ECOLOGICAL STUDIES IN CONTRASTING FOREST TYPES IN CENTRAL AMAZONIA

A thesis presented for the degree of
Doctor of Philosophy at the University of Stirling

by

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I hereby declare that this thesis has been composed by myself and that it contains the results of my own research. Where appropiate I have acknowledged the nature and the extent of the work which has been carried out in collaboration with others.

F. J. Luizão

"Stand still and show yourself attentive to the wonderful works of God."
(Job 37,14).

"We still do not know why species should be so variable in this (wide interspecific variations in nutrient concentrations) respect."
(Dr J. Proctor, 1995).

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Photo credits (Fig. 3.1):

Air photo taken August 1991 by Dr. D. Roberts (University of Washington). Large trees in open sand are specimens of *Aldina heterophylla*.

Landsat satellite image, Thematic Mapper bands 3, 4, and 5 colour composited as blue, green and red, respectively. Date was 21 August 1990 (dry season). The open sand area of the *campina* is shown in red due to the strong reflectance of band 5 from the dry sand. The surrounding *campinarana* is shown as a dark crescent, probably because of having fewer and older leaves on the trees at that time of the year. The red and yellow lines show a road and a power-line cut respectively. Pixels measure 30 m x 30 m.
Source: Brazilian National Space Institute (INPE). Image enhanced and interpreted by Dr. B. Nelson (INPA - National Institute for Amazonian Research).

Contents

Abstract

Most of the Amazonia is covered by the lowland evergreen rain forest (LERF) formation. A small proportion of the region (5-6 % in total) is covered by heath forest, which is particularly common in the Rio Negro basin on Spodosols - white sand soils with a layer of mor humus. The smaller facies of heath forest (SHF) is called `Campina' in Brazil and often lacks the mor humus; the taller facies (THF) is called `Campinarana'. The present study was made in central Amazonia, on a gradient from SHF through THF to well developed LERF. Soil, vegetation, and nutrient dynamics were studied in three 50 m x 50 m plots in each type of forest. Litterfall was measured during one year and litter standing-crop was measured three times a year. Three decomposition experiments, using bagged leaf litter, were made using leaves of two common species from the heath forests and one from the LERF. Fertiliser addition experiments in the field and in the laboratory were carried out to determine the potential nutrient limitations for plants in the three forest types. Annual litterfall was highest in the dry season and was 3.8 t ha^{-1} yr^{-1} in the SHF, 6.3 t ha^{-1} yr^{-1} in the THF and 7.8 t ha^{-1} yr^{-1} in the LERF. The rates of weight loss of the enclosed leaf litter were most rapid in the LERF and slowest in the SHF. The leaves of the LERF species *Clitoria racemosa* decomposed faster than those of the heath forest species. Fine roots penetrating litter-bags differed significantly among forest types and leaf species, and increased the decay rates. There were no significant differences in decomposition rates between the wet and dry season experiments. Significant differences in the release of chemical elements were observed: higher immobilization of iron and aluminium in the LERF; higher potassium and copper release in THF; and lower calcium, but higher boron release rates in SHF. Significantly higher immobilization of iron and aluminium (mainly in LERF) was found in bags penetrated by fine roots, while release of magnesium, calcium, manganese and zinc was significantly increased by fine roots, particularly in the THF. Leaf mass loss and nutrient release were mostly controlled by abiotic factors in the SHF, but organisms were more active in the THF and LERF. Diplopoda were the dominant decomposers, particularly in the THF. Fertiliser addition showed an overall positive effect of liming, especially in heath forest

soils. Nitrogen and phosphorus additions did not induce higher biomass production, while calcium chloride addition invariably induced a high mortality. H^+ ion toxicity, together with a higher concentration of soil phenolics are suggested as causes of the poor growth in the heath forests, but in the SHF, where it lacks mor humus, limitation by nutrients, especially basic cations, may occur.

Chapter 1. GENERAL INTRODUCTION

Amazonia is the name given to the region in South America which is drained by the Amazon river and its tributaries. It is an enormous depression on the Brazilian shield, filled by post-Precambrian sedimentary and volcanic rocks (Putzer 1984), and comprises the area situated between the western parts of the Andes mountains and the Atlantic ocean. Estimates of the area of Amazonia vary from 5 x 10^6 km^2 to 6 x 10^6 km^2 (Daly & Prance 1989). Pires & Prance (1985) estimated that 3.7 x 10^6 km^2 of Amazonia lie in Brazil, of which 3.4 x 10^6 km^2 are covered by forest. The equatorial rain forest which covers 42% of Brazil, goes beyond the Amazon basin and covers much of South America (Leopoldo *et al.* 1987). Despite earlier assumptions of great homogeneity (because most of Amazonia is lowland and has a humid, warm climate), it is now known that there is an important diversity in temperature, precipitation, and seasonality (Bigarella & Ferreira 1985). It follows that soils and vegetation are also diverse.

Forest types in Amazonia

Most of Amazonia that is not seasonally flooded, especially on Oxisols and Ultisols, is covered by the Lowland Evergreen Rain Forest Formation (*sensu* Whitmore 1984), often referred to in Brazil as *terra firme* forest, and characterized by a high species diversity. Prance *et al.* (1976) in an inventory of 1 ha in a forest site 40 km northeast of Manaus, found 179 species of trees with dbh (diameter at breast height) > 15 cm, plus 56 extra species with dbh > 5 cm-14.9 cm in a sub-plot of 400 m^2 within the same 1 ha plot. The 235 species belonged to 43 different families. Tropical rain forests dominated by one or a few species also occur in Amazonia (Anderson 1981; Nascimento 1994), and small patches of lower diversity scleromorphic vegetation generally associated with white sand soils (Spodosols), occur locally throughout Brazilian Amazonia (Ducke & Black 1953; Sombroek 1966; Anderson 1978, 1981), as well as in Surinam (Heyligers 1963), southern Venezuela (Beard 1953; Klinge & Medina 1979), and northeastern Peru (Revilla 1978). The distinctive forest types on Spodosols are designated by a variety of regional names

such as *bana*, *caatinga*, *campina*, *campinarana*, *white sand savannah*, all fitting within the term heath forest (*sensu* Whitmore 1984) which is used throughout this thesis.

According to Whitmore (1984), heath forests are found on soils derived from siliceous parent materials which give rise to podzolised soils inherently poor in bases, highly acidic, lacking buffering capacity due to a shortage of sesquioxides, and commonly coarse textured. The vegetation is distinct floristically, in structure, and in physiognomy. More trees have smaller leaves than in the lowland evergreen rain forest, and many leaves are distinctively sclerophyllous (Ducke & Black 1953; Anderson 1981; Medina *et al.* 1990). Trees of large girth are rare, a bryophyte cover on the ground and ephiphytes on trees are frequent features, and myrmecophytes are abundant, especially in the more open and stunted heath forests. All these characteristics seem to match the ones observed in the two types of heath forest included in the present study.

The most extensive heath forests in the world are in the upper Rio Negro and Rio Orinoco in South America (Whitmore 1990), occupying 5-6 % of Brazilian Amazonia (Braga 1979; Whitmore 1984). Elsewhere in the world, heath forests occur widely in Borneo (Brunei and parts of Indonesia and Malaysia), where they are called *kerangas*, in small areas in Peninsular Malaysia, and on coastal sands in Africa in Gabon, Cameroon, and Ivory Coast (Whitmore 1990). In Borneo, lowland heath forest occurs extensively inland, and on flat sites interdigitation occurs, correlated with differences in soil (Whitmore 1984).

There is no evidence that heath forests are other than natural vegetation-types although there is some evidence of human influence (Prance & Schubart 1978) for *campina* near Manaus.

The causes of heath forests

There are several different views on the possible causes of heath forests within the lowland evergreen rain forest zone. Since the physiognomy of heath forest presents a number of features, such as the small hard leaves, which suggest physiological stress, their cause has been ascribed to one or more of the following factors:

1. Drought (Ducke & Black 1953; Brünig 1974; Lisboa 1975; Reichardt *et al.* 1975; Klinge & Medina 1979; Jordan 1985; Pires & Prance 1985);

2. Waterlogging (Brünig 1974; Herrera 1979; Klinge & Medina 1979; Bongers *et al.* 1985; Jordan 1985);

3. Low nutrients (Richards 1952; Ferri 1960; Rodrigues 1961; Klinge 1965; Anderson *et al.* 1975; Kartawinata 1978; Anderson 1981; Jordan 1985);

4. Soil acidity and phenolics (Rodrigues 1961; Janzen 1974; Anderson *et al.* 1983; Brünig 1983; Proctor *et al.* 1983a; Whitmore 1984).

Brünig (1974) related the series of forest types at Bako, in Sarawak, to decreasing soil depth and increasing variability of water supply; under more favourable conditions, the vegetation type would tend to become similar to the dipterocarp forest. Also periodic drought was considered a major cause of heath forests in Sarawak, and Brünig (1974) regarded it as the main cause for the striking structural and physiognomic features of heath forests such as lower roughness of the canopy surface, smaller mean leaf size, steeply inclined leaves and twigs, and higher reflectance of radiation (the short-wave albedo).

In Venezuela, the existence of the different facies of heath forest has been attributed to the shallow water table in the soil, which could drop quickly during dry spells and cause water shortages (Bongers *et al.* 1985; Jordan 1985). The podzolised quartz sands in the Rio Negro region in Venezuela are located between the flooded forests and lowland evergreen forests (Jordan 1985). Because of the coarseness of the sand, heath forest soils are freely draining and have a low capacity to retain water (Reichardt *et al.* 1975; Klinge & Medina 1979; Jordan 1985; Bravard & Righi 1991). In Venezuelan heath forests, an impermeable iron or humus pan has been described (Klinge & Medina 1979). Lateral drainage occurs quickly following storms, and within a few days without rain, heath forest soils start to become very dry. Klinge & Medina (1979) observed in San Carlos de Rio Negro (Venezuela) that heath forest plants experience water stress in the dry season and suggested this as the cause for the change from tall *caatinga* forest on soils with better water retention, through the smaller stature low *caatinga* to the shrubby *bana* on soils with the least water retention. The heath forests, on soils normally moist but

presenting a fluctuating water table, occupied intermediate positions in space between the flooded forest and the *terra firme.*

There are several features of heath forests which suggest inorganic nutrient deficiency (Whitmore 1984) such as: (a) they are very easily degraded to a low scrub vegetation if burned or cultivated; (b) the abundance of plants with supplementary means of mineral nutrition (myrmecophytes and insectivorous plants); and (c) presence of sclerophylls probably related to shortage of nitrogen and phosphorus (Beadle 1966). In agreement with such features, it has been found that the nutrient supply of heath forest mineral soils is generally low in Brazilian Amazonia (Klinge 1965; Martins & Matthes 1978; Ranzani 1980; Anderson 1981). Elsewhere, Vitousek & Sanford (1986) compared foliar and fine litterfall nutrients of various rain forests, and showed that nitrogen and phosphorus appear to cycle less in heath forest than in other lowland forests, and that heath forest litterfall shows high C:N ratios which suggest that nitrogen is in short supply (Cuevas & Medina 1986, 1988) even though its total amounts in the soil are not unusually low. Phosphorus, generally regarded as having low mobility (Medina & Cuevas 1994) and being probably the most limiting nutrient in tropical rain forests growing on old, leached soils (Vitousek & Sanford 1986), has been linked with tree species distribution and growth in the tropics. In Cameroon, Gartlan *et al.* (1986) and Newbery *et al.* (1988) were able to show strong association between species distribution and gradients of phosphorus availability in the uppermost mineral soil layers. In Sarawak, Baillie *et al.* (1987) suggested that magnesium concentrations in topsoil were the single most important factor associated with species distribution in a mixed dipterocarp forest but their suggestion was criticized by Proctor (1995). The same relationship with one particular nutrient in soil has been supposed for heath forests, but there are no consistent data proving it. In the opposite direction. it has been realized that the soils under heath forests can vary considerably in their chemistry, and have a similar or higher nutrient content of potentially limiting nutrients than neighbouring forests with a larger biomass (Kartawinata 1978; Proctor *et al.* 1983a). In Sarawak, huge dipterocarp forests can be found on very poor soils (Proctor *et al.* 1983a), and the same occurs in central Amazon for lowland evergreen rain forest on nutrient-poor Oxisols (Schubart *et al.* 1984). However, there is a lack of experimental data on limiting

nutrients in lowland evergreen rain forests (Proctor 1992), and this applies to heath forests as well. Recently, Anderson & Spencer (1991) have stated that "there appears to be little evidence that the stature and the productivity of mature forests are related to the inherent fertility of parent soil". Earlier, in a review on rain forest mineral nutrition, Vitousek & Sanford (1986) suggested that `an association between soil fertility and above-ground biomass is unlikely in any but the most extreme cases'. However, there is still a widely accepted view that forest production, if not biomass, is limited by soil nutrient supply (e.g. Jordan 1985), and heath forests in the Rio Negro basin may be one of such extreme cases suggested by Vitousek & Sanford (1986).

In the same way heath forest soils are generally nutrient poor, having a low cation exchange capacity, they also are very acidic, with a pH less than 4.0, and have a low buffering capacity owing to their low concentrations of iron and aluminium sesquioxides (Whitmore 1984; Bravard & Righi 1991), leading some to suggest low pH as a major cause (Rodrigues 1961). Thompson *et al.* (1992) found that Maracá soils had a higher base saturation and were less acid than soils usually described for heath forests (Brünig 1974; Proctor *et al.* (1983a) and concluded that certain features of heath forest soil chemistry such as high acidity (which is likely to have a marked influence on nitrogen supply for example) or toxicity of phenolic compounds are the most likely cause of heath forest features.

Heath forests may be caused by soil toxicity from high concentrations of H^+ or phenolic substances or both (Thompson *et al.* 1992). The low pH might result from a lack of Al-containing minerals since aluminium ions positively buffer the soil pH to about 4.0 (Whitmore 1984; Thompson *et al.* 1992). In addition, phenolic compounds are known to be relatively concentrated in heath forest leaf litterfall (Janzen 1974; Anderson *et al.* 1983; Brünig 1983), and are a potential source of soil toxicity (Kuiters 1990). Janzen (1974) predicted that heath forest leaves would contain exceptionally high concentrations of phenolics and other secondary compounds, and that leachates could prevent plant growth. In Mulu, heath forest leaves had higher polyphenol concentrations, but there was no evidence of a greater toxicity to herbivores, since herbivory rates in the other forest types were similar (Anderson *et al.* 1983). In Manaus, in sites near those of the present

study, Lisboa (1976a) and Anderson & St. John (1981) found evidence of higher concentrations and toxicity of polyphenols from leaves of heath forest species, but further experimental evidence is still lacking for the role of phenolics in determining heath forests.

A possible anthropogenic cause for heath forests, especially the stunted ones, has been suggested by Prance & Schubart (1978) who found evidence of human settlements in heath forest areas in central Amazonia. However, there were no similar records from other areas of heath forest in the tropics to confirm this hypothesis.

In summary, none of the suggested causes of heath forest is accepted generally.

In central Amazonian heath forests, most of the studies have been carried out near Manaus and have been largely descriptive (Takeuchi 1960; Lisboa 1976b; Anderson *et al.* 1975; Braga 1977a; Braga 1977b; Macedo 1977; Anderson 1978; Anderson 1981). Others have studied the general aspects of the ecosystems (Braga & Braga 1975; Lisboa 1975), microclimatological aspects (Ribeiro & Santos 1975), the possible origin of heath forests in the region (Prance & Schubart 1978), the autoecology of dominant species (Lisboa 1976a), the soils (Klinge 1965), root biomass (Klinge 1973b), aspects of soil hydrology and chemistry (Reichardt *et al.* 1975; Santos & Ribeiro 1975), forest streams and stemflow (Ribeiro *et al.* 1978; Santos *et al.* 1981), soil respiration (Martins & Matthes 1978), the phenolic concentrations of tree leaves (Anderson & St. John 1981), the nutrient contents of selected *campina* leaf species (Klinge 1985), and, more recently, the litter invertebrates in *campinarana* (Adis *et al.* 1989) and the phenology of woody species (Alencar 1990). However, more integrated studies on functional aspects of the ecosystems, including the nutrient cycling and limiting factors for plant growth in the heath forests have not yet been made in Brazil apart from the work of R.C.C. Luizão (1994). Published studies on the functioning of heath forests in Amazonia have almost all been made at San Carlos do Rio Negro, Venezuela, including studies on biomass, girth increment, leaf form and limitations to growth, litterfall, nutrient cycling and water relations, (all reviewed by Medina & Cuevas 1989 and Jordan 1989). Forests growing on the podzolised quartz sands in the Rio Negro region are thought to have several nutrient conserving mechanisms which could explain the relative efficiency of nutrient use

(Herrera *et al.* 1978; Herrera 1979; Herrera & Jordan 1981; Klinge & Herrera 1983). However, these current models of rain forest adaptation to low soil nutrients are inadequate in view of recent results from tropical forests, including heath forests (Proctor 1992). Data from Sarawak (Proctor *et al.* 1983a,b; Primack *et al.* 1987), and Maracá Island (Scott *et al.* 1992; Thompson *et al.* 1992) largely contradict that model, and other recent studies are showing similar contradictions (e.g. Green 1992; Burghouts 1993). Thus, it is evident that large gaps remain in our understanding of the fundamental relationships between soil and forests (Proctor 1992).

In Amazonia, few studies on heath forests have examined aspects of their soil processes (Singer & Araujo 1979; Herrera 1979; Jordan & Murphy 1982; Cuevas & Medina 1986, 1988; Medina & Cuevas 1989; Luizão 1994). Among these studies, those in Venezuela were made on heath forests which are located on soils which were subject to periodic waterlogging. Virtually no studies other than that of Luizão (1994) on the dynamics of soil processes have been made on the better-drained heath forests of central Amazonia.

In the present study, *campina* (small facies of heath forest) will be referred to as **SHF**, and *campinarana* (tall facies of heath forest) as **THF**, contrasted with the lowland evergreen rain forest, referred to as **LERF**.

Aims of this study

This study compares the structure and functioning of three contrasting forest types. Examples of a stunted heath forest, a tall heath forest, and a mesophyllous lowland evergreen rain forest were chosen in an area of about 1.5 km^2 where all three forest types occurred. Chapters 2 and 3 concentrate on the characterization of the study sites, including climate, soils and vegetation. Chapters 4 to 6 investigate the dynamics of fine litter production, decomposition, and the associated litter animals acting on organic matter decay and nutrient release. Chapters 7 and 8 investigate which nutrients limit plant growth on heath forest soils. A general discussion including the conclusions is given in Chapter 9.

Chapter 2. SITES AND SOILS

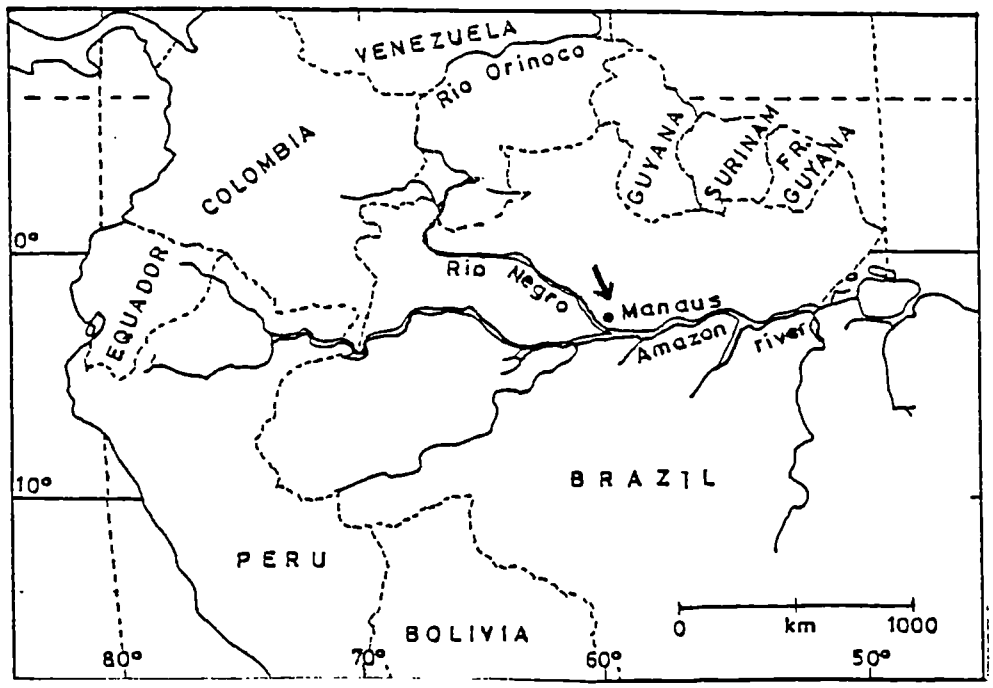
INTRODUCTION

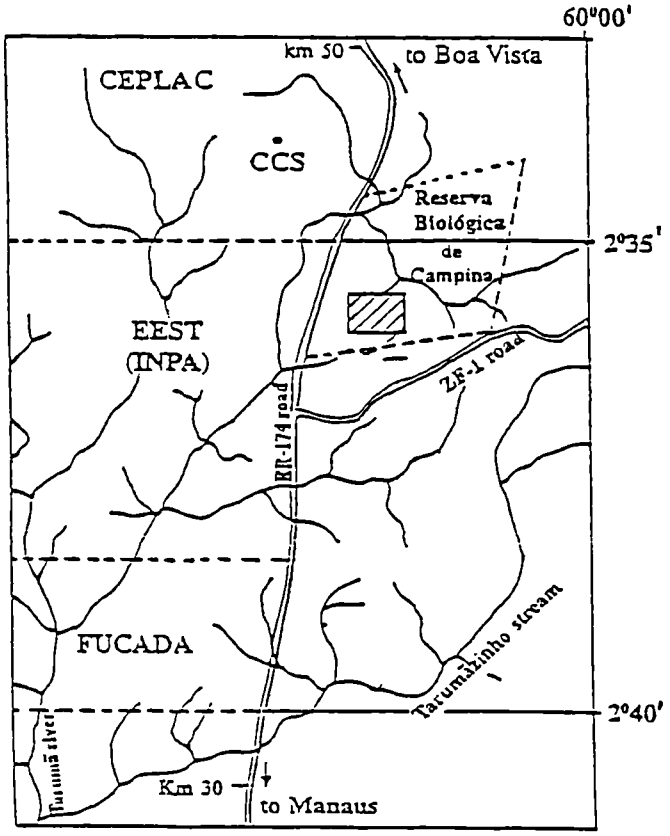
The study was made in the *Reserva Biológica de Campina*, a biological station in the centre of Amazonia, and belonging to the National Institute for Amazonian Research (INPA). The station is located 60 km north of Manaus at about 2° 36' S and 60° 01' W (Figs. 2.1 and 2.2). Of the total *Reserva* area of 900 ha, about 3 ha are SHF (stunted facies of heath forest), 150 ha of THF (tall facies of heath forest) with the rest LERF (lowland evergreen rain forest).

GENERAL FEATURES OF THE STUDY SITES

Climate

The Amazon basin, with an estimated area from 5 x 10^6 km^2 to 6 x 10^6 km^2 (Daly & Prance 1989), corresponds to one third of South America, and 45 % (3.8 x 10^6 km^2) of Brazil. The Amazonian drainage system has more than 1 000 tributaries and flows into the Atlantic Ocean where it accounts for 15-20 % of the world's total fresh water discharge (Leopoldo *et al.* 1987). Most of Amazonia is lowland and has a humid, warm climate, but considerable climatic variations are found. To the north and south there are mountains and as a result, there is a diversity in temperature, precipitation, and seasonality (Bigarella & Ferreira 1985). The total annual precipitation varies from 1 500 mm to 3 500 mm (Salati 1985). The central Amazon plateau, however, with a mean slope of only 2.5 cm km^{-1} is unique in the world (Salati 1985), and has very little temperature variation with rainfalls ranging from 1 800 mm to 2 800 mm. In the city of Manaus (3° 08' S; 59° 00' W) the solar energy is maximum in January and minimum in June. The solar energy input is limited by cloud cover, which is relatively high although variable throughout the year (Salati 1985). The mean cloud cover in central Amazonia is about 50 %, and in Manaus it varies from 30 % in March to 70 % in July-August.





CEPLAC - Cocoa Cropping Development Agency (Ministry of Agriculture)

CCS - CEPLAC's climatological station

EEST - Tropical Forestry Experimental Station of INPA (National Institute for Amazonian Research- Ministry of Science and Technology)

FUCADA - Model Farm for the Agricultural District (Secretary for Regional Development)

Fig. 2.1: Map of the northern part of South America with arrow showing the approximate location of the study sites and, below, the location of the *Reserva Biológica de Campina* and other research stations north of Manaus, Amazonas state, Brazil.

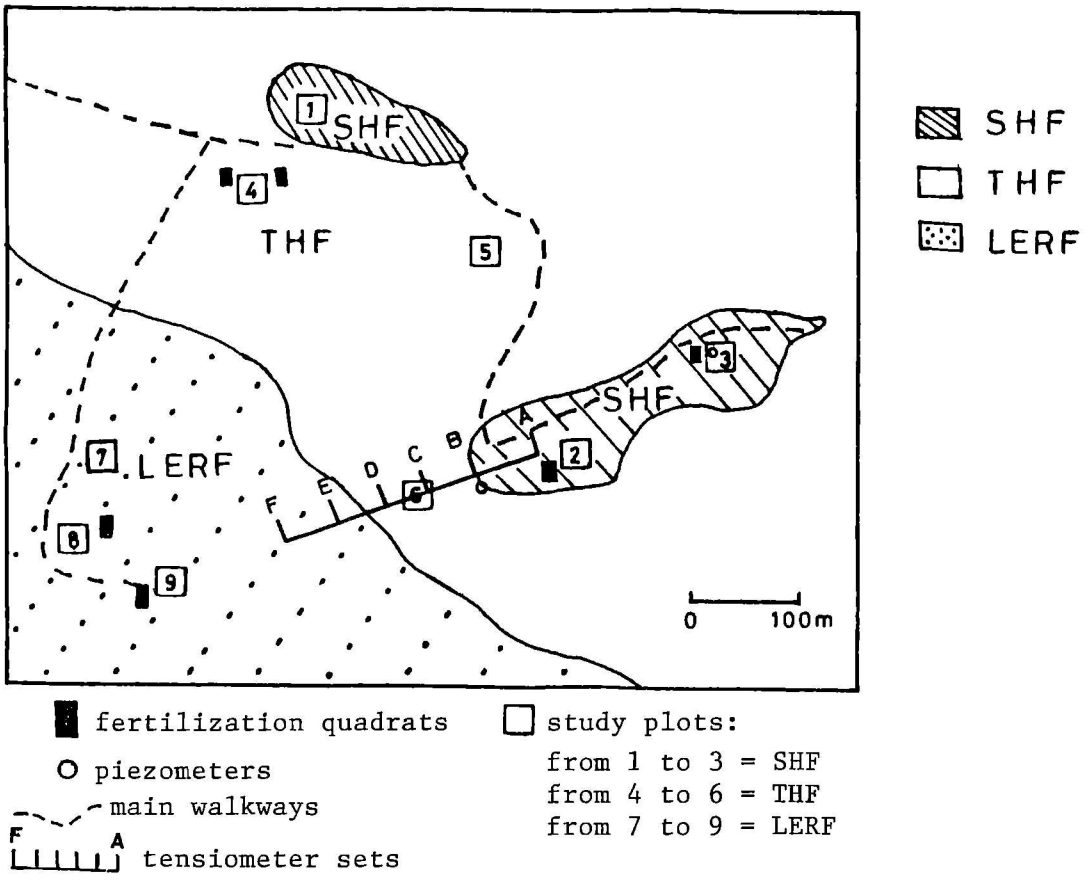


Fig. 2.2: The main entrance of the *Reserva Biológica de Campina* and detailed location of the study plots.

In the central Amazonia plateau, the variation of the mean monthly temperature is small (Salati 1985). In Manaus, the highest mean monthly temperature is 27.9 °C in September, and the lowest is 25.8 °C for February, March and April. The mean annual temperature is 26.7 °C; the mean values of the maximum and minimum temperatures are 31.2 °C and 23.7 °C. The extreme absolute temperatures, recorded over 70 years between 1911 and 1980, were 18.5 °C on 31 July 1955 and 37.8 °C recorded on 3 October 1935 (Salati & Marques 1984). The isothermic condition (very low temperature variation) of the central Amazon plateau is a direct consequence of the water vapour which is always high in the region (Leopoldo *et al.* 1987). The annual mean relative humidity is 84 % with a range of 77-88 % (IPEAAOc 1971). In the *Reserva*, in areas adjacent to the study plots, humidities varied over the year from 81-90 % in the SHF, and from 91-97 % in the THF (Ribeiro & Santos 1975). In the SHF exposed soil (sand) the soil temperatures at the surface layer varied from 25.6 °C to 42.3 °C; in the open SHF under lichens they were 23.6 - 32.4 °C; in the THF they were 23.3 - 29.4 °C. No corresponding measurements were made on the LERF sites which are likely to have a similar but smaller range to that of the THF.

The climate in the Manaus region corresponds to the 'Am' type of the Köppen classification (Ribeiro & Adis 1984), where: A = a tropical rainy climate, where mean monthly temperatures are never below 18 °C; and m = a climate where there is a relatively long dry season, but the total annual rainfall is enough to prevent plants wilting. However, near Manaus, where there is a fairly well defined dry season from June to October, trees on Oxisols begin to lose their leaves after a dry period of 10-15 d, perhaps indicating some deficit of water in the soil (Salati 1985).

During the field study (from 30 December 1991 to 29 September 1993), climatic data were recorded at the CEPLAC Experimental Station, 3 km northwest of the study sites). The mean monthly temperature recorded during 1992 ranged from 24.6 °C in August to 26.6 °C in January. From January-September 1993, the mean monthly temperatures varied from 24.8 °C in March to 25.8 °C in May and September (Table 2.1). The absolute minimum temperature was 18 °C (colder than the absolute minimum temperature in Manaus), recorded in January 1992 and in August 1993, while the absolute maximum was exactly the same (34.8 °C) in seven months during the study. The mean monthly

relative humidity measured in a wide forest gap close to the Station ranged from 84 % in June 1992 to 90 % in December 1992, January and April 1993 (Table 2.1).

Rainfall and water balance in the study area

In the Manaus area, the mean annual rainfall is about 2 100 mm with a rainy season from December to May, and a dry season from June to October (Ribeiro & Adis 1984; Salati 1985). The rainiest months tend to be March and April, with about 300 mm each, and July, August, and September normally receive less than 100 mm each. The mean rainfall for a period of 70 years (1911-1980) was 551 mm in the dry season (June to November), and 1 554 mm in the rainy season (December to May) (Ribeiro & Adis 1984; Salati 1985). Measurements made in a watershed catchment under lowland evergreen rain forest in the `Model basin', located 9 km northwest of the study sites, showed that the rainfall interception by the vegetation was 25.6 %, and 48.5 % was transpired by the plants. Thus, evapotranspiration was 74.1 %, with a daily rate of 4.1 mm. About 70 % of the total precipitation fell in the form of heavy rains and 25.9 % of the total rainfall was drained through the forest streams (Leopoldo *et al.* 1982). There was almost no evaporation from the soil under forest. However, in the study plots, especially in the SHF and THF, which have a lower canopy cover and much sunlight reaching the forest floor, some water evaporation from the forest soil is likely. Rainfall, throughfall, stemflow, and evapotranspiration, should also be different in SHF and in THF. The total rainfall recorded during 1992 was 2 059 mm with a pan evaporation total of 665 mm. The dry season, from May to November, was longer than normally found in the region (Fig. 2.3), with a pan evaporation higher than the total rainfall in June (Fig. 2.4). On the other hand, the following wet season was longer than normally recorded (Ribeiro & Adis 1984; Salati 1985), lasting from December 1992 to July 1993. and the rainfall for the period January-September 1993 was 2 104 mm with a pan evaporation of 448 mm (Fig. 2.4). There were several dry spells (Fig. 2.3), each one with more than seven dry days (`dry' days defined *sensu* Medina *et al.* (1978) as the ones where rainfall was equal or lower than the pan evaporation), especially in the dry season of the first year (Table 2.2). The definition of Medina *et al.* (1978) for `dry day' was adopted because the high evaporation in the study

Table 2.1: Mean monthly temperature (°C) (with the ranges of mean minima and mean maxima in parenthesis) and relative humidity of the air (% RH) in the CEPLAC Station, 3 km northwest of the *Reserva Biológica de Campina* in the period of the main field studies (CEPLAC unpublished).

Years	Months	Temperatures (°C)	% RH
1992	January	26.6 (22.2 - 31.6)	86
	February	25.8 (23.0 - 31.3)	87
	March	25.5 (23.1 - 30.3)	89
	April	25.8 (23.6 - 30.8)	87
	May	26.4 (23.2 - 31.6)	86
	June	25.8 (21.9 - 32.4)	84
	July	25.0 (21.9 - 32.4)	85
	August	24.6 (21.1 - 30.8)	87
	September	26.0 (22.1 - 33.0)	83
	October	26.1 (22.3 - 32.8)	84
	November	26.0 (22.7 - 32.4)	86
	December	25.3 (22.8 - 30.1)	90
1993	January	24.9 (22.4 - 30.1)	90
	February	24.9 (22.4 - 30.6)	89
	March	24.8 (22.5 - 30.0)	89
	April	25.2 (21.8 - 30.5)	90
	May	25.8 (22.1 - 31.6)	88
	June	25.5 (22.1 - 31.3)	88
	July	25.1 (21.4 - 31.6)	86
	August	24.9 (21.4 - 31.7)	87
	September	25.8 (21.4 - 32.3)	86

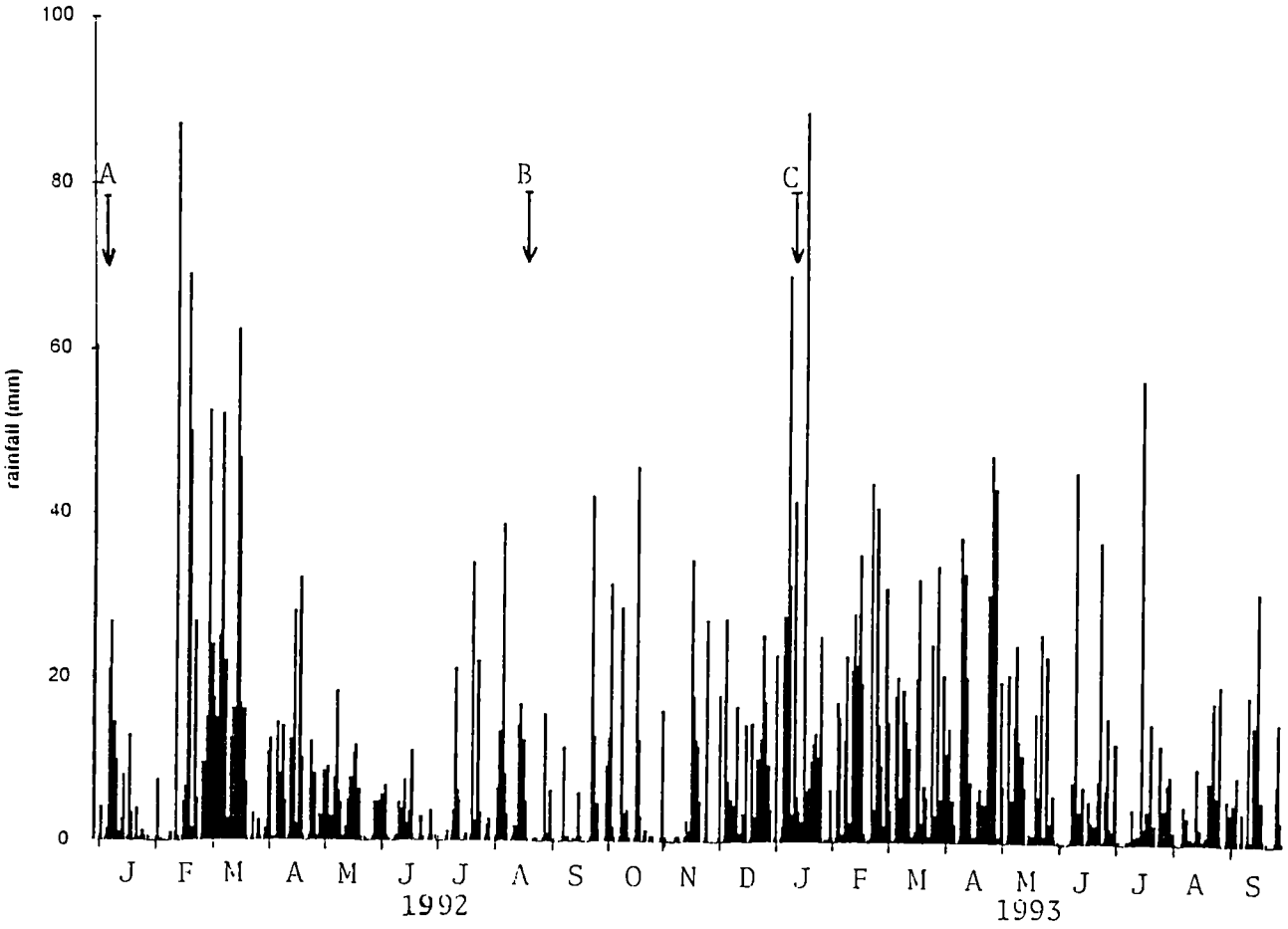


Figure 2.3: Daily rainfall during the period of the main field studies (30 December 1991 until 29 September 1993). Arrows indicate the starting dates of the three decomposition experiments (A.B, and C - Chapter 5); Arrow A mark the starting date of both the 1-year litterfall collection (Chapter 4) and the litter animal study (Chapter 6).

area (generally between 2 and 4 mm d^{-1}) would nullify many 'wet days' if they were defined as days with say rainfall < 0.25 mm. In 1992, three spells of nine dry days each were recorded in February, August and November; two of eleven days each were recorded in October and in June/July; and one of twelve days in October/November. The longest dry spells in 1993 both lasted eight days in May/June and in July/August.

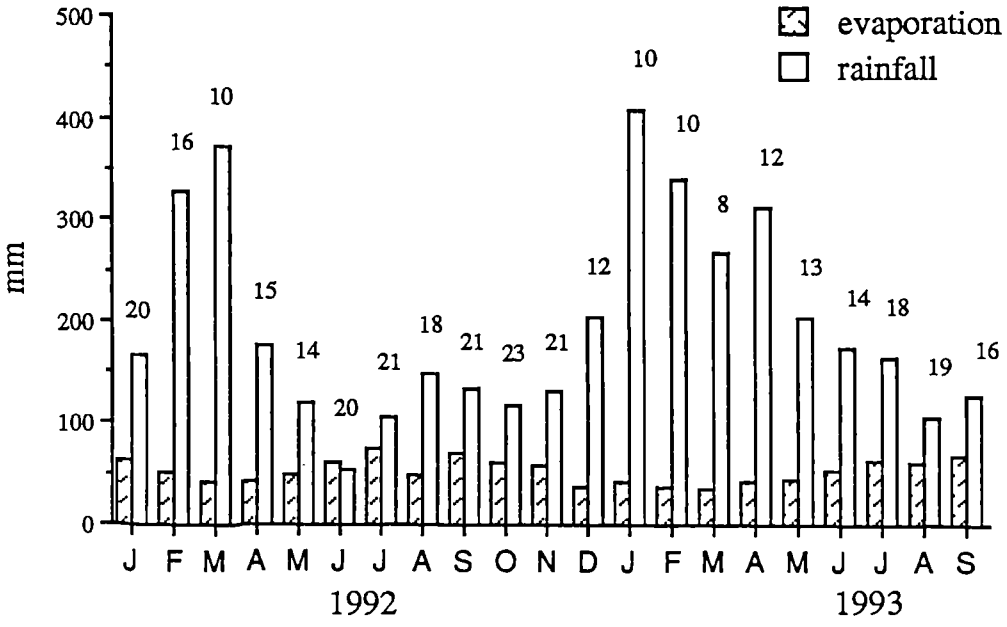


Fig.2.4: Monthly rainfall (mm) (blank bars), and pan evaporation (mm) (hatched bars) in the *Reserva Biológica de Campina* during the field study. The numbers above the bars are the number of dry days in each month.

Geology and geomorphology

The central Amazonia plateau is exceptionally flat, with a maximum slope of 100 m over almost 4,000 km (Salati 1985). In Brazil, the Amazon river bed falls only 60 m, an average of 2 cm km^{-1} from the Brazilian western frontier city of Tabatinga to its mouth at Belém (roughly 3,000 km). The small slope is the reason why the heavy rains from December to May flood the eastern forests to depths of 7-9 m (Leopoldo *et al.* 1987). The geologic basement of the basin is entirely of crystalline rocks of the Precambrian (Putzer 1984). The formation of the modern Amazonian drainage system is assumed to have taken place in the late Tertiary or early Pleistocene (Irion 1989). In the basin area between the Precambrian Brazilian and Guyana shields, sediments weathered from the crystalline rocks of those shields have accumulated since the Paleozoic. The surface is formed by Cretaceous sediments, and outcrops of Paleozoic sediments occur only at the edges of the shields (Irion 1989). At the latitudinal limits of the lowland terrain there are mountains which reach 800 m in the south and 3,000 m in the north (Bigarella & Ferreira 1985). In the middle Amazon basin (from Manaus to the mouth of the river Xingu) the predominant soft Tertiary sediments belong to the *Formation Alter do Chão* (Putzer 1984). However, most of the western parts of the Amazonia lowlands are covered by more recent (Quaternary) sediments eroded from the Andes, and richer in nutrients than the Tertiary sediments, which are predominantly quartzic or kaolinitic. The layer of kaolinitic clay reaches a thickness of 10-20 m. Kaolinite, which consists of silicon, aluminium, hydrogen, and oxygen, is one of the most weathered minerals and is poor in plant mineral nutrients. In the Manaus area, three lithostratigraphic units have been identified: the Trombetas Formation, of the Presilurian, on top of which the late Tertiary *Formation Alter do Chão* is located, locally covered by Quaternary sediments (Dias *et al.* 1980).

Geology and geomorphology of the study area

The *Reserva* has both Tertiary and Quaternary (Pleistocene) sediments (Dias *et al.* 1980). The Tertiary sediments (of the *Formation Alter do Chão*) are sands or clays. The main constituents are resistant minerals such as kaolinite, quartz. and small amounts of oxides of iron and aluminium (Dias *et al.* 1980; Ranzani 1980; Chauvel 1982; Chauvel *et al.*

1987). The predominant weathering process is the complexing of iron with organic material resulting from the action of decomposing roots on the arenites (cemented sandy sediments) with the consequent removal of the sesquioxide cement (Ranzani 1980). The Tertiary sedimentary plain is well dissected by its drainage system, resulting in plateaux, valleys and several slopes (Dias *et al.* 1980). Lucas *et al.* (1987) reported an altitudinal variation of about 50 m between the upper plateau and the lower level of the relief in a toposequence 2 km northwest of the study plots. The sand sediments (from the Pleistocene) are deep deposits of quartzic white sands, possibly of fluvial origin, which may or may not cover a hardpan (Ranzani 1980). However, Lucas *et al.* (1987) and Irion (1989) argue that the quartzitic sands are not of fluvial origin. The Oxisols found in the area result from the weathering of the kaolinitic material of the Tertiary while the Spodosols were formed on the quartzitic white sands (IPEAAOc 1971). The origin of the parent material of the Spodosols in the area is still disputed. According to Klinge (1965) they are alluvial sandy sediments deposited by flooding rivers, and are sandier and more recent than the *Alter do Chão* sediments. The A2 horizons of the Spodsols have gradational contact with the flanking Oxisols, with transitional `leached' soils called `sandy bleached brown loams' and `eluviated brown loams' (Klinge 1965). The white sands of the Spodosols, in some cases, could have been developed from the eluviated brown loams which have a parent material of fluvial sediments (Klinge 1965). However, Lucas *et al.* (1984) and Chauvel *et al.* (1987) suggested that the Spodosols are the result of local weathering and pedogenesis (governed by underground water fluxes, particularly active in the slopes of the terrain), and that a `transformation system' in which Oxisols are progressively replaced by Spodosols is currently taking place. Following the last hypothesis, Bravard & Righi (1989), studying a soil catena (toposequence of 1.7 km with a total slope of less than 3 %) 2 km northwest of the study sites, ascribed the formation of Oxisols mainly to hydrolytic weathering, whereas the genesis of Spodosols was largely governed by organic acids complexing with metals (organic complexation). They argue that several processes of weathering and pedogenesis had been operative. The small amount of SiO_2 in the Oxisols was attributed to the dissolution of quartz without a corresponding hydrolysis of kaolinite. The decreases in clay contents and increases in

quartz in the soils from the upper to the lower end of the toposequence were attributed to the combination of hydrolytic weathering and either clay eluviation or selective erosion or both from that fraction. They suggested that podzolization begins when a critical stage in the clay impoverishment is reached. Destruction of clay minerals continues but the migration of organo-complexes within profiles becomes important (Bravard & Righi 1989). They found that the average concentrations of SiO_2 in the surface and B horizons increase from the Oxisols to the Spodosols, and the reverse is true for Al_2O_3 and Fe_2O_3. The geochemical evolution of the Oxisols reduced the amounts of SiO_2 and increased the relative amounts of Al_2O_3 and Fe_2O_3. In contrast, the Spodosols are marked by a greater accumulation of SiO_2 and apparent loss of Al_2O_3 and Fe_2O_3. The mobility order during the weathering and pedogenesis of the soils of the plateau (leading to the Oxisols) would be $SiO_2 > Al_2O_3 > Fe_2O_3$ but in the lower part of the slope (leading to the Spodosols) it would be $Al_2O_3 > Fe_2O_3 > SiO_2$ (Bravard & Righi 1989). Thus, Spodosols would be the result of strong podzolization processes, being developed on quartzic sands which may be the result of an intense hydrolysis of clays or their impoverishment through eluviation or selective erosion (Bravard & Righi 1990). Evidence was found of a currently active podzolization in the lower part of their toposequence, and that podzolization in Amazonia occurs mainly during the wet season (Bravard & Righi 1990).

The SHF and THF plots are virtually at the same altitude (with slopes < 3 %) and the LERF plots are 2-5 m higher (slopes < 10 %). However, stressing the influence of groundwater levels, slight variations in the topography can reflect a great change in the vegetation, as found in San Carlos do Rio Negro, Venezuela, where three types of heath forests occur on the coarse podzolised sands within an elevational gradient of 2 m or less (Jordan 1985).

Soils

Oxisols and Ultisols are the most common soils in Amazonia (Camargo & Falesi 1975; Sanchez 1976), with Oxisols considered widely predominant. The FAO/UNESCO (1974) map estimated Oxisols to cover 67 % and Ultisols 15 % of Brazilian Amazonia. However, more recent surveys (Richter & Babbar 1991) have shown that the areas covered by

Ultisols are far larger (and Oxisols far smaller) than previously estimated. The current map (EMBRAPA 1981) shows Oxisols occupying 39.1 % of Brazilian Amazonia, and Ultisols 29.9 % (Richter & Babbar 1991). In central Amazonia, Oxisols are common, and Oxisols with clayey texture account for about 60% of the soils in the area between km 30 and km 105 of the BR-174 (national road from Manaus to Boa Vista) in which the study sites are located (IPEAAOc 1971; Dias *et al.* 1980). The soils of the heath forests in central Amazonia have been usually considered either as 'Podzois gigantes', 'Podzois hidromorficos' (Klinge 1965; IPEAAOc 1971)) or 'Areias Quartzosas' (Quartzitic Sands) in EMBRAPA (1981), which would correspond to the Tropaquent/Quartzipsamments of the US Soil Taxonomy (Soil Survey Staff 1975, 1987) (Table 2.2). The Quartzitic Sands are estimated to cover 3.86 % of Brazilian Amazonia (EMBRAPA 1981; Richter & Babbar 1991). The soil is classified as a Quartzitic Sand when the bleached sand layer is beyond the reach of field soil equipment (more than 3 m deep) (Sombroek 1984). This classification seems to be also applied to central Amazonian soils which lack the humus layer (Ranzani 1980).

In the study sites, the soils are not hydromorphic, but they have fast or excessive drainage (Reichardt *et al.* 1975), and do not show evidence of an ochric (yellowish) epipedon or recently formed man-made horizons which characterize the Quartzipsamments (Sanchez 1976). On the other hand (despite not being found in the pits excavated), there was evidence of a hard-pan below the sand. For example, in pit 2 several stones were found in the profile below 40 cm, and plastic tubes introduced nearby to monitor the water-table levels apparently were limited in depth by a hard-pan at 1.8 m and 3.5 m. Also the occurrence of spodic (organically cemented layer) horizons developed on sandy materials, characteristic of the Spodosols, can be observed in road cuts within 1 km of study sites. Thus, the SHF and THF soils were considered to be Spodosols ('Podzols' in EMBRAPA (1981), and the LERF Ultisols are *Solos Podzólicos* (EMBRAPA 1981). Typically, 'Podzols' have extreme sandiness and a hard-pan (Sombroek 1984). while Ultisols generally have better physical properties. In both, the SHF and THF, however. the occurrence of hard-pans if they were present at all was at considerable depth (below 2.5

m), and the groundwater was never observed within 40 cm of the surface, even in the wettest periods.

Table 2.2: The soils of the study sites and surroundings in the three major classification systems for soils (after Sanchez 1976; Richter & Babbar 1991) discussed in relation to the study sites.

Brazilian[1]	**FAO / UNESCO**[2]	**USDA Soil Taxonomy**[3]
Latossolos	Ferralsols	Oxisols
Latossolos Amarelos	Xanthic Ferralsols	Ustox / Udox
Solos Podzólicos	Acrisols	Ultisols
Podzóis	Podzols	Spodosols
Regossolos	Arenosols / Regosols	Psamments / (Entisols)
Areias Quartzosas	Arenosols	Quartzipsamments
Podzóis Gigantes	Arenosols	Albic quartzipsamments
Podzóis Hidromórficos	Arenosols	Tropaquods

[1] EMBRAPA (1981)
[2] FAO / UNESCO (1974)
[3] Soil Survey Staff (1975, 1987)

Study plot selection

Within the *Reserva* three 50 m x 50 m plots were selected at random within the THF and LERF. The positions of the three SHF plots had to be adjusted so as not to include parts of the THF which interdigitates in the limited area of the SHF. The plots were marked with nylon strings, and subdivided into four subplots of 25 m x 25 m. Plots 1 to 3 were in SHF, 4 to 6 in THF, and plots 7 to 9 in LERF (Fig. 2.2). All nine plots were made permanent by marking corners and internal 25 m subplots with plastic tubes, and tagging trees with numbered aluminiun tags.

SOILS OF THE STUDY PLOTS

Soil sampling

A soil auger survey to 2.3 m depth just outside the SHF plot 1, the THF plot 4, and each of the three LERF plots, was made to inspect the soil horizons prior to pit excavation. In September 1993 (dry season), one soil pit 1-m deep was excavated at the side of each of the study plots, and in each pit, 500-g composite samples from the upper organic layer and each of several depths (generally at 10-cm intervals), were taken for analysis. The composite samples were obtained by carefully mixing similar amounts of soil taken from three different walls of the excavated pits at similar depth. Brief descriptive notes were made in the field and are summarized in Appendices 2.1-2.3. The soil samples from the pits were collected on 29 September 1993, following a period which was wetter than usual (123 mm of rain fell from 1-29 September compared with the average September value of 80 mm), and hence the soils were quite moist.

Soil analysis

The samples were air-dried, hand-sorted (using plastic gloves to avoid contamination) for roots, stones, animals and other materials, and sieved through a 2-mm mesh before analysis. Samples of the upper organic layer, composed of litter, root mat and humus, were sieved and ground before the extraction. Particle-size analyses were made using the pipette method (Black *et al.* 1965) on each of the soil samples collected in the nine pits. pH_{H2O} was measured in a 1:2.5 soil:deionized water mix which was shaken for 1 h and allowed to stand for 30 min. pH_{KCl} was measured in an extract obtained by shaking 20 g of soil with 50 ml of 1 M KCl for 1 h, after allowing the mixture to stand for 30 min. Organic carbon was determined colorimetrically by a modified Walkley-Black method (Anderson & Ingram 1993). Total nitrogen was determined by colorimetry following digestion in sulphuric acid and hydrogen peroxide, using selenium as a catalyst. Total phosphorus was extracted using sulphuric acid, and measured colorimetrically, while available phosphorus was measured by colorimetry in Bray-Kurtz extracts (Anderson & Ingram 1989). The exchangeable bases were leached from 10-g subsamples of soil by ten successive additions of 10 ml of 1 M ammonium acetate solution at pH 7.0, and analysed

for potassium, sodium, calcium, and magnesium, using Atomic Absorption Spectrophotometry (AAS). Available aluminium and total acidity were determined by titration. Ten successive additions of 10 ml of 1 M potassium chloride solution were made on 10-g subsamples of soil, and the leachate was treated with 2.5 mM sodium hydroxide solution and phenolphthalein indicator to measure total acidity. After adding 10 ml of 1 M potassium fluoride to the titrated solution, another titration with 5 mM hydrochloric acid gave the values for exchangeable aluminium. Cation-exchange-capacity was calculated from the sum of total exchangeable cations plus total acidity. Two internal reference samples (samples with known concentrations, of material previously analysed against standard certified soil samples from the ISRIC - International Soil Reference Institute, Wageningen) and two blanks were analysed in each batch of 20 samples, keeping the accuracy of the determinations within a range of variation of less than 10 %.

Organic and upper mineral soil moisture

Samples of both organic and upper mineral soil layers were taken regularly (generally every week) from January 1992 to September 1993, for gravimetric determinations of moisture content (Hillel 1982). A stainless-steel corer was designed (Fig. 2.5) and used throughout the study to allow the separation of the organic and mineral layers in the field (Fig. 2.6). Using a narrow knife which was introduced in the side of the corer, firstly a 5-cm deep upper mineral soil sample was separated and placed into a plastic bag; then the remaining organic layer on the top of the corer was placed into a second plastic bag. There was often not enough organic matter for analyses from auger samples from the SHF. To augment these samples, a larger area (50-100 cm^2), at the side of the point selected for the auger samples, was hand-collected in addition to that sampled with the corer. The upper `mineral' soil layer in the THF was generally a mixture of mineral soil and particulate organic matter, included in the sample. In each of the study plots, at each sampling time, ten samples were taken in a stratified random design in which at least two samples were collected in each of the four quadrants of every plot. The ten samples were then mixed in a plastic bag to produce, for each study plot, a composite sample for each of the layers, organic and upper mineral soil. Lack of oven space in the laboratory was the

main reason for using composite samples. Gravimetric moisture was calculated for each layer as the mean of three subsamples dried for 48 h at 105 °C.

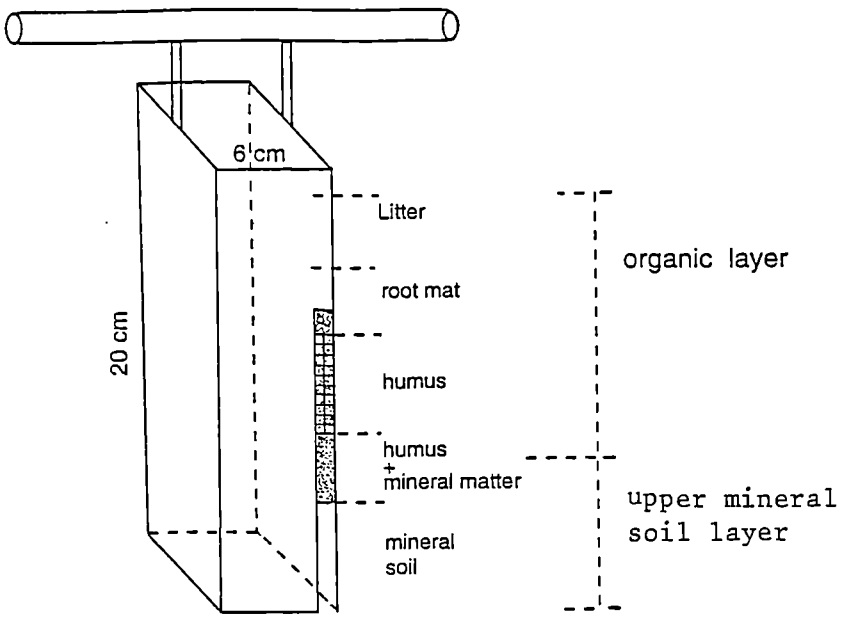


Figure 2.5: Diagram of the stainless-steel corer used for sampling organic and upper mineral soil layers for determinations of gravimetric moisture, showing a typical section of the upper layers in the THF.

Groundwater level

Two 20-cm diameter plastic tubes, 1.75 m and 3.5 m deep in the soil, set up for previous studies (Reichardt *et al.* 1975; Ranzani 1980), were used to monitor the level of the groundwater (Hillel 1982). The first tube was located inside SHF plot 3, and the second between SHF plot 2 and THF plot 6 (Fig.2.2). The levels were assessed nineteen times (generally every week) from early March 1993 (mid wet season) to the end of September (late dry season) 1993, the second and wetter year of the study (Fig.2.3).

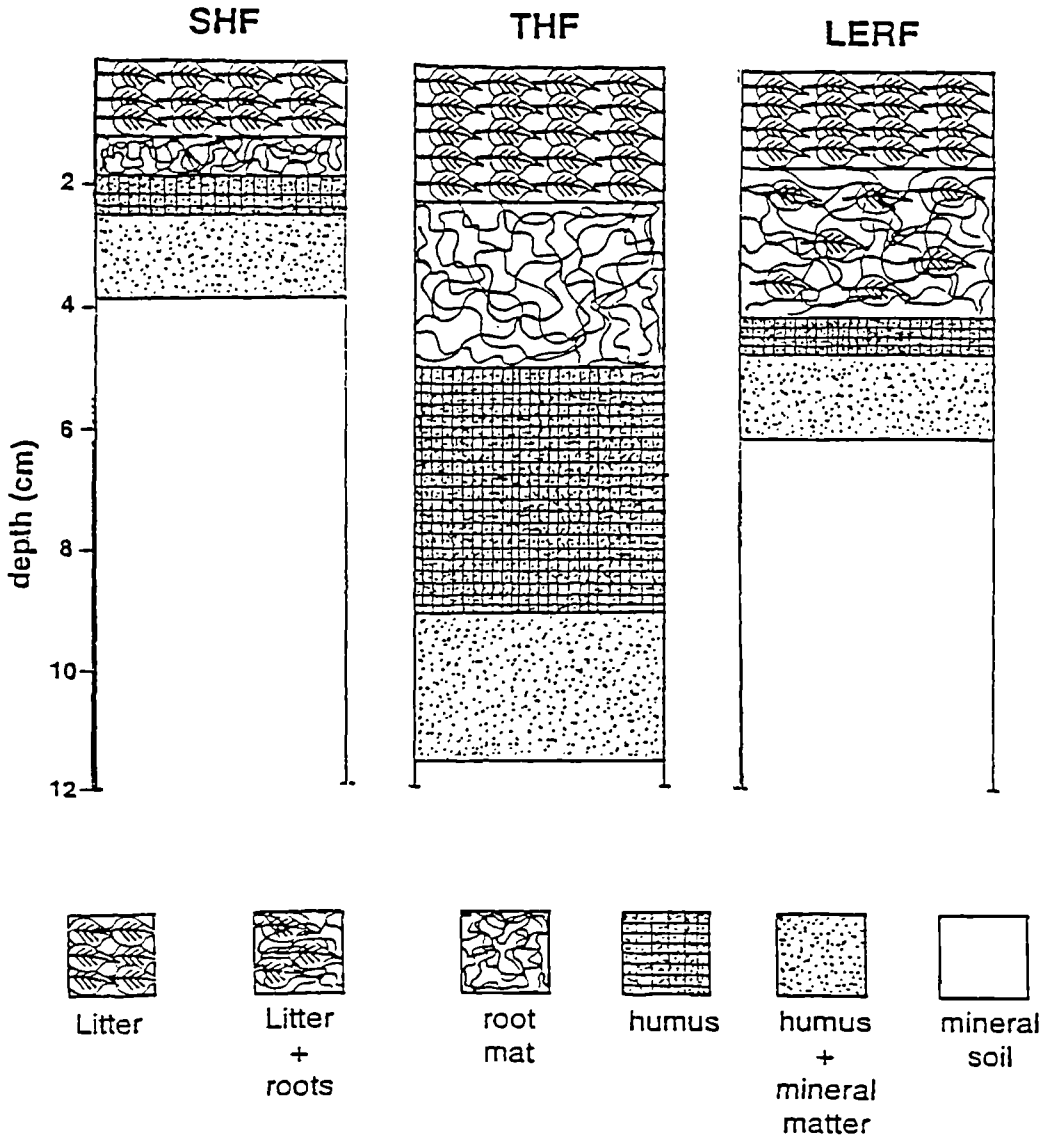


Figure 2.6: Schematic composition of the organic and upper soil mineral layers in the SHF, THF, and LERF.

Soil water tension

The water matric potential (Hillel 1982) was measured in all three forest types at the same time as the groundwater level. Six sets of tensiometers were installed at 50-m intervals in a 250-m long transect spanning the three forest types, but generally not crossing the study plots (Fig. 2.2). Each set was composed of four porous-ceramic cup tensiometers with

mercury columns (pre-tested in the Soil Physics Laboratories at CENA -Atomic Energy Agricultural Centre, Piracicaba, São Paulo) installed at different depths in the soil: 12.5 cm, 37.5 cm, 62.5 cm, and 87.5 cm. The first set `A' was installed in an open SHF area, the second `B' in the transition from SHF to THF, the third `C' inside the THF plot 6, the fourth `D' in the transition from THF to LERF, and the last two `E', and `F' in the LERF (Fig.2.2). A lack of tensiometers prevented the installation of one set in each study plot. At each measurement time, generally at weekly intervals, the height of the mercury columns was recorded, and columns with air bubbles were repaired. The readings were made at the same time as the groundwater records, but an additional daily series of tensiometer measurements was made, once a day, from 4 to 11 May 1994 to assess short-term changes in soil water tension. This time coincided with the availability of field personnel at a time of the year when there are scattered showers but few dry days.

Data analysis

The moisture contents of the organic and the upper mineral soil layers, and the soil water tension were analysed to assess differences among forest types, and months of the year. Nested (plots within forest types) analyses of variance were used for assessing differences in moisture among forest types. Comparisons of soil water tensions among the sites in the transect were made using a repeated measures procedure as a restricted form of the mixed model of analysis of variance (Zar 1984). The F-test degrees of freedom were automatically adjusted by Minitab, on the within-plots tests, being approximated from the linear combination of mean squares and their degrees of freedom. Regression analyses were made to relate soil moisture to climatic factors and correlation coefficients among soil-layer moisture and the climatic events were calculated. All analyses were made using the Minitab (version s 9.2 and 10.1) statistical software.

RESULTS

Profile pits

The descriptions and sampling made in the pits showed that the soils were predominantly sandy, especially in the SHF and the THF which had 90 - 99 % of sand, and 0.4-3.6 % of clay in all mineral layers of the profile down to 1 m (Table 2.3a; Appendix 2.1-2.3). The LERF had between 68 - 83 % sand, with up to 20 % clay at lower 80-100 cm depth (Table 2.3b,c; Appendix 2.4 - 2.9). In the SHF some loose stones were found in pit 2 below 40 cm but there was no hard-pan.

Top organic layer

The upper organic layer differed substantially between the three forest types (Fig. 2.5). In the SHF, it was less than 5 cm deep or even absent (pit 2), the root mat and humus were poorly developed or absent, and some humus was mixed with mineral soil in a gradual transition. In the THF, the upper organic layer was generally deep (> 10 cm), with a substantial root mat and humus, with much fine humus in the dark second and third soil layers (down to 30 cm depth). In the LERF, the abundant fine roots (< 2 mm in diameter) were mainly mixed with the upper litter layer, and a true `root mat' was almost absent; the brown humus formed a shallow layer followed by a mixed layer with humus and mineral soil with no distinct boundary. Fine roots were less abundant in the SHF where they were mainly in the top 30 cm. In the THF they went down to 40-50 cm and in the LERF they occurred down to the bottom of the pit (100 cm).

Soil chemistry

The lowest organic carbon was always recorded in the SHF, in all soil layers down to 1 m depth, and the highest values (34 %) were found in the upper soil layers of the THF (Table 2.3a, b, c; Appendix 2.1-2.9). The pH was lower in the THF than in both the LERF and SHF. A large difference (up to about 1 unit) was found between the pH_{H20} and pH_{KCl} (Table 2.3a, b, c; Appendix 2.1 - 2.9), especially in the organic layers. Total nitrogen and phosphorus were concentrated in the organic layers in all forest types. The highest values

Table 2.3a: The means of soil chemical properties and particle-size composition at a range of depths in pits near the SHF plots. Values are for three pits, unless indicated otherwise, when the depths of the upper layers varied following the distribution of the organic horizons.

	Depths of samples (cm)								
	0-3[1]	0-10[2]	3-10[1]	10-20	20-30	30-40	40-50	50-70	80-100
organic C (%)	10.5	0.20	0.40	0.28	0.15	0.10	0.09	0.08	0.07
pH_{H2O}	3.7	4.7	4.3	4.5	4.9	4.9	5.0	5.0	5.4
pH_{KCl}	2.6	3.5	3.2	3.4	3.6	3.8	4.1	4.4	4.9
N total (mg g^{-1})	4.0	0.40	0.20	0.37	0.30	0.23	0.17	0.17	0.1
P total (μg g^{-1})	232	32	56	118	17	16	14	10	15
P-extr. (μg g^{-1})	20	4.0	4.4	3.0	2.3	2.3	2.2	2.4	2.2
C:N ratio	26	5	20	7.6	5	4.3	5.3	4.7	7.0
Exchangeable cations, CEC and total acidity (m-equiv kg^{-1})									
K^+	2.2	0.0	0.30	0.03	0.0	0.0	0.0	0.06	0.01
Na^+	0.45	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ca^{2+}	0.90	0.5	1.5	0.41	0.82	0.19	0.37	0.75	1.79
Mg^{2+}	3.8	0.06	0.37	0.08	0.10	0.05	0.06	0.18	0.20
H^+	19.7	0.6	3.4	2.9	1.5	1.2	1.0	1.0	1.4
Al^{3+}	0.0	0.0	1.0	0.0	0.2	0.0	0.0	0.0	0.0
CEC	27.1	1.16	6.57	3.4	2.78	1.44	1.47	2.01	3.4
Total acidity ($H^+ + Al^{3+}$)	19.7	0.6	4.4	2.9	1.8	1.2	1.03	1.03	1.4
H^+/Al^{3+}	>100	>6	3.4	>29	7.5	>12	>10	>10	>14
Base saturation (%)	27.2	48.3	29.1	15.0	28.7	17.3	25.5	51.5	58.0
Particle fraction (%)									
clay (< 2 μm)	1.8	1.8	1.8	1.2	0.85	0.80	0.85	1.2	1.0
silt (2-62 μm)	4.1	4.1	4.1	0.46	0.25	0.0	0.85	0.0	0.01
sand (> 62 μm)	94.1	94.1	94.1	98.3	98.7	99.2	98.7	99.0	99.0

[1] values from two pits
[2] values from one single pit with no organic (humus) layer

Table 2.3b: The means of soil chemical properties and particle-size composition at a range of depths in pits near the THF plots. Values are for three pits, unless indicated otherwise, when the depths of the upper layers varied following the distribution of the organic horizons.

	Depth of samples (cm)												
	0-3[2]	0-7[2]	0-12[2]	3-10[2]	10-20[1]	15-20[2]	20-30	30-40	40-50	50-60	60-70	70-80	80-100
organic C (%)	32.0	31.3	27.3	1.0	0.94	2.18	1.22	0.91	0.75	0.38	0.36	0.25	0.26
pH_{H2O}	3.5	3.5	3.4	3.9	4.2	3.9	4.2	4.2	4.3	4.7	4.8	4.8	5.0
pH_{KCl}	2.2	2.3	2.1	2.8	2.8	2.6	2.9	3.1	3.3	3.6	3.7	4.0	4 1
N total ($mg\ g^{-1}$)	12.2	15.2	9.9	0.6	0.45	0.50	0.20	0.03	0.03	0.09	0 03	0.05	0.03
P total ($\mu g\ g^{-1}$)	293	295	1280	11	26	10	19	17	22	15	32	10	15
P-extr. ($\mu g\ g^{-1}$)	20	20	10	3.9	2.9	5.7	1.9	1.2	1.2	1.3	1.1	0.83	0.9
C:N ratio	26	16	27	17	21	44	61	303	250	42	120	50	87
Exchangeable cations, CEC, and total acidity ($m\text{-}equiv\ kg^{-1}$)													
K^+	4.8	2.2	3.9	0.12	0.60	0.14	0.27	0 07	0.13	0.03	0 0	0.0	0 0
Na^+	5.0	3.2	5.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0 0
Ca^{2+}	0.30	0.20	0.10	3.75	1.41	1.50	1.83	2.79	1.71	2.12	2.04	2.00	2.37
Mg^{2+}	4.8	3.20	3.5	0.56	0.38	0.48	0.28	0.43	0.21	0.30	0.25	0.23	0.30
H^+	26.4	62.9	61.1	5.6	7.6	11.9	7.3	4.9	3.2	3.7	1.0	1.0	1.4
Al^{3+}	0.40	16.5	8.0	0.0	0.8	1.5	0.8	0.3	0.0	0.7	0 0	0.0	0.0
CEC	41.7	88.2	82.0	10.0	10.8	15.5	10.5	8.49	5.28	6.85	3 26	3.23	4.07
Total acidity ($H^+ + Al^{3+}$)	26 8	79.4	69.1	5.6	8.4	13.4	8.1	5.2	3.2	4.4	1.0	1.0	1 4
H^+/Al^{3+}	66	3.8	7.6	>56	9.5	7.9	9.1	16	>32	5.3	>10	>10	>14
Base saturation (%)	35.7	9.98	15.7	44.2	23 2	13.7	26.9	37.7	35 8	42.6	73 5	65.9	60 9
Particle fraction (%)													
clay (<2 μm)	na	na	na	na	3.6	3.6	2.2	0.40	2.0	1.20	1 20	1.60	1 40
silt (2-62 μm)	na	na	na	na	0 04	0.04	1.38	1.29	0 0	9.07	0 0	0.81	0 30
sand (> 62 μm)	na	na	na	na	96 3	96.3	96 4	98.3	98 6	98.7	99 0	97 6	98 3

[1] values from two pits
[2] values from a single pit.
na not analysed

Table 2.3c: The means of soil chemical properties and particle size composition at a range of depths in pits near the LERF plots. Values are for three pits, unless indicated otherwise, when the depths of the upper layers varied following the distribution of the organic horizons.

	Depth of samples (cm)										
	0-3[2]	0-6[1]	3-10[2]	10-20	20-30	30-40	40-50	50-60	60-70[1]	70-80	80-100
organic C (%)	18.4	24.6	0.77	1.30	1.10	1.06	1.08	0.94	0 85	0.60	0.64
pH_{H2O}	3.9	3.8	4.2	4.1	4.3	4.6	4.7	4.6	4 5	4.5	4.7
pH_{KCl}	2.7	2.8	3.4	3.5	3.9	4.1	4.2	4.2	4 2	4.2	4 2
N total ($mg\ g^{-1}$)	9.0	11.7	0.8	0.6	0.3	0.57	0.51	0.24	0.35	0.17	0.23
P total ($\mu g\ g^{-1}$)	405	447	164	305	214	183	123	299	249	116	323
P-extr. ($\mu g\ g^{-1}$)	20	25	1.8	2.8	1.8	1.23	0.7	0.5	0 9	0.5	0.3
C:N ratio	20	21	9.6	22	37	19	21	39	24	35	23
Exchangeable cations and CEC ($m\text{-}equiv\ kg^{-1}$)											
K^+	2.7	5.9	0.06	0.15	0.19	0.01	0.11	0.01	0.0	0.04	0.0
Na^+	5.4	4.8	0.0	0.08	0 0	0.0	0.27	1.07	0.75	0.09	0.0
Ca^{2+}	0.2	0.23	2.62	3.41	3.54	2.46	2.54	3.04	2.19	2.75	1.96
Mg^{2+}	2.8	2.5	0.71	0.61	0.47	0.55	0.43	0.56	0 47	0.68	0.38
H^+	26.6	3.0	3.9	4.5	1.6	1.5	0.7	1.0	0 8	1.6	0.9
Al^{3+}	39.0	62.0	14.0	10.6	13.5	11.7	12.3	11.3	10 0	9.0	9.1
CEC	76.7	78.6	21.3	19 4	19 3	16.2	16 3	17.0	14 2	14.2	12.3
Total acidity ($H^+ + Al^{3+}$)	65.6	47.3	17.9	15.1	15.1	13.1	13 0	12.3	10 9	10.6	10.0
H^+/Al^{3+}	0.7	0.05	0.3	0.4	0.1	0.1	0 06	0.1	0 1	0.2	0.1
Base saturation (%)	14.5	19.2	15.9	22.8	21.2	18.5	19 6	25.3	24 3	23.7	17.9
Particle fraction (%)											
clay (< 2 µm)	9.6	9.6	9.6	11.6	10 6	10.4	11.8	12.2	15 8	14.0	19.8
silt (2-62 µm)	19 8	19.8	19.8	7.51	6.01	10.4	13 3	15.3	11 5	9.87	12.5
sand (> 62 µm)	70.6	70.6	70.6	80.9	83 4	79 5	74 9	72.2	73.7	76.4	67.6

[1] values from two pits
[2] values from one single pit

of nitrogen (19 mg g^{-1}) and phosphorus (1.28 mg g^{-1}) were found in the THF. In the mineral layers, the LERF showed the highest values for nitrogen (0.2 - 0.8 mg g^{-1}) and phosphorus (0.12 - 0.32 mg g^{-1}) (Table 2.3a, b, c; Appendix 2.1-2.9). Except for sodium, which usually had very low values and calcium, the exchangeable cations showed higher concentrations in the upper layers (Table 2.3a, b, c; Appendix 2.1-2.9). Exchangeable aluminium in the upper layers was much higher in the LERF than in the other two forest types. Exchangeable potassium was always at low concentrations below 40 cm depth, while exchangeable calcium, magnesium, and aluminium were all highest in the LERF than in the mineral layers (Table 2.3a, b, c; Appendix 2.1-2.9). Exchangeable acidity was always higher in the THF than in both the LERF and SHF. The cation exchange capacity (CEC) was always highest in the organic layer. The base saturation was generally higher in the deeper mineral layers of the SHF and THF, and the deeper THF layers showed values higher than both LERF and SHF (Table 2.3a, b, c; Appendix 2.1-2.9).

Moisture of organic and upper mineral soil layers

The gravimetric moisture (calculated as percentage of water in relation to the wet weight of the sample) in the organic mixture at the soil surface (litter, root mat, and humus) was always higher than in the upper layer of the mineral soil, independent of season and forest type (Fig. 2.7), even taking into account the difference in the bulk density of the two layers. The moisture of both organic and mineral soil layer varied significantly in all three forest types, except for the organic layer in the THF, in 1992 (Fig. 2.7a, b). The moisture of the organic layer was slightly higher in 1993 than in 1992 in both the organic and in the upper mineral soil layers, but no significant difference between the two years was found. For the whole period of measurements (21 months), the moisture of the organic layer was lower in the SHF than in both the THF and LERF (nested ANOVA; $F = 32.2$; $df = 40$; $p < 0.001$), and the same occurred for the upper mineral soil layer ($F = 33.3$; $p < 0.001$). However, the moisture in the LERF was slightly higher than in the THF in the organic layer, but slightly lower in the upper mineral soil layer (Fig. 2.7). In the SHF, plot 2 showed significantly lower moisture in the organic layer ($F = 9.44$; $df = 20$; $p < 0.001$). and slightly lower moisture than both plots 1 and 3 for the upper mineral soil layer. Both

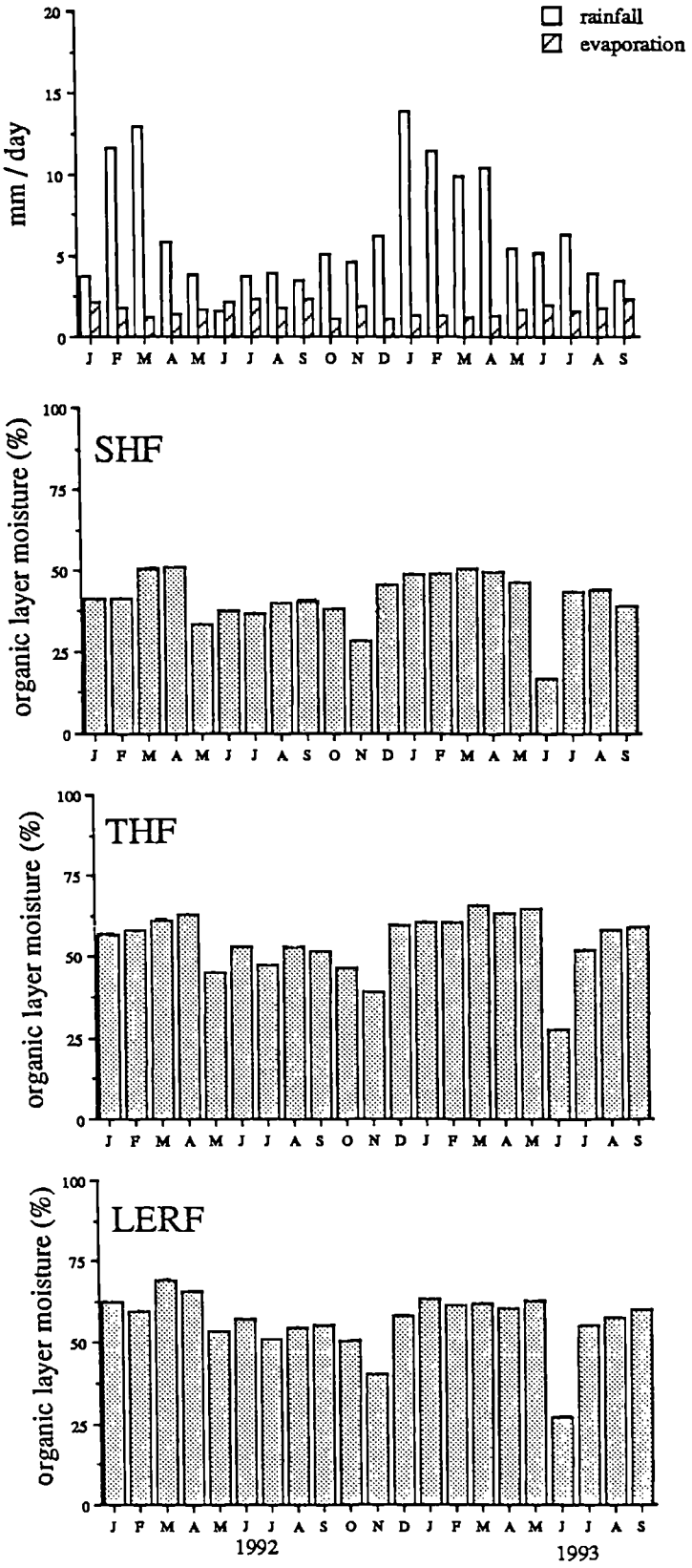


Figure 2.7a: Monthly mean moisture (%) of the organic layer in SHF, THF, and LERF. Values are generally the means of four weekly measurements (except in the last two months with only one or two measurements) for the three plots in each forest type (n = 3). The upper histogram shows the mean daily rainfall and evaporation for the corresponding periods.

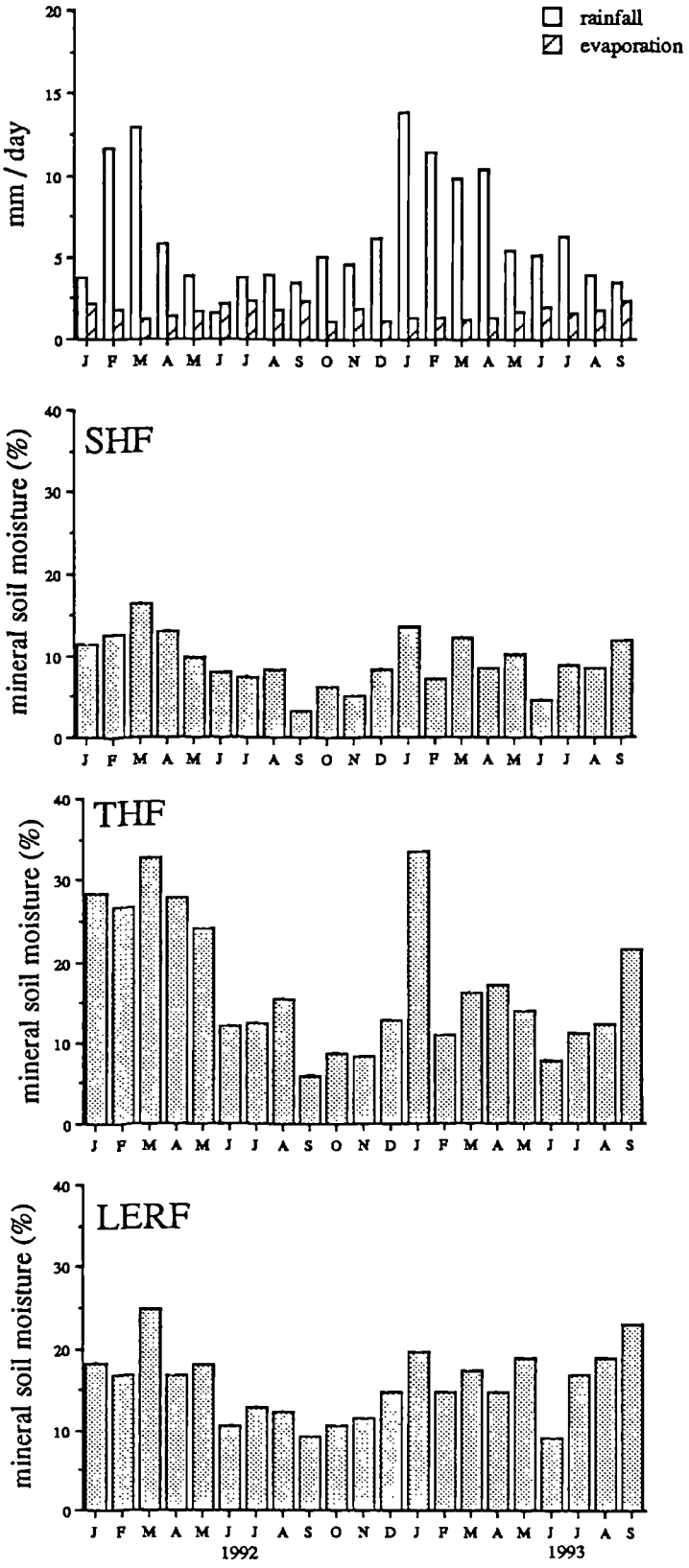


Figure 2.7b: Monthly mean moisture (%) of the upper mineral soil layer in SHF, THF, and LERF. Values are generally the means of four weekly measurements (except in the last two months with only one or two measurements) for the three plots in each forest type (n = 3). The upper histogram shows the mean daily rainfall and evaporation for the corresponding periods.

organic and upper mineral layer moisture were generally slightly higher in plot 1 than in plot 3. Overall in the first year, both layers were drier in June, September and November than in the other months in all three forest types (Fig. 2.7). The highest moisture values were generally found in March. However, considerable variations were found between layers and forest types. The moisture of the organic layer was generally less in November than in September while the opposite was observed for the upper soil mineral layer. In 1993, the lowest values for both layers and all forest types were all found in June while the highest values were generally recorded in January. The moisture of both layers, was related to all climatic factors analysed (mean daily rainfall and evaporation, difference between mean daily rainfall and evaporation, total rainfall for the whole period, rainfall for 3 d and 1 d before the samples were taken, and the number of dry days prior to collection). The moisture of the organic layer was more significantly related to the mean daily evaporation ($r^2 = 8.8$; df = 72; $p < 0.001$), the rainfall of the 3 d before sampling ($r^2 = 6.7$; $p < 0.001$), and to the number of dry days in the period preceding collections ($r^2 = 9.6$; $p < 0.001$). In the upper mineral soil layer, the moisture was more significantly related to the mean daily rainfall ($r^2 = 7.9$; $p < 0.001$), and mean daily evaporation ($r^2 = 9.9$; $p < 0.001$) (all with very low coefficients of determination), and to the number of dry days ($r^2 = 16.6$; $p < 0.001$). Overall, the values found were relatively stable for the top organic layer and unstable in the mineral layer, except for June 1993, when a sharp decrease also occurred in the mineral layer.

