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SUMMARY

A two-year study on leaf litter decomposition and litter invertebrates was carried out in a primary (4 ha ($=4\times10^4$ m^2)) and logged dipterocarp forest plot (2.5 ha) in the Danum Valley, Sabah, Malaysia. Annual leaf litterfall, leaf litter layer mass and leaf litter decomposition, measured as leaf litter mass loss, were not significantly different between plots. Spatial variation among the 30 replicate sites within each plot was high. Annual rates of total litterfall, leaf litterfall and leaf litter mass loss were 11.5, 6.6 and 6.4 t ha^{-1} for the primary forest plot and 11.9, 6.2 and 5.5 t ha^{-1} for the logged forest plot. Rainfall (3000 mm y^{-1}) and litterfall were high throughout the year and rates of litterfall and litter disappearance were not related to the pattern of rainfall.

In the primary and logged forest, leaf litter layer mass and annual rates of leaf litter disappearance increased with annual leaf litterfall. In the primary forest, the abundance of litter invertebrates increased with mass of leaf litter and fine roots.

This invertebrate abundance was higher in the primary forest with a significantly higher abundance of mites, pseudoscorpions and termites. The proportion of mites and pseudoscorpions of the invertebrate fauna was higher in the primary forest; beetles, millipedes and cockroaches were higher in the logged forest. The most abundant invertebrates were ants, springtails, spiders, woodlice and mites.

1. INTRODUCTION

Within many tropical rain forest ecosystems the major proportion of the nutrient capital is incorporated in plant biomass and the forest floor (Whitmore 1984; Vogt *et al.* 1986). Decomposition of litter and the release of nutrients is therefore an important pathway in the rain forest nutrient cycle (Nye 1961; Jordan & Herrera 1981; Edwards 1982; Vitousek 1982; Anderson & Swift 1983; Brassell & Sinclair 1983).

Within temperate forests, the decomposition processes, namely (i) fragmentation, (ii) leaching and (iii) catabolism (Swift *et al.* 1979), are related to the chemical composition of the litter, which is produced by one or a few tree species (Witkamp 1971; Anderson 1973; Herlitzius 1983; Hornung 1985; Kimmins 1985; Miles 1985). Forest floor conditions, such as humidity, pH and physical and chemical composition of the litter determine the composition of the decomposer community. This community affects the balance between the mineralization and immobilization of nutrients in litter and leachates (Swift *et al.* 1979). Litter invertebrates are frequently used as indicators of decomposer activity because of their key role within the decomposition process (Bornebusch 1930; Petersen & Luxton 1982; Seastedt 1984).

In tropical rain forests the relationship between tree species composition, litter invertebrate community and decomposition is not clear because of the diversity and heterogeneity of vegetation (Madge 1965; Fittkau & Klinge 1973; Plowman 1979; Proctor *et al.* 1983). The variable canopy structure affects abiotic factors such as evaporation and humidity within the forest (Richards 1952). Litterfall and canopy leachate (crown-drip) from tree species which differ in chemical composition (Tanner 1977; McKey *et al.* 1978; Coley 1983; Golley 1983*b*; Cuevas & Medina 1988; Proctor *et al.* 1989) and leaf phenology (Madge 1965; Kunkel-Westphal & Kunkal 1979; Schaik & Mirmanto 1985) are expected to affect heterogeneity of the forest floor habitat, the litter layer, and therefore the composition and activity of the invertebrate community.

The aims of the present paper are to relate the quantity of litterfall to leaf litter decomposition, the latter measured as leaf litter mass loss, and to the invertebrate community in a large number of forest sites. In this study an undisturbed dipterocarp forest plot and a selectively logged forest plot were included. We assumed that removal of the emergent trees affects decomposition by changing the quantity and quality of litterfall. This study is part of an extensive research

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programme aiming to relate the quantity and quality of leaf litter in a large number of forest sites to (i) tree species composition and phenology, (ii) leaf litter mass loss, (iii) invertebrate community and (iv) nutrient leaching from canopy, litter layer, root mat, and top soil.

2. STUDY PLOTS AND THEIR ENVIRONMENT

Two research plots were selected near the Danum Valley Field Centre (DVFC), Sabah in Malaysian Borneo (4°58′N and 117°48′E). The first plot (plot 1), 4 hectares (ha)† in size, is located in the Danum Valley Conservation Area in lowland dipterocarp forest. The second (plot 2), 2.5 ha in size and 15 km east of the DVFC is in dipterocarp forest which was selectively logged in 1978. During logging about 20 trees (greater than 40 cm dbh), predominantly dipterocarps, were removed per hectare. Tree (greater than 10 gbh) identifications were available for research sites within plot 1 (D. M. Newbery, personal communication and this symposium) and within plot 2 (L. Y. Fah & L. Madani, personal communication). Plot 1 is 120–150 m ASL, plot 2 between 100–130 m ASL. The soil type of both forest plots is an ultisol developed on weathered sandstone (Burnham 1983; Douglas *et al.* this symposium).

