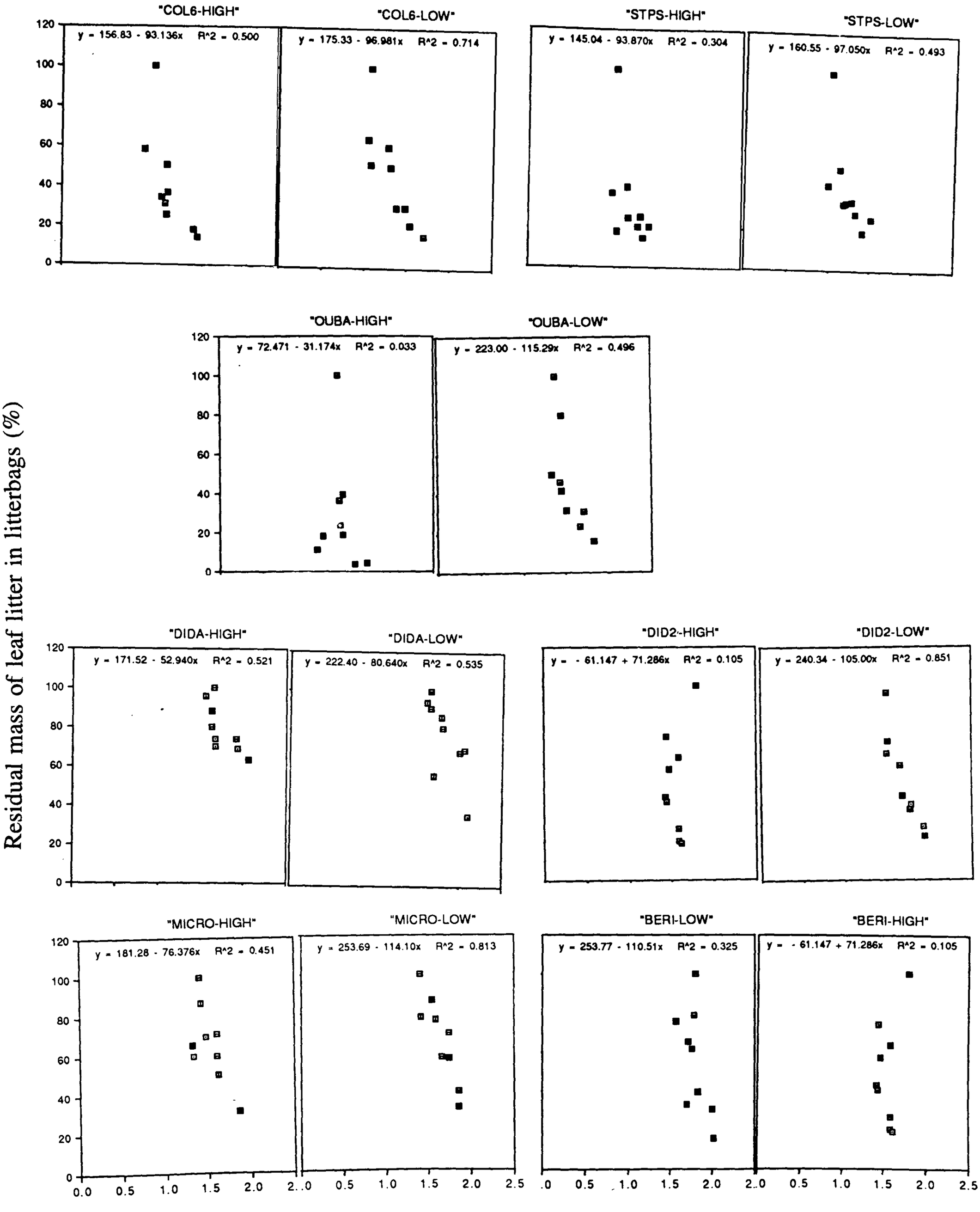


Figure 5.4: The percentage residual mass expressed as a function of N concentration in the residual leaf samples of the seven species in LEM and HEM forests, Korup National Park, Cameroon.

Table 5.10: Regression analysis on rates of nitrogen mineralization in leaf litter of seven selected tree species placed on the forest floor in fine mesh litterbags for eight months (15 July 1991- 14 March 1992) in both LEM and HEM forests, Korup National Park, Mundemba. Comparison between forest types was by student's t test.

			REGRESSION STATISTICS (SINGLE EXPONENTIAL DECAY MODEL)					COMPARISON BETWEEN FOREST TYPES		
SPECIES	FOREST TYPE	SAMPLE SIZE	INTERCEPT	SLOPE†	F-RATIO	p-LEVEL	R^2	t	df	p
Cola verticillata	LEM HEM	27 26	4.56 4.55	0.060 0.047	71.53 25.82	<0.001 <0.001	74.1 51.8	1.13	49	NS
Oubanguia alata	LEM HEM	27 22	4.57 4.58	0.032 0.009	12.42 0.63	<0.01 0.50	33.2 3.0	1.68	45	NS
Strephonema pseudocola	LEM HEM	27 24	4.60 3.57	0.047 0.050	34.87 31.80	<0.001 <0.001	58.2 59.1	0.25	47	NS
*Berlinia bracteosa**	LEM HEM	26 27	4.53 4.47	0.015 -0.007	2.65 0.39	>0.05 >0.05	9.9 1.9	1.79	49	NS
*Didelotia africana**	LEM HEM	24 27	4.57 4.53	0.032 0.029	19.38 24.28	<0.001 <0.001	46.8 49.3	0.33	47	NS
*Tetraberlinia bifoliolata**	LEM HEM	27 27	4.58 4.60	0.037 0.025	58.79 26.92	<0.001 <0.001	70.2 51.9	2.55	50	<0.05
*Microberlinia bisulcata**	LEM HEM	27 27	4.62 4.59	0.035 0.020	28.50 5.55	<0.001 <0.05	53.3 18.2	1.97	50	NS

* Ectomycorrhizal species.
† Positive values indicate net immobilization

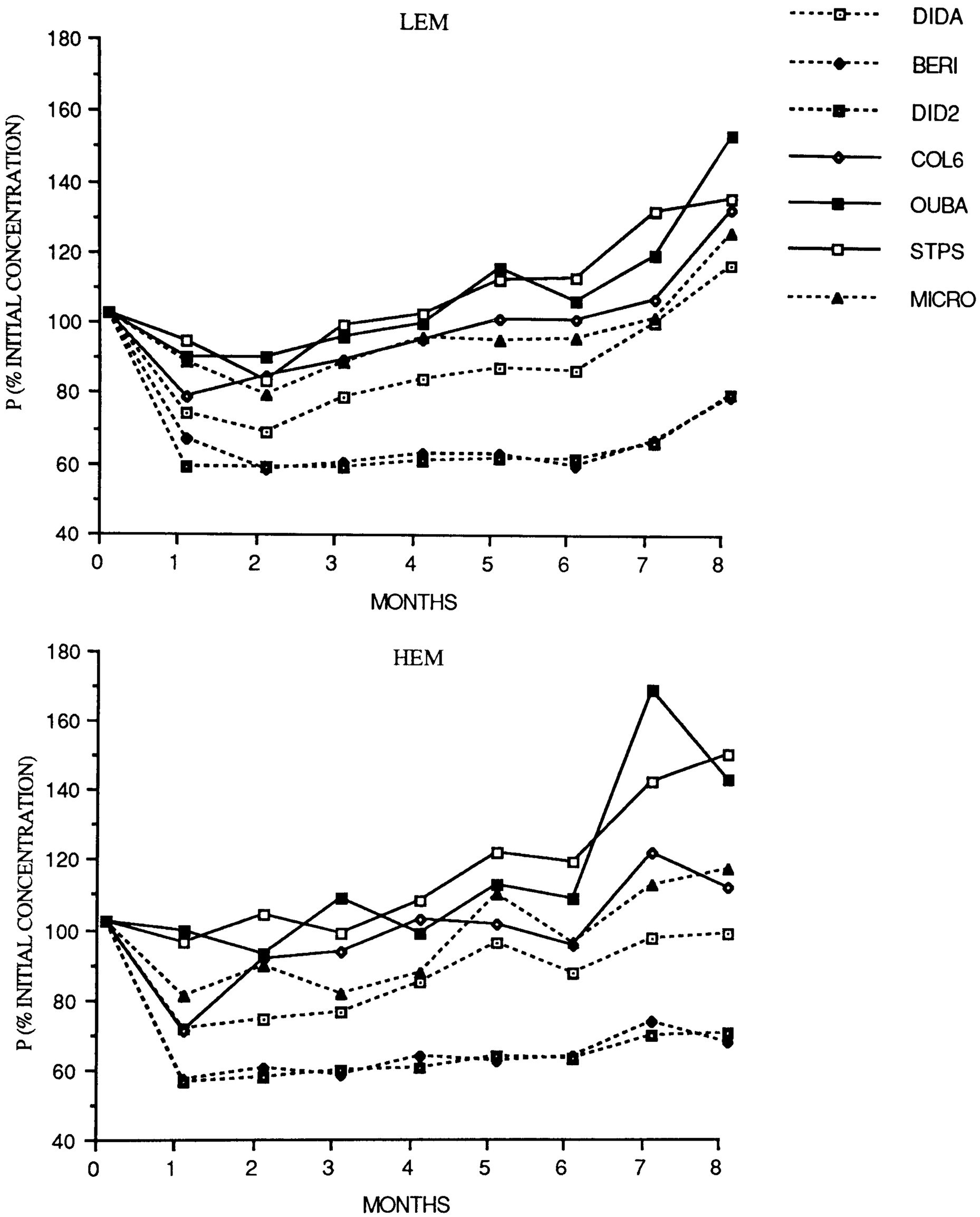


Figure 5.5: Mean phosphorus concentration (% initial concentration) in residual mass of leaf litter in litterbags placed on forest floor after different periods, averaged over the three plots (n=3) in LEM and HEM forests, Korup National Park, Cameroon.

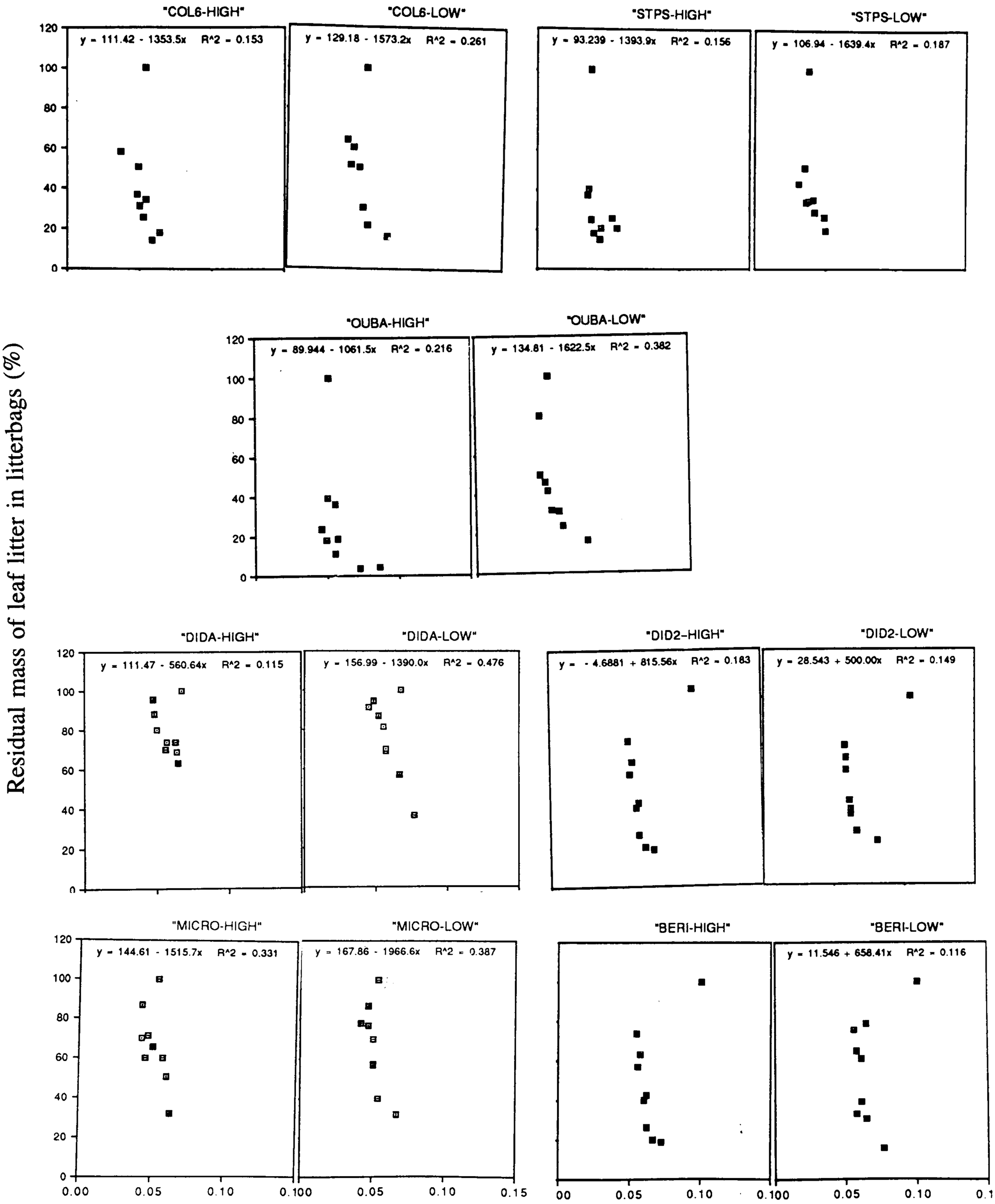


Figure 5.6: The percentage residual mass expressed as a function of P concentration in the residual leaf samples of the seven species in LEM and HEM forests, Korup National Park, Cameroon.

Table 5.11: Regression analysis on rates of phosphorus mineralization in leaf litter of seven selected species placed on the forest floor in fine mesh litterbags for eight months (15 July 1991-14 March 1992) in both LEM and HEM forests, Korup National Park, Mundemba. Comparison between forest types was by student's t test.

			REGRESSION STATISTICS (SINGLE EXPONENTIAL DECAY MODEL)					COMPARISON BETWEEN FOREST TYPES		
SPECIES	FOREST TYPE	SAMPLE SIZE	INTERCEPT	SLOPE†	F-RATIO	p-LEVEL	R^2	t	df	p
Cola verticillata	LEM HEM	27 26	4.39 4.41	0.042 0.034	20.60 5.39	<0.001 <0.05	45.2 18.3	0.47	49	NS
Oubanguia alata	LEM HEM	27 22	4.44 4.49	0.051 0.049	18.63 10.18	<0.001 <0.01	42.7 33.7	0.11	45	NS
Strephonema pseudocola	LEM HEM	27 24	4.45 3.51	0.048 0.049	19.17 10.00	<0.001 <0.01	43.4 31.2	0.05	47	NS
*Berlinia bracteosa**	LEM HEM	26 27	4.25 4.21	-0.021 -0.016	1.94 0.87	>0.05 >0.05	7.5 3.4	0.22	49	NS
*Didelotia africana**	LEM HEM	24 27	4.34 4.32	0.028 0.023	4.01 3.40	>0.05 >0.05	15.4 12.0	0.28	47	NS
*Tetraberlinia bifoliolata**	LEM HEM	27 27	4.19 4.19	-0.008 -0.012	0.28 0.53	>0.05 >0.05	1.0 2.1	0.26	50	NS
*Microberlinia bisulcata**	LEM HEM	27 27	4.43 4.41	0.028 0.033	9.98 7.72	<0.01 <0.05	28.5 23.6	0.48	50	NS

* Ectomycorrhizal species.
† All positive values indicate net immobilisation.

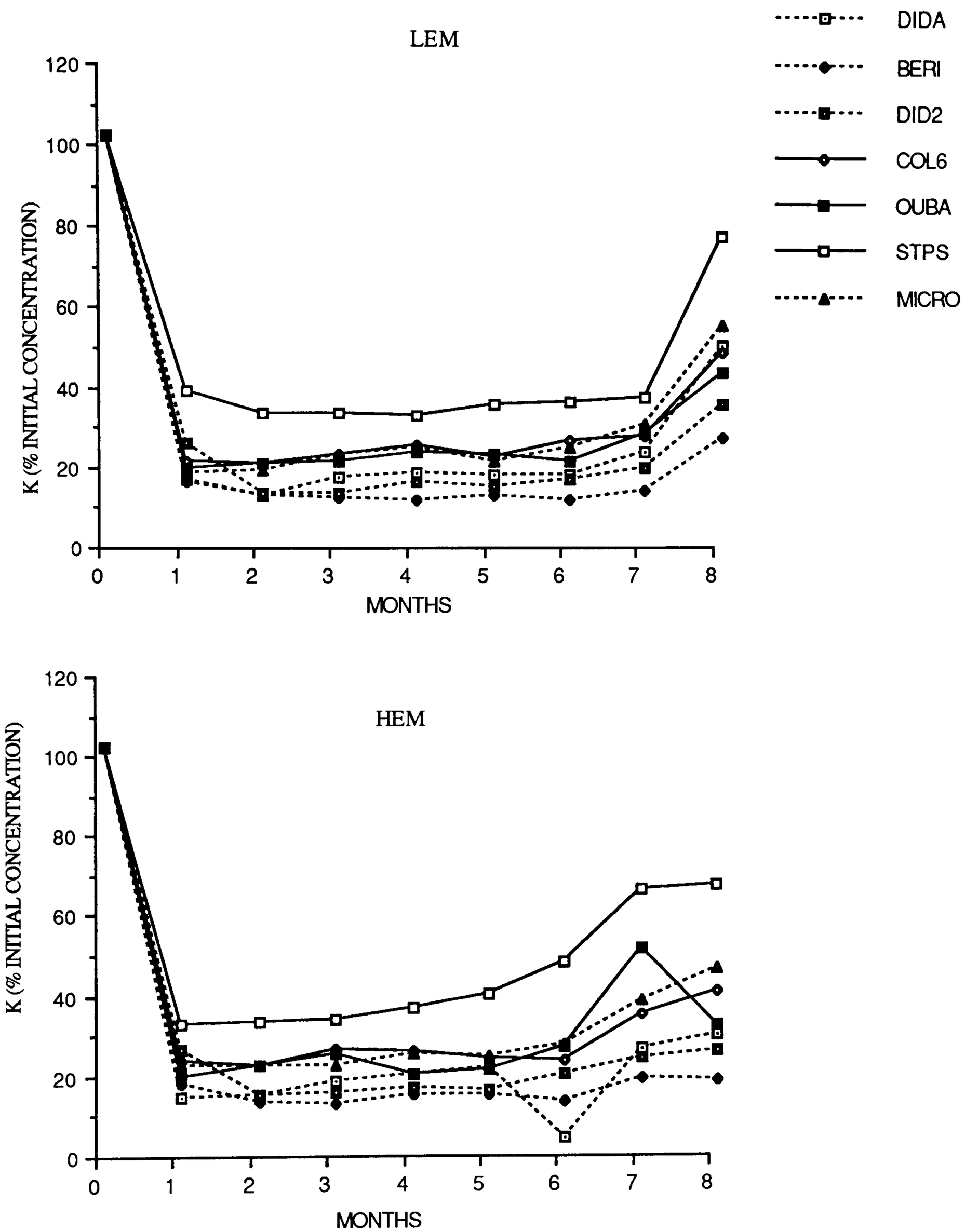


Figure 5.7: Mean potassium concentration (% initial concentration) in residual mass of leaf litter in litterbags placed on forest floor after different periods, averaged over the three plots (n=3) in LEM and HEM forests, Korup National Park, Cameroon.