Soil water potential

The water matric potential, an index of soil-water tension (Hillel 1982) was variable over time and with depth (Fig. 2.8; Table 2.4). Generally, the soil-water matric potential was lower in the LERF and in the deeper layers of soil profile, but there were variations in that pattern (Fig. 2.8). August, a dry month in 1993, had the lowest water potentials of the whole period of study. There were no significant differences among the four different depths over time, and no clear pattern was observed with increased depth of the tensiometers (Table 2.4). Overall the water potentials were not related to either the

depthor the rainfall 1 d or 3 d before the measurements. The mean daily evaporation was the climatic variable most frequently related to the soil-water potentials in all sites. It was the only variable significantly related to water tensions of all sites and depths together. even though with a low coefficient of determination (r^2 = 8.6%; df = 24; $p < 0.001$). It appears that soil-water potentials had a lag-phase after heavy rainfall, and showed much variation several days later (Fig. 2.8).

Table 2.4: Mean water matric potential (kPa) over time in each site along the transect at four depths. Values are means with SE in parenthesis (n=25). Means followed by different letters in each row are significantly different (univariate repeated measures analysis; df = 5; $p < 0.05$).

Depth (cm)	SHF A	SHF/THF B	THF C	THF/LERF D	LERF E	LERF F
12.5	-3.43a (0.24)	-4.60a (0.40)	-3.96a (0.20)	-7.74a (0.83)	-4.62a (0.40)	-6.94a (1.99)
37.5	-2.71a (0.18)	-4.12a (0.29)	-3.07a (0.13)	-7.64a (0.77)	-11.9b (2.47)	-8.38a (1.35)
62.5	-1.81a (0.51)	-6.31b (1.00)	-6.54b (1.31)	-7.75b (0.59)	-8.63b (0.75)	-10.3b (1.22)
87.5	-2.64a (0.39)	-5.62b (0.80)	-4.30bc (0.13)	-8.53bd (0.61)	-8.31bd (0.79)	-8.91bd (0.79)

Groundwater levels

The level of the groundwater was never within 40 cm of the surface, even in the wettest periods (Fig. 2.9). Significant correlations were found between the groundwater levels and all the five climatic variables analysed (mean daily rainfall and evaporation, rainfall of the last week, last three days, and last day prior to the field measurements), but the best correlations were found with the total rainfall of the previous week ($r = -0.421$; $n = 38$; $p < 0.01$, and the mean daily evaporation ($r = -0.469$; $n=38$; $p < 0.01$). The fluctuation of the groundwater levels in both piezometers, in the SHF and in the transition from SHF to THF, were significantly related to either the mean daily rainfall of the period prior to each

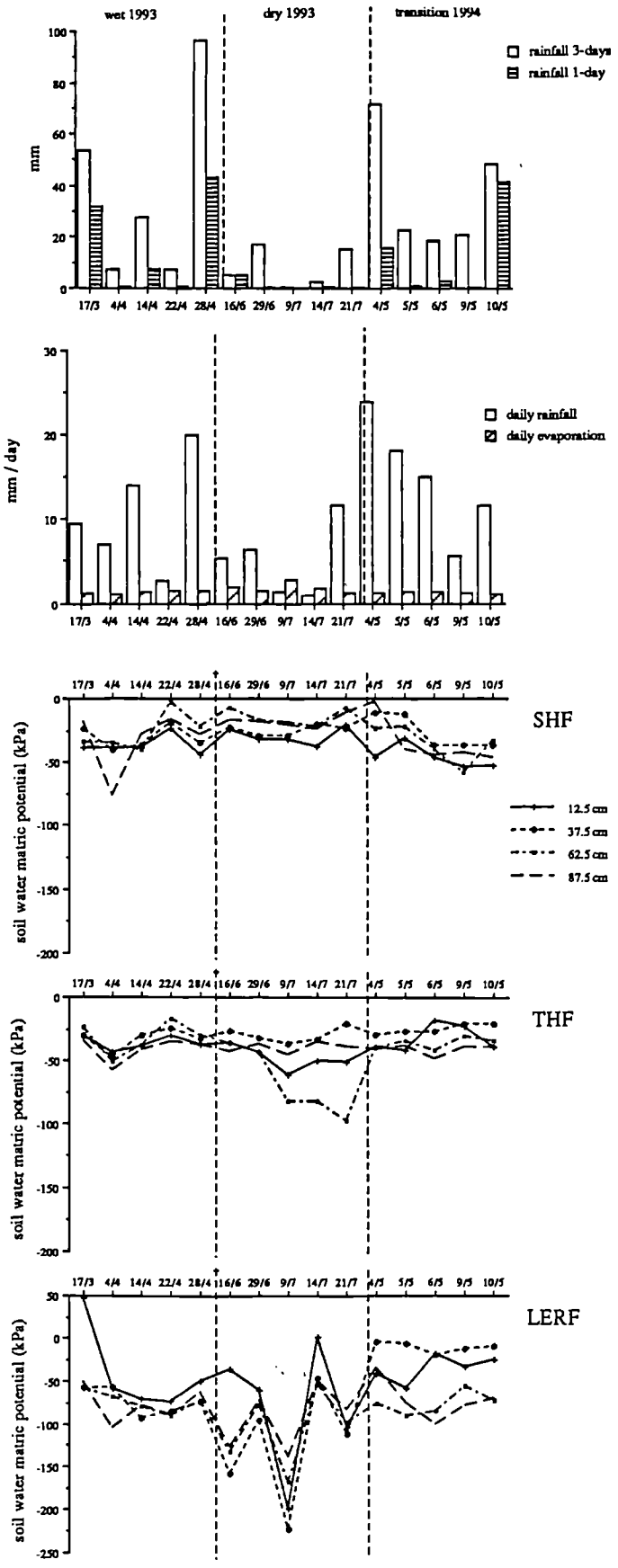


Fig. 2.8: Soil-water matric potential (kPa) at selected periods representing the wet, dry and transitional periods in SHF, THF, and LERF. Upper graph shows climatic variables of days preceding the measurements.

each measurement (generally corresponding to intervals of 7-14 d), the mean daily pan evaporation, or the rainfall of the week prior to the measurements, or the rainfall of shorter previous periods of three days or one day (Table 2.5). The strongest relationships were generally those with rainfall and evaporation of longer periods, but none of them were particularly strong (Table 2.5). The groundwater levels tended to stay closer to the surface in the wet season, falling to levels below the reach of the plastic tubes at 1.75 m and 3.50 m, as the dry season progressed (Fig. 2.9).

Table 2.5: Regression analyses of the rainfall and evaporation amounts in short intervals before measurements, on the groundwater levels over time in the piezometers located in the SHF and in the transition from SHF to THF.

	SHF A			SHF/THF B		
Factors	r^2	df	p	r^2	df	p
Rainfall previous 7-d	25.0%	18	< 0.05	26.6%	18	< 0.05
Rainfall previous 3-d	26.6%	18	< 0.05	26.7%	18	< 0.05
Rainfall previous 1-d	17.5%	18	< 0.05	17.8%	18	< 0.05
Mean daily rainfall	17.5%	18	< 0.05	18.1%	18	< 0.05
Mean daily evaporation	33.1%	18	< 0.01	32.6%	18	< 0.01

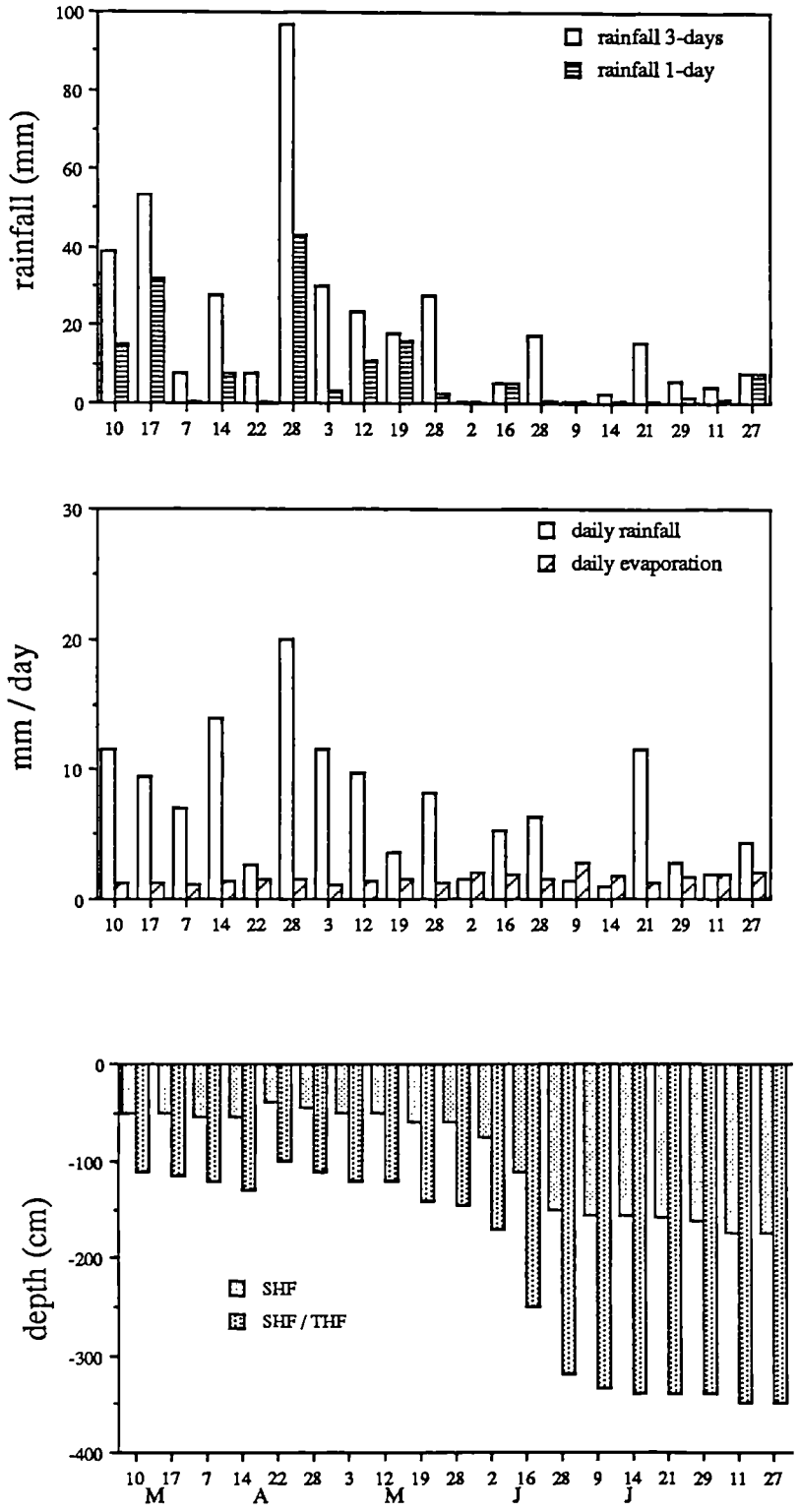


Figure 2.9: Groundwater depth (cm) in the piezometers installed in the SHF and in the transition between SHF and THF in the period March-September 1993. The upper graphs show the climatic variables in the periods preceding the field measurements.

DISCUSSION

The sandy-textured surface soils had some of the lowest clay concentrations recorded from rain forests. The SHF and THF, both with > 94 % sand, were virtually pure coarse white sand, while the LERF Ultisols, with < 20 % of clay down to 1 m depth, were still very sandy, in contrast to the predominant Oxisols under lowland evergreen rain forest in central Amazonia, which often have 60-80 % clay (Ranzani 1980; Chauvel 1982; Chauvel *et al.* 1987).

Soil chemistry

The pH in the three forest types was among the lowest recorded for rain forests on acidic soils, but the concentrations of nutrients (except for sodium in the SHF, and calcium in all three forest types) in the surface soils are not exceptionally low (Table 2.6). The trend of pH values SHF > LERF > THF agrees with previous studies near the present plots (Martins & Matthes 1978). The large differences between pH measured in water and in KCl, especially in the upper (organic) layers implies that H^+ rather than Al^{3+} is dominating the exchange complex. (The term H^+ is used here to include all H-ions, especially H_3O^+). The dominance of H^+ was clearly observed in the heath forests, especially in the SHF, where Al^{3+} concentrations were negligible and the H^+/Al^{3+} quotient was much higher than in the LERF soils. That was the most striking difference observed between the heath forest soils and the LERF soils. The relatively low values obtained for organic carbon in the upper organic layer (litter, root mat and humus) in all forest types, but especially in the heath forests, was probably caused by: (a) the sieving, which has eliminated litter, root mat and some raw humus, leaving a mixture of humus and mineral soil; (b) there was always some white sand mixed with the humus and included with it in the samples; and (c) a relatively small volume of sand may represent a considerable part of the total dry weight of the sample because of the low density of the humus. The CEC of the SHF is in the lower range of those presented in Table 2.6, but the CEC was clearly higher in the LERF, and, as with the base saturation of all three forest types, is in the middle range for tropical forests (Table 2.6). It is noteworthy that base saturation is higher

Table 2.6: Surface soil samples analyses from a range of tropical rain forests on acidic soils ($pH_{H2O} < 5$).

	Africa			Malaysia			Costa Rica	South America						
	Cameroon		Ghana	Pasoh	Danum	Mulu		Maracá	Surinam	Manaus		This study		
	1	2	3	4	5	6	7	8	9	10	11	SHF	THF	LERF
depth (cm)	0-8	0-10	0-15	2-20	1-25	0-10	0-15	0-10	0-7	0-14	0-20	0-5	0-9	0-6
pH_{H2O}	4.2	4.2	4.2	4.3	4.4	4.1	4.2	4.9	4.0	3 9	4 2	3.7	3 5	3 9
C %	3.6	2.7	2.2	0.5	0.3	11	8.9	0.5	2.4	4 1	-	7.1	30 2	22 6
N %	0.31	-	0.21	0.17	0.04	0.51	0.4	0.5	0.13	0.15	-	0.28	1.24	1 08
C:N ratio	12	-	10	3.0	7.5	22	22	1.0	18	27	-	25	24	21
							$\mu g\ g^{-1}$							
P_{total}	-	234	-	200	100	120	940	61	86	-	-	165	623	419
$P_{extr.}$	-	10	6	0	-	-	2.2	5.1	6.1	-	-	15	17	23
							Exchangeable cations and CEC (m-equiv $100\ g^{-1}$)							
K^+	0 17	0.07	-	0.58	0.10	0.25	0.17	0.07	0.07	0.21	-	0.15	0.36	0 49
Na^+	0 13	-	-	0.08	0.09	0.06	0.11	0.005	0.04	0.13	0 01	0 03	0 45	0 50
Ca^{2+}	0.87	0.10	-	0.28	0.25	0.04	1.10	0.23	0.38	0.24	0 04	0.08	0.02	0 02
Mg^{2+}	0 30	-	-	0.10	0.07	0.18	0.29	0.18	0.16	0.18	0 01	0.26	0.38	0 06
CEC	18	-	8	5.6	2.5	37	-	0 85	1.4	9 5	2.0	1.84	7.06	7 82
							Base saturation %							
	8	-	10	18.6	20.4	1.6	-	55.5	46.4	8	-	34.2	20 5	17 5
							Particle size of the mineral matter (%)							
sand	20	88	54	30	-	-	-	76	96	16	91	94	96	71
clay	64	8	27	49	-	-	80	12	4	62	7.7	1.8	2.4	9 6

[1] Hawkins & Brunt (1965) in Sambalang, soil type not determined
[2] Newbery *et al.* (1988) in Korup, soil type not determined
[3] Hall & Swaine (1976), soil type not determined
[4] Allbrook (1973), 'Durian series' soil
[5] Green (1992), Orthic Acrisol
[6] Proctor *et al.* (1983a), Ultisol
[7] Grieve *et al.* (1990), Dystropept
[8] Thompson *et al.* (1992), Grossarenic plinthic Paleudult
[9] Poels (1987), Quartzipsammentic Ultic Haplorthox
[10] Ranzani (1980), Oxisol, 3 km NE of the study sites
[11] Bravard & Righi (1988), Ultisol, 2 km NW of the study sites

in the SHF and THF than in the LERF, but it may only reflect the low CEC of the two heath forests when compared with the LERF. Exchangeable aluminium was relatively high in the LERF, result which agrees with those found by Bravard & Righi (1988): studying a toposequence located 2 km northwest of the present sites they had values of extractable aluminium five-fold higher in the upper horizons of a Spodic Paleudult (Ultisol) than in a Quartzipsamment. The higher concentrations of most nutrients in the upper (organic) layers and very low concentrations in the soil mineral layers is consistent with findings of other studies on nutrients in heath forest soils in Amazonia and Sarawak. Klinge (1975), analysing a Giant Humus Podzol 60 km SW of the study sites, found that the top organic L and F layers, which accounted for only 2% of the total soil dry matter, stored 35% of total water, 27% of total nitrogen, 43% of total phosphorus, 51% of total calcium, 64% of total magnesium, and virtually 100% of total sodium of the soil. The bleached sand (44% of total dry soil mass) stored only 16 % of total water, 13% of total nitrogen, and virtually no other nutrients. In Sarawak, Katagiri *et al.* (1991) also found higher concentrations of total elements in the upper L and H layers with a pH 4: 54.8% of organic carbon, 0.5% of nitrogen, 0.075% of magnesium, and 0.34% of calcium. Their heath forest soil was lower in organic matter and total nutrients than the neighbouring Dipterocarp forest. The results stress the decisive importance of the organic matter, especially the raw humus and the humus proper, for nutrient storage in the highly leached sandy soils.

Very few data exist for other heath forest soils (Table 2.7). The SHF had the lowest values for potassium, sodium, calcium, and CEC in the mineral soil, and it was among the lowest for magnesium. The SHF organic carbon and nitrogen and exchangeable potassium in the organic layer were in the lower range of the values in Table 2.7. Both, the SHF and THF, were in the mid to lower range of pH. The THF ranked mid to high for organic carbon, total nitrogen, exchangeable potassium and sodium (from the organic layer) and low for magnesium, calcium and CEC. Total phophorus in both SHF and THF were lower than in a Sarawak heath forest (Proctor *et al.* 1983a), the only values available for comparison.

Table 2.7: Soil analyses of surface samples from heath forests.

Sites	Depth (cm)	pH_{H2O}	N %	C:N	P_{total} $\mu g\ g^{-1}$	K^+	Na^+	Ca^{++}	Mg^{++}	CEC	Studies
						m-eqiv $100g^{-1}$					
Sarawak	0-5	3.0	1.00	26.0	nd	0.25	0.40	0.54	0.02	15.0	Andriesse (1975)
	5-13	3.3	0.16	30.0	nd	0.17	0.39	0.42	0.02	6.40	
	13-23	4.2	0.02	23.0	nd	0.05	0.33	0.30	0.01	3.00	
San Carlos, Venezuela	0-8	3.8	0.12	68.3	nd	0.57	0.14	2.4	0.32	nd	Herrera (1979)
	8-23	4.1	0.16	28.8	nd	0.12	0.10	0.57	0.18	nd	
Bangka, Sumatra	10-25	3.9	nd	nd	nd	0.03	nd	1.10	0.74	nd	Kartawinata (1978)
Bako National Park, Sarawak	0-5	3.5	0.20	25.5	nd	0.13	nd	0.96	4.52	13.4	Katagiri *et al.* (1991)
	5-10	4.5	0.12	28.6	nd	0.11	nd	0.15	1.94	7.01	
	20-30	4.2	0.03	27.3	nd	0.12	nd	0.36	0.20	1.15	
Manaus SHF	0-7	4.3	nd	nd	nd	0.10	nd	0.30	0.10	nd	Martins & Matthes (1978)
	18-25	4.7	nd	nd	nd	0.04	nd	0.0	0.0	nd	
THF	0-7	3.7	nd	nd	nd	0.18	nd	0.20	0.1	nd	
	18-25	3.4	nd	nd	nd	0.14	nd	0.20	0.10	nd	
Sarawak	0-10	3.6	0.91	33.0	280	0.54	0.11	0.67	1.5	110	Proctor *et al.* (1983a)
	10-30	4.0	0.36	36.0	74	0.08	0.03	0.08	0.16	31	
Manaus SHF	0-5	3.7	0.28	25.4	165	0.15	0.03	0.08	0.26	1.84	This study
	5-10	4.3	0.20	2.0	48	0.03	0.0	0.15	0.04	0.66	
	20-30	4.9	0.30	0.5	17	0 0	0.0	0.08	0.01	0.28	
THF	0-9	3.5	1.24	24.3	623	0.36	0.45	0.02	0.38	7.06	
	9-20	4.2	0.05	18.8	26	0.06	0.0	0.14	0.04	1.08	
	20-30	4.2	0.02	61.0	19	0.03	0.0	0.18	0.03	1.05	

nd no data

In the above comparisons of soil chemistry, it must be taken into account that the lack of information on the season or moisture condition of the soils at the sampling date may limit considerably the validity of such comparisons. Strong seasonal influences can be found on the dynamics, and consequently on the amounts, of exchangeable ions in tropical soils (Grimaldi *et al.* 1992; Forster 1988) altough not invariably so (Luizão *et al.* 1996).

Moisture dynamics in SHF, THF, and LERF soils

Organic and upper mineral soil moisture

Gravimetric moisture measurements have several limitations. However, they continue to be widely used because of their simplicity and cheapness (Hillel 1982; Landon 1991). In the present study, where all soils were low in clay, (which could retain water and interfere in the gravimetric determinations) (A. Chauvel and S.M. Ross, personal communications), the frequent gravimetric moisture measurements were considered to be a useful index of soil moisture.

The higher moisture of the organic layer in relation to the mineral soil can be attributed to the higher water retention capacity of the organic matter. Not surprisingly, the lowest moisture of both layers was found in the SHF, the forest type with the least humus, and most exposed to the sun. That was clear in SHF plot 2, which had the most open vegetation, and the lowest soil moisture. The moisture of the top organic layer was not significantly related to the rainfall of the last day preceding collections, as might be expected. That was probably caused by the strong influence of the rainfall on the same day of the field samplings and which could not be included in the analyses because daily rainfall was only recorded at the end of each day, and samplings were made during the day over a period of about 6 h, for the different plots. and on many occasions rain fell between samplings. The upper mineral soil layer, however. reflected better the medium-term seasonal pattern, especially in the SHF and THF in 1992. with lower moisture values from the drier September to November. Such a pattern is closer to that described by Ranzani (1980) for an Ultisol similar to that of the LERF sites, located 3 km northwest of the study sites, indicating shortage of soil water from August to October.

Although severe water shortages did not occur in the present study, they may do so in the heath forest soils during long dry spells.

Soil water potential

The values found for all study sites were very low, many times below the potential commonly regarded as the 'field capacity' (-10 kPa) (Hillel 1982; Landon 1991). However, the lowest water potential for most depths were generally found in the LERF soils, where the vegetation was more dense and had a higher biomass than the heath forests, and showed no sign of water stress. The higher water tensions in the LERF might be a result of higher mass of roots, more evenly distributed in the soil profile. In the SHF, the higher water potential in relation to all other sites from 37.5 cm to 87.5 cm may reflect the lack of roots in those depths, since they are concentrated in the first 30 cm (Takeuchi 1960; Martins & Matthes 1978). In the same way, the lower water tensions below 30 cm in soil in the transitional SHF/THF and in the THF, than in the transitional THF/LERF and the LERF sites, also may reflect a lower mass of roots below the surface layer in the soil profile of the heath forest. It appears that the top organic layer and the mass of roots in the soil profile are the main controllers of the soil-water potential.

Groundwater fluctuations

The groundwater levels in both piezometers were not clearly related to the rainfall events in the short-term (e.g. the rainfall of the day before the measurements), and stronger relationships were found with rainfall pattern in a longer range (e.g. the mean daily rainfall of the whole period prior to the measurements). This suggests that the groundwater levels are mostly related to the general seasonal pattern during the year, being mainly controlled by regional and seasonal regimes. In this case, the variations of the groundwater level would follow an entirely different pathway to that described by Reichardt *et al.* (1975) who, based on a one-month study in the wet season, claimed heath forest soils had very rapid variations in groundwater levels, totally influenced by immediate rainfall. The short time of observations possibly was responsible for unrealistic estimates of water-table variations in relation to the rainfall. The behaviour of the water-table in the study plots seems similar to that reported by Heyligers (1963) in Surinam for a heath forest where the water-table generally was about 3 m deep He

found that a rise in the groundwater level was observed 6 d after heavy rains, because rain water was retained in the upper layers (by the root mat and finer sands) and only gradually percolated. In the present study, even though the measurements of groundwater levels were all made in the wet year 1993 (which lacked a real dry season), from July on there was a clear and sharp lowering of the water levels, supporting the hypothesis of a wider regional control. These variations were apparently slower than supposed for a Spodosol (Reichardt *et al.* 1975; Jordan 1985), and even very heavy rains did not cause a rise in the groundwater levels within a few hours or even days. However, the fluctuations of the groundwater levels were significantly related to the rainfall of the previous 3-7 d, indicating a response to rainfall events taking place in the previous week.

Chapter 3. VEGETATION

VEGETATION OF THE REGION

The lowland evergreen rain forests in Amazonia have been well studied especially in Brazil and Venezuela, where research projects of large scope and duration have been conducted on forest floristics, soils, soil biology and nutrient cycling (Herrera *et al.* 1978; Herrera 1979; Jordan & Murphy 1982; Chauvel *et al.* 1987; Guillaumet 1987; Leopoldo *et al.* 1987; Luizão & Schubart 1987; Adis 1988, Jordan 1989). The emphasis on the lowland evergreen forest is understandable in view of its extent in Amazonia (over 70 % of total forested area) and its high economic importance either for logging or for land use as pasture or cropping. Much less research effort has been placed on heath forests which occupy a smaller (5-6 %) area of Amazonia.

However, in tropical South America, heath forests on white sand soils are spread over thousands of km^2 of the Negro and Branco river basins (Anderson 1978; 1981), and are also common in the `Serra do Cachimbo' region of southern Pará and northern Mato Grosso states (Lleras & Kirkbride 1978). These heath forests are distinguished from other regional vegetation types by their white-sand soils, (though some heath forests have been described on reddish sands (Heyligers 1963; Lleras & Kirkbride 1978), scleromorphic leaves, and unusual physiognomy and floristic composition (Anderson *et al.* 1975; Anderson 1981). In Brazil, they are locally referred as to *campina* (the stunted facies) and *campinarana* (tall facies). According to Anderson *et al.* (1975), *campina* (in the Indian Tupi language meaning `a dry and low little forest') is defined as a vegetation which occurs on perfectly distinct islands surrounded or close to relatively open areas in exposed sand soil (Fig. 3.1). The tallest trees are lower than 10 m. and the canopy (when existing) is seldom continuous over a large area (Anderson *et al.* 1975). *Campina*, henceforth called SHF, could be divided into two types: `sun-SHF', with vegetation islands < 1 $m^2$ and canopy cover < 50 %, and `shade-SHF', with vegetation islands > 1 m^2 and canopy cover > 50 %. *Campinarana*, henceforth called THF, would be a `false-*campina*', since `rana' in Tupi means `false'. Thus, the THF, also referred to as `high *campina*' (Takeuchi 1960, 1962; Lisboa 1975) is defined as a more continuous vegetation type on sandy soil similar and adjacent to that of the SHF (Anderson *et al.* (1975). The THF is a distinctive, low, relatively

Figure 3.1: Aerial picture and satellite image of the *campina*, showing patches of exposed white sands, and surrounding *campinarana* and forest. The white arrow indicates the position of the area in the upper part of this Figure.

light forest with thin-stemmed trees 10-20 m high with a few exceptionally large girth and with or without butresses. The understorey is patchy, sometimes absent, sometimes well developed, whereas the herbaceous layer is all but absent (Guillaumet 1987).

The most noticeable feature of heath forests in Amazonia is the trend for the dominance of one or a few species (a dominant species is here defined as a species which has at least 10 % of the basal area) (Anderson *et al.* 1975). The heath forests at the *Reserva Biológica de Campina* are dominated by two main species: *Aldina heterophylla* Spr. ex Benth. (Caesalpiniaceae) and *Pradosia schomburgkiana* (A. de Candolle) Cronquist subspecies *schomburgkiana* (Sapotaceae) (Anderson 1978, 1981). These dominant species in heath forest are rare in the surrounding lowland evergreen rain forest. Rodrigues (1967) in an inventory carried out along the AM-010 road (starting 50 km apart from the study sites), found *Aldina* trees reaching diameters larger than 85 cm in lowland evergreen rain forest on Oxisols 70 km southeast of the study sites; in the ZF-2 area (20 km northwest from the study sites), some individuals of *Pradosia* about 30 m high occur (personal observation) on Oxisols also.

In spite of several attempts (Ducke & Black 1953; Lisboa 1975; Anderson 1978; Anderson 1981) to define and name properly the different physiognomies of heath forest in Amazonia (Table 3.1), none is widely accepted. Anderson (1981) proposed the exclusive use of the single term "Amazon *caatinga*" (accompanied by the description of structural phases *caatinga* scrub, *caatinga* woodland, *caatinga* forest), to designate all types of heath forest in Amazonia (Table 3.1), but the local names continue to be used (Klinge 1985; Cuevas & Medina 1986, 1988; Adis *et al.* 1989; Medina & Cuevas 1989; Alencar 1990).

In central Amazonia, the THF is more frequent than the SHF but very little comparative and quantitative data on its range and specific flora exist (Guillaumet 1987). Shade SHF and THF form a continuum with a very gradual transition, but the transition from THF to the lowland evergreen rain forest (henceforth called LERF) is generally sharp and well-defined (Anderson *et al.* 1975). The THF has a regular and distinct understorey of sub-shrubs (dominated by a conspicous Myrtaceae) which becomes denser and more diverse (without the Myrtaceae shrub) in the adjacent LERF, mixing with the other vegetation and becoming indistinct. The sudden appearance of palms in the understory and reduction in the litter layer mass also marks the crossing from THF to LERF. Floristically, shade-SHF differs more from sun-SHF than from

Table 3.1: Regional names and some corresponding characteristics of tropical forests in Amazonia. The names grouped in the first column were judged to be similar vegetation types according to published descriptions 1-15.

Names	Region	Vegetation aspects and characteristic species	Soil and roots
1. *Campina*[1,2,3] *Low Caatinga*[4,5] *Bana*[6] Tall *bana*[7] *Varillal bajo*[8] White sand savannah[9]	Central Amazonia Northwest Amazonia in Brazil and Venezuela Venezuela Venezuela Peru Surinam	Low tree (5-10 m) and shrub layer, with few emergents up to 15 m; patchy canopy with *Aldina heterophylla* (in central Amazonia), *Aspidosperma album*, *Clusia* sp, *Pradosia schomburgkiana*, *Micrandra sprucei*.	Spodosols with thin or thick A1 organic horizon (depending on vegetation cover); bleached sandy horizon ≥ 1m; Bh illuviation horizon may be present; thin root mat may occur in closed patches of vegetation. The more stunted facies lack organic horizon and root mat.
2. *Campinarana*[1,2] *Campina* forest[3] Tall *caatinga*[4,5] *Yuguácanan*[6] *Varillal alto*[8] White sand savannah forest[9]	Central Amazonia Central Amazonia Northwest Amazonia in Brazil and Venezuela Venezuela Peru Surinam	More continuous canopy 8-15 m high, with emergents up to 20 m; high light penetration and dense understorey; typical species are *Aldina heterophylla* (in central Amazonia), *Eperua leucantha* (upper Rio Negro), *Hevea* sp, *Manilkara* sp, *Pradosia schomburgkiana*. *Micrandra sprucei*	Spodosols with thick A1 organic horizon; bleached sandy horizon ≥ 1m; Bh illuviation horizon: dense root mat embebed in organic A0 and A1 horizons.
3. *Floresta arenicola*[10] Tall *caatinga*[4,5]	Central Amazonia Northwest Amazonia in Brazil and Venezuela	Continuous canopy 25-30 m high, with emergents up to 35 m. Typical species are *Eperua leucantha* (upper Rio Negro), *Hevea* sp. *Manilkara* sp	Tropaquods: thick organic horizon; Bh present; root mat embebed in organic A0 and A1 horizons.
4. *Terra firme*[11,12] *Tierra firme*[5,6] *Guaco*[13,14] *Yévaro*[13] Mixed forest[14,15]	Brazil Venezuela	Continuous canopy up to 35 m high, with emergents up to 55 m; low light penetration, understory not dense with frequent palms. Typical species are *Eschweilera odora*, *Protium* sp. *Scleronema micranthum*, *Dinizia excelsa*, *Goupia glabra*. *Licania* sp; *Cariocar* sp. Guaco forests are dominated by *Monopterix macu*. and Yévaro forests by *Eperua purpurea* and *Micrandra spruceana*	Oxisols with thin (in central Amazonia) or thick root mat (upper Rio Negro). Guaco forest found on grey sandy Ultisols, and Yévaro forest on yellow Ultisols, both with a thick root mat above mineral soil.

[1]Ducke & Black 1953; [2]Anderson *et al.* 1975; [3]Prance 1978; [4]Rodrigues 1961; [5]Klinge & Medina 1979; [6]Herrera 1979; [7]Bongers *et al.* 1985; [8]Revilla 1978; [9]Heyligers 1963; [10]Martins & Matthes 1978; [11]Prance *et al.* 1976; [12]Guillaumet 1987; [13]Buschbacher 1984; [14]Medina & Cuevas 1989; [15]Saldarriaga 1985.

THF, but the total number of species increases in the THF (Anderson *et al.* 1975). No estimates of basal area and biomass of heath forests in Brazil are known to date.

In this chapter, a comparative description of three plots in each of the three forest types is made, attempting to characterize their floristics and their structure.

The heath forests under study, which are not normally waterlogged, are not entirely included in the description generally made of Amazonian *caatinga* (Klinge & Medina 1979; Anderson 1981; Medina & Cuevas 1989) of 'a type of forest community which grows on seasonally waterlogged and extremely nutrient-poor bleached white sand, drained by black waters, and characterized by low stature, thin boles, dominance by a few tree species and a relatively high transmission of light to the understorey' (Klinge & Medina 1979). The classic description above perhaps matches most closely the tall *campinarana* (tall *caatinga*) growing close to the forest streams which have sometimes been erroneously considered as *floresta arenicola* (dense forest on sandy soils) for comparisons with the *campina* and *campinarana* (Martins & Matthes 1978; Santos *et al.* 1981; E.P. Oliveira unpublished). This vegetation type was not included in the present study.

VEGETATION OF THE STUDY PLOTS

Sampling

Three 50 m x 50 m plots were randomly chosen in each of the THF and LERF, but boundaries with other vegetation types and steep slopes were avoided. The SHF plots had to be subjectively chosen because of the patchy distribution and small extent of the SHF (Fig. 2.2). One of the SHF plots (2) was relatively open, another (1) was relatively closed, and the third (plot 3) was intermediate. Each 50 m x 50 m plot was marked with nylon cords and divided into four quadrants of 25 m x 25 m for studies other than floristics. For the tree inventory, the plots were subdivided in twenty-five 10 m x 10 m grid squares, and all trees, palms and lianas $\geq$ 10 cm of dbh (diameter at breast height) within each grid square were tagged and numbered (Dellmeier 1992) with aluminium tags, measured, and either identified in the field by Mr. Dionisio Coelho or Mr. José Ramos (Department of Botany, INPA) or had material collected for species determination (not yet completed) at INPA's Herbarium. Aerial biomass were estimated by multiplying the volume (height x radius (at breast height) squared x a form factor

of 0.5) (Whittaker & Woodwell 1968) and by a factor of 0.6 to correct for wood density (Edwards & Grubb 1977). Additionally, 5 m x 5 m grid squares were marked in the SHF plots and the projection of the canopies of the arboreal and shrubby vegetation was plotted on graph paper (by looking up to the canopies) to determine the percentage of cover. For the other two vegetation types, the cover was complete.

RESULTS

Forest structure and floristics

The taxonomic determinations of the collected specimens (most of them sterile material) are still not finished. From the measured trees (diameter ≥ 10 cm), three were not identified at all; thirty-six were identified to the family level only and were separated as morpho-species.

A total of 189 trees (diameter ≥ 10 cm) were found in the the three 50-m x 50-m plots combined in the SHF, while 435 trees were recorded in the THF, and 665 trees in the LERF. In the SHF, the most common identified species were *Aldina heterophylla* (Caesalpiniaceae) and *Pradosia schomburgkiana* (Sapotaceae), each one with 69 individuals out of a total of 189 trees in the three plots. In the THF, the most abundant trees were *Gavarretia terminalis* (Euphorbiaceae), *Pradosia schomburgkiana* and *Aldina heterophylla*, respectively with 93, 73, and 55 individuals out of 435 trees. In the LERF plots, the most common species were *Protium* sp 3 (Burseraceae), *Oenocarpus bacaba* (Arecaceae), and *Ocotea* sp 2 (Lauraceae). respectively with 85, 61, and 53 individuals out of 665 trees (Appendix 3.1).

The total number of species in the 0.75 ha (three plots of each forest type combined) was eleven species (in eight families) in the SHF, forty-nine species (in twenty-five families) in the THF, and 158 species (in forty-five families) in the LERF. The mean number of species per plot varied greatly among the three forest types, from just seven (range 5-9) in the SHF, to twenty four (range 21-29) in the THF, to eighty-two (range 78-84) in the LERF (Table 3.2). Similarly, the mean number of families varied from 4.7 (range 3-7) in the SHF to 17.3 (range 15-20) in the THF and 33.0 (range 29-36) in the LERF (Table 3.2).

The mean tree density varied from 252 ha^{-1} (range 132-312 ha^{-1}) in the SHF to 887 ha^{-1} (range 852-952 ha^{-1}) in the LERF, while the mean basal area varied from 9.52 m^2 ha^{-1} (range 5.76-13.9 m^2 ha^{-1}) in the SHF to 31.0 m^2 ha^{-1} (range 28.2-34.5 m^2 ha^{-1}) in the LERF (Table 3.2). The

estimated aerial biomass was: 71 t ha^{-1} in the SHF; 152 t ha^{-1} in the THF; and 409 t ha^{-1} in the LERF.

The Caesalpiniaceae were the dominant family in terms of % basal area in all three forest types, occupying 78.6 % in the SHF, 47.0 % in the THF, and 17.1 % in the LERF (Table 3.3). In the SHF, the other dominant family (*sensu* Anderson *et al.* 1975) were the Sapotaceae (16.8 %). The Fabaceae had 2.69 % and each of all other families occupied less than 1% in each plot (Table 3.3). In the THF, the second dominant family were the Euphorbiaceae (18.0 %), with the Sapotaceae (8.05 %) ranking third, while in the LERF, the Caesalpiniaceae were followed by the families Burseraceae (13.2 %) and Sapotaceae (12.6 %). In the LERF, two other families (Lauraceae and Chrysobalanaceae) were also dominant with more than 10 % of the basal area (Table 3.3). The variations in tree density and basal area among the three plots of the same forest type were generally high, being higher in the SHF and THF than in the LERF (Table 3.3). The dominance of the Caesalpiniaceae in the tree basal area decreased sharply from the SHF (78.6%) to the LERF (17.1% of the basal area). The opposite was observed for the Burseraceae which were rare in the SHF but occupied 13.2 % of the basal area in the LERF.

Table 3.2: Mean (and range) number of species, number of families, tree (≥ 10 cm dbh) density, tree basal area, and biomass in three replicate 50 m x 50 m plots in each forest type.

	Forest type		
	SHF	THF	LERF
Number of species	7 (5 - 9)	24 (21 - 29)	82 (78 - 84)
Number of families	4.7 (3 - 7)	17.3 (15 - 20)	33 (29 - 36)
Tree density (ha^{-1})	252 (132 - 312)	580 (420 - 748)	887 (852 - 952)
Tree basal area (m^2 ha^{-1})	9.52 (5.76 - 13.9)	16.6 (13.5 - 21.9)	31 0 (28.2 - 34 5
Biomass (t ha^{-1})	71 (24 - 144)	152 (110 - 201)	409 (333 - 461

The dominant species in both the SHF and THF was *Aldina heterophylla* (Caesalpiniaceae) 72.3 % (SHF) and 40.8 % (THF) of the basal area, followed by *Pradosia schomburgkiana* (Sapotaceae) in the SHF (11.2 %), and by *Gavarretia terminalis* (Euphorbiaceae) in the THF (18.0 %). In the THF, *Pradosia schomburgkiana* ranked third (Table 3.4).

Neither *Aldina heterophylla* nor *Pradosia schomburgkiana* occurred in the LERF plots, where the dominant species was *Swartzia polyphylla* (Caesalpiniaceae) (11.6 %), followed by *Ocotea* sp 2 (Lauraceae)(8.6 %) (Table 3.4). There were eight species (belonging to four families) occurring in both the SHF and THF, while twenty-seven species (21 families) occurred in heath forest (either SHF or THF or both) and LERF plots (Table 3.5).

The percent vegetation cover in the SHF plots was 92 % in plot 1, 56 % in plot 2, and 79 % in plot 3, with a mean cover of 75.6 % for the three plots.

Table 3.3: The mean (and range) percentage contribution of each family of tree (≥ 10 cm dbh) to the basal area in three replicate 50 m x 50 m plots in each forest type.

	SHF	THF	LERF
Anacardiaceae	0	0.27 (0.0-0.67)	1.73 (0.0-5.18)
Annonaceae	0	0.91 (0.31-1.66)	1.06 (0.14-1.82)
Apocynaceae	0	2.61 (0.63-3.63)	0.12 (0.0-0.23)
Arecaceae	0	0.81 (0.0-2.42)	4.28 (2.52-6.41)
Bombacaceae	0	0	0.58 (0.0-0.91)
Boraginaceae	0	0	0.61 (0.0-1.05)
Burseraceae	0.08 (0.0-0.23)	0.43 (0.0-1.15)	13.2 (10.2-14.9)
Caesalpiniaceae	78.6 (68.7-80.3)	47.0 (42.5-49.7)	17.1 (2.76-32.4)
Caryocaraceae	0	0	0.32 (0.0-0.83)
Celastraceae	0	0	0.38 (0.0-1.14)
Chrysobalanaceae	0	0.90 (0.0-2.55)	11.0 (8.31-16.0)
Clusiaceae	0.84 (0.0-2.53)	4.59 (1.50-6.90)	0.40 (0.0-0.72)
Combretaceae	0	0	1.25 (0.0-3.74)
Dilleniaceae	0	0	0.03 (0.0-0.12)
Elaeocarpaceae	0	0	0.30 (0.0-0.49)
Euphorbiaceae	0	18.0 (11.8-26.2)	0.05 (0.0-0.15)
Fabaceae	2.69 (0.82-4.62)	0.10 (0.0-0.31)	0.85 (0.25-1.24)
Hippocrateaceae	0	0	0.06 (0.0-0.19)
Humiriaceae	0.40 (0.0-1.21)	0.20 (0.0-0.45)	3.92 (0.69-7.91)
Lauraceae	0	1.22 (0.29-2.68)	11.9 (7.16-18.5)
Lecythidaceae	0	0.58 (0.0-1.74)	0.57 (0.28-0.80)
Linaceae	0	0	1.25 (0.31-2.94)
Malpighiaceae	0	0.16 (0.0-0.47)	0
Melastomataceae	0	0.12 (0.0-0.35)	0.26 (0.14-0.33)
Meliaceae	0	0.07 (0.0-0.22)	0.64 (0.11-1.22)
Menispermaceae	0	0.19 (0.0-0.57)	0.47 (0.0-1.28)
Mimosaceae	0	0	2.21 (0.29-3.68)
Monimiaceae	0	0	0.07 (0.0-0.21)
Moraceae	0	0	3.25 (1.57-5.87)
Myristicaceae	0	0	0.42 (0.12-0.82)

Table 3.2 (cont.)

	SHF	THF	LERF
Myrsinaceae	0	0	0.06 (0.0-0 18)
Myrtaceae	0.09 (0.0-0.26)	0	0.76 (0.51-1.15)
Nyctaginaceae	0	0	0.40 (0.0-0 82)
Ochnaceae	0.58 (0.0-1.73)	2.03 (0.63-3.79)	0.78 (0.10-1.75)
Olacaceae	0	0	0.41 (0.0-0 91)
Quiinaceae	0	0	0.03 (0.0-0 12)
Rhabdodendraceae	0	0	0.07 (0.0-0 12)
Rhizophoraceae	0	0	1.63 (0.0-4 88)
Rubiaceae	0	2.15 (0.0-5.53)	0.70 (0.58-0.81)
Sapindaceae	0	0.95 (0.0-2.54)	0.18 (0.0-0 33)
Sapotaceae	16.8 (8.69-26.9)	8.05 (7.61-8.46)	12.6 (9.05-16.7)
Simaroubaceae	0	4.00 (0.90-7.95)	0.37 (0.0-0 88)
Sterculiaceae	0	0	0.42 (0.14-0 61)
unknown	0	0.21 (0.0-0.49)	0.25 (0.0-0 40)
Verbenaceae	0	0.57 (0.0-1.16)	0.39 (0 0-0 59)
Violaceae	0	0	0.04 (0.0-0 12)
Vochysiaceae	0	3.76 (0.0-5.82)	2.66 (0.0-4 07)

Table 3.4: The mean (and range) percentage contribution of the five most important tree species (≥ 10 cm dbh) to the basal area in each forest type.

Species	SHF	THF	LERF
Aldina heterophylla	72.3 (62.7-81.6)	40.8 (35.7-44.9)	
Pradosia schomburgkiana	11.2 (4.92-14.7)	7.86 (7.50-8.46)	
Swartzia sp 1	5.95 (5.07-7.42)	5.94 (4.07-6.91)	
Manilkara sp	5.62 (0.0-13.1)		
Ormosia sp	2.69 (0.82-4.62)		
Gavarretia terminalis		18.0 (11.8-26.2)	
Simarouba amara		4.01 (0.90-7.95)	
Swartzia polyphylla			11.6 (0.0-29.2)
Ocotea sp 2			9.07 (4.34-14.9)
Protium sp 3			8.61 (8.15-9.40)
Licania sp 1			5.21 (0.29-10.8)
Oenocarpus bacaba			3.83 (2.52-5.08)

Table 3.5: List of the species occurring in heath forest (either SHF or THF or both) and LERF plots in the study sites. The sign + denotes a single occurrence of the species in the corresponding forest type.

Species	Family	Forest types		
Abuta sp	Menispermaceae		THF+	LERF
Aldina heterophylla	Caesalpiniaceae	SHF	THF	
Apocynaceae sp 1	Apocynaceae		THF+	LERF+
Aspisdorperma album	Apocynaceae		THF+	LERF+
Burseraceae sp 1	Burseraceae		THF	LERF
Chrysophyllum sp 1	Sapotaceae		THF+	LERF
Clusia sp	Clusiaceae	SHF	THF	
Eugenia sp 1	Myrtaceae	SHF+		LERF+
Gavarretia terminalis	Euphorbiaceae		THF	LERF+
Guatteria sp	Annonaceae		THF	LERF
Licania sp 1	Chrysobalanaceae		THF	LERF
Licania sp 3	Chrysobalanaceae		THF	LERF+
Macrolobium sp	Caesalpiniaceae	SHF	THF	
Manilkara amazonica	Sapotaceae	SHF	THF+	LERF
Mezilaurus itauba	Lauraceae		THF	LERF+
Miconia sp	Melastomataceae		THF	LERF
Ocotea sp 1	Lauraceae		THF	LERF
Oenocarpus bacaba	Arecaceae		THF	LERF
Ormosia costulata	Fabaceae	SHF	THF+	
Ouratea sp	Ochnaceae	SHF	THF	LERF
Pradosia schomburgkiana	Sapotaceae	SHF	THF	
Protium heptaphyllum	Burseraceae	SHF+		LERF
Qualea sp	Vochysiaceae		THF	LERF+
Remijia sp	Rubiaceae		THF	LERF+
Rubiaceae sp 3	Rubiaceae		THF+	LERF+
Sacoglottis guianensis	Humiriaceae		THF+	LERF+
Sacoglottis sp	Humiriaceae		THF+	LERF
Sapindaceae sp 1	Sapindaceae		THF	LERF
Simarouba amara	Simaroubaceae		THF	LERF
Swartzia sp 1	Caesalpiniaceae	SHF	THF	LERF+
Tapirira guianensis	Anacardiaceae		THF+	LERF+
Vitex sp.	Verbenaceae		THF	LERF+

DISCUSSION

The species richness (a total of 11 species of trees with diameter ≥ 10 cm in the SHF, 49 species in the THF, and 158 species in the LERF) for the 0.75 ha of forests in this study (three plots of each forest type combined), was very low for the SHF and THF, as expected for heath forests in Central Amazonia (Anderson 1981). The number of species was also relatively low for the the LERF plots, compared with the range for rain forests reviewed by Campbell *et al.* (1986) and Gentry (1988) (range of 60-300 species for contiguous 1-ha plots). The number of species in the LERF plots was lower than the 179 species (trees ≥ 15 cm dbh) recorded by Prance *et al.* (1976) in 1 ha of forest on an Oxisol near Manaus, but was higher than that from Maracá, where Thompson *et al.* (1992) recorded 84 species (trees ≥ 10 cm dbh).

The lower species richness found in the SHF and THF plots in the present study confirms findings of other authors (Takeuchi 1960; Anderson *et al.* 1975; Anderson 1978, 1981; Guillaumet 1987) who found low diversity and indicate a pronounced tendency toward a dominance by one of a few species in heath forests in Brazilian Amazonia. There was also a trend to heath-forest endemicity, in agreement with Anderson (1981) who reported that only 23.6% of the woody species of heath forests in central Amazonia also occurred in the lowland evergreen rain forest on Oxisols (Appendices 3.2, 3.3). Thus, a heath forest biota characteristically low in diversity and high in endemism exists in central Amazonia (Anderson 1981), contrasting with a relatively high diversity in many south-east Asian sites, such as in Sarawak (Brünig 1974; Proctor *et al.* 1983a). The species richness in the upper Rio Negro region, where heath forests cover large areas, is also much higher than in central Amazonia (Ducke & Black 1953; Anderson 1981). One likely explanation for the lower diversity in central Amazonia, where heath forests have a scattered occurrence (Anderson 1981), may be linked to the dispersal mechanisms. Macedo & Prance (1977) suggest that only species with long-distance dispersal mechanisms may overcome the barriers such as the Rio Negro and be successfully established in the spatially isolated heath forests in central Amazonia. In the present study, from a total of fifty-one species found in the SHF and THF together, only eight species (15.7 %) were common to both heath forests, and two of these (25 %) involved single individuals in each forest type. From the 180 species in the three forest types together, twenty-seven species (15 %) were common to one or both of SHF and THF, and LERF plots, and

seventeen of these (63 %) involved single individuals in each forest type. The proportion of species common to heath forest and LERF plots (15%) was lower than the 27.2% reported by Brünig (1969) in his extensive survey of heath and dipterocarp forests in Brunei and Sarawak (220 common species out of a total of 849 species). There were large proportions of species recorded as single individuals in the three plots in each forest type of the present study.

The species *Aldina heterophylla* (Caesalpinaceae) and *Pradosia schomburgkiana* (Sapotaceae) were very common in both the SHF and THF, while *Gavarretia terminalis* (Euphorbiaceae) was the commonest tree species in the THF. *Aldina heterophylla* and *Pradosia schomburgkiana* were not recorded in any of the three LERF plots in the present study, while the species *Gavarretia terminalis* occurred once in one of the LERF plots. The tree density in the SHF (252 ha^{-1}) was at the low end of the range reported by Campbell *et al.* (1986) and Gentry (1988) for Amazonian forests (205-858 trees ha^{-1}). That is partially because of the high dbh limit established for such small trees in that forest type. The tree density in the THF (580 ha^{-1}) was intermediate for that range, while the density in the LERF (887 ha^{-1}) was slightly higher than the upper range reported by Campbell *et al.* (1986) and Gentry (1988).

The tree basal area in both the SHF (mean 9.52 m^2 ha^{-1}) and the THF (mean 16.6 m^2 ha^{-1}) was much lower than in the LERF and, as expected, also much lower than the range (30-40 m^2 ha^{-1}) for lowland rain forests in northern South America (Lamprecht 1972; Guillaumet 1987). In the LERF plots, the basal area (mean 31.0 m^2 ha^{-1}, range 28.2-34.5 m^2 ha^{-1}) was at the low end of that range, but higher than the 23.8 m^2 ha^{-1} (range (21.7-26.7 m^2 ha^{-1}) recorded by Thompson *et al.* (1992) on Maracá. The Caesalpiniaceae had the highest basal area in the 0.75 ha of all three forest types, followed by the Sapotaceae and Fabaceae in the SHF, by the Euphorbiaceae and the Sapotaceae in the THF, and by the Burseraceae and Sapotaceae in the LERF plots. Elsewhere in Amazonia, other dominant families have been reported: the Lecythidaceae near Manaus (Prance *et al.* 1976), the Myristicaceae or Euphorbiaceae in Acre. and the Leguminosae in the Rio Xingu, and in Amapá (Campbell *et al.* (1986): and the Moraceae on Maracá (Thompson *et al.* 1992). Only in a monodominant *Peltogyne* forest in Maracá, was there a record of a large (up to 63 %) basal area dominance by the Caesalpiniaceae (Nascimento 1994). It is noteworthy that in the present study, the Lecythidaceae. Moraceae. and Myristicaceae were unimportant in all the plots, the same applying to the Myrtaceae.

regarded as a prominent family in Sarawak (Brünig 1969, 1974). In the present study, the Myrtaceae were only prominent as an understorey shrub in the THF plots.

The dominance of the Caesalpiniaceae in the SHF plots was highly influenced by large (and tall) individuals of *Aldina heterophylla* occurring especially in plot 1 (seven trees with a dbh above 40 cm), the SHF plot presenting the most closed vegetation. Despite the occurrence of these large trees, and the high vegetation cover (92 %), plot 1 must be considered as SHF in view of its floristic composition, low number of species, families, and trees (≥ 10 cm d.b.h.), dissimilar from all three THF plots. The soil was also distinct from those in the THF (Chapter 2), since the soil in plot 1 generally lacked the humus layer and confirmed the plot as SHF. In the LERF plots, the dominant species *Swartzia polyphylla* had a few very large individuals in plots 7 and 8 but it was absent from plot 9. Among the species with a large proportion of the basal area, the most evenly distributed was *Protium* sp 3.

In the heath forests in central Amazonia, *Aldina heterophylla* seems to be the equivalent of the *Shorea* species in the heath forests in Sarawak, reported as frequent by Brünig (1969, 1974), in representing a large proportion of the basal area in heath forest plots.

The aerial biomass estimated for the heath forests in the present study (70 t ha^{-1} in the SHF and 150 t ha^{-1} in the THF) was lower than values recorded in Venezuela (182 t ha^{-1} for stunted facies and 237-266 t ha^{-1} for tall facies) (Medina & Cuevas 1989), and much lower than the 490 t ha^{-1} recorded for tall facies of heath forests in Sarawak (Proctor *et al.* 1983a). In the LERF plots, the estimated biomass (410 t ha^{-1}) was slightly higher than the range of 344-393 t ha^{-1} reported by Klinge *et al.* (1975) for lowland evergreen rain forests on clay-rich soils in Amazonia. It was also well above the values (234-261 t ha^{-1}) reported for mixed forests on Oxisols in Venezuela, but similar to the biomass (423 t ha^{-1}) of a forest on Ultisols in Venezuela (Buschbacher 1984). It is suggested that the forests on Ultisols, like the LERF of the present study, may have a trend for larger biomass than the neighbouring forests on Oxisols because of the high tree density and a few exceptionally large individuals. However, all the biomass values referred to are rough, and the SHF and THF biomass may well be underestimated since *Aldina heterophylla* had a high (but unfortunately not measured) wood density, and largely dominated the basal area in both the SHF and THF.

Chapter 4. FINE LITTERFALL AND LITTER-LAYER IN THE SHF, THF, AND LERF

INTRODUCTION

Litterfall and root turnover are major pathways for the return of organic matter and nutrients from the vegetation to the soil and have an important bearing on soil formation and fertility (Nye 1961; Spain 1984; Vitousek & Sanford 1986). Litter functions as an energy source for many food chains in tropical forest (Fittkau & Klinge 1973) and for the nutrient cycles in the uppermost layers of the soil (Newbould 1967; Swift & Anderson 1989). The importance of litter increases in forest ecosystems on deeply weathered, nutrient-poor soils, where the vegetation is uncoupled from weathering rocks (Nye 1961; Fittkau & Klinge 1973; Herrera *et al.* 1978; Baillie 1989; Burnham 1989).

Despite the fact that fine litterfall studies usually fail to account for leaf material consumed by herbivores, and hence underestimate production (Lowman 1984), litterfall collection remains widely used as a non-destructive technique for assessing production (Newbould 1967). Rain forests usually have a relatively high litterfall (Golley *et al.* 1975; Proctor 1983, 1984; Proctor *et al.* 1983; Vogt *et al.* 1986), but this is not always true, particularly on some lowland spodosols and some montane organic soils (Herrera 1979; Jordan & Murphy 1982; Cuevas & Medina 1986; Medina & Cuevas 1989; Proctor 1984; Luizão 1989). The range in lowland tropical forest litterfall (apart from heath forests) (Proctor 1984 and personal communication; Spain 1984) spans from 5.8 t ha^{-1} yr^{-1} in Venezuela (Jordan & Murphy 1982) to 15.3 t ha^{-1} yr^{-1} in Zaïre (Laudelout & Meyer 1954). Litterfall rates in South American rain forests are generally in the lower range for tropical rain forests (Fittkau & Klinge 1973; Proctor 1984; Vitousek 1984). The relatively low litterfall in lowland evergreeen rain forest in Amazonia has been attributed to the low soil phophorus availability (Vitousek 1984). However, relatively high litterfall production has been found in Amazonian forests on soils with low phosphorus (Scott *et al.* 1992). Since Proctor's (1984) review there have been further Amazonian studies by Luizão & Schubart (1987), Cuevas & Medina (1986), Dantas & Phillipson (1989), Luizão (1989), Medina & Cuevas (1989), Scott *et al.* (1992). Some of the studies have been made in heath forests (Herrera 1979; Jordan & Murphy 1982; Cuevas & Medina 1986; Medina &

Cuevas 1989) giving a range from 2.4 t ha^{-1} yr^{-1} to 5.6 t ha^{-1} yr^{-1}, but none of these was in Brazil.

The aims of the work described in this chapter were to measure the mass and the mineral elements of the fine litterfall and the litter layer in the SHF, THF and LERF, and to estimate the turnover quotients of litter fractions and mineral elements.

MATERIAL AND METHODS

Litterfall was measured using ten 0.5 m x 0.5 m wooden litter-traps randomly distributed in each plot of the three forest types. Litter traps were supported 20 cm above the forest floor by four wooden stakes. The traps were placed in the field on 30 December and emptied at 14 d (occasionally 7 d) intervals from 12 January 1992 to 30 December 1992. Samples were air-dried and sorted into four fractions as recommended by Proctor (1983): leafy material; woody material (up to 2.0 cm in diameter, including twigs, fine branches and bark); reproductive parts (flowers, fruits and seeds); and trash (small fragments of various origins including invertebrate frass, epiphytes, and lichens). After sorting, litterfall samples were dried to constant weight at 65-70 °C for about 3 d and all fractions were individually weighed. Owing to limitations in the number of samples to be analysed, all samples from a given plot within the same season (wet (> 150 mm/month), transitional (100 - 150 mm) or dry (< 100 mm)) were pooled by fraction, finely ground, and stored for chemical analysis. The three months defined as transitional were January (120 mm rainfall measured in 1992), May (129 mm), and November (114 mm).

Litter layer measurements were made using 0.5-m x 0.5-m wooden quadrats close to each litter trap (Anderson & Ingram 1993). Samples were taken on three occasions: 8 April 1992 (wet season), 26 August 1992 (dry season) and 19 February 1993 (early wet season). (Owing to problems in the laboratory, the planned sampling for the transitional month November 1992 was delayed until February 1993). For collecting the samples, a sharp knife was used to cut inside the frame, and all loose litter (but not soil organic matter) was removed (Anderson & Ingram 1993). The litter was sorted into leaves, fine wood and reproductive parts as for litterfall, with a fourth fraction of fine fragments. (The last fraction did not correspond to the trash fraction in the litterfall but consisted of fragments, unsorted into the other fractions, which were retained by a 2-mm sieve). The finer material (which included soil mineral and organic

matter, and which passed through the sieve), was discarded. After drying, the samples were weighed individually, pooled in one sample for each plot and fraction, and then finely ground and stored for chemical analyses.

Chemical analysis of fine litter

Analyses were made in the laboratories of the Centro de Energia Nuclear na Agricultura (CENA), Piracicaba, São Paulo, for nitrogen, phosphorus, potassium, calcium, magnesium. and aluminium, boron, copper, iron, manganese, and zinc. The ground leaves were digested in two ways: 0.20 g of material in concentrated sulphuric acid and hydrogen peroxide with a selenium catalyst (Allen *et al.* 1974) for nitrogen analysis; and 0.50 g of material in a mixture of nitric and perchloric acid (Allen *et al.* 1974) for the other elements. Nitrogen was determined colorimetrically using a FIA (Flow Injection Analysis) system (Reis *et al.* 1980). Potassium was measured by flame emission spectrometry. The other elements, were determined by inductively coupled plasma emission spectrophotometry in a Jarrel-Ash Plasma Atomcomp model 975 ICP. To keep the accuracy of the analyses within a range of error 0-5%, in each batch of 40 samples, three blanks and three samples of standard NBS (National Bureau of Standards, USA) certified material (either pine needles, Standard Reference Material No. 1575 or citrus leaves, Standard Reference Material No. 1572) were included. Additionally. three samples of powdered soya beans were included among the samples as a laboratory reference material.

Data analysis

Important losses of litter mass and mineral elements in the litter traps were not expected because of the short sampling intervals (Luizão 1989), and no correction for decomposition was applied.

The decomposition quotient (k_L) was calculated as

$$k_L = I / X$$

where I is the annual fine-litter input to the forest floor and X is the mean fine-litter layer mass. k_L values for leaves, small wood, reproductive structures, and total litter were calculated separately. Additionally, the corresponding quotients k_E of mineral elements in the litterfall and

in the litter layer were calculated. Nested (plots within forest types) analyses of variance were used to compare the individual values of the fractions and the concentrations of mineral elements in the litterfall and litter layer among the three forest types. Univariate repeated measures analysis (because of samples collected in the same place each time) followed by Tukey's test (Zar 1974) was used to compare the mass of fractions and total fine litterfall and litter layer among seasons and the mean concentrations of mineral elements of litterfall and litter layer (means of ten litter traps or quadrats per plot) among the different fractions. F-test degrees of freedom were automatically adjusted by Minitab, on the within-plots tests, being approximated from the linear combination of mean squares and their degrees of freedom. Data were tranformed (log_e) before running the analyses of variance.

RESULTS

Litterfall

The total fine litterfall ranged from 3.8 t ha^{-1} yr^{-1} in the SHF to 7.8 t ha^{-1} yr^{-1} in the LERF (Table 4.1). The leaf fraction corresponded to 70% or more of the litterfall in the three forest types (Table 4.1 and Fig. 4.1), clearly being the fraction which controls the pattern and the amount of litterfall. Leaf and total litterfall were greater in the dry season, especially from June to August in the THF and LERF (Fig. 4.1). In the open vegetation of the SHF, however, despite a relatively high production in July, the main peak occurred in January which is usually the onset of the wet season. However, in the present study, January was relatively dry, with only 11 rainy days. The wood fraction was significantly lower in December than in the other months. especially in the SHF, while the reproductive parts were higher in May. especially in the THF (Fig. 4.1 and Appendix 4.1). Significant differences in the production of all litter fractions. except trash, were found among all three forest types (Table 4.1) which were ranked: LERF > THF > SHF.

Table 4.1: Estimated fine litterfall (t ha^{-1} yr^{-1}) from ten 0.5 m x 0.5 m traps in each of three replicate plots in the SHF, THF and LERF. Values for individual plots are means ± SE. Values in parenthesis are the percentages (%) of each fraction in relation to the total. Mean values followed by different letters in the same column were significantly different from other forest types ($p < 0.01$) following an univariate repeated measures analysis (df = 2).

	plot	leaf	wood	reproductive parts	trash	total
SHF	1	3.41 ± 0.24	1.07 ± 0.25	0.05 ± 0.02	0.60 ± 0.48	5.13 ± 0.69
	2	1.41 ± 0.29	0.54 ± 0.15	0.07 ± 0.01	0.04 ± 0.01	2.07 ± 0.32
	3	3.14 ± 0.44	0.88 ± 0.18	0.06 ± 0.03	0.18 ± 0.09	4.25 ± 0.50
	mean	2.65a	0.83a	0.06a	0.26a	3.82a
	%	(70.4)	(22.4)	(1.64)	(5.59)	
THF	4	4.01 ± 0.68	1.14 ± 0.13	0.25 ± 0.04	0.11 ± 0.01	5.86 ± 0.75
	5	4.71 ± 0.35	1.68 ± 0.33	0.30 ± 0.08	0.16 ± 0.03	6.83 ± 0.56
	6	4.37 ± 0.46	1.31 ± 0.19	0.27 ± 0.11	0.15 ± 0.04	6.08 ± 0.58
	mean	4.36b	1.38b	0.27b	0.14a	6.26b
	%	(71.2)	(22.1)	(4.44)	(2.27)	
LERF	7	5.13 ± 0.36	1.77 ± 0.33	0.68 ± 0.25	0.10 ± 0.01	7.66 ± 0.55
	8	5.26 ± 0.22	1.41 ± 0.17	0.47 ± 0.15	0.12 ± 0.02	7.25 ± 0.40
	9	5.95 ± 0.40	1.68 ± 0.26	0.51 ± 0.13	0.20 ± 0.04	8.36 ± 0.68
	mean	5.45c	1.62bc	0.55c	0.14a	7.76c
	%	(70.1)	(20.9)	(7.20)	(1.81)	

Mineral elements in litterfall

The concentrations of mineral elements in litterfall are shown in Table 4.2. There were differences among fractions of the litterfall for all mineral elements analysed (Table 4.3). The wood fraction had significantly lower concentrations of nitrogen, phosphorus, potassium, magnesium, and boron, but relatively high concentrations of calcium and zinc (Tables 4.2 and 4.3). The trash fraction had higher concentrations of nitrogen, aluminium, copper, and iron (Table 4.3), and relatively high concentrations of phosphorus, potassium and zinc (Table 4.2). Leaf material showed higher concentrations of boron (Tables 4.2 and 4.3), and relatively high concentrations of nitrogen and aluminium (Table 4.2).

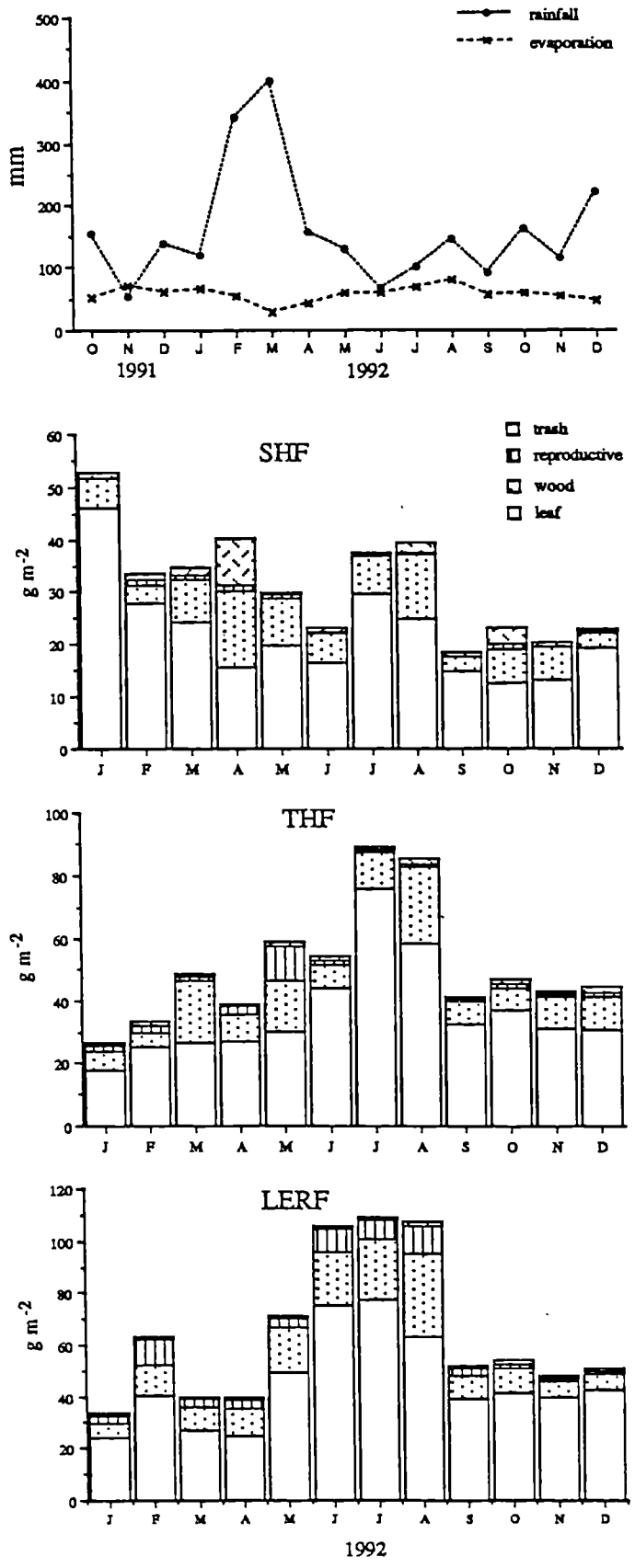


Fig. 4.1: Monthly litterfall production (g m^{-2}) in the SHF, THF, and LERF, with monthly rainfall and evaporation shown in the upper graph

Comparing the forest types, litterfall in the LERF showed higher concentrations of nitrogen than in both THF and SHF ($p < 0.001$ for forest types and $p < 0.01$ for plots nested in forest types); lower concentrations of aluminium in the SHF than both THF and LERF ($p < 0.001$ for forest types and $p < 0.05$ for plots nested in forest types); higher concentrations of calcium ($p < 0.001$ for both forest types and for plots nested in forest types) and apparently higher concentrations of magnesium ($p < 0.001$ for forest types and $p > 0.05$ for plots nested in forest types) in the SHF than both THF and LERF (Table 4.2). No significant differences were found for the other elements analysed.

Table 4.2: Mineral element concentrations in each component of the litterfall in the three forest types. Values are means of three plots with ranges in parenthesis (n=3).

	mg g^{-1}					$\mu g\ g^{-1}$					
	N	P	K	Ca	Mg	Al	B	Cu	Fe	Mn	Zn
SHF											
leaf	9.17 (9.13-10.6)	0.28 (0.23-0.33)	1.39 (1.13-1.80)	4.92 (4.20-6 33)	1.83 (1.67-2.03)	257 (164-305)	51.5 (48-57)	5.21 (4.0-7.6)	98.4 (88.3-106)	69.3 (60-86.7)	21.6 (16-31)
wood	8.43 (7.67-8.93)	0.20	1.08 (0.93-1.17)	6.96 (5.47-8.57)	1.50 (1.20-1.67)	320 (244-365)	25.9 (25-27)	5.44 (4.0-7.4)	128 (103-154)	77 1 (75-80.0)	26.8 (21-38)
reproductive parts	11 6 (11.1-12.1)	0.50 (0.43-0.57)	2.62 (2.30-2.87)	2.97 (2.93-3.00)	1.40 (1.27-1.43)	212 (171-256)	32.2 (31-33)	5.34 (4.6-5.8)	199 (192-208)	58.7 (57-60.7)	17.3 (16-19)
trash	16.0 (12.2-18.2)	0.70 (0.53-0.85)	3.07 (2.47-3.65)	5.12 (4.80-5.57)	1.53 (1.40-1.60)	833 (629-1220)	47.3 (43-54)	8.7 (8.3-8.9)	513 (345-814)	60.8 (52-68)	27.6 (22-32)
THF	11.2	0.60	1.10	2.23	1.30	598	46	4.36 (4.0-	111	62.1	14 8
leaf	(11.0-14.4)	(0.30-0.95)	0.97-1.30)	(2.20-2.27)	(1.20-1.33)	(474-783)	(42-51)	5.1)	(107.-116)	(57-70.7)	(13-17)
wood	8.97 (8.43-9.53)	0.19 (0.17-0.20)	0.80 (0.53-1.13)	3.27 (1.83-3.87)	0.91 (0.60-1.10)	344 (316-391)	24.9 (21-32)	4.19 (4.0-4.6)	98.4 (84-120)	57 .0 (43.7-83)	29 4 (22-38)
reproductive parts	14.3 (13.7-14.9)	0.70 (0.60-0.77)	2.61 (2.40-2.97)	1.85 (1.70-1.93)	1.60 (1.50-1.67)	424 (336-508)	39.4 (30-46)	6.20 (5.6-6.8)	200 (163-220)	49 6 (49-57)	19 5 (17-22)
trash	15.9 (15.2-16.6)	0.56 (0.53-0.57)	2.02 (1.83-2.27)	2.67 (2.50-2.77)	1.45 (1.27-1.57)	1070 (761-1310)	35.4 (33-38)	8.36 (7.3-8.8)	428 (382-504)	55 3 (50.7-58)	25.9 (24-28)
LERF	15.2	0.28	1.08	1.62	1.14	823	47.4	4.34 (4 0-	145	53.2	14 0
leaf	(12.7-16.6)	(0.23-0.30)	(1.03-1.13)	(1.49-1.83)	(1.10-1.20)	(732-874)	(46-49)	5.0)	(115-188)	(47 7-59)	(14-14)
wood	11.5 (10.9-12.2)	0.22 (0.20-0.27)	0.94 (0.83-1.10)	2.56 (2.30-2.87)	1.08 (1.07-1.20)	356 (341-364)	29 3 (28-32)	4.47 (4.0-5.4)	136 (101-183)	67 4 44-82.3)	26 0 (23- 31)
reproductive parts	15.6 (14.6-16.9)	0.68 (0.63-0.73)	3.30 (2.60-4.40)	1.73 (1.53-1.87)	1.66 (1.37-1.87)	276 (256-303)	32.2 (31-34)	7.23 (6.1-7.1)	150 (130-164)	42.5 (37-53 7)	16 8 (16 17)
trash	17.3 (16.5-17.7)	0.56 (0.47-0.60)	2.02 (1.40-2.37)	2.53 (2.50-2.57)	1.45 (1.40-1.53)	2100 (1120-3860)	34 4 (33-35)	7.66 (5.0-7.6)	535 (451-703)	66 2 (59.7-77)	30 0 (26-38)

Table 4.3: Significant differences from a nested analysis of variance on the mean concentrations of mineral elements in the different litterfall fractions for the nine plots in the three forest types.

Element	F	df	p	description of the differences found
N	23.9	3	< 0.001	wood < all others; trash > all others
P	69.5	3	< 0.001	wood, leaf < reproductive parts, trash
K	74.5	3	< 0.001	wood < all others
Ca	7.84	3	< 0.001	reproductive parts < wood, trash
Mg	8.31	3	< 0.001	wood < all others
Al	33.1	3	< 0.001	leaf > wood; trash > all others
B	22.5	3	< 0.001	leaf > all others; wood < all others
Cu	37.8	3	< 0.001	trash > reproductive parts > wood, leaf
Fe	92.9	3	< 0.001	trash > reproductive parts> wood, leaf
Mn	4.46	3	< 0.01	reproductive parts < all others
Zn	26.9	3	< 0.001	leaf, reproductive parts < wood, trash

The estimated annual input of mineral elements to the forest floor was more variable among the SHF plots than among the THF and LERF plots (Table 4.4 and Appendix 4.1). In the SHF, the input of mineral elements was always least in plot 2. The mean annual input of nitrogen ranged from 37.7 kg ha^{-1} (SHF) to 111 kg ha^{-1} (LERF), and phosphorus from 1.11 kg ha^{-1} (SHF) to 2.7 kg ha^{-1} (THF), while the inputs of calcium ranged from 14.2 kg ha^{-1} (LERF) to 21.4 kg ha^{-1} (SHF). The input of calcium was similar in the THF and LERF plots, while inputs of nitrogen, phosphorus, potassium, aluminium, iron, and manganese were clearly higher in LERF (Table 4.4).

Fine-litter layer

The mean annual fine-litter layer mass, estimated from three samplings over a 10-month period including the wet, dry, and early wet seasons, ranged from 5.4 t ha^{-1} yr^{-1} (SHF) to 6.5 t ha^{-1} yr^{-1} (LERF) (Table 4.5). The mean annual mass of the fractions of the fine-litter

Table 4.4: Annual input of mineral elements (kg ha^{-1} yr^{-1}) to the forest floor in the SHF, THF and LERF. Values are means of three plots, with ranges in parenthesis (n=3).

	SHF	THF	LERF
N	37.7 (19.1-53.3)	67.6 (59.8-74.5)	111 (107-116)
P	1.11 (0.56-1.68)	2.70 (0.84-5.29)	2.31 (2.20-2.41)
K	5.65 (2.58-8.99)	6.83 (6.21-7.49)	9.44 (8.90-9.97)
Ca	21.4 (9.31-34.3)	14.3 (14.0-14.5)	14.2 (13.6-14.8)
Mg	6.68 (3.36-9.58)	7.46 (7.04-7.98)	9.07 (8.63-9.82)
Al	1.23 (0.66-2.15)	3.40 (2.43-4.49)	5.54 (5.34-5.89)
B	0.17 (0.08-0.24)	0.25 (0.23-0.26)	0.33 (0.30-0.35)
Cu	0.02 (0.01-0.04)	0.10 (0.02-0.25)	0.03 (0.03-0.04)
Fe	0.57 (0.24-1.02)	0.73 (0.66-0.79)	1.14 (0.93-1.36)
Mn	0.27 (0.13-0.42)	0.37 (0.34-0.39)	0.86 (0.45-1.40)
Zn	0.09 (0.04-0.14)	0.11 (0.10-0.12)	0.13 (0.13-0.14)

layer are also shown in Table 4.5. The total fine-litter layer in the THF and LERF was higher in the dry season than in the early wet season; there was virtually no difference among seasons in the SHF (Fig. 4.2; Table 4.6).

The fine-fragments fraction was significantly lower in the early wet season ($F = 6.94$, $df = 6$, $p < 0.01$), and the same occurred for the total fine-litter layer ($F = 4.15$; $df = 6$; $p < 0.05$). A nested analysis of variance on the litter-layer fractions showed significant differences among the three forest types for the fractions, except fine fragments, but their significances were only confirmed by the Tukey test for wood and reproductive parts (Table 4.5). The SHF had significantly lower values for wood and reproductive parts. In this forest type, plot 2 generally had the lowest quantities of all fractions, except the fine fragments (Fig. 4.2). The lowest value

Table 4.5: Mean ± SE dry weight (t ha^{-1}) of the fine-litter layer in each plot and forest type. Values are means of 10 samples (50 cm x 50 cm) in three replicate plots collected over a year at each of three sample times from each plot within each forest type. Mean values in each column followed by different letters indicate significant differences from other forest type ($p < 0.01$), following Tukey's test ($df = 2$).

forest type	plot	leaf	wood	reproductive parts	fine fragments	total
SHF	1	2.64 ± 0.19	1.19 ± 0.14	0.005 ± 0.002	1.06 ± 0.10	4.90 ± 0.28
	2	2.09 ± 0.28	1.33 ± 0.25	0.049 ± 0.013	1.06 ± 0.18	4.40 ± 0.59
	3	3.60 ± 0.33	2.25 ± 0.70	0.050 ± 0.013	1.75 ± 0.33	6.96 ± 0.60
	mean	2.80a	1.59a	0.035a	1.29a	5.41a
THF	1	3.17 ± 0.25	1.95 ± 0.24	0.16 ± 0.03	1.22 ± 0.11	6.49 ± 0.40
	2	3.34 ± 0.14	1.51 ± 0.10	0.25 ± 0.09	1.22 ± 0.10	6.32 ± 0.25
	3	3.46 ± 0.17	1.90 ± 0.21	0.11 ± 0.02	0.91 ± 0.09	6.38 ± 0.26
	mean	3.32a	1.79ab	0.17b	1.11a	6.40a
LERF	1	3.18 ± 0.18	2.25 ± 0.16	0.18 ± 0.03	1.34 ± 0.13	6.95 ± 0.40
	2	2.74 ± 0.15	2.13 ± 0.18	0.19 ± 0.05	0.97 ± 0.13	6.02 ± 0.41
	3	2.42 ± 0.17	2.38 ± 0.19	0.39 ± 0.09	1.32 ± 0.19	6.52 ± 0.43
	mean	2.78a	2.25c	0.25bc	1.21a	6.50a

Table 4.6: Mean ± SE dry weight mass (t ha^{-1}) of the fine-litter layer in the three forest types at each of the sampling times (n=3).

	wet season			dry season			early wet season		
	SHF	THF	LERF	SHF	THF	LERF	SHF	THF	LERF
litter layer	5.60 =0.60	5.90 ±0.22	7.30 ±0.38	5.60 ±0.54	7.30 ±0.29	5.01 ±0.51	5.00 ±0.51	6.00 ±0.34	4.90 ±0.29

of fine fragments and total litter layer were found in the early wet season (Fig. 4.2), collected after the unusually wet second half of the year 1992 (all months, except June. had more than 100 mm of rainfall (see Fig. 4.1). The percentage composition of the fine-litter layer showed proportions of the wood and fine fragments fractions relatively high in relation to the leafy material (Fig. 4.2).