The climate of northeast Borneo and the microclimate of the rain forest has been described by Marsh & Greer and Brown & Whitmore (this symposium). Annual rainfall over a period of four years suggests a slightly bimodal distribution with a mean of 2500 mm, with the months April and August often having less than 100 mm. From 18h00 to 08h00 the average relative humidity at the DVFC is normally 100%; during the daytime it fluctuates between 60 and 100%. Rainfall and humidity as recorded at the DVFC meteorological station are given in figure 1.

3. MATERIALS AND METHODS

The following variables were measured in each of 30 random sites (314 m^2, radius 10 m) in the primary forest plot from April 1988 until December 1989, and in the logged forest plot from December 1988 until December 1989.

(*a*) *Litterfall*

In the centre of each site, a litter collector of 0.1 mm nylon mesh with a surface area of 0.7 m^2 was installed 30 cm above ground level. The nylon sheet was tied between four 70 cm long PVC poles stuck into the soil.

Monthly total litterfall (TLF) was separated into (i) coarse leaf litterfall (leaf fraction greater than 1 cm; LLF), (ii) trash or fragmented litterfall (leaf fraction and small flower parts less than 1 cm; FLF), (iii) twigs or woody litterfall (less than 2 cm diameter; WLF) and (iv) reproductive parts (fruits and flowers). Litterfall was collected four times a month and bulked into monthly samples; the mass of the fractions was determined after drying to constant mass for 7 days in a solar drying house (65°C).

† 1 ha = 10^4 m^2

(*b*) *Litter layer mass on the forest floor*

Litter layer mass was determined at 3-monthly intervals between December 1988 and December 1989. Two samples of the litter layer were taken per site with a steel corer (diameter 25 cm, height 20 cm) within a three metre radius from the litter collector and were bulked. The litter layer was distinguished from the mineral soil by its loose structure and brown colour in contrast to the compact, yellow mineral soil. After taking the samples the sampling spots were marked with 15 cm PVC poles to avoid resampling during ensuing sampling occasions.

In the laboratory the litter material was first sorted into four fractions before it was oven-dried at 70°C. Litter material (LM) was separated with a 1 cm sieve into (i) recognizable leaf parts (greater than 1 cm; LLM) and (ii) fragmented litter (less than 1 cm; FLM). The latter included a mixture of organic material and soil particles; therefore its mass needs correction for the mineral soil fractions (Burghouts 1992). Woody litter mass (iii) less than 2 cm diameter; WLM) and (iv) fine root mass (less than 3 mm diameter; FRM) were estimated. The moisture content of the litter was estimated as a percentage of dry mass.

(*c*) *Leaf litter disappearance*

Litterfall or litter layer mass (k_L) is often used to describe litter layer mass loss in ecosystems in equilibrium (Golley *et al.* 1978; Swift *et al.* 1979; Proctor 1983). This measure yields correct values when the litter layer is in a steady state but it seems less suitable to describe decomposition when temporal and spatial fluctuations in litterfall and litter layer mass occur. We used 'litter disappearance rates' to estimate the rate of leaf litter decomposition. Leaf litter disappearance (LLD) for four successive periods of three months is calculated as the difference between the sum of LLM at the beginning of the period and LLF during the period, and LLM at the end of the period: $\text{LLD}(t_{1-4}) = \text{LLM}(t_1) + \text{LLF}(t_{1-4}) - \text{LLM}(t_4)$ (Golley *et al.* 1978). LLD includes the physical and chemical disintegration of leaf litter as well as the removal of litter by animals such as leaf litter feeding termites and pheasants.

(*d*) *Litter invertebrate composition and abundance*

Invertebrates were collected in the field from the litter layer only, by hand sorting. They were collected at the same time as the litter layer was sampled to estimate its mass. Large invertebrates were collected by hand from the leaf litter inside the corer, whereas the smaller fauna was sieved with a 2 mm sieve from the litter into a white tray and collected from the tray with a small electric aspirator (3 V batteries). The