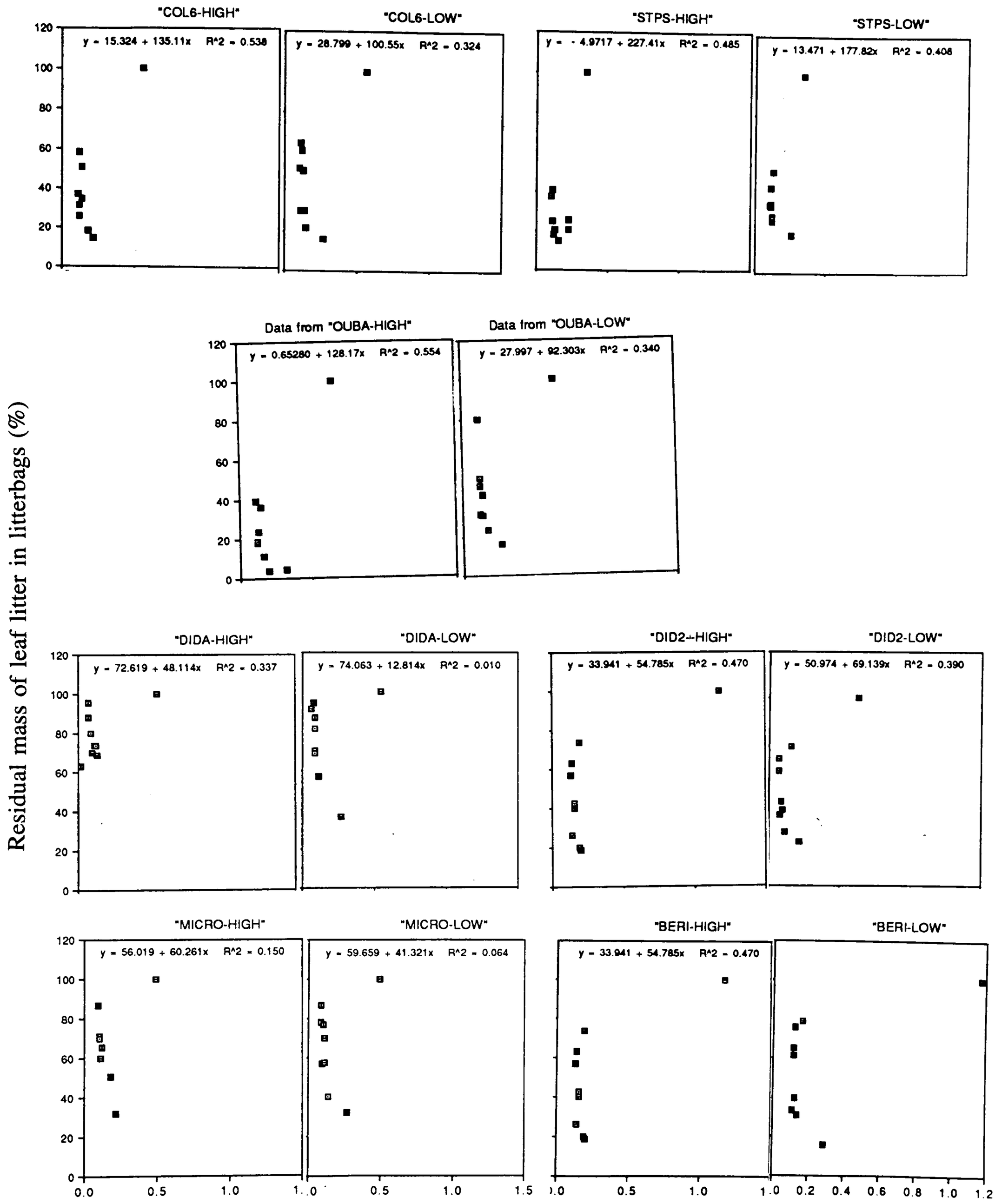


Figure 5.8: The percentage residual mass expressed as a function of K concentration in the residual leaf samples of the seven species in LEM and HEM forests, Korup National Park, Cameroon.

Table 5.12: Regression analysis on rates of potassium mineralization in leaf litter of seven selected species placed on the forest floor in fine mesh litterbags for eight months(15 July 1991-14 March 1992) in both LEM and HEM forests, Korup National Park, Mundemba. Comparison between forest types was by student's t test.

			REGRESSION STATISTICS (SINGLE EXPONENTIAL DECAY MODEL)					COMPARISON BETWEEN FOREST TYPES		
SPECIES	FOREST TYPE	SAMPLE SIZE	INTERCEPT	SLOPE	F-RATIO	p-LEVEL	R^2	t	df	p
Cola verticillata	LEM HEM	27 26	3.44 3.55	-0.030 -0.056	0.52 1.59	>0.05 >0.05	2.0 6.2	0.43	49	NS
Oubanguia alata	LEM HEM	27 22	3.43 3.51	-0.039 -0.061	0.86 1.34	>0.05 >0.05	3.3 6.3	0.30	45	NS
Strephonema pseudocola	LEM HEM	27 24	3.79 3.79	-0.019 -0.005	0.34 0.02	>0.05 >0.05	1.4 0.1	0.28	47	NS
*Berlinia bracteosa**	LEM HEM	26 27	3.18 3.29	-0.129 -0.121	5.27 6.50	<0.05 <0.05	18.0 20.6	0.11	49	NS
*Didelotia africana**	LEM HEM	24 27	3.18 3.23	-0.042 -0.036	0.46 0.56	>0.05 >0.05	2.0 2.2	0.23	47	NS
*Tetraberlinia bifoliolata**	LEM HEM	27 27	3.30 3.40	-0.079 -0.095	2.49 3.97	>0.05 >0.05	9.1 13.7	0.06	50	NS
*Microberlinia bisulcata**	LEM HEM	27 27	3.34 3.45	-0.011 -0.018	0.05 0.20	>0.05 >0.05	0.2 0.8	0.16	50	NS

* Ectomycorrhizal species.

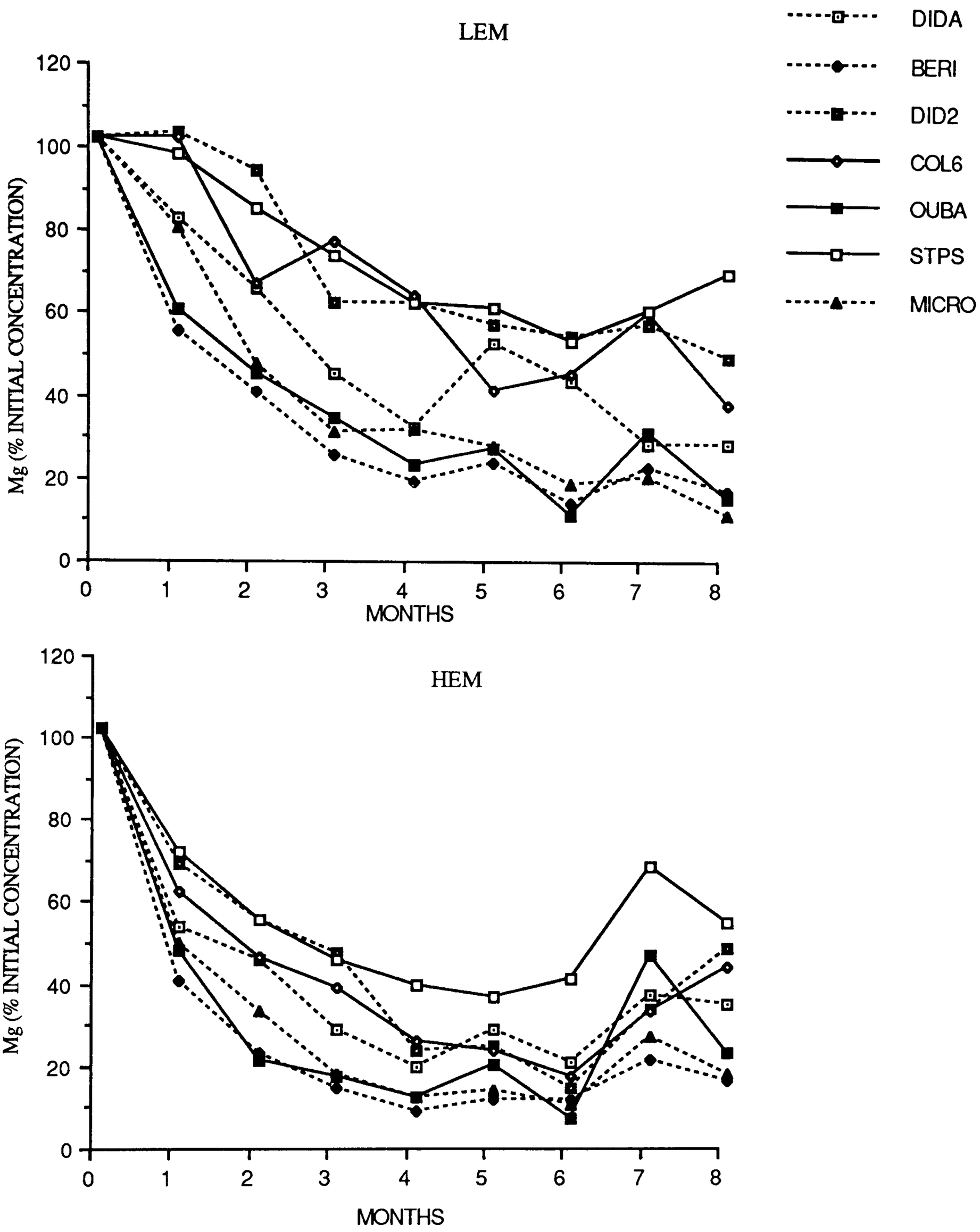


Figure 5.9: Mean magnesium concentration (% initial concentration) in residual mass of leaf litter in litterbags placed on forest floor after different periods, averaged over the three plots (n=3) in LEM and HEM forests, Korup National Park, Cameroon.

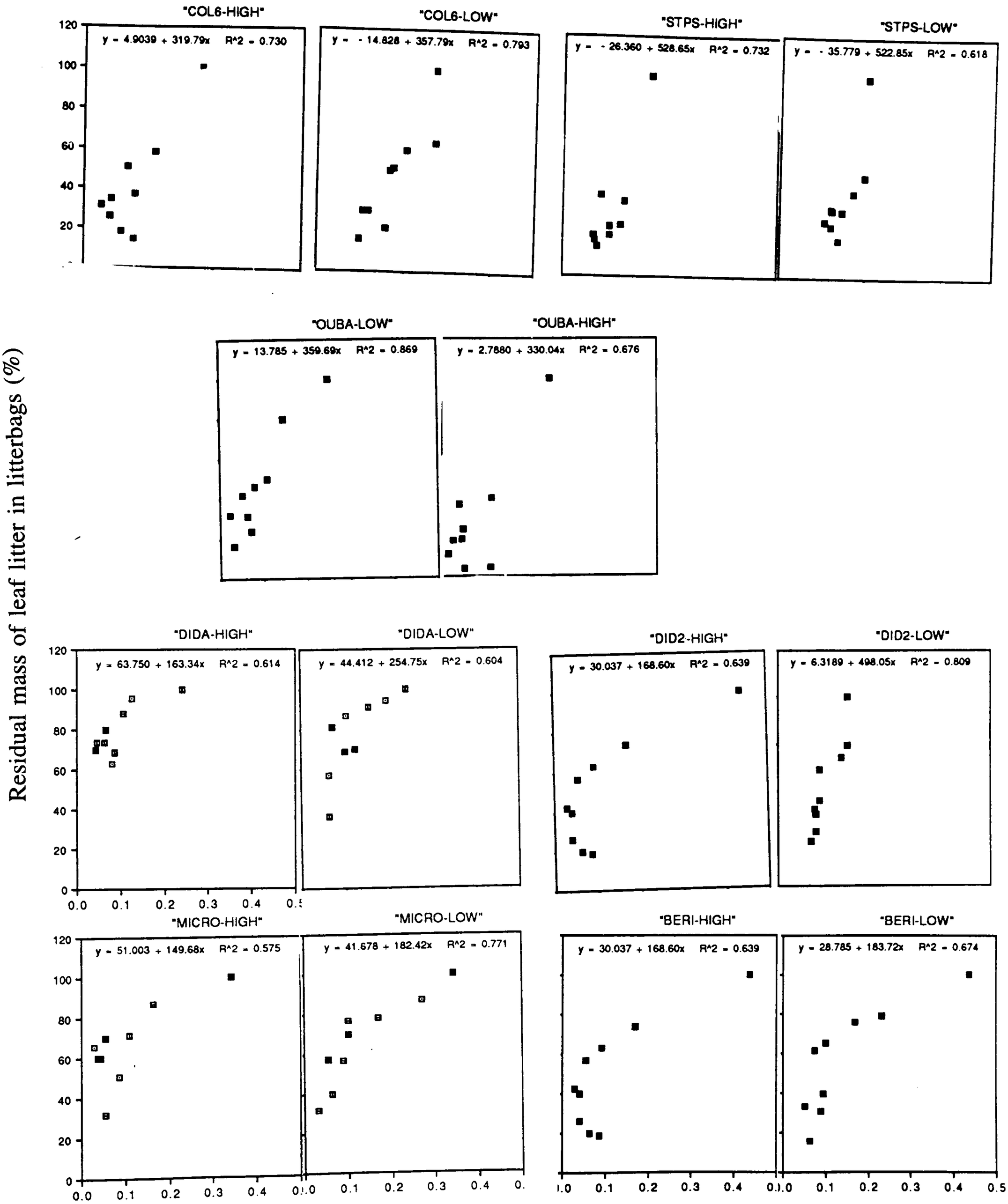


Figure 5.10: The percentage residual mass expressed as a function of Mg concentration in the residual leaf samples of the seven species in LEM and HEM forests, Korup National Park, Cameroon.

Table 5.13: Regression analysis on rates of magnesium mineralization in leaf litter of seven selected species placed on the forest floor in fine mesh litterbags for eight months (15 July 1991-14 march 1992) in both LEM and HEM forests, Korup National Park, Mundemba. Comparison between forest types was by student's t test.

			REGRESSION STATISTICS (SINGLE EXPONENTIAL DECAY MODEL)					COMPARISON BETWEEN FOREST TYPES		
SPECIES	FOREST TYPE	SAMPLE SIZE	INTERCEPT	SLOPE	F-RATIO	p-LEVEL	R^2	t	df	p
Cola verticillata	LEM HEM	27 26	4.57 4.11	-0.128 -0.149	19.19 11.80	<0.001 <0.01	43.4 33.0	0.41	49	NS
Oubanguia alata	LEM HEM	27 22	4.26 3.73	-0.235 -0.182	40.76 7.48	<0.001 <0.05	62.0 27.2	0.74	45	NS
Strephonema pseudocola	LEM HEM	27 24	4.53 4.08	-0.075 -0.079	12.91 1.56	<0.001 >0.05	34.1 6.6	0.06	47	NS
*Berlinia bracteosa**	LEM HEM	26 27	4.12 3.62	-0.247 -0.198	22.53 13.76	<0.001 <0.001	48.4 35.5	0.66	49	NS
*Didelotia africana**	LEM HEM	24 27	4.48 3.98	-0.167 -0.130	32.87 8.40	<0.001 <0.01	59.9 25.2	0.66	47	NS
*Tetraberlinia bifoliolata**	LEM HEM	27 27	4.62 4.26	-0.115 -0.174	24.28 14.53	<0.001 <0.001	49.3 36.8	1.68	50	NS
*Microberlinia bisulcata**	LEM HEM	27 27	4.47 3.83	-0.291 -0.210	44.20 13.82	<0.001 <0.01	63.9 35.6	1.78	50	NS

* Ectomycorrhizal species.

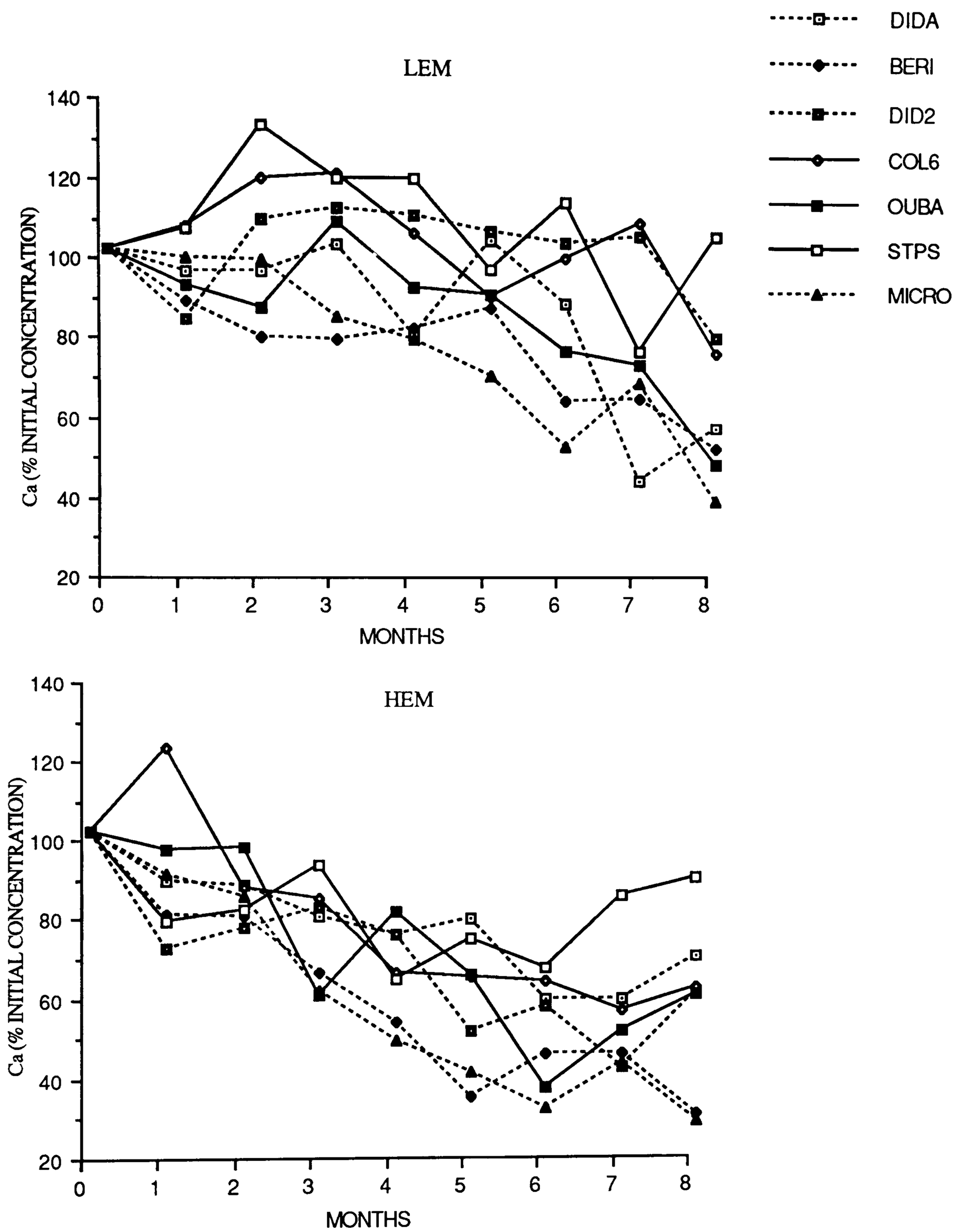


Figure 5.11: Mean calcium concentration (% initial concentration) in residual mass of leaf litter in litterbags placed on forest floor after different periods, averaged over the three plots (n=3) in LEM and HEM forests, Korup National Park, Cameroon.