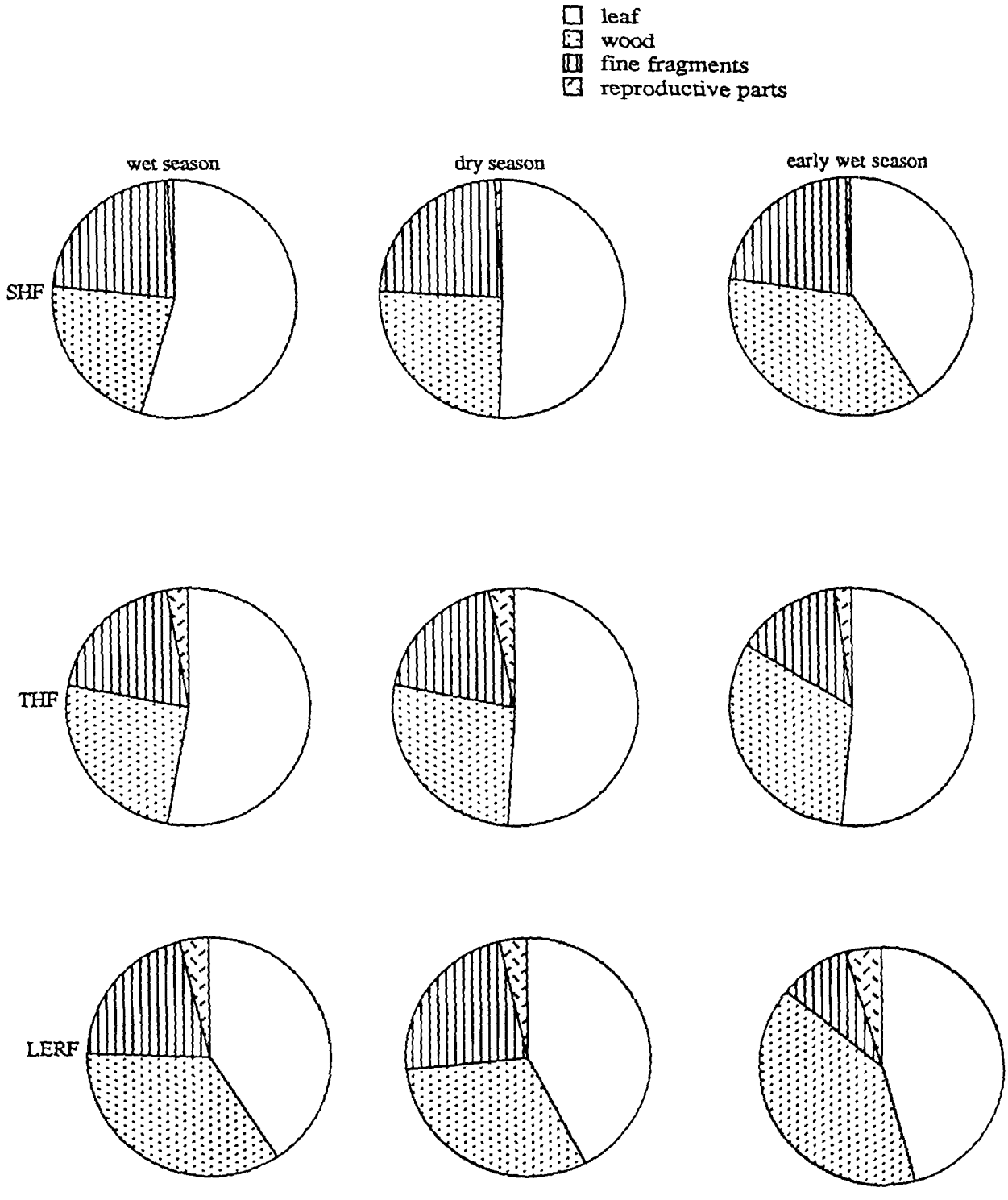


Fig. 4.2: Mean percentage composition of the litter layer in the SHF, THF, and LERF in the wet, dry, and early wet seasons. Values are means of three plots.

The proportions of the wood and fine fragments were higher in the litter layer (Fig. 4.2) than the wood and trash fractions in the litterfall, which is explained by the slower decomposition of wood and the continued breakdown of litter-layer fractions.

Mineral elements in the fine-litter layer

The concentrations of all mineral elements, except copper, in the fine-litter layer showed significant differences among fractions (Table 4.7 and Appendix 4.2). The leaves and fine fragments had the highest concentrations of nitrogen and iron; and for fine fragments only, the highest concentrations of aluminium; wood had the lowest concentrations of phosphorus, aluminium, iron, and boron; and the reproductive parts had the highest concentrations of potassium and boron (Table 4.7 and Appendix 4.2). Among the forest types, there were higher concentrations of nitrogen, and possibly aluminium in the LERF (nested ANOVA; $F = 26.9$; $df = 2$; $p < 0.01$), and of magnesium, and possibly calcium, manganese and zinc in the SHF ($F = 9.40$; $p < 0.05$) (Appendix 4.2).

The quantities of mineral elements in the fine-litter layer showed a similar pattern to those of concentrations, with quantities of nitrogen, iron and aluminium all ranked LERF > THF > SHF, and the quantities of calcium and magnesium ranked SHF > THF > LERF (Table 4.8; Appendix 4.3).

Table 4.7: Significant values from a one-way analysis of variance on the concentration of mineral elements in the litter-layer fractions in the three plots in the three forest types (n=9).

	F	df	p	differences found
N	41.4	3	< 0.001	leaf, fine fragments > wood, reproductive parts
P	14.6	3	< 0.001	wood < other fractions
K	26.1	3	< 0.001	reproductive parts > all others
Ca	12.7	3	< 0.001	wood > leaf, fine fragments
Mg	8.20	3	< 0.05	leaf > fine fragments
Al	3.75	3	< 0.05	fine fragments > wood, reproductive parts
B	10.6	3	< 0.001	reproductive parts > all others
Fe	35.3	3	< 0.001	fine fragments > wood, reproductive parts
Mn	3.69	3	< 0.05	leaf > reproductive parts
Zn	17.9	3	< 0.001	wood > leaf, reproductive parts; fine fragments > leaf

Table 4.8: Quantities of mineral elements (kg ha^{-1}) in the fine-litter layer in the three forest types. Values are means of three plots, with ranges in parenthesis.

Elements	SHF	THF	LERF
N	66.4 (51.0-85.4)	83.4 (80.1-86.6)	105 (91.7-123)
P	1.78 (1.20-2.29)	1.85 (1.78-1.89)	1.74 (1.71-1.89)
K	3.01 (2.09-3.70)	3.42 (2.91-3.94)	3.20 (2.90-3.41)
Ca	29.3 (20.9-36.1)	11.4 (7.80-14.1)	7.55 (7.78-8.13)
Mg	6.47 (4.92-8.24)	4.68 (3.90-5.10)	3.73 (3.47-4.15)
Al	2.08 (1.38-2.94)	6.27 (4.32-9.64)	13.0 (11.5-14.9)
B	0.09 (0.07-0.13)	0.10 (0.09-0.10)	0.09 (0.08-0.10)
Cu	0.03 (0.02-0.04)	0.03 (0.03-0.03)	0.03 (0.03-0.03)
Fe	1.51 (0.96-2.16)	2.31 (1.41-3.58)	4.40 (4.04-4.91)
Mn	0.46 (0.38-0.51)	0.43 (0.33-0.54)	0.34 (0.30-0.36)
Zn	0.13 (0.11-0.16)	0.10 (0.09-0.12)	0.11 (0.09-0.13)

Decomposition quotients

The decomposition quotients (k_L) for litterfall mass in the three forest types were low, especially for the SHF and THF (Table 4.9), and the same occurred with the corresponding quotients for mineral elements, except for potassium and boron in all three forest types, and phosphorus, calcium and magnesium in the THF and the LERF (Table 4.10)

Table 4.9: Decomposition quotients (k_L) (calculated from Tables 4.1 and 4.5) in the three forest types.

forest type	leaf	wood	reproductive parts	total
SHF	0.95	0.52	1.71	0.71
THF	1.31	0.77	1.59	0.98
LERF	1.96	0.72	2.20	1.19

Table 4.10: Mineral element (k_E) quotients (calculated from Tables 4.4 and 4.8) in the three forest types.

	N	P	K	Ca	Mg	Al	B	Cu	Fe	Mn	Zn
SHF	0.57	0.62	1.88	0.73	1.03	0.59	1.90	0.67	0.38	0.22	0.69
THF	0.81	1.46	2.00	1.25	1.59	0.54	2.50	3.33	0.32	0.86	1.11
LERF	1.06	1.33	2.95	1.88	2.43	0.43	3.70	1.00	0.26	2.53	1.20

DISCUSSION

Litterfall

In all three forest types, the proportion of leaves (about 70%) in the total litterfall was similar to most values found in tropical forests (Proctor 1984). The mean fine litterfall in the LERF plots was 7.8 t ha^{-1} yr^{-1} which is at the lower end of the tropical lowland evergreen rain forests (Table 4.11), including those in Brazil investigated by Klinge (1977) near Belém (9.9 t ha^{-1} yr^{-1}) and Scott *et al.* (1992) on Maracá Island (9.3 t ha^{-1} yr^{-1}). The mean fine litterfall in the THF plots (6.3 t ha^{-1} yr^{-1}) was in the mid range for the few other published results for heath forests, varying from 4.8 t ha^{-1} yr^{-1} in Venezuela (Jordan & Murphy 1982) to 9.2 t ha^{-1} yr^{-1} in Sarawak (Proctor *et al.* 1983). The SHF plots apparently had the lowest values of fine litterfall recorded for lowland tropical rain forests: 3.8 t ha^{-1} yr^{-1} (Table 4.11). This is not surprising, taking into account the open vegetation, with low biomass and many open patches of white-sand soil. Plot 2, with the most open vegetation, had the least litterfall (2.1 t ha^{-1} yr^{-1}).

The temporal pattern of the fine litterfall was also distinct in the SHF since the main litterfall peak occurred in January. As mentioned earlier, January usually coincides with the onset of the rains but in 1992 when the measurements were made, January was atypically relatively dry. It is impossible to say if the litterfall peak reflects this unusually dry spell or is a phenological feature which reflects longer term climatic conditions. In both the THF and LERF the litterfall peak was in the dry months from June to September. Dry season peaks in litterfall have been reported elsewhere in Amazonia (Klinge & Rodrigues 1968; Franken *et al.* 1979; Dantas & Phillipson 1989; Luizão 1989; Scott *et al.* 1992) and may be related to water deficits.

Fine-litter layer

The fine litter-layer masses reported in this study include a fine-fragments value which has not been reported by the other studies in Table 4.12. The mean annual litter-layer masses found in the present study (ranging from 4.1 t ha^{-1} in the SHF to 5.3 t ha^{-1} in both THF and LERF) were in the same range of the three other recorded results for Amazonian

Table 4.11: Fine litterfall (t ha^{-1} yr^{-1}) in some tropical rain forests.

Site	Total	Leaf	Wood	Reproductive parts	Trash	Author
Lowland evergreen rain forest						
Australia	9.7	4.9	-	-	-	Spain (1984)
	7.3	4.1	2.3	1.3	-	Lowman (1988)
Brazil - Belém	8.0	-	-	-	-	Dantas & Phillipson (1989)
	9.9	8.0	1.30	0.60	-	Klinge (1977)
	7.3	6.1	0.88	0.31	-	Silva & Lobo (1982)
Manaus	7.9	6.4	1.03	0.47	-	Franken *et al.* (1979)
	7.3	5.6	1.10	0.40	-	Klinge & Rodrigues (1968)
	8.3	5.4	1.56	0.42	0.79	Luizão (1989)
	7.8	5.4	1.62	0.55	0.14	This study
Maracá	9.3	6.3	1.34	1.21	0.42	Scott *et al.* (1992)
	8.6	6.0	1.37	0.93	0.37	Villela (1995)
Costa Rica	9.0	7.6*	1.4	-	-	Heaney & Proctor (1989)
French Guyana	8.7	5.8	-	-	-	Puig (1979)
Ivory Coast - Banco 11.9	8.2	-	-	-	Bernhard (1970)	
Yapo 9.6	7.1	-	-	-		
Panama	11.4	-	-	-	-	Golley *et al.* (1975)
Sarawak	8.8	5.4	-	-	-	Proctor *et al.* (1983b)
Venezuela	10.3	7.6	2.3	0.40	-	Cuevas & Medina (1986)
	5.8	-	-	-	-	Jordan & Murphy (1982)
Zaïre	12.4	-	-	-	-	Laudelout & Meyer (1954)
Heath forest						
Brazil - Manaus, SHF	3.8	2.7	0.83	0.06	0.26	This study
Manaus, THF	6.3	4.4	1.38	0.27	0.14	
Sarawak	9.2	5.6	-	-	-	Proctor *et al.* (1983b)
Venezuela - tall *caatinga*	5.6	4.0	1.36	0.21	-	Cuevas & Medina (1986)
bana	2.4	2.1	0.26	0.12	-	Cuevas & Medina (1986)
caatinga	4.8	-	-	-	-	Jordan & Murphy (1982)

* non-woody fraction, comprising leaf, reproductive parts and miscellaneous fragments.

rain forests. In Manaus, in central Amazonia, Klinge (1973a) found 6.6 t ha^{-1}, while in Maracá, at the northern fringe of Brazilian Amazonia, Scott *et al.* (1992) recorded 4.6 t ha^{-1}, and Villela (1995) 6.4 t ha^{-1} yr^{-1}. The mean annual fine-litter layer found in the THF (5.3 t ha^{-1}) was lower than the value found for heath forest (6.1 t ha^{-1}) in Sarawak (Proctor *et al.* 1983). The higher dry-season values for total and most fractions of the fine-litter layer in the THF and LERF plots reflect the pattern of higher litterfall and slower decomposition rates at that time (Klinge & Rodrigues 1968a; Franken *et al.* 1979; Luizão & Schubart 1987; Dantas & Phillipson 1989; Luizão 1989; Scott *et al.* 1992).

Table 4.12: Fine-litter layer measurements in tropical rain forests. The values in parenthesis for the present study are for the total fine-litter layer including the fine-fragments fraction, not included in the other studies.

Site	Litter layer (t ha^{-1})	Authors
Brazil		
Manaus	6.6	Klinge (1973a)
Maracá	4.6	Scott *et al.* (1992)
	6.4 (7.7)	Villela (1995)
Manaus, LERF	5.3 (6.5)	This study
THF	5.3 (6.4)	
SHF	4.1 (5.4)	
Costa Rica	3.6	Heaney & Proctor 1989
Ivory Coast		
Banco	8.1	Bernhard (1970)
Yapo	6.6	
Sarawak		
Dipterocarp	5.9	Proctor *et al.* (1983b)
Heath forest	6.1	
Zaïre	3.9	Laudelout & Meyer (1954)

Mineral element concentrations in litterfall and litter layer

The two heath forests showed concentrations of nitrogen generally lower than the LERF but higher concentrations of calcium and magnesium (Table 4.15). A similar situation has been observed in comparative heath and LERF studies in Sarawak (Proctor *et al.* 1983b) and Venezuela (Medina & Cuevas 1989). The SHF and THF nitrogen concentrations were higher than those of the heath forests in Venezuela (Medina & Cuevas 1989), which had particularly low nitrogen in the leaf litterfall.

Phosphorus concentrations were similar to most of the other tropical forests, but only half of the values found for Maracá (Scott *et al.* 1992).

Leaf litterfall potassium concentrations were low (Table 4.13), and lower than those for most lowland evergreen rain forests (Proctor 1984). The next lowest values were for Brazilian Amazonia (Klinge 1977; Klinge & Rodrigues 1968). The concentrations of calcium and magnesium were the least recorded in Table 4.13, except those found by Proctor *et al.* (1983) in Sarawak. Leaf litterfall in the SHF and THF plots had lower potassium, but higher calcium and magnesium than heath forests in Venezuela (Medina & Cuevas 1989).

In the fine-litter layer, the higher concentrations of nitrogen, aluminium, iron, and zinc in the fine fragments (in large part constituted by semi-decomposed leaves and wood) is not a surprise, since those elements are known to concentrate in the decomposing litter over time (Attiwill 1968; Luizão & Schubart 1987; Bockheim *et al.* 1991; Attiwill & Adams 1993). However, it was surprising to find relatively high concentrations of potassium and boron in the litter layer, since potassium is the most mobile and leachable nutrient from litter (Attiwill 1968), and boron has also been reported as an easily leachable element from litter in temperate and tropical forests (Luizão & Schubart 1987; Bockheim *et al.* 1991).

Only mineral elements were analysed in the present study; although they are only part of the make-up of litter quality. In his study of freshly fallen litter in lowland evergreen rain forest near Belém, eastern Amazonia, Howard-Williams (1974) showed that the litter was poor in ash and proteins, and rich in cell-wall constituents, polyphenols and calorific value, all unfavourable characteristics for decomposers. If this applies to other Amazonian

litter, one might expect low decompostion rates generally, as seems to be the case for heath forests (although their litter-layer mass has rarely been quantified). However, litter quality and decomposition rates seem variable in Amazonian lowland evergreen rain forest (Klinge 1977; Luizão & Schubart 1987; Luizão & Luizão 1991).

Table 4.13: Concentrations (as % of oven-dry weight) of nitrogen, phosphorus, potassium, calcium, and magnesium in leaf litterfall from tropical forests.

Site	Leaf litterfall $t\ ha^{-1}\ yr^{-1}$	N	P	K	Ca	Mg	Authors
LERF							
Brazil Belém	8.0	1.7	0.041	0.17	0.31	0.28	Klinge (1977)
Manaus	5.6	1.5	0.03	0.18	0.22	0.18	Klinge & Rodrigues (1968)
	5.4	1.8	0.02	0.15	0.38	0.18	Luizão (1989)
	5.4	1.5	0.028	0.11	0.16	0.11	This study
Maracá	6.3	1.3	0.058	0.47	0.74	0.27	Scott *et al.* (1992)
	6.0	1.0	0.034	0.54	0.57	0.18	Villela (1995)
Ivory Coast Banco	8.2	1.5	0.069	0.22	0.56	0.46	Bernhard (1970)
Yapo	7.1	1.4	0.050	0.28	1.32	0.29	
Sarawak (Dipterocarp)	5.4	0.95	0.011	0.45	0.15	0.11	Proctor *et al.* (1983b)
Venezuela	6.5	1.63	0.032	0.24	0.17	0.07	Medina & Cuevas (1989)
Heath forest							
Brazil, SHF	2.7	0.97	0.028	0.14	0.49	0.18	This study
THF	4.4	1.10	0.06	0.11	0.22	0.13	
Venezuela tall *caatinga*	5.2	0.70	0.05	0.21	0.77	0.31	Medina & Cuevas (1989)
low *caatinga*	2.1	0.60	0.02	0.47	0.74	0.25	
Sarawak	5.6	0.57	0.014	0.23	0.89	0.16	Proctor *et al.* (1983b)

Decomposition quotients (k_L) and quotients of mineral elements in litterfall / mineral elements in the litter layer (k_E)

The decomposition quotients (k_L) for the total fine litterfall ranged from 0.71 yr^{-1} (SHF) to 1.19 yr^{-1} (LERF). Decomposition quotients (k_L) must be considered as imperfect indices of the turnover of the fine-litter layer (Spain 1984). They remain, however, a basis for comparison with other published data. The k_L values for leaf (1.96 yr^{-1}) and total small litterfall (1.19 yr^{-1}) in the LERF (Table 4.9) are low compared with values in African lowland evergreen rain forests, and in the lower range of the few other data available for Amazonia. In Ivory Coast, Bernhard (1970) found k_L values of 3.3 yr^{-1} at Banco, and 2.8 yr^{-1} at her Yapo sites, while in Zaïre, Laudelout & Meyer (1954) estimated a k_L value of 3.2 yr^{-1}, for total fine litter. In central Amazonia, Klinge (1973a) found values of 1.5 yr^{-1} for leaves and 1.1 yr^{-1} for total fine litter, while Franken *et al.* (1979) estimated a higher k_L value of 1.9 yr^{-1} for the total litter. Scott *et al.* (1992), working on Maracá Island (northern Brazilian Amazonia), estimated higher k_L values of 2.9 yr^{-1} for leaves and 2.0 yr^{-1} for the total fine litter. In the French Guyana, Puig (1979) found a k_L value of 2.17 yr^{-1} for the total fine litter. The low values of k_L for SHF (0.71 yr^{-1}, total; 0.95 yr^{-1}, leaves) and THF (1.31 yr^{-1}, leaves; 0.98 yr^{-1}, total) are even lower than the ones found for heath forests in Sarawak. Anderson *et al.* (1983) found k_L values of 1.4 yr^{-1} for leaf, 0.10 yr^{-1} for woody material, and 1.3 yr^{-1} for total fine litter. The k_L for the reproductive parts, however, was 10.0, a very high quotient indicating the rapid decomposition of a high quality resource.

The low k_E quotients for nitrogen, iron, manganese (in the SHF and THF) and phosphorus, calcium, and zinc (SHF), and aluminium and iron in all forest types (Table 4.10), indicate a slow cycling of these elements. In the SHF, only potassium and boron (easily leachable elements *sensu* Luizão & Schubart 1987) showed higher quotients. In the THF, phosphorus, potassium, magnesium, boron, and copper had relatively high quotients. In the LERF, potassium, calcium, magnesium, boron, and manganese also showed relatively high k_E quotients.

The low k_E quotients for nitrogen (SHF and THF), phosphorus and calcium (SHF) contrast with values found for Maracá (Scott *et al.* 1992), where they ranged from 1.99

(Ca) to 5.91 (K) for their measured macronutrients. However, their ranking for nutrient release from the fine-litter layer (K > Mg > Ca >= N > P) was similar to that found for both SHF and LERF (K > Mg > Ca > P > N), except for nitrogen and phosphorus, where the rankings were reversed. In the THF, the ranking was: K > Mg > P > Ca > N. In the present study, in all forest types, nitrogen was the most slowly released nutrient, indicating a strong immobilization in the litter layer, a fact already known from studies elsewhere (Attiwill 1968; Klinge 1977; Luizão & Schubart 1987; Attiwill & Adams 1993).

In the present study, among the analysed elements, nitrogen (in all forest types), phosphorus (SHF only), aluminium (all), copper (SHF and LERF), iron (all), and manganese (SHF and THF) showed k_E values lower than k_L quotients (Tables 4.11 and 4.12), indicating some immobilization of these elements. Except phosphorus, all other elements have been found increasing their concentrations in decomposing material (Attiwill 1968; Luizão & Schubart 1987; Swift & Anderson 1989). On the other hand. potassium, magnesium, and boron (in all forest types); phosphorus and calcium (in THF and LERF); copper and zinc (only THF); and manganese (only LERF) showed k_E quotients higher than the k_L values, indicating a relatively high mobilization. Potassium and magnesium have been regarded as the most mobile elements in decomposing material (Anderson *et al.* 1983), and hence the pattern found here is not surprising. However. manganese, a much less studied element (Staaf & Berg 1982; Luizão & Schubart 1987: Bockheim *et al.* 1991) has not been recorded as mobile as is indicated in this study. except in the Scots pine (*Pinus silvestris* L.) needles studied by Staaf & Berg (1982). where calcium and manganese were released from litter faster than nitrogen and phosphorus.

Chapter 5. LITTER DECOMPOSITION AND NUTRIENT RELEASE IN THE THREE FOREST TYPES

INTRODUCTION

The release of nutrients from decomposing litter is one of the most important processes contributing to nutrient cycling in forest ecosystems, and has been studied by several authors (e.g. Anderson & Macfadyen 1976; Swift *et al.* 1979; Swift & Anderson 1989). Swift *et al.* (1979) have emphasized that the rates and pathways of litter decomposition are determined by the qualitative and quantitative composition of the decomposer community, the physical environment (particularly temperature and moisture), and the quality of the resources for animals and micro-organisms. Resource quality depends on the species of trees producing the litter and includes not only the concentration and availability of nutrients and of carbon and energy sources but also its acidity and modifiers, such as tannins, which affect the activity of heterotrophs (King & Heath 1967; Kimmins 1987). Physical features of leaves such as thickness and toughness must be considered as well, to determine the resource quality (Witkamp 1966; Lowman 1986). The lignin and nitrogen concentrations of litter have been considered important controls of the decomposition rate (Meentemeyer 1978; Tanner 1981; Melillo *et al.* 1982). Comparing five leaf species in two sub-tropical forest sites in India, Laishram & Yadava (1988) found that the initial C:N ratios and lignin concentrations were inversely related to decomposition rates and that lignin concentration was the most influential factor in the decomposition rates. On the other hand, Anderson *et al.* (1983) found that mixed leaf species with high lignin concentration in Sarawak decomposed at similar rates of leaf species which were lower in lignin. On a regional or global scale, variations in rates of decomposition across species and sites are correlated with climate and substrate quality (Swift *et al.* 1979; Vitousek *et al.* 1994).

Litter decomposition rates in humid tropical forests, where temperature and moisture supply are generally favourable to decomposers, have been considered very high, with values between six and ten times faster than in temperate forests (Madge 1965). However, this is not always true (*e.g.* Anderson *et al.* 1983), and tropical decomposition rates can be

slow such as on Spodosols in Amazonia, and sometimes variable, where there are seasonal dry periods (Kimmins 1987). In the heath forests, often having small trees and a thick mor humus layer, the relatively slow decomposition may limit the supply of available nutrients. Thus, it is important to know if nutrient flushes are associated with certain leaf species and if such flushes are likely to influence plant growth and hence species composition in heath forests.

Taking into account the complexities of the processes involved, one major problem in decomposition studies is to maintain the identity of the experimental material without altering the litter and soil environment. The use of litter bags partially overcomes this difficulty (Crossley & Hoglund 1962) and despite several drawbacks, including the artefactual within-bag microenvironment (Louisier & Parkinson 1976; St. John 1980), it provides comparative data and remains a widely used technique.

The present study, using litter bags, is an analysis of the decomposition rates and of the main factors involved in the decomposition and nutrient release processes of three different species of leaves in SHF, THF and LERF. The aims in this study are: to investigate the influence of the leaf species, and the forest types on the decomposition of individual leaf substrates in litter-bags; to assess the main factors controlling the decomposition and the nutrient release from the litter; and to assess the seasonal influence on these processes. The term `decomposition' is used to include all the processes which cause the disappearance of the leafy material from the litter bags.

MATERIAL AND METHODS

Litter-bag technique

The litter-bag technique (Bocock & Gilbert 1957; Crossley & Hoglund 1962) was used to assess the decomposition of leaf litter. The technique consists of enclosing plant material, of known weight and chemical composition in mesh bags and placing them in the field. At assigned time intervals, a number of litter bags is retrieved and the litter mass and element concentrations are measured in order to follow the rates of decomposition and nutrient release. The litter bags were 22 cm x 24 cm and made with 1.5-mm nylon mesh. Several 9-mm diameter holes were punched through the bags (near the edges) to permit

larger invertebrates to enter. Freshly fallen leaves of *Clitoria racemosa* Benth. (Mimosaceae), *Pradosia schomburgkiana* (A. DC.) Cronq. (Sapotaceae), and *Aldina heterophylla* Spruce ex Benth. (Caesalpiniaceae) were used. These tree species are henceforth referred to by their generic names only. *Clitoria* is found in LERF and both *Pradosia* and *Aldina* are found in SHF and THF. Leaves of the three species were collected (*Clitoria* at INPA's campus from an old secondary LERF, and the other two species in the Reserve, near the study plots, in both sun and shaded patches of both SHF, and THF) from early September to early December 1991, using large litter traps emptied weekly. The leaves were air dried and stored in a non-sealed insulated box in an air-conditioned (22-25 °C) room until the experiments started. No difference in the air-dried weight of the leaves was recorded after 7-months storage. Fifteen 5.5-g sub-samples of unexposed leaves were oven-dried at 65-70 °C to constant weight to provide an oven-dry weight correction. About the same air-dried weight of leaves (5.5 g) was used in all litter bags. This total quantity (5.5 g) of leaves in each bag was small in relation to the size of the bag and thus tight compression of the leaves was avoided. After filling the bags, they were closed with a fine nylon string, and placed in the the field within 48 h. Sixteen sub-samples of each of the leaf species were used to determine the initial nutrient concentrations.

Experiments A, B and C

Three litter-bag experiments (A, B, C) were made in the three forest types. For all three experiments, a restricted random design (an equal number of litter bags placed in each of the four 25 m x 25 m subplots) was used. A restricted random design was suitable in view of the very variable vegetation cover in the SHF. The same number of litter bags was placed at random in each of the four subplots of the study plots in each forest type for experiments A and B and in one subjectively chosen (as representing the norm for the forest type) study plot in each forest type in experiment C. Twenty-four sets of one bag of each of the three leaf species were tethered in the litter layer after removal of the superficial recently added leaf litter in each replicate plot of the three forest types. At each retrieval four randomly selected litter bags per species of leaves and per plot (or location

within plot for the SHF) were assessed for decomposition rates and nutrient release. Each litter bag was assessed on a subjective eleven-point scale (0-10) for the following 'actions': (i) the overall leaf breakdown and removal; (ii) root penetration among the leaves; (iii) termite activity; (iv) presence of invertebrates; (v) white and black fungal hyphae (strands) or mycelia (tissue) or both; (vi) discoloration and surface area removal of the leaves; and (vii) 'contamination' by soil or organic residues or both. The 0-10 scale used to quantify each observed action was: 0 = absence of the action; 1 = beginning of the action; 2 and 3 = low action; from 4 to 6 = medium; 7 and 8 = intense; and 9 and 10 = very intense. After evaluation, decomposing leaves were gently brushed to remove foreign material (including all fine roots), oven-dried at 65-70 °C to constant weight, ground, and stored in paper bags for chemical analysis. The roots removed from the decomposing leaves inside the litter bags were also dried, weighed and stored for chemical analysis.

Experiment A was installed at the onset of the rainy season to investigate decomposition in relation to forest type and leaf species. The litter bags, containing leaves of *Clitoria*, *Pradosia*, and *Aldina*, were placed in the field on 30 December 1991. A total of 648 litter bags was placed in the field and four litter bags of each leaf species, selected at random, were retrieved from each plot after 30, 60, 120, 180, 270 and 360 d.
Part of this experiment was shared with R.C.C. Luizão (1994), who used the 216 *Clitoria* bags as her undisturbed treatment to study the effect of fine root penetration on the decomposition and nutrient release rates.
In addition to the weighing and chemical analyses mentioned earlier, an extraction of the invertebrates present in the litter bags was made (see Chapter 6).

Experiment B was started in the dry season to compare the decomposition and nutrient release rates among forest types, and to compare the decomposition rates with those found in experiment A which started in the wet season. Former experiments in central Amazonia have shown very fast initial decomposition rates in the wet season, in contrast with relatively low rates in the dry season (Klinge 1977; Luizão & Schubart 1987). Thus,

the hypothesis was that this experiment, starting in the dry season, would show lower decomposition rates than experiment A, started in the rainy season. To allow better comparisons within a period of one year, only *Clitoria* (the fastest decomposing leaf species in the concurrent experiment A) was used. Twenty-four litter bags with *Clitoria* leaves were placed on 3 August 1992 (early dry season) in each replicate plot in each of the three forest types, following the design of Experiment A. The bags were retrieved after 30, 61, 120, 181, 271 and 358 d.

The experiment was shared with R.C.C. Luizão (1994), who used all 216 bags to compare with her paired *Clitoria* bags which were lifted up weekly to prevent fine root penetration.

Experiment C investigated further the decomposition of the two heath forest leaf species, *Pradosia* and *Aldina.* The leaves were collected separately from open (sun-exposed) vegetation patches in the SFH sites, and from closed vegetation sites (shaded parts of the SHF and THF). The litter bags were placed in a paired distribution, with sets of four litter bags (one of each leaf type: sun *Aldina,* shade *Aldina,* sun *Pradosia* and shade *Pradosia,* placed side by side) randomly placed in open and shaded areas in one plot of the SHF and at random in one plot in each of the THF and LERF. The experiment had two aims: (a) to test possible differences in the decomposition rates of each leaf species coming from sun and shaded vegetation, and (b) to test the possible effect of sun exposure on litter decomposition at the SHF site where there were many open areas with short and sparse vegetation. In the LERF and THF plots sixteen sets of four litter-bags each were placed on the forest floor according to the stratified random design used in experiments A and B, while in the SHF plot (sub-divided into sunny and shaded locations) sixteen identical sets were randomly placed, in each subjectively chosen location. A total of 256 litter bags was used in the experiment, starting on 30 December 1992, at the onset of the wet season, and extending over a period of nine months. Four retrievals were made, after 30, 91, 182 and 271 d. At each retrieval four litter-bags of each leaf species and each origin (closed or open vegetation) were removed from each location.

Chemical analysis

The initial concentrations of moisture, ash, proteins, lipids, and fibres were determined at the Aquaculture laboratory, INPA, in the leaf species used in the three experiments. The percentage leaf moisture was measured in three subsamples of each leaf species, oven-dried at 105 °C to constant weight. Ash was determined in three subsamples of 2 g each, ignited at 550 °C in a muffle furnace for 3 h. Total protein was calculated multiplying the Kjeldahl-nitrogen concentration by 6.25 (AOAC 1975). Lipids were determined by continuous digestion, using a Soxleth TE 044-8/25 digestor. Fibres were determined following the method of Weende (AOAC 1975), using the material freed from waxes after lipid determination, which was then digested in both acid (H_2SO_4 0.25 N) and alkaline (NaOH 0.25 N) solutions. The residues produced were vacuum-filtered and then burned in a muffle furnace for 1 h at 550 °C.

The elemental inorganic chemical analyses were made in the same way as described earlier (Chapter 4) for the fine litterfall and litter layer.

Climatic and moisture data

For all three experiments, selected climatic data and weekly gravimetric moisture of the top organic and the upper mineral soil layers were collated. For each period preceding the litter bag collection, the total rainfall, total evaporation, the percentage of rainy days in the period, the daily rainfall, the daily evaporation, and the difference between rainfall and evaporation were calculated using daily data provided by the CEPLAC Experimental Station (Fig 2.2). Gravimetric moisture of the organic layer and mineral soil layers were measured in composite samples taken from each plot. Samples were weighed freshly and then oven-dried up to constant weight (generally during 48 h) at 105 °C. Using the weekly determinations, the mean moisture was calculated for each period preceding the litter-bag retrieval.

Data analysis

The percentage of the initial element content remaining at each retrieval was calculated as the product of mass remaining and element concentration, divided by the initial element

content. The remaining leaf dry matter mass (%) and its nutrient concentration (mg g^{-1} of remaining leaf dry matter), and the nutrient content (mg) of all the leaf dry matter remaining in the bags were tested for differences among forest types, leaf species, locations within plots (for the SHF in experiment C) and over time using either the t-test for means of paired experiments or appropriate analysis of variance models (Zar 1984). Regressions were used to examine possible controls on weight and mineral element losses and correlations among the mineral-element concentrations and between selected element concentrations and both remaining leaf mass and fine root mass in the litter bags. The factors used in the regressions were the remaining mass of decomposing leaves, the concentrations of mineral elements in the decomposing leaves, the dry weight of fine roots per litter bag, the moisture of the organic and the upper mineral soil layer, and several rainfall-related climatic factors (the total rainfall and evaporation in the period preceding the collection, percentage of rainy days, daily rainfall and evaporation, and the difference between rainfall and evaporation in each period preceding collections). The data were transformed either using $\log_e + 1$ (on dry weight of leaves and roots in the litter bags) or arcsin (on the element concentrations and percentage remaining of the mineral elements) transformations of both content and concentrations (Zar 1984) before running the analyses. Decomposition constants, adjustment coefficients, and half-lives of the leaf substrates (Wieder & Lang 1982) were calculated using the best-fitting and simplest models of curves (linear or single negative exponential).

RESULTS

Initial quality of the leaf litter in experiments A, B, and C

The initial chemical composition of the leaves of the three leaf species used in the experiments A, B, and C are shown in Tables 5.1 and 5.2. Moisture was similar in all leaf species, except in experiment C, where *Pradosia* had a slightly higher moisture. *Clitoria* had a higher ash concentration than the two other species, but similar concentrations of

Table 5.1: Mean initial concentrations (%) of moisture, ash and organic constituents of the leaf-litter substrate in the bags (n=3).

	Experiment A			B	Experiment C			
	Clitoria	*Pradosia*	*Aldina*	*Clitoria*	sun *Pradosia*	shade *Pradosia*	sun *Aldina*	shade *Aldina*
moisture	9.37	9.37	9.27	9.35	10.2	10.6	9.60	9.37
ash	11.4	2.60	2.97	11.4	2.10	2.42	2.5	2.37
fibres	31.1	15.8	36.3	31.1	16.4	15.6	36.4	35.3
lipids	3.87	8.67	2.83	387	7.13	6.00	2.37	2.47
proteins	8.13	2.29	7.99	8.13	2.05	2.29	7.50	8.75

Table 5.2: Initial concentrations of mineral elements (mg g^{-1}) in the litter bags in the three experiments. Values are means with SD in parenthesis.

	Experiment A			B	Experiment C			
	Clitoria n=16	*Pradosia* n=16	*Aldina* n=16	*Clitoria* n=18	sun *Pradosia* n=6	shade *Pradosia* n=8	sun *Aldina* n=7	shade *Aldina* n=8
N	12.6 (0.80)	3.80 (0.30)	13.2 (0.60)	13.3 (1.20)	4.50 (0.30)	4.50 (0.30)	13.3 (0.40)	14.6 (1.00)
P	0.40 (0.10)	0.30 (0.05)	0.50 (0.07)	0.40 (0.01)	0.10 (0.05)	0.20 (0.001)	0.50 (0.05)	0.40 (0.07)
K	2.20 (0.30)	2.00 (0.30)	2.50 (0.20)	2.30 (0.50)	0.80 (0.10)	0.60 (0.20)	1.40 (0.30)	1.50 (0.40)
Ca	26.9 (4.80)	4.40 (0.40)	3.80 (0.40)	24.4 (4.70)	3.30 (0.30)	3.50 (0.30)	4.20 (0.30)	3.00 (1.20)
Mg	1.50 (0.30)	1.70 (0.30)	1.10 (0.08)	1.50 (0.20)	1.20 (0.20)	1.30 (0.10)	2.00 (0.10)	1.50 (0.40)
Al	0.20 (0.04)	0.15 (0.04)	0.09 (0.02)	0.21 (0.06)	0.11 (0.02)	0.11 (0.02)	0.09 (0.03)	0.11 (0.05)
B	0.04 (0.007)	0.06 (0.008)	0.06 (0.005)	0.08 (0.02)	0.06 (0.009)	0.07 (0.009)	0.06 (0.005)	0.08 (0.03)
Cu	0.007 (0.002)	0.004 (0.001)	0.01 (0.001)	0.01 (0.001)	0.004 (0.00)	0.004 (0.001)	0.005 (0.001)	0.007 (0.001)
Fe	0.10 (0.02)	0.09 (0.02)	0.08 (0.01)	0.14 (0.07)	0.06 (0.01)	0.06 (0.02)	0.07 (0.01)	0.07 (0.03)
Mn	0.13 (0.03)	0.03 (0.006)	0.05 (0.007)	0.11 (0.02)	0.05 (0.02)	0.02 (0.008)	0.04 (0.005)	0.04 (0.009)
Zn	0.02 (0.05)	0.01 (0.004)	0.02 (0.002)	0.02 (0.006)	0.01 (0.006)	0.01 (0.001)	0.01 (0.001)	0.02 (0.004)

proteins and fibres were found in *Clitoria* and *Aldina* (Table 5.1). *Pradosia* had the highest concentration of lipids, and the lowest concentrations of ash, proteins, and fibres. No large differences were found between sun and shade leaves of both *Pradosia* and *Aldina*, but the fibres were slightly higher and proteins were lower in sun than in shade leaves of both species (Table 5.1). Among the mineral elements, *Clitoria* and *Aldina* had similar concentrations of nitrogen, both more than three times higher than *Pradosia*. *Clitoria* also had exceptionally high calcium concentrations, which were 6-fold those in both *Pradosia* and *Aldina* (Table 5.2). *Pradosia* had the lowest concentrations of phosphorus, potassium, manganese, and zinc, while *Clitoria* had the lowest concentration of boron (Table 5.2). Sun leaves of *Pradosia* had lower concentrations of phosphorus and calcium than shade leaves, while sun leaves of *Aldina* were lower in nitrogen, aluminium and zinc than the shade leaves (Table 5.2). However, sun leaves of *Aldina* showed higher concentrations of phosphorus, calcium and magnesium than the shade leaves of the same species.

Physical and biological features of decomposing leaves in experiments A, B, and C

Observations made immediately after each retrieval in experiments A, B, and C, showed the following:

- (i) that the leaf litter decomposition rates were always fastest in the LERF and slowest in the SHF;
- (ii) that *Clitoria* decomposed faster in all three forest types, while *Pradosia*, with a harder texture and lower initial concentrations of major nutrients, decomposed more slowly. *Pradosia* leaves were frequently found curled inside the litter bags, especially in the SHF, thus decreasing their exposed surface area;
- (iii) that few roots penetrated the litter bags during the experiment in the SHF, but there were many in the THF and, especially, in the LERF, where about 30 % of the litter bags had abundant root penetration. Root penetration was clearly higher among the leaves of *Clitoria* than in the other two species, and higher amounts of roots were generally found in the wet season and in later stages of decomposition (as quantified for this species by R.C.C. Luizão). There were no significant differences between open and closed patches in

the SHF, where only plot 1 (with a higher biomass and more closed vegetation) showed some penetration of roots in the litter bags. Both open and closed patches in the SHF had lower root penetration than both THF and LERF;

- (iv) that only 1-2 % of the bags were severely attacked by termites in the SHF, mostly the *Clitoria*. In general the termites removed little decomposing leaf material in the SHF. However, 3-4.5 % of the bags in the THF and 5-7.5 % in the LERF, especially among those containing *Clitoria* leaves, were severely attacked and much material was removed. In the heath forests, no significant differences in the activity of termites was recorded between either the litter species or origin (sun or shade leaves);

- (v) that litter animals were more abundant after 120 d, when the decomposing material was wetter. The visible fauna in the litter bags was significantly lower ($p < 0.001$) in the SHF than in the other two forest types, but not significantly different between the THF and the LERF. No difference was found either between leaf species or origin in the SHF. Ants were the most noticeable invertebrates inside the litter bags and 2.5-4 % of the bags had ant nests. A low leaf-litter weight loss was recorded in the bags where ant nests occurred. No significant differences in the frequency of ant nests in litter bags was found either between sites or between litter species or origin in the heath forests;

- (vi) that fungal hyphae and mycelia were frequent on the leaves since the beginning of the experiment, especially black fungi on *Clitoria* leaves, and in the THF and LERF plots. White fungi and mycelia were less frequent in the open SHF than elsewhere ($p < 0.01$), and especially low when compared with the THF plots. They were significantly lower ($p < 0.05$) in *Pradosia* leaves than in *Aldina* leaves, but no difference was found between leaves originating from open or closed areas;

- (vii) that about 10 % of the litter bags had a large (>20 g) accumulation of soil which was probably transported by rain drop impacts or faunal activity or both; 26 % of the bags had between 10 and 20 g of soil inside and 32 % of the bags (especially those in the SHF plots) contained smaller amounts of soil. Soil or organic residues inside the bags were highest in the LERF ($p < 0.05$). No differences in the amounts of residues within the bags were evident between the open or closed SHF;

- (viii) that partial discoloration of the leaves was a common feature of the decomposing leaves since the first retrieval: *Clitoria* leaves more accentuatedly in the first stages and *Pradosia* leaves in the last stages, after 120 d. The main apparent causes of discoloration of the leaves were fungal hyphae and mycelia, and the penetration of roots, and, in the SHF, the direct exposure of the material to sunlight. In the SHF, during Experiment C, a significant trend ($p < 0.01$) of decreasing values from the most open to the most closed vegetation type was observed, with the highest values in the sun SHF, owing to exposure to direct sunlight. *Pradosia* leaves were less ($p < 0.001$) discolored than *Aldina* leaves, but no significant differences were found in relation to leaf origin;

- (ix) that the physical breakdown of the leaves was lower in the the SHF than in the other areas ($p < 0.01$), with no significant differences between sun and shade patches in the SHF. *Pradosia* leaves showed lower ($p < 0.001$) breakdown values than *Aldina* leaves;

- (x) that the removal of the leaf surfaces showed a significant ($p < 0.001$) trend to decrease from the most closed (LERF) to the most open type of vegetation (sun SHF). Again, *Pradosia* had lower ($p < 0.001$) surface removal than *Aldina*, but no significant differences were found in relation to leaf origin.

The highest correlations calculated in experiment A (all $p < 0.001$; $n = 648$) were found between leaf breakdown and leaf-surface removal rates ($r = 0.61$); breakdown and leaf discoloration ($r = 0.55$); breakdown and residues accumulated ($r = 0.49$); leaf-surface removal and discoloration ($r = 0.46$); leaf-surface removal and residues ($r = 0.46$); discoloration and residues ($r = 0.40$); leaf-surface removal and termites ($r = 0.31$); white and black fungi ($r = 0.31$); white fungi and residues ($r = -0.19$); black fungi and discoloration ($r = 0.18$); and, white fungi and discoloration ($r = 0.17$). Correlations were similar in experiments B and C.

Despite large visible variation, all samples in the litter bags were used as replicates in the data analyses since litter in natural situations would be expected to experience a similar variety of influences.

EXPERIMENT A

Rainfall, litter and soil moisture during the experiment

The monthly rainfall and evaporation at each period of the experiment, and the mean of the litter and surface soil moisture for the same periods are shown in Fig. 5.1. (The daily rainfall is shown in Fig. 2.3, Chapter 2). The first four months, especially after 30 d, were very wet, and included three out of the six retrievals. After this, it was much drier especially between 180 d and 270 d. The last retrieval (360 d) was made several weeks after the next rainy season started. The total rainfall during the 1-year experiment was 2021 mm. The moisture of the top organic and the upper mineral soil layers were highly correlated ($r = 0.70$; $n = 52$; $p < 0.001$), and both layers followed a similar pattern to the rainfall. The moisture of the organic layer was correlated with the difference between rainfall and evaporation ($r = 0.36$; $n = 52$; $p < 0.05$), while the moisture of the upper mineral soil layer was correlated with evaporation ($r = 0.62$; $n = 52$; $p < 0.001$), with the number of rainy days and the difference between rainfall and evaporation (both $r = 0.54$; $p < 0.001$), and with accumulated rainfall ($r = 0.48$; $p < 0.01$). Significant correlations were found between daily rainfall and the difference between rainfall and evaporation ($r = 1.00$; $n = 6$; $p < 0.001$); daily evaporation and number of rainy days ($r = 0.96$; $p < 0.001$); rainfall and evaporation accumulated since the begining of the experiment ($r = -0.79$; $p < 0.05$); and, daily evaporation and the difference between rainfall and evaporation ($r = 0.70$; $p < 0.05$).

Weight loss, root penetration in the litter bags, and decomposition rates of leaves

The remaining dry mass of leaves and the mass of fine roots penetrating the litter bags were measured in all forest types and are shown in Table 5.3, while decomposition patterns for the three separate substrates are shown in Fig. 5.2. The rates of leaf mass loss were relatively low, especially for *Pradosia*, with no evident initial leaching phase. *Aldina* had a lower weight loss than *Pradosia* in the first periods of the experiment, but the opposite was observed in later periods of decomposition. *Clitoria* decomposed faster than the two other species, and the fastest weight loss was always in the LERF (Table 5.3;

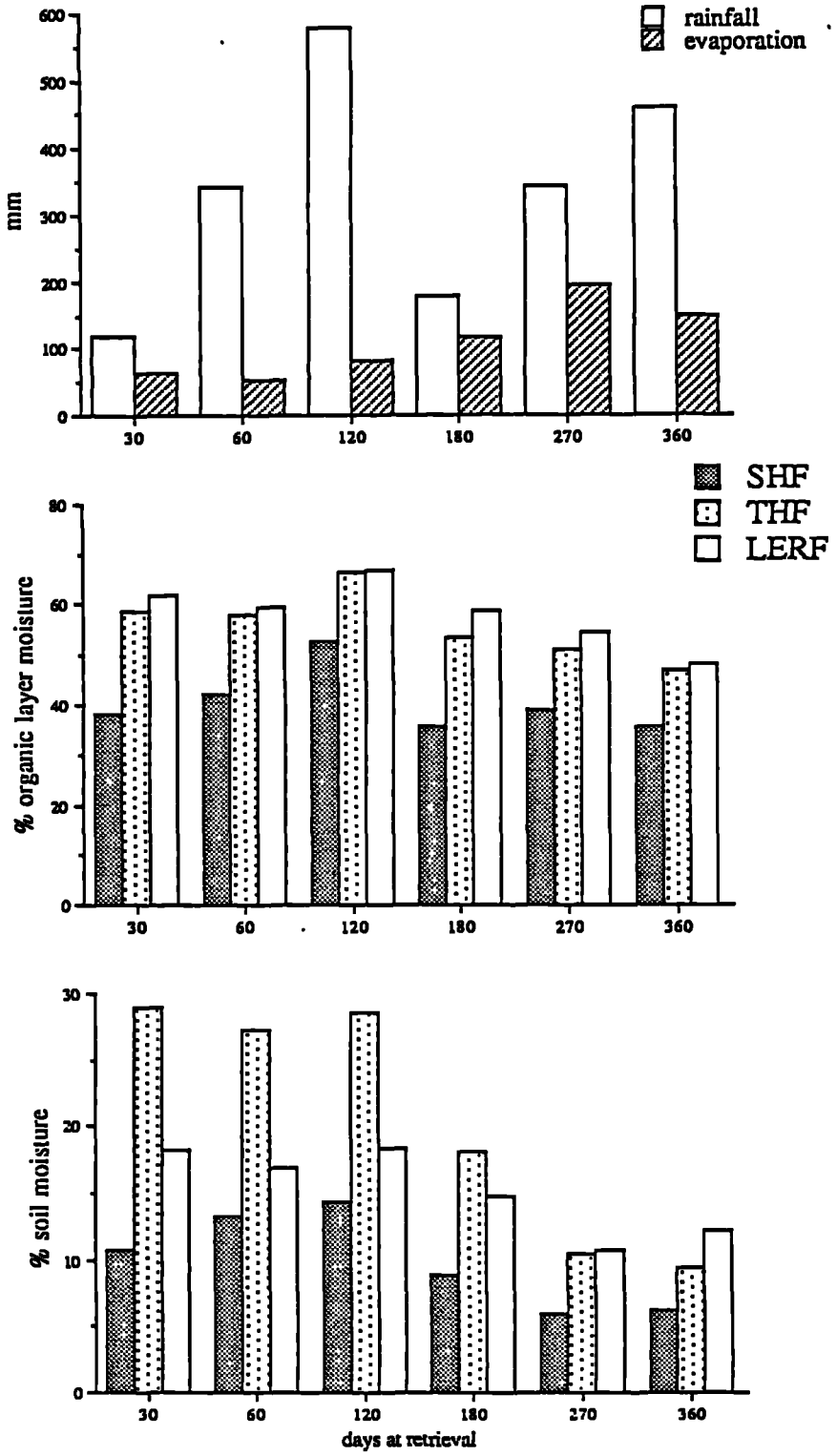


Figure 5.1: Experiment A: rainfall, evaporation, and mean moisture of the top organic and of the upper mineral soil layers in the periods preceding the retrievals. Rainfall and evaporation data are from a climatic station 3 km northwest of study sites (CEPLAC unpublished). The moisture data are means of samples collected weekly and measured gravimetrically as described in the text.

Table 5.3 : Mean remaining mass of leaves (g) and mass of fine roots (g) penetrating the litter bags at each retrieval times. Values are means ± SE (n=12 for all times except 0 d when n=72). The sign - denotes absence of fine roots from the bags.

		leaves			roots		
days		SHF	THF	LERF	SHF	THF	LERF
0	*Clitoria*	5.26 ±0.01	5.29 ±0.01	5.26 ±0.01	-	-	-
	Pradosia	5.28 ±0.01	5.29 ±0.01	5.30 ±0.01	-	-	-
	Aldina	5.24 ±0.01	5.27 ±0.01	5.25 ±0.01	-	-	-
30	*Clitoria*	4.46 ±0.01	4.37 ±0.02	4.51 ±0.02	0.01 ±0.002	0.08 ±0.006	0.07 ±0.007
	Pradosia	4.75 ±0.02	4.62 ±0.02	4.66 ±0.02	0.004 ±0.002	0.05 ±0.009	0.04 ±0.008
	Aldina	4.81 ±0.02	4.64 ±0.02	4.54 ±0.03	0.01 ±0.002	0.10 ±0.02	0.04 ±0.006
60	*Clitoria*	4.13 ±0.02	4.00 ±0.02	3.96 ±0.02	0.01 ±0.002	0.13 ±0.02	0.31 ±0.03
	Pradosia	4.55 ±0.02	4.55 ±0.01	4.37 ±0.02	0.00 ±0.00	0.03 ±0.003	0.25 ±0.02
	Aldina	4.65 ±0.02	4.57 ±0.02	4.41 ±0.02	0.01 ±0.002	0.05 ±0.007	0.18 ±0.01
120	*Clitoria*	3.40 ±0.05	3.32 ±0.03	3.13 ±0.05	0.02 ±0.005	0.94 ±0.11	1.49 ±0.14
	Pradosia	4.19 ±0.03	4.04 ±0.02	3.72 ±0.07	0.01 ±0.002	0.19 ±0.01	0.32 ±0.01
	Aldina	4.07 ±0.03	3.77 ±0.07	3.56 ±0.06	0.03 ±0.008	0.24 ±0.03	0.24 ±0.01
180	*Clitoria*	3.17 ±0.04	2.92 ±0.03	2.54 ±0.05	0.04 ±0.006	0.53 ±0.05	1.21 ±0.11
	Pradosia	3.97 ±0.04	3.76 ±0.02	3.29 ±0.07	0.02 ±0.005	0.17 ±0.02	0.40 ±0.02
	Aldina	3.67 ±0.06	3.56 ±0.04	3.20 ±0.05	0.04 ±0.006	0.19 ±0.02	0.43 ±0.02
270	*Clitoria*	2.30 ±0.05	2.29 ±0.04	2.28 ±0.05	0.03 ±0.007	0.98 ±0.07	1.67 ±0.14
	Pradosia	3.67 ±0.04	3.43 ±0.02	3.27 ±0.03	0.04 ±0.01	0.15 ±0.01	0.51 ±0.02
	Aldina	3.18 ±0.05	2.89 ±0.09	2.12 ±0.09	0.04 ±0.01	0.25 ±0.02	0.52 ±0.03
360	*Clitoria*	1.81 ±0.06	2.02 ±0.05	1.74 ±0.05	0.10 ±0.02	1.51 ±0.10	1.86 ±0.12
	Pradosia	3.20 ±0.05	3.23 ±0.03	2.61 ±0.07	0.04 ±0.008	0.33 ±0.02	0.87 ±0.10
	Aldina	2.59 ±0.04	2.52 ±0.05	2.33 ±0.07	0.06 ±0.009	0.45 ±0.03	0.68 ±0.03

Fig. 5.2). In view of the shape of the curves of the observed data (Fig. 5.2), showing a relatively slow decomposition rate, only the two simplest models (linear and single negative exponential) were tested. A linear model described well the weight loss for *Aldina* and reasonably well for *Clitoria*. *Pradosia* weight losses best fitted an exponential model (Fig 5.2 and Table 5.4). (An example of equation fitted to the data can be found in Fig. 5.5). The estimated half-lives of *Clitoria* leaves ranged from 221 d to 243 d in the

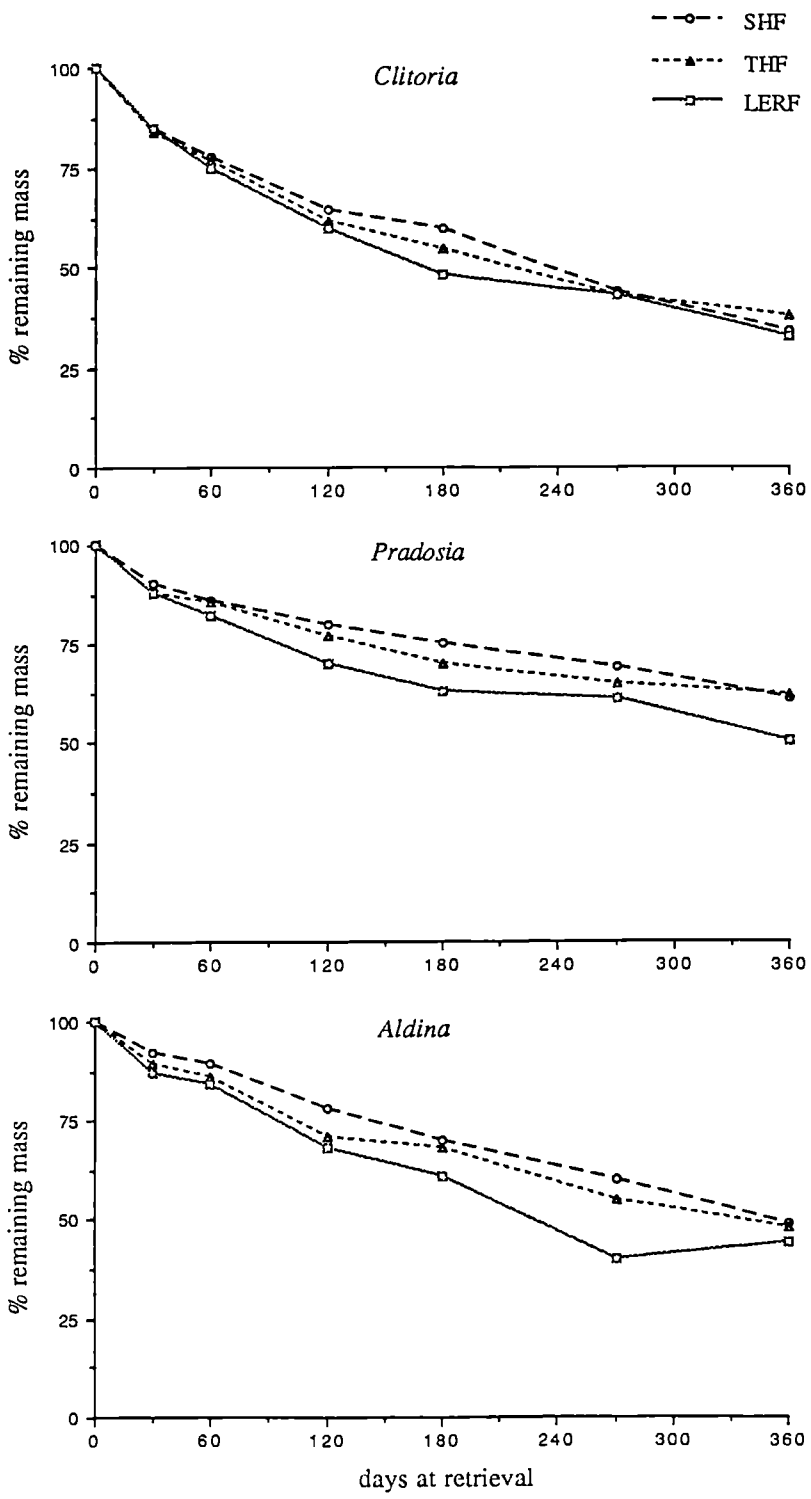


Figure 5.2: Experiment A: mean remaining mass (%) over time in relation to the initial dry mass for each of the leaf litter species in the three forest types (n=12).

Table 5.4: Experiment A: Decay equations and estimated ***k*** and half-life values for the three leaf litter species in the three forest types. The linear equation, which produced the best fit for the observed data, was used to calculated the half-lives. The ***k*** values were always calculated using the exponential equation. The regressions are all significant, $p \leq 0.001$.

	model	equations	F	r^2 %	k	half-life (days)
Clitoria						
SHF	linear	$y = 88.4 - 0.158\ x$	468	86.5		243
	exponential	$y = 94.6\ 10^{-0.0029\ x}$	231	75.9	1.06	
THF	linear	$y = 85.3 - 0.147\ x$	474	86.5		240
	exponential	$y = 89.1\ 10^{-0.00258\ x}$	419	85.0	0.94	
LERF	linear	$y = 85.0 - 0.158\ x$	341	82.1		221
	exponential	$y = 89.1\ 10^{-0.00296\ x}$	220	74.7	1.08	
Pradosia						
SHF	linear	$y = 92.1 - 0.0888\ x$	297	80.2		474
	exponential	$y = 92.8\ 10^{-0.00119\ x}$	258	77.9	0.43	
THF	linear	$y = 89.8 - 0.0874\ x$	408	84.6		592
	exponential	$y = 90.0\ 10^{-0.00117\ x}$	456	86.0	0.43	
LERF	linear	$y = 88.5 - 0.113\ x$	162	68.5		341
	exponential	$y = 90\ 10^{-0.00172\ x}$	116	60.9	0.63	
Aldina						
SHF	linear	$y = 95.9 - 0.133\ x$	474	86.5		345
	exponential	$y = 98.5\ 10^{-0.00193\ x}$	369	83.3	0.70	
THF	linear	$y = 92.4 - 0.133\ x$	285	79.3		319
	exponential	$y = 94.6\ 10^{-0.0020\ x}$	205	73.3	0.73	
LERF	linear	$y = 90.4 - 0.153\ x$	221	74.9		264
	exponential	$y = 93.7\ 10^{-0.00265\ x}$	85.0	53.2	0.97	

three forest types, being lower in the LERF and higher in the SHF (Table 5.4). Half-lives of *Pradosia* leaves ranged from 341 d to 592 d, and of *Aldina* leaves from 264 d to 345 d (Table 5.4). The mass of fine roots in the litter bags was highest in the LERF and lowest in the SHF, and started to increase considerably after the litter bags had been in the field for 60 d (Table 5.3). There were significant effects of all the main factors considered (forest type, leaf species, and time), on the rate of weight loss, and on the mass of fine roots in the litter bags. Significant interactions of leaf species used in the bags and time were also found for leaf mass loss (nested ANOVA; $F = 6.53$; $df = 10$; $p < 0.001$) and fine root mass in the bags ($F = 4.02$; $p < 0.001$). However, for the individual species, *Clitoria* showed no significant differences in leaf mass loss among forest types, while *Pradosia* ($F = 11.8$; $df = 2$; $p < 0.01$) and *Aldina* ($F = 8.58$; $p < 0.05$) showed low significance in the differences of leaf mass loss among forest types.

A total number of 141 samples of fine roots were chemically analysed: 68 samples from *Clitoria* litter bags, 41 from *Aldina*, and 32 from *Pradosia*. Distributed by forest types, 64 came from the THF, 56 from LERF, and 21 from SHF. The LERF plots generally had the highest mass of fine roots (Table 5.3), but not the highest frequency of root penetration in the bags, which was higher in the THF. The masses of fine roots penetrating litter bags were highly significantly different (nested ANOVA; $F = 109$; $df = 2$; $p < 0.001$) among forest types (highest in LERF and lowest in SHF) and among leaf species ($p < 0.001$; $df = 2$; $F = 47.6$) (highest in *Clitoria*, lowest in *Pradosia*). The interaction between leaf species and time was also significant ($F = 4.02$; $df = 10$; $p < 0.001$).

Nutrient release from decomposing leaves

The concentrations of mineral elements in the retrieved leaves were often significantly correlated between one another. The highest correlations calculated ($n = 72$; all $p < 0.001$) were found between aluminium and iron (for *Clitoria* leaves, $r = 0.93$ in the SHF; $r = 0.74$ in THF; and $r = 0.80$ in LERF; for *Pradosia* leaves, $r = 0.88$ in the SHF; $r = 0.81$ in THF; and $r = 0.88$ in LERF; for *Aldina* leaves, $r = 0.89$ in the SHF; $r = 0.74$ in THF; and $r = 0.84$ in LERF). Nitrogen and phosphorus were also generally highly and positively

correlated: r = 0.75 in the SHF for *Clitoria* leaves; r = 0.56 in the SHF; and r = 0.58 in THF for *Pradosia* leaves; r = 0.58 in the SHF; and r = 0.46 in LERF for *Aldina* leaves. Calcium and magnesium were also strongly and positively correlated: r = 0.78 in the THF; and r = 0.83 in LERF for *Clitoria* leaves; r = 0.73 in the SHF; r = 0.82 in THF; and r = 0.92 in LERF for *Pradosia*; and r = 0.72 in the LERF for *Aldina*. Magnesium and aluminium were always negatively correlated in the decomposing leaves: r = -0.50 in the SHF; r = -0.71 in THF; and r = -0.63 in LERF for *Clitoria*; r = -0.76 in the THF; and r = -0.58 in LERF for *Pradosia*; and r = -0.65 in the SHF, r = -0.53 in THF, and r = -0.70 in LERF for *Aldina*. All the above elements (except magnesium) usually increased their concentrations in the leaves during at least one period of the experiment (Appendix 5.1 a,b,c). Among the elements which are known as usually decreasing concentrations in the decomposing leaves, the best correlations were found between potassium and magnesium: r = 0.46 in the SHF and r = 0.64 in LERF for *Clitoria*; r = 0.45 in the THF; and r = 0.64 in LERF for *Pradosia*; and r = 0.66 in the THF and r = 0.83 in LERF for *Aldina*.

The contents of mineral elements in the decomposing leaves are shown in Fig. 5.3 a,b,c. The release rates of nitrogen (nested ANOVA; $F = 4800$; $df = 2$; $p < 0.001$), phosphorus ($F = 420$; $p < 0.001$), potassium ($F = 46.2$; $p < 0.001$), and boron ($F = 143$; $p < 0.001$) differed among leaf species. However they did not differ among forest types. The release rates of calcium ($F = 20.3$; $df = 4$; $p < 0.001$), magnesium ($F = 84.0$; $p < 0.001$), aluminium ($F = 24.3$; $p < 0.001$), iron ($F = 11.1$; $p < 0.001$), manganese ($F = 72.9$; $p < 0.001$), and zinc ($F = 11.3$; $p < 0.001$), all showed significant interactions between forest types and leaf species (Appendix 5.2 a,b,c). Calcium, magnesium and manganese were released slower, in all three leaf species, in the SHF than in LERF (Fig. 5.3 a,b,c). On the other hand, aluminium and iron tended to be released slower in the LERF than in both SHF and THF, while zinc tended to be released slower in the THF (Fig. 5.3 a,b,c). Nitrogen, phosphorus, and calcium were released faster from *Clitoria* leaves and slower from *Pradosia*, but the opposite pattern was observed for aluminium and iron (Fig. 5.3a,b,c). Magnesium was released faster from *Clitoria* than from the other species, while zinc and boron were faster released from *Aldina* (Fig. 5.3a,b,c).

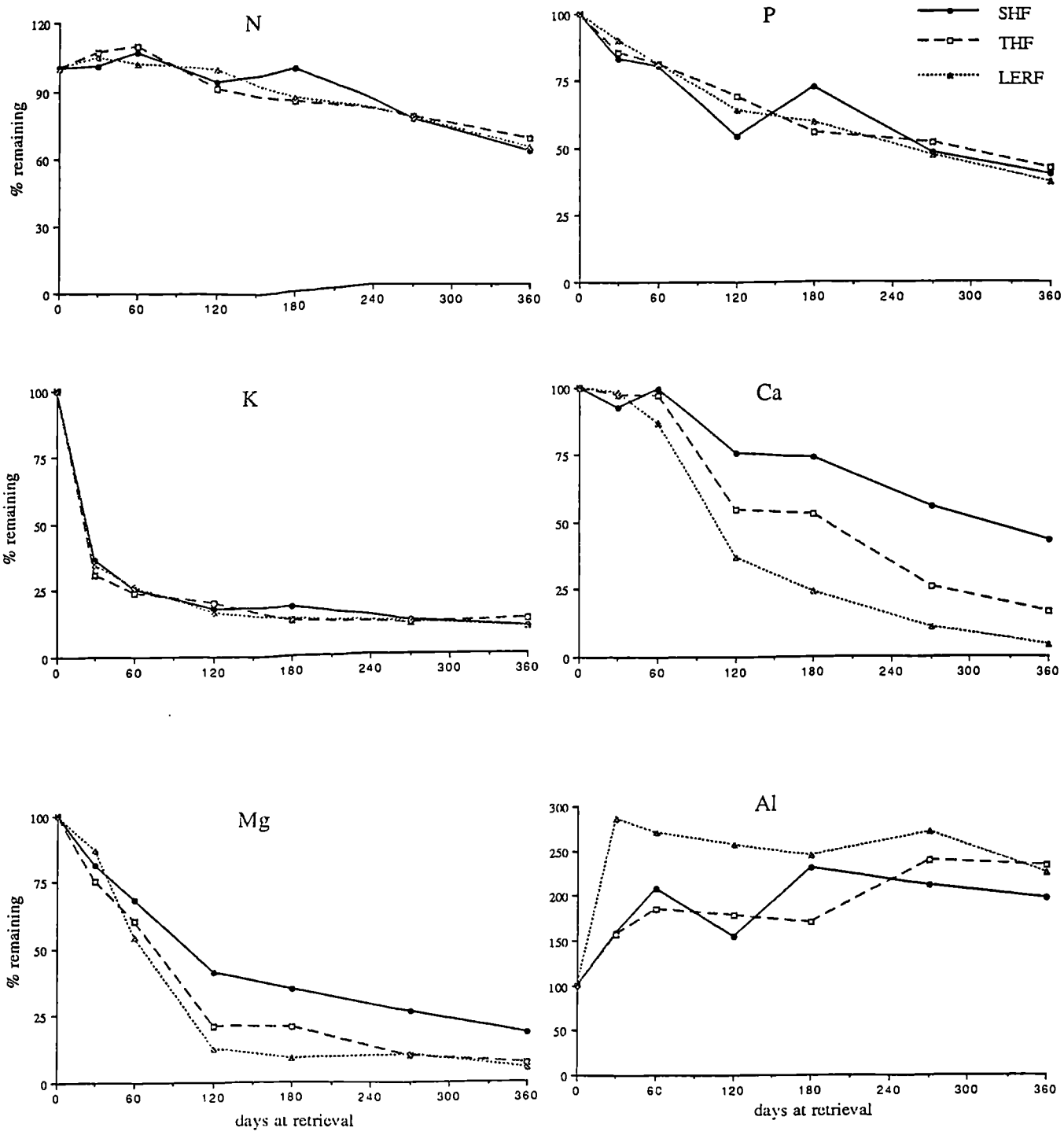


Figure 5.3a: Experiment A: the percentage (%) contents of mineral elements compared with the initial content in decomposing *Clitoria* leaves after each retrieval in the three forest types. Values are means of three plots (n=12).

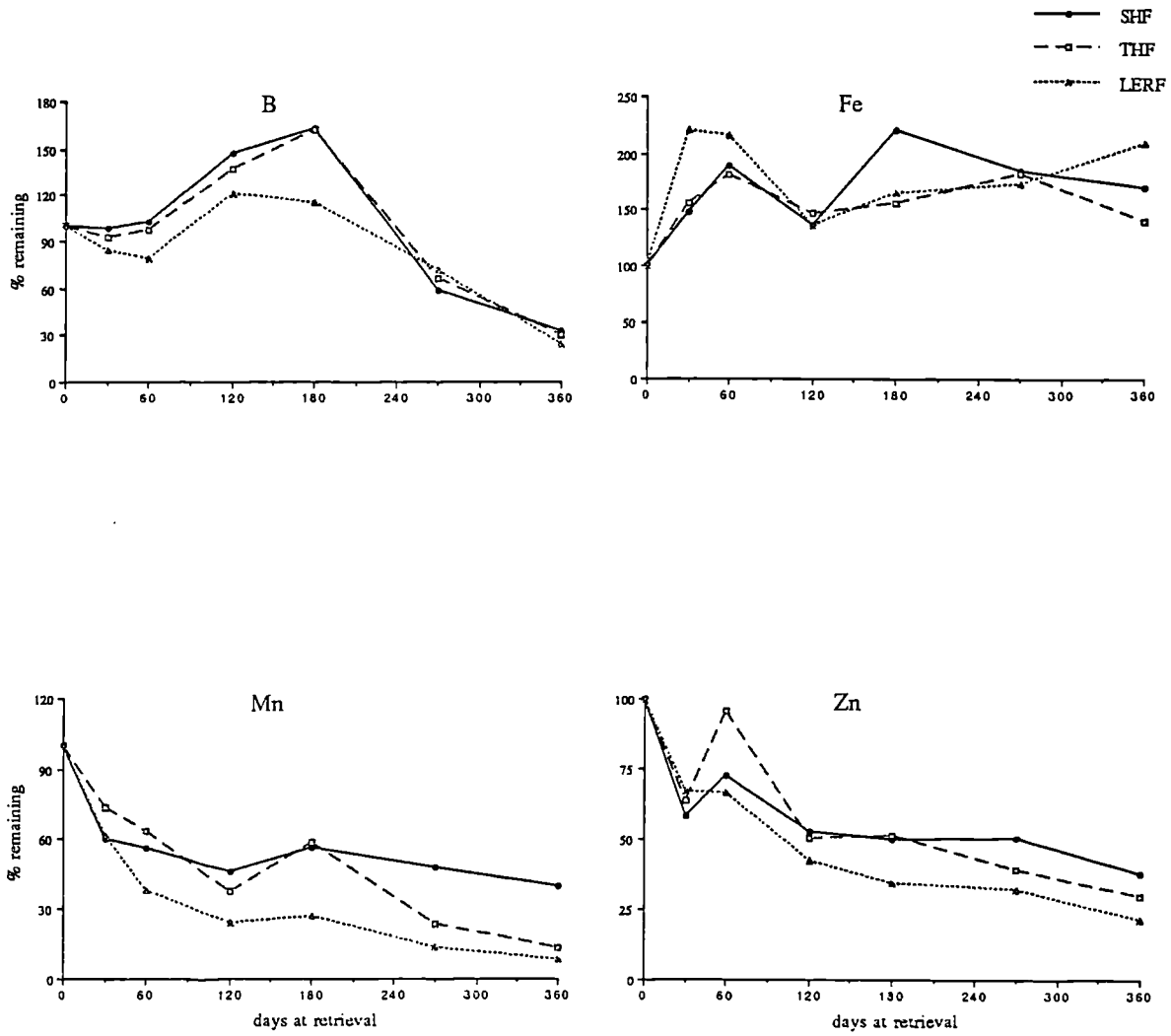


Figure 5.3a (cont.)

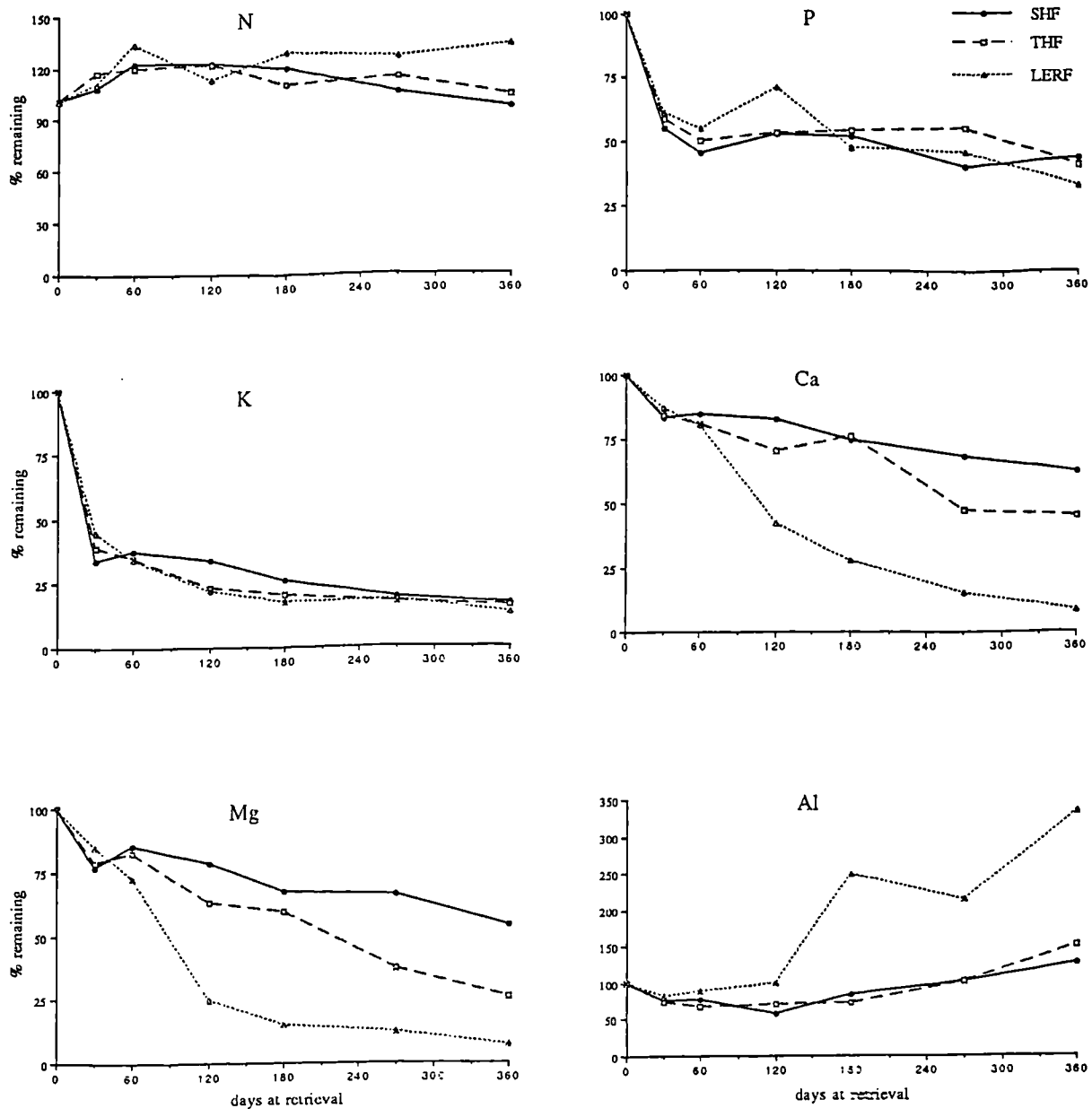


Figure 5.3b: Experiment A: the percentage (%) content of mineral elements compared with the initial content in decomposing *Pradosia* leaves after each retrieval in the three forest types. Values are means of three plots (n=12).

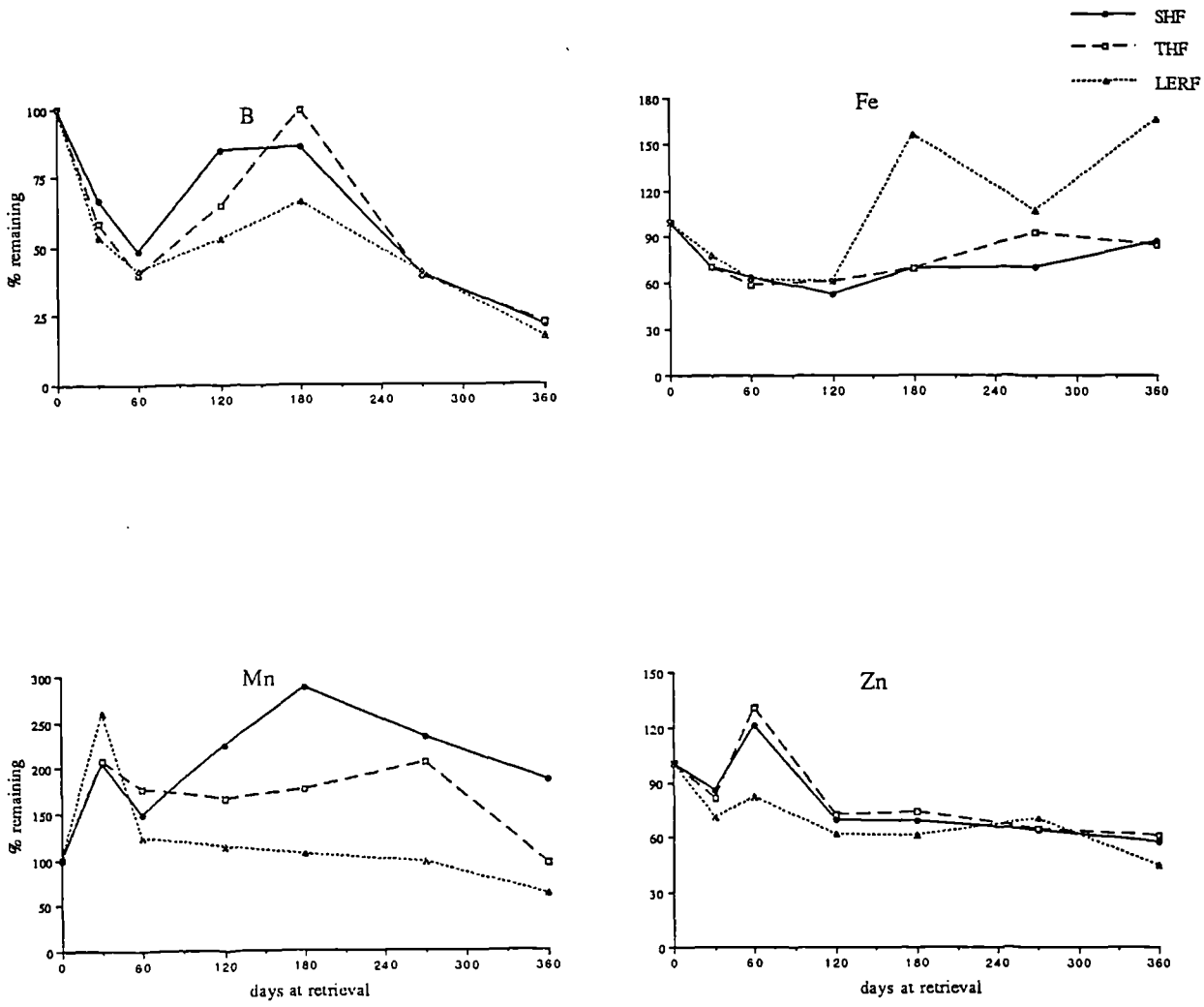


Figure 5.3b (cont.)

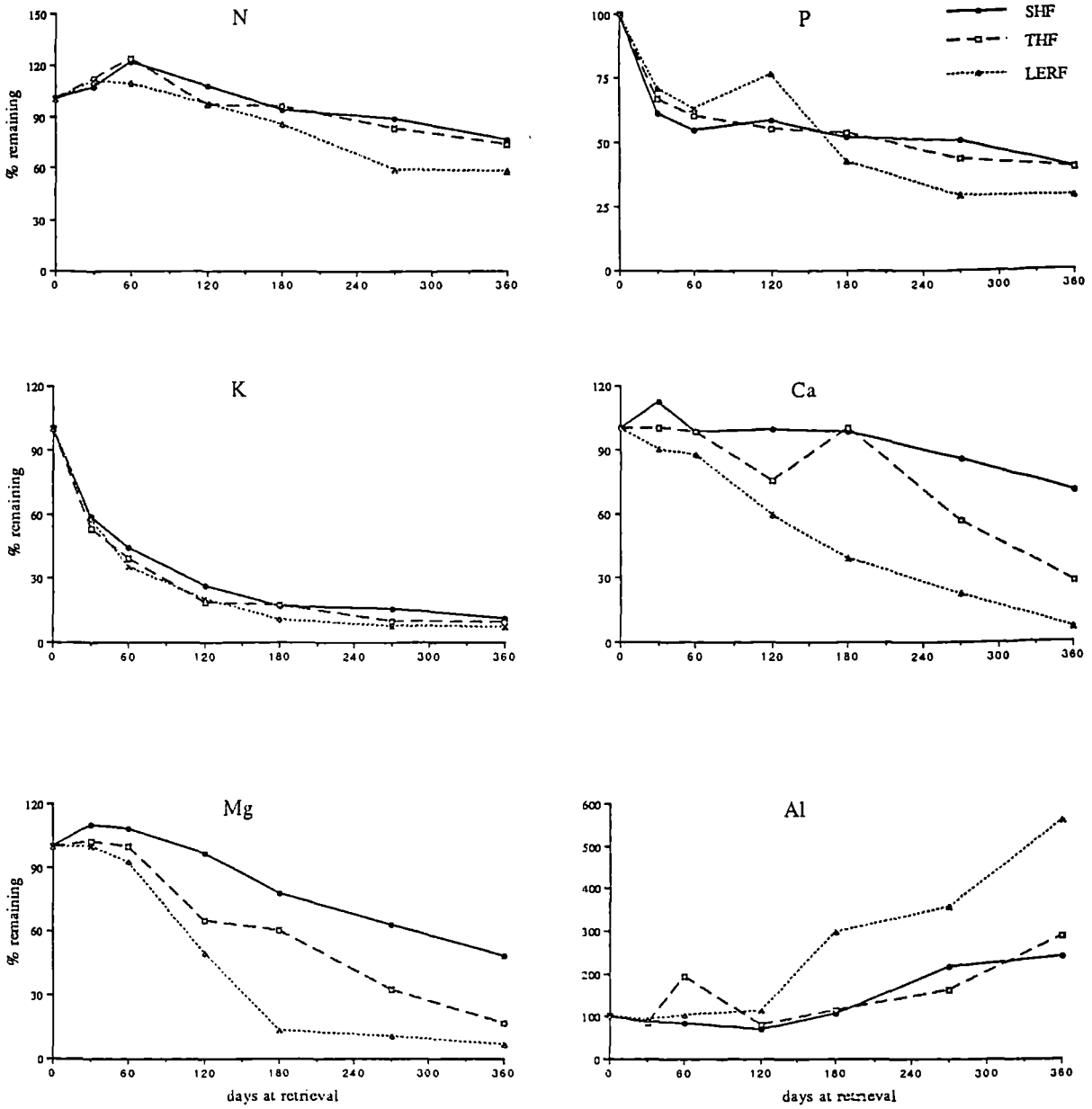


Figure 5.3c: Experiment A: the percentage (%) content of mineral elements compared with the initial content in decomposing *Aldina* leaves after each retrieval in the three forest types. Values are means of three plots (n=12).