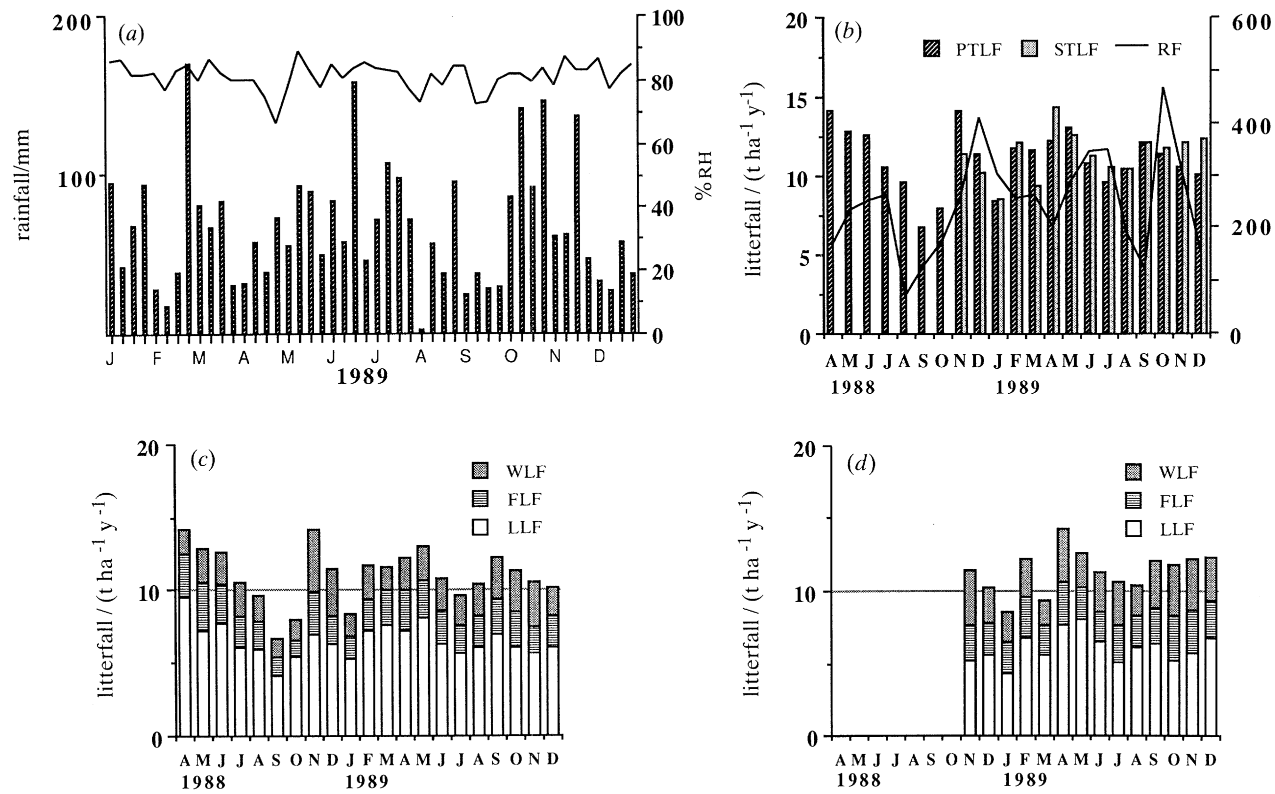

Figure 1. (*a*) Weekly rainfall and relative humidity (10 a.m.–4 p.m.) for the year 1989, Danum Valley Field Centre. (*b*) Monthly rainfall RF and rates of total litterfall for primary (PTLF) and logged (STLF) forest during April 1988–December 1989. (*c*) Monthly litterfall separated into different fractions for the period April 1988–December 1989 in primary forests. (*d*) *Idem* for the period December 1988–December 1989 in logged forest (LLF, leaf litterfall; FLF, fragmented litterfall; WLF, twigs and woody litterfall).

animals were stored in 70% ethanol, identified to the level of order or family (Mackerras 1970; Wallwork 1976; Borror *et al.* 1979), and counted.

Hand sampling undoubtedly underestimates densities of smaller invertebrates such as springtails and mites, especially of those occurring in the fragmented part of the litter layer. Berlese–Tullgren extraction (Macfayden 1961; Huhta 1972) of the 60 sampling units at the laboratory could not be used due to an inadequate and unreliable power supply. Air drying the litter samples appeared to be ineffective due to the high relative humidity inside the DVFC laboratory and as the purpose of the research was a comparison (of plots and of sites within plots) rather than establishing absolute densities, we opted for hand sorting. In addition to hand sorting, litter invertebrates were collected by using a modified pitfall trapping method (BM(NH) 1974) and the results are still being processed.

(*e*) *Chemical analysis*

Leaf litter material collected during the sampling in May 1989 from 30 sites in both forest plots was dried to constant mass (65°C) in a solar drying house, shipped to Amsterdam and ground in a centrifugal ball mill (Retsch, model S2). Total C and N were determined by using a Carlo Erba Strumentazione Elemental Analyzer, model 1106.

The pH and conductivity (measure of total exchangeable nutrients) of the LLM material were determined in the DVFC laboratory from fresh litter (100 g fresh mass) in 500 ml deionized water. In each of 60 sites ten soil samples were collected, in a random manner, to a depth of 8 cm using a 2 cm diameter corer and bulked into one sample per site. pH and conductivity (EC) were measured on 10 g soil suspended in 25 ml deionized water and shaken for 12 hours. Analysis of topsoil samples (200 g fresh mass) on total N (Micro Kjeldahl), total P (Hanson), soluble P (Bray and Kurtz), cation exchange capacity (CEC) (Metson) and soil texture were carried by the Sepilok Forest Research Centre in Sandakan, Sabah (Acres *et al.* 1975).