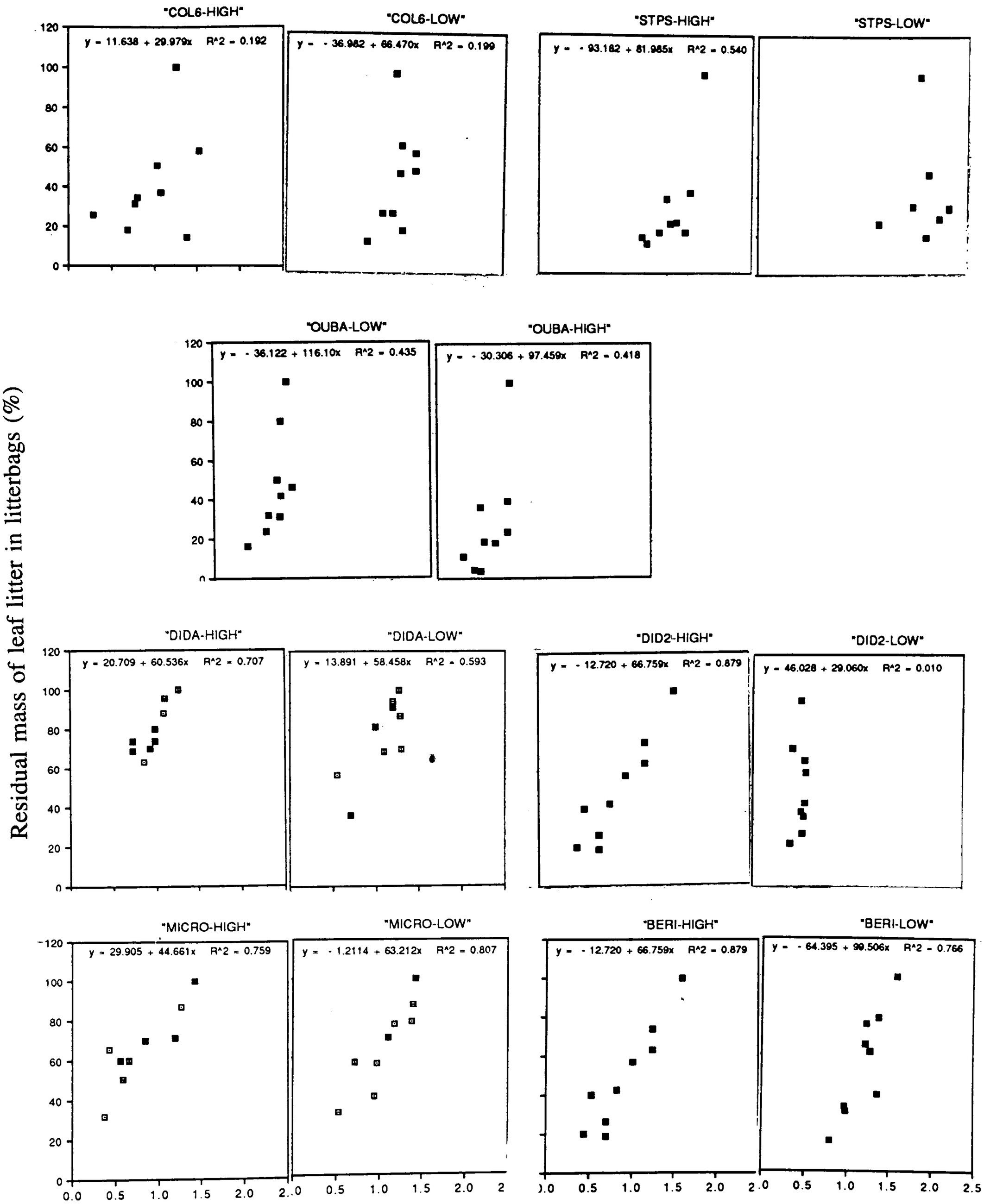


Figure 5.12: The percentage residual mass expressed as a function of Ca concentration in the residual leaf samples of the seven species in LEM and HEM forests, Korup National Park, Cameroon.

LEGEND FOR GRAPHS

DIDA	***Didelotia africana***
BERI	***Berlinia bracteosa***
DID2	***Tetraberlinia bifoliolata***
COL6	***Cola rostrata***
OUBA	***Oubanguia alata***
STPS	***Strephonema pseudocola***
MICRO	***Microberlinia bisulcata***

Table 5.14: Regression analysis on rates of calcium mineralization in leaf litter of selected species placed on the forest floor in fine mesh litterbags for eight months (15 July 1991-14 March 1992) in both LEM and HEM forests, Korup National Park, Mundemba. Comparison between forest types was by student's t test.

			REGRESSION STATISTICS (SINGLE EXPONENTIAL DECAY MODEL)					COMPARISON BETWEEN FOREST TYPES		
SPECIES	FOREST TYPE	SAMPLE SIZE	INTERCEPT	SLOPE	F-RATIO	p-LEVEL	R^2	t	df	p
Cola verticillata	LEM HEM	27 26	4.73 4.57	-0.034 -0.051	4.27 4.54	<0.05 <0.05	14.6 15.9	0.59	49	NS
Oubanguia alata	LEM HEM	27 22	4.68 3.57	-0.077 -0.096	12.34 7.63	<0.001 <0.05	33.0 27.6	0.48	45	NS
Strephonema pseudocola	LEM HEM	27 24	4.76 4.43	-0.035 -0.031	2.03 0.87	>0.05 >0.05	7.5 3.8	0.10	47	NS
*Berlinia bracteosa**	LEM HEM	26 27	4.57 4.56	-0.078 -0.148	6.54 51.24	<0.05 <0.001	21.4 67.2	1.91	49	NS
*Didelotia africana**	LEM HEM	24 27	4.68 3.56	-0.064 -0.065	12.59 16.43	<0.01 <0.001	36.4 39.7	0.20	47	NS
*Tetraberlinia bifoliolata**	LEM HEM	27 27	4.62 4.49	-0.014 -0.084	0.40 14.90	>0.05 <0.01	1.6 37.3	3.19	50	<0.05
*Microberlinia bisulcata**	LEM HEM	27 27	4.73 4.61	-0.125 -0.169	20.67 91.57	<0.001 <0.001	45.3 78.6	1.90	50	NS

* Ectomycorrhizal species.

Table 5.15: Summary of Tukey's multiple comparisons between mass and nutrient loss rates (k) for leaf litter of selected tree species (four ectomycorrhizal and three non-ectomycorrhizal) placed in fine mesh litterbags on the forest floor for a duration of eight months (15 July 1991-14 March 1992) in LEM and HEM forests, Korup National Park, Mundemba. Species with same lower case letters after the k-values indicates that they are not significantly different (critical $q_{0.05, 200, 7}$ =4.17).

SPECIES	Forest type	Weight loss	N	P	K	Mg	Ca
Cola verticillata	LEM	-0.243a	0.060b	0.042bc	-0.030a	-0.128bc	-0.034ab
	HEM	-0.301ab	0.047b	0.034b	-0.056a	-0.149a	-0.051c
Oubanguia alata	LEM	-0.227ab	0.032ab	0.051c	-0.039a	-0.235ab	-0.077ab
	HEM	-0.430a	0.009ab	0.049a	-0.061a	-0.182a	-0.096abc
Strephonema pseudocola	LEM	-0.242ab	0.047ab	0.048bc	-0.019a	-0.075c	-0.035ab
	HEM	-0.209abc	0.050b	0.049a	-0.005a	-0.079a	-0.031c
*Berlinia bracteosa**	LEM	-0.215ab	0.015ab	-0.021a	-0.129a	-0.247ab	-0.078ab
	HEM	-0.230ab	-0.007a	-0.016a	-0.121a	-0.198a	-0.148ab
*Didelotia africana**	LEM	-0.111b	0.032ab	0.028ab	-0.042a	-0.167ab	-0.064ab
	HEM	-0.056c	0.029ab	0.023a	-0.036a	-0.130a	-0.065c
*Tetraberlinia bifoliolata**	LEM	-0.118ab	0.037ab	-0.008ab	-0.079a	-0.115bc	-0.014c
	HEM	-0.104bc	0.025ab	-0.012a	-0.095a	-0.174a	-0.084bc
*Microberlinia bisulcata**	LEM	-0.135ab	0.035ab	0.028ab	-0.011a	-0.291a	-0.125a
	HEM	-0.113bc	0.020ab	0.033a	-0.018a	-0.210a	-0.169a

* Ectomycorrhizal species.

bracteosa, *Oubanguia alata*, *Strephonema pseudocola* and *Cola verticillata*. A similar trend was observed in the HEM forest with the exception of *Berlinia bracteosa* and *Oubanguia alata* which showed relatively higher rates of mass loss.

Pair-wise comparisons of the species-specific decomposition constants (k) between the two forest types showed significantly higher rates of mass loss in the HEM forest for *Oubanguia alata* ($p<0.05$) and for *Didelotia africana* ($p<0.01$) in the LEM forest (Table 5.9b).

The Tukey's multiple comparison test between the species-specific k-values in both forests differentiated two and three significant but overlapping groups amongst the seven species in LEM and HEM forests respectively (Table 5.15). These are in a descending order of decomposition rates from a to c, with rates of mass loss in the species in same lettered group not significantly different from each other. In the LEM forest *Didelotia africana* was significantly different from *Oubanguia alata* ($p<0.05$) with *Strephonema pseudocola, Cola verticillata, Berlinia bracteosa, Microberlinia bisulcata* and *Tetraberlinia bifoliolata* overlapping between these two species. In the HEM forest *Didelotia africana*, *Tetraberlinia bifoliolata* and *Microberlinia bisulcata* (all ectomycorrhizal species) differed significantly from *Oubanguia alata*. *Tetraberlinia bifoliolata* and *Microberlinia bisulcata* were however not significantly different from *Berlinia bracteosa* and *Cola verticillata*. *Strephonema pseudocola* showed no differences from all the other six species.

Judging from the species-specific k-values, some of the non-ectomycorrhizal species appear to decompose faster in the HEM forest than LEM forest. The monthly trends of residual mass (%) showed rapid losses in the non-ectomycorrhizal species compared to the ectomycorrhizal species within the first two months which was relatively high in the HEM forest (Figure 5.2). These trends are best shown in the estimated half-lives ($t_{1/2}$) of these species ranging from 0.94 to 2.9 months and from <0.5 to 1.75 months for the non-ectomycorrhizal species and from 4.98 to 7.28 months and from 4.98 to 11.93 months for the ectomycorrhizal species in LEM and HEM forests respectively. The common slopes however indicated a relatively higher rate of mass loss in the LEM forest though not significantly different from the HEM forest.

5.3.2.3 Mass loss and litter quality.

The substrate quality was defined by the initial concentration of the nutrient elements (labile fractions) in the various leaf litter samples (Table 5.8). The initial concentrations of the various nutrient elements were weakly correlated with the respective k-value describing rates of mass loss in the different species ($p>0.05$, $df=5$). This relationship was negative with the initial concentration of N ($r = -0.37$) and P ($r = -0.34$) but was positive with P:N ratio ($r=0.21$). The relationship was also positive between the respective k-values and the initial concentration of Mg ($r = 0.13$) and Ca ($r = 0.08$).

5.3.3 Rates of mineralization

5.3.3.1 Temporal changes in nutrient concentration in decomposing leaf litter

The initial elemental concentrations of N, P, K, Mg and Ca in the leaf litter of the seven selected species are presented in Table 5.8. Temporal changes in mean concentrations (expressed as per cent of initial concentration) of these elements in the residual leaf samples in the litterbags following different durations the leaf samples were placed on the forest floor in both forests are presented in Figures 5.3-5.7. The dynamics of N, P, K, Mg and Ca in the decomposing leaf samples exhibited varying patterns in the LEM and HEM forest types. The three phases of nutrient dynamics described by Berg and Staaf (1981), which include leaching, accumulation (immobilization) and release phases, were distinguished at varying intervals and durations for the different elements and litter types (species) in both forests. The K-values fitted for the different nutrient elements may not be appropriate but provided the bases for comparing rates of mineralization between the different species and forest types.

Nitrogen dynamics

Concentrations of N increased gradually within the first month the leaf samples were placed on the forest floor in both forests. There was an initial slight loss N concentration through leaching in leaf samples of *Didelotia africana*, *Cola verticillata* and *Berlinia bracteosa* in HEM forest and in *Strephonema pseudocola* in the LEM forest. The increase

in concentration was relatively slower in the HEM forest compared to the LEM forest (Figure 5.3). *Berlinia bracteosa* was the only species in which there was slight drop in concentration within the first two months in the LEM forest and five months in the HEM forest. This was followed by a relatively slower increase in N concentration.

Analysis of covariance showed no significant differences between the common slopes describing N dynamics in both forests nor between the species in each forest type ($p>0.5$). The separate regressions of the percent change in concentration of N against time (months) using the single exponential function were significant for all the species in both forests ($p<0.05$) with the exception of *Berlinia bracteosa* in both forests and *Oubanguia alata* in the HEM forest ($P>0.2$). The regression statistics are presented in Table 5.10. The species-specific k-values describing N dynamics showed that net release (mineralization) of N occurred only from leaves of *Berlinia bracteosa* in the HEM forest and with the lowest accumulation in the LEM forest. The highest rates of N accumulation were in leaves of *Cola verticillata* and *Strephonema pseudocola* in LEM and HEM forests respectively. Pair-wise comparisons between the species-specific k-values showed that net accumulation was significantly higher (higher k-values) in the LEM forest for *Tetraberlinia bifoliolata* ($p<0.05$) compared to the HEM forest (Table 5.10).

Multiple comparisons between the species-specific k-values for all of the species in each forest type differentiated the seven species into two groups with some species overlapping (Table 5.15). In the LEM forest *Berlinia bracteosa* differed significantly from *Cola verticillata* ($p<0.05$) with the other five species overlapping. A similar trend was also exhibited in the HEM forest with *Berlinia bracteosa* differing significantly from *Cola verticillata* and *Strephonema pseudocola* with other the four species overlapping.

The overall net accumulation of N during the eight months period was highest in *Cola verticillata* (57.58%) in the LEM forest and *Strephonema pseudocola* (60.39%) in the HEM forest. The lowest values also coupled with net release were observed in *Berlinia bracteosa* (11.98% and -12.44%) in the LEM and HEM forests respectively. In grouping the species, net accumulations of N were 25.5% and 18.87% in leaf samples of the ectomycorrhizal species, 43.05% and 40.67% in the non-ectomycorrhizal species in both

LEM and HEM forests.

There was a significant inverse relationship ($p<0.05$) between the concentration of N in the residual leaf samples and the residual oven-dried mass in all the species in both forests. The only exception was *Berlinia bracteosa* in the HEM forest (Figure 5.4). The duration of eight months was however short of determining the point at which net release could start.

Phosphorus dynamics

The concentration of P in the residual leaf samples dropped steadily within the first two months on the forest floor in both forests. This was relatively rapid in leaf samples of *Tetraberlinia bifoliolata*, *Berlinia bracteosa*, and *Didelotia africana* (all ectomycorrhizal species) compared to the other species in both forests (Figure 5.5). This was followed by a slow increase in concentration with the magnitude increasing from the sixth month in both forests. There was little or no change in the concentration of P in the residual samples of *Tetraberlinia bifoliolata* and *Berlinia bracteosa* from the second month to the eighth month (end of the experiment) in both forest types.

There was no significant difference between the common slopes describing the temporal changes in P concentration in both forests ($p>0.05$). There were however significant differences in P dynamics in leaf samples of the seven species in each forest type ($F=3.16$ and 3.33, df=6,171 and 6,166, $p<0.01$). Regression statistics of the single exponential function of percent change in P concentration with time, as well as results of the pair-wise comparisons of the species specific k-values between both forests are presented in Table 5.11. The regressions were not significant for *Berlinia bracteosa*, *Didelotia africana* and *Tetraberlinia bifoliolata* in either forest ($p>0.05$) but their intercepts were significant ($p<0.05$). The k-values ranged from -0.021 and -0.061 in *Berlinia bracteosa* to 0.051 and 0.049 in *Oubanguia alata* in both LEM and HEM forests respectively. The negative values indicate net decreases in P concentration and this occurred only in leaf samples of *Berlinia bracteosa* and *Tetraberlinia bifoliolata* (Table 5.11). Following the multiple comparisons between the species-specific k-values in the LEM forest , *Berlinia bracteosa*, *Tetraberlinia bifoliolata*, *Microberlinia bisulcata* and *Didelotia africana* differed

significantly from *Oubanguia alata*. *Cola verticillata* and *Strephonema pseudocola,* in the same group with *Oubanguia alata,* differed significantly from *Berlinia bracteosa* (Table 5.15). The species did not differ significantly from one another in the HEM forest ($p>0.05$).

Net accumulation of P during the eight months period was highest in leaf samples of *Oubanguia alata* (51.58%) and *Strephonema pseudocola* (48.16%) in LEM and HEM forests respectively. Net accumulation occurred in all the non-ectomycorrhizal species in both forests and *Didelotia africana* in LEM forest. Net loss of P from the samples during that period occurred in *Berlinia bracteosa* and *Tetraberlinia bifoliolata* (all ectomycorrhizal species) in both forests and *Didelotia africana* in HEM forest. This was highest in *Berlinia bracteosa* with net loss of 23.02% and 34.83% in LEM and HEM forests respectively. This clearly showed that during the eight months period, the ectomycorrhizal species released P while accumulation occurred in the non-ectomycorrhizal species, both at varying intervals.

The concentration of P in the residual samples showed a weak inverse relationship with the residual mass in all the species (Figure 5.6). This relationship was significant from the second month in all the non-ectomycorrhizal species in both forests ($p<0.05$) with little or no improvement in the ectomycorrhizal species particularly *Berlinia bracteosa* and *Tetraberlinia bifoliolata* which showed net losses of P.

Potassium dynamics

Concentrations of K decreased rapidly from leaf samples of all the species within the first month on the forest floor in both forests. Within this first month, concentrations dropped to 16.77% to 37.0% of the initial concentration in all the species (Figure 5.7). This rapid initial loss is probably through leaching as K is a very mobile element (Parker 1983). Thereafter, little or no change in concentration was observed to the sixth and seventh months in LEM and HEM forests respectively after which slight increase in concentration was observed in all the species. No significant differences were observed in the temporal changes in K concentration between both forests nor between the species in each forest type ($p>0.05$).