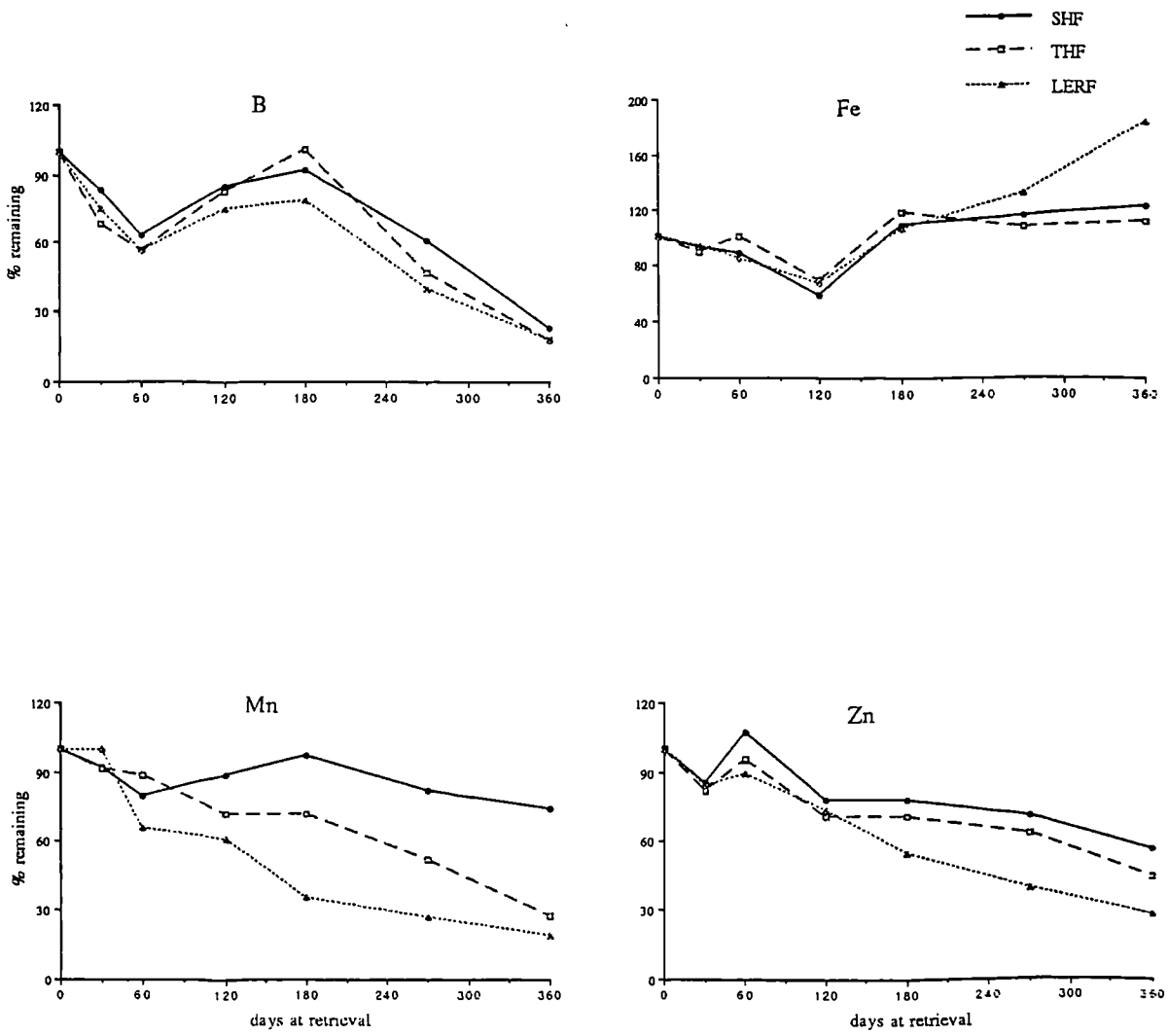


Figure 5.3c (cont.)

Mineral element concentrations in fine roots penetrating litter bags

The concentrations of mineral elements in the fine roots mixed with the decomposing leaves inside the litter bags are in Table 5.5. There were significant differences among the three forest types for all elements analysed, except boron and copper. The most significant differences were found for phosphorus (nested ANOVA; $F = 10.7$; $df = 2$; $p < 0.001$), potassium ($F = 17.8$; $p < 0.001$), and calcium ($F = 127$; $p < 0.001$) concentrations. Among the mineral elements showing significant differences between forest types, nitrogen, phosphorus, and aluminium concentrations in roots were highest in the LERF, while concentrations of potassium, calcium, magnesium, manganese, and zinc, were the highest in the SHF (Table 5.5). Among the leaf species, the fine roots in litter bags containing *Clitoria* had significantly higher concentrations of phosphorus, postassium, calcium, boron, manganese, and zinc, and significantly lower concentrations of magnesium (Table 5.6).

Factors influencing decomposition, fine root penetration, and mineral element release rates

Overall, among the biotic and abiotic factors evaluated, the main factors influencing weight loss rates were the accumulated rainfall since the beginning of the experiment, and the colonization of decomposing leaves by black fungi (both positive relationships), and the moisture of the upper mineral soil layer (negative relationship) (Table 5.7). However, variations were found among the three forest types. Thus, the activity of termites only appeared to be an important factor in the LERF; white fungi colonization was only significantly related to weight losses in the THF, while leaf-surface removal and discoloration were significantly related to weight losses only in the SHF (Table 5.7).

The mass of fine roots penetrating litter bags in all three forest types was related to six different factors: the moisture in the top organic layer of the soil, the breakdown of the decomposing leaves, the residues accumulated on the leaves; the colonization by black and white fungi, and the daily rainfall (Table 5.7). From these factors, only colonization by white fungi was negatively related to the mass of roots in the litter bags. Examining the individual

Table 5.5: Experiment A: concentrations of mineral elements in the fine roots penetrating decomposing leaves of the three different species in the three forest types. Values are means of all six retrievals with SE in parenthesis.

	Clitoria			*Pradosia*			*Aldina*		
	SHF	THF	LERF	SHF	THF	LERF	SHF	THF	LERF
	n=13	n=31	n=20	n=4	n=15	n=11	n=4	n=18	n=15
					mg g^{-1}				
N	19.2 (0.75)	16.0 (0.73)	21.4 (0.94)	14.9 (0.21)	13.5 (0.63)	20.4 (0.43)	15.6 (2.47)	17.0 (0.54)	21.1 (0.80)
P	0.80 (0.04)	0.82 (0.02)	0.74 (0.03)	0.80 (0.00)	0.72 (0.02)	0.68 (0.02)	0.77 (0.03)	0.77 (0.02)	0.57 (0.06)
K	3.92 (0.32)	3.26 (0.13)	2.37 (0.13)	3.43 (0.26)	2.93 (0.33)	2.04 (0.19)	3.20 (0.50)	2.79 (0.23)	1.89 (0.25)
Ca	10.4 (0.26)	5.70 (0.31)	3.03 (0.37)	3.50 (1.00)	1.65 (0.27)	1.40 (0.32)	4.33 (0.17)	1.65 (0.11)	1.11 (0.23)
Mg	1.27 (0.08)	0.81 (0.05)	0.54 (0.05)	1.77 (0.13)	1.29 (0.13)	0.77 (0.07)	1.57 (0.33)	1.18 (0.09)	0.66 (0.01)
					µg g^{-1}				
Al	752 (34.6)	595 (43.1)	1250 (410)	512 (87.7)	801 (237)	1280 (514)	544 (120)	754 (163)	1600 (361)
B	103 (8.82)	86.2 (9.14)	78.3 (6.54)	153 (17.7)	113 (8.84)	109 (9.88)	165 (5.34)	112 (6.98)	85.4 (9.83)
Cu	12.4 (0.61)	8.76 (0.62)	10.6 (0.44)	16.2 (1.40)	13.3 (1.61)	10.1 (0.70)	15.2 (2.37)	14.4 (0.90)	9.73 (1.32)
Fe	272 (11.7)	150 (7.56)	232 (70.4)	157 (15.3)	158 (1.72)	191 (58.4)	184 (12.3)	210 (24.6)	277 (42.9)
Mn	117 (3.97)	42.8 (2.97)	47.4 (5.95)	103 (29.4)	56.7 (10.6)	109 (18.3)	109 (23.0)	55.8 (5.75)	62.7 (7.39)
Zn	30.3 (1.04)	20.5 (0.72)	20.1 (0.87)	32.7 (7.34)	21.7 (2.49)	21.1 (1.08)	34.3 (5.67)	26.7 (1.27)	22.3 (1.80)

Table 5.6: Experiment A: significant values of nested analysis of variance on the concentrations of mineral elements of fine roots between leaf species and forest types (excluding boron and copper, which had no significant results in the previous analysis). The differences found ($p < 0.05$) are shown in the last column.

	Source	F	df	p	differences found
N	leaf species	3.70	4	< 0.05	*Aldina* ≥ *Clitoria* > *Pradosia*
P		7.82	4	< 0.01	*Clitoria* > *Aldina* ≥ *Pradosia*
K		5.84	4	< 0.01	*Clitoria* > *Aldina*
Ca		21.1	4	< 0.001	*Clitoria* > *Aldina* ≥ *Pradosia*
Mg		5.75	4	< 0.01	*Pradosia* > *Clitoria*
B		5.95	4	< 0.01	*Clitoria* > *Pradosia*
Mn		4.20	4	< 0.05	*Clitoria* > *Pradosia*
Zn		3.10	4	< 0.05	*Clitoria* > *Aldina*

forest types, the accumulated rainfall also appeared as an influential factor for penetrating roots in the SHF and LERF (Table 5.7).

Among the mineral elements, nitrogen, phosphorus, and calcium were mainly related to the biotic factors (positively, except for root penetration), while potassium and boron were mainly related (negatively) to the abiotic factors (Table 5.7). Calcium, magnesium, manganese, and zinc were significantly negatively related, and aluminium and iron positively related to fine roots penetrating litter bags.

Table 5.7: Experiment A: Significant regressions of mass loss, root penetration in litter bags, and mineral elements in decomposing leaf litter with selected climatic factors and physical and biological actions on decomposing material for all three forest types and three leaf species together. Mass loss was represented in the analysis by the daily rate of weight loss. Rf = rainfall since last litter-bag retrieval; Rf/d = daily rainfall in the same period; D%Rf = percentage of rainy days; AcRf = total rainfall since the begining of the experiment; EV = evaporation since the last litter-bag retrieval; EV/d = daily evaporation; Lmois = moisture of the organic layer in the top soil in the three weeks preceding retrieval; Smois= moisture of mineral topsoil in the 21 d before retrieval. Term = termites present in litter bags at retrieval; Root = fine roots penetrating litter bags at retrieval; Whitf = white fungi on decomposing leaves; Blackf = black fungi on decomposing leaves; Brdwn = breakdown of decomposing leaves; Disc = discoloration of the leaves; Esk = leaf surface removal; Res = residues (soil and organic) inside the litter bags. The factors with greater influence are presented in order of importance in the last colunm. The italicized factors were negatively related.

		r^2 %	df	p	most influential factors
mass	SHF	86.0	53	< 0.001	AcRf, Blackf, D%Rf, Esk, Disc
	THF	85.5	53	< 0.001	AcRf, Blackf, Brdwn, Whitf
	LERF	86.7	53	< 0.001	AcRf, Black, Term, Rf/d, Brdwn
	all	68.1	161	< 0.001	AcRf, Blackf, *Smois*
root	SHF	29.5	53	< 0.001	Lmois, Rf/d, AcRf, Res, EV
	THF	40.7	53	< 0.001	Brdwn, Blackf, Res
	LERF	56.1	161	< 0.001	Blackf, AcRf, Brdwn
	all	45.4	161	< 0.001	Lmois, Brdwn, Res, Blackf, Rf/d, *Whitf*
N	all	34.2	161	< 0.001	Brdwn, Whitf, Blackf
P		25.7	161	< 0.001	Brdwn, Whitf, Blackf
K		36.2	161	< 0.001	*EV*, *Rf*, *Disc*, Whitf
Ca		59.6	161	< 0.001	Blackf, *Root*, Whitf
Mg		61.7	161	< 0.001	*Root*, *Brdwn*, *EV*, *Term*
Al		56.3	161	< 0.05	Blackf, EV, Res, Root, Brdwn
B		68.7	161	< 0.05	*Rf/d*, *Rf*, *EV*, AcRf, Blackf
Fe		59.6	161	< 0.001	Blackf, EV/d, Res, Brdwn, AcRf, Root
Mn		32.2	161	< 0.001	*Root*, Blackf, Disc, EV/d, *Rf/d*
Zn		14.5	161	< 0.001	Blackf, *Root*, Brdwn, Rf/d

EXPERIMENT B

Rainfall, litter and soil moisture during the experiment

The rainfall and evaporation for each period of experiment B are shown in Fig. 5.4, together with the mean moisture of the top organic and the upper mineral soil layers. (The daily rainfall is shown in Fig. 2.3, Chapter 2). The first four months (three out of six retrievals) of this experiment were relatively dry. Later, high rainfall was recorded and the total during the 358 d was 2491 mm. The moisture of both the organic and the upper mineral soil layers followed a similar pattern to the rainfall, as in experiment A. Overall, correlations found among the abiotic factors were similar to those found in experiment A.

Weight loss of the leaves and fine roots penetration

Leaves of *Clitoria* in the litter bags were decomposed distinctively in the three forest types, ranking LERF > THF > SHF (Table 5.8 and Fig. 5.5). The weight losses in the four first periods of the experiment, up to 120 d, were slower than in the following periods. The linear model, which yielded good fits, especially in the SHF and THF (Fig. 5.5), was used to estimate half-lives from 193 d to 249 d for the leaves in the litter bags in the three forest types (Table 5.9).

There were significant decreases in the mean percentage mass remaining over time associated with the forest type (nested ANOVA; $F = 3.49$; $df = 10$; $p < 0.01$). The SHF showed the lowest leaf mass loss, and the LERF the highest. There were no significant differences between the SHF and the THF, despite rates always being slightly lower in the SHF. Fine root penetration into litter bags varied significantly among forest types (nested ANOVA; $F = 39.6$; $df = 2$; $p < 0.001$), being the lowest in SHF and the highest in LERF.

The leaf mass loss was significantly related ($r^2 = 89.1\%$; $df = 53$; $p < 0.001$) to five of the factors analysed: evaporation, percentage of rainy days, and rainfall in the period preceding retrieval; the mass of fine roots penetrating the litter bags; and, the breakdown rates of the leaves. The mass of fine roots penetrating litter bags was only related to the rates of breakdown of the leaves ($r^2 = 38.7\%$; $p < 0.001$).

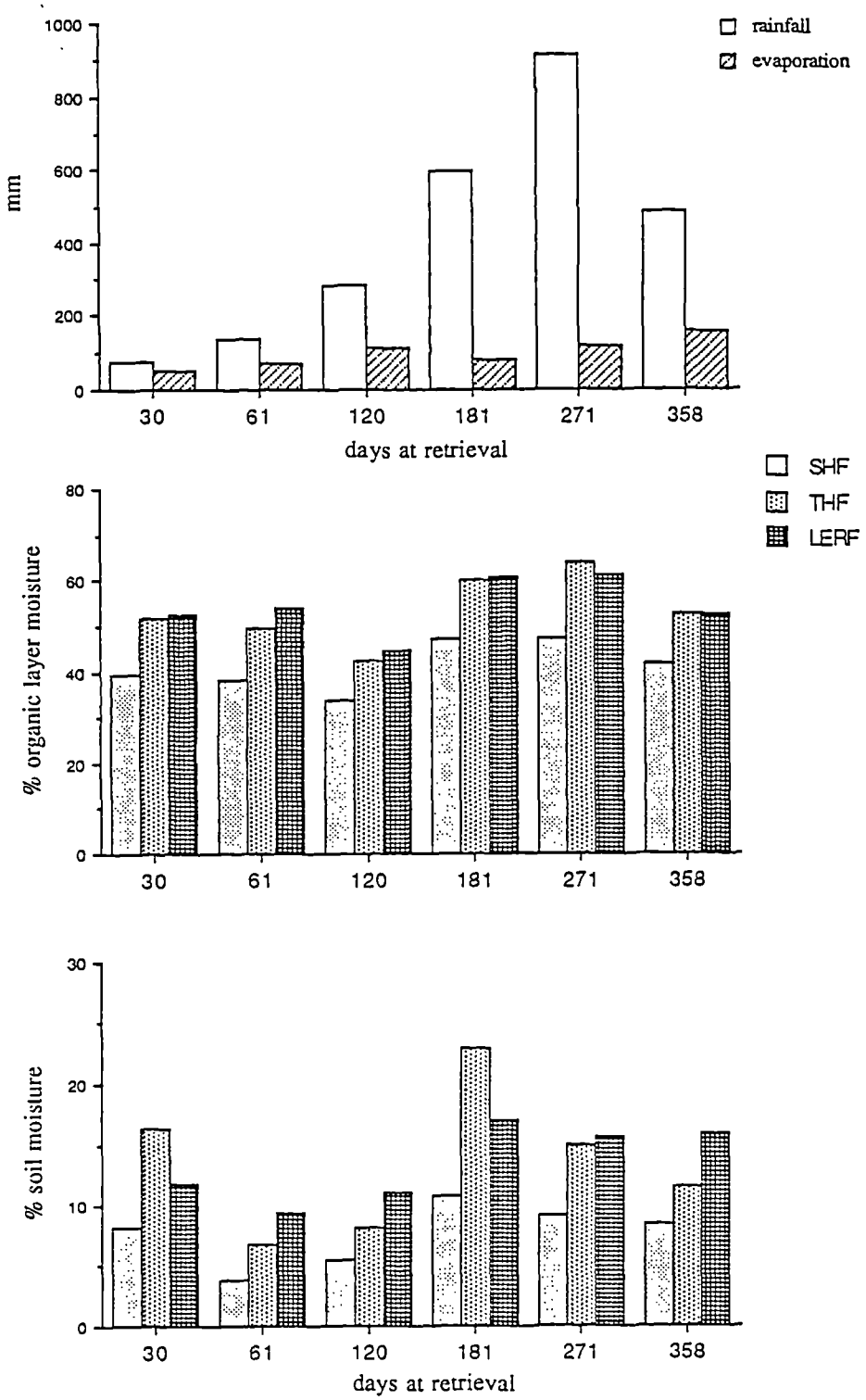


Figure 5.4: Experiment B: rainfall, evaporation, and mean moisture of the top organic and of the upper mineral soil layers in the periods preceding the retrievals. Rainfall and evaporation data from a climatic station 3 km northwest of study sites (CEPLAC unpublished). Moisture data are means of samples collected at 7 d or 14 d intervals and measured gravimetrically as described in the text.

Table 5.8: Experiment B: mean remaining mass of leaves (g) and mass of fine roots (g) penetrating the litter bags at each retrieval time. Values are means with SE in parenthesis (n=12 for all times except 0 d, when n=72). The sign - denotes absence of fine roots from the litter bags.

	mass			roots		
days	SHF	THF	LERF	SHF	THF	LERF
0	5.07 (0.006)	5.08 (0.005)	5.07 (0.006)	-	-	-
30	4.70 (0.01)	4.61 (0.009)	4.56 (0.01)	-	0.02 (0.005)	0.02 (0.005)
61	4.41 (0.01)	4.28 (0.03)	4.04 (0.03)	-	0.05 (0.008)	0.13 (0.01)
120	3.75 (0.03)	3.56 (0.03)	3.15 (0.04)	0.009 (0.003)	0.28 (0.04)	1.62 (0.07)
181	3.09 (0.04)	2.58 (0.04)	2.37 (0.07)	0.04 (0.006)	0.53 (0.04)	1.65 (0.11)
271	2.05 (0.05)	1.85 (0.06)	1.49 (0.08)	0.03 (0.005)	1.42 (0.11)	1.98 (0.18)
358	1.72 (0.06)	1.31 (0.06)	0.92 (0.05)	0.09 (0.01)	1.31 (0.10)	2.39 (0.14)

Table 5.9: Experiment B: decay equations and estimated *k* and half-life values for the leaf litter of *Clitoria* in the three forest types. The linear equation, which produced the best fit for the observed data, was used to calculate the half-lives. The *k* values were calculated using the exponential equation. All 'p' values ≤ 0.001.

	model	**equation**	**F**	**r^2 %**	**k**	**half-life (days)**
SHF	linear	$y = 98.0 - 0.93\ d$	1060	92.7		249
	exponential	$y = 105\ 10^{-0.0033\ d}$	517	86.1	1.20	
THF	linear	$y = 96.5 - 0.213\ d$	1040	92.6		218
	exponential	$y = 106\ 10^{-0.00409\ d}$	449	84.4	1.49	
LERF	linear	$y = 94.5 - 0.231\ d$	819	90.8		193
	exponential	$y = 107\ 10^{-0.00509\ d}$	435	84.0	1.86	

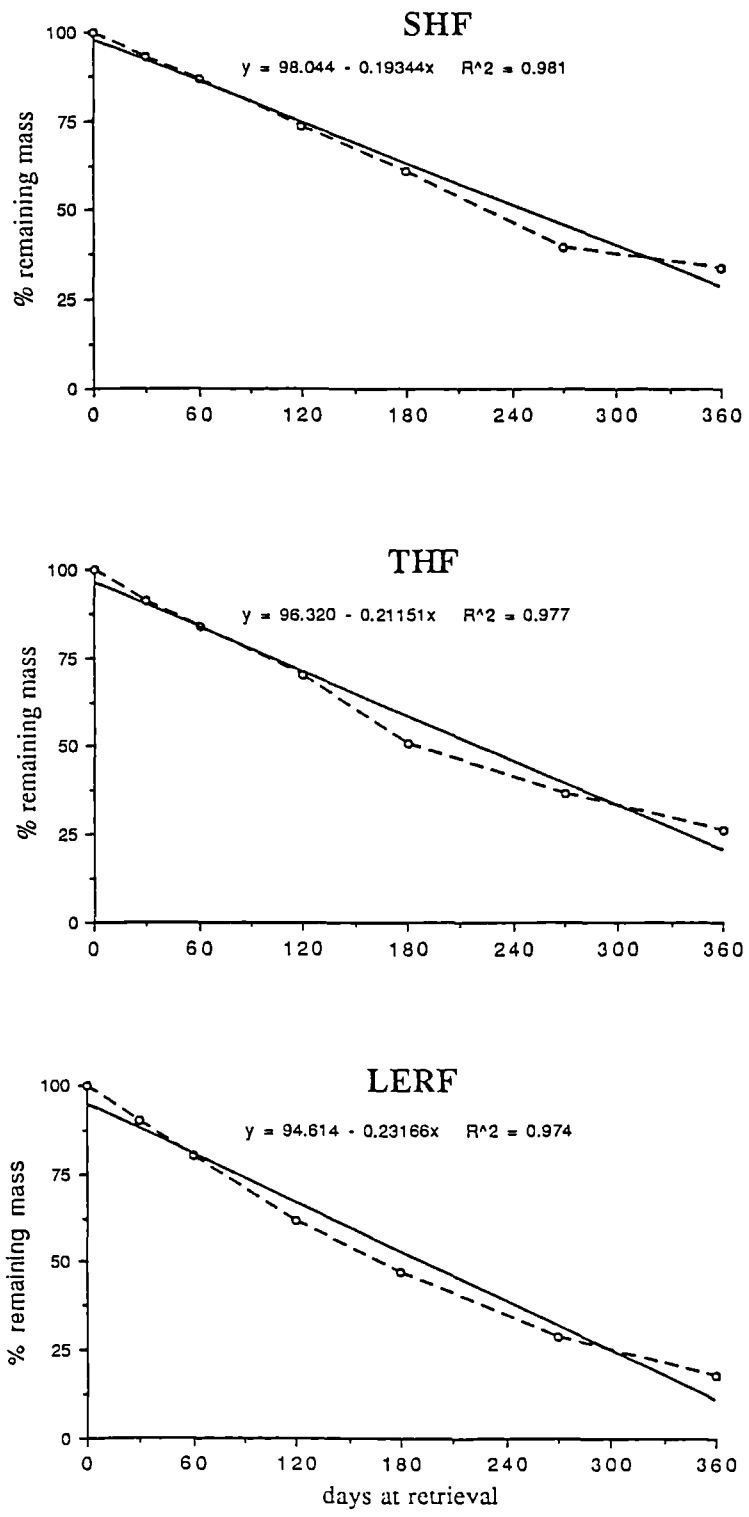


Fig. 5.5: Experiment B: mean remaining mass (%) (dashed line) in relation to the initial dry mass in the three forest types (n=12) and the best-adjusted fits to the curves (solid lines), with their equations.

Nutrient release from decomposing leaves

The concentrations and the final quantities of the mineral elements in the decomposing leaves varied widely with time and among the three forest types (Fig. 5.6; Appendix 5.3). Overall, except for boron and, especially, potassium, the concentrations of the elements in the residual leaves were higher than initially at one or more periods of the experiment (Appendix 5.3). No significant differences in the rates of mineral element release were found among forest types for phosphorus and boron. The release of nitrogen, aluminium and iron were lower in the LERF than in both SHF and THF (Fig. 5.6), while the release of magnesium and zinc were lower in the SHF than in both the THF and LERF. Slower release of calcium and manganese in the SHF than in LERF were also found. The release of potassium was slower in the THF than in both the SHF and LERF.

The biotic and abiotic factors affecting the release of mineral elements from the bagged leaves were broadly the same found in the experiment A, which was started at the onset of the wet season.

The full data for mass and concentrations of mineral elements in the fine roots penetrating litter bags are in Appendix 5.4. Significantly higher concentrations of nitrogen (nested ANOVA; $F = 9.66$; $df = 10$; $p < 0.001$), iron ($F = 4.82$; $p < 0.01$) and aluminium ($F = 8.25$; $p < 0.001$) over time were found in the LERF than in both the THF and the SHF. The THF showed higher concentrations over time than both the SHF and LERF for potassium ($F = 3.83$; $p < 0.05$), and lower than both other two forest types for copper ($F = 6.54$; $p < 0.01$). On the other hand, the SHF showed higher concentrations over time than both the THF and the LERF for magnesium ($F = 7.46$; $p < 0.01$) and zinc ($F = 9.07$; $p < 0.001$), and higher than the LERF for calcium ($F = 22.1$; $p < 0.001$) and manganese ($F = 33.4$; $p < 0.001$). No significant differences among forest types were found for the concentrations of phosphorus and boron. The content of nitrogen and phosphorus, following a net increase at the begining of the study, especially in the THF and LERF, showed a continuous decrease, slower than mass loss for nitrogen and faster than mass loss for phosphorus (Fig. 5.6). Calcium, magnesium, and manganese, all showed similar patterns of release: after a slight net initial increase in content, especially in the SHF and THF, there was a sharp decrease in the following phases (especially between 60 d and 180

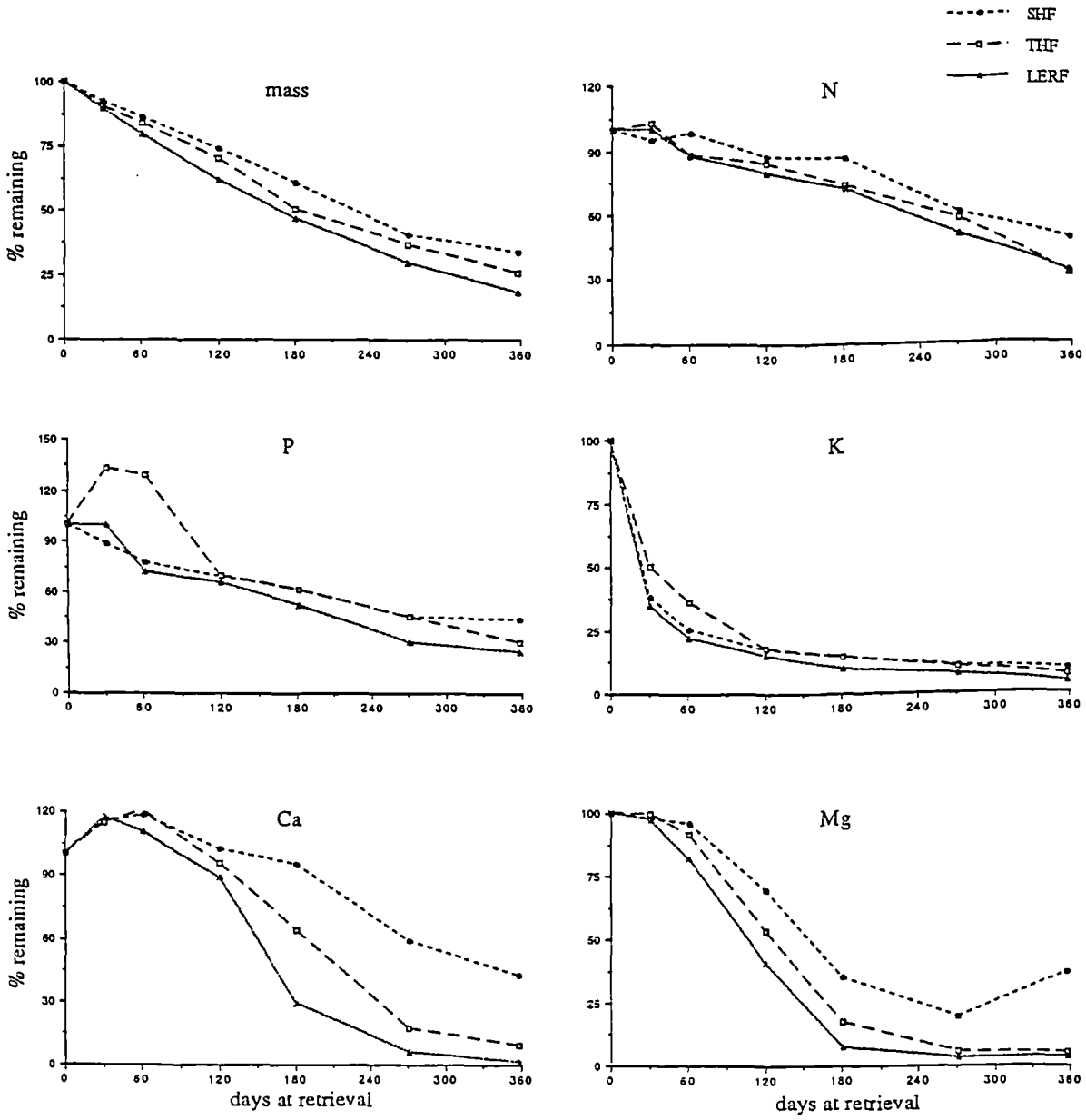


Figure 5.6: Experiment B: mean remaining leaf mass and contents of mineral elements (%) in relation to the initial content in the decomposing leaves after each retrieval, in the three forest types (n=12).

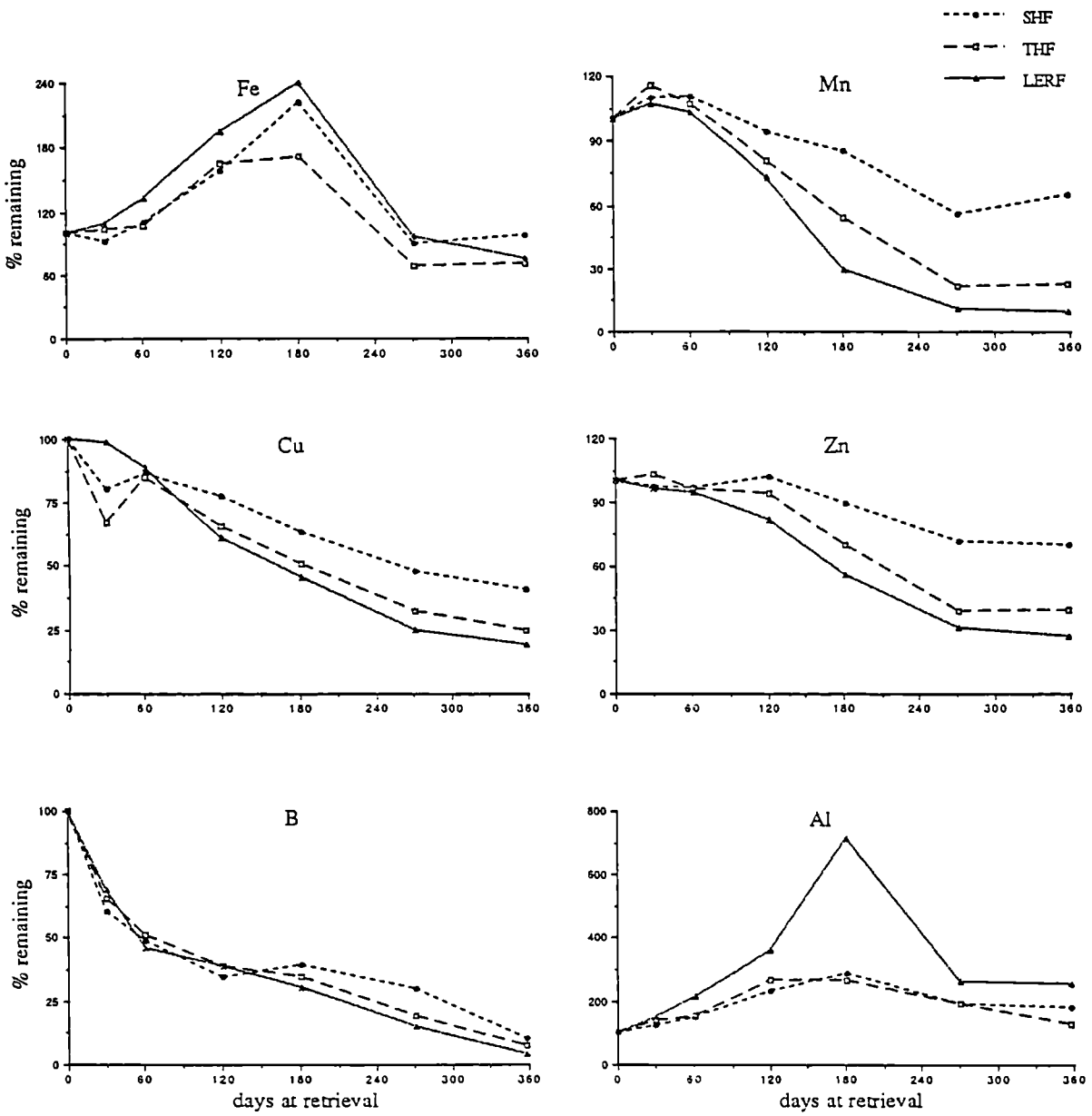


Figure 5.6 (cont.)

d), faster in the LERF than in the THF and SHF for the three elements (Fig. 5.6). Potassium and boron, in contrast, showed sharp decreases of their total contents especially in the first periods. Potassium contents decreased by half of their initial values by 30 d for all forest types, while boron contents did the same by 60 d (Fig. 5.6). Zinc contents increased slightly up to 120 d in the SHF and THF, and decreased continuously in the three last periods, but generally slower than the mass loss (Fig. 5.6). Aluminium and iron showed high increases in their contents, peaking at 180 d and decreasing sharply in the following periods (Fig. 5.6). The increases were higher in the LERF than in both the SHF and THF, and higher for aluminium than for iron. Aluminium contents at the end of one year were higher than the initial ones in all three forest types, but iron contents at the end of one year were slightly lower than the initial ones in the THF and LERF.

The relationships found between mineral element concentrations and physical and biological factors observed in the litter bags (Table 5.10) were broadly similar to the ones found for experiment A (Table 5.7, page 113). The leaf mass loss, and the release rates of potassium and boron were mostly influenced by abiotic factors, while the release rates of nitrogen, phosphorus, calcium, and zinc, were more related to biotic factors such as fungal colonization and root penetration.

Table 5.10: Experiment B: Significant regressions of mass loss, root penetration in litter bags, and mineral elements in decomposing leaf litter with selected climatic factors and physical and biological actions on decomposing material for all three forest types together. Mass loss was represented in the analysis by the daily rate of weight loss. Rf = rainfall since last litter-bag retrieval; Rf/d = daily rainfall in the same period; D%Rf = percentage of rainy days; AcRf = total rainfall since the begining of the experiment; EV = evaporation since the last litter-bag retrieval; EV/d = daily evaporation; Lmois = moisture of the organic layer in the top soil in the 21 d before retrieval; Smois= moisture of mineral topsoil in the 21 d before retrieval. Term = termites present in litter bags at retrieval; Root = fine roots penetrating litter bags at retrieval; Whitf = white fungi on decomposing leaves; Blackf = black fungi on decomposing leaves; Brdwn = breakdown of decomposing leaves; Disc = discoloration of the leaves; Esk = leaf surface removal; Res = residues (soil and organic) inside the litter bags. The factors with greater influence are presented in order of importance in the last colunm. The italicized factors were negatively related.

	r^2 %	df	p	most influential factors
mass loss	89.1	53	< 0.001	EV, %raind, Rf/d, PenRo, Breakd
roots	38.7	53	< 0.001	Breakd
N	34.2	53	< 0.001	Brdwn, Whitf, Blackf
P	25.7	53	< 0.001	Brdwn, Whitf, Blackf
K	36.2	53	< 0.001	*EV*, *Rf*, *Disc*, Whitf
Ca	59.6	53	< 0.001	Blackf, *Root*, Whitf
Mg	61.7	53	< 0.001	*Root*, *Brdwn*, *EV*, *Term*
Al	56.3	53	< 0.05	Blackf, EV, Res, Root, Brdwn
B	68.7	53	< 0.05	*Rf/d*, *Rf*, *EV*, AcRf, Blackf
Fe	59.6	53	< 0.001	Blackf, EV/d, Res, Brdwn, AcRf, Root
Mn	32.2	53	< 0.001	*Root*, Blackf, Disc, EV/d, *Rf/d*
Zn	14.5	53	< 0.001	Blackf, *Root*, Brdwn, Rf/d

EXPERIMENT C

Rainfall, litter and soil moisture during the experiment

The rainfall, evaporation, litter and surface soil moisture during experiment C, are shown in Fig. 5.7. (The daily rainfall is shown in Fig. 2.3, Chapter 2). The first six months (three out of four retrievals) were relatively wet. The total rainfall during the 9-month period of the experiment was 2060 mm. The moisture of both the litter layer and the surface soil followed similar patterns to the rainfall during the corresponding periods.

Weight loss of the leaves

Weight losses of both species, especially of *Pradosia*, were slow in all forest types. The mean percentage mass remaining at the end of the experiment was always greater than 50 % (Tab. 5.11; Fig. 5.8). Taking into account the shorter duration of the experiment, and that only four retrievals were made, the mathematical models often did not fit the observed data well (Table 5.12). Among those fitting well, or reasonably well, the observed data, about half were linear models and the other half exponential (Table 5.18). The estimated half-lives of decomposing leaves varied from 489 d to 911 d in the sun SHF; from 568 d to 1110 d in the shade SHF; from 290 d to 518 d in the THF; and from 348 to 430 in the LERF (Table 5.12). No significant differences in weight losses were found between sun and shade leaves for *Aldina* or *Pradosia* (Table 5.13; Fig. 5.8).

Nutrient release from decomposing leaves

Some of the mineral elements showed indications of faster or slower release in the `sun' than in the `shade' leaves of both *Pradosia* and *Aldina*, especially of *Aldina* (Table 5.13; Fig. 5.9). The final concentrations (concentrations of remaining leaf material in the litter bags after each retrieval) of potassium and manganese were significantly higher in sun leaves than in shade leaves of *Pradosia*. In the *Aldina* leaves, concentrations of phosphorus, calcium, and magnesium, were higher in the sun than in shade leaves, while the opposite was found for nitrogen, iron and zinc (Table 5.13; Fig. 5.9; Appendix 5.5). Among the four forest locations, the LERF generally had the fastest release of calcium, magnesium, and manganese, and the slowest release of aluminium and iron, while the THF showed the slowest release of zinc

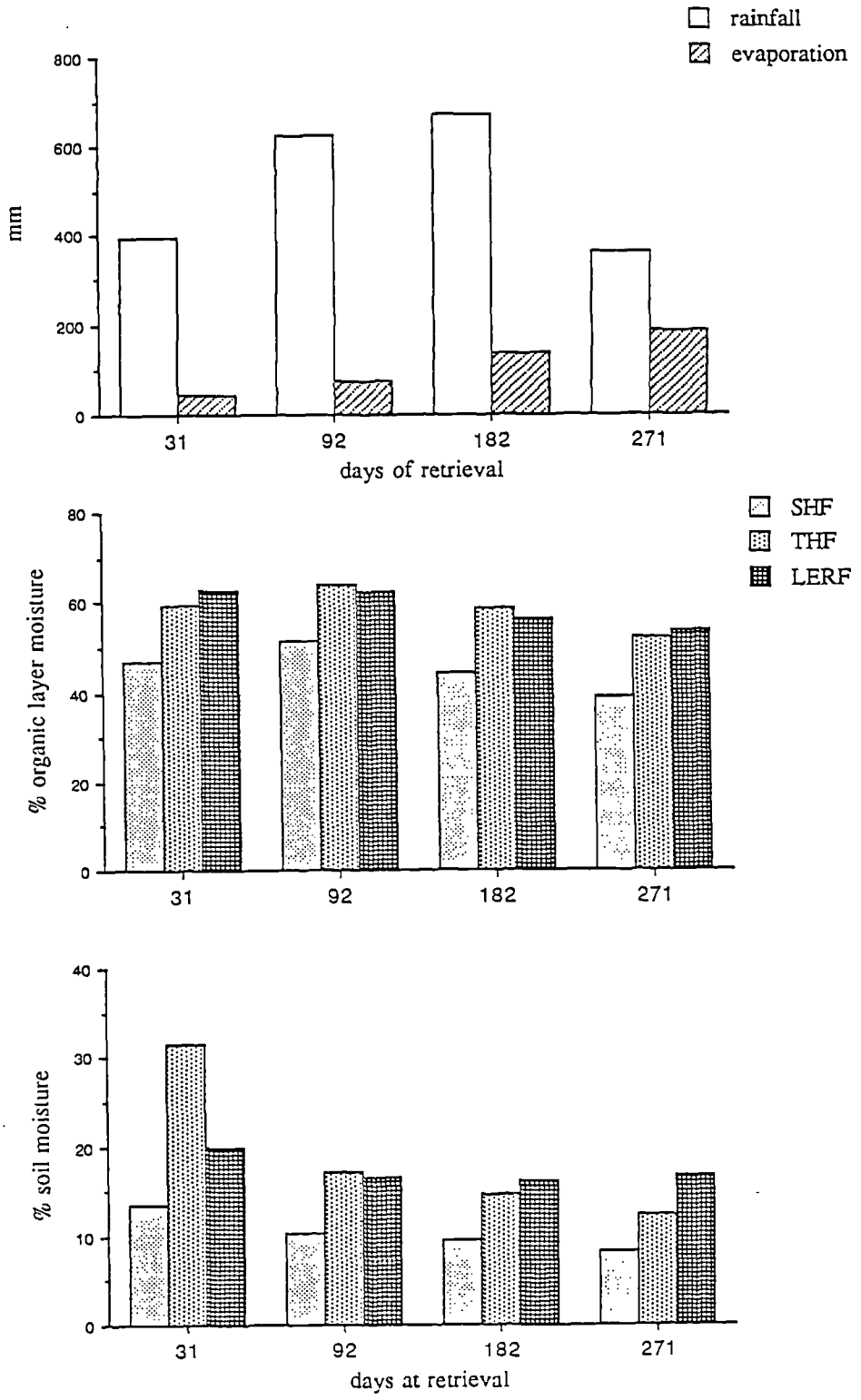


Figure 5.7: Experiment C: rainfall and evaporation (mm), and mean moisture (%) of the top organic layer and upper mineral soil layers in the intervals preceding retrievals. Rainfall and evaporation data are from a climatic station 3 km northwest of study sites (CEPLAC unpublished). The moisture data are means of samples collected every 7 d or 14 d (except the two last months, when there was a 21 d interval) and measured gravimetrically as described in the text.

Table 5.11: Experiment C: mean dry weight of the four different leaf types initially and after each retrieval time in the four forest locations. Values are means ± SE (n = 16 for 0 d, and n = 4 for each of the retrieval times).

leaf type	days	sun SHF	shade SHF	THF	LERF
sun *Pradosia*	0	4.74 ± 0.007	4.74 ± 0.007	4.74 ± 0.007	4.73 ± 0.006
	31	4.40 ± 0.02	4.33 ± 0.03	4.28 ± 0.04	4.30 ± 0.05
	92	4.14 ± 0.06	3.90 ± 0.05	3.99 ± 0.07	3.27 ± 0.52
	182	3.93 ± 0.02	3.83 ± 0.10	3.53 ± 0.14	3.25 ± 0.11
	271	3.66 ± 0.07	3.77 ± 0.11	3.47 ± 0.10	2.92 ±0.31
sun *Aldina*	0	4.72 ± 0.007	4.72 ±0.006	4.72 ± 0.007	4.73 ±0.008
	31	4.35 ± 0.02	4.33 ±0.04	3.90 ± 0.30	4.22 ±0.01
	92	4.06 ± 0.02	4.02 ±0.05	3.85 ± 0.08	3.82 ± 0.03
	182	3.85 ± 0.07	3.91 ± 0.15	3.55 ± 0.13	3.13 ± 0.08
	271	3.68 ± 0.05	3.72 ± 0.15	3.70 ± 0.31	3.00 ± 0.10
shade *Pradosia*	0	4.74 ± 0.07	4.75 ± 0.008	4.75 ± 0.005	4.75 ± 0.006
	31	4.41 ± 0.03	4.39 ± 0.02	4.37 ± 0.03	3.97 ± 0.43
	92	4.11 ± 0.03	3.90 ± 0.04	3.71 ± 0.05	2.82 ± 0.61
	182	3.60 ± 0.16	3.51 ± 0.17	2.99 ± 0.28	3.09 ± 0.09
	271	3.05 ± 0.20	3.14 ± 0.08	2.91 ± 0.18	2.61 ± 0.36
shade *Aldina*	0	4.73 ± 0.007	4.73 ±0.005	4.72 ± 0.007	4.72 ± 0.007
	31	4.48 ± 0.06	4.28 ±0.22	4.35 ±0.04	4.29 ± 0.05
	92	4.19 ±0.06	3.94 ± 0.06	3.98 ± 0.09	3.10 ± 0.25
	182	3.54 ± 0.17	3.51 ± 0.16	3.15 ± 0.16	2.90 ± 0.16
	271	3.50 ± 0.05	3.25 ± 0.08	2.53 ± 0.12	2.71 ± 0.24

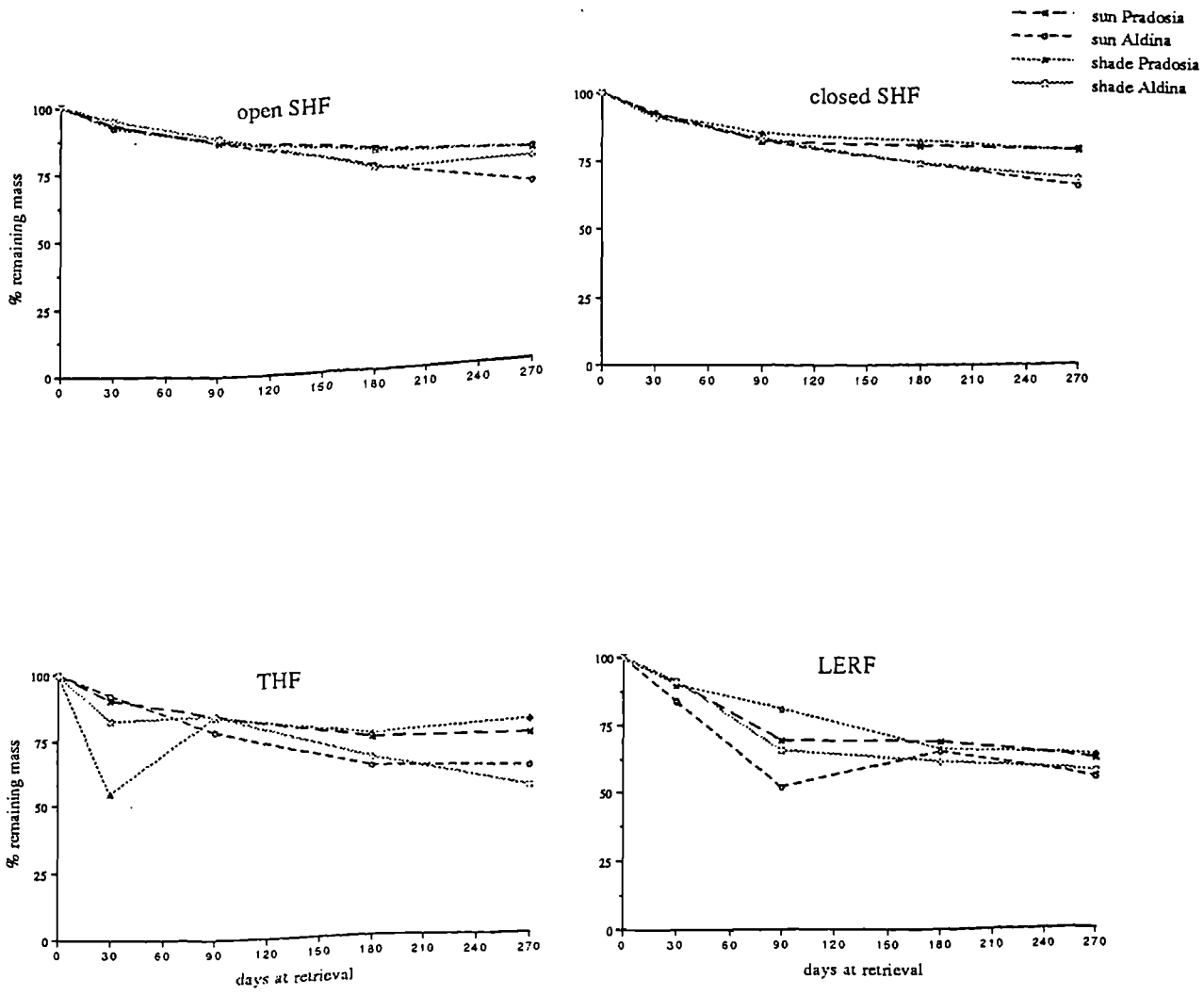


Figure 5.8: Experiment C: mean remaining mass (%) over time in relation to the initial dry mass for each of the litter types in the four vegetation locations (n=4).

Table 5.12: Experiment C: Decay equations and estimated *k* and half-life values for the four leaf litter types in the four areas of forest. The equation which produced the best fit for the observed data (linear or exponential) was used to calculated the half-life. The *k* values (where possible) were calculated using exponential equations. NS = non-significant (no adjustment possible, and further calculations prevented).

leaf type	area	model	equation	F	P	r^2 %	k	half-life (days)
sun *Pradosia*	sun SHF	linear	95.3 - 0.069 x	112	0.000	87.4		
		exponential	95.6 $10^{-0.000801 x}$	117	0.000	87.9	0.29	865
	shade SHF	linear	91.8 - 0.0535 x	20.2	0.000	54.6		
		exponential	91.8 $10^{-0.000623 x}$	20.4	0.000	54.7	0.23	1112
	THF	linear	92.8 - 0.0826 x	47.7	0.000	74.5		518
		exponential	92.8 $10^{-0.00161 x}$	44.1	0.000	72.9	0.37	
	LERF	linear	89.7 - 0.114 x	11.0	0.005	38.5		348
		exponential	88.2 $10^{-0.015 x}$	6.44	0.023	25.4	0.55	
sun *Aldina*	sun SHF	linear	84.8 - 0.290 x	0.90	0.353	0.00	NS	NS
		exponential	83.8 $10^{-0.000372 x}$	0.84	0.375	0.00	NS	NS
	shade SHF	linear	76.9 + 0.0206 x	0.43	0.521	0.00	NS	NS
		exponential	75.9 $10^{+0.0003 x}$	0.58	0.459	0.00	NS	NS
	THF	linear	83.4 - 0.0582 x	2.68	0.122	9.50	NS	NS
		exponential	82.3 $10^{-0.000734 x}$	2.36	0.145	7.80	NS	NS
	LERF	linear	76.0 - 0.0636 x	1.17	0.297	1.00	NS	NS
		exponential	70.8 $10^{-0.000978 x}$	0.55	0.472	0.00	NS	NS
shade *Pradosia*	sun SHF	linear	94.2 - 0.0657 x	86.5	0.000	84.2		
		exponential	94.6 $10^{-0.000776 x}$	94.5	0.000	85.4	0.28	911
	shade SHF	linear	93.3 - 0.0573 x	20.6	0.000	55.0		756
		exponential	93.7 $10^{-0.000673 x}$	20.3	0.000	54.7	0.25	
	THF	linear	85.9 - 0.0383 d	2.39	0.143	8.00	NS	NS
		exponential	85.6 $10^{-0.000464 x}$	2.27	0.152	7.40	NS	NS
	LERF	linear	93.1-0.123x	118	0.000	87.9		
		exponential	93.7 $10^{-0.0016 x}$	121	0.000	88.2	0.59	430
shade *Aldina*	sun SHF	linear	97.1 - 0.0964 x	69.1	0.000	81.0		489
		exponential	97.5 $10^{-0.00115 x}$	61.9	0.000	79.2	0.42	
	shade SHF	linear	93.7 - 0.098 x	41.7	0.000	71.8		
		exponential	93.7 $10^{-0.00122 x}$	42.3	0.000	72.1	0.44	568
	THF	linear	98.4 - 0.167 x	221	0.000	93.2		290
		exponential	101 $10^{-0.00232 x}$	164	0.000	91.1	0.85	
	LERF	linear	89.3 - 0.137 x	25.1	0.000	60.1		360
		exponential	89.1 $10^{-0.0019 x}$	22.1	0.000	56.9	0.69	

Table 5.13: Experiment C: Significant values for t-tests applied to the differences between the final concentrations of mineral elements in sun and shade leaves of *Pradosia* and *Aldina* in all four locations of the study. The differences obtained are described in the last column.

		n	mean	SD	T	p	Differences found
Pradosia	K	64	0.01	0.02	2.23	< 0.05	sun > shade
	Mn	64	0.58	0.55	8.43	< 0.001	sun > shade
Aldina	N	62	-0.06	0.17	-2.83	< 0.01	sun < shade
	P	62	0.01	0.01	5.45	<0.001	sun > shade
	Ca	62	0.14	0.19	5.67	< 0.001	sun > shade
	Mg	62	0.03	0.08	2.90	< 0.01	sun > shade
	Fe	62	-0.31	0.77	-3.21	< 0.01	sun < shade
	Zn	62	-0.18	0.23	-6.16	< 0.001	sun < shade

(Table 5.14; Fig. 5.9). Significant differences in the release rates of mineral elements in sun and shade patches in the SHF, were only found for phosphorus (in shade *Pradosia* leaves) and potassium (in sun *Aldina*). In both cases, faster release were recorded in the sun SHF (Table 5.14; Fig. 5.9).

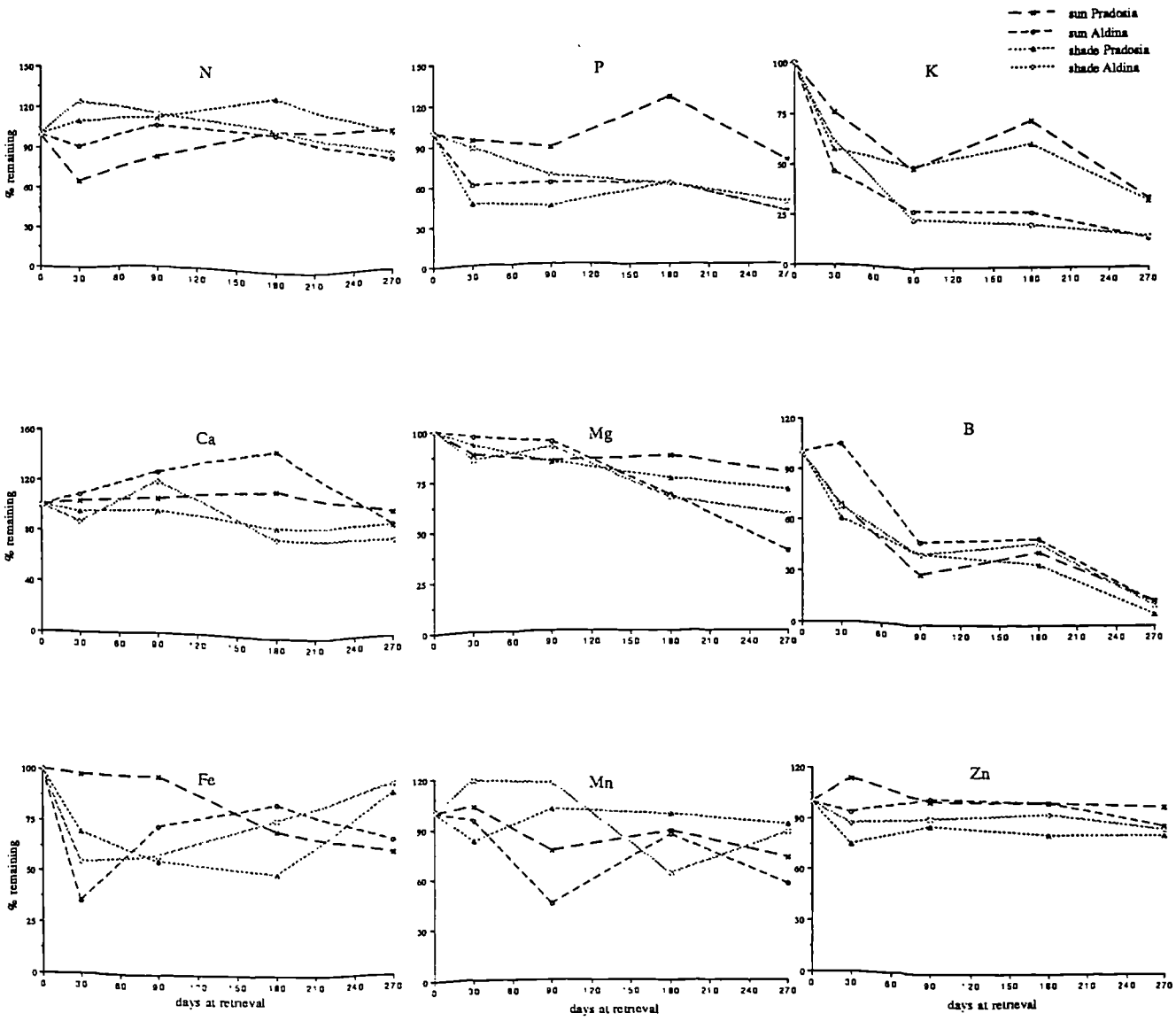


Figure 5.9a: Experiment C: percentage (%) content of mineral elements in relation to the initial content in decomposing leaves after each retrieval in the open SHF (n=4).

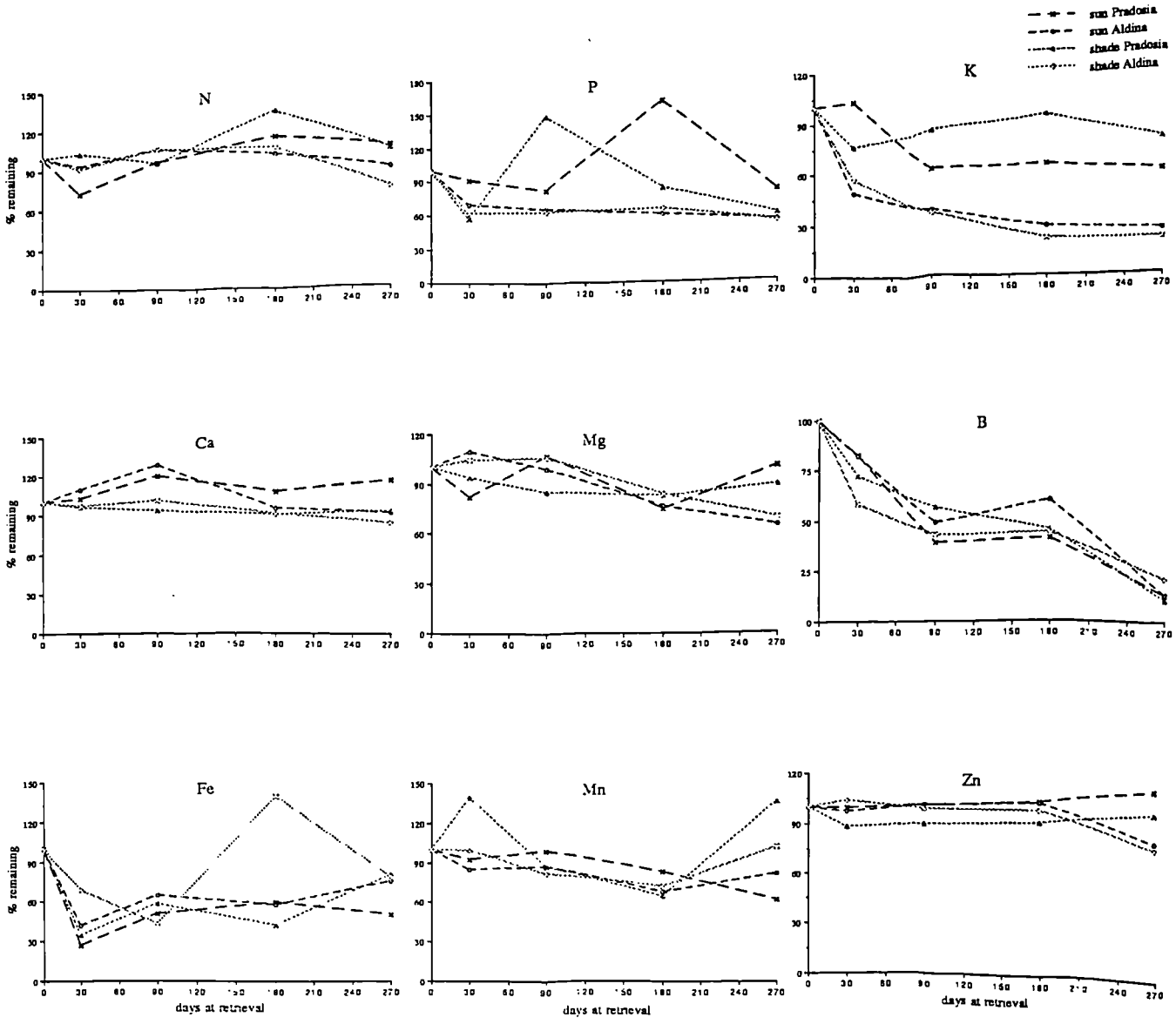


Figure 5.9b: Experiment C: percentage (%) contents of mineral elements in relation to the initial content in decomposing leaves after each retrieval in the closed SHF (n=4).

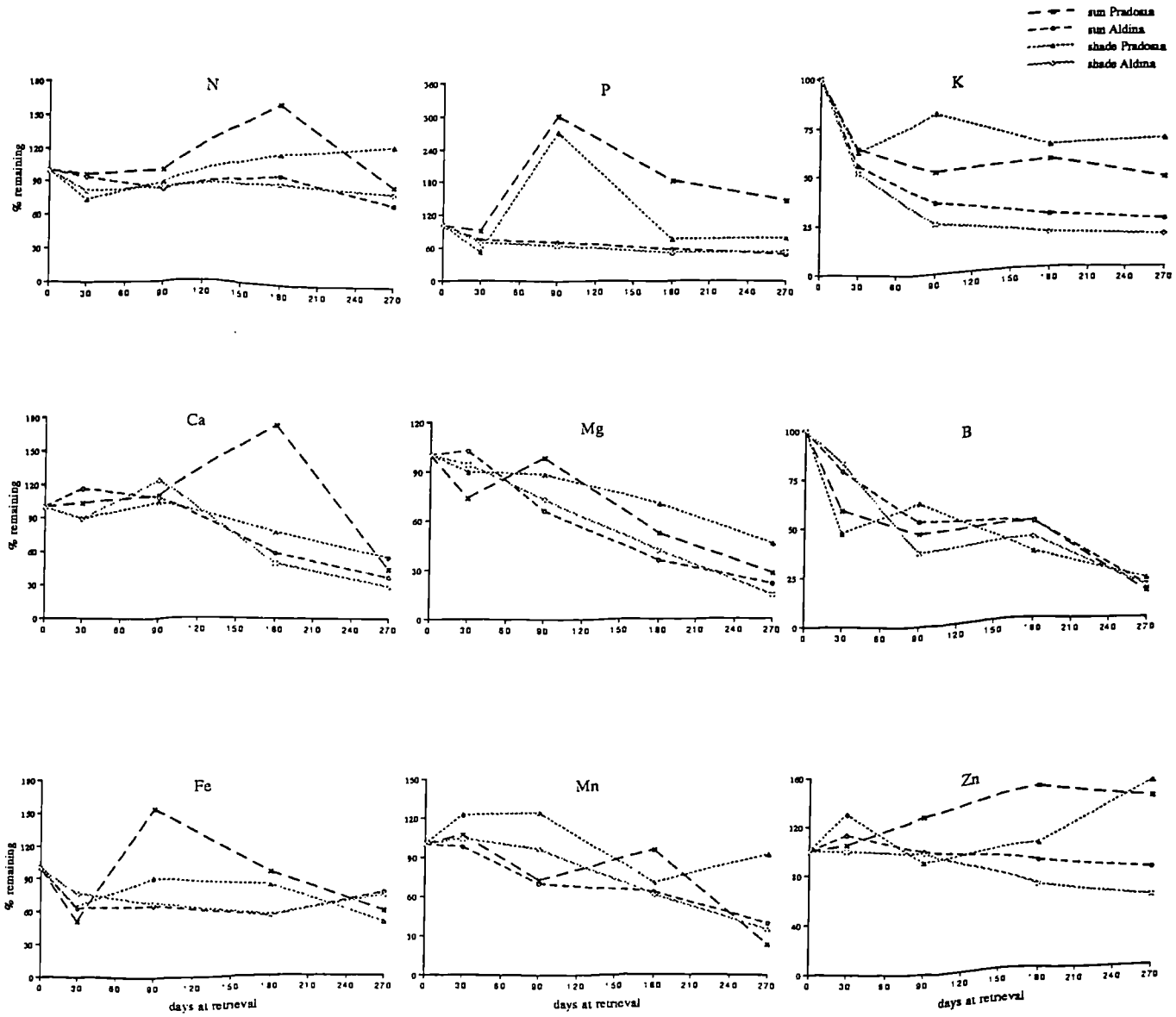


Figure 5.9c: Experiment C: percentage (%) contents of mineral elements in relation to the initial content in decomposing leaves after each retrieval in the THF (n=4).

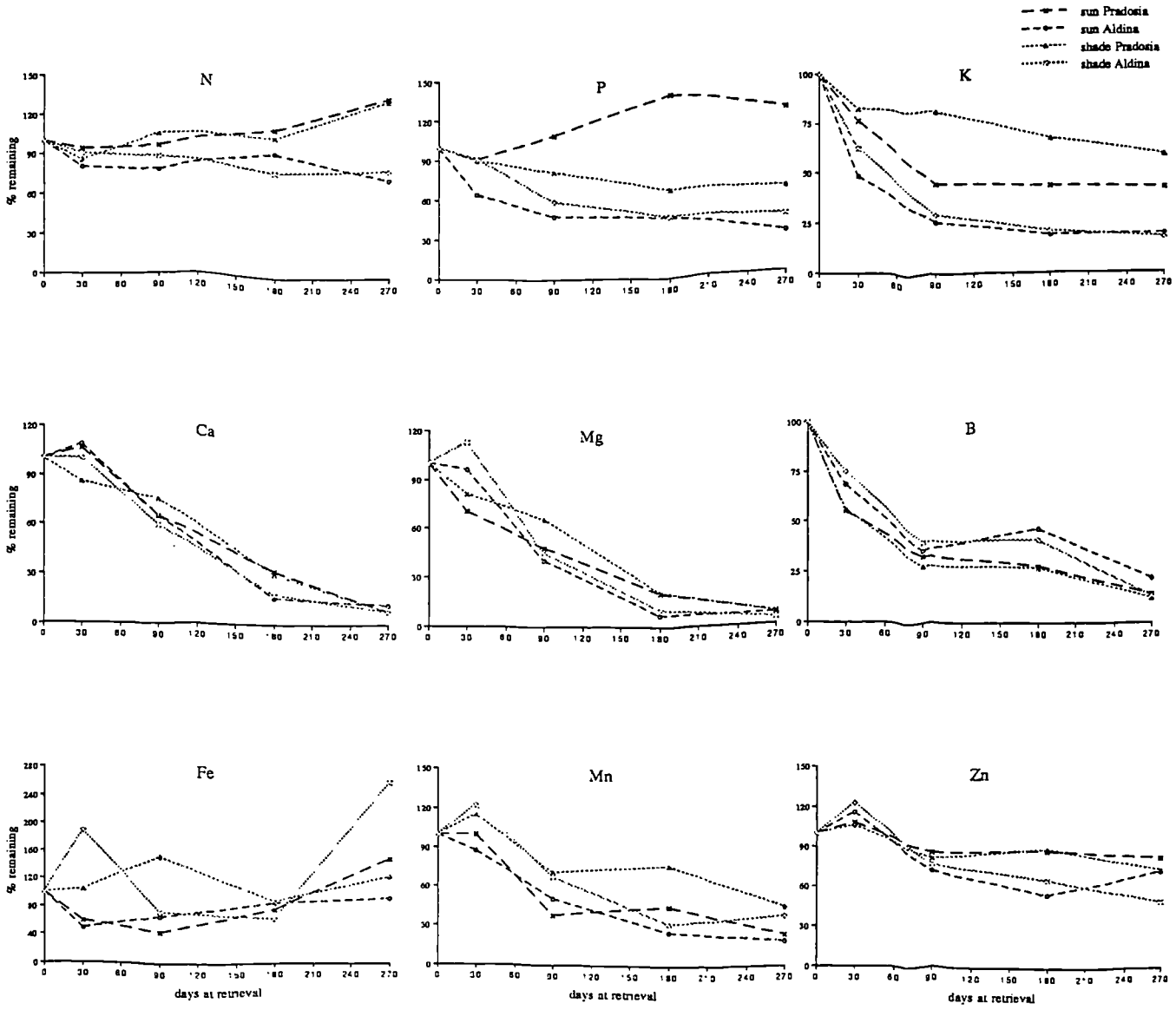


Figure 5.9d: Experiment C: percentage (%) contents of mineral elements in relation to the initial content in decomposing leaves after each retrieval in the LERF (n=4).

Table 5.14: Significant differences among forest locations following one-way analysis of variance on mass losses and residual concentrations of mineral elements in the four different leaf types. Values used included all four sampling times.

leaf type		df	F	P	differences found
sun *Pradosia*	mass	3	4.98	<0.01	LERF > both SHF
	N	3	5.18	<0.01	LERF < both SHF
	P	3	5.06	<0.01	THF < both SHF
	Ca	3	8.11	<0.001	LERF < all others
	Mg	3	16.8	<0.001	LERF < all others; THF < shade SHF
	Al	3	4.84	<0.01	LERF > both SHF
	Fe	3	4.72	<0.01	shade SHF < THF, LERF
	Mn	3	4.47	<0.01	LERF < both SHF
	Zn	3	5.36	<0.01	THF > all others
shade *Pradosia*	mass	3	3.25	<0.05	LERF > sun SHF
	P	3	10.2	<0.001	sun SHF < shade SHF < THF
	K	3	2.89	<0.05	sun SHF < THF
	Ca	3	11.7	<0.001	LERF < both SHF; THF < sun SHF
	Mg	3	9.93	<0.001	LERF < both SHF; THF < shade SHF
	Al	3	3.96	<0.05	shade SHF ≤ THF < LERF
	Mn	3	2.98	<0.05	LERF < shade SHF
sun *Aldina*	mass	3	4.78	<0.01	LERF > both SHF
	K	3	22.0	<0.001	sun SHF < all others
	Ca	3	16.8	<0.001	LERF < all others
	Mg	3	14.3	<0.001	LERF < all others
	Al	3	13.1	<0.001	LERF > all others
	Fe	3	9.93	<0.001	LERF > all others
	Zn	3	5.48	<0.01	THF > both SHF
shade *Aldina*	mass	3	3.62	<0.05	LERF > shade SHF
	Ca	3	8.62	<0.001	LERF < both SHF
	Mg	3	10.8	<0.001	LERF < both SHF; THF < shade SHF
	Al	3	9.32	<0.001	LERF > all others
	Fe	3	5.64	<0.01	LERF > all others
	Mn	3	4.46	<0.01	LERF < both SHF

DISCUSSION

Decomposition rates and patterns

Decomposition rates and patterns were distinct according to the leaf species used and the forest types studied, but they were overall relatively low by tropical standards (Nye 1961; Madge 1965; Bernhard-Reversat 1972; Herrera *et al.* 1978; Anderson & Swift 1983). The decomposition rates in rain forests are usually regarded as high, with pronounced and very fast weight losses in the first weeks of litter-bag exposure, even during the dry season (Olson 1963; Madge 1965; Klinge 1977; Luizão & Schubart 1987; Babbar & Ewel 1989). Two distinct decomposition phases have been often reported: an initial fast mass and nutrient loss in the first few weeks, due to the leaching of more soluble substances (Bocock & Gilbert 1957); and a period of slower decay (Babbar & Ewel 1989). After the first weeks, probably the easily-decomposable substances are 'exhausted' and the substrate then has higher proportions of more recalcitrant materials such as lignins and hemicelluloses, which are slower to decompose (Alexander 1977). In addition to that, the biomass of the decomposer organisms attached to the leaves could represent a considerable proportion of the dry weight and mask the actual decomposition pattern (Swift *et al.* 1979; Babbar & Ewel 1989).

In contrast to the frequently observed pattern just described, in the present study there was no sharp decrease of the initial dry weight of bagged leaves during the first periods of decomposition and the weight loss was rather evenly spread over time. The most likely explanations for these unusual results in the present study may be related to the reduced rates of initial leaf mass loss. In experiment A, although designed to start in the wet season, the first 45 d were unusually dry, and the expected first phase of relatively fast leaf weight loss due to leaching and microbial action (Swift *et al.* 1979) did not occur. In experiment C, started in a real wet season which still lasted for seven months after the experiment was started, only recalcitrant leaves were used, which did not have a sharp initial leaf mass loss. The slow weight loss in the first months was best fitted by the linear models, which is unusual for tropical forests.

None of the currently used regression models (Wieder & Lang 1982) was applicable to all substrates. Single exponential models are theoretically unrealistic given the known heterogeneity of litter and other organic matter (Minderman 1968). The double exponential

model appears the most realistic of the simple models proposed in that it estimates separate rates for an easily decomposable and a more resistant factor, and it has been used for litter weight losses in tropical rain forests (Ezcurra & Becerra 1987; Luizão & Schubart 1987; Spain & Le Feuvre 1987). In tropical rain forests in Australia, Spain & Le Feuvre (1987), using three different leaf species, have fitted different models for different species, and the double exponential model was considered the more biologically realistic, fitting the majority of the curves obtained.

In the present study, the results showing no initial fast decomposition phase prevented the use of double-exponential models for explaining the decomposition patterns. The relatively slow and constant weight losses observed were better described by a linear model for the majority of the data obtained in the three experiments and the distinct leaf types and forest types studied; the other cases were described by the other simplest model, the single exponential model (Olson 1963). The best fits using linear or single exponential models were generally obtained for *Aldina* and *Pradosia* leaves, the substrates of lower quality. The use of linear fits for regression on decomposition over time is not usual, but it has been recorded for some studies in the few last years, showing that for substrates that decompose slowly, as in the present study, the amount of organic matter often decreases linearly with time (Taylor & Parkinson 1988; Tavakol & Proctor 1994).

The fact that a linear model fitted reasonably well most of the observed data means that the amount of remaining substrate and the quality of the decomposing leaves were not the only two decisive factors controlling decomposition over time. The decomposition process may be largely dependent on abiotic factors as well, among which rainfall-related events, causing leaching of organic and mineral leaf constituents, appear to be an important factor in the three forest types, but especially in the SHF. The biological activities of the decomposer organisms did not appear to be more concentrated in one specific period of the process, and were not dependent on the amount or quality of the substrate left in the bags. Rather, they seemed much more dependent on the litter and soil moisture, abiotic factors related to rainfall, which seems to agree with Meentemeyer (1978), who pointed to abiotic factors as the chief controllers of decomposition rates. In the present study, successive periods of drying and wetting the leaves may have broken down the material, followed by rainwater leaching and losses of particles

through meshes, especially in the SHF, the most open vegetation. Periodic drying of the substrate intensifies the decomposition if the desiccation and temperature are not extreme (Anderson *et al.* 1983; Babbar & Ewel 1989).

The **k** (decomposition constant) values estimated for all species and types of leaves in the three experiments varied from 0.23 to 1.20 in the SHF, from 0.37 to 1.49 in THF, and from 0.55 to 1.86 in LERF. These values were lower than the $\mathbf{k_L}$ estimates made from the litterfall and litter layer data (Chapter 4), which were respectively 0.95, 1.31, and 1.96 for leaves, and 0.71, 0.98, and 1.19 for total fine litter.

The low decomposition rates found in the present study appear less surprising when one considers the relatively large litter layer on the soil surface of the three forest types, especially in the SHF (closed patches) and the THF. Other heath forests studied elsewhere in the tropics also showed relatively low decomposition rates. For instance, in Sarawak, Anderson *et al.* (1983) found weight losses in the range 50-77 % after one year for two leaf species in fine mesh bags either in dipterocarp forest (equivalent to LERF) or in heath forest. In Venezuela, Cuevas & Medina (1988) found slow decomposition rates in both heath forests studied, the tall *caatinga* and the low *bana*, estimating respectively 2.6-3.9 years and 3.1-5.9 years as the times required for 95% disappearance of bagged leaf litter. They found **k** values of 0.22-0.44 for the low *bana*, 0.80-1.33 for the tall *caatinga*, and 0.58-5.00 for the lowland evergreen rain forest near San Carlos do Río Negro. Half-life estimates were used to compare decomposition rates (Babbar & Ewel 1989) including those among different leaf species and forest types in the present study. Unfortunately there are few published half-life estimates of decomposing litter in tropical rain forests, which restricts the number of possible comparisons with studies elsewhere.

In the present study, differences in decomposition rates found among foliage types (especially between *Clitoria* and the two heath forest species) were much greater than differences among ecosystems, confirming findings of other authors in tropical forests (Witkamp 1966; Cuevas & Medina 1983; Babbar & Ewel 1993). The initial content of mineral elements and organic compounds in the leaf species may account for such differences (Swift *et al.* 1979), but some other leaf features, like waxiness, thickness, and toughness may be important. Among the mineral elements in the leaves, the most commonly suggested as main controllers of

decomposition rates have been nitrogen (Singh & Gupta 1977; Berg *et al.* 1982; Melillo *et al.* 1982; Taylor *et al.* 1989), and phosphorus (Vitousek *et al.* 1994). However, in a recent study, Prescott (1995), using several fertilizer trials, demonstrated conclusively that nitrogen availability alone, either exogeneous or endogenous, did not control the rate of litter decomposition. Many other authors have often considered nitrogen together with lignin concentrations as the main predictors of decomposition rates, either including or not other organic compounds such as polyphenols (Swift *et al.* 1979; Berg & Staaf 1981; Melillo *et al.* 1982; Palm & Sanchez 1991). However, Spain & Le Feuvre (1987), using three separately bagged leaf species in a lowland tropical rain forest in Australia, found that breakdown rates were not simply related to the initial contents of mineral elements, fibres or lignin. Their most rapid breakdown was found in the litter having a known considerable variety of polyphenols. Cuevas & Medina (1988), studying decomposition in lowland evergreen rainforest and two types of heath forest in Venezuela, using three leaf species from each forest type, found that initial mass losses were inversely correlated with fibre and lignin in the decomposing leaves. At later periods, however, the leaves from lowland evergreen rainforest, even having higher contents of fibres, lignins, and lower concentrations of nitrogen and phosphorus, decomposed faster than leaves from heath forests. In summary, there is still a recognized incomplete understanding of decomposition-rate determinants, particularly in extreme environments (Anderson 1992).

In the present study, *Aldina* leaves, containing higher concentrations of ash, nitrogen and other essential nutrients, and higher fibres, showed slightly lower weight losses than *Pradosia* (with lower protein and higher lipid concentrations) in the first two months of experiment A. From 120 d to the end of the experiment, however, the opposite was always found. The possible reasons for that could be the possible decrease in the concentration of fibres in the decomposing leaves after two months, and the action of white fungi and mycelia, which were more frequent in *Aldina* than in *Pradosia* leaves, and increased considerably in decomposing leaves after 60 d. White fungi may be regarded as one of the two only true decomposers of tropical leaf litter (the other being the earthworms), degrading and transforming organic compounds (F. Toutain, personal communication). The action of white fungi was stronger in the THF than in the other two forest types. *Pradosia* leaves, often curling within the litter bags,

showed a lower rate of physical breakdown than *Aldina*, which increased breakdown especially after the initial 60 d, possibly because of lower fibres in decomposing leaves. The curling of the *Pradosia* leaves may have delayed the decomposition rates, because the leaf surface exposed to decomposers or in contact with the soil was decreased (Babbar & Ewel 1989). In experiment C, sun leaves of both species, *Aldina* and *Pradosia*, even with lower initial concentrations of proteins and higher fibres than shade leaves, had no significantly different rates of weight loss. This result contradicts those found in tropical rain forests in Australia (Lowman 1988), where sun leaves, tougher and thicker than shade leaves, decayed more slowly than shade leaves.

Half-lives for the faster-decomposing species, *Clitoria* (221-243 d) had small and no significant differences among the three forest types in experiment A. In experiment B, the half-lives of *Clitoria* varied from 193 to 243 d in the three forest types (shorter times than in experiment A), showing not very large differences among forest types, with no significant differences in mass losses between LERF and THF. The other two species used in experiment A, especially *Pradosia* (341-562 d) had significant differences in half-lives among the three forest types, and the same occurred with sun and shade leaves of *Aldina* and *Pradosia* used in experiment C. Lower rates of physical breakdown of decomposing leaves always occurred in the SHF, where lower densities of litter animals and lower penetration of fine roots were recorded.

The lack of an evident initial leaching phase in experiment A (starting in the wet season) may be attributed to the lack of rains in the first month of the experiment, when an unusually dry January was observed. In experiment B, low decay rates were observed up to 120 d (dry period), but decomposition was accelerated after that period, when the wet season started.

Other factors influencing mass loss of leaf litter

The abiotic control of breakdown was demonstrated in a shared study (R.C.C. Luizão 1994), where the litter bags with *Clitoria* were weekly uplifted to prevent penetration of fine roots, and still showed considerable breakdown of the leaves.

In addition to the main factors determining decomposition rates discussed in the former sections, namely time, sites and leaf species, some other related factors were found to be

important controllers of rates in the present study. From the three additional factors related to mass losses in experiment A (rainfall accumulated since the beginning of the experiment, colonization of leaves by black fungi, and the moisture of the top organic layer), the first one, accumulated rainfall, is in fact a function of elapsed time which obviously is a very important factor in the estimates of decomposition rates. However, for individual forest types, other factors such as termites in the LERF (especially on *Clitoria* leaves) and leaf-colonization by white fungi in the THF, appeared as important in determining decomposition rates. In the SHF, the significant relationship found with the removal of the leaf surface may not be meaningful, since it is partly a function of elapsed time and of the decomposition process itself. In turn, it may indicate some action of organisms, mainly litter animals, in the leaf disappearance.