(*f*) *Statistical analysis*

Because the data did not follow a normal distribution and because variances were not homogeneous, log transformation was applied. Differences between geometric mean values for chemical parameters of soil and litter collected from the primary and logged forest, as well as between annual mean values for LLF, LLM, LLD, FRM, WLF, FLF, LLM, moisture content, invertebrate abundance (total invertebrate abundance as well as for different taxonomic groups) were tested for significance using the Student's *t*-test. Significance of correlation between various variables was tested for, using Spearman's Rank Correlation test (Sokal & Rohlf 1981).

4. RESULTS

Rainfall and relative humidity were high throughout the period April 1988–December 1989, without clear seasonal variation (figure 1*a*). Even less variation is shown for monthly rates of litterfall (figure 1*b*–*d*). Moreover, total litterfall, leaf litterfall, fragmented litterfall and woody litterfall seem unrelated to rainfall and forest type. In figure 2 invertebrate abundance, and rates of leaf litterfall and leaf litter disappearance are shown to vary little throughout the year although the leaf litter layer mass appears to be lower for the months December 1988–May 1989. LLD equals LLF for each period of three months as shown in figure 2*c* by the LLD/LLF quotient. Only in the period September–December 1989 is the LLD lower in the logged forest compared with the primary forest, but the difference is not significant.

Temporal variation, as shown by the standard deviations indicating spatial and temporal variation in values for the measured variables (table 1), was less than spatial variation. Spatial variation of annual litterfall within a forest type results in a patchy litter layer shown by the variation in LLM (figure 3*a*). In both forest types LLM and LLD increased with LLF ($p < 0.001$) (figure 3*a*, *b*).

Figure 2 and table 1 show no or only small differences between primary forest and logged forest in rates of LLF and LLD and in LLM. Average values of moisture content of the leaf litter layer, the fine root mass and mean abundance of invertebrates in the litter layer appeared to be higher in the primary forest plot compared to the logged forest plot ($p < 0.05$) in spite of high spatial variation.

Average abundance of different taxonomic groups in the two forest types is presented in table 2. Pseudoscorpionida, Scorpionidae and Acarina occurred in a higher abundance in the primary forest. The proportion of Diplopoda, Blattodea and Coleoptera of total invertebrate abundance was higher in the logged forest than in primary forest while Pseudoscorpionida and Acarina showed the reverse. Collembola and Formicidae were abundant in both forests; their abundance was not significantly different between the forest types. In the primary forest especially, some

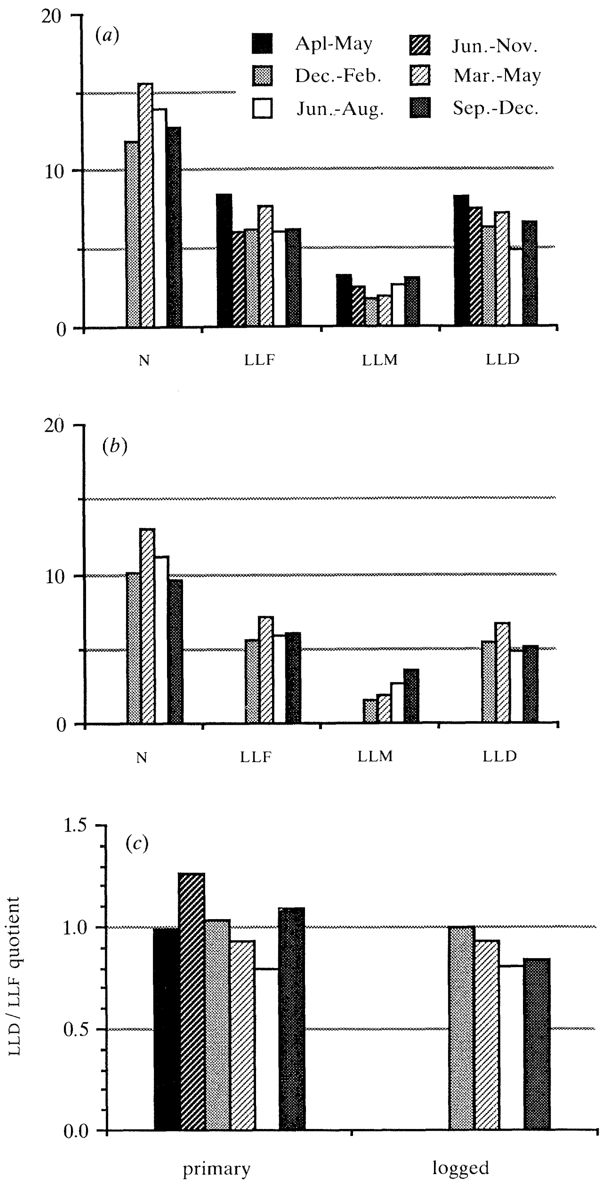

Figure 2. Periodic arthropod abundance, leaf litterfall, leaf litter layer mass and leaf litter decomposition in (*a*) primary and (*b*) logged forest during April 1988–December 1989. N, arthropod abundance (dm^{-2}); LLF, leaf litterfall (ton ha^{-1} y^{-1}); LLM, leaf litter layer mass (ton ha^{-1}); LLD; leaf litter disappearance (greater than 1 cm) (ton ha^{-1} y^{-1}); (*c*) LLD/LLF quotient for primary and logged forest for periods as in (*a*).