The regression statistics for K dynamics and results for the pair-wise comparisons between the species in both forests are presented in Table 5.12. All the regressions were not significant due to the rapid initial drop in concentration which accounted for the very high residuals. Pair-wise comparisons between the species-specific k-values also showed no significant differences between the species in both forest types ($p>0.05$). This non-significant trend was also observed in the multiple comparisons between the species in each forest type.

During the entire eight months period, net loss of K was 53.67% and 64.72% of the initial concentration in LEM and HEM forest respectively.

The concentration of K decreased approximately linearly as a function of the dry mass of the residual samples in most of the species with the exception of *Microberlinia bisulcata* and *Didelotia africana* in the LEM forest. This relationship was particularly significant in the relatively fast decomposing species which include *Oubanguia alata* and *Strephonema pseudocola* (Figure 5.8).

Magnesium dynamics

Concentrations of Mg decreased in all the species in both LEM and HEM forests within the first six months the leaf samples were placed on the forest floor. This was relatively faster in the HEM forest with concentrations dropping to 9.4% of the initial concentrations in *Berlinia bracteosa* and to 39.5% in *Strephonema pseudocola,* compared to 8.9% in *Oubanguia alata* and to 54.4% in *Tetraberlinia bifoliolata* in the LEM forest. Thereafter, Mg concentration increased at varying rates in all the species in the HEM forest and in *Strephonema pseudocola* and *Oubanguia alata* in the LEM (Figure 5.9).

The analysis of covariance showed a highly significant difference between the common slopes describing the temporal changes in Mg concentration in both forests ($F=13.5$, $df=1,361$, $p<0.001$). However, temporal changes in Mg concentration did not differ significantly between the individual species in both forests ($p>0.05$). The regression statistics on changes in Mg concentration in the leaf samples over time are presented in Table 5.13. The regressions were all significant ($p<0.05$) with the exception of *Strephonema pseudocola* in the HEM forest. The species-specific k-values ranged from

0.075 and 0.079 to 0.29 and 0.21 in *Strephonema pseudocola* and *Microberlinia bisulcata* in LEM and HEM forests respectively. Pair-wise comparisons of the species-specific k-values between both forest types showed no significant differences in any of the species (Table 5.13).

In the LEM forest, *Microberlinia bisulcata* differed significantly from *Strephonema pseudocola*, *Tetraberlinia bifoliolata* and *Cola verticillata* ($p<0.05$). *Didelotia africana*, *Oubanguia alata* and *Berlinia bracteosa* were not significantly different from *Microberlinia bisulcata* nor *Tetraberlinia bifoliolata* and *Cola verticillata* but they differed significantly from *Strephonema pseudocola* (Table 5.15). No significant difference was shown among the seven species in HEM forest ($p>0.05$).

Net decrease in concentration of Mg from the decomposing leaf samples on the forest floor during the eight months period were 69.5% and 67.6% in LEM and HEM forests respectively. The rapid initial loss in concentration in the HEM forest was balanced by the sharp rise in concentration from the sixth month. There was no clear distinction between leaf samples of the ectomycorrhizal and non-ectomycorrhizal species in their respective rates of Mg mineralization.

The concentration of Mg in the residual samples decreased linearly with the oven-dried mass in all the species in both forests (Figure 5.10). The decrease in Mg concentration in the residual leaf samples was faster than mass loss in *Oubanguia alata* and *Berlinia bracteosa* in the LEM forest, *Tetraberlinia bifoliolata* in HEM forest and in *Didelotia africana* and *Microberlinia bisulcata* in both forests. This was shown by their relatively higher k-value for Mg mineralization when compared with their respective mass loss constants (k).

Calcium dynamics

Changes in the concentration of Ca in the decomposing leaf samples exhibited varying temporal patterns in the different species and both forests (Figure 5.11). There was an initial drop in concentration within the first month in five of the seven species in both forests. The concentration of Ca increased rapidly within the first two months in leaf

samples of *Strephonema pseudocola* and *Cola verticillata* in LEM forest and in the first month in samples of *Cola verticillata* in HEM forest. This was followed by a gradual and fluctuating fall in concentration which was relatively faster in the HEM forest (Figure 5.11). The concentration increased sharply in *Tetraberlinia bifoliolata* in the second month and was followed by little change to the seventh month before dropping.

There was a significant difference between trends in the temporal changes in Ca concentration in the decomposing leaf litter in both forests with a faster rate of decrease in concentration in the HEM forest ($F=3.84$ df=1,361, $p=0.05$). This was however not significant between the species in each forest type ($p>0.05$). The regressions were significant for all the species with the exception of *Strephonema pseudocola* in both forest types and *Tetraberlinia bifoliolata* in LEM forest (Table 5.14). The species specific k-values ranged from 0.014 in *Tetraberlinia bifoliolata* to 0.125 in *Microberlinia bisulcata* in LEM forest and 0.031 in *Strephonema pseudocola* to 0.169 in *Microberlinia bisulcata* in the HEM forest. Loss of Ca was significantly higher in the HEM forest for *Tetraberlinia bifoliolata* ($p<0.05$).

In the LEM forest, *Microberlinia bisulcata* differed significantly from the *Tetraberlinia bifoliolata* with the other species overlapping. In the HEM forest *Microberlinia bisulcata* and *Berlinia bracteosa* differed significantly from *Strephonema pseudocola*, *Cola verticillata* and *Didelotia africana* with *Tetraberlinia bifoliolata* and *Oubanguia alata* overlapping (Table 5.15).

Net loss of Ca during the eight months period was 36.56% and 37.07% in LEM and HEM forests respectively. Net loss appeared to be relatively faster in the ectomycorrhizal species compared with the non-ectomycorrhizal as exhibited in their higher k-values (Table 5.14).

The concentration of Ca decreased linearly as a function of mass loss of the residual leaf samples in most of the species and in both forest types. Exceptions to this trend were *Strephonema pseudocola* and *Tetraberlinia bifoliolata* in the LEM forest and *Cola verticillata* in both LEM and HEM forests (Figure 5.12). This was as a result of the net

increase in concentration leaf samples of these species at different intervals during the eight months period.

5.3.3.2 Initial concentration and rates of mineralization

Correlation analysis showed significant relationships between the initial concentrations and rates of mineralization of the elements in the decomposing leaf litter. Significant and negative relationships were found between rates of N mineralization and the initial concentrations of N and Mg. The coefficients were r= -0.78 and r= -0.56 for N and Mg respectively ($p<0.05$ and <0.01 respectively, df=12). Significant correlations were also found between rates of P mineralization and the initial concentrations of N, P and P:N with coefficients (r) of -0.65 ($p<0.05$), -0.92 and -0.83 respectively ($p<0.001$, df=12). Rates of Ca mineralization was also significantly negatively correlated to the initial concentration of Mg (r=-0.66 $p<0.05$, n=14). The general trend was that of negative relationships between rates of mineralization and initial concentrations of N and P. The highest accumulation of N were in *Strephonema pseudocola* and *Cola verticillata* and P in *Oubanguia alata* which all had the lowest initial concentration of these elements (Table 5.8). No correlation was found between the rates of mineralization of K, Mg and Ca and their respective initial concentrations. These elements however showed net release during decomposition in both forests.

5.3.3.3 Element mobility

The mean net decrease in concentration of nutrients from all the decomposing leaf samples in each forest type showed that Mg was mineralized faster than the other elements (69.6% and 67.6% in LEM and HEM forests respectively). Meanwhile, N showed the highest increase in concentration (133.0% and 128.2% in LEM and HEM forests respectively) during the eight months period. The general mobility sequence observed in both forests was in the following descending order:

Mg > K > Ca > P > N.

K was loss rapidly within the first month and was followed by little or no change in concentration in both forests.

Based on the scores for the non-significant groupings among the species from the multiple comparisons of mineralization rates of the different nutrient elements, the species were also ranked for their overall rates of mineralization. The results showed that leaf samples of *Microberlinia bisulcata* were mineralized relatively faster in both forests and the least in *Tetraberlinia bifoliolata* and *Cola verticillata* were mineralized the slowest in the LEM and HEM forests respectively. The species were ranked in the following descending order in each forest:

LEM: *Microberlinia bisulcata* > *Berlinia bracteosa* > *Didelotia africana* > *Oubanguia alata* > *Strephonema pseudocola* > *Cola verticillata* > *Tetraberlinia bifoliolata.*

HEM: *Microberlinia bisulcata* > *Berlinia bracteosa* > *Oubanguia alata* > *Tetraberlinia bifoliolata* > *Didelotia africana* > *Strephonema pseudocola* > *Cola verticillata.*

5.4 DISCUSSION

5.4.1 Forest floor litter layer and turn-over rates.

Results from sampling the litter layer showed no significant difference in the amount of litter on the forest floor in the HEM forest compared to the LEM forest (Table 5.1). Litter input estimates for both forest types (chapter 3) were also not significantly different between both forest types. Looking at the different fractions of the litter layer, greater amounts of the small wood and reproductive were accumulated in the HEM forest. The small wood input in the LEM forest consisted of mostly small twigs and branches which were long dead and were already in advance stages of decomposition before being dropped. Since they were already colonized by decomposer organisms, the process of décomposition would have been expected to proceed even faster on the forest floor. In the HEM forest, the greater part of the small wood input comes from the 'physiological pruning' in the large legumes and will require longer periods to be colonized or acted upon by decomposer organisms. Similar situations were also found for the reproductive fractions. The large legumes (caesalpinioids) which are dominant in the HEM forest produce highly lignified pods which decompose very slowly and will tend to accumulate over the years on the forest floor.

The high spatial and temporal variation in the litter layer in both forests could be a function the variable litter input to the forest floor with the different fractions decomposing at different rates (Spain 1984, Vogt *et al.* 1986). The amount and proportion of the different fractions of the litter input are dependent on the phenological patterns of the different tree species. This is also dependent on the prevailing climatic 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 surpasses the rate of breakdown and results in net accumulation of litter. The rate of decomposition is highly reduced during this period as a result of the dry conditions which cause desiccation of the litter layer as the canopy cover is greatly reduced following leaf fall. The dry conditions

are, not favourable to the decomposer organisms. Luizão and Schubart (1987) reported lower mass loss in leaf samples from litterbags in the dry season. They recorded a half-life of 218 days for leaf samples in the dry season compared to 32 days in the wet season in central Amazon.

Turnover was very rapid in both forests within the first two months of the rainy season. Different reasons have put forth to explain this rapid breakdown of the accumulated litter. Swift *et al.* (1979) related this loss to the relatively high nutrients in the canopy leachates and available moisture which stimulated decomposition. Gosz (1984) also related the high rates of respiration in the F layer of the forest floor to the added supply of nutrients in the canopy leachates having a priming effect on the decomposition of the older organic matter. Additional nutrients also came from the nutrient-rich flowers and insect frass in the litter input during this period in both forest types.

The role of the macro/mesofauna in litter breakdown has been reported by many authors (Anderson and Ineson 1983, Anderson *et al.* 1983, Collins 1983, Seastedt 1984, Jones 1990, Blair *et al.* 1991, Burghouts *et al.* 1992). Though not investigated in the present study, it was observed that humus feeding termites were very active during this period gathering enough food that will serve them during the subsequent wet months. Aber (1979) estimated that 32% of the litter input in the Pasoh Forest Reserve in Peninsular Malaysia was removed by termites. Irmler and Furch (1979) estimated that 6% of the annual litter input in the inundated forests in Brazil were consumed by the cockroach (*Epilampra irmleri*). Nye (1961) in Ghana and Hopkins (1966) in Nigeria both attributed the rapid disappearance of litter on the forest floor to the activities of termites but gave no estimates as the population of termites were not determined. The role played by termites in litter breakdown was clearly shown in the rapid loss of leaf samples in the first decomposition experiment with the relatively larger mesh-size litterbags. These bags were laid-out on the onset of the first rain at the start of the wet season. Net accumulation of the reproductive fractions in the rainy season resulted from the profuse fruit fall during this period in some species such as *Irvingia gabunensis, Staudtia stipitata, Poga oleosa* and the immature pods from the large legumes in the HEM forest. These were rapidly decomposed as well.

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ORIGINAL

The amount of litter on the forest floor and turn-over coefficients in a range of tropical forests were summarized by Anderson *et al.* (1983) and Proctor *et al.* (1983) showing a range from 1.0 - 11.2 t ha^{-1} for litter layer and turnover coefficients between 0.9 to 3.8 for leaf litter and 0.6 to 3.3 for small litter. The estimates for both LEM and HEM forests were comparable to that reported for the other African tropical forests and were in the lower (litter layer) and upper (turn-over coefficients) range for other tropical forests. Results of the present study confirm previous reports by Anderson *et al.* (1983) that decomposition rates in West African forests appears to be generally higher than those of the New World and of the Far East (Table 5.17). Few reports are available on the turn-over rates of the reproductive fractions on the forest floor of most tropical forests. Swift *et al.* (1979) however classified this fraction as decomposing relatively faster compared to other fractions irrespective of the climatic conditions or rate at which decomposition proceeds. In the present study the reproductive fractions followed that trend in both forests despite the high amounts of lignified pods in the HEM forest. The turnover rate of the reproductive fractions recorded for Maraca Island by Scott *et al.* (1992) was comparatively lower.

The problems of standardized limits in size range for litter fractions (Proctor 1987) and the intervals between sampling of the forest litter layer (UNESCO 1978) should be considered when making comparisons with other studies. In the present study, organic matter below the size of 2 mm was considered as soil organic matter. Due to the high seasonality in litter input monthly k_l values were computed for the different fractions which were then summed to obtain the annual turnover coefficients. This approach when compared with the conventional method in which the annual estimates of litterfall and the mean litter on the forest floor are used (Olson 1963) showed an over-estimation of the turnover coefficients by 6 and 16% in the LEM and HEM forests respectively.

5.4.2 Mass loss in leaf litter confined in litterbags.

The litter on the forest floor consist of litter fractions at different stages of decomposition. The monitoring of fresh leaf litter through the process of decomposition provides an insight into the other regulating factors whose effects are generally masked when sampling the litter layer. This also provides the possibility of comparative assessment of the effects of microsites on rates of decomposition.

Results from the study showed that mass loss in leaf samples varied for the different species and between LEM and HEM forests for some species. This indicated the influence of litter quality and other local effects in both forests on the rates of decomposition. The leaf litter of the seven species varied in their initial nutrient concentrations. Possible relationships have been reported between rates of mass loss and the initial concentration of N (Tanner 1981, Melillo 1982); P (Tanner 1981, Meentemeyer and Berg 1986) and Ca (Upadhyay *et al.* 1989). No significant relationship was shown in the present study between the initial concentrations these nutrients and the respective rates of mass loss (k values) for the different litter types (species). The initial concentration of P in the leaf samples used by Meentemeyer and Berg (1986) ranged from 0.014-0.025% and were low compared to the leaf samples used in the present study (initial P concentration ranging from 0.04-0.11% for the leaf litter of the seven species). Tanner (1981) also observed an increase in rates of mass loss in leaf litter on addition of N (10% KNO_3) and P (10% NaH_2PO_4). The results of the present study seem to contradict these findings. *Didelotia africana* and *Tetraberlinia bifoliolata* which showed relatively slower rates of mass loss were at the upper margin for the range of initial concentrations of all the five nutrients been investigated. Khiewtam and Ramakrishnan (1993) also observed similar trends in *Engelhardtia spicata* which had the highest initial concentration of N and decomposed comparatively slower than the other species.

The leaf samples of *Didelotia africana, Tetraberlinia bifoliolata* and *Microberlinia bisulcata* (all ectomycorrhizal species) were thick and leathery indicating high amounts of structural constituents. Estimates of these recalcitrant fractions (1-A) from the double exponential model confirmed these high proportions in leaf samples of the

ectomycorrhizal species (55-74%). These organic (recalcitrant) fractions are known to retard the process of decomposition (Cromack 1973, Fogel and Cromack 1977, Aber and Melillo 1982, Kuiters 1990). It could be concluded that the relatively slower rates of mass loss in leaf litter of ectomycorrhizal species (with exception of *Berlinia bracteosa)* was as a result of their higher proportions of the recalcitrant structural constituents. These slower rates also result in the relatively higher accumulation of leaf litter on the forest floor in the HEM forest where they are the dominant species.

Gadgil and Gadgil (1971) attributed slower rates of decomposition to the effects of mycorrhizal fungi on the forest floor and in top layer of the soil. In the present study, the difference in rates of breakdown of leaf litter was marginal as leaves of *Oubanguia alata* decomposed faster in the HEM forest and leaves of *Didelotia africana* in the LEM forest. However some allelopathic effects at the level of the forest floor cannot be ruled out (Newman 1983, Rai and Tripathi 1984).

5.4.3 Rates of mineralization in leaf litter in both forest types.

Nutrient dynamics in decomposing leaf litter tend to follow three sequential phases: (i) an initial release phase predominated by leaching, (ii) net accumulation (immobilisation) phase (iii) net release phase (Gosz *et al.* 1973, Swift *et al.* 1979, Staaf and Berg 1982, Upadhyay and Singh 1989). Most of the nutrient elements examined in the present study showed at least one of these phases in the decomposing litter in both forests. The patterns however varied between the different species in each forest type and within the same species in both forest types. This reflects the influence of both the litter quality and local site characteristics on the rates of nutrient mineralization (Vitousek *et al.* 1994).

Looking at the general trends of the five nutrient elements, there was net accumulation of N and P and net release of K, Mg and Ca in both forests though at varying magnitudes. Mineralization of nutrient elements were more or less similar in both forests for N, P and K and differed for Mg and Ca. N accumulation in decomposing litter has been observed in most decomposition studies in temperate forests (Gosz *et al.* 1973, Berg and Staaf 1981, Blair *et al.* 1991, Van Vuuren *et al.* 1992, Rustad 1994) and in a few tropical

forests (Songwe 1984, Cuevas and Medina 1988). In some tropical forests N has been reported to be released at rates similar to the loss of leaf biomass (Berhard-Reversat 1972, Swift *et al.* 1981) and in some cases N was 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. These includes addition of N in one or more of the following: N fixation (Woods 1974); absorption of atmospheric ammonia; contamination from insect frass, green litter and throughfall; microbial translocation and or immobilization (Gosz *et al.* 1973). P was generally released or conserved with little or no addition from the decomposing litter in most of the tropical studied reported (Swift *et al.* 1981 Anderson *et al.* 1983 Upadhyay and Singh 1989).