In experiment B (started in the dry season), both climatic and biotic factors related to weight loss of decomposing leaves differed from experiment A. The rainfall and the evaporation in the period preceding retrievals, plus the percentage of rainy days in the same period, are correlated themselves, and suggest a strong abiotic control of decomposition rates in the initial phases of the experiment, during the dry period. That is emphasized by the next significant factor related to weight losses, the physical breakdown of the decomposing leaves, which is partly a result of climatic action.

The penetration of fine roots was the only biological factor significantly related to weight losses of bagged leaves, and root masses (for the three leaf species pooled) were positively correlated with the physical breakdown of the leaves. This result contradicts those of R.C.C. Luizão (1994) who found no significant differences in mass loss rates of *Clitoria* leaves between bags where roots were allowed or prevented to enter by weekly uplifitings. In the present study, fine roots penetrating litter bags appeared to be partly responsible for the breakdown of bagged leaves, confirming results obtained in Venezuela (Cuevas & Medina 1983), where two out of three leaf species studied had higher mass losses in presence of roots.

Comparison of decomposition rates between experiments A and B

The weight loss of bagged *Clitoria* leaves exposed at the onset of the wet season (experiment A), was slower overall than leaves of the same species similarly exposed in the same plots in the dry season (experiment B) (Table 5.15). This result contradicts the suggestion made by

Wiegert & Murphy (1970) that the apparent effect of season on litter decomposition would be a function only of the starting time of the experiment. This suggestion has been supported in some studies on tropical litters, showing significantly higher decomposition rates for litter exposed in the wet season than for litter exposed in the dry season (Luizão & Schubart 1987; Lowman 1988). In the present study, differences in weight losses were visible in first four months of each experiment, but at the end of the 1-year experiments, the expected difference did not appear. After 360 d the experiment started in the dry season had the highest mass losses, especially in the THF and LERF (Table 5.15), but the difference was not significant. The half-lives found for the three forest types studied varied from 221 to 243 d in experiment A and from 193 to 249 in experiment B. It is noteworthy that the half-lives for the SHF showed the opposite trend, being shorter in experiment A.

In experiment A, started at the onset of the wet season, the rainfall in the first 30 d was only 120 mm (a small amount for the time of the year, and half fell in the day the experiment was installed), and was relatively low for a further 15 d, but it reached 1040 mm by the end of 120 d. In experiment B, started in the dry season, the rainfall was 77 mm in the first 30 d, reaching 495 mm by the end of 120 d. Thus, the first 45 d of experiment A were unusually dry (with the three following months very wet), while in experiment B the first 30 d were dry as expected but the three following months were not really dry, and followed by seven very rainy months. The rainfall pattern observed certainly had an important role in determining the lack of significant differences in the decomposition rates in the experiments started in the dry and wet seasons. However, despite the unusual climatic pattern, the seasonal effects on decomposing leaves were evident in the two experiments, each one with a distinctive pattern of decomposition. In the THF and LERF, in experiment B there was an apparently important process of breakdown during the initial four months of the 'dry' period. The sucessive periods of drying and wetting the leaves (by the scattered and sometimes heavy rains) apparently caused the breakdown of the material, followed by leaching and losses of particles through the mesh of the bags (Babbar & Ewel 1989). This process was followed by a phase of more intense biological activity when the wet season started. In the most open vegetation type, the SHF, apparently there was no such intense biological activity (as in the other two forest types), in the early wet season, which followed four months of the dry season, when leaching and

Table 5.15: Mean percentage leaf mass remaining and mass of fine roots (g) in the litter bags after 120 d and 360 d in the field, and the estimated half-lives of *Clitoria* litter in the experiments starting in the dry and the wet season. Values are means and SE's (n=12).

	After 120 d		**After 360 d**		**half-life (days)**	
SHF	dry	wet	dry	wet	dry	wet
mass (%)	74.0 (1.15)	65.0 (2.31)	34.0 (3.17)	34.5 (2.89)	249	243
roots (g)	0.01 (0.01)	0.02 (0.01)	0.09 (0.03)	0.10 (0.05)		
THF						
mass (%)	70.0 (1.15)	62.5 (1.44)	26.0 (2.89)	38.0 (2.31)	218	240
roots (g)	0.28 (0.09)	0.94 (0.26)	1.31 (0.25)	1.52 (0.24)		
LERF						
mass (%)	62.0 (2.02)	60.0 (2.31)	18.0 (2.60)	33.0 (2.60)	193	221
roots (g)	0.62 (0.18)	1.50 (0.33)	2.39 (0.35)	1.86 (0.30)		

physical breakdown had occurred. Thus, the limited biological action slowed down the decomposition rates in later periods of the experiment in the SHF, where apparently the decomposition would be actually always faster when starting in the wet season. Interestingly, the litterfall in that forest type peaked in January, in the early wet season, which could suggest a synchrony between litterfall and decomposition processes in the SHF, in the same way as it appears to exist in the THF and LERF. For both the THF and LERF, taking into account that the litterfall peaked in the dry season (Chapter 4), it seems that experiment B better represented the natural process of leaf litter decomposition in those two forest types, where the rates over one year are higher when starting decomposition by physical breakdown of leaves in the dry season. The results of the present study highlight the need of longer experiments to assess properly the decomposition rates (Swift & Anderson 1989; Anderson & Ingram 1993) in tropical forests.

Fine roots penetrating litter bags and mineral elements in roots

The mass of fine roots penetrating litter bags was higher in the LERF, and increased considerably after 60 d in experiments A and B, and it was always related to the physical breakdown of leaves, as discussed above. The lack of root penetration in most samples from the SHF may account for the lower decomposition rates, despite a presumed higher abiotic action on the breakdown in SHF where, because of its more open vegetation, the litter bags were more exposed to the direct impact of rains and heath.

There were relatively high concentrations of the main essential nutrients, except for potassium, in the fine roots penetrating the litter bags in the present study, especially in bags with *Clitoria* leaves, compared with fine roots from the Danum Valley, Malaysia (Green 1992). In fine roots ≤ 2 mm in diameter in the upper soil layers, he found concentrations (%) of N = 1.41; P = 0.052; K = 0.52; Ca = 0.59; and Mg = 0.24. In the present study, the highest concentrations of phosphorus, potassium, calcium, magnesium, boron, manganese, and zinc in fine roots, were found in those penetrating bags with *Clitoria*, while the lowest values for nitrogen were found in those with the nitrogen-poor *Pradosia* leaves. These results indicate a significant variation among different leaf-litter species in the bags as well as a similarity with the initial concentrations of mineral elements in the corresponding leaves present in the litter bags. This suggests that fine roots growing inside the litter bags were actually participating in the nutrient release processes, either causing faster release of elements, such as calcium, magnesium, manganese, and zinc, or causing accumulation of other elements, such as nitrogen, aluminium, and iron.

Comparing concentrations of mineral elements in fine roots among the forest types, it was clear that the LERF roots showed the highest concentrations of nitrogen, phosphorus, and aluminium, elements more abundant in LERF soils than in soils of the SHF. On the other hand, the SHF roots had the highest concentrations of potassium, calcium, magnesium, manganese, and zinc, and SHF soils are poorer in such elements than LERF soils. Thus, it could be suggested that there is a limitation of bases in the SHF soils, with fine surface roots absorbing elements from decomposing organic material, as indicated by Went & Stark (1968), Herrera *et al.* (1978); Cuevas & Medina (1983, 1988). However, it must be considered that the

concentrations of bases (and other mineral elements) in the SHF roots themselves could be originally higher than in the LERF soils. In fact, that was already found in central Amazonia by Klinge (1975) who, comparing heath forest on Spodosols with lowland evergreen rain forest on Oxisols, always recorded higher concentrations of mineral elements in roots (with diameter up to 6 mm) from heath forests. Further data are needed before the results of the present study can be used to support the idea of direct nutrient cycling and nutrient limitation for root or plant growth.

Nutrient release from decomposing leaves

Nitrogen in the leaves, as a constituent of proteins and nucleic acids, retained in the protoplasm of decomposers, was shown to be little leachable, presenting net increases in the initial phases of the experiments, decreasing later on, but slower than dry weight losses of leaves. Increases of nitrogen contents in the leaves is commonly found in decomposition studies (Nye 1961; Gosz *et al.* 1973; Luizão & Schubart 1987; Laishram & Yadava 1988; Babbar & Ewel 1989; Attiwill & Adams 1993), as result of a progressive reduction in the amount of organic C present and different external sources to the leaves: from the soil, the canopy through leaching, the fungal hyphae, and nitrogen fixation (Anderson 1973; Lousier & Parkinson 1978; Howard & Howard 1980; Luizao & Schubart 1987; Babbar & Ewel 1989).

Phosphorus, like nitrogen, is subject to immobilization by microorganisms in decomposing leaf litter (Gosz *et al.* 1973), and this immobilization during the first two months of the experiments probably occurred in the present study. In fact, phosphorus is an element with variable behaviour in decomposing leaves: it can be lost at similar rates to the dry weight (Ewel 1976; Swift *et al.* 1981) or can increase concentrations in the leaves (Anderson *et al.* 1983; Luizão *et al.* 1996). Upadhyay & Singh (1989) reported nitrogen and phosphorus accumulation in some litter types in India, especially during the first stages of decomposition. A pattern of nitrogen and often phosphorus immobilization, followed by a net release, particularly for phosphorus, from leaves of tropical forests growing on nutrient-poor soil has been reported by Vitousek & Sanford (1986). This pattern was confirmed in the present study, when after the initial apparent immobilization of both nitrogen and phosphorus, once release has started it is proportional to the decomposition rate (Berg & Staaf 1981; van Vuuren *et al.*

1993), but faster for phosphorus than for nitrogen. The phosphorus release was especially fast in the THF and LERF after 60 d of the experiments.

Potassium showed very high mobility, in the same way as recorded by many workers (Nye 1961; Attiwill 1968; Bernhard-Reversat 1972; Gosz *et al.* 1973; Luizão & Schubart 1987; Cuevas & Medina 1988; Babbar & Ewel 1989; Luizão *et al.* 1996). Potassium is not bound as a structural component in leaves and is highly water soluble (Gosz *et al.* 1973) and hence susceptible to leaching. In the present study, there was a very fast initial loss, with most of the content lost in 30-60 d, and showing slower decreases in the following phases.

Calcium, manganese, and, to a lesser extent, magnesium showed similar patterns of release from decomposing material in the litter bags. Calcium, a structural component of the leaves, is usually retained up to the breakdown of cell walls (Attiwill 1968), and often shows little leaching in decomposing litter (Babbar & Ewel 1989). Magnesium can show a variable behaviour: it can be either easily leached from leaves similar to potassium (Anderson *et al.* 1983; Gosz *et al.* 1973) or be very stable in the material, with a weight loss similar to the mass and calcium losses (Attiwill 1968; Bernhard-Reversat 1972), depending on the composition of the substrate (concentrated in the structures or in the chlorophyll molecules) (Babbar & Ewel 1989). On Maracá Island, Brazil, Luizão *et al.* (1996) found the first pattern, with magnesium showing a continuous and rapid release from leaf litter, a result which agrees with many of the studies on nutrient release which considered it as one of the most mobile elements (e.g. Attiwill 1968; Anderson *et al.* 1983). On Maracá, the release of magnesium was faster than that of calcium. However, in Venezuela, Cuevas & Medina (1988) reported similar release rates for calcium and magnesium. In the present study, calcium, magnesium, and manganese, all showed a pattern of initial accumulation in decomposing leaves, followed by a net decrease phase but slower than the weight loss rates. The release rates of the three elements was slower in the SHF. The slowest release of calcium, magnesium and manganese (in both experiments, A and B) in all three leaf species exposed in SHF may be attributed to two factors: the slow penetration of fine roots and the apparently stronger abiotic control of decomposition in that forest type. Litter decomposition in the SHF appears much more governed by the leaching and physical breakdown of the decomposing material. Calcium, magnesium, manganese, and zinc, more concentrated in the leaf structural parts, are little affected by physical action, and depend

more on decomposers. The slower penetration of fine roots in the litter bags in SHF means that there was a slower physical breakdown of leaves (perhaps one major action of roots in decomposition, either direct or indirect), and consequently less surface area of the leaves was exposed to removal.

Zinc, a minor structural element of the leaves, showed a pattern of release somewhat related to other structural elements such as calcium, magnesium, and manganese: increase in the first phases, when soluble organic compounds and leachable mineral elements were quickly lost, followed by a net release later on. However, the increase lasted longer than for the other three elements, and the release started after 120 d, and even so, at slower rates than for weight losses of decomposing leaves. Thus, an accumulation of zinc may be expected in the old litter and humus in the forest floor, and that was already found in temperate forests in Sweden, where higher concentrations of zinc in the humus than in the litter were found (Laskowsky & Berg 1993).

Boron, for most of the time in the experiments, showed a similar pattern of release to that of potassium, as an element strongly subject to leaching. However, there were periods of the decomposition when, without a plausible explanation, boron was accumulated in the leaves, just to be again quickly released in the next period. There were no good correlations with rainfall events to explain such behaviour.

Increases in iron concentration and mass during litter decay is well doccumented (Gosz *et al.* 1973; Lousier & Parkinson 1978; Staaf 1980; Luizão & Schubart 1987), but it has been seldom recorded for aluminium (Luizão & Schubart 1987; Rustad & Cronan 1988; Rustad 1994). Rustad & Cronan (1988) found indication that aluminium accumulation in decaying litter is primarily an abiotic process in which aluminium is strongly adsorbed onto the litter exchange sites, and that these exchange sites increase during the humification process. Potential sources of aluminium and iron to decaying litter include throughfall and stemflow, inputs of aluminium-rich and iron-rich litter or fungal hyphae, upward diffusion from underlying mineral soils, and inputs of mineral soil (Rustad 1994). Throughfall inputs could account for a large part of the aluminium and iron accumulated in the litter bags during the study, but it is possible that inputs of aluminium-rich and iron-rich litter or fungal hyphae have also contributed as well as the transport (by raindrops or litter animals) of soil particles to the

litter bags, thus adhering to decomposing leaves. Even a small amount of mineral soil contamination to the litter bag could result in a large increase in the aluminium and iron concentrations in the litter, since their concentrations in the mineral soil can be high, as in the LERF plots. In the present study, the accumulation, and very slow release of aluminium and iron observed in the LERF, produced dramatic increases in the mass of these elements, especially aluminium, and may be more related to higher root penetration, since roots are relatively rich in such elements and may be exuding them on decomposing leaves, and probably to the active transport of soil residues by soil and litter animals to the litter bags. These two factors actually have a considerable overlap: root penetration facilitates the litter bag colonization by animals which in turn can transport more soil particles to the litter bags. The result of the accumulation of aluminium and iron in decomposing litter should be increased concentrations of these elements in the humus layers, and that has been recorded in old litter and humus in Brazilian Amazonia (Lucas *et al.* 1993; F.J. Luizão unpublished). In temperate forests, in Sweden, Laskowsky & Berg (1993) found concentrations of iron in the humus 18-fold higher than that in the litter, attributing such high concentrations to the toxicity of iron and other metals to soil microorganisms and invertebrates.

Among the three leaf species, *Clitoria* showed the fastest release of nitrogen, phosphorus, calcium, and magnesium, all important nutrients. The initial concentrations of calcium in this species was much higher than in the other two species, and this accounts in part for the faster release observed. Additionally, *Clitoria* leaves were more rapidly colonized by litter animals and attacked by termites, which may have removed both leaf surface (richer in nitrogen and phosphorus) and structural parts (rich in calcium and magnesium). Aluminium and iron release was very slow, and, in fact, a large accumulation of these elements was observed on *Clitoria* leaves, caused especially by contaminating soil residues. *Pradosia* leaves showed a faster release of aluminium and iron than the other two species, but as the other species had very large accumulations of these elements, this could simply be translated as `having a smaller increase in concentration than the others'. The possible explanation for such smaller increases would be the much higher waxiness of *Pradosia* leaves that prevents the aluminium-rich and iron-rich soil residues adhering to the leaves (especially in the LERF). Additionally the curling of these leaves decreased the surface exposed to both decomposers and soil residues. *Aldina*

leaves showed the fastest release of the micronutrients boron and zinc, and two possible causes can be suggested. Boron was never found increasing concentrations in the experiments, always being released, which suggests a strong influence of leaching. Zinc, partly a structural element of the leaves, is less subject to leaching, and may be more biologically removed from the leaves, especially after 60 d, when mass losses of *Aldina* increased considerably.

In experiment C, testing the differences between sun and shade leaves of *Aldina* and *Pradosia*, the significant differences found in the final concentrations of some mineral elements may not imply a faster or slower release of such elements, since differences in final concentrations match those in the initial concentrations of the same elements, except for iron which had identical initial concentrations in sun and shade leaves of *Aldina*. In fact, both initial and final concentrations of potassium and manganese were higher in sun than in shade leaves of *Pradosia*; phosphorus, calcium and magnesium concentrations were higher in sun leaves of *Aldina* at the begining and at the end of the experiment; and initial and final concentrations of nitrogen, iron, and zinc, were higher in shade than in sun leaves of *Aldina*. Thus, it is not possible to speculate on different rates of release of mineral elements from sun or shade leaves.

The increased concentrations of mineral elements in decomposing leaves in the initial phases of the study were most common in experiment B, started in the dry season, than in experiment A. The reason for these increases would be the reduced leaching which would cause only a slight increase in the concentrations of other constituents, and the soil residues which are looser on the forest floor during the dry season, and more susceptible to be transported to litter bags. Soil contamination of bagged leaves is probably the main responsible for the large increases in the concentrations of aluminium and iron in the decomposing leaves. Soil contamination seems to be linked to litter animals, especially the larger ones such as earthworms, millipedes, and termites, and to root penetration and growth in the litter bags.

Factors influencing nutrient release from decomposing litter

The release (or immobilization) of nitrogen, phosphorus, and calcium were mainly affected by biotic factors (positively, except for root penetration), which means these elements were added to the decomposing leaves by biological activities (fungi colonization, faeces of arthropods, and transport of soil residues). On the other hand, the release of potassium and boron was

positively related to abiotic factors, indicating that leaching was a predominant factor for their release. The fine roots penetrating litter bags were mainly related to the release (or immobilization) of calcium, magnesium, manganese, zinc (positively), and aluminium and iron (negatively). This results suggest that roots were absorbing calcium, magnesium, manganese, and zinc from leaves, and adding aluminium and iron to the decomposing leaves which they penetrated. In fact, the mass of fine roots penetrating litter bags was higher in the LERF, and increased considerably after 60 d in experiments A and B, coinciding with the decrease of calcium in the decomposing leaves. These findings agree with Cuevas & Medina (1983) who reported that the disappearance rates of calcium, which in decomposing leaves is either bound in organic matter or held in crystalline form, were significantly influenced by contact with roots. According to those authors, for all leaf species together, the presence of roots induced similar turnover times for calcium and potassium, both fast. In the absence of roots, however, the release of calcium was much slower than of potassium (Cuevas & Medina 1983). Among the three leaf species studied, they found faster mass losses in two species, and no significant difference in the third one in contact with roots. Therefore, they affirm that their results did not support the hypothesis of Gadgil & Gadgil (1975) which indicate inhibition of litter decomposition by mycorrhizal roots.

However, many times, especially in the THF and in the bags containing *Aldina* or *Pradosia* leaves, the roots growing among decomposing leaves were not actually penetrating the leaves. It may be possible that in the THF the roots were absorbing the nutrient solution on the surface of the leaves or the leaf drops rather penetrating the leaves (Toutain 1987, and personal communication). The leaf drops from white fungal formations are very rich in calcium and other nutrients (Toutain 1987).

Finally, it seems that the slow decomposition rates in the present study, especially in the SHF, may be related to three factors: (i) the reduced penetration of fine roots; (ii) the composition of the heath forest leaves themselves, showing pronounced sclerophylly, with high waxiness and hard texture; (iii) the reduced populations of soil and litter animals, especially of important litter decomposers like termites and earthworms. Additionally, the higher production of secondary products by the SHF trees (and partly by THF trees as well) may influence the palatability of the leaves to decomposers (King & Heath 1965) and consequently the

decomposition rates. In a study conducted in the same areas of the present study, Lisboa (1976a) and Anderson & St. John (1981) found relatively high concentrations of polyphenols in the *Pradosia* leaves as well in leaves of several other species from SHF and THF. Their findings support the hypothesis of Janzen (1974) and Toutain (1987) that a high production of tannins and other phenolics should be expected from trees under stress either from nutrient or water shortage. However, the source of stress for trees, especially in the SHF, can be different, as discussed later (Chapters 7 and 8), which may or may not have a bearing on the above hypothesis.

Possible limiting nutrients for plant growth

The fast release of calcium and magnesium (together with other cations such as manganese, iron and aluminium) in the second half of the experiment B (from 180 d on), when the biological activity is stronger, suggests that these cations could be limiting elements for the microflora and the decomposer animals. Calcium, magnesium and manganese content, all showed a net increase in the first stages of the decomposition (in the dry period), but as soon as the rainy season started (around the time of the 120 d collection) they decreased sharply. That period corresponded to higher root penetration and higher frequency and abundance of litter animals. Significant relationships between fine root penetration and the release of calcium. magnesium and manganese was found in a parallel study (Luizão 1994). She also found that soil microbial biomass and soil respiration responded positively to additions of calcium to the soil. However, the apparent limiting effect of calcium and manganese for soil and litter organisms does not imply these elements are also limiting for plant growth, a subject discussed later (Chapters 7 and 8). Also, an observed loss of nutrients from decomposing litter cannot be simply interpreted as mineralization (Attiwill & Adams 1993).

Virtually all of the studies of nutrient release from decomposing forest litter show that nitrogen is immobilized during the first stages of decomposition (Attiwill & Adams 1993). According to these authors, 'the emphasis on nitrogen immobilization in decomposing litter appears to be intrinsically linked with the hypothesis that forest growth is limited by nitrogen, but if forest growth **is** limited by nutrients, then for much of the tropical forests growing on older, well-

weathered soils, the limiting element is most likely to be phosphorus. However, it can only be speculated as to limiting factors' (Attiwill & Adams 1993).

Chapter 6. LITTER ANIMALS COLONIZING DECOMPOSING LEAVES IN SHF, THF, AND LERF

INTRODUCTION

The decomposition of organic matter has been considered as a synergistic relationship between the invertebrate fauna and the microflora, following an initial period of leaching of soluble nutrients and polyphenols (Petersen & Luxton 1982). Efficient decay is dependent upon a preliminary fragmentation of the organic matter, usually by the fauna or sometimes mainly by abiotic processes, which enables further leaching of soluble minerals by rainwater, and increases the surface area available for exploitation by the microflora (Anderson 1973a, b). There is a sequence of phases of colonization, exploitation, invasion, and post invasion, which occurs in the decomposition of more recalcitrant material such as leaf litter, tree branches, twigs, or stumps (Swift *et al.* 1979). Among the biota, there is a sequence of primary decomposers and then fauna feeding upon them in the rhizosphere and bulk soil regions, and the qualitative and quantitative composition of the decomposer community has much influence on the rates and pathways of litter decomposition (Swift *et al.* 1979). As shown in Chapter 5, the litter quality and moisture are important factors influencing decomposition rates. Thus, they must affect the composition of microbial and faunal populations as well (Witkamp 1966; Howard & Howard 1980). The soil on which the litter decomposes may also influence the process, for example by acting as a reservoir of microrganisms which can colonize the litter (Howard & Howard 1980). Among the soil and litter invertebrates which colonize decomposing leaves, Acari (mites) and Collembola (springtails) are generally the most abundant groups (Wallwork 1976; Levings & Windsor 1982; Petersen & Luxton 1982; Vannier 1987), which has been confirmed by studies in central Amazonia (Beck 1971; Adis 1988; Adis *et al.* 1989). Acari and Collembola generally are non-specific feeders (Anderson 1975; Wallwork 1976; Vannier 1987), but species of both the Oribatid mites and Collembola can be primarily fungivorous, feeding on organic debris and associated fungi. Larger Oribatid mites are capable of fragmenting and comminuting litter (Seastedt 1984) and may play an important role in processing recalcitrant litter, while smaller species feed more selectively on fungi. Collembola generally have small populations in tropical forests, but when a thick

organic topsoil is present, densities can be much higher (Goffinet 1975). Unfortunately few investigations of the soil fauna associated with decomposing leaf litter have been carried out. Thus, the useful information on the microhabitat development and successional changes in soil organism communities during the breakdown and decomposition of organic materials in the soil, which could provide insights towards the understanding of such processes, is still fragmented and insufficient (Swift & Anderson 1989; Blair *et al.* 1992). One reason for the few studies of this kind is the complexity of the processes involved, and one major problem is to maintain the identity of the experimental material without altering the litter and the soil environment. The use of litter bags partially overcomes this difficulty (Crossley & Hoglund 1962) and despite several drawbacks, including the altered within-bag microenvironment (Lousier & Parkinson 1976; St John 1980), it provides comparative data and remains a widely used technique.

The aim of the present study, using litter bags, was to investigate the influence of the leaf species, and the forest type on the colonization of distinct substrates by the litter and soil invertebrates, and to assess the main factors controlling the colonization of the litter bags in SHF, THF, and LERF. Additionally, an attempt was made to assess the main groups of litter animals involved in the decomposition and nutrient release in each forest type. Henceforth the mixture of soil and litter invertebrates colonizing the litter bags will be referred to as 'litter animals'.

MATERIAL AND METHODS

The litter animals were extracted from samples of the experiment A (Chapter 5) which was started in the wet season. Briefly, litter bags measuring 20 cm x 24 cm in size and made with 1.5-mm nylon mesh, had been filled with about 5.5 g (air-dried weight) of freshly fallen leaves and exposed on the forest floor. Several 9-mm diameter holes were punched through the bags (near the edges) to permit the entry of larger invertebrates. A total of 648 litter bags were placed in the field on 30 December 1991, at the onset of the rainy season, and retrieved after 30, 60, 120, 180, 270 and 360 d. At each retrieval four litter bags of each leaf species, selected at random, were removed from each plot (one from each of the quadrants). A Berlese-Tullgren apparatus (Macfadyen 1961; Edwards & Fletcher 1971) was used for extracting the litter

animals from three of the four samples from each study plot. (All four could not be extracted because of a shortage of funnels). In the Berlese-Tullgren funnel apparatus (Macfadyen 1963), an electric lamp bulb (25 W) positioned 20 cm above the samples was used as a heat source over 4-5 d to drive the animals into a collecting jar with dilute (1%) formaldehyde solution. After extraction, the animals were stored in 70% ethanol, identified to broad taxonomic groups (Wallwork 1976), and counted. Climatic data for the study period are given in Fig 2.3 and 2.4. In addition to the calculations described in Chapter 5, total rainfall, and the moisture of the organic and upper mineral soil layer in shorter periods preceding each retrieval were calculated, since they could directly affect the presence of litter animals in the bags. Thus, rainfall for 3 d, 7 d, 14 d, and 21 d before bag retrieval, and the moisture of the organic and upper mineral soil layers for the 7 d, 14 d, and 21 d intervals before retrieval, were each calculated.

This experiment was also shared with R.C.C. Luizao (1994), who used the *Clitoria* bags (one third of the experiment) to evaluate the effects of fine root penetration in the bags on animal colonization of that species.

Data analysis

The frequency of each litter animal group was expressed simply as the percentage of retrieved bags in which they occurred. The density of each group was calculated for each retrieval time as the mean number of individuals per litter bag. The oven dry biomass of each group was estimated by multiplying the mean density by the typical published values for each group (Petersen & Luxton 1982). The densities of litter animals in the bags were tested for differences among forest types, leaf species, and over time using appropriate analysis of variance models. Regressions were used to determine the possible controls on the density of the litter animals and related activities, and correlations between the most frequent litter animal groups were calculated. The factors used in the regressions were the remaining mass of decomposing leaves, the concentrations of mineral elements in the decomposing leaves, the dry weight of fine roots penetrating the litter bags, the moisture of the organic and upper mineral soil layer, and several rainfall-related climatic factors (the total rainfall and evaporation in the period preceding the collection, percentage of rainy days, daily rainfall and

evaporation, and the short-term values of rainfall and soil and litter moisture). Correlations and regressions were also calculated between the densities of litter animal groups and both the concentrations and the contents of the mineral elements in the residual leafy material in the litter bags. The data were transformed either using $\log_e$ (for the dry weights of leaves and roots in the litter bags, and for the concentrations and contents of mineral elements), or arcsine (on the percent dry weight of remaining leaves), or square-root (on the densities of litter animals) transformations (Zar 1984) before running the analyses.

RESULTS

Rainfall, litter and soil moisture during the experiment

The total rainfall, and moisture of litter and soil for shorter periods prior to each retrieval are shown in Fig. 6.1 and Table 6.1, while the climatic data for each sampling interval were shown in the previous chapters (Fig. 2.3 and 5.1). The retrieval made at 60 d corresponded to the wettest period of the study, while the 180 d sampling was at the driest period (Fig. 6.1 and Table 6.1). The last week prior to the retrievals of 30 d, 120 d, and 270 d had low rainfall, but if the two weeks prior to these samplings are combined, there was much rainfall, except in the 14 d before the 180 d retrieval (Fig. 6.1). Overall, the litter bags retrieved from the SHF were drier than in the other two forest types.

Litter animals colonizing decomposing leaves

Frequency

A total of forty-one taxonomic groups of litter animals were found colonizing the decomposing leaves in the litter bags (Table 6.2 and Appendix 6.1). The five groups most frequently recorded were: Acari (95.5 % of the litter bags extracted), Collembola (76.9 %), Pseudoscorpionida (34.1 %), Formicidae (33.4 %), and Diptera larvae (30 %). Five other groups (in order of decreasing frequency: Copepoda, Psocoptera, Diplopoda, Araneae, and Homoptera juveniles) were each one found in more than 20 % of the bags, while nine other

groups were present in more than 5.8 % (Table 6.2). In Table 6.2, 'other' groups include Chilopoda, Diptera adults, Enchytraeidae, Hemiptera and Lepidoptera juveniles, and the fifteen further groups listed in Appendix 6.1. A general trend LERF > THF > SHF was observed for the percentage of litter bags colonized by the major litter animal groups, but this trend was reversed for Psocoptera, and did not apply for Isopoda, Isoptera, Protura, Pauropoda, and Symphyla (Table 6.2). Some groups such as Araneae, Collembola, Coleoptera adults and larvae, Copepoda, Diptera larvae, earthworms, Phalangida, Protura, and Thysanoptera, were much more frequent in LERF than in SHF and THF.

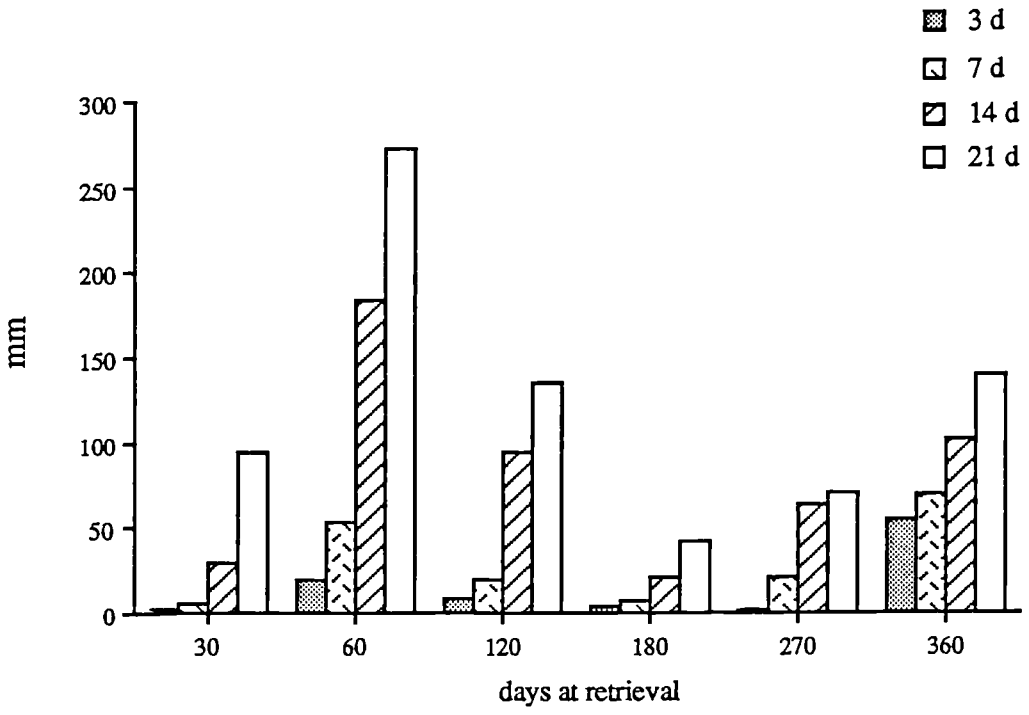


Fig. 6.1: Rainfall (mm) in short intervals (3 d; 7 d; 14 d; and 21 d) prior to each of the six collections of litter bags.

Table 6.1: Moisture (%) of the organic layer and upper mineral soil layers 7 d, 14 d, and 21 d before litter bag collection (n = 3).

		Organic layer			Upper mineral soil		
		7 d	**14 d**	**21 d**	**7 d**	**14 d**	**21 d**
SHF	30 d	48.4	45.4	40.5	11.1	11.8	10.6
	60 d	48.1	48.4	46.3	9.78	15.3	14.9
	120 d	54.1	50.0	51.5	9.72	10.0	12.3
	180 d	26.4	29.0	34.2	4.58	4.66	5.42
	270 d	43.5	43.7	41.3	4.55	4.64	3.68
	360 d	48.5	45.3	45.3	6.19	10.2	8.67
THF	30 d	58.9	60.5	58.6	22.4	25.6	28.9
	60 d	67.9	65.8	62.5	28.7	26.4	27.8
	120 d	62.4	61.6	63.1	25.1	24.7	26.5
	180 d	44.8	45.7	50.5	10.1	8.85	8.31
	270 d	53.8	54.3	52.7	8.26	7.86	6.51
	360 d	64.5	60.8	60.5	7.38	14.5	12.4
LERF	30 d	68.8	64.0	63.7	27.6	21.0	18.2
	60 d	61.9	62.2	63.2	15.1	16.6	16.9
	120 d	64.6	62.1	65.2	16.4	14.9	15.2
	180 d	49.9	51.9	55.0	8.37	8.80	9.83
	270 d	55.7	56.3	56.1	10.5	10.5	9.64
	360 d	57.5	57.0	56.9	12.6	17.1	15.4

Table 6.2: The frequency (%) of animal groups for all litter bags retrieved in each forest type. The ranking of the groups in each forest type is given in parentheses and the groups are ordered in the ranking of their means for all forest types combined.

	SHF	THF	LERF	Mean	Ranking
Acari	88.4 (1)	97.4 (1)	100 (1)	95.5	(1)
Collembola	62.6 (2)	74.7 (2)	92.0 (2)	76.9	(2)
Pseudoscorpionida	19.1 (5)	29.9 (4)	51.5 (3)	34.1	(3)
Formicidae	27.9 (4)	30.5 (3)	41.1 (6)	33.4	(4)
Diptera larvae	15.0 (7)	22.1 (9)	50.9 (4)	30.0	(5)
Copepoda	14.3 (8)	24.7 (8)	44.2 (5)	28.2	(6)
Psocoptera	31.3 (3)	29.1 (5)	19.6 (13)	26.5	(7)
Diplopoda	18.4 (6)	27.3 (6)	30.7 (9)	25.7	(8)
Araneae	10.9 (11)	21.4 (10)	38.7 (4)	24.1	(9)
Homoptera juveniles	6.80 (13)	25.3 (7)	35.6 (8)	23.1	(10)
Thysanoptera	13.6 (10)	14.3 (12)	23.9 (11)	17.5	(11)
Coleoptera adults	6.12 (14)	14.3 (13)	29.5 (10)	17.0	(12)
Isopoda	13.6 (9)	17.5 (11)	16.0 (16)	15.7	(13)
Coleoptera larvae	7.50 (12)	8.44 (16)	22.1 (12)	12.9	(14)
Diplura	2.72 (19)	13.6 (14)	19.6 (14)	12.3	(15)
Phalangida	3.40 (18)	4.55 (18)	16.6 (15)	8.41	(16)
Protura	6.12 (15)	2.60 (19)	15.3 (17)	8.19	(17)
Pauropoda	4.76 (16)	11.7 (15)	6.13 (18)	7.54	(18)
Symphyla	4.76 (17)	6.49 (17)	6.13 (19)	5.82	(19)
Earthworms	0.68 (21)	1.30 (21)	4.91 (20)	2.37	(20)
Isoptera	2.04 (20)	1.95 (20)	1.83 (21)	1.94	(21)
Other 20 minor groups	17.0	32.5	43.6	36.0	

Density

Some animal groups showed big changes in their rankings for density compared with those for frequency. For instance, Copepoda, which ranked sixth in frequency, were more abundant than Formicidae, Pseudoscorpionida, and Diptera larvae, in the bags with *Pradosia* and *Aldina* in the LERF (Table 6.3). The percentage of Collembola in the SHF was higher than in the THF and LERF, but the opposite occurred for Acari (Table 6.3). The percentage of Formicidae was higher in SHF than in THF and much higher than in LERF, except for *Pradosia* bags, which had more Formicidae in LERF. Copepoda had a greater share of the total in *Aldina* and *Pradosia* than in *Clitoria* leaves, especially in the LERF (Table 6.3). The animal density in each litter bag is given in the Appendix 6.2, and the total density of the 'other' groups (found less frequently) in each litter bag in Appendix 6.1. Both the total litter animal densities and the number of taxonomic groups found in the litter bags were ranked: LERF > THF> SHF (Table 6.3; Fig. 6.2; Appendix 6.2). Thedifferences between forest types were generally consistent for all six retrievals spanning both wet and dry seasons (Fig. 6.2). The Diplura and Protura differed among forest types (nested ANOVA; Diplura: $F = 11.1$; $df = 2$; $p < 0.001$ among forest types, and $F = 1.06$; $df = 6$; $p < 0.05$ among plots nested into forest types; Protura: $F = 10.7$; $df = 2$; $p < 0.001$ among forest types, and $F = 1.57$; $df = 6$; $p < 0.05$ among plots nested into forest types). Only Coleoptera larvae and Protura had a slightly higher density in SHF than in THF; all other groups had slightly lower densities in the SHF. Higher densities in LERF than in SHF (but not significantly higher than in THF) were recorded for Homoptera juveniles ($p< 0.01$). No significant differences between the three forest types were found for Araneae, Collembola, Diplopoda, Formicidae, Isopoda, Isoptera, Pauropoda, Psocoptera, Symphyla and Thysanoptera. Earthworms were seldom found in the litter bags. Acari and Collembola together were more than 80 % of the total number of litter animals in the bags of all leaf species (Fig. 6.2), but some variations were observed among the three forest types. In the SHF, Acari were 69 % of the total, and Collembola 17-20%; in the THF, Acari were 76-79 % and Collembola 10-12.5 %; and in the LERF, Acari were 76-78 % and Collembola 7-11 %. Acari and Collembola were generally strongly correlated (Appendix 6.3).

Table 6.3: Mean density of litter animals per litter bag in each leaf species and forest type (n=18). The mean of the three forest types for each leaf species is also shown. Values are the means for all six retrieval times (from 30 d to 360 d). Different letters following the mean values indicate significant differences (Tukey's test; $p < 0.05$) among forest types for each leaf species.

	Clitoria				*Pradosia*				*Aldina*			
	SHF	THF	LERF	mean	SHF	THF	LERF	mean	SHF	THF	LERF	mean
Acari	43.4a	83.4b	170c	98.9	28.4a	42.8b	77.3c	49.5	44.1a	68.9b	82.4b	65.0
Collembola	12.3a	12.0a	24.4b	16.2	7.33a	5.64a	6.96a	6.64	12.6a	11.3a	9.38a	11.1
Pseudoscorpionida	0.45a	0.71b	1.30c	0.82	0.25a	0.36ab	0.44b	0.35	0.36a	0.28a	0.73b	0.46
Formicidae	2.69a	3.73a	4.89a	3.77	1.43a	1.42a	4.06b	2.30	2.96a	3.02a	1.51b	2.50
Diptera larvae	0.37a	0.29a	1.02b	1.68	0.12a	0.23b	0.93c	0.43	0.21a	0.40b	0.78c	0.46
Copepoda	0.49a	0.84a	2.69b	1.34	1.20a	1.28a	5.44b	2.64	1.30a	1.50a	5.05b	2.62
Psocoptera	0.47a	0.35b	0.20c	0.34	0.57a	0.91b	0.26c	0.58	0.36a	0.48b	0.42b	0.42
Diplopoda	0.39a	0.98b	0.72b	0.70	0.25a	0.13b	0.32a	0.23	0.32a	1.66b	0.73c	0.90
Isopoda	0.18a	0.59b	0.48b	0.42	0.31a	0.17b	0.13b	0.20	0.19a	0.18a	0.15a	0.17
Others	1.92a	6.95b	15.8c	8.22	1.50a	1.64a	3.72b	2.29	1.23a	2.34b	5.49c	3.02
Total	62.7a	110b	221c	131.2	41.4a	54.6a	99.5b	65.2	63.7a	90.1b	107c	86.9

Comparing the different leaf species, the densities of litter animals were usually ranked: *Clitoria* > *Aldina* > *Pradosia* (Table 6.3; Appendix 6.2 a-i). The densities were significantly higher in *Clitoria* than in both *Aldina* and *Pradosia* leaves for the number of taxonomic groups, the total number of litter animals, Collembola, Diplura, Pseudoscorpionida, 'others' (nested ANOVA; df = 2; all $p < 0.001$); Acari, Homoptera juveniles, Pauropoda, Protura ($p < 0.01$); Coleoptera larvae, Isopoda, and Symphyla ($p< 0.05$). In general, the litter animal density was slightly higher in *Aldina* than in *Pradosia* leaves for most of the groups, but this difference was significant ($p< 0.001$) only for Collembola. Of the twenty-one major groups of litter animals, the following showed no significant differences in their densities among the three leaf species: Araneae, Coleoptera adults, Copepoda, Diplopoda, Diptera larvae, earthworms, Formicidae, Isoptera, Phalangida, Psocoptera and Thysanoptera.

Factors affecting litter animal densities in the litter bags

All the main factors: the forest type, the time of retrieval, and the leaf species, showed significant effects on most of the litter animals in the bags. However, multiple regression analyses ($df = 53$; $p < 0.05$) showed no direct relationship between the residual dry weight of leaves and either the number of taxonomic groups, or the total of litter animals, or the densities of the most abundant groups of litter animals. The number of taxonomic groups, the density of the two most abundant groups, Acari and Collembola, and the total density of litter animals in the bags seem to be related to the mean moisture of the organic and upper mineral soil layers in the two weeks before each collection (Fig. 6.1 and 6.2; Tables 6.1 and 6.4). The 180-d retrieval corresponded to the driest period of the study, with very low rainfall in the two weeks prior to collection, but the two last retrievals (even the 270 d collection, still during the dry season) were both made after two weeks with higher rainfall and moisture of the organic layer (Fig. 6.1; Table 6.1). The total litter animals were related especially to the moisture of the organic layer, the mean daily rainfall and evaporation ($r^2 = 10.8$ %; $df = 53$; $p < 0.001$) but some important variations were found

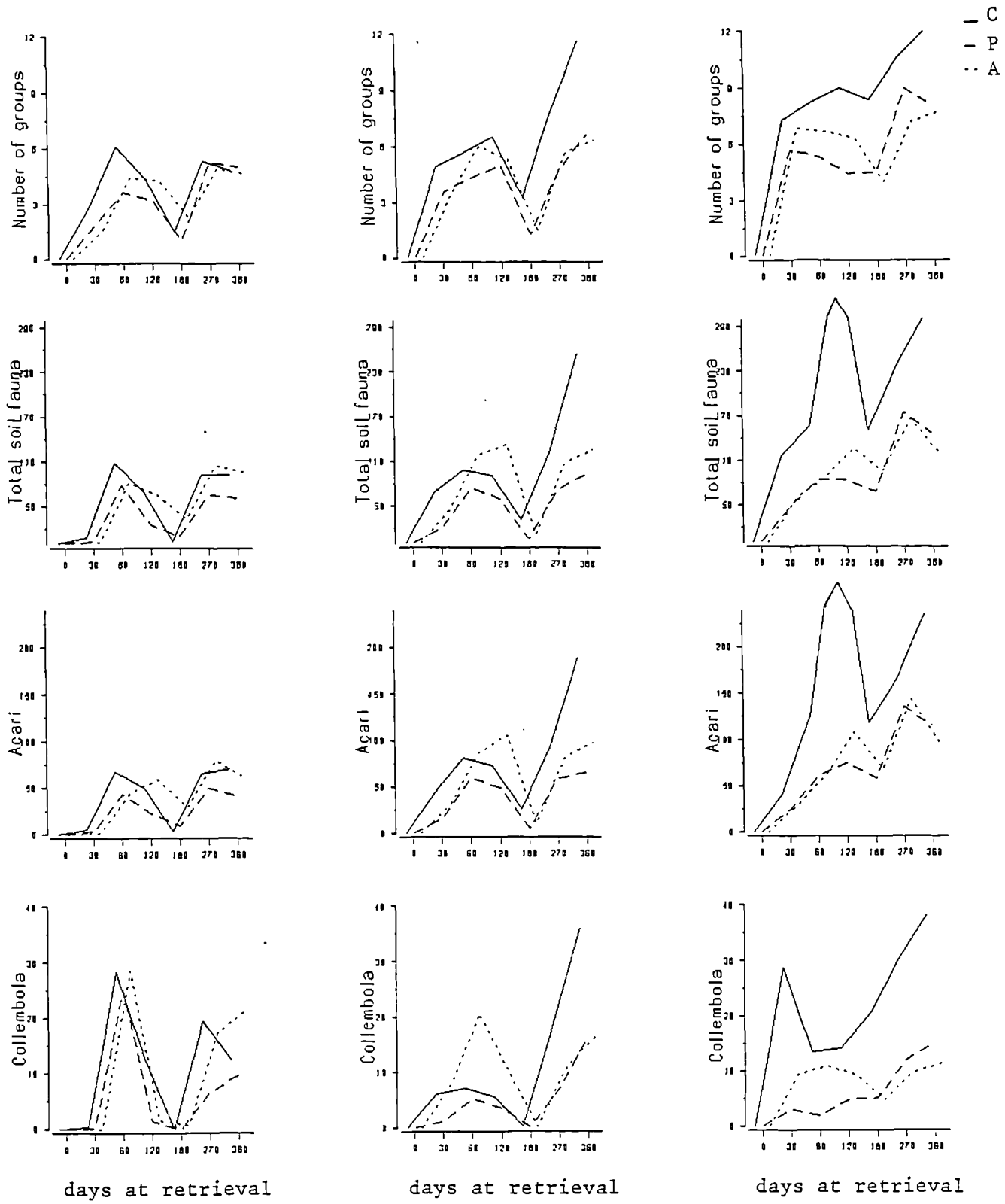


Fig. 6.2: Mean number of taxonomic groups, total litter animals, and individuals of the taxonomic groups per litter bag of each leaf species in the three forest types. Values are generally the means of nine bags (n = 9). C = *Clitoria*; P = *Pradosia*; A = *Aldina*.

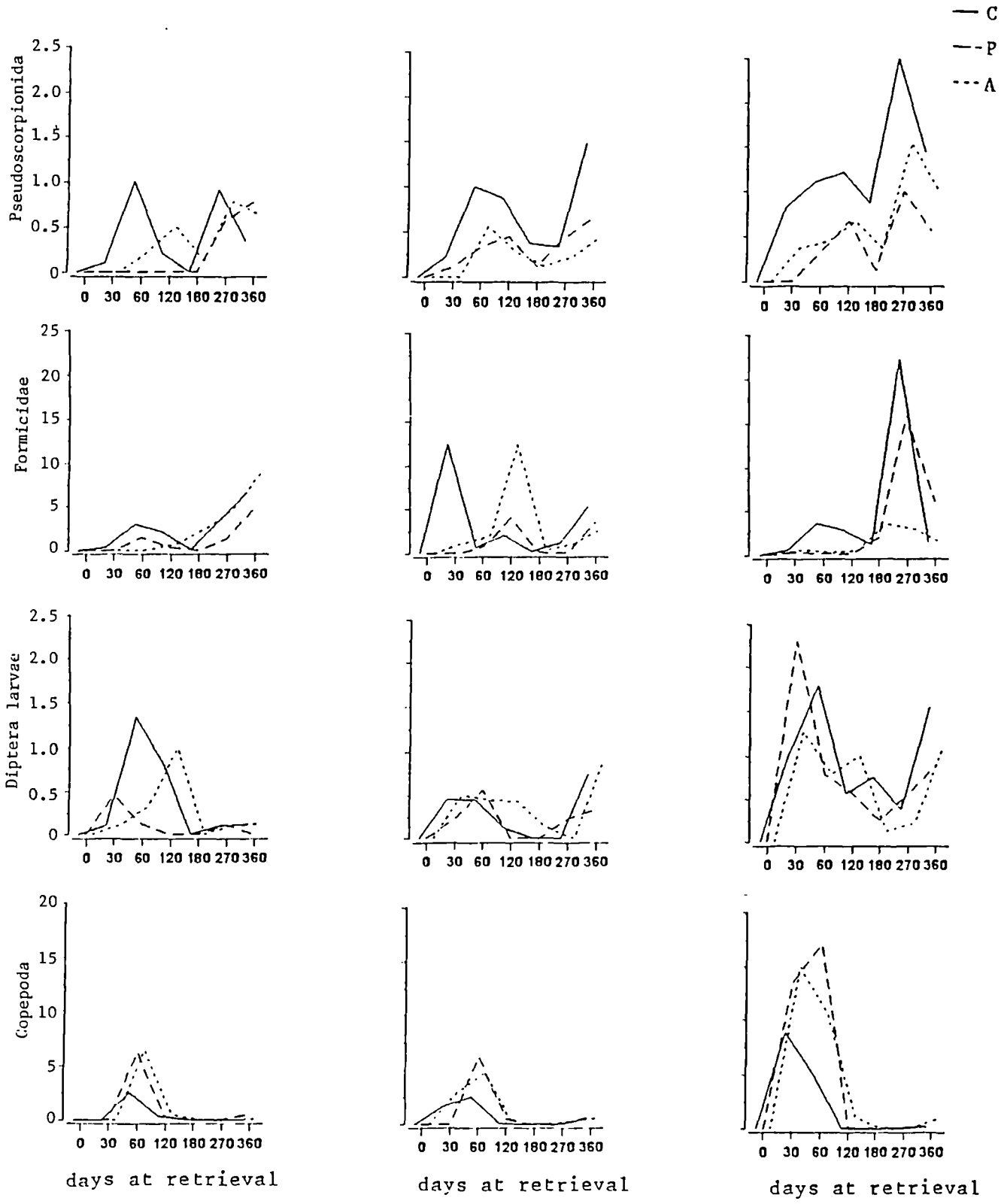

C
P
A
Pseudoscorpionida
Formicidae
Diptera larvae
Copepoda
0 30 60 120 180 270 360
days at retrieval

Fig.6.2: (cont.)

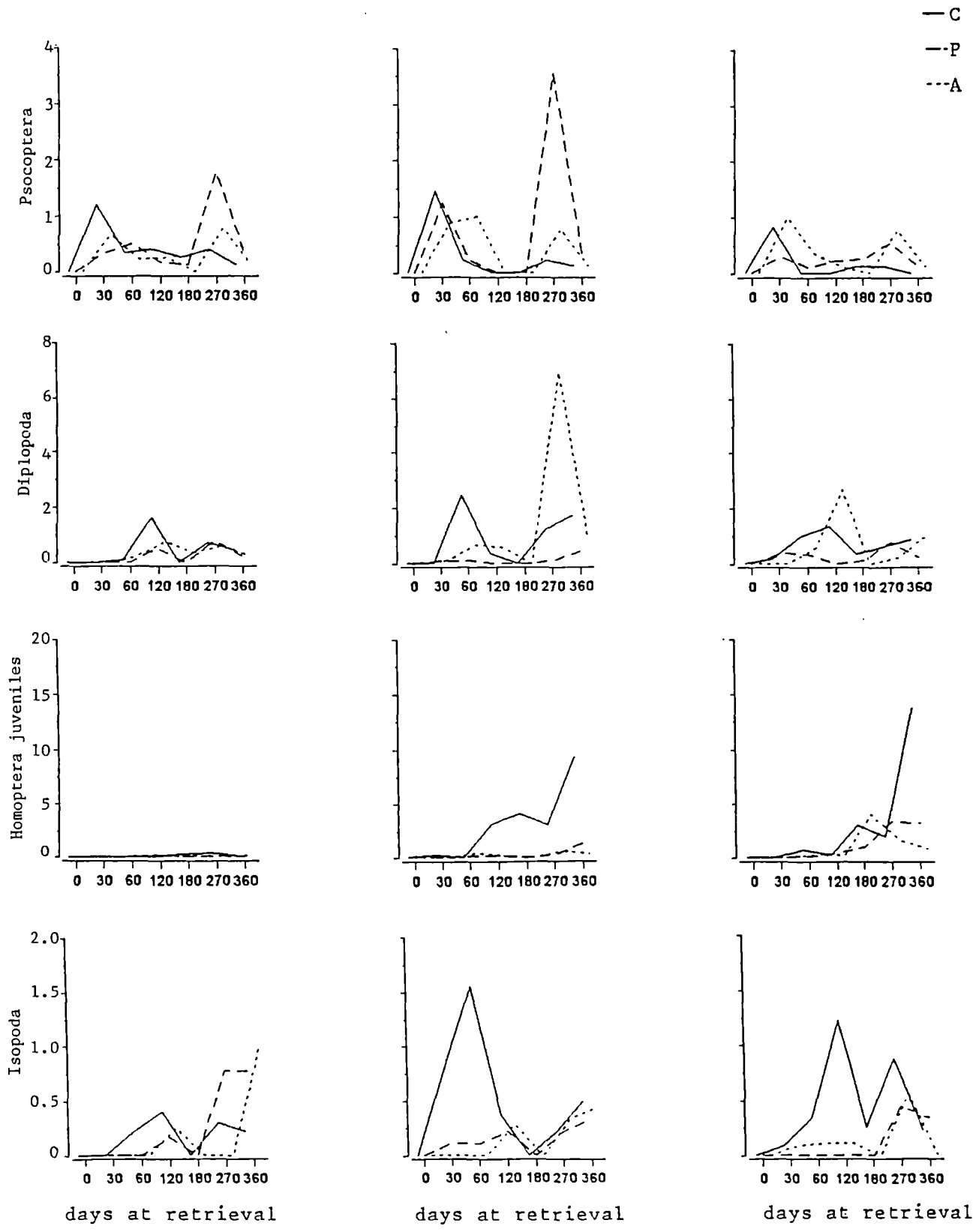

—C
—-P
---A
Psocoptera
Diplopoda
Homoptera juveniles
Isopoda
0 30 60 120 180 270 360
days at retrieval

Fig. 6. 2. (cont.)

between the three forest types. In the SHF, the total litter animals were more strongly related to the percentage of rainy days in the period before collection and the mean daily rainfall ($p < 0.001$), which explained 35.6 % of the variation in the values. In the THF, the percentage of rainy days, together with the rainfall and the mean daily evaporation, explained 24.7 % of the variation. In the LERF, however, the relation was weakly significant ($p < 0.05$), and showed no relationship with rainfall events or with soil moisture, and explained only 5 % of the variation. For each individual animal group, the most outstanding factor influencing densities overall seemed to be the moisture of the organic layer, followed by the mean daily evaporation and the mean daily rainfall (Tab. 6.4). However, Isopoda were mainly related to the moisture of mineral soil ($p < 0.001$), while some other groups, such as Araneae, Coleoptera larvae, Formicidae and Isoptera, showed no relation with the climatic factors analysed. Some significant correlations were found between the litter animal densities and both the residual mass of decomposing litter and the mass of fine roots penetrating the litter bags. The total density of litter animals was negatively correlated with the residual mass in the SHF ($r = -0.45$; $n = 147$) and in the THF ($r = -0.48$; $n = 154$), but less strongly in the LERF ($r = -0.25$; $n = 163$). It was also correlated (positively) with fine root mass, especially in the THF ($r = 0.58$; $n = 154$). Among the various groups compared, the highest correlations were found between Thysanoptera and Diplopoda ($r = 0.93$; $n = 154$), between Protura and earthworms ($r = 0.70$; $n = 154$), and between Acari and Collembola ($r = 0.67$; $n = 154$) in the THF, and between Formicidae and Pauropoda in the LERF ($r = 0.71$; $n = 163$).

Biomass of litter animals colonizing the litter bags

Diplopoda were ranked first for biomass, and Formicidae second, while the most abundant litter animal group, Acari, was placed in an intermediate position, and the second most abundant, Collembola, had a low biomass (Table 6.4). Earthworms, despite their low frequency, were ranked fourth in litter animal biomass in the LERF at the last retrieval.

Table 6.4: Estimated biomass (mg) per litter bag of some litter animal groups, using mean individual oven-dry weights given by Petersen & Luxton (1982). Values in parenthesis are the mean individual weights used for calculations.

	SHF	THF	LERF	Mean
Acari (0.0043)	0.17	0.28	0.47	0.31
Collembola (0.0027)	0.03	0.03	0.03	0.03
Formicidae (0.5)	1.18	1.35	1.74	1.43
Diptera larvae (0.7)	0.17	0.22	0.64	0.35
Diplopoda (14)	4.49	12.7	8.25	8.53
Araneae (0.8)	0.21	0.39	2.13	0.94
Coleoptera adults (0.9)	0.08	0.12	0.42	0.21
Isoptera (0.6)	0.01	0.14	0.41	0.28
Earthworms (17)	0.11	0.22	1.25	0.55

Succession of litter animals on decomposing leaves

Overall, the fastest and most diverse colonization of the litter bags was in the LERF, and the slowest and least diverse in SHF (Fig. 6.2). In the SHF, the colonization by litter animals was small in the first (30 d) dry period before the first retrieval, but a peak in the numbers of taxonomic groups and of the total fauna was recorded at 60 d, in the following rainy period (Fig. 6.2). This was followed by a decrease in the numbers of taxonomic groups and of the total of litter animals in the SHF, but in the THF and especially in the LERF they both continued to increase up to the third collection (120 d). In all forest types and leaf species, a sharp decrease of the numbers of groups and total fauna was observed at the fourth collection (180 d) which represented the driest period of the study (Fig. 6.1 and 6.2). However, the decrease was least in the LERF, and greatest in the SHF (Fig. 6.2). After the relatively dry period of about 80 d (covering the period between 160 and 240 d of the experiment), an increase in numbers of groups and total fauna was observed in the last two collections. The same pattern just described for the number of taxonomic groups and of the total fauna was also found for the two most abundant groups of litter animals,

the Acari and Collembola, as well as for Pseudoscorpionida (Fig. 6.2). The third most abundant group in the litter bags, Formicidae, showed no clear pattern of colonization. However, some other major groups of litter animals such as Copepoda, Homoptera juveniles and Psocoptera, showed clear temporal trends (Fig. 6.2). The number of taxonomic groups colonizing the litter bags as well as the densities of Acari and the total fauna were significantly lower ($p < 0.001$), especially in the SHF and THF, at the 30 d collection, and after 180 d, the driest period of the study (Fig. 6.2), when the litter bags were retrieved following a week with only 7.1 mm of rainfall (41.7 mm in the 21 d preceding retrieval). The general trend, excepting the 180 d collection, was an increase with time, producing the highest numbers of groups, density of Acari, and density of the total fauna after 240 d, despite the considerable weight loss of the decomposing leaves. Collembola had densities significantly higher (nested ANOVA; $F = 10.8$; $df = 5$; $p < 0.001$) in the second (60 d) and the two last (270 d and 360 d) periods of the study. Several other groups had significantly higher densities in the two last periods: Pseudoscorpionida ($F = 9.31$; $p < 0.001$), especially in the LERF; Diplura ($F = 5.42$; $p < 0.01$), Diptera larvae ($F = 4.92$; $p < 0.01$), and Symphyla ($F+ 5.03$; $p < 0.01$), especially in the THF and LERF; and Isopoda ($F = 2.03$; $p < 0.05$), especially in the THF and in LERF. Formicidae ($F = 4.11$; $p < 0.01$) and Pauropoda ($F = 4.52$; $p < 0.01$) showed higher densities in the two last retrievals, but only in the LERF. Coleoptera adults ($F = 5.12$; $p < 0.01$) and Homoptera juveniles ($F = 5.62$; $p < 0.01$) were found in their highest density only in the last collection of the study, but Homoptera juveniles had no significantly higher density in the SHF. Higher density after 360 d was recorded for earthworms in the LERF. Protura showed higher densities in the THF and LERF ($F = 4.02$; $p < 0.01$) in the last three retrievals, while Psocoptera had two major peaks, with significantly higher densities ($F = 7.84$; $p < 0.001$) in the first (60 d) and in the fifth (270 d) collections in all three forest types. Phalangida presented no defined pattern of colonization, despite a non-significant trend for higher densities in the later stages of decomposition (the general trend followed by most of the litter animal groups). Noticeable exceptions to that trend were Copepoda and Isoptera. Copepoda were significantly more abundant ($F = 11.7$; $p < 0.001$) in the two initial retrievals (at 30 d and 60 d), while Isoptera were more abundant

in the litter bags at the 180d collection, in the driest period of the year, and more abundant in the more open and dry forest type, the SHF.

Relationships between litter animals, mass loss, and nutrient release rates

Among the twenty-one major litter animal groups, nine which were more abundant or had a high biomass were used for additional analyses. Except for nitrogen and phosphorus, and partly for calcium, the mass and the mineral element contents remaining after each retrieval, and the densities of litter animals in the bags, were strongly correlated (Appendix 6.3). The concentrations and the contents of copper were generally either weakly or not correlated to the large majority of the litter animal groups, and were not included in further analyses. The correlations were negative with the remaining mass and all mineral elements but iron and aluminium, which showed positive and generally stronger correlations with the densities of animals in the bags (Appendix 6.3). Alone among the litter animal groups, the Copepoda showed a strong positive correlation with mass and mineral elements. Acari, Collembola, Copepoda, Diplopoda, Diplura, earthworms, Isopoda, Protura, and Pseudoscorpionida, were the groups of litter animals more significantly related to the remaining mass and mineral element contents or concentrations (Appendices 6.4 and 6.5). Mass losses of *Pradosia* and *Aldina* in the SHF were directly related to the abundance of Copepoda and to the total of litter animals in the bags; in the THF, the mass loss of *Clitoria* was mainly related to the Symphyla; and in the LERF, mass losses of *Clitoria* were related to several groups, especially the Copepoda and Acari; mass losses of *Pradosia* were mostly related to the Copepoda and Diptera larvae; and the mass losses of *Aldina* were mainly related to the Protura densiaties (Table 6.5). In all three forest types, the Copepoda were inversely related to mass losses. In the SHF, the Collembola, Copepoda, and Symphyla were the groups more strongly related to the mineral element concentrations in the remaining material (Table 6.7). Diplopoda and Isopoda were only related to the concentrations of aluminium and iron in the *Pradosia* leaves, and to manganese in *Aldina*. In the THF, the Collembola, Copepoda, and Symphyla were also the groups most often related to the mineral element concentrations in all three leaf species, while the total litter animals were especially related to the mass

losses of *Pradosia* (Table 6.5). The Acari, Collembola and Copepoda were related to most of the mineral elements, especially on Clitoria leaves, where earthworms also showed a good relationship with mass loss and concentrations of calcium, boron, and iron. Some noticeable differences were found among the three leaf species used in the study. In the bags containing *Clitoria* leaves, mass loss was mostly related to Collembola, Copepoda, and earthworms. In the bags with either *Pradosia* or *Aldina*, mass losses were related to the Acari, Copepoda, Protura, and Pseudoscorpionida (Appendix 6.4). The mineral elements of the *Clitoria* leaves were more related to the Copepoda (six elements), Collembola and Diplura (four elements each), and Acari and Diplopoda (three elements each). In the bags with *Pradosia* leaves, they were more related to the Acari (six elements), Copepoda (five elements), earthworms (four elements), Isopoda (three elements), and Protura (two elements). In the *Aldina* leaves, mineral elements were mainly related to the Protura (six elements), Acari, Copepoda, and earthworms (five elements each), Collembola (four elements), and Diplura (two elements). The Copepoda were always positively related to either the mass or mineral element concentrations (except for iron and aluminium) of the remaining leafy material in the litter bags (Appendix 6.4).

Table 6.5: Regression analyses between the densities of the litter animals and the remaining mass and concentrations of mineral elements in the litter bags for each forest type and leaf species. Levels of significance for each group were: * $p < 0.05$; ** $p < 0.01$; and *** $p < 0.001$

SHF	r^2	df	p	Groups significantly related to mass or mineral elements
Clitoria				
Fe	73.4	17	< 0.05	Homoptera juveniles*
Zn	86.3	17	< 0.01	Collembola* Diptera larvae* Homoptera juveniles* Protura*
Pradosia				
mass	60.3	17	< 0.05	Copepoda*
P	72.3	.17	< 0.05	Collembola* Acari* Earthworms* Isopoda* Symphyla*
K	63.9	17	< 0.05	Copepoda** Total*
Fe	89.0	17	< 0.001	Isopoda*** Symphyla*** Diplura** Earthworms** Acari* Collembola* Diplopoda*
Al	87.9	17	< 0.01	Earthworms*** Isopoda*** Symphyla*** Diplopoda** Diplura*
Aldina				
mass	75.1	17	< 0.01	Copepoda* Total*
N	83.5	17	< 0.01	Acari*** Total*
Mn	71	17	< 0.05	Pseudoscorpionida** Isopoda*
Zn	72.1	17	< 0.05	Collembola*

THF	r^2	df	p	Groups significantly related to mass or mineral elements
Clitoria				
mass	63.6	17	< 0.05	Symphyla*
N	65.7	17	< 0.05	Symphyla*
P	70.8	17	< 0.05	Earthworms** Symphyla*
K	67.3	17	< 0.05	Total** Copepoda*
Ca	66.3	17	< 0.05	Total* Diplura*
Al	71.9	17	< 0.05	Pseudoscorpionida* Symphyla*
Mn	78 8	17	< 0.01	Acari* Diplura*
Pradosia				
N	58.5	17	< 0.05	Total*
Ca	59.4	17	< 0.05	Total** Collembola* Copepoda* Homoptera juveniles*
Mg	61.9	17	< 0.05	Total** Copepoda** Collembola*
Zn	74.3	17	< 0.01	Copepoda**
Al	59.7	17	< 0.05	Total** Collembola* Copepoda*
Aldina				
Mg	62.5	17	< 0 05	Symphyla*
Al	62.7	17	< 0.05	Symphyla** Protura*
Fe	70.2	17	< 0.05	Protura** Diplopoda* Isopoda* Symphyla*
Mn	64 2	17	< 0.05	Symphyla*

(cont.)

(cont.)

LERF	r^2	df	p	Groups significantly related to mass or mineral elements
Clitoria				
mass	85.1	17	< 0.01	Copepoda*** Acari** Collembola* Diptera larvae* Earthworms* Homoptera juveniles*
N	79.6	17	< 0.01	Copepoda** Homoptera juveniles** Collembola* Diptera larvae*
P	66.0	17	< 0.05	Copepoda**
K	72.2	17	< 0.05	Copepoda*** Acari* Collembola*
Mg	84.1	17	< 0.01	Copepoda*** Acari** Collembola** Diptera larvae*
Al	64.3	17	< 0.05	Acari* Copepoda* Homoptera juveniles*
B	62.2	17	< 0.05	Collembola** Earthworms*
Fe	69.6	17	< 0.05	Earthworms* Homoptera juveniles*
Pradosia				
mass	73.5	17	< 0.05	Copepoda* Diptera larvae*
N	83.1	17	< 0.05	Collembola* Symphyla*
K	69.2	17	< 0.05	Copepoda* Diptera larvae*
Ca	86.7	17	< 0.01	Copepoda** Collembola* Homoptera juveniles*
Mg	83.5	17	< 0.01	Copepoda*** Diptera larvae** Collembola*
Aldina				
mass	66.7	17	< 0.05	Protura*** Copepoda* Diptera larvae* Total*
P	80.8	17	< 0.01	Diplopoda***
K	77.6	17	< 0.01	Copepoda***
Mg	67.6	17	< 0.05	Copepoda** Diptera larvae* Protura*
Al	87.7	17	< 0.01	Protura*** Diptera larvae*
Fe	92.8	17	< 0.001	Protura*** Diptera larvae* Homoptera juveniles*

DISCUSSION

It is admitted that the Berlese-Tullgren extraction method used in the present study was not efficient for several groups of litter animals. Bearmann funnels would be more appropriate for the extraction of Copepoda and Enchytraeidae, while the Kempson system would also be better for those two and some other groups (Adis 1988). Bearmann funnels were not used because the liquid used in the extraction technique would have interfered with the chemical analyses, while the Kempson system was not available in INPA for a large number of simultaneous samples. Berlese-Tullgren funnels are not efficient for

Coleoptera adults, Copepoda, and Phalangida (Opiliones) (Wallwork 1976), Symphyla (Edwards 1990), but are good for Acari, Araneae and Collembola (Edwards & Fletcher 1971). However, since the Berlese-Tullgren method was used throughout it provides a valid comparison among treatments. The proximity of the forest types allowed a comparison of litter animals without the confounding effects of differences in weather and times of collection. Besides the extraction method used, it is also possible that the bags have limited the colonization of the decomposing leaves. Despite the 9-mm holes perforated in the bags, it is possible that the artificial confinement of the leaves into the bags altered the microenvironment (Lousier & Parkinson 1976; St John 1980) and restricted the access of some litter animals.

Density of litter animals

The densities of litter animals colonizing the decomposing leaves were different in the three forest types, as well as on the three species of leaves. The densities of most of the litter animal groups were significantly related to climatic factors, and the fluctuations in the density of all three leaf species were generally synchronous suggesting an important influence of rainfall, evaporation, and the moisture of the organic and upper mineral soil layers. The results obtained broadly agree with the statements that: `within a climatic region, the main factors determining the abundance of soil microarthropods include the type and quantity of decomposing organic residues, and the soil water regime' (Wallwork 1976); and `the numbers of animals associated with leaf litter bags are likely to be affected by two main phenomena: the seasonal abundance of the animals in the litter layers and successional differences in the suitability of the substrate for colonization by the animals' (Anderson 1975).

The number of individuals and taxonomic groups of litter animals were relatively high, especially in the LERF. In a former study of invertebrate densities of the litter layer along a transect within 1 km of the present plots, with five collections made over a year, and using the same Berlese-Tullgren apparatus for extraction, the highest litter-animal densities were found in the THF (50 600 m^{-2}), and the lowest in the LERF (34 300 m^{-2}). The SHF had an intermediate density of 45 200 m^{-2} (E.P. Oliveira, unpublished). In her

study, the proportions of the two most abundant groups, Acari and Collembola, varied widely among the three forest types, and together they represented from 87-92 %. She observed distinct seasonal variations across the three forest types: higher densities were recorded in the wet season and lower in the transitional period in the SHF, while the opposite occurred in the LERF. In the THF, the highest densities were found in the dry season, while the lowest occurred in the transitional period. It must be noted, however, that her LERF site was a few metres lower and more prone to waterlogging than the one in the present study. In another study made in THF within 1 km of the study plots, Adis *et al.* (1989), using Kempson extractors, found higher densities of arthropods in the wet (74 000 m^{-2}) than in the dry season (58 000 m^{-2}) and Acari plus Collembola were 75-80 % of the total number of individuals collected. Formicidae, Diplura and Pauropoda, in rank order, were the other most abundant groups. Acari, Collembola, and Protura had lower densities in the dry season, while Coleoptera, Diplopoda, and Pauropoda had higher densities in the dry season. No indication of vertical migration as a result of abiotic factors was found in their study. In the present study, there were seasonal influences on the densities of most groups of litter animals. The total litter fauna density was highly influenced by the two most abundant groups, Acari (mites), especially, and Collembola, which broadly agrees with results recorded elsewhere (Beck 1971; Dickinson & Pugh 1974; Adis 1988). Acari constituted about 70 % of the total number of litter animals in the SHF, and nearly 80 % in THF and LERF. Other studies in central Amazonia showed that 70-77 % of the Acari extracted in Berlese-Tullgren funnels were Oribatidae (Beck 1971; Ribeiro & Schubart 1989), decomposer mites which were less abundant in the dry season. In the present study, Acari populations were always low when it was dry and least in the SHF. Acari were present in all bags retrieved from the LERF, but their numbers were related to the moisture of the organic layer. They did occur in drier conditions, especially in the LERF and THF, with closed vegetation and a thicker organic layer, where presumably it remained moist enough for them to feed. Acari can have more general feeding habits during certain times of the year, and may have `feeding refuges' during periods of scarcity, such as drought, when they have to leave their surface soil habitat (Anderson 1975). This could account for the relatively high densities of Acari in the drier periods, especially in

the LERF. It must be noted that the group classified here as Acari includes animals at different trophic levels with many predators of litter animals (Wallwork 1976). In contrast to the Acari, even when greatly reduced in the driest period (180 d), Collembola still had large populations in the more open and dry forest type, the SHF. Higher densities of Collembola during the dry season were similarly recorded in a lowland evergreen rain forest on Oxisol with high clay content close to the present study plots (Oliveira 1983). The third most abundant group of litter animals in the present study, Formicidae, showed no significant differences among the three forest types, no relationships with litter and soil moisture, and no relationships with rainfall, all of which reflect the high mobility of ants. Tropical ants, with a diversity of food types and nest sites can be considered as the dominant predators and competitors for resources in tropical lowland forests (Levings & Windsor 1982; Olson 1994). Leaf-cutting ants (Attini) contribute to litter breakdown, carrying large amounts of leaf material to their nests, where the material is fragmented (Edwards 1974). In central Amazonia, one species of Attini, *Atta sexdens*, was found foraging 27 % of its time on dead leaves from the litter layer of a lowland evergreen rain forest (Vasconcelos 1990). Ants occur with a fairly high diversity and density in some neo-tropical forest sites. On Mount Silam, Sabah, Leakey & Proctor (1987) found that the Formicidae dominated the numbers of litter macrofauna in four of the six plots (Collembola and Isoptera were the most numerous groups in the other two plots). In Mulu, Sarawak, Anderson *et al.* (1983) reported higher densities of Formicidae in heath forest than in dipterocarp forest, and that they largely influenced the total fauna in the litter. In the present study, despite the lack of significant differences in density among the three forest types, the relative frequency of Formicidae in the litter bags was higher in the SHF and THF than in the LERF, indicating ants as more conspicuous and important predatory groups in the two heath forests than in the LERF. In forest ecosystems of central Amazonia, higher densities were found in the dry season (Adis & Schubart 1984), but this trend was not observed in the present study in the litter bags, which of course do not necessarily reflect the populations in the litter layer.

Colonization and succession of functional groups of litter animals

The assignment of litter animals to gross trophic categories based on coarse taxonomic resolution (such as class, order or families) is difficult, owing to the variability in the trophic habits within major groups and due to uncertainties regarding the feeding habits of many taxa. The classification is imprecise, since some species (or taxonomic groups) are omnivorous (Blair *et al.* 1994; Robertson *et al.* 1994). Litter animals have been classified into herbivores, detritivores, and predators based on their known behaviour, or that of known related species (Raw 1967; Edwards 1974; Wallwork 1976; Moran & Southwood 1982; Petersen & Luxton 1982; Dindal 1990; Blair *et al.* 1994; Robertson *et al.* 1994). Henceforth in the present study 12 out of 21 major taxonomic groups (Acari, Coleoptera larvae, Collembola, Copepoda, Diplopoda, Diptera larvae, earthworms, Isopoda, Isoptera, Protura, Psocoptera, and Symphyla) will be referred to as `decomposers', six groups (Araneae, Diplura, Formicidae, Pauropoda, Phalangida, and Pseudoscorpionida) as `predators', and three (Coleoptera adults, Homoptera juveniles, and Thysanoptera) as `herbivores'.

Among the animals acting mainly as decomposers, six groups (Acari, Coleoptera larvae, Copepoda, Diptera larvae, earthworms, and Protura) followed the same pattern of the total number of litter animals, with significantly higher densities in the LERF than in both the THF and the SHF. Contrary to the findings of Lewings & Windsor (1982) in lowland evergreen rain forests in Panama, the densities of the decomposers in the litter bags were generally not related to the residual mass of leaves. They were mostly related to the moisture of the organic and upper soil layers. Diptera larvae and Copepoda are neglected components of the litter fauna, and considered as having a low biomass in tropical ecosystems but are sometimes abundant (Petersen & Luxton 1982), as in the present study, where they ranked respectively fifth and sixth overall in density. They both were especially frequent in the LERF. Diptera larvae were related to moisture of both organic and upper soil layers, while Copepoda were more closely related with the moisture of the organic layer and rainfall than any other group, and were virtually only found in the bags during the wettest period (from 30 d to 120 d). The lack of a seasonal pattern for Coleoptera larvae contrasts with Morais (1985), who found, for forests in central

Amazonia, that about two thirds of all Coleoptera larvae were collected during the dry season. Psocoptera showed a different pattern from most of the litter animal groups, being more frequent and abundant in the THF (and to a lesser extent also in the SHF) than in the LERF. The reasons for that can be related to their eating algae, lichens (more abundant in the SHF), and organic matter particles (more abundant in the THF) (Aldrete 1990). Lewings & Windsor (1982) reported higher densities of Psocoptera in dry-season conditions, which can happen more frequently in the less closed SHF and THF. The densities were related only to the daily evaporation and they seem to be more dependent on the air humidity than on litter or soil moisture. Air humidity is not regarded as a limiting factor in any of the forest types (Ribeiro & Santos 1975). Two groups of decomposers, Diplopoda and Isopoda, showed relatively high densities, while two other important groups of decomposers, earthworms and Isoptera, showed very low densities in the litter bags. Diplopoda and Isopoda are generally considered as having a low biomass in tropical forests (Petersen & Luxton 1982). However, Lawrence (1953) regarded Diplopoda as probably as important as earthworms for decomposition in some African forests, and the present study indicates they are more important than earthworms in the SHF, THF and LERF. Diplopoda were related to the moisture of the organic layer, while Isopoda, typically soil animals (Dindal 1990; Fragoso & Lavelle 1992), were related to the soil moisture. The relatively higher frequency and density of Diplopoda and Isopoda in the THF than in LERF could be related to the higher humus content of the THF which maintains the moist conditions suitable for these groups (Raw 1967). In Mulu, Anderson *et al.* (1983) found higher densities of litter-feeding Diplopoda in heath forest than in dipterocarp forest, confirming the present study, which suggests they were not limited by the lower pH of heath forest soils. On the other hand, Hoffman (1990) suggested Diplopoda are restricted by pH < 5. Atkin & Proctor (1988), studying altitudinal variations in the litter and soil fauna of Volcán Barva in Costa Rica, found that Isopoda densities were second only to Formicidae at 100 m altitude, while Diplopoda ranked fifth. Thus, new studies in tropical forests tend to contradict the idea of low densities of Diplopoda, and their importance is now appreciated (Hoffman 1990). The relatively high frequency and abundance of these two moisture-limited groups also suggest that the

moisture of the upper organic and mineral layers is not likely to be a limiting factor for most of the litter invertebrates in the SHF and THF, but it might be important for some groups, such as Copepoda and earthworms. Earthworms, considered as one of the main decomposers in temperate areas, and in a number of tropical ecosystems with a high abundance of epigeic and anecic populations (Fragoso & Lavelle 1992) were restricted to a few bags in the LERF, and they were at the last retrieval. This observation agrees with Fittkau & Klinge (1973) for central Amazonia, as well as for other tropical rain forests on acid soils (pH < 5), where estimates of their densities and biomass are generally low (Petersen & Luxton 1982), and they seem especially limited by low pH and soil moisture. Anderson *et al.* (1983) reported that earthworms did not seem to be involved in litter breakdown in Mulu. However, relatively high biomasses in tropical forests have been recorded even under conditions of pH < 5 (Leakey & Proctor 1987; Atkin & Proctor 1988). In the present study, the soil pH was generally below 4, which, in addition to periodic short-term droughts, could restrict earthworm populations. Isoptera are generally considered to be very important decomposers in tropical forests (Fittkau & Klinge 1973; Swift *et al.* 1983; Lavelle 1984). Matsumoto & Abe (1979) suggested that termites could remove 32% of the leaf litter on forest floor while Luizão & Schubart (1987) estimated that termites removed 42% of leaf litter in a forest on Oxisol in central Amazon. In the present study, however, Isoptera were uncommon in the bags. The absence could be attributed to: (a) their high mobilility, resulting in a short residence time; (b) their largely nocturnal foraging activity; (c) the lower frequency, in sandy soils, of soil-gallery inhabiting litter-feeding termites; (d) the high frequency of the most conspiscuous termite-predators, the ants; and (e) a predominance of humus-feeding termites, which do not feed on intact litter. In Mulu, Sarawak, the Isoptera biomass in the dipterocarp and heath forest was mainly of humus-feeding termites (Anderson *et al.* 1983). In the present study, the termite effect on the decomposition of the leaves was visibly more pronounced, especially in the LERF and THF, than is suggested by their low density in the bags (which were always collected during the daytime). The higher densities of termites recorded in the driest period of the experiment (180 d), in the more open and dry forest type (SHF), agree with report of Menaut *et al.* (1985), who indicated that termites in African savanas tended

to have high surface activities during dry periods. However, such results suggest that the species of termites in the SHF are not the same as the litter-feeding *Syntermes* commonly found in the nearby clay soils, where they are more prominent during the rainy season (Luizão & Schubart 1987).

Among the predators of litter animals, two groups (Phalangida and Pseudoscorpionida) were more abundant in LERF than in the other two forest types, one (Diplura), was more abundant in the SHF, and the other three groups (Araneae, Formicidae, and Pauropoda) showed no significant difference among the three forest types. Phalangida (Opiliones) and Pseudoscorpionida populations have been seldom estimated, and are considered as having a low biomass in tropical forests (Petersen & Luxton 1982). However, Lavelle & Kohlmann (1984) have found Phalangida to be relatively abundant in American rain forests, and more recent studies have shown relatively high numbers of Pseudoscorpionida in forests (Blair *et al.* 1994). Adis (1988) reported high densities of this group in the upper litter-soil layer of central Amazonian forests. This was confirmed in the present study for all forest types, especially for the LERF, where the Pseudoscorpionida were the third most frequent group, and the most frequent predator. It must be pointed, however, that Pseudoscorpionida were frequent but (as with other typical predators in the litter bags) generally in small numbers (often only one individual) in the samples. The densities of Pseudoscorpionida and Phalangida were related to the moisture of the organic layer. As a typical non-specialized predator of the litter fauna, the densities of Pseudoscorpionida followed closely the pattern recorded for the total litter fauna, and especially that of the most frequent groups, Acari and Collembola. Diplura showed an opposite trend from the majority of the litter animal groups, and had higher densities in the SHF than in both the THF and the LERF, and were related to the moisture of the organic layer in the period preceding the litter bag retrieval. The findings of the present study, with higher densities in the SHF, contrast with those of Anderson *et al.* (1983) in Mulu, where the densities of Diplura were lower in heath forest than in dipterocarp forest. Among the groups categorized as herbivores, Coleoptera adults and Homoptera juveniles showed higher densities in the LERF, and Thysanoptera, despite being more frequent in the LERF, showed no significant difference in density among the forest types. Thysanoptera showed

no direct relationship with the moisture of either the organic or the upper mineral soil layers, which can account for the lack of difference among the forest types.

