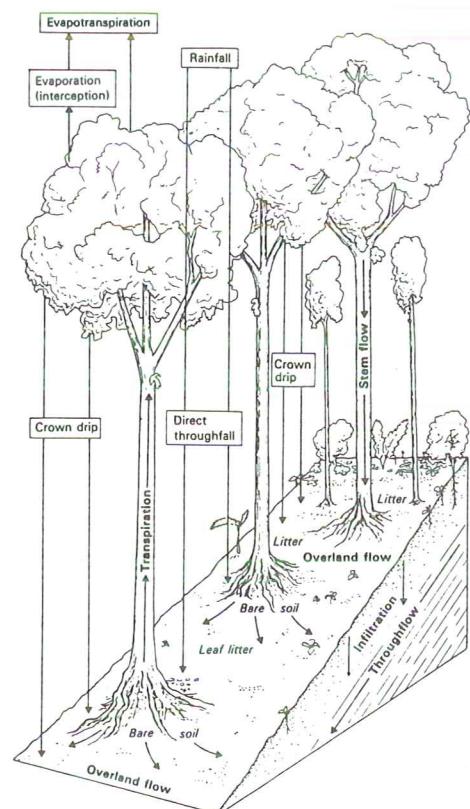
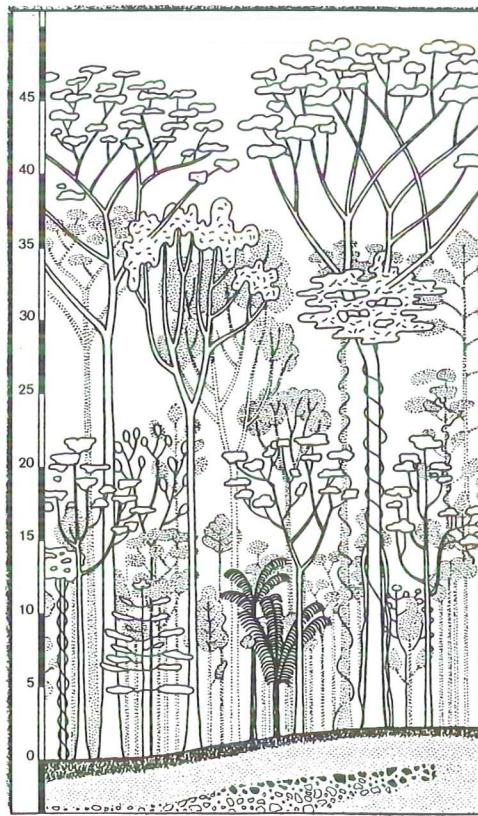


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NUTRIENT DYNAMICS IN INTACT AND LOGGED TROPICAL RAIN FOREST ON AN ACID SANDY SOIL IN GUYANA

Leo C. Brouwer¹

ABSTRACT

In tropical forests growing on nutrient poor and acid soils nutrient cycling is tight and ecosystem nutrient losses are low. In this paper the effects of selective logging on leaf decomposition rates and soil nutrient leaching are evaluated. Two logging gaps of different size (730 m^2 and 3440 m^2) were each divided into three zones: skidder (open, disturbed soil), crown (debris, no soil disturbance) and undisturbed (small trees still present, no soil disturbance). Decomposition and nutrient release from brown (recently shed) *Chlorocardium rodiei* leaves was slower than from green (fresh) leaves. Compared to closed canopy forest, decomposition was slower in the skidder zone of the gap but did not differ in the crown zone of the gap.

The soils in the gaps were wetter than in closed canopy forest, especially during dry periods. This led to about 50% more water percolation in the skidder zone of the gaps during the first two years. Also $\text{NO}_3\text{-N}$, Al, Ca, K, Mg, Mn, Na and Cl concentrations of the soil water at 120 cm depth were significantly higher, and the pH lower than in closed canopy forest, particularly during the first 15 months after logging. Nutrient losses through leaching in the large gap were higher and extended for a longer period than in the small gap. The rise in soil water nutrient concentrations was most pronounced in the skidder zones of the two gaps and in the crown zone of the large gap. The importance of nitrification with regard to acidification, cation leaching and soil Al levels is discussed.

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1. INTRODUCTION

In large parts of Guyana, soils are poor and the low nutrient availability hampers land use other than extensive forestry. The most common practice in the forestry belt of Guyana is selective logging, and increasingly large areas are given out as timber concessions. Traditionally the forestry sector has concentrated on a few hardwood species, of which *Chlorocardium rodiei* (Greenheart) is by far the most important. This species has a clumped distribution and during heavy exploitation fairly large clearings (up to 5000 m²) are created.

In relation to nutrient cycling, selective logging has been classified as a disturbance of moderate intensity (JORDAN, 1985, BRUIJNZEIJER, 1985). Nevertheless there is much variation in the intensity of selective logging, depending for example on the proportion of trees that can be harvested commercially. In Guyana the proportion of commercial trees is generally low. The average exploitation intensity for hardwoods rarely exceeds 50% (PARKER, 1985). However, not only the average intensity but also the spatial distribution of newly created gaps is important. At a given exploitation intensity, a distributed cut may have completely different effects than a cut in one concentrated area (PARKER, 1985).

Selective logging can cause a disruption of the nutrient cycle. Large amounts of organic debris reach the forest floor, where it is decomposed and nutrients are released in mineral form. If the exchange capacity of the soil is low and the soil is not very abundant, the risk of leaching is high and valuable nutrients will be lost.