In the present study, net release of N occurred only in *Berlinia bracteosa* which had the highest initial concentration of N. It was also observed that the highest rates of immobilization were in the litter samples of *Cola verticillata* and *Strephonema pseudocola* which also had the lowest initial concentrations of N. A similar trend was also seen for P mineralization. This negative relationship indicated that the initial concentrations of the different litter types were a more important regulating factor in N and P mineralization than local site characteristics. The significantly lower rates of N accumulation in *Oubanguia alata, Tetraberlinia bifoliolata* and *Microberlinia bisulcata* and the relatively higher rate of N release in *Berlinia bracteosa* in the HEM forest is an indication of minor local differences between the two forest types. Net release of P occurred only in litter samples of the ectomycorrhizal species which had relatively high initial concentrations P. This shows that the turn-over of P is relatively rapid in the HEM forests where they dominate the leaf litter input to the forest floor. Similar situations have been reported for leaf litter in Bakundu Forest Reserve by Songwe (1984). N was released from the decomposing leaf samples of *Celtis zenkeri* and *Cola lepidota* both having initial N content of 1.73 and 1.4% respectively compared to 0.95 for *Desbordesia glaucescens* which showed the highest initial N accumulation. These species were comparatively rich in P but still showed net P accumulation.

Mineralization of K was very rapid in all the species in both forests with more than 60% of its initial concentration released within one month on the forest floor. K is a highly mobile and readily leached element (Swift *et al.* 1981, Parker 1983). Korup National Park has one of the highest rainfalls recorded for lowland tropical forests (annual rainfall > 5000 mm). This high precipitation will enhance rapid release of K through leaching.

Mineralization of Mg and Ca in the decomposing leaf litter proceeded rapidly irrespective of their initial concentrations. Mg showed the fastest rate of net release among the five nutrient elements investigated. Trends in the mineralization of Mg and Ca in Korup National Park were similar to the those reported in the Terra Firme forest in the Amazon by Cuevas and Medina (1988). They observed faster release of Ca and Mg from the litter when in contact with fine roots from the root mat and concluded that there must be a nutrient release mechanism mediated by these roots or their associated microorganisms. The litterbags in the HEM forests were invaded by numerous fine roots which characterized the forest floor in this forest. Root growth is affected by Mg deficiency leading to an increase in root/shoot ratio (Marschner 1986). The results of Cuevas and Medina (1988) also showed strong and positive correlations between fine root growth and the Mg and Ca concentrations of litter. Trees tend to produce excessive roots to explore wider areas in search of nutrients. The comparatively rapid release of Mg and Ca may be attributed to their higher requirement in the HEM forest by the large legumes for the development of extensive fine root systems which scavenge for nutrients on the forest floor (Stark and Jordan 1978, Jordan and Escalante 1980, Khiewtam and Ramakrishnan 1993). A net accumulation Ca (51.9%) and a slight release of Mg (36%) probably through leaching was observed from leaf samples of *Microberlinia bisulcata* in an extra litterbag that was left suspended on a branch near to the replicate block in plot 3A during the entire eight months period. No firm conclusion can be drawn from this single sample but it shows an enhanced release of Ca at the soil level surface.

Results of the present study seem not to show a clear cut impact of the role played by the ectomycorrhizas in the mineralization of N and P in the decomposing litter in the HEM forest where they are dominant in association with the large legumes. With the rapid loss of Mg and Ca in the HEM forest from the decomposing leaf litter, more investigations

are needed to ascertain whether they play any role in the uptake of either Mg or Ca. So far in the literature, much of the focus has been on N and P. Looking at the overall rates of mineralization of five nutrient elements in the decomposing litter samples, leaf litter from *Microberlinia bisulcata* showed a relatively faster release in both the LEM and HEM forests. This species alone contributes approximately 37.8 % of the annual leaf litter input to the forest floor in the HEM forest (Table 3.9). This is an indication of rapid turnover of nutrients from decomposing litter in the HEM forest.

CHAPTER SIX

NUTRIENT INPUT

IN

THROUGHFALL AND STEMFLOW

6.1 INTRODUCTION

Rainfall is another important pathway for nutrient input to the forest ecosystems (Nye 1961, Likens *et al.* 1977, Parker 1983, Bruijnzeel 1989). Regardless of the amount of dissolved nutrients in rainfall, significant amounts are added and transferred from various plant parts to the forest floor as the rainwater passes through the canopy (Easton *et al.* 1973, Manokaran 1979, 1980, Prebble and Stirk 1980, Lewis 1981, Edwards 1982). These nutrients are transferred to the forest floor in throughfall and stemflow (together referred to as total rain water by Parker 1983). Throughfall refers to that part of gross rainfall which passes through the forest canopy either directly in gaps or interacting with the foliage before reaching the forest floor (Helvey and Patric 1965, Carlisle *et al.* 1966, Lee 1980, Parker 1983, Lloyd and Marques 1988, Bruijnzeel 1989). Stemflow is that which is funnelled down the trunk of the trees to the forest floor (Carlisle *et al.* 1967, Easton *et al.* 1973, Jordan 1978, Manokaran 1980, Herwitz 1986).

Fluxes of nutrients in throughfall and stemflow are very rapid as they are in forms which can readily be taken up by the plants. The immediate availability of nutrients plays an important role in the dynamics of various ecosystem processes such as the priming of decomposition processes on the forest floor (Gosz 1984). Throughfall and stemflow are both determinants of interception loss which is an important parameter in water balance studies (Gash and Morton 1978, Lee 1980, Lloyd and Marques 1988, Bruijnzeel 1991).

It is widely acknowledged that the alteration of the composition of rainwater results from washoff of deposited particles and gases, uptake and release of substances by the plants and their associated epiphytes (Wittwer and Teubner 1959, Carlisle *et al.* 1966, Lang *et al.* 1976, Pike 1978, Lewis 1981, Lovett and Lindberg 1984).

The amount of throughfall and stemflow, as well as the nutrients therein in most forests, are reported to be dependent on many factors, the most important ones which include: the

intensity and duration of gross rainfall (Easton *et al.* 1973, Lloyd and Marques 1988), forest structure as a function of species composition and form (Kimmins 1973, Vis 1985, Herwitz 1986) and soil fertility (Tsutsumi and Nishitani 1984). These factors are highly variable in time and space and they affect throughfall and stemflow to the same order.

Results of most interception studies in tropical forests have been reported to be highly diverse and differ in their reliability (Clarke 1987, Lloyd and Marques 1988, Bruijnzeel 1989). Lloyd and Marques (1988) attributed the high variability to the use of improper sampling designs which did not take full account of the high spatial and sometimes temporal heterogeneity of the canopy in tropical forests. Much attention has been given to the variability in throughfall with recommendations for a wider catchment under the forest canopy through random relocations of the collectors during the sampling period (Kimmins 1973, Lloyd and Marques 1988). Stemflow studies have received far less attention to that respect.

Korup National Park has one of the highest rainfalls recorded (5460 mm) for lowland tropical forests. It is expected that this will constitute an important pathway for the transfer of nutrients to the forest floor. This chapter focuses on:

(i) the quantification of inputs of N, P, K, Mg and Ca in gross rainfall and their transfer to the forest floor in throughfall and stemflow in LEM and HEM forests.

(ii) examination of the different factors which affect volume and nutrient enhancement in throughfall and stemflow in both LEM and HEM forests.

An elaborate sampling design was adopted to provide estimates within the required confidence limits.

6.2 Materials and methods.

6.2.1 Sample plot selection and layout.

Two blocks of 50 m × 50 m (0.25 ha) each were demarcated in LEM and HEM forests. Block 1 was located in the LEM forest, south of plot 3A and 100 m away from transect P. Block 2 was located in the HEM forest, south of plot 15A and 50 m away from the transect P. The aim was to locate the blocks quite close to the plots within which the other aspects of nutrient studies were in progress. These blocks were free of any wind damage and located away from transect P in order to prevent any interference with collectors from passersby. The square shape and size of the blocks allowed the inclusion of whole crowns of several dominant species, some of which reached approximately 25 m in diameter.

Within each block, a complete inventory was carried out on all the trees above 5 cm diameter at breast height (dbh). A total of 303 and 331 trees were enumerated in blocks 1 and 2 in LEM and HEM forest respectively. The trees were classified into twenty-two diameter classes (5 cm intervals). The number of sample trees required for mounting the stemflow collars that will yield stemflow volumes within an acceptable standard error was computed using the equation of Freese (1962) where:

$$n = \frac{t^2 * SD^2}{E^2}$$

where: t = the student's t value for a desired confidence interval at 95% probability level (usually taken to be 2),

SD = the estimated standard deviation, and

E = the acceptable standard error level (%).

Table 6.1: Size class frequency distribution of all trees above 5 cm at breast height and the number of sample trees selected for stemflow studies in blocks 1 and 2 (0.25 ha each) in LEM and HEM forests respectively, Korup National Park, Mundemba, Cameroon.

	LEM		HEM	
Diameter classes (cm)	Frequency	No of sample trees	Frequency	No of sample trees
5 - 9.9	183	6	212	7
10 - 14.9	48	4	45	3
15 - 19.9	26	2	22	3
20 - 24.9	15	1	15	1
25 - 29.9	8	1	11	2
30 - 34.9	2	0	9	1
35 - 39.9	7	1	4	0
40 - 44.9	4	0	4	1
45 - 49.9	2	0	0	0
50 - 54.9	0	0	1	0
55 - 59.9	3	1	2	1
60 - 64.9	1	0	1	0
65 - 69.9	2	0	1	0
70 - 74.9	0	0	0	0
75 - 79.9	0	0	0	0
80 - 84.9	1	1	2	0
85 - 89.9	0	0	0	0
90 - 94.9	0	0	1	1
95 - 99.9	0	0	1	0
100 - 104.9	0	0	0	0
105 - 109.9	1	1	0	0
<110	0	0	0	0
Total	303	18	331	20

Based on the estimated standard deviation of the diameter distribution and a desired sampling error of 5.0%, sample sizes of 18 and 20 trees were obtained for both LEM and HEM forests respectively. This gave a sampling fraction of approximately 6% in both forests. The sample trees for stemflow collars were then selected randomly and more or less proportionally for each diameter class in both blocks. The frequency distribution and number of sample trees for stemflow studies in each diameter class are presented in Table 6.1. A full description of these sample trees including the species, diameter at breast height (dbh), crown position, branching habit, bark texture and nature of latex (if it exists) are given in appendix 2a and 2b.

Stemflow collection.

The design of the stemflow collar used in both forests was similar to that of Herwitz (1986). This consisted of a 25 mm diameter high quality rubber hose slit longitudinally and sealed to the trunk in an upward spiral with U-shaped steel clips and an inert silicon sealant (SILASTIC®). The unslit portion directed the stemflow into a black 50 l jerrycan (Plate 6.2). The collars were mounted at the breast height position (1.3 m above the forest floor). For trees with buttresses or any malformation at that position, the collar was mounted 0.3 m above that point. The spirals were steep enough to allow rapid flow of the water once it entered into the collar. The collars were checked regularly for leakages and all debris trapped therein removed.

Throughfall collection.

The throughfall collector consisted of a steep-angle polyethylene funnel (20 cm in diameter) mounted on 16 l plastic buckets standing on the forest floor (Plate 6.1). The funnels were held upright by stoppers from the solidified inert silicon sealant at the centre of the lids of the buckets. The rim of the funnels were 0.7 m above the forest floor to prevent water droplets and soil particles from splashing in as large drops hit the forest floor. The steep angle of the collecting funnels also minimized 'splash-outs' from the funnels during rain storms (Lloyd and Marques 1988). In the neck of each funnel was placed a 2 mm nylon gauze which prevented litter and debris from entering into the collectors. These nylon gauzes were cleaned regularly to avoid any blockage.

Plate 6.1: **16 l plastic bucket and plastic funnel used for throughfall collection.**

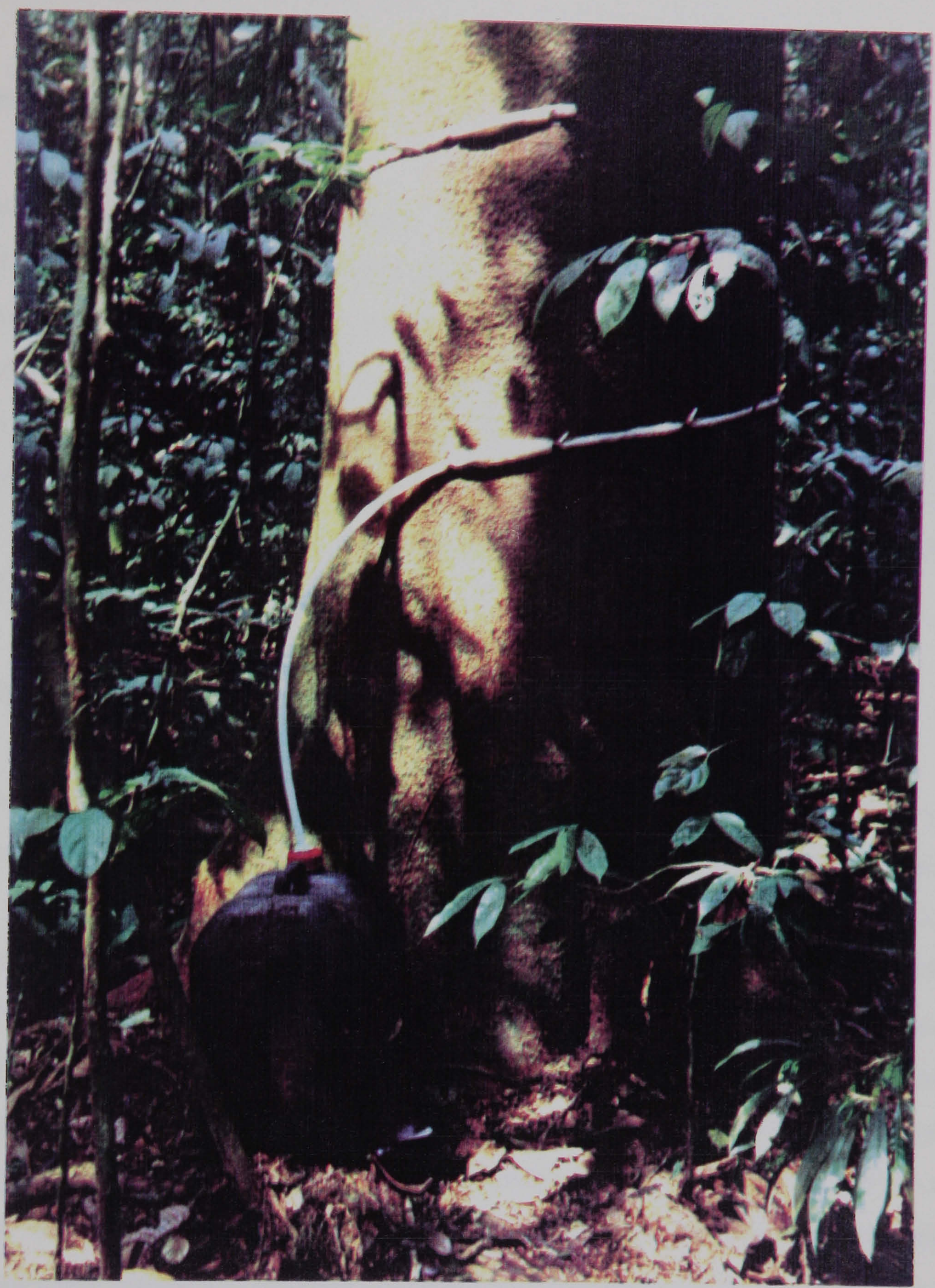

Plate 6.2: Spiral collar and 50 l storage can for stemflow collection.

Ten throughfall collectors were laid-out in each block in systematic pattern to sample throughfall. Each block was subdivided into five strips (5 m × 50 m) with nylon strings in an E-W direction. Two throughfall collectors were located within each strip and were randomly relocated though restricted within the same strip after each measurement (Kimmins 1973, Lloyd and Marques 1988).

Gross rainfall collection.

Gross rainfall was sampled by a similar steep angle polyethylene funnel (20 cm in diameter) mounted on a 3 m wooden pole and fixed at the top of crownless tree approximately 35 m tall. The crown had been snapped off by another falling tree. The funnel was connected by a long 20 mm diameter rubber hose into a collecting bucket placed on the forest floor. The gross rainfall collector was placed between both blocks and around the science camp where some trees had been felled. This area was relatively clear and with less chance of contamination from splashes of rain drops from neighbouring crown foliage.

6.2.2 Collection preservation and storage of samples.

Throughfall, stemflow and gross rainfall were measured from February 1992 to January 1993. The three variables were all measured during each sampling occasion the duration of which varied with the different rainfall intensities. Initially, volume measurements were taken for all the collectors within the middle and end of month from March 1992 to June 1992. During this period, the rainfall intensity was relatively low and the chances of the collectors overflowing was very small. However the number of measurements were increased to 6-7 occasions from July to October 1992 following the increase in rainfall intensity and duration which resulted in substantial amounts of both stemflow and throughfall. This necessitated more frequent measurements and inspection of the collars for blockages and leakages. This then dropped to 4 occasions in November 1992. In December 1992 and January 1993, rainfall amounts had dropped drastically and could neither generate throughfall nor stemflow in both forests.

Stemflow and throughfall were measured using a 10 l graduated bucket (0.5 l graduation) and the gross rainfall a 500 ml measuring cylinder (5 ml graduation). The funnels, nylon mesh, collecting buckets and jerrycans were thoroughly cleaned after each measurement with the remaining water samples. Due to the remoteness of the plots it was not possible for deionized water to be carried in for such cleaning purposes.

Subsamples of 30 ml were collected from each collector in the middle and end of months in 30 ml polyethylene bottles. These were taken to the Forest Research Station Kumba and kept below 3°C after addition of five drops of chloroform to each sample. The addition of chloroform to the samples was a preservative technique to minimize microbial degradation in storage. In the laboratory, the two samples collected for a particular month and collector were bulked and a final sub-sample of 30 ml stored for chemical analysis. These were stored below 3°C in polyethylene bottles with very tight caps to prevent volatilization and diffusion of gases. Photochemical changes were also minimized by storing these bottles in black polythene bags.

In March 1993, all the stored water samples were packed in a well designed box which reduced the chances of any damage to the bottles and air-freighted to the University of Stirling, where they were stored in a cold room below 3°C prior to chemical analysis.

6.2.3 Chemical analysis.

Sub-samples were bulked for the months of March/April, June/July and September/October of stemflow samples of three of each of the following category of trees; large, medium and small trees in each forest type; throughfall samples for each forest type; and gross rainfall samples. 30 ml of each bulked sample were sent to the Institute of Hydrology, Wallingford, UK for cation and anion analysis (courtesy of C. Neal). The results obtained were used as references in comparing the values from the chemical analysis of the rest of the individual samples at the University of Stirling.

The ten throughfall samples collected for each month and block were bulked and 25 ml of the composite samples acid digested. Stemflow samples of the individual trees were

bulked for the months of: March/April, June/July, September/October and May/August/November and 25 ml of each composite sample was also acid digested. 25 ml of each composite sample was acid digested in clean (acid washed) digestion tubes on a Tecam DG-1 block digestor using 1.0 ml of the digestion mixture (same mixture used for plant material in chapter 4.2). These were in batches of forty samples (thirty-eight composite samples, one reagent blank and one phosphate control) per run. The block digestor was initially raised to 100°C and the samples were gradually concentrated by heating for three hours. The temperature was then raised to 250°C and the concentrated samples digested for three hours (to white fume stage). The samples were being checked constantly to avoid dry-outs. Glass beads were put in each tube to reduce frothing.