Biomass of litter animals

When the density of litter animals was transformed to biomass (Petersen & Luxton 1982), Diplopoda were ranked first, followed by Formicidae and Araneae. Earthworms also were ranked high, which reflects the population of the LERF, at the last retrieval. Of the two most abundant groups of litter animals, the Acari were ranked in the middle range of biomass and the Collembola one of the last. These biomass estimates are rough, but allow some comparisons with results from other forests. For instance, the Formicidae, the second in the biomass ranking, match closely the results of alcohol-wet weights quoted by Anderson *et al.* (1983) in Mulu, Sarawak, for dipterocarp and heath forests, where Formicidae were respectively 20.8 % and 13.9 % of total biomass. On the other hand, the estimates there for Araneae (19.6% in the dipterocarp and 10 % in the heath forest), and Isoptera (15 % in the dipterocarp and 1.6 % in the heath forest) were far above, and the estimates presented for Diplopoda (0.4 % for dipterocarp and 5.8 % for heath forest) were far below the values found in the present study. Blattaria, which had the highest biomass in Mulu, were seldom recorded in the litter bags, but that probably reflects the low chance of capturing these highly mobile animals. The biomass estimates for the SHF, THF, and LERF suggest a higher importance for the Diplopoda and Isopoda than generally thought (Petersen & Luxton 1982; Dindal 1990), confirming recent reports from other tropical rain forests where Diplopoda has been regarded as important decomposers (Lavelle & Pashanasi 1989).

Influence of leaf species on litter animals

Both the number of taxonomic groups and the total numbers of litter animals were significantly different among the three leaf species, being higher in *Clitoria* and lower in *Pradosia*. The same was found for several of the groups of litter bag animals, including the three most frequent (Acari, Collembola, and Pseudoscorpionida), but 11 of the 21 groups showed no significant differences in densities among the three leaf species. These

11 groups include some important decomposers such as Diplopoda, Diptera larvae, earthworms and Isoptera, as well as some predatory groups such as Araneae and Phalangida.

The differences in density and biomass must reflect the ways in which different decomposer species are affected by the resource quality and the micro-environment produced inside the litter bags by the interaction of the substrate and its colonizers. In a shared study, R.C.C. Luizão (1994), using a standard leaf species, *Clitoria racemosa*, found considerable differences for several litter animal groups, when the colonizing fauna of litter bags left in permanent contact with the litter layer was compared with that in the bags regularly lifted up to avoid fine root colonization of the decomposing leaves. The resource quality within litter bags includes not only the concentration and availability of nutrients, and of carbon and energy sources, but also modifiers, such as tannins, which affect the activity of heterotrophs (Swift *et al.* 1979). Undoubtedly there are chemicals (including tannins, phenols, and volatile terpenoids) released from leaves and leaf litter which are capable of inhibiting the activity of microrganisms (Attiwill & Adams 1993), but overall, it is difficult to assess the role of allelopathy in the decomposition and mineralization processes. In a litter bag study in temperate forests, Anderson (1973a, b) found that beech leaves were more palatable to soil animals and more resistant to microbial decomposition than chestnut leaves, and that some leaf species on the forest floor were not attacked by soil animals during the first six months because of the toughness of the undecomposed tissues and their high polyphenol and tannin content. Harrison (1971) showed that the growth of many of the major cellulolytic fungi is inhibited by leaf tannins, but that some of the colonists of freshly fallen litter were tolerant and even stimulated by high tannin concentrations. Anderson *et al.* (1983) suggested that the higher consumption of *Ficus* and *Parashorea* leaves, of higher nutritional value, were preferentially selected instead of mixed litters of lower nutritional quality in Mulu. That was particularly observed in a forest on limestone with relatively high populations of snails, millipedes and woodlice. In the present study, some groups, such as Copepoda, Psocoptera, and Diplopoda were more frequently found on the more sclerophyllous and slowly-decomposed leaf species (*Pradosia schomburgkiana* and *Aldina heterophylla*)

than on the more palatable species, *Clitoria racemosa*. Copepoda and Psocoptera were more abundant on leaves of *Pradosia*, the most slowly-decomposed leaf species, which has the highest concentrations of both lignin and polyphenols (Lisboa 1976a; Anderson & St. John 1981). This could indicate that Copepoda act as a decomposer group only in the first stages of decomposition, when the 'brown pigments' produced by the formation of polyphenol-protein complexes (Toutain 1987) are the dominant feature of that leaf species. However, the greater abundance of Copepoda on *Pradosia* leaves could also be a simple result of the greater retention of films of water on that leaf species.

Succession of litter animals on decomposing leaves

Succession is generally related to an increase in both the number of species and the density of most groups of the soil fauna (Usher 1985). With time, population sizes and structures change as a function of the greater range of microhabitats formed by the interaction of the organisms and the environment. The reduction in polyphenol concentrations with time can also contribute to such increases (Anderson 1975). Competition between soil arthropods is generally asymmetrical (one species adversely affected, the other species unaffected), and predation probably plays an important role in regulating populations of the grazing species. Little is yet understood about more complex interactions in the soil ecosystem (Usher 1985).

In the present study, overall there was no significant relationship between the weights of residual litter in the bags and the numbers of animals they contained. This finding agrees with the results of Anderson (1975) for temperate forests, but contradicts those of Lewings & Windsor (1982). In the present study, significant negative correlations were found between the residual weight of litter and both the number of groups colonizing the litter bags and the total number of litter animals, indicating the amount of remaining material in litter bags as a minor influence on the presence and densities of litter animals. The seasonal and temporal patterns appeared as the main factors influencing the succession of the litter animals.

The colonization of the litter bags by representatives of several groups of litter animals was not particularly fast, and no groups could be recognized as pioneers. Because of the

relatively long initial period and the broad taxonomic levels used, it was impossible to verify a possible initial invasion of the litter by a few species of mycophagous microarthropods, followed by an increase in species diversity, as reported by Crossley & Hoglund (1962). A general trend for increasing populations of most groups with time was observed in the present study, only interrupted in the driest period (180 d). In the two last stages, after the short dry period, a considerable increase took place. The 180 d retrieval illustrates well how the litter animal densities can be affected by a short but severe dry period: the two months since the last retrieval were not especially dry, but the two weeks, and particularly the week immediately before the retrieval were very dry. That retrieval resulted in the lowest numbers of groups and animal densities in the litter bags. Thus, climate is likely to be the main factor controlling the colonization of the leaves, especially in the more open SHF. The litter animals in the humus and upper soil layers are probably less affected by short dry spells than the bagged leaves on the litter layer.

The seasonal control on decomposition is well known. Levings & Windsor (1982) found that the numbers of soil fauna and microarthropods in Barro Colorado Island, Panama, decreased sharply at the onset of the dry season, but rose sharply at the begining of the wet season. The numbers of most soil faunal groups were strongly associated with litter moisture. In central Amazonia, Luizão & Schubart (1987) found higher decomposing activity of the litter fauna, especially of large *Syntermes* termites, in the rainy season. Lavelle (1993) suggested that both the number and activity of decomposer soil organisms show a distinct seasonal pattern in relation to moisture supply. Adis (1988) suggested that in central Amazonia the presence of arthropods on the forest floor fluctuates throughout the year and is mainly influenced by abiotic factors, particularly the short but pronounced dry season. However, in most of the evergreen tropical rain forests, where moisture is not commonly limiting, substrate quality is likely to be the most important determinant of decomposition pathways and dynamics (Lavelle *et al.* 1993). This would be especially true in spodosols, where large amounts of secondary compounds (e.g., tannins and other polyphenols) are present in the litter and have been used to explain the low abundance of soil fauna in some Southeast Asian heath forests (Collins *et al.* 1984). In Mulu, Anderson *et al.* (1983) reported that the freshly fallen leaf litter used in their experiments (with 27-

40 % of lignin) had 0.46-2.50 mg 100 mg^{-1} of polyphenols (as tannic acid equivalents). In a comprehensive survey on central Amazonian leaf litters, Howard-Williams (1974) reported concentrations of polyphenols (as tannic acid equivalents) of freshly fallen litters in the range of 2.06-3.50 mg 100 mg^{-1}, which is higher than the values found in Mulu.

Only a few groups showed clear successional trends unrelated to the seasonal patterns: Diplopoda, earthworms, Homoptera juveniles, Isopoda, Protura, and Symphyla, among the major groups; and Chilopoda, Embioptera and Enchytraeidae, among the minor groups. All were more frequent and abundant in the litter bags in the later stages of decomposition. These groups possibly are those with a preference for advanced stages of organic matter decomposition. On the other hand, Copepoda were present virtually only in the two initial stages, indicating a strong preference for the initial stages of decomposition when the leaves hold a surface water film needed for the Copepoda. However, in the present study, this phase (from 30 d to 120 d) coincided with the wettest period, and may only reflect a seasonal pattern. Anderson (1975) reported that Copepoda disappeared when free water was no longer present between the leaves and the litter bags. He also found that Enchytraeidae showed the clearest evidence of a successional change in their status with a three-fold increase in numbers of individuals per bag in one year. That was similar to the results obtained in the present study, but here with much lower densities of animals (possibly because of a less efficient method of extraction).

Overall, besides differences found among litter species, there were significant effects of forest type and dates of collection on total numbers of litter animals in the litter bags, a result similar to that found by Blair *et al.* (1994) for the microarthropods extracted from litter and soil of the top 10 cm of a temperate forest. Their data suggested that total microarthropod densities are positively related to the pool of organic matter and moisture, and to the soil pH and bulk density. Considering bulk density, pH and moisture all as functions of organic matter concentration, they suggested the last as the most important determinant of litter fauna on a local scale. In the present study, taking into account the conditions of soil pH and litter and soil moisture in the three forest types, the densities of soils animals in the SHF and the THF could be considered relatively high. The THF has the lowest soil pH and the highest humus concentration in the surface soil, and generally

had high soil and litter moisture. The SHF had the highest soil pH and high humus concentration only in the forested patches, and had the lowest values of soil and litter moisture. Both, the THF and the forested patches of the SHF had a `mor' humus, in contrast with the LERF which had a `moder' humus. Thus, soil pH may be less important for litter animals than adverse micro-climatic conditions in the SHF and THF. During the dry season, the combination of greater temperature and variations of soil and litter moisture may have created a microclimate that was suboptimal for the decomposer community, affecting both primary (bacteria and fungi) and secondary (fauna) decomposers (Blair & Crossley 1988). Maximum temperatures above 40 °C, which have been recorded at the soil-litter interface in the open heath forest (Ribeiro & Santos 1975) could have adverse effects on litter animals, but the presumed main factor involved, moisture (Raw 1967), seems not to be limiting, since soil and litter moisture were never very low nor were the air humidities of the heath forests (monthly mean 81-97 %) (Ribeiro & Santos 1975). The low litter animal density found in the SHF may result from the lower soil organic matter and the many patches without any vegetation cover. The upper organic and mineral layers of the SHF soil clearly had lower populations of litter animals than the corresponding layers in THF and LERF (R.C.C. Luizão 1994) and this may have contributed to reduced decomposition rates. Decay rates were most reduced for *Pradosia* litter, which was the slowest to decompose in all three forest types, especially in the SHF. This agrees with the observation that microarthropods have a greater effect on the litter species more resistant to decomposition (Seastedt 1984). The low pH of the soils in the three forest types may have contributed to a slower litter animal colonization and the generally low decomposition rates, since pH influences the success of colonization of various Collembola, Acari and Enchytraeidae (Hågvar & Abrahamsen 1980). However, other factors such as the moisture of the organic and topsoil layers, and the toxicity of secondary compounds and the acidity of the litter itself, all acting together and interacting, may be of more importance. That could explain the lower densities of litter animals in the THF when compared with the LERF which has similar soil and litter moisture, but distinct litterfall and litter layer composition.

Relationship between litter animals and mass loss, and mineral element release rates

The results of the present study must be interpreted with extreme care, and any conclusion drawn must consider the wide range of factors interacting to produce such results. These factors are often correlated, and generally cannot be properly separated in the statistiscal analysis. For instance, the several significant values found in the regression analyses may better reflect the simultaneous processes occurring in the litter bags as a function of time elapsed and seasonal patterns, than the actual effects of the litter animals on the decomposition and mineral element release rates. For example, the Copepoda were virtually only found in the litter bags up to 120 d (all retrievals in the wet season), when the concentrations of some mineral elements, such as potassium, calcium, and magnesium, were higher, but this may be due to the high litter moisture in that period, and moisture is a requisite for the Copepoda (Anderson 1975; Dindal 1990). In spite of correlated events taking place on the decomposing leaves, consistently significant relationships found in the present study suggest that greater or lesser importance can be assigned to some groups of litter animals involved in the dynamics of organic matter and nutrients. Thus, Collembola, and especially Copepoda seem to be the most important decomposers involved in mass loss and nutrient release or accumulation in the SHF, while Diplura are probably the most important predatory group. In the THF, Acari, Collembola, Copepoda, Symphyla, and to a lesser extent Diplopoda, would be important decomposers, and again Diplura important predators. In the LERF, Acari, Collembola, Copepoda, and earthworms are the most important decomposers, while the Pseudoscorpionida appear to be an important predatory group, instead of Diplura. Especially in the THF and LERF, the groups more related to mineral element changes are partly distinct from those more strongly related to the remaining leaf mass. This is not surprising, since reviewers have drawn different conclusions about the overall effects of invertebrates on litter nutrient fluxes (Blair *et al.* 1992). Anderson & Ineson (1984), citing indirect evidence from litter-bag studies, concluded that the mesofauna (Acari and Collembola) may be more important in mobilizing nutrients than in contributing to mass loss. On the other hand, Seastedt (1984), based on a short-term (up to one year) litter-bag study, concluded the opposite. He suggested that mineralization of nutrients should be increased by invertebrate feeding

activities in the later stages of decomposition. The fact is that little is known of the way invertebrates influence forest floor dynamics, particularly on acidic soils (Blair *et al.* 1992), where fungi are considered as the dominant primary decomposers (Anderson & Ineson 1984). In the present study, the evidence points to some specific groups of litter animals as key decomposers. Thus, Collembola, possibly including many fungivorous species, are important in all three forest types, and in the tall heath forest (THF), which has a root mat and a large humus layer, Acari, Diplopoda, and Symphyla also appear as key decomposers. In the LERF, Diplopoda are replaced by earthworms as important decomposer groups, possibly because of the pH, higher than in the THF, together with the higher water retention potential of the mineral soil which contains more clay. Comparing the three leaf species, Acari appear to be decomposers of all of them, while the Collembola appear more important for *Clitoria* and *Aldina*, the Isopoda more important for *Pradosia*, and the Protura especially important *for Aldina*. The Diplura are probably important predators on all three leaf species. Most of the groups of potentially important litter decomposers were either not related or weakly related to litter nitrogen and phosphorus, but generally related to the release of calcium, magnesium, boron and manganese, and to the immobilization of iron and aluminium. The increase in the concentrations of iron and aluminium in decomposing leaves has been noted before (Luizao & Schubart 1987; Rustad 1994), and can be partly attributed to the transport of soil residues to the litter bags by the colonizing fauna. The relationship between the densities of decomposer groups and the decrease of concentrations of cations such as calcium and magnesium could be further evidence that these elements limit activities of litter and soil organisms, as suggested in the shared study on the microflora and litter animals (R.C.C. Luizão 1994). In this case, the surprising element is manganese, which is an essential micronutrient but is generally regarded as potentially toxic. In the present study there is evidence that it is in short supply and limiting. In addition to the groups of litter animals identified above as potentially important, the present study (despite the criticisms of the extraction methods discussed earlier), found considerable densities of Copepoda in the litter bags, suggesting they are important decomposers in all forest types and leaf species. They were always positively related to the remaining mass and mineral

element concentrations (except for iron and aluminium), suggesting they are immobilizing nutrients in decomposing leaves. Since the Copepoda do not feed and stay in the internal parts of the leaves (I. Walker, personal communication), the nutrient immobilization possibly would be caused by their faeces and dead bodies left on leaves surface by an imperfect extraction, and also by the fungal mycelia and exudates on which Copepoda feed (Dindal 1990). Extraction systems which are efficient for Copepoda (and for other litter animal groups, such as Enchytraeidae and some insect larvae, which need films of water to colonize leafy material), together with microcosm experiments, are necessary to fully elucidate their role in decomposition.

Chapter 7. NUTRIENT ADDITION EXPERIMENTS WITHIN THE THREE FOREST TYPES

INTRODUCTION

For most acidic soils under tropical rain forest, phosphorus is often thought of as the main limiting nutrient for production (Vitousek 1984; Lathwell & Grove 1986; Vitousek & Sanford 1986). Heath forest soils are thought to be more limited by nitrogen (Grubb 1989; Medina & Cuevas 1989). However, there is little direct evidence that natural tropical forests are nutrient limited (Lathwell & Grove 1986; Proctor 1992). It is difficult to make experiments to assess nutrient limitation without disrupting natural ecosystems, and presumptive evidence of nutrient limitation results from experiments in which native ecosystems have been converted to agriculture, where additions of phosphorus or nitrogen or both invariably increase production (Lathwell & Grove 1986). In the few fertilization experiments in native tropical forests, there was evidence of nutrient limitation, especially by nitrogen. Nitrogen supply is always critical in determining the levels of organic matter production, and its availability could be one of the limiting factors causing reduced growth in upper montane forests (Medina & Cuevas 1994). In Jamaica and in Venezuela, additions of nitrogen or phosphorus or both significantly increased trunk growth in montane forests (e.g. Tanner *et al.* 1990, 1992). For lowland tropical forests, however, there is no experimental evidence of such responses. In the last years more detailed reviews and new studies on nutrient cycling have suggested that neither low soil nutrients nor water regime could explain the constraint for plant growth in heath forests. It has been realized that the soils under heath forests in Southeast Asia vary in their chemistry and have either a similar or even higher content of nutrients than the soils of neighbouring large-stature forests (Proctor *et al.* 1983a; Whitmore 1989). Recent studies on soil and litter nutrients on Maracá Island, northern Brazil, characterized by low concentrations of soil nutrients, found no evidence that nutrients were limiting either plant growth in the forest nor seedling survival and growth in gaps (Thompson *et al.* 1992; Scott *et al.* 1992). There is no simple relationship between soil nutrient concentrations and biomass or species richness (Proctor *et al.* 1983a; Vitousek & Sanford (1986; Primack *et al.* 1987;

Anderson & Spencer 1991; Proctor 1992; Medina & Cuevas 1994), and new hypotheses must be put forward to provide an explanation on the limiting factors for plant establishment and growth.

Soil acidity and related effects could reduce or even prevent plant growth in very acid forest and crop soils (Ritchie 1989). Soil pH has a powerful influence on plant community composition, controlling the establishment or exclusion of plant species (Fitter & Hay 1991; Falkengren-Grerup & Tyler 1993). However, even for crop plants (far more studied than natural-forest trees), it is still unknown which of the many different effects of soil acidity reduces plant growth (Ritchie 1989). Soil acidity could reduce growth either through induced nutrient (e.g. phosphorus, calcium, molybdenum) deficiencies or by the toxicities of Al^{3+}, Mn^{2+}, or H^{+} ions, the toxicities being recognized as the most common cause of reduced yields (Ritchie 1989). Aluminium and nitrogen have been identified as two major pH-linked soil chemical factors, and nitrate ions can enhance aluminium uptake and toxicity in the soil through an increasing aluminium solubilization by the H^{+} ions, which increase together with nitrate (Rorison 1985). Aluminium toxicity is generally regarded as a common feature of acid soils, and a strong limitation for plant growth. Schmehl *et al.* (1952) pointed out high levels of Al^{3+} in the soil solution as responsible for deleterious effects on plants, by reducing calcium uptake by roots. Similarly, Brenes & Pearson (1973) concluded that root inhibition in acid humid-tropical soils was primarily a result of soil solution Al^{3+} toxicity. Probably Al^{3+} interferes with normal root elongation and function and thus limits growth (Lathwell & Grove 1986). However, aluminium in acid soils has a very variable behaviour, interacting with both organic matter and H^{+} (Ritchie 1989; Kinraide 1993), and it could not be assumed that aluminium, even in high concentrations in the soil solution, is necessarily causing toxicity to plant roots because aluminium may form complexes with organic matter or be adsorbed on to exchange sites (Ritchie 1989).

The pH of soils under heath forests is low, even by tropical standards (Whitmore 1989) and heath forests studied in the central Amazon were considered as having strongly acid soils (Klinge 1965; Lisboa 1975, 1976a), and around pH 3.0 H^{+} ions are directly toxic for

most plants (Fitter & Hay 1991). Therefore, it can be supposed that a change of a unit in soil pH could cause considerable change in soil conditions to plant roots.

In order to test the hypothesis that nutrients or low pH or both limit plant growth and survival in heath forest, nutrient addition experiments were made on two types of heath forest and one lowland evergreen tropical rain forest in central Amazonia. It was hypothesized that (a) seedlings would respond to N but not P or other nutrient addition; and (b) increasing soil pH through liming would cause a significant increase in plant growth, and the addition of both lime and nutrients should produce the best seedling survival and growth.

MATERIAL AND METHODS

Two 8 m x 5 m quadrats were selected close to the permanent plots in each of the three forest types (Fig. 2.2). At the THF and LERF sites, small natural gaps were used, after clearing the fallen tree branches. At the SHF sites, open spaces at the side of the `islands' of vegetation were used. The selected quadrats were all virtually flat, and it could be assumed that there was no lateral movement of the applied treatments. Twenty-eight 1 m x 1 m sub-quadrats were marked, in each of the quadrats for nutrient addition and control treatments. Half of the sub-quadrats were used for planting seeds of *Diniza excelsa* Ducke (Mimosaceae), a fast-growing tree, and the other half contained only seedlings occurring naturally in the quadrats, and belonging to many different species (especially in the THF and LERF). Two replicates of each of seven treatments (including a control) were used in each of the quadrats. The seven treatments were randomly located inside each quadrat. The rates of chemical addition used were the ones generally recommended for growing seedlings in forestry nurseries (Reis 1989), and were in the lower part of the range commonly used elsewhere for mature trees in forestry (Tanner *et al.* 1990). The seven treatments were (ha^{-1}): nitrogen as 150 kg of urea (NH_2CONH_2); phosphorus as 50 kg of sodium phosphate (NaH_2PO_4); potassium as 60 kg of potassium chloride (KCl); calcium as 2,000 kg of calcium chloride ($CaCl_2$); calcium as 2 000 kg of calcium carbonate ($CaCO_3$); a combination of 1, 2, 3, and 5; and a control with no added chemicals.

Nitrogen, phosphorus, and potassium were added freshly dissolved in 1 500 ml of water, while calcium chloride and calcium carbonate powders were firstly spread on the soil surface and then 1 500 ml of water were added. Controls received only water. The chemicals were added to the soil during the rainy season (1 March 1993), to ensure that the planted seedlings did not dry out. The nitrogen was added in three stages (0, 50 and 90 days), while the other chemicals were applied in equal amounts at 0 (1 March 1993) and 50 d (20 April 1993).

The number of replicate quadrats (each one with the treatments replicated twice) was limited because of the shortage of *Diniza excelsa* seeds, and of suitable natural gaps.

Plant-test assay

Fresh seeds of *Diniza excelsa* were obtained from the Department of Tropical Silviculture at INPA. This species was selected because of its ready germination, fast growth, and small seeds (with a small nutrient reserve) which would respond quickly to the nutrient additions. (Fast-growing species, generally growing on more fertile soils, respond quicker to the addition of nutrients (Chapin 1980). Just before sowing the seeds were treated with a 3 M sulphuric acid solution for 10 min to break the dormancy, and then washed in cold tap water. The treated seeds were buried 1 cm deep in the soil which had just received the first application of the treatments. Twenty-five seeds were sown in the central 80 cm x 80 cm area of each sub-quadrat (to avoid edge effects) at regular spacing, using a wooden frame with crossed strings to guide the planting. A minimum number of ten viable seedlings per sub-quadrat was envisaged to assure a good estimate of growth and biomass production. The sown areas were kept moist during all the germination period (only 7-10 days) by regular watering of the soils in case of lack of rain, using water from the nearest forest stream, stored in three large drums placed near the quadrats. It was planned to make a second application of the treatments after 50 d of planting the seeds, with a final recording of the height and number of leaves of each seedling after six months.

Native seedlings fertilization assay

At the time of the nutrient addition, all seedlings naturally growing in the central 80 cm x 80 cm area of each sub-quadrat were tagged with small aluminium tags, and their height and number of living leaves were recorded. After 180 d the seedlings were again measured. From the original 273 seedlings, 16 % were missed in the final recording, because the tags were lost. The survival (as a percentage of the initial number of seedlings) and growth rates of those that were refound were calculated. The growth indices used were: (a) the quotient final/initial number of living leaves, and (b) the quotient final/initial height of the seedling. The quotients were considered appropriate because the native seedlings had a wide variation of species and sizes which did not allow the evaluation of simple increases of height or number of living leaves in the seedlings.

Data analyses

Nested analyses of variance, using the GLM (General Linear Model) because of the unbalanced design of the experiment, were made to verify the influence of forest types and treatments on survival and growth of the seedlings. Additionally, one-way ANOVA's coupled with the Dunnett's test for differences of the treatments in relation to the control, and with the Tukey's test for differences between plots, were made to assess the significance of differences in survival and growth of the seedlings.

RESULTS

Planted seedlings

The seeds of *Diniza* germinated well: from 60-70 % in the SHF and THF, and from 70-90 % in the LERF. However, within the eight days of germination, virtually all seedlings planted in the quadrats were eaten by insects (especially leaf-cutter ants and a small black cockroach). Only a few seedlings remained in the LERF, insufficient for any treatment evaluation.

Natural seedlings

The overall comparison of the quadrats used as replicates for each forest type, showed a significant influence of both main factors analysed, forest type and the treatments applied to the seedlings (Fig. 7.1), but the interaction of the two factors was not significant (Appendix 7.1). No significant differences between the two quadrats were found either in the SHF or in the LERF, but there were significant differences in the survival ($F = 10.8$; $df = 1$; $p < 0.001$) and in the quotient final/initial height of the seedlings ($F = 8.51$; $p < 0.001$) between replicate quadrats in the THF. These differences were mainly because of significant differences in the treatments receiving additions of nitrogen, and possibly those receiving potassium (Appendix 7.1). In the SHF, the greatest survival and growth were observed in quadrat 2 with a thicker humus layer, especially in the sub-quadrats receiving nitrogen and phosphorus additions, but these were not significantly different from the control. No significant differences in the quotient final/initial number of leaves were found between quadrats in any of the three forest types. In each of the forest types, treatments always produced significant differences in the SHF and THF, but only affected the number of living leaves in the LERF (Fig. 7.1). For all forest types together, calcium chloride additions significantly decreased the seedling survival ($F = 7.82$; $df = 5$; $p < 0.001$), number of living leaves ($F = 4.87$; $p < 0.001$) and growth ($F = 6.01$; $p < 0.001$). Phosphorus addition significantly decreased the survival of the seedlings ($F = 7.82$; $p < 0.001$).

The survival of the seedlings in the SHF quadrats did not increase significantly with any of the treatments used. On the contrary, there was a trend for negative effects of phosphorus addition ($F = 2.75$; $df = 1$; $p < 0.05$) and a significantly higher mortality of seedlings with calcium chloride addition ($F = 6.52$; $p < 0.001$), which killed all the seedlings (Fig. 7.1). In the THF quadrats, the survival of the seedlings was reduced under all treatments, except for the NPK + $CaCO_3$ addition, but the only significant decrease was caused by calcium chloride ($F = 4.0$; $p < 0.01$). which killed most of the seedlings. In the LERF plots. none of the six chemical treatments increased the survival rate of the

seedlings, and the decreases observed, of 69 % with calcium chloride, and 64 % with phosphorus, were not significantly different from the control.

The final number of living leaves in the seedlings in SHF quadrats increased 31 % ($F = 2.90$; $df = 1$; $p < 0.05$), in relation to the initial number of leaves under NPK + calcium carbonate treatment and was reduced ($F = 4.69$; $p < 0.01$) to nil by calcium chloride (Fig. 7.1; Appendix 7.1). In the THF quadrats, the number of leaves in the seedlings showed a general trend to decrease after treatments, but the only significant decrease in relation to the control was observed after the addition of calcium chloride ($F = 2.70$; $p < 0.05$). In the LERF quadrats, the final number of living leaves in the seedlings increased by 61 % with calcium carbonate, and by 78 % with the addition of NPK + calcium carbonate, decreasing sharply with the addition of calcium chloride. However, no significant differences in relation to the control were found.

The height of the seedlings in the SHF was significantly increased by 27 % under the NPK + calcium carbonate treatment ($F = 4.54$; $p < 0.01$), while the calcium chloride addition reduced it to nil ($F = 4.98$; $p < 0.001$), by killing all the seedlings (Fig. 7.1; Appendix 7.1). Nitrogen addition caused a 22 % increase in seedling growth in relation to the control, but the increase was not significant. In the THF, the final height of the seedlings was generally lower (except for the NPK + calcium carbonate addition with a 21 % increase), but only significantly lower with calcium chloride ($F = 3.30$; $p < 0.01$). In the LERF plots, the height of the seedlings was 72 % lower than in the control when receiving calcium chloride, and slightly higher when nitrogen was added, but no significant differences were found.

Overall, there were a few positive responses of the natural seedlings to nutrient addition. in the three forest types. That was particularly true in the LERF. Only the addition of the NPK plus calcium carbonate appeared to have a positive effect on seedling growth. On the other hand, there was a clear and generally significant negative effect of calcium chloride addition on the survival and growth of the seedlings of most species, especially in the SHF plots, where they were all killed.

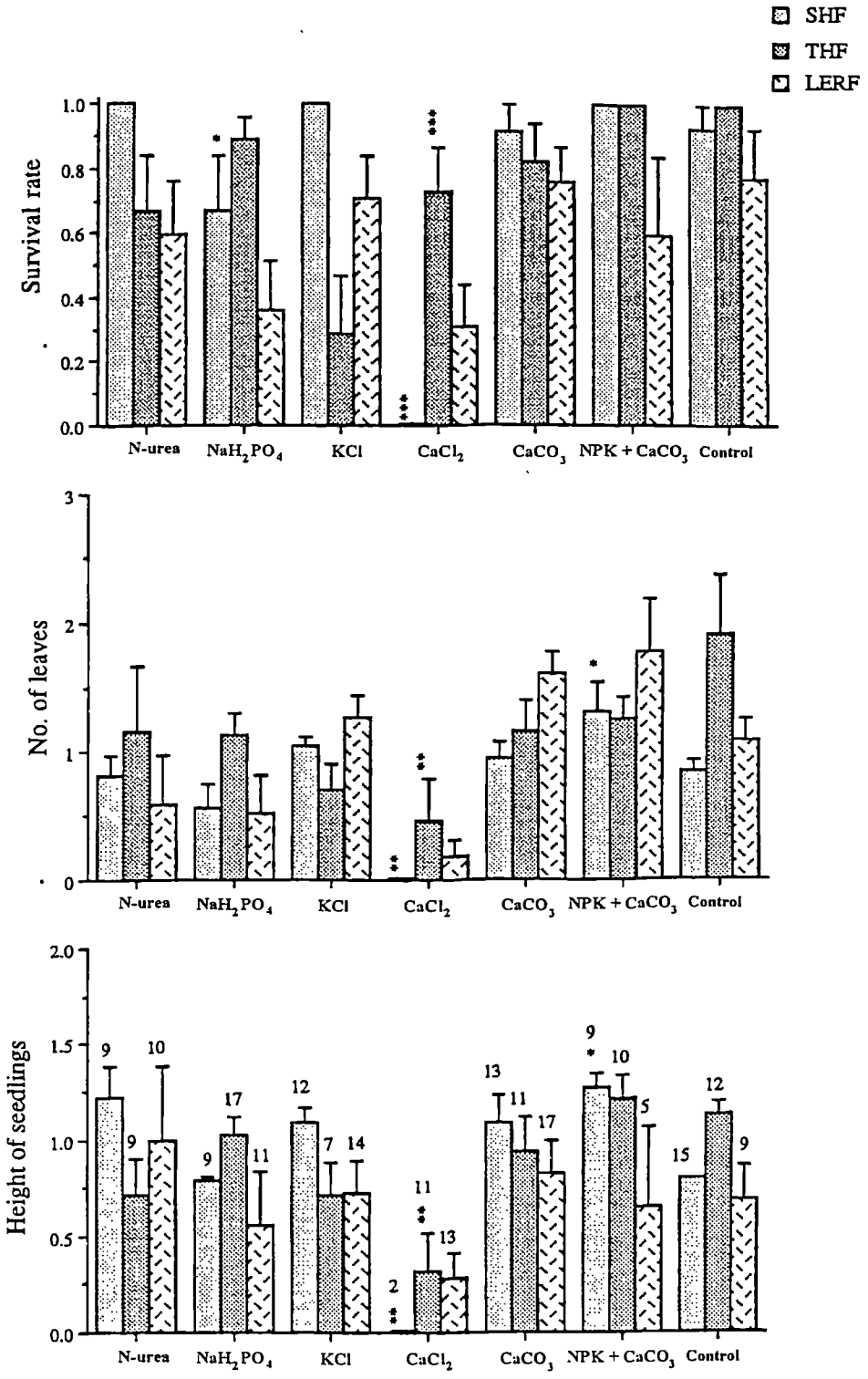


Fig. 7.1: Survival rate, and the quotients final/initial number of living leaves and final/initial height of the seedlings after 180 d in the seven treatments in the SHF, THF, and LERF. Values are means with SE. The significance levels for the analysis of variance (*0.05; **0.01; and ***0.001) and n values are indicated above the bars. The survival rate varies from 0 (no seedlings survived) to 1 (all survived).

DISCUSSION

The results of fertilization on native seedlings in heath forests in the present study were very similar to those of recent studies carried out in temperate forests in France (Ranger *et al.* 1994) and Sweden (Brunet & Neymark 1992; Falkengren-Krerup & Tyler 1992, 1993; Staaf 1992). They all found that any addition of mineral nutrients was unsuccessful in promoting plant survival or growth, unless the treatment involved an increase in soil pH. In the present study, overall there were no beneficial effects of the nutrient addition, if not associated with soil pH raising (by addition of calcium carbonate). In fact, in most cases there was a trend for a negative effect on seedling growth when nutrients such as phosphorus or nitrogen were added, and a significant increase in plant mortality or reduced growth with addition of calcium chloride. The exception was the positive growth of seedlings in the LERF plots, less acid (pH 0.3-0.6 higher pH) than the THF in the upper soil layers (Tables 2.3b, c - Chapter 2), and the best supplied in nutrients in the mineral soil (Tables 2.3a, b, c). The addition of calcium carbonate and NPK + calcium carbonate yielded consistent increases in seedling growth. The results seem to fit the statment that "beneficial effects of liming on forest plants in highly acidic soils seem, therefore, mainly to be a direct or indirect effect of the pH increase rather than of calcium or magnesium addition" (Falkengren-Krerup & Tyler 1993). They argued that the high acidity of the rhizosphere solution, possibly aggravated by harmful levels of easily reacting, mainly monomeric Al^{3+}, obstructs the uptake or retention of mineral nutrients by the roots in the more acid soils. They found an overall close inverse correlation between pH, or H^+ ion concentration, and Al^{3+} concentration of the soil solution (Falkengren-Krerup & Tyler 1993). In their study, there were no indications that the calcium or magnesium concentrations of the soil were below the minimum, or even suboptimal, for plant growth, indicating that the higher pH of the treated soils made it possible for the plants to utilize the native calcium and magnesium pools for normal development (Falkengren-Krerup & Tyler 1993). In a former study (Falkengren-Krerup & Tyler 1992), investigating to what extent soil acidity as such, aluminium concentration, or mineral nutrient deficiency were factors limiting the survival and performance of the forest

herbaceous species *Galium odoratum*, found that the plant was unable to survive unless the pH was raised (in both glasshouse and outdoor experiments). When phosphate plus nitrogen together with lime were supplied, no additional growth was observed, and nitrogen and phosphorus additions without lime caused no growth at all. They found that most of the neutralizing effect of $CaCO_3$ happened within 3 d, and that smaller amounts of $CaCO_3$ raising the pH to less than 3.3-3.4 (in KCl) did not much improve the growth, but raising the pH to 4.4 caused a 100 % survival of plants. Exclusion of aluminium from the soil solution did not influence growth significantly. They concluded that addition of nutrients, singly or in combination, did not increase survival and growth of plants unless the pH was raised, and that a high H^+ ion concentration in the soil limits survival and growth of *Galium*. Later, studying a range of seedlings of native species, a critical pH range of 3.5-4.3 (in KCl) was identified. At pH 3.5 (about 3.9 in water), only one species was frequent; all the other 12 species studied were absent (Falkengren-Krerup & Tyler 1992).

In the acid soils, adsorbed aluminium ions maintain an equilibrium with aluminium ions in soil solution. Then, the pH is maintained by the movement of aluminium ions from clay to the solution, producing a buffering action to soil pH. Adding basic nutrients such as potassium or calcium chloride, will cause aluminium ions in solution to precipitate as the hydroxide (Kennedy 1986). Calcium chloride additions to the soil do not raise the pH, while potassium chloride addition can cause nutrient deficiencies in some acid soils, as chloride will carry away Ca^{2+} and Mg^{2+} if they are leached (Rowell 1988). In the present study, the decrease of soil pH by the release of hydrogen ions probably happened, induced by additions of potassium chloride, and especially by the larger addition of readily soluble calcium chloride. Those results contradict some studies in other tropical forests. Cuevas & Medina (1988), in contrasting rain forests in the Rio Negro basin in Venezuela, found that the fine root growth in bags placed on the soil surface responded positively to nitrogen additions in the low *bana* and to phosphorus and calcium additions in the *tierra firme* forest. They concluded that *bana* forests were limited by nitrogen and the *tierra firme* forest by calcium and magnesium. In Sabah, Green (1992) found no effect of added nitrogen, phosphorus and potassium to fine root growth in bags in the surface soil. In

Costa Rica, Denslow *et al.* (1987) always found positive responses for forest species growth with complete nutrient fertilization, but there were no responses of shrubby species to phosphorus additions. Lack of response to phosphorus addition was attributed either to the mycorrhizal associations of the species or to their low natural requirements of the nutrient. In fact, assessment of the actual requirements of trees would be necessary in connection with nutrient addition experiments, but it has never been done.

In the present study, as the addition of nutrients to the soil showed no positive effects on seedling growth unless calcium carbonate was added, and some of the nutrients had a clear negative effect on plants, there was no evidence of nutrient limitation, especially nitrogen and phosphorus, for seedling growth in the SFH and THF. Thus, toxicity induced by soil acidity seems to be the main cause for the high seedling mortality or poor growth in the nutrient addition treatments. Aluminium toxicity would appear as a possibility. However, as pointed by Rorison (1985), if aluminium is most effectively toxic in the presence of nitrate ions, what role does it play in excluding non-calcifuge species from acidic soils in which nitrate ions are in relatively low supply? In the soils of the study areas, the amounts of nitrate ions are very low (R.C.C. Luizão 1994). A second question is that of aluminium tolerance by tropical plants. Sobrado & Medina (1980), after a survey in Venezuela, found that species of most tropical lowland rain forests seem to be tolerant of high soil concentrations of mobile aluminium. This was later confirmed in several other studies (e.g. Cuenca *et al.* 1990) in tropical forests in South America. It is also recognized that plant species can have large differences in response to aluminium toxicity (Brenes & Pearson 1973). The question of plant tolerance to aluminium, with a wide range of response from different species, should also be linked with the fact that "chelated aluminium in upper soil horizons is not as toxic as free aluminium in solution, which may partly account for the lower critical pH values for plant growth in organic soils and the significance of organic matter additions in the management of soil acidity" (Rowell 1988). Lower total amounts of aluminium in organic soils may also lower the critical pH values (Rowell 1988). Aluminium may form soluble or insoluble complexes with organic matter or it may be non-specifically adsorbed onto exchange sites. Displacement of aluminium from organic matter (by non-complexing cations such as

potassium) leads to electrostatic adsorption at exchange sites (Ritchie 1989). Hoyt (1977) found that for soils of similar pH even though the exchangeable aluminium decreased with increasing organic matter, there was a concomitant increase in the exchangeable acidity due to the buffering ability of the organically complexed aluminium. The removal of the aluminium forms by addition of bases would cause a decrease in the soil pH. Also, the removal of hydrolysed aluminium from solution would induce further solution hydrolysis of aluminium and therefore a lowering of the pH (Ritchie 1989). In the present study, the pH values were similar in the three forest types, but the soil organic matter in the SHF was much lower than in the THF and LERF, and the H^+ saturation of the LERF soils was infinitely lower than in the heath forest soils, and especially the SHF soils. There is increasing evidence of the toxicity of H^+ *per se* (Alva *et al.* 1986). Toxic effects of aluminium in the soil solution appear to occur at a lower Al^{3+} activity because of a concomitant H^+ ion effect on root growth. Injurious effects of H^+ at pH 4 to 5 can be offset by additional calcium but not at pH 3 (Alva *et al.* 1986; Ritchie 1989). In the present study, it is possible that the addition of bases to the very acid soil, especially calcium (applied in larger amounts as calcium chloride), have displaced aluminium from exchange sites, broken the soil-pH buffering and inducing a strong toxicity of H^+ in the soil. That would be in agreement with suggestions made by Proctor *et al.* (1983a) for soils under heath forests in Sarawak. It also would help to explain the negligible amounts of potassium in the soil of the study sites (Table 2.3a, b, c - Chapter 2), with pH generally below 4 in the upper layers, since K^+ in acid soils (pH < 5) is displaced from exchange sites by H^+ and leached from soil (Fitter & Hay 1991).

The H^+ toxicity as a major feature in acid and organic soils is also supported by recent findings by Skyllberg (1990, 1991) in a study of a Haplic Podzol in a boreal coniferous forest in Sweden. He found that the humus layer (O) had a pH significantly and positively correlated with aluminium. He suggested in acid humus layers and organic horizons, with a pH below 4.0, that aluminium cations act as any "base cation", through a H^+-displacement at cation exchange sites. Thus, instead of acidifying effects, aluminium ions in soil would be beneficial, buffering the pH at levels not toxic to plants, and the lack or displacement of such ions would cause strong toxicity for plant

roots. In the present study, Al^{3+} concentrations were very low in both heath forests, SHF and THF, and H^{+} concentrations high (Tables 2.3a, b, c). Then, the addition of bases to soil, especially the large additions of readily soluble calcium chloride, may have caused a strong toxicity to plant roots, through the displacement of the little aluminium in soil in the SHF and THF, but much less in the LERF, with a higher soil aluminium concentration.

Because of the wide range of natural seedlings' species, ages, and heights in the study plots, each likely to have different requirements and producing distinct responses to the nutrient additions, together with the failure of the experiment with *Diniza excelsa*, it is not possible to draw firm conclusions. In addition, light usually plays an important role in the seedling survival and growth. However, the fact that small gaps were used for the experiments, and that in such small quadrats similar amounts of light were likely for all treatments, validating the results found here. Nevertheless, other experiments must be made to allow further insights on the possible nutrient or pH limitations for plant growth in the heath forest soils. In long-term fertilization experiments on montane forests in Jamaica, the responses of adult trees to nitrogen addition were species-dependent (Tanner *et al.* 1990), and the same dependence on species may have occurred in the seedlings in the present study. It must be also pointed that possible toxicities caused by phenolics in the soil were not evaluated, and may have contributed to the strong negative effect of calcium chloride in the SHF and THF, where they are particularly abundant (Lisboa 1976a; Anderson & St. John 1981). Whitmore (1990) indicates that phenols are abundant in heath forest leaves and litter, and that these may be toxic or inhibit uptake when they leach into the soil. Soil phenolics directy affect germination and especially the growth of higher plants, and concentrations of soluble phenolics are correlated with organic matter content, and highest in the superficial L and F organic layers (Kuiters 1990). In the organic layers of the THF soils, evidence was found of phenolic leachates, in the form of green-brownish bubbles (R.C.C. Luizao 1994). These were certainly released by the decomposition of either the litter on the soil surface or the fine roots, the main originators of phenolics in soil (Kuiters 1990). However, in the present study, using pre-existing natural seedlings, and where control

plots showed no strong mortality, the putative toxicity of phenolic compounds would have interacted with the added nutrients, making it still more difficult to explain the mechanisms involved. The role of phenolic substances is closely related to pH and soil nutrient status, and plant growth is especially affected under acidic soil conditions, where several mechanisms act additionally or even synergistically (Kuiters 1990). Although phenolics are generally not high enough to be strongly toxic, they are more physiologically active at low pH (Kuiters 1990) and, in the present study, they may have interacted with H^+ to produce the high mortality of seedlings in the SHF and THF when pH buffer was probably overwhelmed by the large additions of calcium chloride.

Chapter 8. PLANTED SEEDLINGS IN GLASSHOUSE EXPERIMENTS USING SHF, THF, AND LERF SOILS

INTRODUCTION

Field experiments (Chapter 7) had been made on SHF, THF, and LERF and had shown positive effects with calcium carbonate additions but consistent negative effects with additions of calcium chloride. However the results were somewhat difficult to interpret because of the high diversity of the experimental plants and the death of the planted seedlings of the tree species selected. This chapter reports a further experiment made using "Dryland rice" as a bioassay in a glasshouse experiment on the soils from the SHF, THF, and LERF.

MATERIAL AND METHODS

Humus (including decomposing litter and raw humus material) and top soil layers were collected separately from each of the three forest types, air-dried and sieved through a 2-mm mesh. Eight 7-cm diameter (200-ml volume) pots were prepared for each of seven experimental treatments for each soil type. Four of the eight pots were filled only with soil, and the other four with soil plus a top layer of humus of a thickness which matched that of the soil in the field. A total of 168 pots was used for the experiment, which had six addition treatments and one control. The seven treatments were randomly located on wooden benches inside a glasshouse. The rate of fertilizer addition was at the lower end of the generally recommended ranges (Anghinoni & Volkeweiss 1984) for farmers in acidic soils in Brazil (except it included calcium chloride, not used by farmers). The added chemicals and their rates of application were: nitrogen as 150 kg of urea (NH_2CONH_2); phosphorus as 50 kg of sodium phosphate (NaH_2PO_4); potassium as 60 kg of potassium chloride (KCl); calcium as 2,000 kg of calcium chloride ($CaCl_2$); calcium as 2,000 kg of calcium carbonate ($CaCO_3$); a combination of 1, 2, 3, and 5; and, a control with no added chemicals.

All nutrients were added to the pots freshly dissolved or suspended in 20 ml of water. Controls received only 20 ml water. The nitrogen was added initially and after 21 d and

35 d to make up the total; the other chemicals were applied initially and the total made up after 21 days. Just after receiving the first treatment, the pots were planted with selected seeds of "Dryland rice" (Brazilian variety IAC-47) (ICEA 1987). Ten seeds were placed in the top 1-cm of soil (or at the bottom of the humic layer) in each pot. The pots were kept moist and ten days after initial planting, the germination was assessed. At the same time the number of individuals per pot was adjusted to six. After 50 d the rice plants were assessed and harvested. At harvest, the whole plant (shoot and root parts) was carefully removed, brushed to remove the soil particles, divided into shoot and root sections, and oven dried (70 °C) to constant weight. The shoot and root biomass, as well the numbers of surviving and dead seedlings were calculated. The soils in a series of non-planted duplicate pots treated with calcium carbonate were measured for pH (5 g soil:10 ml distilled water). The pH measurements were made on one composite sample initially and on four samples from each forest type after 20 d and 50 d.

Multiple analyses of variance were made to test significant influences of the treatments, the forest types, and the interaction between these factors. One-way analysis of variance connected to Dunnett's test was used to assess possible differences between treatments and the control in soils of each forest type, and also to test significant differences for each treatment and forest type between the pots with and without the inclusion of a humus layer. Square-root transformations were applied to the numbers of germinated and dead seedlings, while the shoot and root biomasses were log-transformed for normality before analysis.

RESULTS

The pH values measured in the soils of the two heath forests were higher than those usually mentioned or measured in the sites of the present study (Ranzani 1980; Anderson 1981; Luizão 1994).

In the non-planted pots, the addition of $CaCO_3$ raised the pH_{H2O} from 4.6 to 7.0 in the SHF; from 4.0 to 5.9 in THF; and from 3.9 to 7.6 in LERF, especially where the humus layer was present (Table 8.1). From 20 d to 50 d, pH values decreased from 7.0 to 6.2 in the SHF; from 5.9 to 4.6 in THF; and from 7.6 to 7.1 in LERF. Both the increase in the first 20 d and the decrease between 20 d and 50 d were fastest in the pots with the humus layer, except in the LERF soils, where the decrease was slower (Tab 8.1).

Table 8.1: Values of pH_{H2O} measured in a composite sample of soils from each forest type prior to the addition of calcium carbonate, and in non-planted pots (n=4) 20 d and 50 d after the addition of the calcium carbonate. Values in parenthesis are SE.

		0 d	20 d	50 d
SHF	without humus	4.27	6.06 (0.93)	6.20 (0.77)
	with humus	4.28	7.00 (0.34)	6.21 (1.18)
THF	without humus	3.71	5.16 (0.89)	4.82 (0.96)
	with humus	4.03	5.92 (0.73)	4.64 (0.45)
LERF	without humus	4.52	7.16 (0.26)	6.18 (1.22)
	with humus	3.94	7.57 (0.04)	7.12 (0.22)

In the planted pots (Fig. 8.1), rice seedlings virtually stopped growth in all treatments after 35-40 d. The inclusion of the humus layer produced a few significant differences in the number of germinated and dead seedlings, and in biomass, but varied with soil type and the treatment. In the SHF soils, only the treatment NPK + $CaCO_3$ produced a lower biomass of both shoots ($F = 23.0$; $df = 1$; $p < 0.01$) and roots ($F = 18.1$; $df = 1$; $p < 0.01$), in the pots with humus than in the pots without humus layer. In the THF, significant negative effects of the humus layer were found when KCl and $CaCl_2$ were added. Pots with the humus had higher seedling mortality ($F = 7.51$; $p < 0.05$), and lower root mass ($F = 7.28$; $p < 0.05$) when KCl was added, and lower germination ($F = 26.1$; $p < 0.01$) and lower root mass ($F = 13.3$; $p < 0.05$) with $CaCl_2$. In contrast, the LERF soils showed a positive influence of the humus layer on seedling germination and growth, in several treatments. The number of germinated seedlings in pots with the humus layer was higher with the addition of $CaCl_2$ ($F = 37.2$; $p < 0.01$) and $CaCO_3$ ($F = 6.64$; $p < 0.05$). The shoot mass was higher in the pots with humus and NaH_2PO_4 ($F = 12.6$; $p < 0.05$), $CaCl_2$ ($F = 9.45$; $p < 0.05$), $CaCO_3$ ($F = 16.2$; $p < 0.01$), and NPK + $CaCO_3$ ($F = 19.0$; $p < 0.01$). The mass of roots was higher ($F = 16.8$; $p < 0.01$) only where NaH_2PO_4 was added. It must be noted, however, that most of the results of the treatments with and without the inclusion of a top humus layer generally showed the same trend (both greater or both smaller than the control) with no consistent results (Appendix 8.1). Thus, additional statistics for differences between treatments and forest types were made combining those with and without a humus layer.

The two main factors analysed, the soil type and the treatment, generally had a significant influence on the germination, survival and growth (Fig. 8.2; Table 8.2). However, there was no significant effect of soil type on the total number of germinated seedlings. Overall, the shoot and root biomass were less with $CaCl_2$ and greater with $CaCO_3$ and NPK + $CaCO_3$ (Fig. 8.2). In the SHF and THF, the few survivors in the $CaCl_2$ pots grew well, but generally $CaCl_2$ inhibited germination and killed seedlings (Fig. 8.2 and Appendix 8.1). Germination was not significantly affected by any treatment in the SHF soils, but it was significantly lower in the THF soils with both urea and $CaCl_2$ ($F = 5.39$; $df = 6$; $p < 0.001$), and lower in the LERF soils with $CaCl_2$

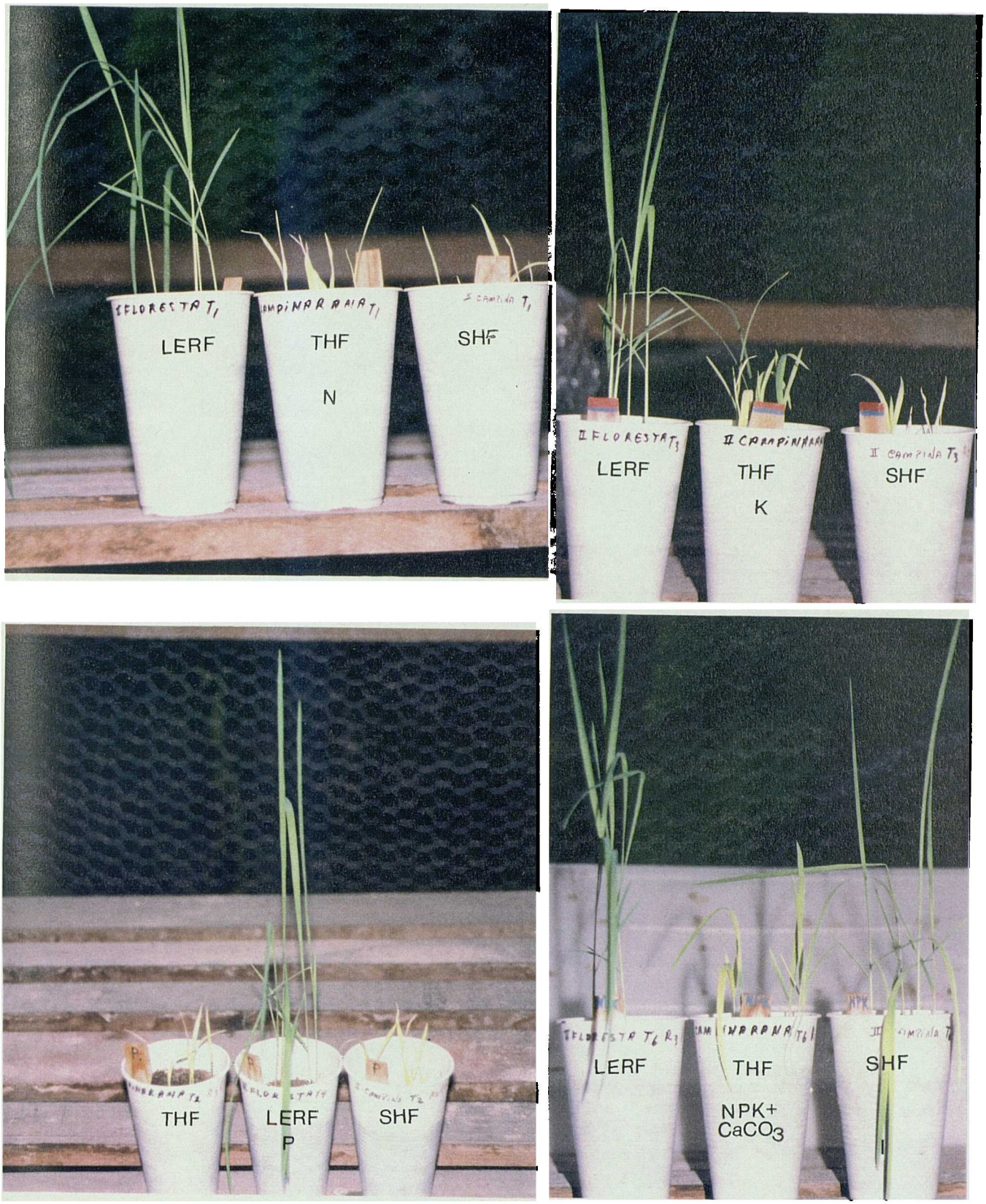


Figure 8.1: Rice seedlings 20 d after planted in glasshouse on soils from the SHF, THF, and LERF, showing the treatments 1 (N-urea), 2 (P-NaH_2PO_4), 3 (K-KCl), and 6 (NPK + $CaCO_3$).

($F = 2.43$; $p < 0.05$). The number of dead seedlings was increased by $CaCl_2$ in the three soil types (SHF: $F = 14.4$; $p < 0.001$; THF: $F = 10.3$; $p < 0.001$; and LERF: $F = 24.3$; $p < 0.001$). In the THF soils, addition of urea increased mortality ($F = 10.3$; $p < 0.001$). The seedling mortality was lower in the SHF than in THF soils and lower than in the control when N, P or NPK + $CaCO_3$ were added, but the difference was not significant. In SHF soils, significantly higher shoot biomass occurred with $CaCO_3$ and NPK + $CaCO_3$ ($F = 16.1$; $p < 0.001$). In the THF soils, higher shoot biomass was found only with $CaCO_3$ ($F = 7.66$; $p < 0.001$). In the LERF soils, higher shoot biomass was produced with NPK + $CaCO_3$, but $CaCl_2$ caused a significant decrease ($F = 28.4$; $p < 0.001$). Root biomass was significantly increased in the SHF soils by both $CaCO_3$ and NPK + $CaCO_3$ ($F = 9.23$; $p < 0.001$), but only by $CaCO_3$ ($F = 5.91$; $p < 0.001$) in the THF soils. The shoot and root biomass were both higher in the SHF soils than in THF soils when NPK + $CaCO_3$ were added (both $p < 0.01$). In the LERF soils no significant increase in root biomass was found with any treatment, but additions of urea and $CaCl_2$ caused a significant reduction ($F = 19.9$; $p < 0.001$).

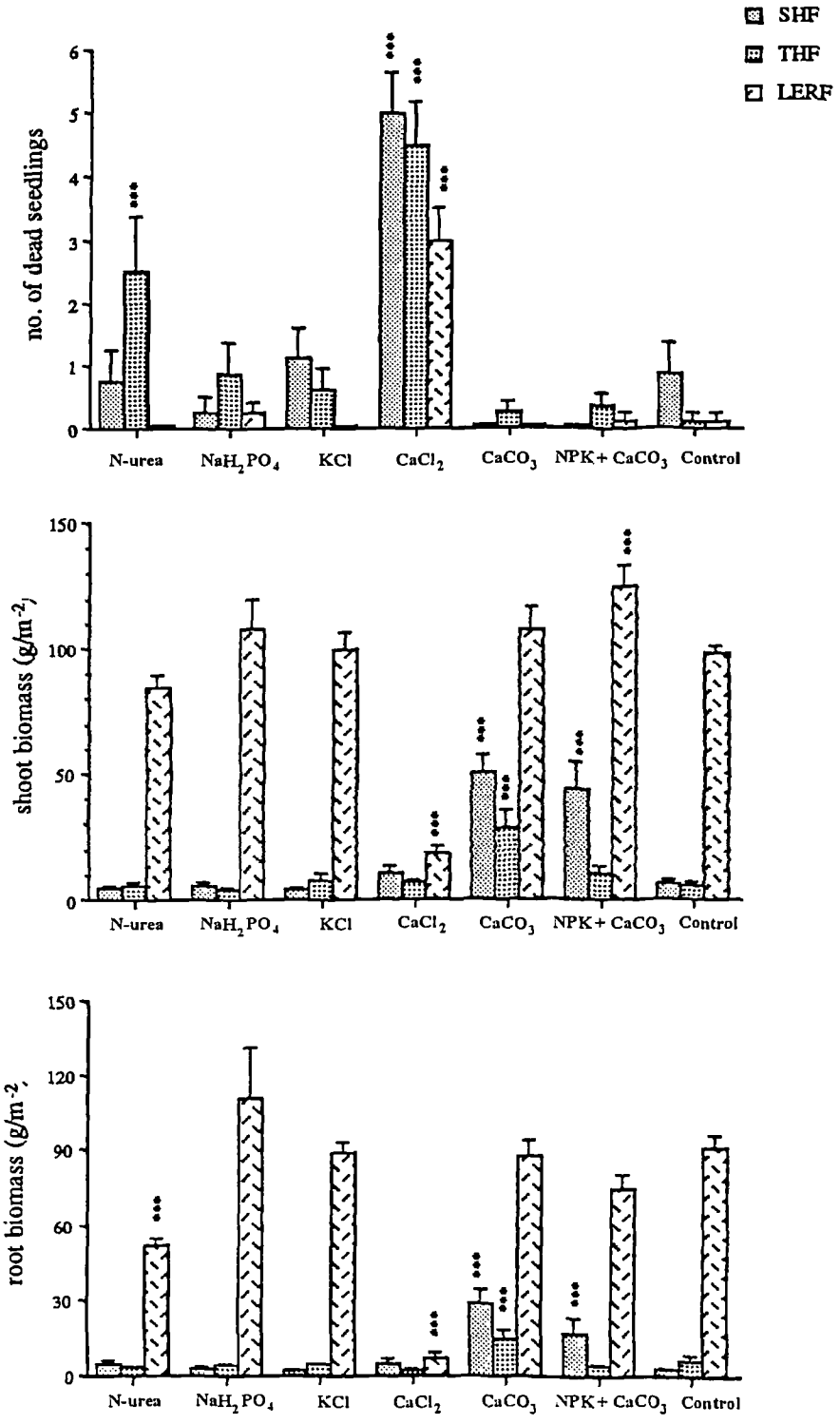


Figure. 8.2: Number of dead rice seedlings, and shoot and root dry mass ($g\ m^{-2}$) in each treatment after 50 d, using soils from the SHF, THF, and LERF. Values are means and SE, and significant differences in relation to the control are indicated by asterisks: $^{*}0.05$; $^{**}0.01$; and $^{***}0.001$.

Table 8.2: Summary table of the multiple analyses of variance for the number of germinated and dead seedlings, and the aerial and root biomass of rice seedlings after 50 d.

Number of germinated seedlings				
Source	df	SS	F	p
Treatment	6	2.35	4.80	< 0.001
Forest type	2	0.30	1.81	> 0.05
Treatment * Forest type	12	2.51	2.56	< 0.01
Residual	21	12.0		
Total	41	17.2		
Number of dead seedlings				
Source	df	SS	F	p
Treatment	6	31.9	36.9	< 0.001
Forest type	2	2.45	8.54	< 0.001
Treatment * Forest type	12	3.55	2.6	< 0.05
Residual	21	21.1		
Total	41	59.0		
Shoot biomass				
Source	df	SS	F	p
Treatment	6	278	37.9	< 0.001
Forest type	12	1347	551	< 0.001
Treatment * Forest type	12	220	15.0	< 0.001
Residual	21	180		
Total	41	2025		
Root biomass				
Source	df	SS	F	p
Treatment	6	207	30.3	< 0.001
Forest type	2	1218	535	< 0.001
Treatment * Forest type	12	227	16.6	< 0.001
Residual	21	167		
Total	41	1819		

DISCUSSION

The relatively high pH values measured in the mixed soils of the SHF and THF prior to the treatment application might be related to the sample preparation for the experiment. The physical structure as well as the biological composition of the soil influence considerably its fertility and other characteristics (Healey 1989). Thus, mixing and sieving the soils might have induced changes in their pH's because of the disruption of soil microsites. The LERF soil showed a better capacity to buffer the pH (initially increased by the addition of calcium carbonate) especially when a humus layer was present. The THF soil, with a thicker humus layer, had the lowest capacity to keep the pH levels obtained by the calcium carbonate addition, and its pH decreased sharply between 20 d and 50 d.

Overall, the results found in the glasshouse experiment using rice seedlings confirmed those found in the field study on natural seedlings (Chapter 7): the only general positive effect on seedling growth was caused by the addition of calcium carbonate, while addition of calcium chloride had a general deleterious effect on seedlings, inducing high mortality rates. The high mortality rate was less than that associated with calcium chloride in the field experiment, possibly because it was readily leached from the pots by the frequent watering (C. Grimaldi, personal communication), which allowed the later-germinating seedlings to survive and grow. Initially, it is likely that calcium chloride caused a release of H^+ and Al^{3+} held on the exchange complex, causing a strong unbalance in the nutrient solution and consequently toxic effects on plants. At very low pH there is a direct H^+ toxicity in soil (Fitter & Hay 1991; Kinraide 1993; C. Grimaldi, personal communication). The amelioration of H^+ toxicity by Al^{3+} ions is reciprocal (Kinraide 1993), and Al^{3+} decreases solute leakage at low pH, then producing a growth enhancement (Foy 1984; Rowell 1988; Staaf 1992). The result of the aluminium complexation would then be an increase of soil toxicity because of lack of protective aluminium ions.

The reasonable germination rate followed by poor development or even death of the seedlings on soils with humus layer agrees with observations by Staaf (1992) who, studying survival and growth of seedlings of four different forest species in field and laboratory experiments in Sweden, found that seedlings of all species grew poorly on mor soils, and that no seedlings survived for more than two years. He concluded that mor soil is, indeed, a very unfavourable substrate seedling survival and growth, and that mechanisms related to soil acidity prevented the four studied plant species from growing on the mor soil. Virtually only liming had positive effects, and these were restricted to the organic horizons (L, O_1, O_2) (Staaf 1992). In highly acidic mor soils, plant establishment from seeds and growth of seedlings were more sensitive to low pH than survival and growth of adult plants (Falkengren-Krerup & Tyler 1993).

The negative effects of the humus layer included in part of the pots may also be the result of phenolic compounds (leached by the frequent watering of the pots), affecting seedling roots, especially in the heath forest soils. In Sarawak, Brünig (1983) reported that heath forest soils have high concentrations of secondary metabolites, which may produce toxic effects on the vegetation and reduce available nitrogen in soil. Also in the study sites evidence has been found of high phenolic concentrations in heath forest soils (Lisboa 1976a; Anderson & St John 1981; Luizão 1994). In studies made in the same forests from where soils were collected for the present study, Anderson & St John (1981) found that the important heath forest species *Pradosia schomburgkiana* (Sapotaceae), had a high content of polyphenols, and Lisboa (1976a) reported that leachates of its leaf litter inhibited the growth of lettuce seedlings and apparently the establishment of seedlings of other tree species under the *Pradosia* canopies.

The general coincidence of the results observed in the glasshouse (using a cultivated crop) with the field experiment (using varied native species) was reassuring. According to Chapin *et al.* (1986), few native species from nutrient-poor soils seem to have the ability to respond quickly and positively to the enhanced nutrient supply, which is perhaps not surprising in a community that evolved in low nutrient conditions. On the other hand, Dryland rice, though having mid to high tolerance to low pH (Yu 1991;

Weischet & Caviedes 1993), is a crop and will have relatively high nutritional requirements.

The results found in the present study agree with recent studies on central Kalimantan heath forest soils. In a pot experiment, also using a type of dryland rice as test-plant, and basically the same nutrients added to soils, Smith (1994) found no seedling root growth in any treatment in the heath forest organic soil, except when calcium carbonate was added. However, there was some seedling germination and growth when nitrogen (as urea) was added to the soil in concentrations lower than 150 kg ha^{-1} (the amount used in the present study). This result may suggest that nutrient-poor acid soils can only respond to smaller additions of nutrients which do not disrupt the functioning of the system. Smith (1994) speculated that poor growth of rice on heath forest soils was due to toxins in soil and not due to a low soil nutrient status, and that toxic effects of the organic and mineral heath forest soils could be ameliorated by the addition of calcium carbonate, which raises the pH.

The results of bioassays must be considered as having limits to the extent to which they can be used to draw firm conclusions about the relative fertility of the tested soils or their effects on seedlings (Healey 1989). However, in view of the comparative approach used in the present study, it is possible to draw a few tentative conclusions. The soils with no top organic layer in the SHF may be nutrient limited. A better response, though not always significant, was observed for the SHF soils than for THF soils when nutrients were added. For the THF soils (which invariably have a mor humus layer) there is no evidence of nutrient deficiencies as the chief cause of limited plant growth. However, it is possible that calcium and other bases (including aluminium and other metals such as manganese and zinc) may be limiting seedling establishment and growth, especially in the heath forest soils. The mechanisms of this potential limitation are still not well known, but they do appear to have an important role in tropical acid soils (P.M. Vitousek, personal communication). Additionally, there was some evidence of toxic effects of soil pH and secondary compounds, as illustrated by the slight negative responses to the inclusion of a humus layer in the pots with heath forest soils, and by the largely positive response to the addition of calcium carbonate to the soils.

Chapter 9: GENERAL DISCUSSION

Soils and vegetation

The distribution and physiognomy of vegetation have been often related to the soils under the trees, but studies of such relationships have given contrasting results. In Pasoh, peninsular Malaysia, Wong & Whitmore (1970) found no evidence of links between forest composition and soil types. A reinvestigation by Ashton (1976), using a greatly enlarged sampling area, concluded that floristic composition was linked to environmental factors, including soil. In Sarawak, Newbery & Proctor (1984), although recognizing that soil differences among the plots were the likely cause of their contrasting vegetation, found that soil factors had only a limited impact on the floristics.

Contrary to many previous assumptions, a lack of direct relationship between soil nutrients and biomass or species richness for lowland evergreen rain forests has recently begun to be accepted. For instance, Primack *et al.* (1987), evaluating 15-year's data of plant growth in three natural forests in Sarawak, found that `the anticipated relationship between soil fertility and growth rate is not demonstrable, and other factors, such as local weather patterns, elevation, tree competition, pests and pathogens also play a role in controlling tree growth rates'. Thus, the use of nutrient contents of superficial soil layers to explain species distribution is of limited value (Medina & Cuevas 1994). Organic matter production by the vegetation strongly modifies surface soil chemistry (Lugo *et al.* 1990), and these influences are also reflected in the mineral soil, and can be associated with differences in the amount and quality of litter produced (Medina & Cuevas 1994). In Maracá, northern Brazil, Thompson *et al.* (1992) showed that complex, non-sclerophyllous forests can develop on coarsely sandy, apparently nutrient-deficient soils. The Maracá data showed that in rain-forest trees there is likely to be little correlation between foliar and soil nutrient concentrations (as conventionally measured), and therefore cast doubts on whether sclerophyllous leaves are a response to low soil nutrient supply (Thompson *et al.* 1992). Thus, existing data suggest there is little correlation between soil chemistry and forest stature (Proctor 1992), and no simple relationship between soil nutrient element concentrations and biomass or species richness, neither for

lowland evergreen rain forest nor for heath forest. One major cause of the large variation in heath forest chemistry may be the presence or absence of the distinct organic layer on top of the mineral soil. Where a thick organic layer is present, as generally occurs in San Carlos, Venezuela (Herrera 1979; Klinge & Medina 1979), the supply of nutrient may be very different from that of sites where the organic layer is absent, as in most of the stunted heath forests in central Amazonia (Anderson 1981). In tropical Spodosols, organic matter contains the principal cation exchange sites and is generally recognized as a major pool of nitrogen and phosphorus (Sanchez 1976; Proctor *et al.* 1983a). In heath forest soils in Sarawak, Katagiri *et al.* (1991) found higher nitrogen, potassium, calcium, and cation exchange capacity in the more organic surface (0-10 cm) layer. Their data were similar to those obtained in the present study, and confirmed that heath forests in particular are highly dependent on the nutrient recycling from organic matter of the top soil, and once heath forest is felled the soil organic layer degenerates very quickly (Whitmore 1990). After organic matter depletion, the remaining white sand is highly unfavourable chemically (since it has few nutrients) and physically because of its coarse texture and excessive drainage. This rapid and easy soil degradation is one of the reasons why agriculture on old heath forest sites is virtually impossible (Whitmore 1990). However, little is still known of the mechanisms acting on the surface soil or in the litter-soil interface in tropical heath forests. It is recognized a need to base further comparative studies on nutrient availability on the fractionation of the nutrients into biologically meaningful forms (Attiwill & Adams 1993).

The sandy-textured surface soils of the SHF, THF, and LERF had some of the lowest pHs and clay concentrations recorded from rain forests on acidic soils, but the concentrations of nutrients (except for calcium in all three forest types) in the surface soils were not exceptionally low. Among the three forest types studied, the main differences were in the values of CEC and concentrations of exchangeable aluminium, both much higher in the LERF than in the heath forest soils. The quotient H^+/Al^{3+} was much higher in the heath forests, especially in the SHF, than in LERF, indicating that even having similar pHs the soils differed greatly in organic matter and exchangeable aluminium, with a much higher

potential pH toxicity in the heath forest soils because a lack of the buffering capacity of the organically complexed aluminium (Hoyt 1977).

Despite the high water retention capacity of the soil organic layer, as found also in the present study, especially in the THF with a thick humus layer, it is a fact that most (if not all) heath forests experience droughts from time to time and their unusual leaf features could be adaptations for those specific periods (Brünig 1974). However, Peace & Macdonald (1981), testing eight species of detached leaves from Sarawak heath forest, found no evidence that those leaves had a special ability to avoid or resist desiccation, despite their unusual structure. In Sarawak (Proctor *et al.* 1983a), and in Maracá Island, in distinctly seasonal northern Brazilian Amazonia (Thompson *et al.* 1992) found indirect evidence against the drought hypothesis. In the present study, no evidence was found to suggest that drought is limiting plant growth in the heath forest, since the soil was never excessively dry, and lower water potentials were recorded in the LERF as a result of its higher mass of roots. However, considering that the two years of the study were not very dry , it is possible that important soil water deficit can occur in drier years, especially in the SHF. Long-term observations are required to confirm this suggestion. The longest dry spell observed affected the densities of litter animals acting on the soil surface, but apparently not directly the plants rooting in the mineral soil. That is possibly because sandy soils can have low water contents, but most of it is available to plant roots (Killham 1994). However, drainage in the coarse sandy soil of heath forest may cause important changes in soil chemistry, and these may affect plants.

As a result of its patchy distribution in the SHF, the vegetation of this forest type had very low tree ($\geq$ 10 cm dbh) density, diversity, and biomass, compared with the LERF, and the THF showed an intermediate density of trees and biomass, but still a low species richness. The SHF and THF had a high dominance of few species, and apparently a high endemism as observed for central Amazonia (Anderson 1981). This contrasts with a relatively high diversity in some south-east Asian heath forests, such as in Sarawak (Brünig 1969, 1974; Proctor *et al.* 1983a). The heath forests in the upper Rio Negro have an intermediate species richness (Anderson 1981). The lower diversity in the scattered heath forests in central Amazonia (Anderson 1981) may be the result of the isolation of small areas of

heath forests and the inadequacy of the long-distance dispersal mechanisms (Macedo & Prance 1977). The LERF was unusually dominated by the Caesalpiniaceae, and had a relatively low species richness (Campbell *et al.* 1986; Gentry 1988), and a basal area (31.0 m^2 ha^{-1}) which is at the lower end of the range for lowland rain forests in northern South America (Lamprecht 1972; Guillaumet 1987). In spite of that, the LERF showed a tree density (887 ha^{-1}) slightly higher than the upper range reported by Campbell *et al.* (1986) and Gentry (1988) for Amazonian rain forests. The estimated biomass (410 t ha^{-1}) of the LERF was slightly higher than the range of 344-393 t ha^{-1} reported by Klinge *et al.* (1975) for lowland evergreen rain forests on clay-rich soils in Amazonia. This suggests that forests on Ultisols, like the LERF, may have a trend for larger biomass than the neighbouring forests on Oxisols. Higher biomass of forest on Ultisols was also found in Venezuela by Buschbacher (1984), and the reason for that was the high tree density together with a few exceptionally large individuals. There was no evidence of limitation imposed by soil chemistry for plant growth on the sandy soils in the LERF, despite soil nutrients mostly similar to the heath forest soils. The most important difference perhaps was the big difference in the quotient H^+/Al^{3+}, which was much lower in the LERF soils, indicating the higher soil aluminium may buffer pH and ameliorate H^+ toxicity. However, other factors related to soils, such as the topography and drainage may exert a strong influence on vegetation, since plant species are likely to vary in their responses to soil changes, and interactions between these factors are likely to be important (Proctor 1995). The heath forests investigated in the present study are not normally waterlogged unlike some heath forests in Borneo (Whitmore 1984), Brazil (Ducke & Black 1953), and Venezuela (Herrera 1979; Klinge & Medina 1979). Also, the stunted facies show a patchy vegetation with a lack of an organic layer in open areas, indicating that the mechanisms for the organic matter and nutrient cycling may be distinct from other heath forests.

Nutrient cycling

Overall, the nutrient cycling via litter, in the SHF, THF and LERF, was slower than previously measured for some Amazonian rain forests (Klinge 1977; Herrera *et al.* 1978;

Jordan 1985; Luizão & Schubart 1987), and the amounts of nutrients cycled were relatively low.

The fine litterfall in the LERF was at the lower end of values for tropical lowland evergreen rain forests, while THF ranked in the middle of the few other published results for heath forests. The SHF apparently had the lowest value of fine litterfall recorded for a lowland tropical forest: 3.8 t ha^{-1} yr^{-1}, not surprising in view of the open vegetation of low biomass. The concentrations of nitrogen in litterfall were generally much lower in the heath forests, especially in the SHF than in LERF, but both SHF and THF had higher concentrations of calcium and magnesium. These results agree with studies made in Sarawak (Proctor *et al.* 1983b) and Venezuela (Medina & Cuevas 1989). In Sarawak, Proctor *et al.* (1983b) found that the most distinctive feature of the heath forest litterfall was its low nitrogen concentration, and they argued that the distinctively low pH of the highly organic surface soils of heath forest may limit the nitrogen mineralization. In the present study, leaf litterfall of the important heath forest species *Pradosia schomburgkiana* had exceptionally low concentrations of nitrogen. Phosphorus concentrations in SHF, THF, and LERF were within the range recorded for other tropical forests, while the concentrations of calcium and magnesium were the least recorded, except those found by Proctor *et al.* (1983) in Sarawak.

The k_L values for leaf litterfall were in the lower range of the few other data available for Amazonia, and for the SHF and THF they were lower than the values for a heath forest in Sarawak (Anderson *et al.* 1983), indicating a slow turnover of organic matter in the SHF and THF. The turnover of nitrogen, iron, manganese (in both SHF and THF), and the turnover of phosphorus, calcium, and zinc (in SHF), were all slower than in the LERF. In all forest types, nitrogen was the most slowly returned nutrient, indicating a strong immobilization in the litter layer, as often reported elsewhere (Attiwill 1968; Klinge 1977; Luizão & Schubart 1987; Attiwill & Adams 1993). On the other hand, copper and zinc appeared to be faster released in the THF than in LERF.

In contrast to many other studies in tropical rain forests, there was no sharp decrease of the initial dry weight of bagged leaves during the first periods of decomposition, partly because of the unusual climatic pattern of the wet season experiment. As a consequence,

the weight losses observed were better described by a linear model, especially for *Aldina* and *Pradosia* leaves, the substrates of lower quality. An important feature of the decomposition process in the heath forests, and especially in the SHF, the most open vegetation type, was the strong abiotic control of decomposition rates in the initial phases of the experiment, during the dry period. There were successive periods of drying and wetting the leaves which may have broken down the material, followed by rainwater leaching and losses of particles through meshes, intensifying the decomposition (Anderson *et al.* 1983; Babbar & Ewel 1989).

The differences in decomposition rates found among foliage types (especially between *Clitoria*, with lower waxiness, thickness, and toughness, and the two heath forest species) were much greater than differences among ecosystems, confirming findings of other authors in tropical forests (Witkamp 1966; Cuevas & Medina 1983; Babbar & Ewel 1989). Among the major factors inducing decomposition, the action of white fungi and mycelia (which were stronger in the THF than in the other two forest types) was very important, and increased considerably on decomposing leaves after 60 d. Sun leaves of both species, *Aldina* and *Pradosia* had no significantly different rates of weight loss in relation to shade leaves, contrasting with results found in tropical rain forests in Australia (Lowman 1988). Lower rates of physical breakdown of decomposing leaves always occurred in the SHF, where lower densities of litter animals and lower penetration of fine roots occurred.

In the LERF, the activity of termites was important, especially for *Clitoria*, while in the SHF, there was a limited effect of termites and other litter animals. In the THF and LERF, fine roots penetrating litter bags appeared to contribute to the decomposition of bagged leaves, confirming results obtained in Venezuela (Cuevas & Medina 1983).

The unusual rainfall pattern observed in 1992, with a shorter wet season and a dry season interrupted by unusually wetter months, certainly played an important role in determining the lack of significant differences in the decomposition rates of bagged *Clitoria* leaves in the experiments starting in the wet and dry seasons. However, the slightly faster decomposition over a 1-year period of leaf litter exposed in the dry season, when the litterfall was higher in the THF and LERF, suggests a synchrony of processes in these

types of vegetation in a steady state. Interestingly, the decomposition in the SHF was slightly faster when starting in the wet season, and litterfall in that forest type peaked in January, in the early wet season, which could further support the synchrony hypothesis. Such synchrony has recently been shown to exist in lowland evergreen rain forests in Cameroon (Chuyong 1994), where periods of highest litterfall were followed by periods of highest decomposition rates of litter. The results of the present study stress the need for decomposition experiments with a duration longer than one year to assess properly the rates and patterns of tropical forest decomposition.

The release rates of calcium, magnesium, and manganese were slower in the SHF, probably because of low penetration of fine roots and the apparently stronger abiotic control of decomposition in that forest type. Litter decomposition in the SHF appears much more governed by leaching and physical breakdown of the decomposing material. Large increases in the concentration and mass of iron and aluminium during litter decay were found, especially in the LERF, a fact seldom recorded for aluminium (Luizão & Schubart 1987; Rustad 1994). The increases were likely to be the result of the transport (by raindrops or litter animals) of soil particles to the litter bags and the penetration of litter bags by fine roots, which were relatively rich in such elements, contaminating the decomposing leaves.

Among the three leaf species, *Clitoria*, which was more rapidly colonized by litter animals and attacked by termites (which may remove both leaf surface and structural parts) showed the fastest release of the macronutrients nitrogen, phosphorus, calcium, and magnesium.

The fine roots penetrating litter bags were positively related to the release of calcium, magnesium, manganese, zinc, and negatively to aluminium and iron, suggesting that they were causing a faster release of some elements or causing accumulation of others. However, such results are not sufficient to support the idea of direct nutrient cycling (Went & Stark 1968; Herrera *et al.* 1978) and nutrient limitations for root or plant growth (Cuevas & Medina 1983, 1988), since higher concentrations of mineral elements in the heath forest roots themselves (with diameter up to 6 mm) has been recorded (Klinge 1975). It is rather suggested that the main role of fine roots in decomposition is indirect.

facilitating access and action of decomposers (fungi and animals) into litter bags, and the accumulation of soil residues and organic matter within the bags.

Though the colonization of the decomposing leaves by litter animals was not particularly fast, and no groups could be recognized as pioneers, the number of individuals and taxonomic groups of litter animals were relatively high, especially in the LERF. Overall there was no significant relationship between the weights of residual litter in the bags and the numbers of animals they contained. The animals were mostly related to the moisture of the organic and upper soil layers, and were affected by short but severe dry periods, confirming suggestions made by Adis (1988) and Adis *et al.* (1989) that in central Amazonia the presence of arthropods on the forest floor fluctuates throughout the year mainly influenced by abiotic factors, particularly the short but pronounced dry season. Thus, climate was likely the main factor controlling the colonization of the leaves, especially in the more open SHF. The Diplopoda and Isopoda were apparently not limited by the lower pH of heath forest soils, showed higher densities than expected, while two other important groups of decomposers, earthworms and Isoptera, showed very low densities in the litter bags. The Diplopoda were ranked first in biomass in all three forest types, suggesting them as important decomposers, especially in the SHF and THF. The relatively high frequency and abundance of the Diplopoda and Isopoda, two moisture-limited groups, also suggest that the moisture of the upper organic and mineral layers, even when fluctuating considerably, is not likely to be a limiting factor for some of the litter animals in the SHF and THF, but it might be important for some groups, such as Copepoda and earthworms. The Isoptera were uncommon in the bags, especially in the SHF and THF, probably because of the high frequency of the most conspicuous termite-predators, the ants, and the predominance of humus-feeding termites, which do not feed on intact litter.