Table 1. *Average values (including spatial – s.d.*[1] *– and temporal variation – s.d.*[2]*) for the variables that were studied from December 1988 to December 1989 for three-month periods in the comparison between the primary and logged forest plot*

(Differences between geometric means for both forest types were tested for significance using Student's *t*-test (*, $p < 0.05$).)

	primary forest			logged forest			
variable[a]	average	s.d.[1]	s.d.[2]	average	s.d.[1]	s.d.[2]	*p*
N	1317	767	167	1051	351	194	*
LLF	6.6	1.8	0.6	6.2	1.7	0.6	
LLM	2.4	0.6	0.5	2.4	0.6	0.8	
LLD	6.4	1.6	0.9	5.5	1.6	0.7	
LLM % water	180	24	15	156	24	10	*
LLD/LLF (%)	97	11	4	89	8	5	
k_L	2.7	0.5		2.6	0.5		
FLF	2.2	0.8		2.5	1.6		
WLF	2.3	1.3		2.8	2.3		
FRM	1.4	0.8		0.9	0.7		*

[a] N, abundance of arthropods in litter layer (per square metre); LLF, periodic leaf litterfall (greater than 1 cm, ton ha^{-1} y^{-1}); LLM, periodic leaf litter layer mass $(t_{1,4}) = (\text{LLM}(t_1) + \text{LLM}(t_4))/2$ (less than 1 cm; ton ha^{-1})); LLD, periodic leaf litter decomposition $(t_{1,4}) = \text{LLM}(t_1) + \text{LLF}(t_{1,3}) - \text{LLM}(t_4)$ (ton ha^{-1} y^{-1}); LLM, moisture content: moisture content as percentage of dry mass; k_L, annual LLF/annual LLM; FLF, fragmented leaf litterfall (less than 1 cm, ton ha^{-1} y^{-1}); WLF, woody litterfall (less than 2 cm diameter; ton ha^{-1} y^{-1}); FRM, fine root mass in litter layer (less than 3 mm; ton ha^{-1}).

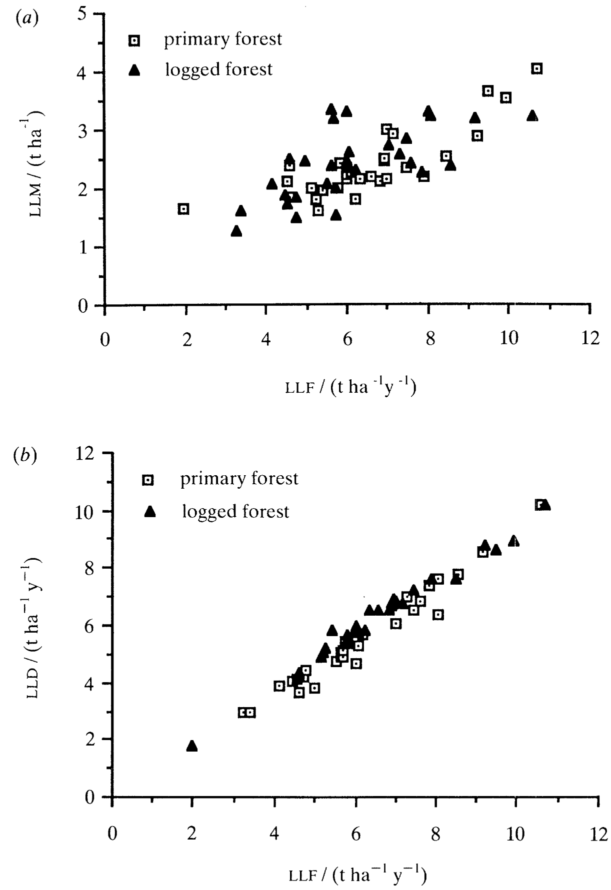

Figure 3. Relationships between annual leaf litterfall (LLF) and (*a*) leaf litter layer mass (LLM), and (*b*) leaf litter disappearance (LLD) for 30 sites in primary and logged forest.

species of Formicidae seem important as fragmentors of leaf litter (T. Burghouts, personal observations). Isoptera occurred in higher abundance in the primary forest plot compared with the logged forest plot. Litter-feeding termites were observed in the primary forest but none occurred in the samples: they had a highly aggregated distribution.

In the primary forest the total litter invertebrate abundance increased with LLF, FLF, WLF, LLM, LLD and fine root mass (FRM) but not with moisture content of the litter (table 3). In the logged forest total invertebrate abundance was related to the FLF and WLF. Abundance of Collembola, insect larvae, Coleoptera, Araneae, Pseudoscorpionida, Hemiptera and Chilopoda were related to LLF and LLM in the primary forest; in the logged forest abundance of some of these groups increased with moisture content of the leaf litter. The abundance of Isoptera in both forest types increased with LLM rather than with humidity of the leaf litter. Diplododa and Isopoda increased with FLF and WLF in both forest types. In both forests the abundance of Coleoptera were related to LLF, WLF and FLF and LLM. Abundance of litter dwelling Annelida were related to WLF in both forest types but showed a decrease with LLM in primary forest.