The digested samples were allowed to cool for two hours and then filtered through a Whatman filter paper (N° 44) into a volumetric flask. The digestion tubes were thoroughly rinsed with deionized water and also filtered into the flask. The filter paper was then rinsed well to make up the solution to 20 ml which was shaken and stored in labelled plastic bottles for elemental analysis. Each sample was analyzed for total N and P, K, Mg and Ca following the procedures described in chapter 4.2.4 (for litter samples). The detection range was 0 - 1.0 mg/l for N and P as their concentrations were quite low in the samples.

6.2.4 Data analysis

The amount of rainfall collected in the standard rainfall gauge (0.0127 m^2 collecting area) at Bulu weather station (PAMOL Ndian), located approximately 10 km away from the blocks was extrapolated over the entire block (0.25 ha). This was converted to litres (since throughfall and stemflow were measured in litres) by multiplying with 31.83. Using the standard rainfall measure, 31.83 l of rainwater is equivalent to 1 mm depth of rainfall (Meteorological Office 1982, Rodda 1985). Throughfall was also estimated for the entire block in each forest and corrected for stem basal area. The total basal areas were 8.2 m^2 and 8.9 m^2, representing 0.33% and 0.36% of the total area of blocks 1 and 2 in LEM and HEM forests respectively. The samples trees were grouped into size diameter classes (5-10, 10-15, 15-25, 25-40, 40-65 and 65 cm dbh and above). Mean

stemflow volumes were calculated for these respective diameter classes which were then multiplied by the number of trees in those respective size classes in each block. These were all summed to provide estimates of the total stemflow for both blocks. These were used to calculate the proportions of throughfall and stemflow to gross rainfall and the interception loss in both forests.

Throughfall variability in each forest type was examined by expressing the throughfall catch of the individual collectors at each sample point as per cent gross rainfall recorded for the same duration. Mann-Whitney U test (adjusted for ties as sample sizes were not equal) was carried out to compare these relative proportions of throughfall in both forests as their distributions were positively skewed. Paired-wise t testing was also carried out between the monthly estimates of throughfall (mm) in LEM and HEM forests.
Stemflow from each sample tree was summed over the entire period and the total volume used in computing the funnelling ratio of each of the trees. These were calculated using the equation of Herwitz (1986) whereby:

$$F = \frac{V}{(BG)}$$

where F = funnelling ratio, V = stemflow volume (l), B = basal area (m^2) and

G = the depth equivalent of rainfall (mm).

These ratios were used to compare the magnitude of stemflow in the different trees and individuals of the same species.

Three form attributes of the sample trees were investigated in relation to their respective stemflow amounts over the entire period. These included branching angle, crown position in relation to general canopy level and basal area. The branching angles were classified in a nominal scale from 1-4 in the following increasing order: 1-obtuse (>90° from the vertical), 2-perpendicular (75°≤90°), 3-oblique (45°≤75°), 4-very oblique (<45°). The crown positions of the trees in relation to the canopy level were also scaled from 1-4 in

the following increasing order: 1-understorey, 2-lower canopy, 3-upper canopy and 4-emergents. A principal component analysis (PCA) was carried out between these form attributes in each forest type. Rank correlations were also carried out between the individual stemflow volume, funnelling ratio and the scores of the of principal axis 1 and 2 of the principal components which accounted for more than 90% of the variability in the sample trees (on the basis of the three form attributes used) in both forests.

The annual inputs of N, P, K, Mg and Ca in gross rainfall, throughfall and stemflow for both forests were obtained by multiplying their respective weighted mean concentrations and estimated volumes for each block. These were then expressed per unit area of the forest. Net nutrient transfer from plant parts were obtained by subtracting the inputs in gross rain from the sum of throughfall and stemflow inputs. Stemflow inputs of the each sample tree were summed over the entire period and expressed per unit basal area. These were then used in comparing nutrient inputs of the different species and of individuals of the species.

6.3 RESULTS

6.3.1 Gross rainfall.

The gross rainfall recorded within the park for the period February 1992 to January 1993 was 3704.6 mm. This was however an lower than the mean annual rainfall record of about 5000 mm for Mundemba (Gartlan *et al.* 1986). Gross annual rainfall recorded for the study period at Bulu weather station (PAMOL) located approximately 10 km away from the research plots was 5368 mm. Rainfall was however recorded during each month of the study period though less frequently in the dry season. Rainfall was quite low in February 1992 (dry season) and increased sharply from April to the peak in July 1992. This was then followed by a gradual drop in rainfall amounts until the dry season set in December 1992. In all, a total of 204 rainy days were recorded and with the highest number of rainy days in August 1992 (Table 6.2). This, however, did not coincide with the month with the highest rainfall indicating different patterns in amount and frequency distribution patterns of rainfall in Korup National Park.

6.3.2 Throughfall

The total amounts of throughfall recorded from February 1992 to January 1993 were 5187.0 mm and 4961.7 mm in LEM and HEM forests respectively. These constituted 96.6% and 92.4% of gross rainfall in LEM and HEM forests respectively (Table 6.2). Rainfall was quite low in the months February 1992, December 1992 and January 1993 and was just enough to wet the forest canopy with no generation of throughfall (Table 6.2). There were considerable spatial and temporal variations in the amount of throughfall recorded in both forests. The relocations of the throughfall collectors resulted in 410 and 400 individual sample points in both LEM and HEM forests respectively. The individual throughfall catch at each sample point was expressed as a percentage of gross rainfall, the frequency distribution of which is shown in Figure 6.1. These ranged from 0% (in the dry season with little or no rain) to 810% of gross rainfall in both forests with medians of 94.2% and 105.3% in the LEM and HEM forests respectively. In all, 41% and 49%

of these individual points recorded throughfall greater than gross rainfall and 9% and 12% were more than twice the gross rainfall in LEM and HEM forests respectively. Comparison of these percent point records showed significant differences between both forests in rainfall interception ($p<0.05$).

The monthly throughfall ranged from 78% to 142% and 63% to 141% of the monthly gross rainfall in LEM and HEM forests respectively. The amount of throughfall recorded were strongly correlated with gross rainfall in both forests ($r=0.91$ and 0.90 for LEM and HEM forests respectively, $p<0.001$, $n=12$). A pair-wise comparison of the monthly amounts of throughfall also showed significant differences between both forest types ($t=2.92$, $P<0.05$, $n=12$).

6.3.3 Stemflow

Total stemflow (expressed in mm of gross rainfall) estimated for the period from February 1992 to January 1993 was 79.4 mm and 120 mm in LEM and HEM forests respectively. Stemflow was relatively negligible and constituted 1.5% and 2.2% of the annual gross rainfall in LEM and HEM forests respectively. The monthly estimates of total stemflow (Table 6.2) were significantly and positively correlated with the respective monthly gross rainfall ($r=0.91$ and 0.94 for LEM and HEM forests respectively, $p<0.001$, $n=12$). The amount of rainfall in the months of February 1992, December 1992 and January 1993 were below the threshold limit expected to generate stemflow. The highest monthly amount of stemflow for both forests was recorded in August 1992 which had the highest number of rainy days for the entire sampling period (Table 6.2). Variations in total stemflow of the individual species were relatively higher in the LEM forest compared to HEM forest (coefficient of variation of 73% and 65% for LEM and HEM forests respectively). Pairwise comparisons of the monthly stemflow estimates showed significant differences between both forests in enhancing the flow of rainwater to the forest floor along the tree trunk.

The high variability in stemflow enhancement among the different trees was reflected in the their respective funnelling ratios (F). These ratios ranged from 0.02 (for *Strephonema*

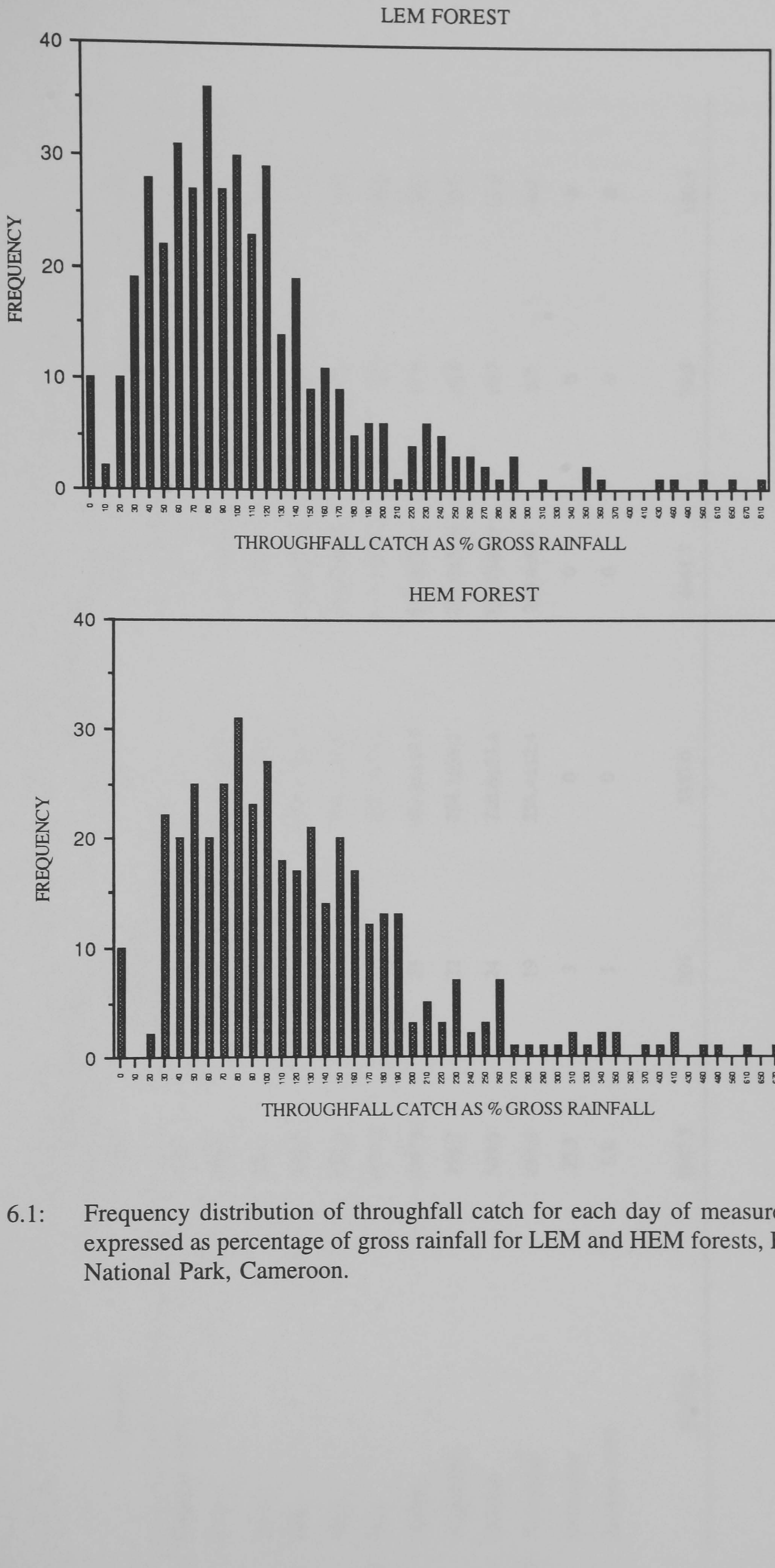

Figure 6.1: Frequency distribution of throughfall catch for each day of measurement expressed as percentage of gross rainfall for LEM and HEM forests, Korup National Park, Cameroon.

Table 6.2: Monthly records (mm) of gross rainfall, throughfall and stemflow from February 1992 to January 1993 in LEM and HEM forests, Korup National Park, Mundemba, Cameroon. Throughfall and stemflow volumes are expressed in depth equivalence of gross rainfall, (means of throughfall ± SE, n=10). Stemflow values are for the estimated total volume for each block in LEM and HEM forest respectively.

Months	Gross rainfall (mm)		Throughfall (mm)		Stemflow (mm)	
	Amount	No of rainy days	LEM	HEM	LEM	HEM
February 1992	1.8	1	0	0	0	0
March	168.5	15	153.7±14.6	113.9±11.4	1.9	1.6
April	226.7	19	230.1±12.7	176.3±10.2	2.8	2.7
May	339.7	20	266.1±14.9	214.8±15.6	3.7	3.4
June	830.6	25	680.1±32.8	653.4±36.6	8.9	14.2
July	1197.2	26	1091.3±71.0	1165.5±89.1	15.0	26.5
August	1047.6	29	986.0±112.9	918.5±75.1	17.8	28.2
September	750.7	22	794.7±58.2	754.0±35.6	14.9	23.2
October	509.0	24	726.6±33.4	719.9±29.9	10.7	15.6
November	254.6	19	258.4±12.4	245.4±9.9	3.7	4.9
December	35.3	3	0	0	0	0
January 1993	5.8	1	0	0	0	0
TOTAL	5367.5	204	5187.0	4961.7	79.5	120.3

Table 6.3: Principal component analysis on three form attributes of the sample trees, the correlations (Spearman's rank correlations) between principal axis 1 and 2, the individual stemflow volumes recorded between March 1992 and November 1992 and their respective funnelling ratios in LEM and HEM forests, Korup National Park, Mundemba, Cameroon.

	principal component axis	
	1	2
LEM		
Eigenvalue	1.75	0.98
Proportion	0.58	0.33
Correlation coefficient (r_s)		
stemflow volume	0.30	0.54*
Funnelling ratio (F)	0.72**	0.06
HEM		
Eigenvalue	1.96	0.84
Proportion	0.65	0.28
Correlation coefficient (r_s)		
Stemflow volume	-0.49*	-0.44*
Funnelling ratio	-0.41*	-0.46*

* $p \leq 0.05$ ** $p \leq 0.01$

pseudocola) to 11.8 (for *Cola semecarpophylla*) in LEM forest and from 0.14 (for *Cola rostrata*) to 13.5 (for *Strombosia glaucescens*) in the HEM forest. The funnelling ratio (F) relates stemflow volume to the expected volume from a raingauge with a collecting area equivalent to the trunk basal area (Hertwitz 1986). Trees with ratios exceeding unity indicated that rain water funnelling occurred. In all 67% of the sample trees in LEM forest had funnelling ratios greater than unity and 60% in the HEM forest.

The results of the principal component analysis (PCA) of basal area, branching angle and crown position in relation to the general forest canopy showed that 91% and 93% of the variability among the sample trees (for the three form attributes only) are explained in principal axis 1 and 2 (Table 6.3). Total stemflow of the individual trees were significantly and positively correlated with principal axis 2 and the funnelling ratios with axis 1 in LEM forest (Table 6.3). The reverse was however observed in the HEM forest where the stemflow volume and funnelling ratios were significantly and negatively correlated with both principal axis 1 and 2 (Table 6.3). This parallel trend again reflects the differences between the two forests in stemflow enhancement.

The estimated interception losses in both forests were 1.6% and 5.4% in the LEM and HEM forests respectively.

6.3.4 Nutrient concentration and fluxes

The concentration of the various elements in gross rainfall, throughfall and stemflow fluctuated through the year following the different amounts of incident rainfall. The annual volumetric weighted mean concentration of N, P, K, Mg and Ca in gross rainfall collected above the forest canopy are presented in Table 6.4. The concentrations of these nutrient elements in gross rainfall were in the following descending order:

$$Ca > K > Mg > N > P.$$

The weighted concentration of these nutrient elements were considerably higher in throughfall (Table 6.5) and stemflow (Table 6.6) compared to gross rainfall in both

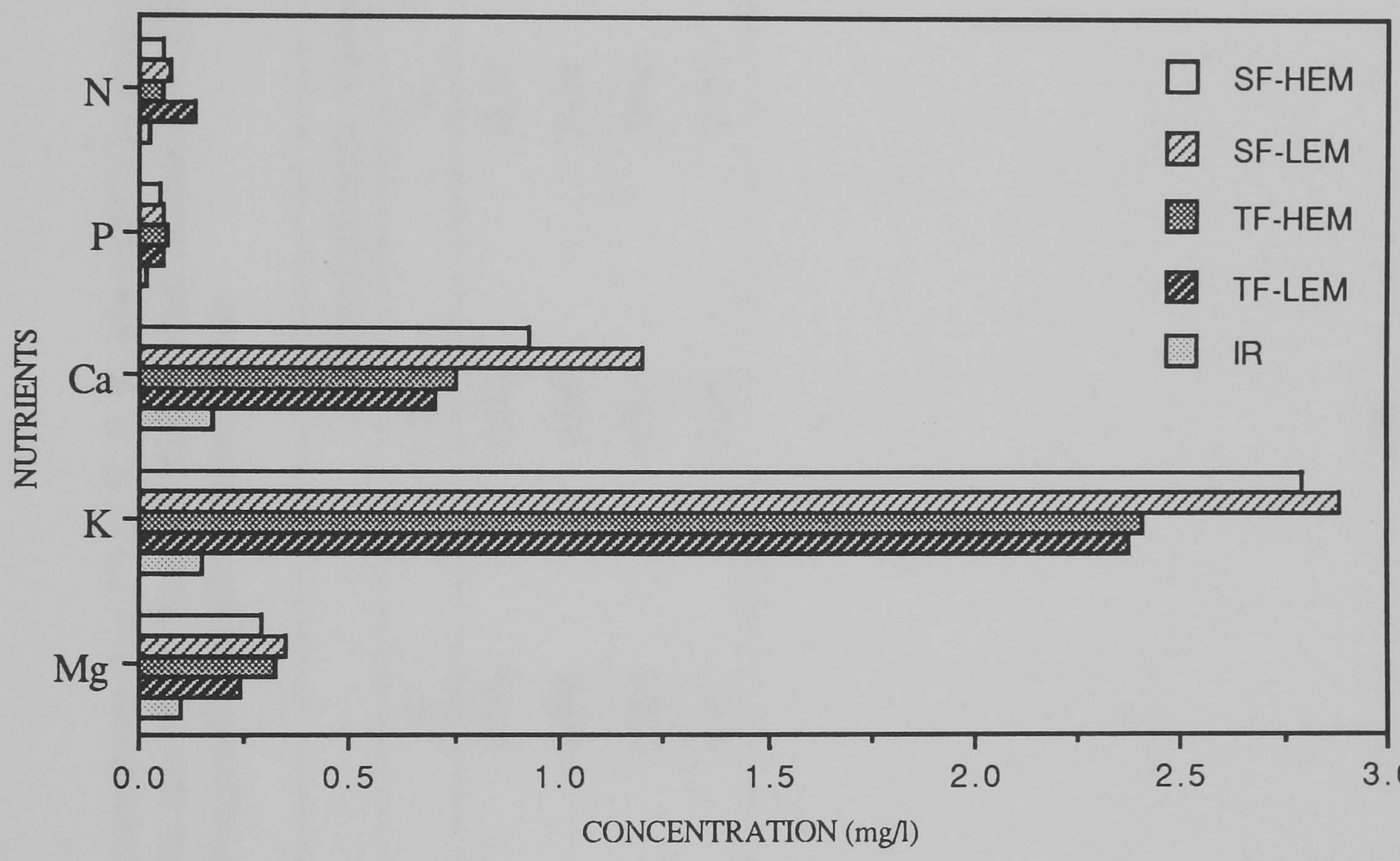

Figure 6.2: Weighed mean concentrations (mg l^{-1}) of the nutrient elements in gross rainfall (IR), throughfall (TF) and stemflow (SF) samples collected in LEM and HEM forests, Korup National Park, Cameroon.