Both the number of taxonomic groups and the total numbers of litter animals were generally lower in the heath forest leaf species. especially in *Pradosia.* However important decomposers such as Diplopoda, earthworms, and Isoptera, showed no lower densities in the heath forest species, and Copepoda. Psocoptera, and Diplopoda were more frequently found on the more slowly-decomposed leaf species (*Pradosia* and *Aldina*) than

on the more palatable species, *Clitoria*, and are then indicated as important decomposers of heath forest litter. Copepoda and Psocoptera were more abundant on leaves of *Pradosia*, the most slowly-decomposed leaf species, which has the highest concentrations of both lignin and polyphenols (Lisboa 1976a; Anderson & St John 1981).

The low litter animal density found in the SHF may result from the lower soil organic matter and the many patches without any vegetation cover, and this may have contributed to reduced decomposition rates, especially for *Pradosia* litter, since microarthropods have a greater effect on the litter species more resistant to decomposition (Seastedt 1984). The low pH of the soils in the three forest types may have contributed to a slower litter animal colonization (Hågvar & Abrahamsen 1980) and the generally low decomposition rates. However, other factors such as the moisture of the organic and topsoil layers, and the toxicity of secondary compounds and the acidity of the litter itself, all acting together and interacting, may be of more importance. That could explain the lower densities of litter animals in the THF when compared with the LERF which has similar soil and litter moisture, but distinct litterfall and litter layer composition.

The most important decomposers were Collembola and Copepoda in the SHF; Acari, Collembola, Diplopoda, and Symphyla in the THF; and Acari, Collembola, Copepoda, and earthworms in the LERF. These results contradict most of the assumptions made based on studies in temperate forests (Petersen & Luxton 1982; Dindal 1990), but confirm some recent studies in tropical ecosystems showing a higher importance of earthworms and Diplopoda in acid soils (Lavelle & Pashanasi 1989; Fragoso & Lavelle 1992).

Nutrient limitation for plant growth

The faster release of calcium, magnesium, and manganese, when the biological activity is stronger, suggests that these elements could be limiting for the microflora and the decomposer animals. Also, significant relationships between fine root penetration and the release of calcium, magnesium and manganese were found here and in a shared study (R.C.C. Luizão 1994), in which it was also found that soil microbial biomass and soil respiration responded positively to additions of calcium to the soil. However, the apparent limiting effect of calcium and manganese for soil and litter organisms does not imply

these elements are also limiting for plant growth, since other factors may be involved (Attiwill & Adams 1993).

For instance, Grubb (1989) suggested that in nutrient-poor tropical soils, an important interaction between shade and nutrients (especially phosphorus) occurs, and that was partly confirmed in recent bioassays in lowland dipterocarp rain forests in Singapore. Highly positive responses of two shrubby species were found when phosphorus was added (Burslem *et al.* 1994), but seedlings of four shade-tolerant species showed either no response or a negative response to phosphorus additions (Burslem *et al.* 1995). They suggested phosphorus and major cations as limiting factors in nutrient-poor soils (Burslem *et al.* 1994), and that shade-tolerant tree seedlings which have mycorrhizas are not limited by phosphorus supply because of the mycorrhizas or because they have a low demand for nutrients when growing in the shade (Burslem *et al.* 1995). The latter suggestion was also made by Denslow *et al.* (1987), who found positive responses of seedling growth with complete nutrient fertilization on nutrient-richer soils, but no responses of shrubby species to phosphorus additions. In fact, assessment of the actual nutrient requirements of trees is a necessary information in connection with nutrient addition experiments, but these requirements are virtually impossible to ascertain.

In the present study, native seedlings in the field experiment showed either no or a negative response to nitrogen, phosphorus, and potassium addition, as well as a high mortality when calcium chloride was applied.

The results in the SHF and THF were very similar to those of recent studies carried out in temperate forests on acidic sandy soils in Sweden (Brunet & Neymark 1992; Falkengren-Krerup & Tyler 1992, 1993; Staaf 1992). They all found that any addition of mineral nutrients was unsuccessful in promoting plant survival or growth, unless the treatment involved an increase in soil pH. In the present study, overall there were no beneficial effects of the nutrient addition, if not accompanied by an increase in soil pH (by addition of calcium carbonate), in the SHF and THF, and a very limited effect in LERF. Thus, there was no direct evidence of nutrient limitation for seedling growth in the SFH and THF, and other factors must be involved. The high toxicity induced by soil acidity was

likely to be the main cause for the death or poor seedling growth in the nutrient addition treatments.

Falkengren-Krerup & Tyler (1992) identified a critical pH range of 3.5-4.3 (in KCl) for seedling survival; at pH 3.5 (about 3.9 in water), only one out of thirteen species was frequent. In soils well supplied with aluminium, pH is buffered by the movement of aluminium ions from clay to the solution (Kennedy 1988), and lower total amounts of aluminium in organic soils may also lower the critical pH values (Rowell 1988). Hoyt (1977) found that for soils of similar pH even though the exchangeable aluminium decreased with increasing organic matter, there was a concomitant increase in the exchangeable acidity due to the buffering ability of the organically complexed aluminium. The removal of the aluminium forms by addition of bases (such as potassium chloride and especially calcium chloride, which was used in much larger concentrations) may have caused a decrease in the soil pH, increasing the H^+ toxicity. It must be reminded that amelioration of H^+ toxicity by Al^{3+} ions is reciprocal (Kinraide 1993), and that Al^{3+} decreases solute leakage at low pH, then producing a growth enhancement (Foy 1984; Rowell 1988; Staaf 1992). In studies of Haplic Podzols in a boreal coniferous forest in Sweden, Skyllberg (1990, 1991) found that the humus layer (O horizon) had a pH positively correlated with aluminium. He suggested in acid humus layers and organic horizons, with a pH below 4.0, that aluminium cations act as any "base cation", through a H^+-displacement at cation exchange sites. Thus, instead of acidifying effects, aluminium ions in soil would be beneficial, buffering the pH at levels not toxic to plants, and the lack or displacement of such ions would cause strong toxicity for plant roots.

In the present study, the very low concentration of aluminium in the heath forest soils, especially in the SHF where the mor humus is often lacking, may be a major reason for the poor control of H^+ toxicity.

In the glasshouse experiment using rice seedlings, the results overall confirmed those found in the field study on natural seedlings: the only general positive effect on seedling growth was caused by the addition of calcium carbonate, while addition of calcium chloride had a general deleterious effect on seedlings, inducing high mortality rates. The

general coincidence of the results observed in the glasshouse (using a cultivated crop) with the field experiment (using varied native species) was reassuring.

The results found in the present study agree notably with recent studies on central Kalimantan heath forest soils. In a pot experiment, Smith (1994) found no seedling root growth in any treatment in the heath forest organic soil, except when calcium carbonate was added, speculating that poor growth of rice on heath forest soils was due to toxins in the soil and not due to a low soil nutrient status.

The negative effects of the humus layer included in part of the pots may also be the result of phenolic compounds (leached by the frequent watering of the pots), affecting seedling roots, especially in the heath forest soils. In Sarawak, Brünig (1983) reported that heath forest soils have high concentrations of secondary metabolites, which may have two effects: production of toxic effects on the vegetation, and reduction of available nitrogen in the soil. Whitmore (1990) indicated that phenols are abundant in heath forest leaves and litter, and these may be toxic or inhibit uptake when they leach into the soil. Soil phenolics directly affect germination and especially the growth of higher plants, and concentrations of soluble phenolics are correlated with organic matter content, and highest in the superficial L and F organic layers (Kuiters 1990). In the organic layers of THF soils, evidence was found of phenolic leachates, in the form of green-brownish bubbles (Luizão 1994), certainly released by the decomposition of either the litter on the soil surface or the fine roots, the main originators of phenolics in soil (Kuiters 1990). However, in the field experiment, using pre-existing natural seedlings, and where control sub-quadrats showed no strong mortality, the putative toxicity of phenolic compounds would have interacted with the added nutrients, making it still more difficult to explain the mechanisms involved. The phenolic substances are closely related to pH and soil nutrient status, and although phenolics are generally not high enough to be strongly acidic, they are more physiologically active at low pH (Kuiters 1990) and, in the present study, they may have interacted with H^+ to produce the high mortality of seedlings in the SHF and THF when the pH buffer was probably swamped by the large additions of calcium chloride.

In conclusion, it is possible that the soils in the SHF are nutrient limited, considering that they have virtually no top organic layer (where the nutrients are mainly found in the THF soils), and that a better response, though not always significant, was observed for the SHF soils than for THF soils when nutrients were added. The seedling mortality was smaller in the SHF than in THF when nitrogen, phosphorus, or NPK plus calcium carbonate were added, while the shoot and root mass were higher in the SHF than in THF soils when NPK plus calcium carbonate were added.

There was little evidence of nitrogen or phosphorus limitation, as suggested for acidic tropical soils generally (Sanchez 1976; Vitousek & Sanford 1986; Tanner *et al.* 1990, 1992), as the chief cause of poor plant growth in the SHF and THF. It is possible also to speculate that there was some evidence of toxic effects of soil pH and secondary compounds, as illustrated by the slight negative responses to the inclusion of a humus layer in the pots with heath forest soils, and by the largely positive response to the addition of calcium carbonate to the soils.

Thus, the view of Whitmore (1984) that heath forests occur on sites which have a number of unfavourable characteristics, acting together or separately, is substantiated. Even not being frequent, droughts may occur; the extremely acid soils, with pH < 4 at surface would be toxic to many plants; the soil has low amounts of aluminium and iron sesquioxides, and consequently a low ability to absorb H^+; phenols occur at high levels in leaves and litter, leaching into the soil; and, the amounts of nutrients in fine litter are low and slowly cycling. All these severe conditions, together or separately, restrict the production of heath forest and select only those species which are resistant to its many adverse conditions.

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APPENDICES

Appendix 1.1: Sample of the repeated measures procedure of analysis of variance for differences in leaf litterfall (log_e transformed) among forest types (Chapter 4).

Source	df	MS	F	p
Between-plots				
forest types	2	151	10.4	< 0.001
residual	6	14.5		
Within-plots				
date	26	462	5.82	< 0.001
forest*date	52	142	7.71	< 0.001
residual	155	43.4		
total	242			

Appendix 1.2: Sample of the nested analysis of variance used to compare forest types with plots nested within forest type, applied on the analysis of leaf mass in the experiment B (Chapter 5).

Source	df	SS	MS	F	p
forest type	2	2.78	1.39	32.3	< 0.01
plot (forest)	6	0.26	0.04	0.14	> 0.05
residual	207	65.6	0.32		
total	215	68.7			

Appendix 2.1: Soil chemical properties and particle-size composition at a range of depths in the pit outside of plot 1 in the SHF.

	Depths of samples in the pits (cm)							
	0-3	3-10	10-20	20-30	30-40	40-50	50-70	80-100
organic C (%)	5.5	0.16	0.01	0.0	0.0	0.0	0.0	0.0
pH_{H2O}	3.7	4.3	4.5	5.1	4.9	4.7	4.7	5.2
pH_{KCl}	2.7	3.3	3.5	3.6	3.7	4.3	4.3	4.8
N total ($mg\ g^{-1}$)	2.1	0.20	0.20	0.30	0.20	0.20	0.20	0.20
P total ($\mu g\ g^{-1}$)	142	44	22	22	20	13	10	19
P-extr. ($\mu g\ g^{-1}$)	20	4.3	2.9	2.1	1.9	1.1	0.4	1.6
Exchangeable cations, CEC, and total acidity (m-equiv kg^{-1})								
K^+	1.30	0.40	0.10	0.0	0.0	0.0	0.0	0.0
Na^+	0.20	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ca^{2+}	1.10	0.25	0.0	0.0	0.10	0.0	1.12	1.12
Mg^{2+}	2.30	0.12	0.0	0.0	0.06	0.0	0.02	0.06
H^+	13.9	3.4	2.1	1.9	1.1	1.1	0.4	0.6
Al^{3+}	0.0	0.0	0.0	0.20	0.0	0.0	0.0	1.0
CEC	18.8	4.17	2.20	2.1	1.26	1.10	1.54	2.78
Total acidity ($H^+ + Al^{3+}$)	13.9	3.4	2.1	1.9	1.1	1.1	0.4	1.6
Base saturation (%)	26.1	18.5	4.50	0.0	12.7	0.0	74.0	42.4
Particle fraction (%)								
clay (< 2 μm)	1.8	1.8	1.2	0.80	0.80	1.6	1.2	1.0
silt (2-62 μm)	4.1	4.1	0.46	0.25	0.0	2.27	0.00	0.01
sand (> 62 μm)	94.1	94.1	98.3	99.0	99.3	98.1	99.0	99.0
Colour	10YR 3/2 very dark greyish brown	10YR 5/2 greyish brown	10YR 6/2 light brownish grey	10YR 6/1 grey	10YR 6.5/1 light grey	10YR 6.5/1 light grey	10YR 6.5/1 light grey	10YR 7/1 light grey

Descriptive notes: A_0 horizon (0-3.4 cm) of a mixture of litter, a little humus and white coarse sand. Below, down to 1 m deep, only slight variations of the A_2 horizon. Common roots up to 1 cm diameter found up to 40 cm deep in the profile; few roots below 50 cm in depth. Porosity high in all layers sampled. Colours were greyish/brown in the upper 20 cm and light grey below 30 cm.

Appendix 2.2: Soil chemical properties and particle-size composition at a range of depths in the pit outside of plot 2 in the SHF.

	Depth of the samples (cm)					
	0-10	10-20	20-30	30-50	50-70	80-100
organic C (%)	0.17	0.07	0.18	0.09	0.04	0.04
pH_{H2O}	4.7	5.0	5.1	5.4	5.5	6.2
pH_{KCl}	3.5	3.7	3.8	4.0	4.6	5.2
N total (mg g^{-1})	0.40	0.30	0.20	0.30	0.30	0.10
P total (μg g^{-1})	32	23	10	19	10	10
P-extr. (μg g^{-1})	3.9	2.4	2.1	2.2	2.2	2.4
Exchangeable cations, CEC, and total acidity (m-equiv kg^{-1})						
K^+	0.0	0.0	0.0	0.0	0.0	0.0
Na^+	0.0	0.0	0.0	0.0	0.0	0.0
Ca^{2+}	0.50	0.37	0.87	0.37	0.87	2.37
Mg^{2+}	0.06	0.04	0.08	0.06	0.12	0.31
H^+	1.6	1.4	0.9	0.9	1.6	1.4
Al^{3+}	0.0	0.0	0.5	0.0	0.0	0.0
CEC	2.16	1.81	2.33	1.33	2.59	4.08
Total acidity ($H^+ + Al^{3+}$)	1.6	1.4	1.4	0.9	1.6	1.4
Base saturation (%)	25.9	22.7	39.9	32.3	38.2	65.7
Particle fraction (%) clay (< 2 μm)	1.8	1.2	0.80	0.80	1.2	1.0
silt (2-62 μm)	4.1	0.46	0.25	0.0	0.00	0.01
sand (> 62 μm)	94.1	98.3	99.0	99.3	99.0	99.0
Colour	10YR 3/2 very dark greyish brown	10YR 5/2 greyish brown	10YR 6/2 light brownish grey	10YR 6/2 light brownish grey	10YR 7/1 light grey	10YR 7.5/1 white

Descriptive notes: A_0 horizon slightly darker (0-10 cmm) above white-sandy A_2 horizon with diffuse boundary. Few roots up to 6 mm, mostly in the upper 30 cm. High porosity in the whole profile. Some small stones from 50 cm to 100 cm in depth. Few dark spots along the profile. Greyish brown colour in the upper 20 cm; light colour to white downward.

Appendix 2.3: Soil chemical properties and particle-size composition at a range of depths in the pit outside of plot 3 in the SHF.

	Depths of samples (cm)							
	0-3	3-10	10-20	20-30	30-40	40-50	50-70	80-100
organic C (%)	15.6	0.65	0.75	0.26	0.22	0.18	0.19	0.16
pH_{H2O}	3.7	4.3	4.0	4.6	4.6	5.0	4.9	4.8
pH_{KCl}	2.5	3.0	3.1	3.5	3.7	3.9	4.1	4.7
N total (mg g^{-1})	6.0	0.20	0.60	0.40	0.20	0.0	0.0	0.0
P total (μg g^{-1})	322	67	322	20	10	10	10	15
P-extr. (μg g^{-1})	20	4.4	3.4	2.5	1.9	2.0	1.6	1.6
Exchangeable cations (m-equiv kg^{-1})								
K^+	3.10	0.20	0.0	0.0	0.0	0.0	0.17	0.02
Na^+	0.70	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ca^{2+}	0.70	2.75	0.87	1.6	0.10	0.75	0.25	1.87
Mg^{2+}	5.3	0.62	0.21	0.21	0.02	0.12	0.39	0.23
H^+	25.4	3.4	5.1	2.1	1.6	1.1	1.1	1.1
Al^{3+}	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0
CEC	35.2	8.97	6.18	3.91	1.72	1.97	1.91	3.22
Total acidity ($H^+ + Al^{3+}$)	25.4	5.4	5.1	2.1	1.6	1.1	1.1	1.1
Base saturation (%)	27.8	39.8	17.5	46.3	6.98	44.2	42.4	65.8
Particle fraction (%)								
clay (< 2 μm)	1.8	1.8	1.2	0.80	0.80	1.60	1.2	1.0
silt (2-62 μm)	4.1	4.1	0.46	0.25	0.0	0.27	0.00	0.01
sand (> 62 μm)	94.1	94.1	98.3	99.0	99.3	98.1	99.0	99.0
Colour	10YR 3/2 very dark greyish brown	10YR 4.5/2 dark greyish brown	10YR 5/2 greyish brown	10YR 5.5/1 grey	10YR 6/1 grey	10YR 7/1 light grey	10YR 7/1 light grey	10YR 7.5/1 white

Descriptive notes: A_0 horizon (0-5 cm) above slightly dark layers up to 30 cm in depth. From 40 cm to 1 m only white sand with some organic dark spots. Common roots up to 8 mm in diameter are found in the upper 50 cm; below 50 cm they become very few. High porosity in the whole profile. Greyish brown colour in the upper 40 cm; pale colour to white downwards.

Appendix 2.4: Soil chemical properties and particle-size composition at a range of depths in the pit outside of plot 4 in the THF.

	Depths of samples (cm)								
	0-7	7-18	20-30	30-40	40-50	50-60	60-70	70-80	80-100
organic C (%)	31.3	1.44	1.71	1.21	0.86	0.41	0.41	0.40	0.41
pH_{H2O}	3.5	3.9	3.5	4.1	4.1	4.6	4.3	4.5	4.6
pH_{KCl}	2.3	2.7	2.7	2.9	3.3	3.5	3.5	3.9	4.0
N total ($mg\ g^{-1}$)	15.2	0.70	0.30	0.0	0.0	0.04	0.0	0.04	0.0
P total ($\mu g\ g^{-1}$)	295	44	38	26	19	10	16	10	10
P-extr. ($\mu g\ g^{-1}$)	20	4.6	3.4	2.1	1.7	1.8	1.6	0.8	1.5
Exchangeable cations, CEC, and total acidity ($m\text{-}equiv\ kg^{-1}$)									
K^+	2.2	1.20	0.80	0.0	0.0	0.03	0.0	0.0	0 0
Na^+	3.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ca^{2+}	0.20	0.20	1.75	1.50	0.75	1.75	1.62	0.75	0.75
Mg^{2+}	3.2	0.41	0.31	0.29	0.06	0 25	0.19	0.08	0 10
H^+	62.9	9.9	10.1	6.4	2.9	1.6	1.4	1.0	1.9
Al^{3+}	16.5	0.5	0.5	1.0	0.0	0.5	0.0	0.0	0.0
CEC	88.2	12.2	13.5	9.19	3.71	4.13	3.21	1.83	2.75
Total acidity ($H^+ + Al^{3+}$)	79.4	10.4	10.6	7.4	2.9	2.1	1.4	1.0	1.9
Base saturation (%)	9.98	14.8	21.2	19.5	21.8	49.2	56.4	45.4	30.9
Particle fraction (%)									
clay (< 2 μm)	0.0	3.6	2.2	0.40	2.0	1.20	1.20	1.60	1.40
silt (2-62 μm)	0.0	0.04	1.38	1.29	0.0	9.07	0.0	0.81	0.30
sand (> 62 μm)	0.0	96.3	96.4	98.3	98.6	89.7	99 0	97.6	98.3
Colour	10YR 3/1 very dark grey	10YR 3/1 very dark grey	10YR 3/1 very dark grey	10YR 4/1 dark grey	10YR 5/2 greyish brown	10YR 5.5/2 greyish brown	10YR 6/2 light brownish grey	10YR 7/1 light grey	10YR 7/1 light grey

Descriptive notes: 0 horizon (0-10 cm) of litter plus a root mat and humus. A_2 horizon with bleached white sand between 10-18 cm above a darker gray B_h horizon up to 40 cm. A B_2 horizon of white sand follows up to 1 m; roots up to 2 mm in diameter occur mostly up to 40 cm; below 40 cm only few and finer roots were found. Overall high porosity. Dark grey-brown colour up to 60 cm; light grey below.

Appendix 2.5: Soil chemical properties and particle-size composition at a range of depths in the pit outside of plot 5 in the THF.

	Depths of samples (cm)								
	0-12	12-20	20-30	30-40	40-50	50-60	60-70	70-80	80-100
organic C (%)	27.3	2.18	1.79	1.36	1.40	0.60	0.58	0.19	0.18
pH_{H2O}	3.4	3.9	4.3	4.3	4.2	4.6	5.2	5.0	5.3
pH_{KCl}	2.1	2.6	2.7	3.0	3.1	3.5	3.7	3.8	4.1
N total ($mg\ g^{-1}$)	9.9	0.50	0.20	0.0	0.0	0.02	0.0	0.0	0.0
P total ($\mu g\ g^{-1}$)	1280	10	10	10	37	25	54	10	10
P-extr. ($\mu g\ g^{-1}$)	10	5.7	2.3	1.4	1.8	2.0	1.6	1.7	1.2
Exchangeable cations, CEC, and total acidity ($m\text{-}equiv\ kg^{-1}$)									
K^+	3.9	0.14	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Na^+	5.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ca^{2+}	0.1	1.5	0.0	1.75	1.12	1.12	1.75	2.62	2.37
Mg^{2+}	3.5	4.80	0.0	0.35	0.19	0.21	0.19	0.27	0.27
H^+	61.1	11.9	9.4	4.6	4.4	8.4	0.1	1.6	0.8
Al^{3+}	8.0	1.5	1.5	0.0	0.0	0.5	0.0	0.0	0.0
CEC	82.0	19.8	10.9	6.70	5.71	10.2	2.04	4.49	3.44
Total acidity ($H^+ + Al^{3+}$)	69.1	13.4	10.9	4.6	4.4	8.9	0.1	1.6	0.8
Base saturation (%)	15.7	32.5	0.0	31.3	22.9	13.0	95.1	64.4	76.7
Particle fraction (%)									
clay (< 2 μm)	0.0	3.6	2.2	0.40	2.0	1.20	1.20	1.60	1.40
silt (2-62 μm)	0.0	0.04	1.38	1.29	0.0	9.07	0.0	0.81	0 30
sand (> 62 μm)	0.0	96.3	96.4	98.3	98.6	89.7	99.0	97 6	98.3

Colour	10YR 3/1 very dark grey	10YR 3/1 very dark grey	10YR 3/1 very dark grey	10YR 4/1 dark grey	10YR 4/2 dark grey	10YR 5/2 greyish brown	10YR 6/2 light brownish grey	10YR 7/1 light grey	10YR 7/1 light grey

Descriptive notes: 0 horizon (0-15 cm) of litter, root mat and humus. A_2 horizon has a strip of white sand at 15-20 cm in depth, above a darker B_h horizon from 20 to 40 cm. Below 40 cm, the sand layers (B_2 horizon) became clearer, with diffuse boundaries and organic dark spots. Common roots up to 1.5 cm in diameter were found in the upper 40 cm, with the larger ones mainly in the upper 20 cm. Overall high porosity. Dark grey-brown colour up to 50 cm; paler colour downwards.

Appendix 2.6: Soil chemical properties and particle-size composition at a range of depths in the pit outside of plot 6 in the THF.

	Depths of samples (cm)									
	0-3	3-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-100
organic C (%)	32.0	1.0	0.43	0.16	0.16	0.0	0.13	0.10	0.15	0.18
pH_{H2O}	3.5	3.9	4.4	4.7	4.2	4.5	4.8	4.8	4.9	5.0
pH_{KCl}	2.2	2.8	3.0	3.3	3.3	3.6	3.7	3.9	4.2	4.1
N total (mg g^{-1})	12.2	0.60	0.20	0.10	0.10	0.10	0.20	0.10	0.10	0.10
P total (µg g^{-1})	293	11	25	10	14	10	10	25	11	25
P-extr. (µg g^{-1})	20	3.9	1.2	0.0	0.0	0.1	0.0	0.1	0.0	0.0
Exchangeable cations, CEC, and total acidity (m-equiv kg^{-1})										
K^+	4.8	0.12	0.0	0.0	0.20	0.40	0.05	0.0	0.0	0.0
Na^+	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ca^{2+}	0.30	3.75	2.62	3.75	5.12	3.25	3.50	2.75	2.62	4.0
Mg^{2+}	4.8	0.56	0.35	0.52	0.66	0.37	0.43	0.37	0.33	0.52
H^+	26.4	5.6	5.4	2.4	3.6	2.4	1.1	1.4	0.4	1.5
Al^{3+}	4.0	0.0	1.0	0.5	0.0	0.0	1.0	0.0	0.0	0.0
CEC	45.3	10.0	9.37	7.17	9.58	6.42	6.08	4.52	3.35	6.02
Total acidity (H^++Al^{3+})	30.4	5.6	6.4	2.9	3.6	2.4	2.1	1.4	0.4	1.5
Base saturation (%)	32.9	44.2	31.7	59.5	62.4	62.6	65.5	69 0	88 0	75.1
Particle fraction (%)										
clay (< 2 µm)	0.0	0.0	3.6	2.2	0.40	2.0	1.20	1.20	1.60	1.40
silt (2-62 µm)	0.0	0.0	0.04	1.38	1.29	0.0	9.07	0.0	0.81	0.30
sand (> 62 µm)	0.0	0.0	96.3	96.4	98.3	97.6	89.7	98.0	97 6	98.3
Colour	10YR 3/1 very dark grey	10YR 4/2 dark grey	10YR 5/2 greyish brown	10YR 5/2 greyish brown	10YR 6/2 light brownish grey	10YR 7/2 light grey	10YR 7/2 light grey	10YR 7/2 light grey	10YR 7/2 light grey	10YR 7/2 light grey

Descriptive notes: 0 horizon (0-5 cm) composed by litter, root mat and humus. Clear A_2 horizon (5-10 cm) mixing humus and white sand above a darker B_h horizon down to 30 cm. Below 40 cm, the clearer white sand layers of the B_2 horizon were frequently spotted by dark organic matter. Common roots up to 1.2 cm in diameter were found in the upper 40 cm, becoming fewer and finer downwards. Overall high porosity. Dark grey-brown colours in the upper 20 cm; paler colour below 40 cm.

Appendix 2.7: Soil chemical properties and particle-size composition at a range of depths in the pit outside of plot 7 in the LERF.

	Depths of samples (cm)									
	0-3	3-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-100
organic C (%)	18.4	0.77	0.28	0.78	0.72	0.81	0.62	0.52	0.51	0.49
pH_{H2O}	3.9	4.2	4.2	4.5	4.6	4.8	4.7	4.6	4.7	4.7
pH_{KCl}	2.8	3.4	3.6	3.9	4.1	4.2	4.2	4.2	4 3	4.2
N total ($mg\ g^{-1}$)	9.0	0.80	0.70	0.70	0.70	0.70	0.50	0.50	0.40	0.20
P total ($\mu g\ g^{-1}$)	405	164	307	260	1100	134	272	201	215	323
P-extr. ($\mu g\ g^{-1}$)	20	1.8	2.3	1.5	0.9	0.5	0.7	1.7	0.5	0.3
Exchangeable cations, CEC, and total acidity ($m\text{-}equiv\ kg^{-1}$)										
K^+	2 7	0.06	0.04	0.13	0.0	0.03	0.0	0.0	0.13	0.0
Na^+	5 4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ca^{2+}	0 2	2.62	2.87	3.87	3.37	3.75	3.75	4.00	4 87	2.37
Mg^{2+}	2.8	0.71	0.56	0.46	0.56	0.33	0.44	0.42	0.54	0.23
H^+	26.6	3.9	3.6	1.4	0.4	1.9	2.1	1.6	1.6	0.9
Al^{3+}	39.0	14.0	9.5	14.0	12.0	10.0	8.5	7.5	7.5	7.8
CEC	76.7	21.3	16.6	19.9	16.3	16.0	14.8	13.5	14.6	11.3
Total acidity ($H^+ + Al^{3+}$)	65.6	17.9	13.1	15.4	12.4	11.9	10.6	9.1	9.1	8.7
Base saturation (%)	14.5	15.9	20.9	22.5	24.1	25.7	28.3	32.7	37.9	23.0
Particle fraction (%)										
clay (< 2 µm)	9.6	9.60	11.6	10.6	10.4	11.8	12.2	15.8	14.0	19.8
silt (2-62 µm)	19.8	19 8	7.51	6.01	10.4	13.3	15.3	11.5	9.9	12.5
sand (> 62 µm)	70.6	70.6	80.1	83 4	79 2	74.9	72.2	72.7	76.4	67.7
Colour	10YR 3/1 very dark grey	10YR 4/2 dark greyish brown	10YR 4/3 dark brown	10YR 4/4 dark yellowish brown	10YR 4/4 dark yellowish brown	10YR 4/3 dark brown	10YR 4/3 dark brown	10YR 4/4 dark yellowish brown	10YR 4/4 dark yellowish brown	10YR 5/4 yellowish brown

Descriptive notes: A_0 horizon (0-5 cm) of litter and humus with abundant roots. A_2 horizon (3.5-20 cm) is grey-yellowish, sandy-textured, above a B_h horizon, darker up to 60 cm and gradually becoming yellow; the 80-100 cm layer is yellow. Clay content increases with depth. Charcoal was found from 30-60 cm. Roots up to 2 cm in diameter down to 1 m. Dark grey colours in the upper 10 cm; dark brown below 10 cm with yellowish shades below 20 cm and dominant below 80 cm.

Appendix 2.8: Soil chemical properties and particle size-composition at a range of depths in the pit outside of plot 8 in the LERF.

	Depth of samples (cm)							
	0-6	6-20	20-30	30-40	40-50	50-60	70-80	80-100
organic C (%)	14.7	1.48	1.18	1.08	1.05	1.02	0.86	1.08
pH_{H2O}	3.8	4.0	3.9	4.6	4.6	4 6	4.6	4.6
pH_{KCl}	3.0	3.6	4.0	4.1	4.2	4.2	4.2	4.2
N total ($mg\ g^{-1}$)	7.5	0.10	0.10	0.20	0.02	0.01	0.01	0.40
P total ($\mu g\ g^{-1}$)	355	289	168	193	143	279	67	298
P-extr. ($\mu g\ g^{-1}$)	20	3.2	1.8	1.3	0.8	0.7	0.7	0.4
Exchangeable cations, CEC, and total acidity ($m\text{-}equiv\ kg^{-1}$)								
K^+	5.9	0.20	0.06	0.01	0.30	0 04	0.0	0.0
Na^+	4.1	0.0	0.0	0.0	0.70	2.4	0.26	0.0
Ca^{2+}	0.20	4.12	3.12	4.00	3.87	5 37	3.37	3.50
Mg^{2+}	2.20	0.66	0.48	0.56	0.56	0.71	1.08	0.44
H^+	0.0	3.9	0.9	1.4	0.0	0 9	1.1	0.9
Al^{3+}	89.5	7.5	14.0	10.5	13.0	13 0	10.0	10.0
CEC	102	16.4	18.6	16.5	18.4	22.4	15.8	14.8
Total acidity ($H^+ + Al^{3+}$)	53.6	11.4	14.9	11.9	12.9	13.9	11.1	10.9
Base saturation (%)	12.2	30.4	19.7	27.7	29.5	38.0	29.8	26.6
Particle fraction (%)								
clay (< 2 µm)	9.60	11.6	10.6	10.4	11.8	12.2	14.0	19.8
silt (2-62 µm)	19 8	7.51	6.01	10.4	13.3	15 3	9.9	12.5
sand (> 62 µm)	70.6	80.1	83.4	79 2	74.9	72 2	76 4	67.7
Colour	10YR 3/2 very dark greyish brown	10YR 4/3 dark brown	10YR 4/4 dark yellowish brown	10YR 4/4 dark yellowish brown	10YR 4/3 dark brown	10YR 4 3 dark brown	10YR 4/4 dark yellowish brown	10YR 4/4 dark yellowish brown

Descriptive notes: A_0 horizon (0-5 cm) of litter and humus with abundant fine roots. Loose sandy soil immediately below A_0 horizon. B horizon was light yellow down to 60 cm, darker from 60-80 cm, and again lighter from 80-100 cm. Clay content increase gradually with depth. Common roots up to 2 cm in diameter were distributed up to 1 m. Dark grey-brown colours down to 20 cm.; yellowish downwards.

Appendix 2.9: Soil chemical properties and particle-size composition at a range of depths in the pit outside of plot 9 in the LERF.

	Depth of the samples (cm)								
	0-6	6-20	20-30	30-40	40-50	50-60	60.70	70-80	80-100
organic C (%)	34.6	2.13	1.33	1.37	1.39	1.18	1.14	0.44	0.36
pH_{H2O}	3.8	4.1	4.5	4.6	4.6	4.6	4.5	4.2	4.7
pH_{KCl}	2.7	3.4	3.9	4.1	4.1	4.2	4.2	4.2	4.2
N total ($mg\ g^{-1}$)	15.9	1.0	0.10	0.80	0.80	0.20	0.0	0.10	0.10
P total ($\mu g\ g^{-1}$)	539	319	215	246	91	346	298	67	349
P-extr. ($\mu g\ g^{-1}$)	30	2.9	2.0	1.5	0.8	0.1	0.1	0.2	0.3
Exchangeable cations, CEC, and total acidity (m-equiv kg^{-1})									
K^+	6.0	0.21	0.0	0.02	0.0	0.0	0.0	0.0	0.0
Na^+	5.6	0.23	0.0	0.0	0.10	0.80	1.50	0.0	0.0
Ca^{2+}	0.25	3.25	3.62	0.0	0.0	0.0	0.37	0.0	0.0
Mg^{2+}	2.8	0.60	0.48	0.52	0.41	0.54	0.52	0.43	0.46
H^+	6.0	6.1	2.6	2.6	0.10	0.0	0.1	2.10	0.90
Al^{3+}	35.0	14.8	12.5	12.5	14.0	12.5	12.5	9.50	9.50
CEC	55.7	25.2	19 2	15.6	14.6	13.8	15.0	12.0	10.9
Total acidity (H^++Al^{3+})	41.0	20.9	15.1	15.1	14.1	12.5	12.6	11.6	10.4
Base saturation (%)	26.3	17.0	21.4	3.46	3.49	9.71	15.9	3.57	4.23
Particle fraction (%)									
clay (< 2 µm)	9.60	11.6	10.6	10.4	11.8	12.2	15.8	14.0	19.8
silt (2-62 µm)	19.8	7.51	6.01	10.4	13.3	15.3	11.5	9.9	12.5
sand (> 62 µm)	70.6	80.1	83.4	79.2	74.9	72.2	72.7	76.4	67.7
Colour	10YR 3/2 dark grey	10YR 3/3 greyish brown	10YR 4/4 dark yellowish brown	10YR 4/4 dark yellowish brown	10YR 4/4 dark yellowish brown	10YR 4/4 dark yellowish brown	10YR 4/4 dark yellowish brown	10YR 5/6 yellowish brown	10YR 5/8 yellowish brown

Descriptive notes: A_0 horizon (0-10 cm) of litter and humus with abundant fine roots. Dark yellow B horizon with little variation in colour down to 70 cm, becoming pale yellow below 70-80 cm. Clay content increases gradually with depth. Common roots up to 1.8 cm in diameter down to 1 m. Dark grey-brown colours in the upper 20 cm; yellowish below 20 cm.

Appendix 3.1: List of species within each family of trees (≥ 10 cm dbh) found in the study sites with their respective number of individuals in each of the nine plots.

	SHF			THF			LERF		
Family/Species	1	2	3	4	5	6	7	8	9
ANACARDIACEAE									
Anacardium spruceanum Benth. ex Engl.	0	0	0	0	0	0	0	0	1
Tapirira guianensis Aubl.	0	0	0	0	0	1	0	0	1
Tapirira sp.	0	0	0	0	1	0	0	0	0
ANNONACEAE									
Ephedranthus amazonicus R.E. Fries	0	0	0	0	0	0	1	0	1
Guatteria discolor R.E. Fries	0	0	0	0	0	0	0	1	0
Guatteria recurvisepala R.E. Fries	0	0	0	0	0	0	0	0	1
Guatteria sp	0	0	0	2	1	2	0	2	3
Unonopsis sp	0	0	0	0	0	0	0	1	1
Annonaceae sp 1	0	0	0	0	0	0	0	0	1
APOCYNACEAE									
Anacampta rigida (Miers) Markgraf	0	0	0	0	0	0	1	0	0
Aspidosperma album (Vahl.) R. Ben.	0	0	0	0	1	0	0	0	0
Aspidosperma excelsum Benth.	0	0	0	0	0	0	0	1	0
Lacmellea sp 1	0	0	0	3	5	1	0	0	0
Lacmellea sp 2	0	0	0	0	2	0	0	0	0
Apocynaceae sp 1	0	0	0	0	1	0	0	0	1
ARECACEAE									
Maximiliana martiana Karst.	0	0	0	0	0	0	1	0	0
Oenocarpus bacaba Mart.	0	0	0	0	8	0	27	14	20
BOMBACACEAE									
Scleronema micranthum Ducke	0	0	0	0	0	0	1	0	1
BORAGINACEAE									
Cordia sp	0	0	0	0	0	0	1	0	2
BURSERACEAE									
Dacryodes roraimensis Cuatr.	0	0	0	0	0	0	0	2	0
Protium aracouchini (Aubl.) March.	0	0	0	0	0	0	1	1	1
Protium. decandrum (Aubl.) March.	0	0	0	0	0	0	1	0	1
Protium grandifolium Engl.	0	0	0	0	0	0	1	2	0
Protium heptaphyllum (Aubl.) March.	0	0	0	0	0	0	1	2	0
Protium paniculatum Engl.	0	0	0	0	0	0	1	1	0
Protium polybotryum Engl.	0	0	0	0	0	0	0	1	0
Protium subserratum Engl.	0	0	0	0	0	0	0	2	0

(cont.)

Family/Species	SHF			THF			LERF		
	1	2	3	4	5	6	7	8	9
Protium sp 1	0	0	0	1	0	0	0	0	0
Protium sp 2	0	0	0	0	0	0	3	4	2
Protium sp 3	0	0	0	0	0	0	27	30	27
Protium sp 4	0	0	0	0	0	0	2	11	7
Protium sp 5	0	0	0	0	0	0	1	1	0
Burseraceae sp 1	0	0	0	0	3	0	0	1	2
CAESALPINIACEAE									
Aldina heterophylla Spruce ex Benth.	21	21	27	24	14	17	0	0	0
Macrolobium sp	1	0	1	2	0	0	0	0	0
Peltogyne paniculata subsp. *paniculata* Benth.	0	0	0	0	0	0	0	3	3
Swartzia dolicopoda Cowan.	0	0	0	0	0	0	0	2	0
Swartzia ingifolia Ducke	0	0	0	0	0	0	0	1	1
Swartzia laevicarpa Amsh.	0	0	0	0	0	0	0	1	0
Swartzia polyphylla A. DC.	0	0	0	0	0	0	3	1	1
Swartzia recurva Poepp. & Endl.	0	0	0	0	0	0	14	0	1
Swartzia cf. *tessmannii* Harms	0	0	0	0	0	0	0	1	0
Swartzia sp 1	10	4	8	30	14	7	0	0	0
Swartzia sp 2	0	0	0	0	0	0	2	0	3
Tachigalia myrmecophylla (Ducke) Ducke	0	0	0	0	0	0	1	0	0
Tachigalia paniculata Aubl. var. *paniculata*	0	0	0	0	0	0	1	0	0
Tachigalia sp	0	0	0	0	0	0	1	0	1
Caesalpiniaceae sp 1	0	0	0	0	0	0	1	0	0
CARYOCARACEAE									
Caryocar glabrum (Aubl.) Pers.	0	0	0	0	0	0	0	1	1
CELESTRACEAE									
Goupia glabra Aubl.	0	0	0	0	0	0	0	1	0
CHRYSOBALANACEAE									
Couepia bracteosa Benth.	0	0	0	0	0	0	0	3	1
Couepia canominensis (Mart.) Mez	0	0	0	0	0	0	6	1	1
Couepia sp	0	0	0	0	0	0	0	0	1
Licania apetala (E. Mey.) Fritsch	0	0	0	0	0	0	0	4	0
Licania heteromorpha Benth.	0	0	0	0	0	0	0	1	0
Licania latifolia Benth. ex Hook.	0	0	0	0	0	0	1	3	3
Licania leptostachya Benth.	0	0	0	0	0	0	1	0	0
Licania sp 1	0	0	0	1	2	1	2	5	15

(cont.)

Family/Species	SHF			THF			LERF		
	1	2	3	4	5	6	7	8	9
Licania sp 2	0	0	0	0	0	0	5	2	4
Licania sp 3	0	0	0	0	2	3	0	0	0
Lilavia sp	0	0	0	0	0	0	0	0	1
Parinari excelsa Sabine	0	0	0	0	0	0	0	0	1
Chrysobalanaceae sp 1	0	0	0	0	0	0	0	0	1
CLUSIACEAE									
Clusia insignis Mart.	0	0	0	0	0	0	1	1	0
Clusia sp 1	3	0	0	6	0	0	0	0	0
Clusia sp 2	0	0	0	4	3	7	0	0	0
Tovomita macrophylla (Poepp. ex Endl.) Walp.	0	0	0	0	0	0	0	1	0
Clusiaceae sp 1	0	0	0	0	0	0	1	0	0
ELAEOCARPACEAE									
Sloanea guianensis (Aubl.) Benth.	0	0	0	0	0	0	0	1	1
EUPHORBIACEAE									
Gavarretia terminalis Baill.	0	0	0	58	33	22	0	0	1
Euphorbiaceae sp 1	0	0	0	0	0	0	1	0	0
FABACEAE									
Alexa sp	0	0	0	0	0	0	0	0	1
Andira cf. *micrantha* Ducke	0	0	0	0	0	0	0	0	1
Andira sp	0	0	0	0	1	0	0	1	0
Diplotropis purpurea (Rich.) Amsh.	0	0	0	0	0	0	1	0	0
Diplotropis rodriguesii Lima	0	0	0	0	0	0	0	0	1
Machaerium sp	0	0	0	0	0	0	1	0	0
Ormosia sp	2	1	2	0	0	1	0	0	0
Fabaceae sp 1	1	1	1	1	1	1	0	1	0
HIPPOCRATEACEAE									
Salacia sp	0	0	0	0	0	0	0	1	0
HUMIRIACEAE									
Duckesia verrucosa (Ducke) Cuatr.	0	0	0	0	0	0	1	0	0
Humiria sp	2	0	0	0	0	0	0	0	0
Sacoglottis guianensis Benth.	0	0	0	1	0	0	0	1	0
Sacoglottis sp	0	0	0	0	1	0	0	1	8
Humiriaceae sp 1	0	0	0	0	0	0	1	0	0
LAURACEAE									
Aniba sp	0	0	0	0	0	0	2	1	2

(cont.)

Family/Species	SHF			THF			LERF		
	1	2	3	4	5	6	7	8	9
Licaria aritu Ducke	0	0	0	0	0	0	1	0	1
Mezilaurus itauba (Meisn.) Taub. ex Mez	0	0	0	2	1	1	1	0	0
Mezilaurus synandra (Mez) Kosterm.	0	0	0	0	0	0	1	0	1
Ocotea aciphylla Mez	0	0	0	0	0	0	0	1	0
Ocotea canaliculata (Rich.) Mez.	0	0	0	0	0	0	0	0	1
Ocotea sp 1	0	0	0	6	0	0	0	0	2
Ocotea sp 2	0	0	0	0	0	0	26	18	8
Ocotea sp 3	0	0	0	0	0	0	4	4	2
Lauraceae sp 1	0	0	0	0	0	0	0	1	0
LECYTHIDACEAE									
Eschweilera fracta R.Knuth	0	0	0	0	0	0	1	0	0
Holopyxidium jarana (Hub.) Ducke	0	0	0	0	0	1	0	0	0
Lecythis sp	0	0	0	0	0	0	1	1	0
Lecythidaceae sp 1	0	0	0	0	0	0	0	0	1
LINACEAE									
Hebepetalum humirifolium (Planch.) Benth.	0	0	0	0	0	0	1	2	4
Roucheria callophylla Planch.	0	0	0	0	0	0	1	0	0
SAPOTACEAE									
Chrysophyllum balata (Ducke) Baheni	0	0	0	0	0	0	0	0	1
Chrysophyllum guyanense (Eyma) Baheni	0	0	0	0	0	0	1	0	0
Chrysophyllum sanguinolentum (Pierre) Baehni	0	0	0	0	0	0	1	0	0
Chrysophyllum sp 1	0	0	0	0	1	0	4	3	4
Chrysophyllum sp 2	0	0	0	0	0	0	5	7	5
Chrysophyllum sp 3	0	0	0	0	0	0	1	1	0
Chrysophyllum sp 4	0	0	0	0	0	0	1	1	0
Ecclinusa cf. *guianensis* Eyma	0	0	0	0	0	0	1	1	0
Manilkara sp	0	2	10	0	1	0	1	2	0
Micropholis guyanensis (A. DC.) Pierre	0	0	0	0	0	0	1	2	1
Micropholis sp	0	0	0	0	0	0	4	3	6
Neoxythece elegans (A. DC.) Aubr.	0	0	0	0	0	0	0	0	1
Pouteria cuspidata (A. DC.) Baehni	0	0	0	0	0	0	1	2	0
Pouteria sp	0	0	0	0	0	0	1	0	0
Pradosia schomburgkiana (A. DC.) Cronq.	37	5	27	35	20	18	0	0	0
Ragala spurea (Ducke) Aubr.	0	0	0	0	0	0	6	1	1
Ragala sp	0	0	0	0	0	0	10	4	7

(cont.)

	SHF			THF			LERF		
Family/Species	1	2	3	4	5	6	7	8	9
Richardella manaosensis (Aubr.) Pellegr.	0	0	0	0	0	0	2	0	0
Sapotaceae sp 1	0	0	0	0	0	0	0	0	3
SAPINDACEAE									
Matayba inelagans Radlk.	0	0	0	1	0	0	0	0	0
Matayba sp	0	0	0	2	0	0	0	0	0
Toulicia guianensis Aubl.	0	0	0	0	0	0	0	1	0
Sapindaceae sp 1	0	0	0	0	5	0	0	0	2
UNKNOWN									
undetermined liana sp. 1	0	0	0	1	0	0	0	0	0
undetermined liana sp. 2	0	0	0	0	0	0	0	1	0
unknown	0	0	0	0	1	0	0	1	1
MYRTACEAE									
Eugenia diplocampta Diels.	0	0	0	0	0	0	2	0	0
Eugenia sp 1	1	0	0	0	0	0	0	0	1
Eugenia sp 2	0	0	0	0	0	0	1	4	2
Myrcia eximia DC.	0	0	0	0	0	0	0	1	0
OCHNACEAE									
Ouratea discophora Ducke	0	0	0	0	0	0	1	0	0
Ouratea sp	0	0	3	2	5	11	5	1	3
Ochnaceae sp 1	0	0	0	1	0	0	0	0	0
SIMAROUBACEAE									
Simaba palyphylla (Cavac.) W. Thomas	0	0	0	0	0	0	5	0	0
Simarouba amara Aubl.	0	0	0	3	8	1	1	2	0
MELIACEAE									
Guarea sp 1	0	0	0	0	0	0	0	2	0
Guarea sp 2	0	0	0	0	0	0	1	2	0
Trichilia septentrionalis C. DC.	0	0	0	0	0	0	0	1	3
Meliaceae sp 1	0	0	0	0	1	0	0	0	0
MELASTOMATACEAE									
Miconia splendens (Sw.) Griseb.	0	0	0	0	0	0	0	0	1
Miconia sp	0	0	0	2	0	0	0	2	1
Mouriri nigra (A. DC.) T. Morley	0	0	0	0	0	0	1	0	0
RUBIACEAE									
Chimarrhis sp	0	0	0	0	0	0	3	1	0
Duroia macrophylla Hub.	0	0	0	0	0	0	0	0	1

(cont.)

Family/Species	SHF			THF			LERF		
	1	2	3	4	5	6	7	8	9
Duroia saccifera (Benth.) Hook.	0	0	0	0	0	0	0	0	1
Duroia sp 1	0	0	0	1	0	0	0	0	0
Duroia sp 2	0	0	0	1	0	0	0	0	0
Ferdinandusa elliptica Pohl	0	0	0	0	0	0	1	0	0
Ferdinandusa lanceolata K. Schum.	0	0	0	0	0	0	1	0	0
Ferdinandusa sp	0	0	0	0	0	0	1	2	0
Remijia amazonica K. Schum.	0	0	0	0	0	0	0	1	0
Remijia sp	0	0	0	0	0	2	0	0	0
Rubiaceae sp 1	0	0	0	0	0	1	0	0	0
Rubiaceae sp 2	0	0	0	0	0	0	0	1	0
Rubiaceae sp 3	0	0	0	1	0	0	0	0	1
VOCHYSIACEAE									
Erisma uncinatum Warm.	0	0	0	0	0	0	1	0	0
Erisma sp	0	0	0	0	0	0	3	0	0
Qualea paraensis Ducke	0	0	0	0	0	0	0	0	1
Qualea retusa	0	0	0	0	0	1	0	0	0
Qualea sp	0	0	0	0	2	1	1	0	0
Vochysia sp	0	0	0	0	2	5	0	0	0
VERBENACEAE									
Vitex triflora Vahl.	0	0	0	0	0	0	1	0	0
Vitex sp	0	0	0	0	3	0	0	1	0
Verbenaceae sp 1	0	0	0	0	0	1	0	0	0
MENISPERMACEAE									
Abuta sp	0	0	0	0	1	0	0	1	3
MALPIGHIACEAE									
Malpighiaceae sp 1	0	0	0	0	0	1	0	0	0
STERCULIACEAE									
Theobroma sylvestris Aubl. ex Mart.	0	0	0	0	0	0	1	5	2
MIMOSACEAE									
Enterolobium sp	0	0	0	0	0	0	0	0	1
Inga sp	0	0	0	0	0	0	0	0	1
Parkia decussata Ducke	0	0	0	0	0	0	0	1	0
Parkia sp	0	0	0	0	0	0	2	0	1
Pithecolobium pedicellare (Benth.) Hook.	0	0	0	0	0	0	0	0	1
Pithecolobium racemosum Ducke	0	0	0	0	0	0	3	0	1

Family/Species	SHF			THF			LERF		
	1	2	3	4	5	6	7	8	9
COMBRETACEAE									
Buchenavia sp	0	0	0	0	0	0	0	3	0
MYRISTICACEAE									
Iryanthera tricornis Ducke	0	0	0	0	0	0	1	0	0
Virola calophylla Warb.	0	0	0	0	0	0	0	0	1
Virola elongata (Benth.) Warb.	0	0	0	0	0	0	1	0	0
Virola venosa (Benth.) Warb.	0	0	0	0	0	0	0	1	0
Virola sp	0	0	0	0	0	0	0	2	0
MORACEAE									
Brosimum rubescens Taubert	0	0	0	0	0	0	0	0	1
Brosimum sp	0	0	0	0	0	0	0	2	0
Helicostylis podogyne Ducke	0	0	0	0	0	0	1	0	0
Helicostylis cf. *scabra* (Macbr.) C.C. Berg	0	0	0	0	0	0	1	0	0
Helicostylis tomentosa (Planch. & Endl.) Rusby	0	0	0	0	0	0	0	2	0
Naucleopsis sp	0	0	0	0	0	0	2	1	0
Pourouma minor Benoist	0	0	0	0	0	0	0	1	2
Pourouma sp	0	0	0	0	0	0	1	1	0
Trymatococcus turbinatus (Baill.) Ducke	0	0	0	0	0	0	1	0	0
Moraceae sp 1	0	0	0	0	0	0	1	2	1
NYCTAGINACEAE									
Neea sp	0	0	0	0	0	0	0	1	1
MONIMIACEAE									
Siparuna cristata, var. *macrophylla* A. DC.	0	0	0	0	0	0	0	1	0
OLACACEAE									
Heisteria laxiflora Engl.	0	0	0	0	0	0	2	0	0
MYRSINACEAE									
Cybianthus cf. *pseudoicacoreus*	0	0	0	0	0	0	1	0	0
VIOLACEAE									
Paypayrola grandiflora Tul.	0	0	0	0	0	0	1	0	2
Violaceae sp 1	0	0	0	0	0	0	1	0	2
RHIZOPHORACEAE									
Sterigmapetalum obovatum Kuhlman	0	0	0	0	0	0	0	0	3
QUIINACEAE									
Lacunaria jenmani (Oliv.) Ducke	0	0	0	0	0	0	0	0	1
RHABDODENDRACEAE									
Rhabdodendrum amazonicum (Spruce ex Benth.) Hub.	0	0	0	0	0	0	1	0	1

Appendix 3.2: Some species of plants found in both SHF and THF in the *Reserva Biológica de Campina*, INPA (Braga 1979). The asterisked species were also recorded by Anderson (1978).

Plant species	Family
* *Aldina heterophylla* Spr. ex Benth.	Caesalpiniaceae
* *Annona nitida* Mart.	Annonaceae
Borreria capitata (R. et P.) A. DC.	Rubiaceae
Clusia aff. *columnaris* Engl.	Clusiaceae
Clusia grandiflora Splitg.	Clusiaceae
Conomorpha cf. *grandiflora* Mez.	Myrsinaceae
* *Doliocarpus spraguei* Cheesm.	Dilleniaceae
* *Erythroxylum campinense* Amaral Jr.	Erythroxylaceae
* *Eugenia patrisii* Vahl.	Myrtaceae
* *Pradosia schomburgkiana* (A. DC.) Cronquist	Sapotaceae
* *Henriettea maroniensis* Sagot	Melastomataceae
Heteropterys aff. *acutifolia* Adr. Juss.	Malpighiaceae
* *Hirtella racemosa* Lam. var. *racemosa*	Chrysobalanaceae
* *Humiria balsamifera* St Hil	Humiriaceae
* *Macrolobium arenarium* Ducke	Caesalpiniaceae
* *Mandevilla ulei* K. Schum	Apocynaceae
* *Manilkara amazonica* (Hub.) Standl.	Sapotaceae
Matayba opaca Radlk.	Sapindaceae
* *Miconia lepidota* A.DC.	Melastomataceae
Mouriri nervosa Plig.	Melastomataceae
* *Ormosia costulata* (Miq.) Kleinh.	Fabaceae
* *Ouratea spruceana* Engl.	Ochnaceae
* *Pagamea duckei* Standl.	Rubiaceae
* *Palicourea nitidella* (M. Arg.) Standl.	Rubiaceae
Parkia auriculata Spr. ex Benth	Mimosaceae
* *Protium heptaphyllum* (Aubl.) March	Burseraceae
* *Qualea retusa* Spr. ex Warm.	Vochysiaceae
Sandemania hoehnei (Cogn.) Wurdack	Melastomataceae
* *Swartzia dolichopoda* Cowan	Caesalpiniaceae
Talisia cerasina (Bth) Radlk.	Sapindaceae
* *Vernonia grisea* Baker	Compositae

Appendix 3.3: List of the plant species from SHF and THF on Spodosols which are also found in LERF on Ultisols in the *Reserva Biológica de Campina* (Anderson 1978).

Plant species	Family
Aldina heterophylla Spr. ex Benth.	Caesalpinaceae
Couepia racemosa Bth. ex Hook.f.	Chrysobalanaceae
Humiria balsamifera St Hil	Humiriaceae
Manilkara amazonica (Hub.) Standl.	Sapotaceae
Miconia lepidota A.DC.	Melastomataceae
Palicourea nitidella (M.Arg.) Standl.	Rubiaceae
Pera schomburgkiana (Bth.) M.Arg.	Euphorbiaceae
Protium heptaphyllum (Aubl.) March.	Burseraceae
Simaba cuspidata Spr. ex Engl.	Simarubaceae
Talisia cerasina (Bth.) Radlk.	Sapindaceae

Appendix 4.1: Annual input of mineral elements (kg ha^{-1} yr^{-1}) to forest floor in total fine litterfall in each plot of the three forest types.

	SHF			THF			LERF		
	1	2	3	4	5	6	7	8	9
N	53.3	19.1	40.6	59.8	74.5	68.4	116	112	107
P	1.68	0.56	1.08	5.29	1.97	0.84	2.41	2.27	2.23
K	8.99	2.58	5.36	7.49	6.77	6.21	8.90	9.45	9.96
Ca	34.3	9.31	20.4	14.3	14.5	14.0	14.7	13.6	14.1
Mg	9.58	3.36	7.09	7.04	7.35	7.98	8.78	8.62	9.81
Fe	1.02	0.24	0.44	0.66	0.80	0.74	0.93	1.36	1.21
Cu	0.04	0.01	0.02	0.02	0.04	0.25	0.03	0.03	0.04
Mn	0.42	0.13	0.27	0.34	0.37	0.38	1.40	0.72	0.45
Zn	0.09	0.04	0.14	0.12	0.11	0.10	0.13	0.12	0.14
B	0.24	0.08	0.19	0.23	0.25	0.27	0.33	0.30	0.35
Al	2.15	0.66	0.86	2.43	4.49	3.27	5.38	5.34	5.90

Appendix 4.2: Mineral element concentrations in each fraction of the litter layer in the three forest types. Values are means and SE of three composite samples from each of three plots, collected three times a year (n=9).

	mg g^{-1}					μg g^{-1}					
	N	P	K	Ca	Mg	Fe	Cu	Mn	Zn	B	Al
leaf											
SHF	13.1	0.37	0.63	5.43	1.43	272	5.63	103	18.0	20.0	395
	(0.64)	(0.06)	(0.15)	(0.71)	(0.12)	141	(2.83)	(21.5)	(1.73)	(3.61)	183
THF	14.3	0.30	0.60	1.80	0.90	407	4.47	67.3	11.7	17.7	1222
	(0.80)	(0.00)	(0.10)	(0.52)	(0.17)	355	(0.81)	(9.81)	(1.15)	(0.58)	812
LERF	18.5	0.30	0.50	1.17	0.70	772	4.00	55	13.0	18.0	2290
	(0.96)	(0.00)	(0.00)	(0.06)	(0.00)	791	(0.00)	(1.00)	(1.00)	(1.73)	1414
wood											
SHF	9.77	0.23	0.40	6.27	0.97	204	5.23	65.0	33.3	13.0	254
	(0.58)	(0.06)	(0.00)	(1.29)	(0.15)	709	(1.16)	(7.55)	(4.73)	(3.00)	102
THF	10.00	0.20	0.33	2.00	0.57	227	4.47	73.0	23.0	10.3	552
	(0.82)	(0.00)	(0.06)	(0.61)	(0.06)	208	(0.81)	(29.5)	(5.57)	(1.52)	173
LERF	12.9	0.20	0.40	1.40	0.47	302	4.70	59.7	18.3	10.7	670
	(2.7)	(0.00)	(0.00	(0.26)	(0.06)		(1.21)	(17.8)	(1.53)	(1.15)	114
						46.6					
reproductive parts											
SHF	12.97	0.37	0.80	2.40	0.93	270	9.67	51.0	18.7	38.3	311
	(1.27)	(0.06)	(0.10)	(0.66)	(0.15)	144	(7.52)	(19.9)	(4.62)	(10.1)	133
THF	11.17	0.53	1.63	1.10	0.87	233	6.37	46.7	16.0	28.0	387
	(1.3)	(0.23)	(0.49)	(0.53)	(0.38)	675	(2.97)	(21.2)	(5.00)	(10.4)	131
LERF	12.03	0.33	1.17	0.67	0.70	293	4.93	21.3	10.0	17.7	705
	(2.63)	(0.06)	(0.15)	(0.15)	(0.26)	139	(1.62)	(6.11)	(1.00)	(2.31)	537
fine fragments											
SHF	13.0	0.33	0.53	4.57	0.90	404	5.87	78.7	26.0	13.0	558
	(0.70)	(0.06)	(0.06)	(0.47)	(0.00)	190	(0.81)	(11.5)	(2.64)	(0.00)	252
THF	14.50	0.37	0.50	1.43	0.50	450	4.47	60.0	19.0	15.3	1038
	(0.46)	(0.06)	(0.10)	(0.38)	(0.10)	162	(0.81)	(16.8)	(6.08)	(2.31)	157
LERF	17.80	0.30	0.50	0.80	0.43	122	4.00	38.0	20.3	10.7	4153
	(1.31)	(0.00)	(0.00)	(0.10)	(0.17)	9	(0.00)	(3.61)	(5.86)	(1.15)	1756
						151					

Appendix 4.3: Quantities of mineral elements (kg ha^{-1}) in the litter layer in each plot of the three forest types. Values are means of three composite samples from each of three plots, collected three times a year.

	SHF			THF			LERF		
	1	2	3	4	5	6	7	8	9
N	62.8	51.0	85.4	83.5	86.6	80.1	123	101	91.7
P	1.84	1.20	2.29	1.89	1.89	1.78	1.89	1.60	1.72
K	3.23	2.09	3.70	3.94	3.41	2.91	3.41	2.90	3.30
Ca	31.0	20.9	36.1	14.1	7.80	12.1	8.13	7.78	6.72
Mg	6.23	4.92	8.24	5.04	3.90	5.10	4.15	3.47	3.57
Fe	2.15	0.96	1.40	1.94	3.59	1.41	4.91	4.25	4.04
Cu	0.04	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03
Mn	0.51	0.38	0.50	0.54	0.33	0.42	0.36	0.36	0.30
Zn	0.11	0.11	0.16	0.12	0.10	0.09	0.13	0.09	0.10
B	0.08	0.07	0.13	0.09	0.10	0.10	0.10	0.09	0.08
Al	2.94	1.38	1.92	4.32	9.64	4.84	11.5	12.6	14.9

Appendix 5.1a: Experiment A: mean initial (n=16) and final (n= 12) concentrations of mineral elements in *Clitoria* leaves in the litter bags. Values are the means with SD in parenthesis..

		%					μg g^{-1}					
		N	P	K	Ca	Mg	Al	B	Cu	Fe	Mn	Zn
0 d	SHF	1.26 0.08	0.04 0.01	0.22 0.03	2.69 0.48	0.15 (0.03	198 (41.9)	39.5 (7.45)	7.04 (2.53	99.6 (20.0)	12.6 (29.8)	20.0 (5.37)
	THF	1.26 (0.08)	0.04 (0.01)	0.22 (0.03)	2.69 (0.48)	0.15 (0.03)	198 (41.9)	39.5 (7.45)	7.04 (2.53)	99.6 (20.0)	12.6 (29.8)	20.0 (5.37)
	LERF	1.26 (0.08)	0.04 (0.01)	0.22 (0.03)	2.69 (0.48)	0.15 (0.03)	198 (41.9)	39.5 (7.45)	7.04 (2.53)	99.6 (20.0)	12.6 (29.8)	20.0 (5.37)
30 d	SHF	1.51 (0.09)	0.04 (0.003	0.09 (0.02)	2.93 (0.23)	0.14 (0.01)	372 (69.8)	46.0 (6.84)	5.20 (0.75)	175 (20.6)	89.2 (49.0)	13.7 (1.91)
	THF	1.62 (0.08)	0.04 (0.00)	0.08 (0.01)	3.12 (0.32)	0.13 (0.03)	372 (56.4)	43.9 (6.73)	4.95 (1.19)	186 (31.7)	110 (50.9)	15.3 (2.06)
	LERF	1.56 (0.08)	0.04 (0.00)	0.09 (0.00)	3.10 (0.30)	0.15 (0.01)	667 (314)	392 (102)	5.28 (1.20)	259 (80.8)	92.3 (60.4)	15.9 (3.09)
60 d	SHF	1.71 (0.18)	0.04 (0.01)	0.07 (0.01)	3.37 (0.43)	0.13 (0.02)	530 (116)	51.4 (15.9)	5.08 (0.66)	240 (51.8)	86.2 (55.6)	18.6 (4.10)
	THF	1.81 (0.08)	0.04 (0.00)	0.06 (0.01)	3.40 (0.46)	0.11 (0.03)	481 (87.3)	50.5 (8.65)	6.10 (0.80)	237 (44.0)	103 (56.3)	25.0 (14.3)
	LERF	1.72 (0.13)	0.04 (0.00)	0.07 (0.00)	3.11 (0.32)	0.11 (0.04)	716 (234)	41.8 (797)	6.48 (1.12)	287 (62.2)	64.2 (429)	18.0 (7.46)
120 d	SHF	1.83 (0.11)	0.03 (0.01)	0.06 (0.01)	3.16 (0.46)	0.09 (0.02)	487 (187)	89.5 (16.7)	7.04 (1.26)	215 (78.5)	90.4 (33.6)	16.5 (2.94)
	THF	1.85 (0.17)	0.04 (0.00)	0.07 (0.00)	2.36 (0.56)	0.05 (0.02)	567 (162)	86.7 (7.14)	6.24 (1.50)	236 (68.0)	74.8 (35.2)	16.2 (2.38)
	LERF	2.10 (0.14)	0.04 (0.00)	0.06 (0.00)	1.66 (0.50)	0.03 (0.02)	837 (227)	79.5 (21.2)	7.70 (3.06)	225 (29.5)	53.0 (33.1)	14.2 (2.26)
180 d	SHF	2.08 (0.31)	0.05 (0.01)	0.06 (0.01)	3.25 (0.86)	0.08 (0.02)	754 (240)	107 (37.0)	6.62 (2.87)	366 (124)	115 (64.7)	16.6 (3.60)
	THF	1.95 (0.15)	0.04 (0.00)	0.05 (0.00)	2.61 (0.74)	0.06 (0.02)	621 (170)	115 (38.0)	7.43 (1.57)	288 (91.3)	134 (47.2)	18.8 (3.10)
	LERF	2.25 (0.07)	0.05 (0.00)	0.06 (0.00)	1.32 (0.60)	0.03 (0.01)	1010 (207)	95.5 26.6	7.13 1.24	346 120	70.5 47.2	14.3 4.49
270 d	SHF	2.12 (0.24)	0.05 (0.01)	0.06 (0.01)	3.43 (0.46)	0.09 (0.03)	9.79 (2.83)	53.6 (15.5)	9.20 (4.33)	432 (141)	141 (52.5)	23.3 (4.81)
	THF	2.18 (0.10)	0.04 (0.00)	0.07 (0.02)	1.15 (0.70)	0.03 (0.01)	1090 (206)	60.9 (12.6)	8.68 (5.53)	362 (148)	71.4 (49.1)	18.3 (4.96)
	LERF	2.16 (0.19)	0.04 (0.00)	0.06 (0.03)	0.69 (0.44)	0.04 (0.02)	1250 (234)	65.2 (16.4)	8.14 (2.42)	413 (161)	40.0 (28.3)	15.7 (7.25)
360 d	SHF	2.18 (0.15)	0.05 (0.00)	0.06 (0.02)	3.33 (0.71)	0.08 (0.01)	1150 (210)	37.3 (7.42)	6.43 (1.78)	514 (165)	144 (46.7)	22.0 (1.48)
	THF	2.17 (0.13)	0.05 (0.01)	0.06 (0.00)	1.68 (1.02)	0.03 (0.01)	1230 (134)	31.3 (4.73)	5.67 (1.43)	417 (101)	45.8 (22.7)	15.8 (3.21)
	LERF	2.34 (0.41)	0.04 (0.00)	0.06 (0.01)	0.34 (0.22)	0.02 (0.00)	1340 (39.6)	29.5 (2.07)	5.40 (0.92)	621 (45.8)	33.0 (19.6)	13.0 (2.89)

Appendix 5.1b: Experiment A: mean initial (n=16) and final (n=12) concentrations of mineral elements in the leaves of *Pradosia* in the litter bags. Values are the means and SD.

		%					μg g^{-1}					
days		N	P	K	Ca	Mg	Al	B	Cu	Fe	Mn	Zn
0	SHF	0.38 (0.03)	0.03 (0.005)	0.20 (0.03)	0.44 (0.04)	0.17 (0.03)	148 (36.2)	59.6 (8.51)	4.23 (0.88)	94.9 (23.2)	7.51 (6.51)	10.8 (4.17)
	THF	0.38 (0.03)	0.03 (0.005)	0.20 (0.03)	0.44 (0.04)	0.17 (0.03)	148 (36.2)	59.6 (8.51)	4.23 (0.88)	94.9 (23.2)	27.5 (6.51)	10.8 (4.17)
	LERF	0.38 (0.03)	0.03 (0.005)	0.20 (0.03)	0.44 (0.04)	0.17 (0.03)	148 (36.2)	59.6 (8.51)	4.23 (0.88)	94.9 (23.2)	27.5 (6.51)	10.8 (4.17)
30	SHF	0.46 (0.03)	0.02 (0.00)	0.08 (0.03)	0.41 (0.05)	0.14 (0.03)	124 (26.2)	44.2 (6.27)	5.82 (3.82)	74.2 (14.9)	62.7 (16.3)	10.2 (2.63)
	THF	0.51 (0.04)	0.02 (0.00)	0.09 (0.03)	0.42 (0.09)	0.15 (0.03)	123 (29.8)	39.7 (5.43)	4.00 (0.00)	76.5 (21.2)	65.8 (18.9)	10.0 (2.59)
	LERF	0.48 (0.03)	0.02 (0.00)	0.10 (0.03)	0.43 (0.06)	0.16 (0.03)	137 (34.9)	36.4 (9.18)	4.23 (0.81)	84.0 (20.3)	81.6 (35.4)	8.75 (0.75)
60	SHF	0.54 (0.07)	0.01 (0.00)	0.09 (0.03)	0.43 (0.07)	0.17 (0.02)	131 (51.0)	33.0 (3.78)	4.17 (0.39)	70.2 (18.9)	47.7 (12.3)	15.0 (8.01)
	THF	0.54 (0.10)	0.02 (0.00)	0.08 (0.02)	0.41 (0.08)	0.16 (0.03)	115 (27.4)	27.7 (5.12)	4.65 (0.90)	64.5 (15.8)	56.7 (15.0)	16.7 (12.2)
	LERF	0.62 (0.06)	0.02 (0.00)	0.08 (0.02)	0.45 (0.08)	0.15 (0.03)	159 (70.5)	29.9 (5.87)	4.58 (1.05)	72.2 (14.3)	41.2 (18.6)	10.7 (1.29)
120	SHF	0.59 (0.08)	0.02 (0.00)	0.08 (0.03)	0.46 (0.03)	0.17 (0.02)	106 (69.7)	63.0 (17.1)	3.97 (1.19)	63.1 (30.4)	77.8 (21.2)	9.50 (1.45)
	THF	0.60 (0.16)	0.02 (0.00)	0.06 (0.01)	0.40 (0.12)	0.14 (0.04)	134 (54.2)	50.4 (15.4)	4.12 (0.43)	75.9 (27.0)	59.4 (27.3)	10.2 (1.64)
	LERF	0.62 (0.05)	0.03 (0.02)	0.06 (0.00)	0.26 (0.07)	0.06 (0.03)	237 (273)	45.6 (11.9)	4.33 (0.79)	85.4 (40.5)	46.3 (19.7)	9.67 (1.23)
180	SHF	0.61 (0.08)	0.02 (0.01)	0.07 (0.03)	0.44 (0.06)	0.15 (0.03)	162 (122)	68.2 (21.5)	4.39 (0.93)	79.6 (32.0)	104 (30.9)	10.0 (1.81)
	THF	0.60 (0.08)	0.02 (0.00)	0.06 (0.01)	0.48 (0.12)	0.14 (0.04)	151 (30.8)	84.7 (18.6)	4.00 (0.00)	94.4 (21.6)	68.7 (22.7)	11.3 (3.08)
	LERF	0.78 (0.07)	0.02 (0.01)	0.06 (0.02)	0.20 (0.06)	0.04 (0.02)	562 (504)	66.7 (31.0)	5.16 (1.85)	2.33 (1.24)	47.6 (39.8)	10.8 (2.85)
270	SHF	0.59 (0.12)	0.02 (0.00)	0.06 (0.02)	0.44 (0.12)	0.16 (0.04)	231 (203)	35.2 (10.6)	5.57 (1.72)	101 (65.5)	93.7 (21.3)	10.0 (1.92)
	THF	0.67 (0.05)	0.02 (0.00)	0.05 (0.00)	0.32 (0.07)	0.09 (0.04)	229 (80.8)	36.0 (6.00)	4.44 (0.89)	136 (47.4)	86.9 (44.0)	10.7 (1.42)
	LERF	0.78 (0.10)	0.02 (0.00)	0.06 (0.01)	0.11 (0.05)	0.03 (0.01)	512 (318)	39.8 (13.6)	5.27 (2.01)	166 (70.8)	45.2 (37.0)	12.4 (5.43)
360	SHF	0.61 (0.08)	0.02 (0.00)	0.05 (0.01)	0.45 (0.07)	0.15 (0.03)	313 (185)	20.8 (2.04)	5.25 (1.47)	137 (81.9)	84.2 (16.0)	10.2 (1.40)
	THF	0.64 (0.06)	0.02 (0.00)	0.05 (0.00)	0.32 (0.11)	0.07 (0.02)	361 (107)	215 (4.03)	4.43 (1.01)	129 (53.0)	42.0 (11.8)	10.7 (1.30)
	LERF	1.02 (0.18)	0.02 (0.00)	0.05 (0.00)	0.07 (0.03)	0.02 (0.00)	991 (269)	20.5 (3.06)	4.00 (0.00)	328 (169)	32.8 (15.0)	9.83 (0.94)

Appendix 5.1c: Experiment A: mean initial (n=16) and final (n=12) concentrations of mineral elements in the leaves of *Aldina* in the litter bags. Values are means and SD.