Preliminary chemical analysis of LLM and topsoil (table 4) showed high variation among sites. None the less, the two forest plots differed significantly in pH and CEC and in content of C, N, total and exchangeable P and clay particles ($p < 0.05$). Comparison of relatively undisturbed sites in both forest plots may reveal whether differences between the two plots in chemical composition of litter and soil are a consequence of logging or caused by a different composition of mineral soil. Soil fertility, as indicated by total and soluble phosphorus, the cation exchange capacity and carbon and nitrogen content of the topsoil of both forest plots is low when compared to other soil types elsewhere in Sabah (Acres *et al.* 1975; Whitmore 1984, 1989). Although the C/N quotient of the leaf litter is similar for both forest types, pH and EC are lower whereas carbon and nitrogen are higher for leaf litter in the primary forest. The C/N quotient declines steeply with depth from leaf litter to topsoil.

5. DISCUSSION

Litter layer mass and litter disappearance rates are within the range of values reported for rain forests elsewhere in the world (Proctor 1983: Vogt *et al.* 1986). Leaf litter layer mass and leaf litter disappearance are similar in primary and logged forest being positively related to leaf litterfall. The high variation of the measured variables among the 30 sites within each forest type indicates effects of the composition and structure of the vegetation on forest floor processes and nutrient availability.

The horizontal heterogeneity of the forest floor influences regeneration processes and habitat diversity (Whitmore 1984; Golley 1983*a*, *b*) and it is therefore important to analyse it. Dependent on the intensity of disturbance, logging operations and natural gap formation affect the composition of the vegetation, by favouring light-demanding pioneer species and decreasing the number of shade bearers (Brown & Whitmore, this symposium; Kennedy & Swaine, this symposium). The logging operations in 1978 removed *ca.* 20 dipterocarp trees (greater than 40 cm diameter) per hectare†, resulting in patches with *Macaranga* spp. and other fast growing species overgrowing the disturbed and often compacted soil (Van der Plas 1991).

As has been shown in research on herbivory and leaf characteristics (McKey *et al.* 1978; Coley 1983; Lowman & Box 1983), leaf quality of many of the emergent trees differs from leaf quality of pioneer species in chemical and physical aspects such as higher toughness, higher tannin and lignin concentrations, lower nutrient concentrations and C/N quotients (Ewel 1976; Coley 1983; Dantas & Phillipson 1989). Pioneer tree species differ from emergent trees in quality of leaf litter and patterns of leaf flushing, flowering and fruiting (Whitmore 1984) causing these trees to affect forest floor processes in a different way from emergent trees.

The impact of litter quality on litter invertebrates and decomposition processes has been shown in temperate forests within the range between mor and mull humus types (Anderson 1973; Swift *et al.* 1979).

† 1 hectare (ha) = 10 000 m²

Table 2. *Arithmetic mean abundance (per square metre) of litter arthropods according to different taxonomic (ecological functional) groups for five sampling occasions between December 1988–December 1989*

(s.d.[1] indicates spatial variation among annual values for 30 sites within forest type; s.d.[2] indicates temporal variation among successive three months values for each forest type. Differences between both forest types were tested for significance using Student's *t*-test following log transformation (*, $p < 0.05$; ***, $p < 0.001$). Taxa, not significantly different between forest types and representing less than 3% of the total density, are not listed.)

	primary forest			logged forest			
taxa[a]	average	s.d.[1]	s.d.[2]	average	s.d.[1]	s.d.[2]	*p*
Crustacea							
Isopoda (woodlice)	71	50	21	72	35	26	
Arachnida							
Acarina (mites)	54	24	29	29	11	18	***
Araneae (spiders)	74	21	6	71	25	21	
Phalangida (harvestmen)	6	6	6	4	3	3	
Pseudoscorpionida (pseudoscorpions)	56	51	24	18	10	8	***
Scorpionidae (scorpions)	1	2	1	0	0	0	***
Myriapoda							
Chilopoda (centipedes)	15	8	6	13	12	6	
Diplopoda (millipedes)	27	22	9	28	16	12	
Insecta							
Blattodea (cockroaches)	6	5	3	10	7	5	
Coleoptera (beetles)	61	24	21	80	37	36	
Collembola (springtails)	252	109	123	184	58	70	
Formicidae (ants)	465	466	124	364	209	122	
Hemiptera (bugs)	19	13	7	17	11	6	
Isoptera (termites)	60	71	30	24	54	22	*
larvae	24	13	17	21	11	13	
Orthoptera (crickets)	5	4	1	6	5	2	
Annelida (earthworms)	14	15	8	9	7	1	
Total	1231	650	301	967	310	298	*