Table 6.4: Volumetric weighted mean concentrations (mg l^{-1}) of N, P, K, Mg and Ca in gross rainfall samples collected from February 1992 to January 1993 above the forest canopy in Korup National Park Mundemba, Cameroon. The arithmetic mean, minimum and maximum values are for the unweighted monthly concentrations.

	Nutrient element concentration (mg l^{-1})				
	N	P	K	Mg	Ca
Volumetric weighted mean	0.03	0.02	0.15	0.10	0.17
Arithmetic mean	0.04	0.03	0.29	0.13	0.52
Minimum	0.001	0.001	0.01	0.03	0.01
Maximum	0.07	0.08	0.79	0.34	2.50

Table 6.5: Volumetric weighted mean concentrations (mg l^{-1}) of N, P, K, Mg and Ca in throughfall samples collected from February 1992 to January 1993 in LEM and HEM forests Korup National Park, Mundemba, Cameroon. Arithmetic means, minimum and maximum values are for the monthly composite samples.

	Forest type	Nutrient element concentration (mg l^{-1})				
		N	P	K	Mg	Ca
Volumetric weighted mean	LEM	0.13	0.06	2.37	0.34	0.70
	HEM	0.06	0.07	2.41	0.32	0.75
Arithmetic mean	LEM	0.11	0.10	3.73	0.37	1.14
	HEM	0.71	0.11	4.14	0.45	1.14
Minimum	LEM	0.04	0.22	1.10	0.13	0.20
	HEM	0.04	0.03	1.23	0.18	0.43
Maximum	LEM	0.44	0.45	12.5	1.16	3.54
	HEM	0.13	0.33	13.4	1.18	3.66

Table 6.6: Volumetric weighted mean concentrations (mg l^{-1}) of N ,P, K, Mg and Ca in stemflow samples collected from February 1992 to January 1993 in LEM and HEM forests, Korup National Park, Mundemba, Cameroon. The arithmetic, means minimum and maximum values are for the four composite samples of each sample tree.

		Nutrient element concentration (mg l^{-1})				
	Forest type	N	P	K	Mg	Ca
Volumetric weighted mean	LEM	0.07	0.06	2.88	0.34	1.20
	HEM	0.06	0.05	2.78	0.29	0.93
Arithmetic mean	LEM	0.09	0.11	3.98	0.50	1.58
	HEM	0.11	0.11	5.07	0.42	1.51
Minimum	LEM	0.01	0.001	0.13	0.01	0.19
	HEM	0.001	0.001	0.06	0.01	0.20
Maximum	LEM	0.86	1.35	14.2	3.21	9.10
	HEM	1.26	0.78	61.6	1.70	10.4

forests. The weighted concentrations of these elements in throughfall and stemflow were in the following descending order:

$$K > Ca > Mg > N > P.$$

The highest concentration was recorded for K in throughfall and stemflow in LEM and HEM forests and differed from the ranking observed in gross rainfall. The weighted concentration of P was however higher than N in throughfall in the LEM forest. The concentration of these nutrient elements showed little or no differences in both throughfall and stemflow between LEM and HEM forests (with the exception of N in throughfall in LEM forest which was slightly higher). The weighted concentrations of K in both throughfall and stemflow were 16-20 fold that of gross rainfall, while Ca was 4-7 fold and Mg 3-3.5 fold greater as well. The difference was however considerably lower for N and P indicating low leachability of these two elements (Figure 6.2).

The annual input estimates of N, P, K, Mg and Ca to the forest floor in both forests are presented in Table 6.7. Considerable amounts of Ca, Mg and P were brought into the forest canopy in gross rainfall (24-45% of total input to the forest floor). The highest amount of nutrient input in both forests were K and Ca with high proportions (94% and 75% of K and Ca respectively) resulting from the interactions of rainwater with plant parts as it passed through the canopy to the forest floor (Table 6.7). A substantial amount of N was also removed from the canopy in the LEM forest (Table 6.7). This was approximately 51% of the total input of N to the forest floor in the LEM forest.

Stemflow inputs also followed patterns of rainfall amounts with higher amounts being washed down the trunks in June and July 1992. High intra-specific and inter-specific differences were observed for the different trees in both forests. The high inter-specific difference can partly be explained by the differences in stemflow volume. The highest variations were in N and Ca in LEM forest (coefficients of variation of 158% and 129% respectively) and K and Mg in the HEM forest (coefficients of variation of 113% and 98% respectively). The variation in input from the different trees were relatively lower in the HEM forest for all the nutrients (coefficients of variation ranging from 70-113%) compared to the LEM forest (coefficient of variation ranging from 89-159%). Typical

Table 6.7: Annual estimates of nutrient fluxes (kg ha^{-1}) in gross rainfall, throughfall and stemflow in LEM and HEM forests, Korup National Park, Mundemba, Cameroon. Net rainfall loading is the difference in nutrient inputs between throughfall + stemflow and gross rainfall.

		Nutrient fluxes (kg ha^{-1})				
	Forest type	N	P	K	Mg	Ca
Gross rainfall		1.50	1.07	7.77	5.25	9.27
Throughfall	LEM	6.93	2.95	122	12.3	36.1
	HEM	2.87	3.31	119	15.8	37.2
Stemflow	LEM	0.06	0.04	2.22	0.27	0.92
	HEM	0.07	0.06	3.27	0.34	1.09
Net rainfall loading	LEM	5.49	1.92	117	7.27	27.8
	HEM	1.44	2.32	114	10.9	29.1
Total input	LEM	6.99	2.99	125	12.5	37.1
	HEM	2.94	3.39	122	16.2	38.3

intra-specific variations were found in *Cola rostrata* in which two individuals had N input of 0.37 g m^{-2} of basal area and 2.94 g m^{-2} of basal area, P inputs of 0.67 and 3.88 g m^{-2} and Ca inputs of 7.73 and 60.86 g m^{-2} of basal area respectively. Similar situations were also found in *Didelotia africana* and *Hymenostegia afzelii*, both of which had more than one individual in the sample.

6.4 DISCUSSION

6.4.1 Nutrient fluxes in gross rainfall, throughfall and stemflow.

The results of the present study show that gross rainfall is not only an important source of nutrient input to the forest ecosystem but also an important route for nutrient transfer to the forest floor. Inputs of P, K and Mg in gross rainfall ranged from 17%-26% of their respective input estimates in litterfall in both LEM and HEM forests (Table 4.3). Ca had the highest input in gross rainfall though it constituted 9% of litterfall estimates in both forests. The proportion of nutrients finally reaching the forest floor as throughfall and stemflow (net rainwater) were enhanced as the rainwater interacted with the plant parts. The total input in throughfall and stemflow relative to litterfall inputs in LEM and HEM forests were: 5% and 2% N; 49% and 55% P; 316% and 353% K; 64% and 82% Mg; 345 and 40% Ca respectively.

The nutrients inputs in gross rainfall are dissolved gaseous elements, aerosols and dust particles of both natural and anthropogenic origin washed out of the atmosphere by the raindrops. Gross rainfall chemistry has been reported to vary from area to area depending on the origin of the air mass (Easton *et al.* 1973, Galloway 1982, Parker 1983). High concentrations of Na, Cl and Mg in gross rainfall have been associated with maritime air masses (Attiwill 1966, Carlisle *et al.* 1966, Manokaran 1980, Brassell and Sinclair 1983). The study area is close to the sea and probably experiences some maritime effect on the airmasses causing rainfall. The Ca/Mg ratio in gross rainfall in the present study was 1.77. This was higher than that observed in seawater (0.196) but should not be considered as coming entirely as from continental air masses (Easton *et al.* 1973). The Ca/Mg ratio for the site reported by Brassell and Sinclair (1983) for their site closer to the sea was 1.0 which was closer to that recorded in the present study. Lovett and Lindberg (1984) in determining mean airborne particulate concentration concluded that Ca was generally associated with airborne soil dust while the source of K was the vegetation itself. These sources may be applicable to Ca and K in the present study. The source of P in the gross

rainfall is still questionable. Nitrogen compounds are primarily produced by lightning discharges (Manorakan 1980), discharge of gaseous nitrogen into the atmosphere from the process of denitrification and other organic sources such as pollen grains.

The amount of P, K and Ca reaching the forest floor in stemflow and throughfall were more or less of the same magnitude in both LEM and HEM forests. Enhancement of N was slightly higher in LEM forest and Mg in HEM forest. These differences may reflect the relative availability of the nutrients in both forests. Jordan *et al.* (1980) observed negative net throughfall deposition for N, K and S in one of their sites and Ca and P in another. They suggested that the 'scavenging' of nutrients from the rainwater was a nutrient conservation strategy in that oligotrophic forest. Bernhard-Reversat (1975) also observed net loss of P from rainfall samples at the plateau sites in Banco, Ivory Coast. In the present study, no evidence of nutrient scavenging was found though the enhancement of N was comparatively lower in the HEM forest. In using the magnitude of nutrient enhancement as an index of stand trophic level (Parker 1983), both forests can be considered to be of the same status.

In both forests throughfall was the major pathway of transfer of nutrients to the forest floor. Approximately 97-99% of the net nutrient transfer was in throughfall and the rest 1-3% in stemflow. Stemflow is quite variable and difficult to quantify particularly in mixed tropical forests (Parker 1983). Though the transfer of nutrients in stemflow may appear negligible (1-3%) compared to throughfall, it is more significant in locating concentrated solutions of nutrient elements in a small area around the base of the tree (Easton *et al.* 1973, Jordan 1978, Prebble and Stirk 1980, Herwitz 1986). Ford and Dean (1977) had reported greater concentrations of fine roots around the region close to the tree stem. The low transfer is a function of the low proportion of gross rainwater reaching the forest floor as stemflow.

The review on nutrient cycling in primary and secondary rainforests by Proctor (1987) showed that nutrient input in gross rainfall in tropical forests ranged between; 5-21.7 kg ha^{-1} yr^{-1} for N; 0.5-26.9 for P; 2.6-24.6 for K; 0.2-19.8 for Mg and 3-30 kg ha^{-1} yr^{-1}. Canopy enrichments ranged between; 6.9-2.9 for N; 2.9-3.4 for P; 124.6-122.2 for K;

12.5-16.2 for Mg and 37.1-38.3 kg ha^{-1} yr^{-1} for Ca. The values obtained for Korup was relatively low for N in both gross rainfall and enrichment while the other nutrients were within the tropical range. Edwards (1982) reported the high adsorption of N and P to the walls of the plastic containers in storage. P in the present study showed no mark drop in concentration indicating that the low concentrations of N was actually as a result of its low leachability and not from adsorption nor microbial degradation. The high amount of rainfall in Korup favours luxuriant growth of the epiphytic mosses and lichens on leaves, branches, trunk and other plant parts (Plate 6.3). Results from litterfall studies showed a comparatively higher production of mosses and lichens in the HEM forests. They greatly increase the capacity of plant parts to absorb water and may explain in part the relatively lower throughfall catch and high net rainfall loss in the HEM forest. Lang *et al.* (1976) showed that lichens can absorb ammonium and nitrate from solution and lost Ca, K and Mg to the solution. These exchanges can greatly alter the nutrient content of the rainwater as it passes over these plant parts.

The amount of nutrients transferred to the forest floor is a function of the amount of rainfall reaching the forest canopy, the duration, the residence time of the rainwater and nature of the forest canopy. This implies that the reliability of the estimates of nutrient input and enrichment will depend on how well the rainwater is sampled. The high variability in estimates for the tropical forests (Clarke 1987, Proctor 1987, Bruijzneel 1989, 1991, Forti and Neal 1992) has been attributed to poor sampling designs. This is also confounded with chemical changes in storage (Galloway and Likens 1978, Galloway 1982, Parr *et al.* 1988) and analytical contamination as the samples are very dilute (Galloway and Likens 1978). Studies in a remote area such as Korup are bound to have such shortcomings.

Collection of gross rainfall above the forest canopy was grossly under-estimated due to air turbulence resulting from eddies generated by the uneven canopy layer (Mueller and Kidder 1972, Brinkmann 1985). To overcome this effect, volumetric data from Bulu weather station (PAMOL, Ndian) was used in all the computation while the elemental analysis was on the samples collected from the Park. It is not known exactly whether the rainfall on transect P is the same as that at Bulu. Forti and Moreira-Nordermann (1991)

B

Plate 6.3: **Mosses and lichens growing on (A) leaves and (B) tree trunk of trees in Korup National Park.**

also reported 'washout effects' of the rough canopy layer which enriches the collected samples. This effect was reduced by placing the gross rainfall collector in an area relatively clear taller crowns.

6.4.2 Temporal and spatial variability in inputs

The strong relationship between rainfall amounts and magnitude of nutrient enhancement (Carlisle *et al.* 1966, Easton *et al.* 1973, Prebble and Stirk 1980, Parker 1983) show that temporal variations in throughfall and stemflow amounts were also reflected in their respective nutrient fluxes. Though throughfall was generally higher in the LEM forest, greater amounts were recorded in the HEM forest in July when nutrient inputs were at their peaks. Washoff was probably the dominant process of enhancement in both forests within the first month of the rainy season. The lower amounts within the first months with low rainfall amounts were balanced by high concentrations of all the nutrients. The nutrients washed off must have come from dry deposition or concentration by evaporation during the dry months. The later part of the rainy season was dominated by leaching and the relatively mobile elements (K and Mg) were removed faster.

The degree to which elements are removed from the crowns of trees also vary to some extent between species (Easton *et al.* 1973). This will also be depend on the elemental content of the leaves. The higher returns of Mg in the HEM forest may reflect its high content in leaves of the dominant species in the HEM forest as shown in their leaf litter contents. Phenological changes in the canopy may also affect nutrient enhancement. Tukey *et al.* (1958) found that very young leaves were less susceptible to leaching than older leaves. Easton *et al.* (1973) also found high concentrations of Ca and Mg in throughfall prior to leaf fall which declined after leaf fall. This showed that the high concentrations in the month of March 1992 were more or less from rainwash as the trees were just putting out new leaves.

Stemflow inputs were variable not only in volume but also as a result of the high species diversity. No direct relationship could be arrived at for nutrient inputs of the different species. The understorey species however showed relatively higher nutrient returns per unit basal area due to their high stemflow amounts and small basal area. The results of the PCA analysis showed that there may be more important factors controlling the rates of stemflow funnelling in the HEM forest.

CHAPTER SEVEN

GENERAL DISCUSSION

AND

CONCLUSION

7.1 Nutrient input and availability.

The major routes of nutrient transfer from the above-ground biomass to the forest floor were through litterfall, throughfall and stemflow. Estimates of the annual returns of nutrients to the forests floor through these major routes showed that relatively higher amounts of N, K and Ca were returned to the forest floor in the LEM forest and higher amounts of Mg in the HEM forests (Table 7.1). The amount of P returned was more or less equal in both forests (Table 7.1). The results also show that while greater amounts of N, P and Ca were returned in litterfall, a higher amount of K was returned in throughfall in LEM and HEM forests. The amount of Mg returned was approximately equal for both routes in LEM and HEM forests. The return of nutrients in stemflow was comparatively small in both forests. This was not considered negligible as the supply of these small amount of nutrients were restricted to the small region around the bole of the individual trees.

A remarkable feature was the fact that the amount of litterfall returned to the forest floor in both forests were approximately the same though with different concentrations of the nutrient elements. Litterfall has however been reported not to be closely related to ecosystem nutrient status (Jordan and Herrera 1981, Brassell *et al.* 1983, Proctor 1983b). The disparity in the amount of nutrient returned to the forest floor was therefore a reflection of the variation in concentration of the different nutrient elements in foliage and litterfall in both forests. The different tree species vary in their phenological cycles, nutrient requirement and economy. These, in turn determine the elemental composition of their litter. The differences in nutrient input in both forests was further highlighted by the variation in proportion of the different litter fractions (Table 3.8) which also had different concentrations of the nutrient elements (Table 4.1).

These above-ground nutrient inputs to the forest floor determined the extent to which nutrients were made available to the plants. The returns of nutrients in throughfall and stemflow therefore constituted a rapid pathway of transfer since the nutrients were probably, mostly in dissolved forms readily available for plant uptake. Therefore

Table 7.1: Estimates of the quantities (kg ha^{-1} yr^{-1}) of mineral elements returned annually in litterfall, throughfall and stemflow in LEM and HEM forests, Korup National Park, Mundemba, Cameroon.

	Forest type	Nutrients				
		N	P	K	Mg	Ca
Litterfall	LEM	150	6.1	39.5	19.7	111
	HEM	136	5.9	34.7	19.7	96.0
Throughfall	LEM	6.93	2.95	122	12.3	36.1
	HEM	2.87	3.31	119	15.8	37.2
Stemflow	LEM	0.06	0.04	2.22	0.27	0.92
	HEM	0.07	0.06	3.27	0.34	1.09
Total	LEM	157	9.09	164	32.2	148
	HEM	139	9.27	157	35.7	134

approximately 70% of K, 40% of Mg and 35% of P of their annual returns were in form that readily be absorbed by the plants. However, the amount of rainfall was high for a greater part of the year and exceeding the water retention capacity of the soil. This often led to a lost in some proportion of these nutrients in surface runoff and soil drainage to streams (Bruijnzeel 1991). However that proportion was not estimated in this study.

The litter has to undergo a series of transformation processes before the nutrients therein can be made available for uptake by the plants. These processes therefore, have a key role in regulating nutrient availability to the plants. Breakdown of litterfall was relatively slower in the HEM compared to the LEM forest as shown by the higher forest floor litter mass. The highly lignified pods of the legumes decomposed much more slowly and were abundant on the forest floor in the HEM forest (chapter 5). Results of the rates of breakdown of leaf litter of the abundant species in both forests showed that leaves of *Didelotia africana, Tetraberlinia bifoliolata* and *Microberlinia bisulcata* decomposed relatively slower. Leaf litter of these species constituted 3% and 45% of annual leaf litter in the LEM and HEM forests respectively. These leaves are highly sclerophyllous and had lower decomposition rates as a result of their low substrate quality (higher structural components) (Anderson *et al.* 1983, Lavelle *et al.* 1993). This characteristic feature has been reported as a nutrient conservation strategy for species on nutrient-poor soils which renders the leaves to decompose at very slow rates thereby reducing the chances of nutrient loss through leaching (Jordan and Herrera 1981). Contrarily, mineralization of P was relatively faster in these species in the LEM and HEM forests as the initial concentration of this nutrient was high. This could be due to a higher proportion of labile or inorganic fractions of P which was readily released. This further stresses the need for further comparative studies on the nutrient availability to be based on the fractionation of the nutrients into biological meaningful forms (Attiwill and Adams 1993).

In the HEM forest the leaf litter in the litterbags were invaded by ectomycorrhizal roots, a situation earlier reported by Newbery *et al.* (1988) for the ectomycorrhizal groves in the Park and by Singer and Araujo (1979, 1986) for Terre firme forest in the Amazon. It was expected that the rate of mineralization of P will comparatively be higher in the HEM forest due to the activity of the surface phosphatase reported to be released by the

ectomycorrhizas which enhances the exploitation of organic P from the decomposing litter (Harley and Smith 1983). This was not witnessed possibly as a result of interaction in the highly heterogenous natural environment which could hamper its effectiveness.