		%					μg g^{-1}					
days		N	P	K	Ca	Mg	Al	B	Cu	Fe	Mn	Zn
0	SHF	1.32 (0.06)	0.05 (0.007)	0.25 (0.02)	0.38 (0.04)	0.11 (0.008)	91.0 (16.5)	56.4 (5.10)	10.6 (1.52)	78.3 (15.8)	50.4 (6.94)	16.3 (1.94)
	THF	1.32 (0.06)	0.05 (0.007)	0.25 (0.02)	0.38 (0.04)	0.11 (0.008)	91.0 (16.5)	56.4 (5.10)	10.6 (1.52)	78.3 (15.8)	50.4 (6.94)	16.3 (1.94)
	LERF	1.32 (0.06)	0.05 (0.007)	0.25 (0.02)	0.38 (0.04)	0.11 (0.008)	91.0 (16.5)	56.4 (5.10)	10.6 (1.52)	78.3 (15.8)	50.4 (6.94)	16.3 (1.94)
30	SHF	1.54 (0.05)	0.03 (0.00)	0.16 (0.03)	0.46 (0.09)	0.13 (0.02)	87.5 (22.8)	50.6 (5.37)	9.40 (2.19)	78.9 (11.1)	50.3 (8.98)	15.0 (1.38)
	THF	1.66 (0.06)	0.04 (0.00)	0.15 (0.02)	0.42 (0.08)	0.13 (0.01)	86.7 (20.5)	43.0 (4.18)	9.70 (1.74)	78.4 (9.92)	51.6 (9.38)	15.0 (2.04)
	LERF	1.69 (0.12)	0.04 (0.00)	0.17 (0.02)	0.39 (0.13)	0.13 (0.01)	98.1 (22.0)	48.3 (9.16)	9.88 (1.06)	84.5 (10.2)	58.0 (14.4)	15.7 (1.05)
60	SHF	1.82 (0.22)	0.03 (0.00)	0.12 (0.03)	0.42 (0.09)	0.13 (0.01)	85.4 (20.6)	39.9 (3.94)	8.75 (1.31)	77.7 (12.7)	45.2 (12.2)	19.7 (3.46)
	THF	1.90 (0.17)	0.03 (0.00)	0.11 (0.02)	0.43 (0.08)	0.13 (0.02)	202 (37.1)	36.7 (5.31)	9.26 (1.11)	91.1 (83.0)	51.8 (14.5)	18.0 (3.23)
	LERF	1.71 (0.06)	0.04 (0.00)	0.10 (0.02)	0.39 (0.07)	0.12 (0.02)	113 (25.6)	37.5 (5.25)	9.67 (1.23)	78.7 (16.0)	39.4 (8.61)	17.2 (2.52)
120	SHF	1.84 (0.13)	0.04 (0.00)	0.08 (0.02)	0.48 (0.07)	0.13 (0.01)	84.3 (49.8)	61.3 (8.77)	10.6 (1.08)	59.5 (17.2)	57.2 (10.3)	16.2 (1.14)
	THF	1.78 (0.17)	0.04 (0.00)	0.06 (0.01)	0.40 (0.12)	0.10 (0.04)	104 (38.7)	65.7 (10.8)	9.97 (1.64)	75.2 (15.1)	50.2 (19.7)	16.2 (1.64)
	LERF	1.89 (0.05)	0.05 (0.04)	0.07 (0.02)	0.33 (0.12)	0.08 (0.03)	154 (48.2)	62.2 (7.65)	13.7 (1.86)	76.7 (14.8)	45.3 (16.2)	17.7 (3.54)
180	SHF	1.79 (0.15)	0.04 (0.00)	0.06 (0.02)	0.54 (0.09)	0.12 (0.02)	145 (70.5)	75.7 (25.1)	10.0 (2.82)	127 (49.8)	70.7 (15.9)	18.3 (3.65)
	THF	1.89 (0.20)	0.04 (0.00)	0.06 (0.02)	0.60 (0.30)	0.09 (0.03)	161 (95.5)	85.4 (22.0)	10.1 (2.38)	139 (55.4)	54.2 (15.9)	17.0 (2.66)
	LERF	1.87 (0.11)	0.03 (0.00)	0.04 (0.00)	0.25 (0.07)	0.02 (0.00)	459 (329)	73.2 (16.3)	11.5 (1.33)	139 (52.9)	29.7 (7.95)	14.7 (3.55)
270	SHF	1.96 (0.11)	0.04 (0.01)	0.06 (0.02)	0.54 (0.11)	0.11 (0.03)	340 (171)	56.5 (11.9)	12.6 (2.98)	155 (64.5)	69.2 (18.5)	19.0 (2.84)
	THF	2.02 (0.17)	0.04 (0.01)	0.05 (0.01)	0.41 (0.14)	0.07 (0.02)	278 (134)	47.7 (16.8)	10.8 (2.40)	153 (31.4)	50.2 (20.0)	18.9 (4.64)
	LERF	1.95 (0.16)	0.04 (0.00)	0.05 (0.00)	0.22 (0.08)	0.03 (0.01)	815 (306)	57.6 (11.5)	11.5 (2.29)	265 (144)	33.3 (13.5)	15.9 (4.19)
360	SHF	2.05 (0.04)	0.04 (0.00)	0.05 (0.00)	0.54 (0.16)	0.11 (0.04)	453 (251)	26.0 (2.95)	11.5 (2.25)	200 (87.7)	75.5 (15.5)	18.5 (2.74)
	THF	2.03 (0.08)	0.04 (0.03)	0.05 (0.00)	0.23 (0.09)	0.04 (0.02)	537 (176)	215 (132)	8.77 (1.98)	180 (111)	2.97 (6.95)	15.3 (3.39)
	LERF	1.72 (0.54)	0.03 (0.00)	0.04 (0.01)	0.06 (0.02)	0.02 (0.00)	1170 (278)	23.2 (3.09)	7.90 (1.48)	346 (168)	22.3 (5.00)	10.5 (1.00)

Appendix 5.2a: Experiment A: percentage (%) remaining quantities of mineral elements in *Clitoria* leaves after each retrieval time in relation to the initial content. Values are means with SE in parenthesis (n=12).

days	forest	N	P	K	Ca	Mg	Al	B	Cu	Fe	Mn	Zn
30	SHF	101	83.1	36.4	92.4	81.1	159	98.7	62.6	148	60.2	58.3
		(1.81)	(2.00)	(2.80)	(2.33)	(1.91)	(8.98)	(4.33)	(2.64)	(4.99)	(9.64)	2.46
	THF	107	85.3	31.0	97.0	75.4	157	92.9	58.9	156	73.7	64.1
		(1.32)	(1.79)	(1.17)	(2.80)	(4.53)	(7.16)	(4.22)	(4.33)	(7.62)	(9.84)	(2.61)
	LERF	105	90.3	34.5	98.3	87.0	286	84.4	64.0	221	61.7	67.4
		(1.75)	(2.62)	(1.05)	(2.79)	(2.61)	(39.8)	(6.23)	(4.53)	(20.0)	(11.3)	(3.41)
60	SHF	107	80.2	25.2	99.3	68.0	207	103	56.7	190	56.1	72.9
		(3.29)	(3.90)	(1.26)	(3.64)	(3.12)	(13.8)	(9.87)	(2.12)	(12.0)	(9.76)	(4.45)
	THF	110	81.4	23.8	97.1	60.3	185	97.9	66.9	181	63.2	95.9
		(1.86)	(5.48)	(1.59)	(4.33)	(5.14)	(9.06)	(4.96)	(2.39)	(8.69)	(10.2)	(15.9)
	LERF	102	81.2	26.1	86.8	54.3	271	79.4	68.9	216	37.9	67.0
		(2.25)	(3.35)	(0 93)	(2.71)	(5.57)	(24.8)	(4.10)	(3.00)	(12.9)	(6.96)	(7.48)
120	SHF	94.1	54.1	17.6	75.6	40.9	154	147	64.1	136	46.0	52.8
		(2.63)	(12.7)	(0.95)	(2.62)	(2.19)	(11.8)	(10.4)	(2.70)	(10.2)	(4.82)	(2.00)
	THF	91.6	69.1	20.1	54.9	21.1	178	137	55.2	147	37.3	50.7
		(2.34)	(3.00)	(0.74)	(14.3)	(2.97)	(14.1)	(4.73)	(3.75)	(11.5)	(5.43)	(8.59)
	LERF	100	63.8	16.5	36.8	12.7	257	121	66.4	136	24.2	42.7
		(13.4)	(2.94)	(0 57)	(3.12)	(2.44)	(27.7)	(11.3)	(8.63)	(7.65)	(12.6)	(2.59)
180	SHF	99.1	72.4	18.0	73.6	34.6	230	163	57.8	221	56.0	50.2
		(5.86)	(4 76)	(1.39)	(6.75)	(2.86)	(25.1)	(16.6)	(9.38)	(24.5)	(10.0)	(4.79)
	THF	84.7	55.8	13.0	52.8	20.5	169	162	57.5	156	58.2	51.5
		(1.82)	(2.34)	(0.55)	(4.24)	(2.43)	(11.2)	(18.5)	(3.50)	(11.3)	(5.71)	(2.73)
	LERF	86.5	59.5	13.6	23.9	8.93	244	115	48.6	165	27.0	34.6
		(3.49)	(2.59)	(0.74)	(3.88)	(1.58)	(13.0)	(9.29)	(2.31)	(15.3)	(5.22)	(3.43)
270	SHF	73.2	48.3	12.0	55.8	26.4	210	58.8	55.1	185	47 8	50.6
		(3.32)	(2.97)	(0.81)	(2.97)	(2.33)	(13.6)	(5.02)	(6.55)	(15.1)	(4.23)	(3.20)
	THF	74.5	51.7	11.4	25.8	9.92	238	66.1	51.6	182	23.5	39.2
		(2.80)	(1.80)	(0.60)	(4.21)	(1.36)	(16.8)	(1.12)	(8.37)	(16.7)	(4.21)	(2.78)
	LERF	74.1	47.2	11.9	10.8	10.3	270	71.3	49.0	173	13.2	32.3
		(3.95)	(2.08)	(1.46)	(1.84)	(1.44)	(16.8)	(6.73)	(3.78)	(16.4)	(2.46)	(2.82)
360	SHF	59 7	40.4	9.60	42.9	18.4	196	33.0	30.7	170	39.7	38.0
		(4.82)	(3.43)	(0.95)	(4.76)	(2.06)	(14.9)	(3.32)	(2.63)	(16.5)	(4.70)	(3.12)
	THF	65.1	42.4	12.8	16.5	6.78	233	30.3	30.5	139	13.5	29.7
		(3.95)	(2.94)	(1.27)	(3.26)	(0 78)	(16 0)	(2.52)	(2.94)	(19.1)	(1.84)	(2.13)
	LERF	61.3	37 6	9.91	4 41	5.27	225	24.8	25.2	209	8.60	21.5
		(5.54)	(3 17)	(0 90)	(0 84)	(0 68)	(17.1)	(2.03)	(2.12)	(17.1)	(1.40)	(1.81)

Appendix 5.2b: Experiment A: percentage (%) remaining quantities of mineral elements in *Pradosia* leaves after each retrieval time in relation to the initial content. Values are means with SE in parenthesis (n=12).

days	forest	N	P	K	Ca	Mg	Al	B	Cu	Fe	Mn	Zn
30	SHF	108	54.6	34.3	83.1	76.9	75.4	66.6	124	702	205	85.4
		(2.18)	(3.26)	(3.26)	(3.20)	(4.10)	(4.44)	(2.97)	(24.2)	(4.24)	(15.8)	(6.75)
	THF	117	58.2	39.4	84.1	79.0	73.1	58.5	83.0	70.5	208	81.0
		(2.87)	(4.79)	(3.61)	(4.88)	(94.1)	(4.85)	(2.24)	(0.21)	(5.28)	(15.9)	(5.69)
	LERF	111	60.9	44.8	86.7	85.2	81.2	53.4	87.6	77.5	260	71.0
		(2.10)	(2.70)	(4.24)	(3.67)	(4.79)	(6.00)	(3.78)	(4.82)	(5.43)	(33.5)	(1.91)
60	SHF	123	45.4	37.7	84.6	85.5	76.8	47.9	85.2	63.7	149	121
		(4.27)	(4.10)	(3.84)	(3.75)	(3.06)	(8.57)	(1.51)	(2.47)	(4.62)	(11.1)	(19.4)
	THF	120	49.8	34.9	80.7	82.9	66.8	39.8	93.8	58.2	176	131
		(6.32)	(5.11)	(1.99)	(4.59)	(4.53)	(4.70)	(2.19)	(4.88)	(4.18)	(13.6)	(15.8)
	LERF	134	54.6	34.4	80.3	73.0	89.0	41.3	89.2	62.6	123	81.9
		(3.72)	(4.50)	(3.29)	(4.30)	(4.42)	(11.8)	(2.36)	(6.12)	(3 61)	(15.8)	(2.97)
120	SHF	123	52 7	34.3	82.8	78.4	56.8	84.8	74.4	52.5	225	69.7
		(4 04)	(2.94)	(3.46)	(2.11)	(3.58)	(10.1)	(6.99)	(6.21)	(6.87)	(17.9)	(2.84)
	THF	122	53 2	23.4	70.5	63.1	69.9	65.1	74.9	61.5	165	72.3
		(9.81)	(4 79)	(1.68)	(5.95)	(5.51)	(8.66)	(6.09)	(2.60)	(6.49)	(22.4)	(3.35)
	LERF	113	70.9	22.0	42.4	24.7	100	52.8	71.5	61.0	114	62.0
		(6.09)	(14.4)	(1.20)	(3.93)	(3.62)	(23.7)	(4.62)	(5.28)	(6.49)	(13.2)	(3.00)
180	SHF	120	52.0	26.4	74.7	67.4	826	86.2	77.2	69.6	287	68.9
		(3.41)	(5.14)	(3.12)	(2.54)	(3.72)	(19.4)	(8 05)	(3.81)	(6.09)	(27.5)	(2.86)
	THF	110	54.4	20.6	76.0	59.2	71.9	99.7	66.4	69.5	175	73.7
		(3.64)	(2.97)	(1.15)	(5.43)	(5.74)	(4 6)	(6 23)	(1.07)	(4.18)	(17.0)	(5.97)
	LERF	129	47.8	17.8	28.0	15.1	249	66.4	74 3	156	105	61.2
		(8.23)	(3.43)	(1.38)	(2.44)	(2.60)	(6.87)	(7.04)	(6.70)	(27 6)	(24 6)	(3.72)
270	SHF	105	40.7	19.1	68.9	65.9	101	40.1	89.9	70.4	233	63.5
		(4.07)	(3.00)	(1.75)	(4.47)	(4.10)	(2.18)	(2.97)	(7.27)	(10.5)	(15.1)	(2.17)
	THF	114	55 6	17.5	47.7	36.8	101	39.2	68.3	93 3	205	64.6
		(2.22)	(2 74)	(0 74)	(3.06)	(4.56)	(10.8)	(1.76)	(4 01)	(9.50)	(3 03)	(2.22)
	LERF	126	46.2	18 0	15 2	12.0	215	40.8	76.2	107	97.1	70.1
		(6.00)	(3.32)	(1.92)	(1.97)	(1.66)	(4.10)	(4.16)	(8.54)	(14 1)	(21.2)	(9.09)
360	SHF	97 0	43.9	16 7	62.8	53.9	126	21.4	74.8	87 1	185	57.4
		(4 04)	(2.41)	(0 91)	(3 93)	(3.87)	(20.9)	(1.16)	(5 60)	(14 6)	(9.93)	(2.97)
	THF	104	41.1	16 0	45 2	25.5	150	22.2	64.9	84 6	94 8	61.1
		(3.84)	(0 81)	(4 62)	(4 62)	(2.29)	(13.0)	(1.08)	(4.82)	(10 2)	(8.37)	(2.81)
	LERF	134	33.2	13 3	8.49	6.94	334	17.1	47.0	166	61.4	44.7
		(11.9)	(2.23)	(0 99)	(1.30)	(0 90)	(36 7)	(1.40)	(3.15)	(23 3)	(9.61)	(2.58)

Appendix 5.2c: Experiment A: percentage (%) remaining quantities of mineral elements in *Aldina* leaves after each retrieval time in relation to the initial content. Values are means with SE in parenthesis (n=12).

days	forest	N	P	K	Ca	Mg	Al	B	Cu	Fe	Mn	Zn
30	SHF	107	61.6	59.1	112	110	88.0	82.8	81.9	93.0	92.2	85.5
		(0.99)	(2.68)	(3.09)	(6.15)	(4.10)	(6.73)	(2.54)	(5.46)	(3.72)	(4.73)	(2.35)
	THF	112	66.9	53.5	99.9	102	84.8	67.9	81.8	89.2	91.5	81.9
		(1.81)	(2.62)	(2.15)	(5.66)	(3.46)	(5.72)	(1.87)	(4.68)	(3.23)	(5.25)	(3.06)
	LERF	111	71.0	58.0	89.5	100	93.5	74.5	80.9	93.6	99.8	84.0
		(2.53)	(1.82)	(2.62)	(8.77)	(3.52)	(5.95)	(4.18)	(2.26)	(2.89)	(7.04)	(1.89)
60	SHF	122	54.6	44.3	98.2	108	83.1	62.7	73.3	88.0	79.4	107
		(3.90)	(3.93)	(2.77)	(5.97)	(3.26)	(5.48)	(1.53)	(3.38)	(3.78)	(5.97)	(5.17)
	THF	124	60.3	39.1	97.9	100	193	56.1	75.3	100	88.5	95.3
		(3.20)	(2.38)	(2.22)	(3.68)	(4.91)	(10.4)	(2.40)	(2.34)	(27.0)	(6.81)	(3.98)
	LERF	109	63.2	35.4	87.4	92.7	105	56.1	77.0	84.7	65.8	88.9
		(1.56)	(2.97)	(2.29)	(4.21)	(5.43)	(6.93)	(2.41)	(2.85)	(4.88)	(3.98)	(3.93)
120	SHF	108	58.2	26.4	99.0	96.3	71.0	84.8	77.8	58.7	88.4	77.9
		(1.09)	(2.04)	(1.68)	(4.47)	(2.37)	(10.9)	(3.23)	(2.19)	(4.10)	(4.30)	(1.94)
	THF	96.5	55.1	18.7	75.2	64.6	82.3	82.7	67.4	69.1	71.5	70.7
		(5.05)	(3.93)	(1.00)	(7.62)	(7.48)	(9.27)	(5.17)	(4.53)	(5.31)	(9.27)	(3.72)
	LERF	97.5	76.6	20.0	59.5	49.6	116	74.6	88.1	67.0	60.3	73.7
		(4.30)	(17.0)	(2.48)	(6.64)	(6.99)	(12.4)	(3.06)	(4.82)	(4.96)	(6.38)	(4.73)
180	SHF	93.9	52.1	17.1	97.9	77.2	106	91.9	65.1	109	96.9	77.8
		(2.17)	(1.86)	(0.52)	(0.55)	(4.85)	(11.3)	(7.65)	(4.42)	(8.60)	(5.95)	(3.87)
	THF	96.3	53.8	17.5	99.6	59.9	116	101	64.7	118	72.0	70.8
		(2.28)	(2.39)	(1.92)	(13.0)	(6.69)	(18.0)	(7.24)	(4.30)	(12.1)	(5.28)	(3.72)
	LERF	85.8	42.4	10.7	39.0	13.6	298	78.4	66.1	106	35.5	54.2
		(3.46)	(2.43)	(0.54)	(3.23)	(1.20)	(57.1)	(5.69)	(3.55)	(11.1)	(2.72)	(4.24)
270	SHF	89.3	50.6	15.5	85.4	62.6	217	60.3	71.8	115	81.6	70.5
		(3.15)	(3.17)	(1.23)	(4.88)	(5.51)	(27.0)	(4.21)	(5.54)	(9.67)	(5.43)	(3.90)
	THF	83.4	43.6	10.2	56.6	32.4	162	46.4	55.3	107	51.8	62.6
		(3.98)	(2.19)	(0.59)	(3.78)	(3.64)	(23.5)	(5.63)	(3.55)	(8.40)	(4.47)	(4.82)
	LERF	59.9	29.4	8.07	22.5	10.5	357	39.9	44.7	132	26.8	39.5
		(6.44)	(3.12)	(0.84)	(2.85)	(1.72)	(50.8)	(3.61)	(5.54)	(20.5)	(4.07)	(5.22)
360	SHF	76.6	39.5	11.1	70.1	48.5	239	22.8	53.2	123	73.8	56.2
		(3.43)	(1.81)	(0.53)	(7.22)	(6.03)	(3 72)	(1.27)	(3.72)	(14.9)	(5.40)	(3.78)
	THF	73.4	39.5	9.46	28.2	16.8	287	18.0	38.7	112	27.6	44.1
		(2.94)	(1.59)	(0.37)	(2.73)	(1.79)	(33.5)	(0.82)	(20.7)	(22.5)	(1.64)	(2.36)
	LERF	58.4	28.9	7.35	6.76	6.58	559	17.8	32.7	184	19.2	28.2
		(7.76)	(1.98)	(0.70)	(0.82)	(0.69)	(52.2)	(1.17)	(2.80)	(21.7)	(1.58)	(2.02)

Appendix 5.3. Experiment B: mean concentrations of mineral elements in the leaves of *Clitoria* in the litter bags at the begining of the experiment (n=16) and after each retrieval time (n=12). Values are means and SD.

		N	P	K	Ca	Mg	Fe	Cu	Mn	Zn	B	Al
				%					$\mu g\ g^{-1}$			
0 d	SHF	1.33	0.04	0.23	2.44	0.15	138	7.43	109	16.7	84.9	213
		0.12	0.00	0.05	0.47	0.02	72.1	1.00	25.0	5.80	19.3	56.8
	THF	1.33	0.04	0.23	2.44	0.15	138	7.43	109	16.7	84.9	213
		0.12	0.00	0.05	0.47	0.02	72.1	1.00	25.0	5.80	19.3	56.8
	LERF	1.33	0.04	0.23	2.44	0.15	138	7.43	109	16.7	84.9	213
		0.12	0.00	0.05	0.47	0.02	72.1	1.00	25.0	5.80	19.3	56.8
30 d	SHF	1.36	0.04	0.09	3.04	0.16	138	6.46	129	17.6	55.4	282
		0.12	0.004	0.03	0.23	0.02	25.6	1.31	26.1	3.20	5.38	55.5
	THF	1.50	0.06	0.13	3.10	0.16	158	5.47	138	19.0	61.4	328
		0.10	0.08	0.04	0.37	0.02	36.4	1.26	21.2	3.07	13.2	68.2
	LERF	1.48	0.04	0.09	3.20	0.16	169	8.17	130	18.0	65.6	355
		0.12	0.03	0.03	0.22	0.01	46.7	2.33	25.9	2.45	17.6	45.0
60 d	SHF	1.51	0.04	0.07	3.33	0.17	176	7.40	139	18.7	47.8	369
		0.07	0.005	0.02	0.35	0.02	60.4	1.47	23.3	2.71	8.63	117
	THF	1.39	0.06	0.10	3.49	0.16	177	7.55	138	19.2	51.2	396
		0.11	0.08	0.13	0.35	0.02	24.9	1.23	27.2	2.72	8.25	86.7
	LERF	146	0.04	0.06	3.37	0.15	230	8.19	140	19.7	49.0	569
		0.09	0.00 5	0.01	0.28	0.02	31.1	1.67	23.9	2.26	10.4	112
120 d	SHF	1.56	0.04	0.05	3.38	0.14	298	7.77	139	23.1	39.7	679
		0.11	0.01	0.01	0.51	0.03	107	1.17	32.7	4.03	12.4	236
	THF	1.59	0.04	0.06	3.34	0.11	327	6.97	125	22.5	47.0	815
		0.13	0.00	0.01	0.34	0.02	119	1.17	13.0	4.17	10.7	255
	LERF	1.72	0.04	0.06	3.49	0.10	437	7.35	129	22.0	52.7	1270
		0.12	0.004	0.00	0.53	0.02	148	2.29	45.0	3.98	13.3	575
180 d	SHF	1.88	0.04	0.05	3.86	0.09	509	7.75	154	24.7	54.5	1030
		0.18	0.01	0.01	0.92	0.02	281	1.67	38.8	3.60	24.7	632
	THF	1.96	0.05	0.07	3.05	0.05	482	7.37	115	22.9	57.5	1170
		0.16	0.01	0.01	1.05	0.02	182	0.81	31.3	7.19	19.9	651
	LERF	2.08	0.04	0.05	1.58	0.02	690	7.23	68.5	20.8	55.7	3240
		0.30	0.01	0.01	0.77	0.01	696	1.18	30.6	9.02	13.9	3880
270 d	SHF	1.98	0.05	0.06	3.55	0.07	303	9.17	155	30.2	66.0	1030
		0.13	0.01	0.02	0.87	0.01	136	2.89	35.9	6.34	20.6	377
	THF	2.09	0.05	0.07	1.08	0.02	257	6.42	57.9	17.6	44.4	1110
		0.11	0.01	0.01	0.80	0.01	91.8	1.11	36.1	4.98	14.7	287
	LERF	2.27	0.04	0.06	0.60	0.02	573	7.14	44.8	19.3	50.7	2270
		0.13	0.01	0.01	0.85	0.01	407	3.28	38.3	6.57	23.1	1550
360 d	SHF	1.89	0.05	0.06	3.09	0.15	408	8.85	206	34.5	25.2	1140
		0.16	0.004	0.00	0.66	0.24	62.4	1.17	46.5	6.46	6.25	213
	THF	1.66	0.04	0.06	0.91	0.03	365	7.33	96.7	26.0	23.7	1060
		0.06	0.01	0.02	0.31	0.01	207	1.60	48.3	5.75	11.3	329
	LERF	2.40	0.07	0.06	0.25	0.03	588	7.77	54.3	24.7	20.7	3000
		0.23	0.10	0.00	0.10	0.01	291	1.03	21.0	1.77	6.95	798

Appendix 5.4: Experiment B: mean concentrations of mineral elements in the fine roots penetrating litter bags. Values are means and SD. The sign - denotes absence of roots from the litter bags or insuficient mass for chemical analysis.

days		mass	%						μg g^{-1}				
			N	P	K	Ca	Mg	Al	B	Cu	Fe	Mn	Zn
30	SHF	-	-	-	-	-	-	-	-	-	-	-	-
	THF	0.02	-	-	-	-	-	-	-	-	-	-	-
		0.04											
	LERF	0.03	1.95	0.05	0.11	0.42	0.05	569	44.0	5.10	123	69.0	14.0
		0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
61	SHF	-	-	-	-	-	-	-	-	-		-	-
	THF	0.05	1.83	0.11	0.57	0.43	0.14	265	106	12.0	121	58.0	28.0
		0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	LERF	0.13	3.13	0.06	0.21	0.24	0.04	1290	4.00	6.40	136	81.0	24.0
		0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
120	SHF	0.01	-	-	-	-	-	-	-	-	-	-	-
		0.03											
	THF	0.28	1.81	0.11	0.54	0.43	0.13	315	101	11.6	126	60.4	27.7
		0.32	0.05	0.01	0.08	0.00	0.00	159	16.8	0.00	16.1	7.59	0.95
	LERF	0.62	1.50	0.09	0.55	0.43	0.12	374	102	11.5	151	78.0	19.0
		0.63	0.61	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
181	SHF	0.04	-	-	-	-	-	-	-	-	-	-	-
		0.05											
	THF	0.53	2.13	0.08	0.33	0.49	0.05	635	47.5	9.82	136	69.2	27.7
		0.33	0.83	0.02	0.09	0.23	0.03	406	14.0	2.41	41.4	49.4	4.50
	LERF	1 65	1.97	0.08	0.30	0.36	0.06	1840	56.8	9.32	222	86.0	27.0
		0.94	0.45	0.02	0.08	0.25	0.01	1910	14.1	2.12	185	49.7	7.32
271	SHF	0.03	1.70	0.08	0.30	0.47	0.11	610	99.0	10.9	91.0	66.0	30.0
		0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	THF	1.42	1.45	0.06	0.20	0.43	0.04	387	48.0	6.37	91.5	36.0	19.4
		0.98	0.43	0.01	0.10	0.14	0.01	200	20.8	0.94	45.7	21.6	6.95
	LERF	1.98	2.10	0.06	0.16	0.18	0.04	1270	40.7	8.54	142	62.1	21.7
		1.56	0.42	0.010	0.03	0.10	0.01	1010	13.6	1.86	75.8	44.5	5.08
358	SHF	0.09	1.70	0.07	0.37	1.11	0.20	661	87.0	11.5	248	156	48.0
		0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	THF	1.31	1.76	0.06	0.25	0.34	0.05	557	37.8	6.01	118	58.0	24.1
		0.86	0.73	0.01	0.11	0.13	0.01	375	24.1	1.21	40.5	29.0	9.55
	LERF	2.39	2.37	0.05	0.14	0.12	0.04	1510	20.7	9.14	170	44.2	29.1
		1.22	0.45	0.01	0 03	0.06	0.01	1400	9.95	2.19	192	26.7	8.18

Appendix 5.5a: Experiment C: mean initial and final concentrations of mineral elements in bagged sun and shade leaves of *Pradosia* and *Aldina* exposed in the open patches of the SHF. Values are means and SD.

		%					μg g^{-1}					
days		N	P	K	Ca	Mg	Fe	Cu	Mn	Zn	B	Al
0	sun	0.45	0.01	0.08	0.33	0.12	64.21	4.00	55.0	9.00	62.3	109
	Pradosia	0.03	0.005	0.01	0.03	0.02	1.8	0.00	15.9	0.63	9.60	22.4
0	shade	0.45	0.02	0.06	0.35	0.13	59.7	4.30	22.4	10.4	69.7	111
	Pradosia	0.03	0.00	0.02	0.03	0.01	19.2	0.56	8.52	1.19	9.44	22.0
0	sun	1.33	0.05	0.14	0.42	0.20	67.3	5.06	44.7	12.6	57.7	88.7
	Aldina	0.04	0.005	0.03	0.03	0.01	12.9	1.16	5.02	1.27	5.56	28.8
0	shade	1.46	0.04	0.15	0.30	0.15	72.0	7.35	38.7	16.9	76.1	108
	Aldina	0.10	0.007	0.04	0.12	0.04	28.7	1.53	8.90	3.87	27.9	55.2
31	sun	0.32	0.01	0.06	0.37	0.11	67.2	4.00	60.7	11.0	45.7	80.7
	Pradosia	0.02	0.00	0.01	0.02	0.01	71.0	0.00	12.7	2.16	14.0	5.62
31	shade	0.54	0.01	0.04	0.36	0.13	45.0	4.00	20.0	8.50	45.7	82.5
	Pradosia	0.05	0.00	0.10	0.03	0.02	37.9	0.00	4.55	1.29	8.38	12.5
31	sun	1.31	0.03	0.07	0.49	0.21	25.5	4.30	45.2	12.7	65.0	70.0
	Aldina	0.05	0.005	0.02	0.04	0.01	4.80	0.60	5.38	0.96	20.8	10.4
31	shade	1.93	0.04	0.10	0.27	0.15	41.2	6.37	48.2	15.5	54.5	76.2
	Aldina	0.11	0.01	0.02	0.06	0.03	7.68	0.67	3.40	1.91	22.3	16.1
92	sun	0.42	0.01	0.04	0.40	0.11	72.0	4.55	48.0	10.5	21.0	106
	Pradosia	0.01	0.00	0.02	0.01	0.02	27.7	0.63	10.4	0.58	2.31	0.58
92	shade	0.52	0.01	0.03	0.39	0.12	38.5	4.00	26.0	10.5	33.5	110
	Pradosia	0.02	0.00	0.02	0.00	0.01	11.0	0.00	3.46	0.58	0.58	5.77
92	sun	1.61	0.03	0.04	0.61	0.21	56.5	5.25	22.9	15.02	32.5	129
	Aldina	0.05	0.01	0.01	0.07	0.02	4.04	0.17	15.3	.31	4.04	10.4
92	shade	1.87	0.03	0.04	0.40	0.15	47.5	6.92	50.7	17.5	35.5	109
	Aldina	0.02	0.00	0.00	0.05	0.00	17.0	1.05	2.50	1.00	1.00	0.00
182	sun	0.57	0.01	0.07	0.46	0.12	55.5	4.00	58.5	11.0	32.5	132
	Pradosia	0.00	0.01	0.01	0.04	0.01	6.35	0.00	7.51	1.15	12.1	8.08
182	shade	0.71	0.01	0.04	0.37	0.12	37.0	4.00	27.0	10.5	30.5	79.0
	Pradosia	0.06	0.01	0.01	0.02	0.01	6.93	0.00	6.93	0.58	1.73	9.24
182	sun	1.81	0.04	0.05	0.84	0.17	77.0	7.80	51.0	17.0	38.5	146
	Aldina	0.28	0.00	0.00	0.37	0.02	20.8	0.92	11.5	2.31	1.73	81.2
182	shade	2.13	0.03	0.04	0.32	0.14	76.7	6.47	33.3	22.0	50.3	127
	Aldina	0.13	0.01	0.01	0.02	0.01	0.58	0.46	2.31	1.73	1.15	0.58
271	sun	0.60	0.01	0.03	0.42	0.12	50.5	4.00	51.0	11.5	11.5	107
	Pradosia	0.01	0.00	0.01	0.01	0.00	4.04	0.00	4.62	0.58	4.04	15.0
271	shade	0.59	0.01	0.02	0.39	0.11	69.5	4.00	26.5	11.0	6.00	116
	Pradosia	0.02	0.00	0.01	0.02	0.01	12.1	0.00	2.89	1.15	2.31	9.24
271	sun	1.70	0.03	0.03	0.57	0.12	70.0	4.75	39.0	17.0	12.0	140
	Aldina	0.06	0.00	0.00	0.08	0.00	21.9	0.87	0.00	2.31	2.31	13.3
271	shade	1.72	0.02	0.03	0.31	0.11	92.0	7.30	45.5	19.5	12.0	161
	Aldina	0.06	0.01	0.01	0.02	0.01	23.1	0.92	0.58	0.58	6.93	17.3

Appendix 5.5b: Experiment C: mean initial and final concentrations of mineral elements in bagged sun and shade leaves of *Pradosia* and *Aldina* exposed in the closed patches of the SHF. Values are means and SD.

		%					μg g^{-1}					
days		N	P	K	Ca	Mg	Fe	Cu	Mn	Zn	B	Al
0	sun	0.45	0.01	0.08	0.33	0.12	64.2	4.00	55.0	9.00	62.3	109
	Pradosia	0.03	0.005	0.01	0.03	0.02	11.8	0.00	15.9	0.63	9.60	22.4
0	shade	0.45	0.02	0.06	0.35	0.13	59.7	4.30	22.4	10.4	69.7	111
	Pradosia	0.03	0.00	0.02	0.03	0.01	19.2	0.56	8.52	1.19	9.44	22.0
0	sun	1.33	0.05	0.14	0.42	0.20	67.3	5.06	44.7	12.6	57.7	88.7
	Aldina	0.04	0.005	0.03	0.03	0.01	12.9	1.16	5.02	1.27	5.56	28.8
0	shade	1.46	0.04	0.15	0.30	0.15	72.0	7.35	38.7	16.9	76.1	108
	Aldina	0.10	0.007	0.04	0.12	0.04	28.7	1.53	8.90	3.87	27.9	55.2
31	sun	0.36	0.01	0.10	0.37	0.11	18.5	4.55	55.2	9.75	56.2	68.7
	Pradosia	0.03	0.00	0.05	0.04	0.01	8.23	1.10	15.1	0.50	20.3	8.42
31	shade	0.50	0.01	0.05	0.36	0.13	22.2	4.85	34.0	10.0	54.7	72.2
	Pradosia	0.03	0.005	0.01	0.01	0.01	6.08	1.06	22.3	2.16	10.9	10.6
31	sun	1.35	0.04	0.07	0.50	0.24	30.0	5.05	41.0	13.2	51.2	53.0
	Aldina	0.35	0.005	0.04	0.03	0.04	19.8	0.78	0.82	2.06	11.9	11.1
31	shade	1.48	0.03	0.09	0.32	0.17	54.5	7.00	42.5	19.2	49.0	84.5
	Aldina	0.16	0.005	0.02	0.05	0.02	13.8	0.20	2.65	3.86	8.52	18.6
92	sun	0.53	0.01	0.06	0.48	0.15	39.0	4.00	66.0	11.0	29.5	88.5
	Pradosia	0.00	0.00	0.00	0.00	0.01	1.15	0.00	2.31	1.15	0.58	12.1
92	shade	0.51	0.03	0.06	0.38	0.13	40.5	4.00	23.0	11.0	46.0	104
	Pradosia	0.12	0.03	0.01	0.02	0.01	6.35	0.00	4.62	1.15	2.31	1.15
92	sun	1.72	0.04	0.06	0.65	0.24	52.5	5.60	47.5	15.5	34.0	94.5
	Aldina	0.01	0.00	0.01	0.01	0.01	6.35	0.58	5.20	0.58	9.24	4.04
92	shade	1.87	0.03	0.06	0.36	0.19	37.0	7.30	38.0	20.0	39.0	97.5
	Aldina	0.01	0.00	0.01	0.09	0.03	0.00	0.58	1.15	2.31	3.46	17.9
182	sun	0.64	0.02	0.06	0.44	0.11	47.0	4.00	56.5	11.5	31.5	116
	Pradosia	0.09	0.00	0.01	0.01	0.02	2.31	0.00	2.89	0.58	1.73	9.24
182	shade	0.73	0.02	0.07	0.38	0.13	30.5	4.00	17.5	11.5	38.0	108
	Pradosia	0.03	0.00	0.01	0.04	0.01	0.58	0.00	0.58	1.73	1.15	1.15
182	sun	1.82	0.04	0.05	0.53	0.20	52.0	6.80	41.0	17.5	46.0	137
	Aldina	0.04	0.00	0.02	0.09	0.01	4.62	0.23	8.08	0.58	10.4	34.6
182	shade	2.10	0.03	0.04	0.37	0.17	137	9.65	37.5	22.5	45.0	109
	Aldina	0.06	0.01	0.02	0.08	0.02	60.6	1.21	8.66	0.58	3.46	3.46
271	sun	0.59	0.01	0.06	0.48	0.15	40.5	4.00	42.5	12.5	10.0	94.5
	Pradosia	0.00	0.00	0.01	0.01	0.00	2.89	0.00	7.51	2.89	1.15	0.58
271	shade	0.58	0.01	0.06	0.41	0.14	61.0	4.00	38.5	13.0	9.00	100
	Pradosia	0.01	0.01	0.00	0.03	0.01	3.46	0.00	4.04	2.31	1.15	6.35
271	sun	1.78	0.04	0.05	0.58	0.19	77.5	5.35	55.5	15.5	11.0	128
	Aldina	0.03	0.00	0.01	0.01	0.02	14.4	0.17	0.58	1.73	3.46	20.2
271	shade	1.58	0.03	0.04	0.36	0.15	83.5	6.60	58.0	19.0	22.5	192
	Aldina	0.18	0.00	0.01	0.01	0.00	11.0	0.58	19.6	2.31	4.04	60.0

Appendix 5.5c: Experiment C: mean initial and final concentrations of mineral elements in bagged sun and shade leaves of *Pradosia* and *Aldina* exposed in the THF. Values are means and SD.

		%					μg g^{-1}					
days		N	P	K	Ca	Mg	Fe	Cu	Mn	Zn	B	Al
0	sun	0.45	0.01	0.08	0.33	0.12	64.2	4.00	55.0	9.00	62.3	109
	Pradosia	0.03	0.005	0.01	0.03	0.02	11.8	0.00	15.9	0.63	9.60	22.4
0	shade	0.45	0.02	0.06	0.35	0.13	59.7	4.30	22.4	10.4	69.7	111
	Pradosia	0.03	0.00	0.02	0.03	0.01	19.2	0.56	8.52	1.19	9.44	22.0
0	sun	1.33	0.05	0.14	0.42	0.20	67.3	5.06	44.7	12.6	57.7	88.7
	Aldina	0.04	0.005	0.03	0.03	0.01	12.9	1.16	5.02	1.27	5.56	28.8
0	shade	1.46	0.04	0.15	0.30	0.15	72.0	7.35	38.7	16.9	76.1	108
	Aldina	0.10	0.007	0.04	0.12	0.04	28.7	1.53	8.90	3.87	27.9	55.2
31	sun	0.48	0.01	0.06	0.38	0.10	36.5	4.25	65.2	10.5	41.2	67.2
	Pradosia	0.03	0.00	0.04	0.02	0.00	8.66	0.50	14.0	1.73	3.77	14.6
31	shade	0.39	0.01	0.04	0.38	0.14	46.5	4.25	34.5	16.0	39.7	72.5
	Pradosia	0.04	0.005	0.10	0.04	0.02	4.93	0.50	12.3	12.0	4.99	8.10
31	sun	1.36	0.04	0.08	0.53	0.22	45.7	4.27	47.5	15.5	49.7	55.5
	Aldina	0.06	0.00	0.01	0.06	0.02	9.57	0.55	5.45	1.29	4.99	8.35
31	shade	1.29	0.03	0.08	0.29	0.15	59.7	6.25	43.7	18.2	68.7	73.5
	Aldina	0.16	0.00	0.02	0.07	0.02	10.2	0.50	3.20	1.71	51.0	20.4
92	sun	0.53	0.03	0.05	0.43	0.14	118	4.00	47.5	13.5	35.0	117
	Pradosia	0.06	0.03	0.02	0.02	0.01	82.6	0.00	4.04	0.58	0.00	16.2
92	shade	0.49	0.06	0.06	0.44	0.14	66.0	4.00	34.0	11.5	55.5	114
	Pradosia	0.09	0.09	0.01	0.04	0.00	3.46	0.00	5.77	0.58	48.4	11.0
92	sun	1.39	0.04	0.06	0.58	0.17	56.5	5.40	40.0	16.0	39.5	99.0
	Aldina	0.06	0.01	0.01	0.02	0.03	7.51	0.20	3.46	0.00	1.73	25.4
92	shade	1.45	0.03	0.04	0.43	0.13	58.0	6.25	44.0	19.5	34.0	107
	Aldina	0.01	0.00	0.01	0.21	0.01	13.9	0.29	12.7	0.58	3.46	35.2
182	sun	1.01	0.02	0.06	0.80	0.08	83.0	5.00	71.0	18.0	42.0	188
	Pradosia	0.35	0.01	0.00	0.47	0.01	27.7	1.15	6.93	5.77	13.9	90.6
182	shade	0.72	0.02	0.05	0.36	0.12	65.5	11.6	21.0	14.0	31.5	120
	Pradosia	0.13	0.00	0.00	0.05	0.03	7.51	8.78	4.62	4.62	0.58	13.3
182	sun	2.11	0.04	0.06	0.38	0.10	53.7	5.50	44.5	17.0	44.5	103
	Aldina	0.20	0.01	0.00	0.11	0.06	31.2	0.23	0.58	0.00	5.20	26.6
182	shade	2.00	0.03	0.04	0.22	0.09	58.0	7.20	34.3	16.7	46.7	140
	Aldina	0.33	0.00	0.00	0.01	0.01	17.3	1.39	11.0	0.58	2.89	24.8
271	sun	0.56	0.02	0.05	0.20	0.04	52.0	4.00	17.0	16.5	11.5	136
	Pradosia	0.06	0.00	0.00	0.11	0.03	3.46	0.00	8.08	7.51	1.73	21.9
271	shade	0.73	0.02	0.05	0.25	0.07	40.2	4.00	26.5	20.0	18.0	152
	Pradosia	0.05	0.00	0.01	0.02	0.02	25.8	0.00	7.51	6.93	6.93	20.2
271	sun	1.61	0.04	0.05	0.25	0.06	82.0	4.80	27.5	16.0	15.5	174
	Aldina	0.03	0.00	0.00	0.09	0.04	15.0	0.92	14.4	1.15	0.58	39.8
271	shade	2.300	0.04	0.04	0.16	0.04	98.0	8.05	24.5	17.5	23.0	267
	Aldina	0.11	0.00	0.01	0.06	0.01	10.4	0.98	8.66	2.89	9.24	41.0

Appendix 5.5d: Experiment C: mean initial and final concentrations of mineral elements in bagged sun and shade leaves of *Pradosia* and *Aldina* exposed in the LERF. Values are means and SD.

		%					μg g^{-1}					
days		N	P	K	Ca	Mg	Fe	Cu	Mn	Zn	B	Al
0	sun	0.45	0.01	0.08	0.33	0.12	64.2	4.00	55.0	9.00	62.3	109
	Pradosia	0.03	0.005	0.01	0.03	0.02	11.8	0.00	15.9	0.63	9.60	22.4
0	shade	0.45	0.02	0.06	0.35	0.13	59.7	4.30	22.4	10.4	69.7	111
	Pradosia	0.03	0.00	0.02	0.03	0.01	19.2	0.56	8.52	1.19	9.44	22.0
0	sun	1.33	0.05	0.14	0.42	0.20	67.3	5.06	44.7	12.6	57.7	88.7
	Aldina	0.04	0.005	0.03	0.03	0.01	12.9	1.16	5.02	1.27	5.56	28.8
0	shade	1.46	0.04	0.15	0.30	0.15	72.0	7.35	38.7	16.9	76.1	108
	Aldina	0.10	0.007	0.04	0.12	0.04	28.7	1.53	8.90	3.87	27.9	55.2
31	sun	0.47	0.01	0.07	0.39	0.09	42.2	4.00	60.5	10.7	38.0	70.5
	Pradosia	0.03	0.00	0.01	0.05	0.06	18.5	0.00	9.95	0.96	6.38	21.1
31	shade	0.43	0.02	0.05	0.33	0.12	69.5	4.62	28.7	12.2	43.5	83.7
	Pradosia	0.03	0.00	0.00	0.05	0.01	39.7	1.25	11.3	2.06	7.42	4.11
31	sun	1.26	0.04	0.08	0.54	0.23	38.2	4.25	46.2	17.5	47.5	51.5
	Aldina	0.09	0.005	0.01	0.08	0.00	10.3	0.50	5.56	2.65	14.2	10.5
31	shade	1.45	0.04	0.10	0.33	0.18	148	6.50	51.7	22.7	62.2	92.0
	Aldina	0.19	0.01	0.01	0.12	0.07	147	0.60	14.4	8.02	15.2	28.5
92	sun	0.62	0.01	0.05	0.30	0.08	38.5	4.00	30.0	11.0	28.5	109
	Pradosia	0.05	0.01	0.01	0.04	0.02	8.66	0.00	4.08	1.15	9.81	23.1
92	shade	0.58	0.02	0.06	0.32	0.10	112	4.00	19.5	10.5	24.0	147
	Pradosia	0.01	0.00	0.00	0.02	0.03	62.3	0.00	5.20	1.73	0.00	16.7
92	sun	1.74	0.04	0.06	0.47	0.14	78.5	5.75	38.5	15.5	36.0	198
	Aldina	0.01	0.00	0.00	0.10	0.02	26.0	0.63	4.04	1.73	6.93	136
92	shade	1.91	0.03	0.06	0.26	0.10	80.0	8.55	39.0	19.5	45.5	290
	Aldina	0.25	0.01	0.02	0.05	0.02	17.3	1.33	5.77	1.73	15.0	66.4
182	sun	0.73	0.02	0.05	0.15	0.03	70.5	4.00	36.0	11.5	25.5	191
	Pradosia	0.01	0.00	0.00	0.05	0.01	0.58	0.00	19.6	0.58	2.89	10.4
182	shade	0.72	0.02	0.06	0.16	0.04	78.5	4.60	26.0	14.0	28.0	331
	Pradosia	0.00	0.00	0.00	0.06	0.02	0.58	1.20	8.08	1.15	5.77	31.2
182	sun	1.92	0.03	0.04	0.10	0.02	87.5	4.50	17.0	10.5	41.5	437
	Aldina	0.09	0.01	0.00	0.01	0.00	24.8	1.00	2.31	0.58	13.3	301
182	shade	1.89	0.03	0.05	0.09	0.02	74.0	6.40	20.0	18.0	51.0	314
	Aldina	0.09	0.00	0.00	0.00	0.01	8.08	0.46	0.00	1.15	10.4	145
271	sun	1.01	0.02	0.05	0.04	0.01	149	4.50	21.0	12.0	14.0	1240
	Pradosia	0.15	0.00	0.01	0.01	0.01	60.0	0.58	5.78	0.00	1.15	634
271	shade	0.96	0.02	0.05	0.04	0.01	118	4.80	15.5	12.0	13.5	615
	Pradosia	0.06	0.00	0.01	0.01	0.01	31.1	0.92	1.73	1.15	0.58	247
271	sun	1.83	0.03	0.05	0.08	0.02	103	5.22	15.0	17.0	21.7	672
	Aldina	0.74	0.005	0.01	0.08	0.02	78.6	0.94	3.27	3.56	8.62	685
271	shade	2.07	0.03	0.04	0.04	0.01	326	6.60	25.0	14.5	17.0	2530
	Aldina	0.20	0.00	0.01	0.00	0.00	45.6	0.00	1.15	0.58	1.15	57.7

Appendix 6.1: Total number of individuals of the 'other' (less frequently found) litter animals at the different times of collection and for the whole experiment. The percentage of total samples where the groups were recorded is given in parenthesis.

	30 d	60 d	120 d	180 d	270 d	360 d	Total
Lepidoptera juveniles	0	3	7	8	14	5	37 (5.8)
Hemiptera juveniles	1	0	6	3	14	12	36 (5.6)
Diptera adults	8	7	4	2	2	7	30 (5.2)
Chilopoda	0	0	1	2	4	19	27 (4.5)
Hemiptera adults	1	5	2	0	8	7	23 (4.5)
Orthoptera	8	2	3	1	1	0	15 (3.0)
Embioptera	0	0	1	0	7	7	15 (2.4)
Microhymenoptera	2	0	4	3	2	2	13 (2.4)
Opilioacaridae	0	0	2	4	4	3	13 (2.2)
Enchytraeidae	2	0	1	0	1	9	13 (1.7)
Thysanura	0	0	3	2	0	1	6 (1.3)
Polyxenus	0	1	0	2	0	2	5 (1.1)
Homoptera adults	0	1	0	0	0	3	4 (0.9)
Palpigradrae	1	0	1	0	0	0	2 (0.4)
Trichoptera	2	0	0	0	0	0	2 (0.4)
Odonata	1	0	0	0	0	0	1 (0.2)
Scorpionidae	0	0	1	0	0	0	1 (0.2)
Ostracoda	0	0	0	0	0	1	1 (0.2)
Nematoda	0	0	0	0	1	0	1 (0.2)
Onychophora	0	0	1	0	0	0	1 (0.2)

Appendix 6.2a: Mean number of litter animal individuals in several taxonomic groups per litter bag of *Clitoria* leaves for each retrieval time in the SHF. Values are means ± SD.

	Days at retrieval						
Taxonomic groups	30 d	60 d	120 d	180 d	270 d	360 d	Total
Acari	5.2±4.9	67±53	50±61	2.9±4.7	65±46	70±68	43±52
Collembola	0.3±0.9	28±29	12±19	0.0±0.0	20±13	12±8.9	12±18
Pseudoscorpionida	0.1±0.3	1.0±1.0	0.2±0.4	0.0±0.0	0.9±1.4	0.3±0.7	0.4±0.9
Formicidae	0.4±0.7	3.0±2.8	2.0±4.5	0.1±0.3	3.5±8.3	6.7±20	2.7±9.1
Diptera larvae	0.1±0.3	1.3±1.9	0.8±1.1	0.0±0.0	0.1±0.3	0.1±0.3	0.4±1.0
Copepoda	0.0±0.0	2.6±4.9	0.4±0.5	0.0±0.0	0.0±0.0	0.0±0.0	0.5±2.2
Psocoptera	1.2±1.2	0.3±0.5	0.4±0.9	0.2±0.5	0.4±0.7	0.1±0.3	0.5±0.8
Diplopoda	0.0±0.0	0.1±0.3	1.6±3.0	0.0±0.0	0.7±1.2	0.4±0.7	0.4±1.1
Araneae	0.0±0.0	0.1±0.3	0.4±0.9	0.0±0.0	0.2±0.6	0.2±0.4	0.1±0.4
Homoptera juveniles	0.0±0.0	0.0±0.0	0.0±0.0	0.2±0.7	0.4±0.7	0.1±0.3	0.1±0.4
Thysanoptera	0.0±0.0	2.2±3.1	0.0±0.0	0.1±0.3	0.3±0.5	0.3±1.0	0.5±1.5
Coleoptera adults	0.2±0.6	0.4±1.0	0.0±0.0	0.0±0.0	0.0±0.0	0.2±0.4	0.2±0.5
Isopoda	0.0±0.0	0.2±0.4	0.4±0.5	0.0±0.0	0.3±.5	0.2±0.4	0.2±0.4
Coleoptera larvae	0.4±1.3	0.4±1.0	0.0±0.0	0.1±0.3	0.2±0.4	0.1±0.3	0.2±0.7
Diplura	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.2±0.4	0.04±0.2
Phalangida	0.0±0.00	0.1±0.3	0.2±0.4	0.0±0.0	0.2±0.4	0.1±0.3	0.1±0.3
Protura	0.0±0.0	0.4±1.0	0.0±0.0	0.0±0.0	0.1±0.3	0.3±0.7	0.2±0.5
Pauropoda	0.0±0.0	0.1±0.3	0.0±0.0	0.0±0.0	0.3±0.7	0.2±0.7	0.1±0.4
Symphyla	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.2±0.6	0.2±0.4	0.08±0.3
Earthworms	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Isoptera	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.3	0.0±0.0	0.0±0.0	0.02±0.1
Others*	0.4±1.0	0.1±0.3	0.2±0.4	0.0±0.0	0.1±0.3	0.3±1.0	0.2±0.6
TOTAL	8.3±7.9	108±74	69±84	3.9±6.0	92±56	93±74	63±70
No. of groups	2.7±1.4	6.1±1.8	4.4±2.7	1.5±1.3	5.3±2.4	4.8±2.6	4.2±2.5
n	10	9	5	8	10	9	51

* the 20 minor taxonomic groups pooled together were: Chilopoda, Diptera adults, Embioptera, Enchytraeidae, Hemiptera adults, Hemiptera juveniles, Homoptera adults, Lepidoptera juveniles, Microhymenoptera, Nematoda, Odonata, Opilioacaridae, Orthoptera, Ostracoda, Palpigradrae, Onychophora, Scorpionidae, Trichoptera, Thysanura.

Appendix 6.2b: Mean number of individuals in several taxonomic groups per litter bag of *Clitoria* for each retrieval time in the THF. Values are means ± SD.

	Days at retrieval						
Taxonomic groups	30 d	60 d	120 d	180 d	270 d	360 d	Total
Acari	43±27	81±63	73±47	26±29	92±65	190±145	83±86
Collembola	6.1±11	7.1±3.9	5.5±5.5	0.2±0.7	18±12	36±25	12±17
Pseudoscorpionida	0.2±0.4	1.0±0.8	0.9±1.1	0.4±1.1	0.3±0.5	1.5±2.0	0.7±1.1
Formicidae	12±37	0.7±1.7	2.0±2.6	0.2±0.5	1.2±2.2	5.4±6.8	3.7±16
Diptera larvae	0.4±0.5	0.4±0.7	0.1±0.3	0.0±0.0	0.0±0.0	0.7±1.2	0.3±0.6
Copepoda	1.7±3.5	2.6±3.5	0.1±0.3	0.0±0.0	0.0±0.0	0.5±0.8	0.8±2.2
Psocoptera	1.4±1.0	0.2±0.4	0.0±0.0	0.0±0.0	0.2±0.4	0.1±0.3	0.3±0.7
Diplopoda	0.0±0.0	2.4±4.5	0.4±0.7	0.0±0.0	1.2±1.3	1.7±1.6	1.0 ±2.2
Araneae	0.4±1.0	0.1±0.3	1.4±1.7	0.1±0.3	0.9±0.9	2.2±2.2	0.8±1.4
Homoptera juveniles	0.2±0.7	0.0±0.0	3.1±8.0	4.1±7.4	3.1±4.7	9.4±9.6	3.2±6.5
Thysanoptera	0.9±0.8	0.3±1.0	0.0±0.0	0.5±0.5	0.2±0.4	0.0±0.0	0.3±1.6
Coleoptera adults	0.0±0.0	0.0±0.0	0.2±0.5	0.0±0.0	0.7±1.0	0.6±0.7	0.2±0.6
Isopoda	0.8±2.0	1.6±3.6	0.4±1.1	0.0±0.0	0.2±0.4	0.5±0.8	0.6±1.8
Coleoptera larvae	0.3±1.0	0.1±0.3	0.0±0.0	0.0±0.0	0.1±0.3	0.4±0.5	0.2±0.5
Diplura	0.0±0.0	0.2±0.7	1.5±1.5	0.0±0.0	0.8±1.0	0.7±0.5	0.5±0.9
Phalangida	0.0±0.00	0.1±0.3	0.1±0.3	0.0±0.0	0.0±0.0	0.0±0.0	0.04±0.2
Protura	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.2±0.5	0.04±0.2
Pauropoda	0.1±0.3	0.0±0.0	0.0±0.0	0.2±0.5	0.6±0.7	1.1±1.7	0.3±0.8
Symphyla	0.0±0.0	0.0±0.0	0.1±0.3	0.0±0.0	0.2±0.7	1.0±0.9	0.2±0.6
Earthworms	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.2±0.5	0.04±0.2
Isoptera	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.3	0.0±0.0	1.6±4.6	0.3±1.8
Others*	0.1±0.3	0.2±0.4	0.9±0.8	0.5±0.8	1.3±1.3	1.2±0.7	0.7±0.9
TOTAL	68±60	98±70	89±60	32±38	121±72	255±181	110±111
No. of groups	4.9±2.4	5.7±2.5	6.5±2.2	3.2±2.5	7.8±2.7	11±3.2	6.6±3.6
n	9	9	8	8	9	8	51

* the 20 minor taxonomic groups pooled together were: Chilopoda, Diptera adults, Embioptera, Enchytraeidae, Hemiptera adults, Hemiptera juveniles, Homoptera adults, Lepidoptera juveniles, Microhymenoptera, Nematoda, Odonata, Opilioacaridae, Orthoptera, Ostracoda, Palpigradrae, Onychophora, Scorpionidae, Trichoptera, Thysanura.

Appendix 6.2c: Number of individuals per litter bag of *Clitoria* for each retrieval time in the LERF. Values are means ± SD.

	Days at retrieval						
Taxonomic groups	30 d	60 d	120 d	180 d	270 d	360 d	Total
Acari	41±19	125±79	354±757	118±58	166±61	237±105	170±318
Collembola	29±30	13±16	14±14	20±22	30±19	38±20	24±22
Pseudoscorpionida	0.8±0.7	1.1±1.3	1.2±1.4	0.9±1.0	2.5±1.4	1.4±1.1	1.3±1.2
Formicidae	0.6±0.8	3.7±8.4	2.8±0.8	1.2±1.3	22±47	1.4±2.0	4.9±19
Diptera larvae	1.0±1.4	1.8±1.5	0.6±1.0	0.7±0.7	0.4±0.5	1.6±1.7	1.0±1.3
Copepoda	8.8±7.5	4.9±3.4	0.1±0.3	0.0±0.0	0.1±0.3	0.2±0.4	2.7±5.0
Psocoptera	0.8±1.1	0.0±0.0	0.0±0.0	0.1±0.3	0.1±0.3	0.0±0.0	0.2±0.6
Diplopoda	0.2±0.4	1.0±1.4	1.3±1.2	0.4±0.5	0.6±1.1	0.9±1.2	0.7 ±1.0
Araneae	32±103*	0.7±1.0	1.3±1.7	0.6±0.5	1.9±2.8	0.7±0.9	7.3±47
Homoptera juveniles	0.0±0.0	0.8±2.0	0.2±0.4	3.0±5.3	2.0±2.1	14±25	3.2±11
Thysanoptera	0.4±0.7	0.8±1.1	0.7±0.9	0.1±0.3	0.1±0.3	0.7±1.3	0.5±0.9
Coleoptera adults	0.2±0.4	0.3±0.5	0.8±1.3	0.1±0.3	0.4±0.5	1.2±1.9	0.5±1.0
Isopoda	0.1±0.3	0.3±0.5	1.2±1.8	0.2±0.5	0.9±1.1	0.2±0.4	0.5±1.0
Coleoptera larvae	0.2±0.4	0.1±0.3	0.4±0.7	0.0±0.0	0.7±0.1	0.4±0.5	0.3±0.6
Diplura	0.2±0.4	0.2±0.4	1.3±1.6	0.5±0.9	1.0±1.1	1.2±1.9	0.7±1.2
Phalangida	0.2±0.4	0.0±0.0	0.2±0.4	0.0±0.0	1.3±2.4	0.4±0.5	0.3±1.0
Protura	0.0±0.0	0.1±0.3	0.0±0.0	1.6±2.0	2.2±2.5	1.4±2.1	0.8±1.7
Pauropoda	0.0±0.0	0.0±0.0	0.1±0.3	0.1±0.3	0.9±2.5	0.3±0.5	0.2±1.0
Symphyla	0.0±0.0	0.0±0.0	0.1±0.3	0.1±0.3	0.5±1.1	0.6±0.7	0.2±0.6
Earthworms	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.4±0.7	0.07±0.3
Isoptera	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	1.1±3.2	0.0±0.0	0.2±1.2
Others**	0.6±0.7	0.9±1.3	1.4±1.7	1.4±1.4	2.0±2.1	2.2±1.7	1.4±1.6
TOTAL	116±93	155±97	382±758	150±76	237±120	305±117	221±322
No. of groups	7.3±1.4	8.2±2.4	9.0±3.1	8.4±2.8	11±2.1	12±2.7	9.2±2.9
n	11	9	9	8	8	9	54

* 1 nest in one of the samples

** 20 minor taxonomic groups of Appendix 6.1 pooled.

Appendix 6.2d: Number of individuals per litter bag of *Pradosia* for each retrieval time in the SHF. Values are means ± SD.

	Days at retrieval						
Taxonomic groups	30 d	60 d	120 d	180 d	270 d	360 d	Total
Acari	2.7±3.4	43±37	22±27	9.6±16	50±33	40±45	28±34
Collembola	0.11±0.3	25±24	1.3±1.9	0.0±0.0	6.7±7.2	9.8±11	7.3±14
Pseudoscorpionida	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.6±0.7	0.8±1.3	0.2±0.7
Formicidae	0.0±0.0	1.5±2.7	0.3±0.9	0.0±0.0	1.3±3.3	4.9±12	1.4±5.6
Diptera larvae	0.4±1.0	0.1±0.3	0.0±0.0	0.0±0.0	0.1±0.3	0.0±0.0	0.1±0.5
Copepoda	0.11±0.3	6.2±9.9	0.3±0.5	0.0±0.0	0.1±0.3	0.6±1.7	1.2±4.4
Psocoptera	0.3±0.5	0.5±0.8	0.1±0.4	0.1±0.3	1.8±2.0	0.3±0.7	0.6±1.1
Diplopoda	0.0±0.0	0.0±0.0	0.5±0.8	0.0±0.0	0.8±1.3	0.2±0.7	0.2 ±0.7
Araneae	0.1±0.3	0.0±0.0	0.0±0.0	0.0±0.0	1.4±4.3	1.3±1.7	0.5±2.0
Homoptera juveniles	0.0±0.0	0.0±0.0	0.2±0.4	0.0±0.0	0.1±0.3	0.0±0.0	0.04±0.2
Thysanoptera	0.0±0.0	0.7±2.1	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.3	0.1±0.9
Coleoptera adults	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.2±0.7	0.04±0.1
Isopoda	0.0±0.0	0.0±0.0	0.2±0.4	0.0±0.0	0.8±1.4	0.8±1.7	0.3±1.0
Coleoptera larvae	0.0±0.0	0.0±0.0	0.1±0.4	0.0±0.0	0.0±0.0	0.0±0.0	0.02±0.1
Diplura	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.3	0.02±0.1
Phalangida	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Protura	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.9±1.8	0.2±0.8
Pauropoda	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Symphyla	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.8±2.3	0.1±0.3	0.2±1.0
Earthworms	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.3	0.02±0.1
Isoptera	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.3	0.0±0.0	0.0±0.0	0.02±0.1
Others*	0.1±0.3	0.1±0.3	0.3±0.5	0.0±0.0	0.7±1.0	0.8±1.4	0.3±0.8
TOTAL	3.9±3.9	78±49	25±30	9.9±16	65±43	61±61	41±48
No. of groups	1.9±1.3	3.6±1.3	3.2±2.0	1.0±0.8	5.2±2.2	5.0±2.8	3.4±2.4
n	9	8	6	8	9	9	49

* 20 minor taxonomic groups of Appendix 6.1 pooled.

Appendix 6.2e: Number of individuals per litter bag of *Pradosia* for each retrieval time in the THF. Values are means ± SD.

	Days at retrieval						
Taxonomic groups	30 d	60 d	120 d	180 d	270 d	360 d	Total
Acari	16±15	60±69	49±50	4.7±4.6	59±30	65±39	43±45
Collembola	1.1±1.6	5.2±8.8	3.4±2.6	0.0±0.0	7.0±5.5	16±10	5.6±8.0
Pseudoscorpionida	0.1±0.3	0.3±1.0	0.4±0.5	0.1±0.3	0.4±1.0	0.7±1.0	0.4±0.8
Formicidae	0.0±0.0	0.7±1.3	4.0±10	0.1±0.3	0.0±0.0	3.6±8.6	1.4±5.6
Diptera larvae	0.2±0.4	0.6±0.7	0.0±0.0	0.0±0.0	0.2±0.7	0.3±0.5	0.2±0.5
Copepoda	0.0±0.0	6.4±7.1	0.6±1.7	0.0±0.0	0.1±0.3	0.7±1.3	1.3±3.7
Psocoptera	1.2±1.6	0.2±0.4	0.0±0.0	0.0±0.0	3.6±6.6	0.3±0.5	0.9±0.3
Diplopoda	0.1±0.3	0.1±0.3	0.0±0.0	0.0±0.0	0.1±0.3	0.4±0.7	0.1 ±0.4
Araneae	0.1±0.3	0.0±0.0	0.3±0.5	0.0±0.0	0.0±0.0	1.9±1.9	0.4±1.0
Homoptera juveniles	0.0±0.0	0.1±0.3	0.2±0.4	0.0±0.0	0.2±0.4	1.3±1.2	0.3±0.7
Thysanoptera	0.1±0.3	0.0±0.0	0.3±0.7	0.1±0.3	0.1±0.3	0.0±0.0	0.1±0.3
Coleoptera adults	0.1±0.3	0.1±0.3	0.1±0.3	0.0±0.0	0.3±0.5	0.2±0.4	0.1±0.4
Isopoda	0.1±0.3	0.1±0.3	0.2±0.7	0.0±0.0	0.2±0.4	0.3±0.5	0.2±0.4
Coleoptera larvae	0.0±0.0	0.3±0.7	0.1±0.3	0.0±0.0	0.0±0.0	0.1±0.3	0.09±0.3
Diplura	0.0±0.0	0.0±0.0	0.1±0.3	0.0±0.0	0.0±0.0	0.0±0.0	0.02±0.1
Phalangida	0.1±0.3	0.0±0.0	0.1±0.3	0.0±0.0	0.0±0.0	0.0±0.0	0.04±0.2
Protura	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Pauropoda	0.0±0.0	0.0±0.0	0.1±0.3	0.0±0.0	0.0±0.0	0.0±0.0	0.02±0.1
Symphyla	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.2±0.7	0.04±0.3
Earthworm	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Isoptera	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Others*	0.8±1.2	0.0±0.0	0.7±1.3	0.1±0.3	0.4±0.5	0.6±0.7	0.4±0.8
TOTAL	20±18	74±72	60±57	5.2±4.6	71±34	92±49	55±53
No. of groups	3.6±2.8	4.3±1.9	5.0±2.7	1.2±1.0	4.7±1.1	6.7±2.4	4.3±2.6
n	9	9	9	8	9	9	53

* 20 minor taxonomic groups of Appendix 6.1 pooled.

Appendix 6.2f: Number of individuals per litter bag of *Pradosia* for each retrieval time in the LERF. Values are means ± SD.

	Days at retrieval						
Taxonomic groups	30 d	60 d	120 d	180 d	270 d	360 d	Total
Acari	24±23	60±29	75±36	58±36	135±63	115±69	77±58
Collembola	3.0±3.7	1.9±1.8	4.9±5.1	5.1±4.0	12±4.2	15±9.4	7.0±7.0
Pseudoscorpionida	0.0±0.0	0.3±0.5	0.7±0.5	0.1±0.3	1.0±1.2	0.6±0.9	0.4±0.7
Formicidae	0.3±0.7	0.2±0.7	0.1±0.3	2.0±5.3	16±25	6.0±13	4.0±12.4
Diptera larvae	2.3±2.9	0.8±0.7	0.6±0.9	0.2±0.5	0.6±0.7	0.9±1.0	0.9±1.5
Copepoda	14±12	17±25	0.0±0.0	0.1±0.3	0.1±0.3	0.2±0.7	5.4±13
Psocoptera	0.3±0.7	0.1±0.3	0.2±0.7	0.2±0.5	0.6±0.7	0.1±0.3	0.3±0.6
Diplopoda	0.4±0.7	0.3±0.5	0.0±0.0	0.1±0.3	0.8±1.0	0.2±0.4	0.6±0.6
Araneae	0.4±0.5	0.0±0.0	0.3±0.5	0.0±0.0	0.3±0.5	0.3±0.5	0.2±0.4
Homoptera juveniles	0.0±0.0	0.1±0.3	0.4±1.3	1.0±0.3	3.3±3.0	3.2±3.4	1.3±2.4
Thysanoptera	0.0±0.0	0.7±1.1	0.1±0.3	0.4±0.7	0.3±0.5	0.1±0.3	0.3±0.6
Coleoptera adults	0.6±0.8	0.4±1.0	0.3±0.7	0.1±0.3	0.9±1.2	1.0±1.2	0.6±0.9
Isopoda	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.4±1.0	0.3±0.7	0.1±0.5
Coleoptera larvae	0.6±1.1	0.2±0.4	0.1±0.3	0.1±0.3	0.4±0.7	0.7±0.7	0.4±0.7
Diplura	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.3	0.9±1.2	0.0±0.0	0.2±0.6
Phalangida	0.2±0.4	0.2±0.4	0.2±0.4	0.0±0.0	0.3±0.1	0.0±0.0	0.2±0.5
Protura	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.0	0.1±0.3	0.4±0.7	0.1±0.3
Pauropoda	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.3	0.0±0.0	0.02±0.1
Symphyla	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.2±0.4	0.04±0.2
Earthworms	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.4±0.9	0.07±0.4
Isoptera	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Others*	0.1±0.3	0.1±0.3	0.3±0.5	0.1±0.3	0.8±1.3	0.9±0.9	0.4±0.8
TOTAL	46±35	83±42	83±40	67±41	174±73	146±80	99±69
No. of groups	5.7±0.9	5.3±1.9	4.4±1.8	4.5±1.6	9.0±3.0	8.0±2.6	6.2±2.6
n	10	9	9	8	9	9	54

* 1 nest in one of the samples

** 20 minor taxonomic groups of Appendix 6.1 pooled

Appendix 6.2g: Number of individuals per litter bag of *Aldina* for each retrieval time in the SHF. Values are means ± SD.

	Days at retrieval						
Taxonomic groups	30 d	60 d	120 d	180 d	270 d	360 d	Total
Acari	1.7±1.6	44±34	59±39	29±65	80±21	60±43	44±45
Collembola	0.0±0.0	29±38	1.5±1.3	0.6±1.4	17±14	21±22	13±22
Pseudoscorpionida	0.0±0.0	0.2±0.4	0.5±1.0	0.1±0.3	0.8±1.4	0.6±1.8	0.4±1.0
Formicidae	0.0±0.0	0.1±0.3	0.7±1.5	2.5±6.7	4.8±12	9.0±25	3.0±12
Diptera larvae	0.1±0.3	0.3±0.7	1.0±1.1	0.0±0.0	0.1±0.3	0.1±0.3	0.2±0.5
Copepoda	0.0±0.0	6.4±12	0.5±1.0	0.0±0.0	0.0±0.0	0.1±0.3	1.3±5.5
Psocoptera	0.7±0.7	0.2±0.4	0.2±0.5	0.0±0.0	0.8±1.1	0.1±0.3	0.4±0.7
Diplopoda	0.0±0.0	0.2±0.4	0.7±1.0	0.4±1.1	0.6±0.7	0.2±0.5	0.3 ±0.7
Araneae	0.0±0.0	0.1±0.3	0.2±0.5	0.0±0.0	0.2±0.7	0.2±0.5	0.1±0.4
Homoptera juveniles	0.0±0.0	0.1±0.3	0.0±0.0	0.1±0.3	0.0±0.0	0.1±0.3	0.06±0.2
Thysanoptera	0.0±0.0	1.0±1.4	0.0±0.0	0.1±0.3	0.1±0.3	1.4±3.5	0.5±1.6
Coleoptera adults	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.3	0.1±0.3	0.1±0.3	0.06±0.2
Isopoda	0.0±0.0	0.0±0.0	0.2±0.5	0.0±0.0	0.0±0.0	1.0±1.2	0.2±0.6
Coleoptera larvae	0.0±0.0	0.1±0.3	0.0±0.0	0.0±0.0	0.1±0.3	0.1±0.3	0.06±0.2
Diplura	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.3	0.0±0.0	0.0±0.0	0.02±0.1
Phalangida	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Protura	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.3	0.1±0.3	0.0±0.0	0.04±0.2
Pauropoda	0.0±0.0	0.1±0.3	0.0±0.0	0.0±0.0	0.2±0.7	0.2±0.7	0.1±0.4
Symphyla	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.3	0.1±0.3	0.04±0.2
Earthworms	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Isoptera	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.3	0.0±0.0	0.0±0.0	0.02±0.1
Others*	0.1±0.3	0.1±0.3	0.0±0.0	0.1±0.3	0.2±0.4	0.6±1.1	0.2±0.5
TOTAL	2.6±2.1	81±64	64±42	33±75	105±22	96±66	64±62
No. of groups	1.6±1.0	4.4±1.3	4.2±3.0	2.2±2.9	4.9±1.8	4.6±3.4	3.6±2.5
n	9	9	4	8	9	8	47

* 20 minor taxonomic groups of Appendix 6.1 pooled.

Appendix 6.2h: Number of individuals per litter bag of *Aldina* for each retrieval time in the THF. Values are means ± SD.

	Days at retrieval						
Taxonomic groups	30 d	60 d	120 d	180 d	270 d	360 d	Total
Acari	29±47	86±51	106±136	10±17	81±44	98±42	70±74
Collembola	7.7±15	21±23	10±13	0.13±0.3	11±9.6	17±16	11±15
Pseudoscorpionida	0.0±0.0	0.6±0.5	0.3±0.5	0.1±0.3	0.2±0.4	0.4±0.7	0.3±0.5
Formicidae	1.1±2.8	1.9±4.6	12±26	0.4±0.7	1.1±2.7	2.8±8.3	3.0±11
Diptera larvae	0.5±1.1	0.4±0.5	0.4±0.8	0.1±0.35	0.0±0.0	0.9±1.3	0.9±1.5
Copepoda	3.0±8.1	4.8±4.3	0.0±0.0	0.0±0.0	0.3±0.5	0.6±0.7	1.5±4.0
Psocoptera	0.9±0.8	1.0±1.0	0.0±0.0	0.0±0.0	0.8±1.0	0.1±0.3	0.5±0.8
Diplopoda	0.1±0.3	0.7±0.7	0.6±1.0	0.0±0.0	7.0±20	1.0±0.9	1.7±8.6
Araneae	0.7±2.1	0.0±0.0	0.7±1.2	0.0±0.0	0.0±0.0	0.0±0.0	0.2±1.0
Homoptera juveniles	0.0±0.0	0.4±1.3	0.1±0.4	0.0±0.0	0.6±0.7	0.3±0.7	0.3±0.7
Thysanoptera	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.3	2.9±7.6	0.0±0.0	0.5±3.3
Coleoptera adults	0.0±0.0	0.0±0.0	0.1±0.4	0.0±0.0	0.1±0.3	0.2±0.4	0.08±0.3
Isopoda	0.0±0.0	0.0±0.0	0.3±0.5	0.0±0.0	0.3±0.7	0.4±0.7	0.2±0.5
Coleoptera larvae	0.0±0.0	0.1±0.3	0.3±0.5	0.0±0.0	0.0±0.0	0.0±0.0	0.06±0.2
Diplura	0.0±0.0	0.1±0.3	0.0±0.0	0.0±0.0	0.0±0.0	0.3±0.5	0.08±0.3
Phalangida	0.0±0.0	0.0±0.0	0.6±1.0	0.0±0.0	0.1±0.3	0.0±0.0	0.1±0.4
Protura	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.2±0.4	0.04±0.2
Pauropoda	0.0±0.0	0.1±0.3	0.3±0.8	0.0±0.0	0.3±0.5	0.1±0.3	0.1±0.4
Symphyla	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.2±0.4	0.04±0.2
Earthworms	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Isoptera	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	2.4±7.3	0.4±3.1
Others*	0.2±0.5	0.0±0.0	0.6±0.8	0.0±0.0	0.6±1.0	0.6±1.0	0.3±0.7
TOTAL	44±60	117±62	132±155	11±17	106±64	126±88	90±90
No. of groups	3.4±1.2	6.0±1.3	5.3±3.8	1.5±1.1	5.7±1.7	6.3±2.6	4.8±2.6
n	8	9	7	8	9	9	50

* 1 nest in one of the samples

** 20 minor taxonomic groups of Appendix 6.1 pooled.

Appendix 6.3: The most significant Spearman's correlation coefficients (r) for major litter animal groups with other groups in the litter bags. Levels of significance are:
$^{*} < 0.05$; $^{**} < 0.01$; and $^{***} < 0.001$.

	SHF	THF	LERF
	n=147	n=154	n=163
Acari x Collembola	0.50***	0.67***	0.24**
Araneae	0.19*	0.48***	-0.03
Pseudoscorpionida	0.28***	0.41***	0.13
Diplopoda	0.44***	0.15	0.08
Pauropoda	0.31***	0.54***	0.12
Collembola x Araneae	0.10	0.51***	0.39***
Pseudoscorpionida	0.33***	0.32***	0.39***
Pauropoda	0.17*	0.42***	0.21**
Copepoda	0.47***	0.08	-0.03
Formicidae x Pauropoda	-0.04	0.03	0.71***
Protura x earthworms	-0.02	0.70***	0.13
Diplura	0.47***	0.08	0.14
Pauropoda	0.20*	0.10	0.47***
Thysanura x Diplopoda	-0.02	0.93***	0.00
Araneae x Isopoda	0.53***	0.11	-0.02
Diplopoda	0.42***	-0.01	-0.02

Appendix 6.4: Regression analyses between the densities of the litter animals and the remaining mass and concentrations of mineral elements in the litter bags for each leaf species. Levels of significance for each group were: *0.05; **0.01; and ***0.001; NS = not significant

Clitoria	r^2	df	P	Groups significantly related to mass or mineral elements
mass	40 8	155	< 0.001	Collembola**; Copepoda***; Earthworms***
N	35 8	155	< 0 001	Collembola*; Copepoda***; Protura*
Ca	51.0	155	< 0.001	Acari***; Copepoda***; Diplura*; Earthworms**; Protura***; Pseudoscorpionida**
Mg	45.9	155	< 0.001	Acari***; Copepoda***; Diplopoda*; Diplura**
Fe	26 2	155	< 0.001	Collembola***; Copepoda***; Diplopoda*; Isopoda*
Mn	17.6	155	< 0.001	Acari*; Diplura*; Pseudoscorpionida*
B	15.8	155	< 0.001	Collembola***; Earthworms**
Al	39 3	155	< 0.001	Collembola***; Copepoda***; Diplopoda*
Pradosia	r^2	df	P	Groups significantly related to mass or mineral elements
mass	35.7	155	< 0.001	Acari***; Copepoda***; Protura*; Pseudoscorpionida*
N	37.7	155	< 0.001	Acari***; Copepoda***; Earthworms**; Pseudoscorpionida**
K	15.9	155	< 0.001	Acari*; Copepoda***
Ca	39.7	155	< 0.001	Acari***; Copepoda***; Diplura***; Eartworms*; Isopoda*
Mg	30 6	155	< 0.001	Acari***; Copepoda***; Diplura*; Earthworms*; Isopoda*
Fe	31.6	155	< 0.001	Acari***; Copepoda**; Earthworms***; Protura*
Mn	14.9	155	< 0.001	Acari***; Isopoda*
B	18.8	155	< 0.001	Collembola***; Protura*
Al	41.7	155	< 0.001	Acari***; Collembola**; Copepoda***; Earthworms**
Aldina	r^2	df	P	Groups significantly related to mass or mineral elements
mass	31.9	151	< 0.001	Acari**; Copepoda***; Protura**; Pseudoscorpionida*
N	17.2	151	< 0.001	Collembola***; Copepoda***
K	30 8	151	< 0.001	Acari***; Copepoda***
Ca	23 1	151	< 0.001	Acari***; Collembola*; Earthworms*; Protura*
Mg	34.1	151	< 0.001	Acari***; Copepoda***; Earthworms*; Protura**
Fe	20.4	151	< 0 001	Copepoda*; Diplura*; Isopoda**; Protura***
Mn	16.5	151	< 0.001	Acari***; Earthworms*; Protura*
B	15.1	151	< 0.001	Collembola***
Al	37 6	151	< 0 001	Acari***; Copepoda***; Diplura**; Earthworms*; Protura***

Appendix 6.5: Regression analyses between the densities of the litter animals and the remaining mass and concentrations of mineral elements in the litter bags for each forest type. Levels of significance for each group were: * $p < 0.05$; ** $p < 0.01$; and *** $p < 0.001$; NS = not significant

SHF	r^2 %	df	p	Groups significantly related to mass or mineral elements
mass	29.4	146	< 0.001	Collembola*; Copepoda***; Diplura*; Isopoda*
N	7.8	146	< 0.01	Collembola**; Copepoda*
P	5.3	146	< 0.05	Collembola*
K	7.6	146	< 0.05	Copepoda**
Ca		146	NS	
Mg	10.7	146	< 0.001	Collembola*; Copepoda**; Diplura*
Fe	18.3	146	< 0.001	Collembola***; Copepoda**; Diplura*
Mn	8.2	146	< 0.01	Collembola*; Copepoda*
Zn	18.3	146	< 0.001	Collembola**; Copepoda*
B	16.6	146	< 0.001	Collembola**; Diplopoda***; Isopoda*
Al	18.3	146	< 0.001	Copepoda***
THF n=154	r^2 %	df	p	Groups significantly related to mass or mineral elements
mass	33.4	153	< 0.001	Collembola**; Copepoda***; Diplopoda*; Diplura**
N	12.3	153	< 0.001	Diplopoda**; Diplura**
P	8.1	153	< 0.01	Diplopoda**; Diplura*
K	8.2	153	< 0.01	Acari*; Copepoda***
Ca	6.4	153	< 0.01	Collembola**; Diplura**
Mg	33.3	153	< 0.001	Collembola***; Copepoda***; Diplura***
Fe	27.0	153	< 0.001	Acari*; Diplopoda**; Diplura**
Mn	10.6	153	< 0.001	Collembola***; Isopoda*
Zn	6.0	153	< 0.01	Diplopoda**
B	23.4	153	< 0.001	Collembola**; Diplura***
Al	31.3	153	< 0.001	Acari*; Diplura***
LERF n=163	r^2 %	df	p	Groups significantly related to mass or mineral elements
mass	47.2	162	< 0.001	Acari**; Copepoda***; Earthworms**; Protura**
N	24.9	162	< 0.001	Collembola***; Protura*; Pseudoscorpionida**
P	11.8	162	< 0.01	Collembola**; Diplopoda**
K	36.3	162	< 0.001	Acari***; Copepoda***
Ca	13.2	162	< 0.001	Collembola*; Copepoda***; Earthworms*
Mg	60.5	162	< 0.001	Acari***; Copepoda***
Fe	37.1	162	< 0.001	Collembola***; Copepoda***; Earthworms*; Protura*
Mn	12.6	162	< 0.001	Acari**; Copepoda**
Zn	3.0	162	< 0.05	Collembola*
B	9.4	162	< 0.001	Copepoda**;Earthworms**
Al	44 8	162	< 0.001	Collembola***; Copepoda***; Earthworms*; Protura*

Appendix 7.1: Means ± SE of the survival rate, number of living leaves and height of seedlings at the start and end of the experiment, and quotients final/initial number of leaves and final/initial height of seedlings in the three forest types and all seven treatments. The seedling survival is the proportion surviving and has values from 0 (all dead) to 1 (all alive) after 180 d in the field.

SHF	n	Treatments	Seedling survival	Number of living leaves			Height of the seedlings (cm)		
				initial	final	quotient	initial	final	quotient
	9	N	1.0±0.0	35.2±6.61	31.1±9.09	0.82±0.15	19.4±9.10	22.0±2.98	1.22±0.16
	9	P	0.67±0.17	19.6±3.10	9.89±3.14	0.56±0.19	32.4±9.10	14.9±4.06	0.79±0.21
	12	K	1.0±0.17	18.4±3.48	19.7±4.30	1.04±0.07	19.6±1.20	21.1±1.63	1.09±0.07
	2	CaCl2	0.0±0.0	12.5±3.50	0.0±0.0	0.0±0.0	20.3±12.8	0.0±0.0	0.0±0.0
	13	$CaCO_3$	0.92±0.08	22.3±3.54	22.9±5.43	0.95±0.12	23.7±2.99	23.7±2.41	1.10±0.14
	9	NPK + $CaCO_3$	1.0±0.0	18.8±3.70	27.0±9.65	1.31±0.22	21.7±2.39	26.6±2.01	1.27±0.07
	15	Control	0.93±0.07	25.3±3.76	23.4±3.76	0.85±0.08	32.9±4.33	22.0±2.32	0.80±0.08
THF									
	9	N	0.67±0.17	8.0±3.27	7.44±3.67	1.15±0.51	14.3±2.32	9.01±2.87	0.71±0.19
	17	P	0.89±0.07	8.88±2.19	8.41±1.67	1.12±0.17	15.4±2.12	14.0±1.96	1.02±0.10
	7	K	0.29±0.18	5.43±1.45	4.29±2.77	0.41±0.32	17.4±2.82	4.29±2.88	0.32±0.20
	11	CaCl2	0.73±0.14	9.0±2.49	4.64±1.29	0.71±0.19	16.8±4.43	10.7±2.46	0.71±0.17
	11	$CaCO_3$	0.82±0.12	6.55±2.50	8.64±3.53	1.15±0.24	14.6±1.81	14.4±4.0	0.94±0.18
	10	NPK + $CaCO_3$	1.0±0.0	12.8±3.28	12.5±1.21	1.25±0.17	14.8±2.53	15.6±1.40	1.21±0.12
	12	Control	1.0±0.0	6.58±0.93	9.75±1.65	1.91±0.47	17.1±1.96	18.7±1.73	1.13±0.06
LERF									
	10	N	0.60±0.16	4.20±0.47	2.80±1.04	0.59±0.19	15.8±4.68	11.5±4.52	1.0±0.38
	11	P	0.36±0.15	4.64±0.41	1.61±0.70	0.52±0.24	5.32±2.16	4.86±2.78	0.55±0.29
	14	K	0.71±0.13	3.79±0.77	3.86±1.0	1.27±0.35	12.7±3.85	7.68±1.65	0.72±0.17
	13	CaCl2	0.31±0.13	4.92±0.92	1.92±1.25	0.18±0.11	14.5±2.23	6.38±3.16	0.28±0.13
	17	$CaCO_3$	0.77±0.11	5.24±0.62	4.88±0.92	1.61±0.80	19.7±3.33	16.2±3.38	0.83±0.17
	5	NPK + $CaCO_3$	0.60±0.25	4.80±1.39	4.20±1.83	1.78±0.98	21.9±12.1	11.9±5.46	0.65±0.41
	9	Control	0.78±0.15	3.44±0.44	4.0±0.91	1.08±0.25	14.0±2.75	11.6±3.53	0.69±0.17

Appendix 7.2: Survival rate, and quotients final/initial number of living leaves and final/initial height of the seedlings in the seven treatments in the two THF plots. Values are means with SE in parenthesis. The significant levels of differences for analyses of variance coupled with Tukey's test are: ** 0.01 and *** 0.001.
- denotes data not calculated.

	n	n	Seedlings survival		Quotient final/ initial leaves		Quotient final/ initial heights	
Treatment	Plot 3	Plot 4	Plot 3	Plot 4	Plot 3	Plot 4	Plot 3	Plot 4
N	6	3	1.0*** (0.0)	0.0 (0.0)	1.73** (0.65)	0.0 (0.0)	1.07*** (0.12)	0.0 (0.0)
P	12	5	0.93 (0.07)	0.80 (0.20)	1.20 (0.19)	0.92 (0.36)	1.09 (0.12)	0.84 (0.22)
K	1	6	1.0 -	0.17 (0.17)	2.14 -	0.19 (0.19)	1.17 -	0.17 (0.17)
$CaCl_2$	5	6	1.0 (0.0)	0.50 (0.22)	1.01 (0.21)	0.46 (0.28)	1.02 (0.15)	0.46 (0.24)
$CaCO_3$	8	3	0.87 (0.12)	0.67 (0.33)	1.31 (0.28)	0.72 (0.43)	1.01 (0.17)	0.76 (0.50)
NPK + $CaCO_3$	8	2	1.0 (0.0)	1.0 (0.0)	1.02 (0.10)	2.20 (0.0)	1.24 (0.15)	1.12 (0.10)
Control	7	5	1.0 (0.0)	1.0 (0.0)	1.30 (0.35)	2.76 (0.08)	1.22 (0.08)	1.01 (0.08)

Appendix 8.1: Number of germinated and dead rice seedlings, and their shoot and root dry mass 50 d after planting. Values are means ± SE of four pots.

	N-urea	NaH_2PO_4	KCl	$CaCl_2$	$CaCO_3$	NPK + $CaCO_3$	Control
SHF				without top organic layer			
germination	4.25±0.63	3.75±0.48	3.75±0.48	5.75±0.25	5.0±0.0	5.0±0.41	5.50±0.29
mortality	1.5 ± 0.96	0.5±0.5	1.25±0.75	5.25±0.48	0.0±0.0	0.0±0.0	1.5±0.96
aerial mass	5.85 ±1.19	3.95±1.66	3.87±1.70	8.33±3.0	59.2±6.47	68.0±10.4	8.04±2.19
root mass	3.73±1.34	3.43±0.83	2.05±1.27	6.72±4.59	31.4±7.39	30.0±7.58	2.56±0.36
				with top organic layer			
germination	5.25±0.48	5.50±0.29	4.5±0.64	4.75±0.48	5.25±0.75	5.0±0.41	5.50±0.29
mortality	0.0±0.0	0.0±0.0	1.0±0.71	4.75±1.31	0.0±0.0	0.0±0.0	0.25±0.25
aerial mass	4.38±0.84	7.31±2.53	4.38±0.84	13.1±3.87	40.2±12.4	19.0±4.54	4.38±0.25
root mass	6.21±2.95	2.12±0.50	1.5±0.52	3.07±1.08	26.3±9.47	3.65±1.11	2.63±1.18
THF				without top organic layer			
germination	4.25±0.85	4.50±0.87	5.75±0.25	4.25±0.63	5.5±0.29	4.0±1.08	5.75±0.25
mortality	3.25±1.49	1.0±1.0	0.0±0.0	5.75±0.85	0.25±0.25	0.50±0.29	0.25±0.25
aerial mass	7.31±1.46	5.11±0.73	11.0±5.25	8.04±0.73	38.0±12.1	13.9±5.25	7.31±0.84
root mass	2.92±0.0	4.60±1.24	6.58±1.40	3.65±0.7	16.8±6.0	4.38±1.46	5.12±1.40
				with top organic layer			
germination	3.25±0.63	5.0±0.41	5.0±0.41	1.25±0.25	5.25±0.25	5.25±0.48	5.5±0.29
mortality	1.75±1.03	0.75±0.48	1.25±0.48	3.25±0.75	0.25±0.25	0.25±0.25	0.0±0.0
aerial mass	4.38±0.84	4.02±1.1	4.38±1.46	5.99±1.93	09.0±4.54	7.31±1.89	4.38±1.46
root mass	3.65±0.63	3.65±0.73	2.92±0.0	1.02±0.37	12.4±5.64	3.65±0.73	8.04±1.46
LERF				without top organic layer			
germination	5.25±0.47	5.75±0.25	5.0±0.0	20.±0.41	6.0±0.0	5.25±0.48	4.75±0.48
mortality	0.0±0.0	0.25±0.25	0.0±0.0	3.25±0.48	0.0±0.0	0.0±0.0	0.0±0.0
aerial mass	80.4±5.4	81.8±7.26	94.3±13.0	13.1±3.04	86.2±6.14	104±7.14	96.5±4.62
root mass	51.9±4.83	65.8±1.89	88.4±6.13	6.58±1.4	88.4±3.65	70.1±9.91	82.6±5.12
				with top organic layer			
germination	4.75±0.63	4.75±0.48	4.75±0.48	5.0±0.29	4.75±0.48	5.5±0.5	5.5±0.29
mortality	0.0±0.0	0.25±0.25	0.0±0.0	2.75±1.03	0.0±0.0	0.25±0.25	0.25±0.25
aerial mass	89.1±8.48	134±13.1	104±7.39	24.1±0.73	128±8.47	145±4.22	98.6±4.68
root mass	52.6±3.16	155±25.1	88.4±7.39	7.82±3.14	86.2±13.8	79.6±3.24	99.4±6.86