Mor humus often develops as a matted surface layer on sandy or other nutrient-poor soils: under tree species such as pine (*Pinus nigra* Arnold), oak (*Quercus petraea* (Mattuschha) Liebl.) and beech (*Fagus sylvatica* L.) the litter layer consists of low quality litter and low pH, and initial fragmentation rates are low. In these forests fungal biomass is high, fungivorous Collembola and mites are abundant and dominate the invertebrate community while invertebrates that fragment leaf litter are less abundant. By their grazing activity on fungi, Collembola and mites play an important role in the slow but gradual mineralization of nutrients (Teuben & Roelofsma 1990). In a mull humus type, under tree species such as birch (*Betula lenta* L.) and hickory (*Carya ovata* (Miller) K. Koch), litter is of higher quality and neutral pH. High initial fragmentation rates, through the combined activity of bacteria and earthworms and larger invertebrates such as woodlice and millipedes, result in high mineralization rates (Anderson 1973; Herlitzius 1983) and high potential for leaching of nutrients. In tropical rain forests different decomposition rates for different types of leaf litter have been reported (Madge 1965; Ewel 1976; Lohdi 1978; Tanner 1981; Anderson *et al.* 1983; Gong & Ong 1983; Luizão & Schubart 1987; Spain & Le Feuvre 1987; Cuevas & Medina 1988; Brasell *et al.* 1989). It is unknown to what extent tree species cause quantitative and qualitative differences in leaf litterfall, in composition of the invertebrate community and in decomposition mechanisms (Golley 1983*c*). Leaf litterfall depends on tree species, as shown by high rates of leaf litterfall under clusters of emergent trees such as *Shorea pauciflora* King, *Shorea argentifolia* Sym. and *Shorea fallax* Meijer (Dipterocarpaceae) and species of Lauraceae and Fagaceae (*ca.* 6 ton ha^{-1} per 3 months). High rates of leaf litter disappearance equal the high rates of leaf litterfall over a one year period, but the fragmented litter fraction (less than 1 cm) tends to accumulate on top of the mineral soil under the parent trees, thus the fragmented litter fraction is an important part of the forest floor layer. In the present study we have excluded the fraction less than 1 cm from the estimation of litter disappearance rates because its dry mass is difficult to measure due to mixing with soil particles. After correction for the content of mineral soil this fraction will to be included in further calculations of turnover rates of organic matter and nutrients within the litter layer.

Average values for total litterfall, leaf litterall, leaf

Table 3. *Significance levels of the relationships between different taxonomic groups and measured variables as described in table 2*

(The significance of Spearman's coefficient of rank correlation is given: *, $p \leqslant 0.05$; **, $p \leqslant 0.005$; ***, $p \leqslant 0.001$; — = not significant. For abbeviations see table 1.)

primary forest	LLM	LLF	LLD	WLF	FLF	% water	FRM
Crustacea							
Isopoda	—	—	*	*	***	—	*
Arachnida							
Acarina	*	*	**	*	*	—	*
Araneae	***	*	*	—	—	—	*
Pseudoscorpionida	*	*	*	**	—	—	***
Myriapoda							
Chilopoda	**	***	***	—	*	—	*
Diplopoda	—	—	—	*	*	*	*
Insecta							
Blattodea	—	—	—	—	—	—	**
Coleoptera	***	**	**	—	—	—	*
Collembola	*	**	***	***	*	—	—
Formicidae	—	—	—	*	*	—	—
Hemiptera	***	*	*	—	*	—	*
Isoptera	**	—	—	—	—	—	—
larvae	**	***	***	—	*	—	*
Annelida	—	—	—	*	—	—	—
Total	***	**	***	—	*	—	**
logged forest	**LLM**	**LLF**	**LLD**	**WLF**	**FLF**	**% water**	**FRM**
Crustacea							
Isopoda	—	—	—	**	*	*	—
Arachnida							
Acarina	—	**	—	—	—	—	—
Araneae	—	—	—	*	*	—	—
Pseudoscorpionida	—	—	—	—	—	—	—
Myriapoda							
Chilopoda	—	—	—	—	—	—	*
Diplopoda	—	—	—	**	*	—	*
Insecta							
Blattodea	—	—	—	—	—	—	—
Coleoptera	*	***	***	***	***	*	—
Collembola	*	—	—	—	—	***	—
Formicidae	—	—	—	—	—	—	—
Hemiptera	—	—	—	—	—	*	—
Isoptera	*	—	—	—	—	—	*
larvae	—	—	—	—	—	—	—
Annelida	—	—	—	*	*	—	—
Total	—	—	—	*	**	—	—

litter layer mass and leaf litter disappearance are similar to values reported by Anderson *et al.* (1983) and Proctor *et al.* (1983) for dipterocarp forest in Gunung (Mount) Mulu in Sarawak, Malaysian Borneo. The dipterocarp forest in Gunung Mulu is characterized by the same tree families as our study plot but has a higher annual rainfall of over 5000 mm y^{-1} and a higher soil organic matter content. Abundance of most groups of macro-invertebrates in Gunung Mulu were similar to abundance in our primary and logged forest except for termites, woodlice and millipedes. The most striking difference was found for the termites which in our study had a much lower abundance (*ca.* 100 m^{-2}) than those reported by Matsumoto & Abe (1979), Wood *et al.* (1982) and Anderson *et al.* (1983) for other rain forests in Asia and Africa (greater than 1000 m^{-2}). This may be related to the low organic matter content of the soil