Magnesium and Calcium were the only nutrient elements that were released more rapidly in the HEM forest compared to the LEM forest (Chapter 5). Cuevas and Medina (1988) in examining the relationship between fine root growth, rate of litter decomposition and nutrient release in three contrasting forests in the Amazon, also found that Mg and Ca were released relatively faster in the 'Terra Firme' forest where the leaves were in contact with the root mat. They concluded that there must be release mechanism mediated by the roots and/or its microorganisms. The root mat is well developed in the HEM forest and strongly associated with the ectomycorrhizas. Mg is also an important requirement for fine root formation (Marschner 1986, Cuevas and Medina 1988). This may reflect a higher demand for this nutrients for the formation of fine roots which scavenge the forest floor for nutrients. Some ectomycorrhizas have also been reported to accumulate Ca (Lapeyrie and Bruchet 1986) which suggests that nutrients other than P and N may also be of interest in mycotrophy.

7.2 Nutrient redistribution.

Redistribution of nutrients within the plant is a means of regulating the nutrient fluxes in litter (Staaf 1982, Chapin 1983, kost and Boerner 1985). It is expected that nutrients in short supply to the plants will be efficiently retranslocated from senescing plant parts to sites of active growth which will be evident in low nutrient concentrations in litterfall (Chapin 1983, Chapin *et al.* 1986, Vitousek and Sanford 1986). P, N and K were withdrawn from senescent leaves but to a lesser extent for Mg which were occasionally accumulated. The extent of withdrawal of N, P, K and Mg were relatively lower in the ectomycorrhizal compared to the non-ectomycorrhizal species (Table 4.4 and 4.6). This in part, explains the high nutrient concentrations (particularly N and P) in leaf litter of the ectomycorrhizal species. Some differences may be due to variations in foliar concentration.

Three reasons can be proposed for this behaviour: (i) The ectomycorrhizal species are not adapted to internal re-distribution of nutrients; (ii) The nutrients in question are not in short supply to these ectomycorrhizal species since the ectomycorrhizas aid the plants in nutrient uptake from soil solution; (iii) the period of study coincided with the 'luxury' year of the species during which the nutrient requirements were at their lowest level. If the first proposal is right, then the situation will be further complicated on how these plants meet up their nutrient requirements from the nutrient-poor soils. With the vast literature on the possible active role of the ectomycorrhizas in nutrient uptake from the soil (Harley and Smith 1983, Alexander 1983, 1989a, Högberg 1986, Brundrett 1991), the second proposal may be a possible explanation.

During the first year of this study (May 1990-1991) there was that sharp drop in nutrient concentration in leaf litter in both forests in the dry season when peak litterfall was recorded. This was however not so drastic in the second year during which flower and fruit production were quite high in both forests for most of the species used in this study. The nutrient requirements for flower and fruit production is usually very high (Schaik 1985, Ernst and Tolsma 1989) which would contradict the idea of a 'luxury' year. This also highlights the complexity in nutrient allocation in the trees. Most above-ground biomass studies have often focused on the proportion of nutrients invested in wood and leaves while ignoring the proportion that is invested in reproductive structures. Flowering and fruit production are very irregular in most tropical trees and may require a particular threshold level of nutrients in the tree for its initiation (Schaik 1985). With the concentration of nutrients in flowers and fruits, the plants nutrient economy as well as nutrient cycling sub-processes may be completely altered during such a year. This necessitates some caution in the interpretation of these results.

Scott *et al.* (1992) on examining rates of nutrient retranslocation in six species in an evergreen forest in Maraca island, Brazil, found a wide range of values from 17% to 73% for N and from 41% to 82% for P. Their conclusion was that the trees were not efficient in retranslocating N and P from the leaves before abscission and that neither element was limiting in that forest. The lower values obtained in the present study are the annual estimates and in such seasonal forests redistribution may be of much significance just

within the short period before the dry season and the early part of it when the greater number of the tree species and lianes shed their leaves.

Application of the litterfall dry mass/nutrient ratios as indicative of within-stand nutrient use efficiency (Vitousek 1984, Vitousek and Sanford 1986, Singh 1989) also showed low efficiencies in the use of N, P, K, Mg and Ca (Table 4.6) making it difficult to believe that any of these nutrients could be limiting in both forests. The use of throughfall enhancement as an index of forest trophic status (Parker 1983) showed no specific selection for any of the nutrient elements in LEM and HEM forests as reported for the oligotrophic forests in northern Amazon (Jordan *et al.* 1980).

Another striking feature was the synchronization of sub-processes in both forests. Nutrient fluxes were strongly seasonal, with the bulk of the litterfall in the dry season followed by the throughfall and stemflow inputs in the wet season. Decomposition was very rapid from the onset of the rainy season during which the thick litter mass on the forest floor was rapidly decomposed.

This was also the period during which the trees were putting on new leaves and flower buds and the nutrient requirement by the plants is expected to be quite. Nutrient uptake during this period will be high thereby reducing losses through leaching. In the HEM forest, the root mat in association with the ectomycorrhizas which is reported to have high storage capacity for nutrients (Harley and Smith 1983, Alexander 1989a, 1989b) may be quite effective in trapping nutrients during this period.

7.3 Conclusions

Considering the amount of nutrients returned to the forest floor in litterfall, throughfall and stemflow; it can be concluded that higher amounts of N, K and Ca are cycled annually in the LEM and higher amounts of P and Mg are cycled in the HEM forest. The rapid mineralization of Mg and Ca in leaf litter on the forest floor in the HEM forest indicated a faster rate cycling of these nutrients in the HEM forest compared with the LEM forest. None of these nutrients actually showed any indication of limited availability in LEM and HEM forest. The role of ectomycorrhizas in nutrient acquisition was however not clearly shown. However this association may prove beneficial to the host plants in terms of storage since the input of nutrients to the forest floor were in flushes. The possible nutrient conserving mechanism was the formation of the root mat which was better developed in the HEM forest. More work is required at the level of the soil and on roots to properly ascertain the role of the ectomycorrhizas in plant nutrition.

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APPENDIX

Appendix 1a: List of the different species in the leaf litter, the other fractions in total litterfall and the code numbers used in classifying them.

Code No.	SPECIES	FAMILY
1	*Acioa sp. (Dactyladenia)*	CHRY
2	*Afzelia bipindensis* Harms.	CAES
3	*Afzelia pachyloba* Harms	CAES
4	*Ageleae sp.*	CAES
5	*Alstonia congensis* Engl.	APOC
6	*Amanoa strobiliaceae* Mull. Arg	EUPH
7	*Anisophyllea laurina* R. Br. ex Sabine	RHIZ
8		
9	*Anthocleista vogelli* Planh	LOGA
10	*Anthonotha fragrans* (Bak.F) Exell & Hi.	CAES
11	*Anthonotha lamprophylla* (Harms) J. Leonard	CAES
12	*Antidesma vogelianum* Mull Arg	EUPH
13	*Aphanocalyx marginervetus*	
14	*Aulacocalyx jasminiflora* Keay	RUBI
15	*Baikiaea insignis* Benth	CAES
16	*Baphia laurifolia* Baill.	PAPI
17	*Baphia nitida* Lodd.	PAPI
18	*Beilchmiedia sp.*	LAUR
19	*Berlinia bracteosa* Harms	CAES
20	*Berlinia confusa* Hoyle	CAES
21	*Calamus sp.*	AREC
22	*Calancoba glauca* (P. Beauv.) Gilg	FLAC
23	*Calpocalyx dinklagei* Harms	MIMO
24	*Canthium sp.* Lam	RUBI
25	*Carapa procera* Aubl.	MELI
26	*Coelocaryon preussii* Warb.	MYRI
27	*Cola cauliflora*	STER
28	*Cola lateritia* K. Schum	STER
29	*Cola lepidota* K. Schum	STER

Code No.	SPECIES	FAMILY
30	*Cola rostrata* K. Schum	STER
31	*Cola semecarpophylla* K. Schum	STER
32	*Cola verticillata* (Thonn) Stapf ex A. Chev.	STER
33	*Cola sp.*	STER
34	*Coula edulis* Baill.	OLAC
35	*Cissus sp.*	VITA
36	*Cyrtogonone argentea* (Pax) Prain	EUPH
37	*Dacryodes edulis* Vahl	BURS
38	*Dasylepis blackii* (Oliv.) Chipp	FLAC
39	*Dalbergia sp.*	PAPI
40	*Dialium pachyphyllum* Harms	CAES
41	*Dialium sp.*	CAES
42	*Dichostemma glaucescens* Pierre	EUPH
43	*Didelotia africana* baill.	CAES
44	*Diogoa zenkeri* (Engl) Exell & Mend.	OLAC
45	*Diospyros gabunensis*	EBEN
46	*Diospyros gracilescens* (Gürke)	EBEN
47	*Diospyros hoyleana* F. White	EBEN
48	*Diospyros iturensis* (Gürke) Let.& White	EBEN
49	*Diospyros* sp.1	EBEN
50	*Diospyros* sp.2	EBEN
51	*Discoglypremna caloneura* (Pax) Prain	EBEN
52	*Drepetes sp.*	EUPH
53	*Enantia chlorantha* Oliv.	ANNO
54	*Ancistrocladus korupensis*	
55	*Erismadelphus exsul* Midbr.	VOCH
56	*Erythrophleum ivorense* A.Chev	CAES
57	Epiphytes (leafy)	
58	*Fagara tessmannii* Engl.	RUTA
59	*Ficus* sp.	MORA
60	*Garcinia manni* Oliv.	GUTT
61	*Garcinia polyantha* Oliv.	GUTT
62	*Garcinia* sp.	GUTT
63	*Gilbertiodendron mayombense* (Baill.)	CAES

Code No.	SPECIES	FAMILY
64	*Gilbertiodendron sp.*	CAES
65	*Homalium letestui* Pellegr.	SAMY
66	*Hymenostegia afzelii* (Oliv.) Harms	CAES
67	*Hymenostegia bakeriana* Hutch. & Dalz.	CAES
68	*Hypodaphnis zenkeri* (Engl.) Stapf.	CAES
69	*Irvingia gabonensis* (O'Rorke) Baill.	IXON
70	*Irvingia grandifolia* (Engl.) Engl.	IXON
71	*Irvingia roboo*	IXON
72	*Klaineanthus gaboniae* Pierre ex Prain	EUPH
73	*Klainedoxa gabonensis* Pellegr	IXON
74	*Landolphia* sp.	APOC
75	*Larvegeria* sp. ?	
76	*Lecomtedoxa klaineanum*	SAPO
77	*Lophira alata* Banks ex Gaertn.f	OCHN
78	Liane4	
79	Liane5	
80	Liane12	
81	Liane21	
82	Liane31	
83	*Maesobotrya dusenii* (Pax) Hutch.	EUPH
84	*Magnistipula glaberima* Engl.	CHRY
85	*Mammea africana* Sabine	GUTT
86	*Manilkara multinervis* (Bak.)	SAPO
87	*Mareyopsis longifolia* (Pax)	EUPH
88	*Memecylon normadii*	MELA
89	*Microberlinia bisulcata* A.Chev.	CAES
90	*Milletia* sp.	PAPI
91	*Monopetalanthus* sp.	CAES
92	*Napoleonaea* sp.	LECY
93	*Newtonia duparquetiana* (Baill.) Keay	MIMO
94	*Oubanguia alata* Bak.f.	SCYT
95	*Pachypodanthium staudtii* Engl. & Diels	ANNO
96	*Parkia bicolor* D.Chev.	MIMO
97	*Pausinystalia johimbe* K.Schum	RUBI

Code No.	SPECIES	FAMILY
98	*Poga oleosa* Pierre	ANIS
99	*Protomegabaria macrophylla* Hutch.	EUPH
100	*Rinorea oblongifolia* Marquand ex Chipp	VIOL
101	*Salacia* sp.	HIPP
102	*Scytopelalum klaineanum*	SCYT
103	*Sorindeia* sp.	
104	*Soyauxia gabonensis* Oliv.	MEDU
105	*Staudtia stipitata* Warb.	MYRI
106	*Strephonema pseudocola* A.Chev.	COMB
107	*Strombosia glaucescens* Engl.	OLAC
108	*Strombosia scheffleri* Engl.	OLAC
109	*Strychnos sp.*	LOGA
110	*Syzygium owariense* (P.Beauv.)	MYRT
111	*Tabernaemontana contorta* Stapf.	APOC
112	*Tetracera sp.*	DILL
113	*Tetraberlinia bifoliolata* (Harms) Hauman	CAES
114	*Tetraberlinia moreliana* Aubr.	CAES
115	*Uapaca staudtii* Pax	EUPH
116	*Uvariastrum zenkeri* Engl. & Diels	ANNO
117	*Vitex grandofolia* Gürke	VERB
118	*Vitex* sp.	VERB
119	*Warneckea memecyloides* (Benth.) Jac Fél.	MELA
120	*Xylopia aethiopica* (Dunal.) A.Rich	ANNO
121	*Xylopia quintasii* Engl. & Diels	ANNO
122	*Xylopia villosa* chipp.	ANNO
123	Unidentified	
124	Wood,Bark,Twigs	
125	Reproductive part	
126	Moss,Lichen	
127	Trash	

Appendix 1b: List of the families of different species sorted from the leaf litter. The abbrevations are those used in Appendix 1a and in Text.

Family	**Abbreviation**
Apocynaceae	APOC
Anacardiaceae	ANAC
Annonaceeae	ANNO
Arecaceae	AREC
Burserceae	BURS
Caesalpinioideae	CAES
Chrysobalanceae	CHRY
Cannaraceae	CANN
Combretaceae	COMB
Ctenlophonaceae	CTEN
Dilleniaceae	DILL
Ebenaceae	EBEN
Euphorbiaceae	EUPH
Flaucourtiaceae	FLAC
Guttiferae	GUTT
Hippocrateaceae	HIPP
Hypericaceae	HYPE
Ixonanthaceae	IXON
Lauraceae	LAUR
Lecythidaceae	LECY
Loganiaceae	LOGA
Medusandraceae	MEDU
Melastomataceae	MELA
Meliaceae	MELI
Mimosoideae	MIMO
Monimiaceae	MONI
Moraceae	MORA
Myristicaceae	MYRI
Ochnaceae	OCHN
Olacaceae	OLAC
Papilionoideae	PAPI
Passifloraceae	PASS
Rhizophorceae	RHIZ
Rubiaceae	RUBI
Rutaceae	RUTA
Samydaceae	SAMY
Sapidaceae	SAPI
Sapotaceae	SAPO
Scytopetalaceae	SCYT
Sterculiaceae	STER
Tiliaceae	TILI
Verbenaceae	VERB
Violaceae	VIOL
Vochysiaceae	VOCH
Vitaceae	VITA

Appendix 2a: Morphological features of sample trees in the LEM forest for stemflow studies.

Species	Dbh (cm)	crown position & shape	Branching habit (angle & arrangement)	Leaves & arrangement	bark texture	Exudate
Strombosia glaucescens	8.0	lower multiple flabelate	perpendicular alternate	simple alternate	rhytidome, circular flakes	no
Diospyros gabunensis	18.6	middle, umbellate	oblique alternate	simple alternate	without, cracked	no
Strephonema pseudocola	107.5	emergent	oblique alternate	simple alternate	flakes, irregular scales	no
Vitex sp.	17.0	middle, umbellate	oblique alternate	simple	lamellate rytidome	no
Warneckea memecyloides	9.7	understorey	obtuse verticullate	simple	without, smooth	no
Hymenostegia afzelii	13.7	lower, multiple flabellate	very oblique alternate	compound alternate	without, smooth	no
Diospyros iturensis	12.5	lower	very oblique alternate	simplealternate	without, lenticellate	no
Hymenostegia afzelii	22.0	lower	very oblique alternate	compound alternate	without, slightly rough	no
Dichostemma glaucescens	9.0	middle, umbellate	perpendicular verticullate	simple	spotted, without	white latex, sticky
Didelotia africana	37.0	emergent	perpendicular alternate	compound	spotted, without	no
Cola rostrata	9.8	middle	oblique verticullate	simple digitate	without, slightly rough	no
Diospyros iturensis	8.7	lower	oblique alternate	simple	cracked, without	no
Didelotia africana	82.5	emergent	perpendicular alternate	compound	without, lenticillate	no
Berlinia bracteosa	59.0	Top	oblique	compound	with irregular flakes	no
Garcinia polyantha	11.8	lower, spherical	perpendicular opposite	simple	without, smooth	no
Cola sermacarpophylla	6.8	understorey, turfed	very oblique	simple (rossettes)	without, smooth	no
Sorindiea sp.	26.8	middle	perpendicular alternate	compound	without, slightly rough	no
Cola rostrata	14.5	middle	very oblique alternate	simple digitate	without, slightly rough	no

Appendix 2b: Morphological features of the sample trees in the HEM forest for stemflow studies.

Species	Dbh(cm)	Crown position & shape	Branching habit	leaves	Bark texture	Exudate
Garcinia sp.	15.4	middle, umbellate	very oblique alternate	simple alternate	without, cracked	No
Strombosia glaucescens	13.0	middle, conical	perpendicular alternate	simple	rhytidome, circular flakes	No
Didelotia africana	56.5	top, multiple flabelate	very oblique alternate	compound	without, lenticellate	No
Strombosia glaucescens	9.9	middle, conical	perpendicular alternate	simple	with circular flakes	No
Didelotia africana	28.6	top, multiple flabellate	oblique alternate	compound	without lenticellate	No
Cola rostrata	26.4	lower	oblique alternate	simple obligate	without slightly rough	No
Cola lateritia	14.5	lower	obtuse alternate	simple	without, irregular scales	No
Coula edulis	43.2	top	oblique allenate	simple	without, smooth regular folds	No
Diogoa sp.	16.4	lower	perpendicular	simple	with rhytidome lamellate	No
Strombosia glaucescens	8.2	Middle	perpendicular allenate	simple	rhytidome, circular flakes	No
Diospyros gabunensis	21.0	middle	obtuse verticullate	simple	with rectangular flakes	Dark No
Warneckea memecyloides	7.5	understorey	oblique verticulte	simple	without, smooth	No
Maesobotrya dusenni	9.6	low	perpendicular allenate	simple	with irregular flakes	No
Pausynistalia johimbe	19.4	middle	obtuse opposite decussate	simple	with irregular flakes	No
Hymenostegia afzelii	8.2	middle	very oblique	compound	without, smooth	No
Memecylon normardii	12.5	lower, multiple flabellate	perpendicular	simple	without, smooth	No
Dichostemma glaucescens	32.0	middle	perpendicular verticullate	simple	without, spotted	white latex
Cola sermacarpophylla	8.0	understorey	very oblique allenate	simple (rossettes)	without, smooth	No
Tetraberlinia moreliana	95.0	emergent umbelliform	oblique allenate	compound	without, lenticellate	No
Cola rostrata	9.9	low	perpendicular alternate	simple	without, slightly rough	No