Table 4. *Chemical characteristics of leaf litter layer mass and topsoil for primary and logged forest*

(Differences in pH, EC, C, N (except litter), C/N (except litter), total P and soluble P (for B-layer only) were significant ($p < 0.05$). Average values are presented including standard deviations (s.d.^{0}, standard deviations for values of EC and pH for ten sites; at each site five random samples were bulked into one sample per site; for C and N concentrations the standard deviations are calculated for 30 sites; s.d.^{1}, standard deviation for average values of 30 sites; at each site ten random samples were bulked into one sample per site); EC, conductivity in $\mu\Omega\ cm^{-1}$; CEC, cation exchange capacity (me %), total P, total phosphorous (p.p.m.); sol. P, easily soluble phosphorous (p.p.m.).)

forest type	pH	EC	C (%)	N (%)	C/N	CEC	total P	sol. P
Primary forest								
leaf litter	4.4	64	46.90	1.53	30.9			
s.d.^{0}	0.3	18	2.02	0.13	3.4			
soil 0–3 cm	4.6	73	3.08	0.30	11.1	10.6	155.7	9.4
s.d.^{1}	0.4	21	0.97	0.10	4.7	4.8	31.6	4.6
soil 3–8 cm	4.7	42	2.04	0.26	9.8	9.8	137.8	6.4
s.d.^{1}	0.5	11	0.71	0.09	3.4	4.0	29.2	3.2
Logged forest								
leaf litter	6.1	155	42.18	1.42	30.4			
s.d.^{0}	0.6	89	3.43	0.27	4.6			
soil 0–3 cm	5.2	43	2.20	0.26	8.7	10.0	121.2	8.9
s.d.^{1}	0.6	19	0.86	0.09	3.2	2.9	26.7	3.9
soil 3–8 cm	5.0	27	1.30	0.19	7.6	9.2	121.5	8.3
s.d.^{1}	0.3	16	0.49	0.10	2.8	4.3	25.8	3.4

in the Danum Valley dipterocarp forest. The opposite was found for millipedes and woodlice. A difference in composition of the decomposer community does not necessarily affect the rate of litter disappearance. Compensatory activity by other groups of organisms, including microflora, is a possible explanation for the similarity of litter disappearance rates in the Mulu and Danum forests. Our data on mesofauna such as mites and Collembola show low abundance compared with abundance in other rain forests in Peninsular Malaysia (Chiba 1978), Australia (Plowman 1979), and Amazonia (Beck 1971), because of differences in sampling methods (hand-sorting versus Berlese-Tullgren extraction) these data are difficult to compare. The low abundance of Collembola and mites may possibly be explained by the absence of humus accumulation in topsoil. Collembola and mites collected in our study were species obviously living in the leaf litter layer. Preliminary sampling of invertebrates in the topsoil showed very low numbers.

Our results showed only minor differences in litterfall, litter disappearance rates and composition of the invertebrate community between both primary and logged forest. Exchangeable nutrients and pH of forest floor litter were higher in logged forest than in primary forest while the fine root mass and moisture content of leaf litter showed the reverse. Equal litter disappearance rates, lower litter humidity and a lower fine root mass suggest higher leaching rates of nutrients from the litter layer into the mineral soil of the logged forest compared with the primary forest, whether these differences are effects of selective logging is as yet unclear. Differences between the primary and logged forest plot in chemical and physical characteristics of the soil (Van der Plas 1991), may be due to minor differences in geological origin. It should be noted that the density of emergent dipterocarp trees in our primary forest plot is low compared with other lowland dipterocarp forest in Sabah (Newbery, this symposium), and that this is comparable with that of our logged forest plot 12 years after logging (L. Madani, personal communication). The complex and heterogeneous geology and its effect on vegetation composition in the Danum Valley (Marsh & Greer, this symposium) requires an analysis of the spatial heterogeneity of the vegetation within each forest plot, as indicated by our results on leaf litterfall, forest floor litter and invertebrate abundance. Within our primary forest plot abundance of invertebrates, especially of predators, such as spiders and pseudoscorpions, and fungivorous invertebrates, such as springtails, increased with leaf litter layer mass and leaf litterfall and suggests favourable conditions in sites with a high litter layer mass. For the earthworms the opposite was found, though it is not statistically significant. In the logged forest, abundance of various invertebrate taxa increased with litter humidity and with woody and trash litterfall. These differences between primary and logged forest indicate that the canopy structure and composition of tree species affect forest floor processes in both forest types in a different way. Further multivariate analysis of effects of vegetation composition on litterfall and forest floor processes within the two forest plots, may reveal to what extent natural disturbance and selective logging affect abundance of litter invertebrates and litter decomposition.

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