The aims of this study were 1) to estimate decomposition rates of leaf litter present on the soil surface after a selective logging operation and 2) to evaluate nutrient losses through leaching after a selective logging operation. In addition, we evaluated whether gap size does influence leaching rates. A decomposition study using litterbags was used to monitor dry weight and nutrient loss of *Chlorocardium rodiei* leaves, the major timber tree in the area. Leaching of nutrients in two gaps of different size and in undisturbed closed canopy forest (CCF) was evaluated by monitoring soil water nutrient contents below the soil surface, combined with soil moisture suction measurements and a vertical nutrient balance model.

2. STUDY AREA

The study area is located in the forestry belt of north-central Guyana, South America (5°N, 59°W, elevation < 100m). Average annual rainfall is 2500 mm, distributed over two wet and two relatively dry seasons. The driest month is usually October, with an average precipitation of about 100 mm. The wettest months are June and July. The average annual temperature is 26 °C with a small monthly variation.

The topography consists of gently rolling hills which rise up to 30 m above the river level, with the exception of some higher landscape elements. The well-drained soils at the study site have formed on sandy sediments of Pliocene/Pleistocene age which cover the underlying rocks of the Precambrian Guyana shield. The soils are classified as ferrallitic Arenosols or haplic Ferralsols (FAO classification) or as Paleudults (USDA Soil Taxonomy). These acid soils are characterised by a low content of weatherable minerals, low cation exchange capacity, low exchangeable bases, high content of Al and Fe and low P availability (DRIESSEN and DUDAL, 1989). Some basic soil chemical characteristics are shown in table 1.

(Table 1)

A mixed species tropical lowland rain forest is found on this soil, with sometimes a local dominance of a few species (TER STEEGE, 1993). The trees have an average height of 30 -35 m and the average basal area is about $30 \text{ m}^2/\text{ha}$ (VAN ZANTEN, 1991).

3. METHODS

3.1 Plot Preparation, Division

An area containing a rich stock of commercial trees (mainly *Chlorocardium rodiei*) was selected for the experiment. Within the area two, more or less circular shaped, logging gaps of different size were created on 30 and 31 January 1992, by felling the commercial trees and extracting them using a heavy type skidder with rubber tyres. The largest gap (canopy opening sensu BROKAW, 1982, 3440 m^2) resulted from the removal of an estimated 65 m^3 of timber in 17 trees. The comparatively small gap (canopy opening 730 m^2) resulted from the removal of 16 m^3 of timber in five trees. A third area located about 60 m from the small gap and 200 m from the large gap was selected as control (CCF). The two gaps were subdivided into three zones depending on the amount of debris and the damage to vegetation and soil. The three zones, that occupied about equal surface areas in the gaps, were:

- 1) the skidder zone; this is the area where skidder movement took place. It is characterised by more or less bare soil which is compacted. There was no vegetation remaining in this zone except for some shade adapted seedlings that died within a few weeks. Most of the skidder zone was located near the centre of the gaps.
- 2) the crown zone; this is the area where the crowns of the felled trees were deposited. Except for a few large trees all vegetation in this zone was damaged and covered by a large amount of debris. The soil in this zone was generally not disturbed although locally there was some uprooting of smaller

trees that had been smashed by falling larger trees. Most of the crown zone was located near the gap edges. 3) the undisturbed zone; in this zone there was no soil disturbance and no disruption of the "smaller" vegetation (seedlings, saplings, trees with a diameter < 15 cm). The major difference with the pre-logging situation was the absence of large canopy trees, with consequently a much higher irradiation at ground level.

3.2 Decomposition

To investigate leaf litter decomposition rates in the gaps and the closed canopy forest (CCF) a litterbag experiment was carried out. Both green (picked from felled trees) and recently shed (collected daily from well drained netting) brown leaves of *Chlorocardium rodiei* were used. The leaves were dried at 40 °C, cut into pieces of 5-10 cm² and mixed. Several pieces were put in one litterbag up to a weight of 2 g (green leaves) or 1.3 g (brown leaves). The 10 * 7 cm litterbags were prepared from 1 mm² polyethylene mesh, excluding soil macrofauna that could transport the leaf material but allowing access for soil mesofauna and microfauna. In total 140 litterbags were prepared, one half of them filled with green leaves and the other half of them filled with brown leaves. The first group of bags was divided between the crown zone of the large gap and the CCF; whereas the second group was divided between the open zone of the large gap and the CCF. Wherever possible the litterbags were incorporated into the existing litter layer. Five replicate litter bags were recovered after 0, 2, 5, 9, 20, 34 and 49 weeks. After recovery the leaves were dried for 48 hours at 70 °C and weighed to 0.001 g. The samples were sealed and shipped to the laboratory of Physical Geography of Utrecht University in the Netherlands, where they were analysed for P, N, K, Ca, Mg and Na. Extracts were made by boiling the samples in a mixture of concentrated H₂SO₄ and H₂O₂. Cations and P were determined using an ICP-AES, N was determined using flow injection analysis.

3.3 Water Flux Estimation

Ten clusters of tensiometers were installed in the CCF (2), the large gap skidder (LGS, 2), crown (LGC, 2) and undisturbed (LGU, 1) zone and the small gap skidder (SGS, 1), crown (SGC, 1) and undisturbed (SGU, 1) zone. Each cluster consisted of three tensiometers at 30, 75 and 120 cm depth. Readings of soil water tension were taken weekly during two periods: February - April 1992 (a dry period) and March - June 1993 (a wet period). The readings from the tensiometers were used to calibrate a one-dimensional water balance model called SOAP (SOil Atmosphere Plant model). Details on this model can be found in JETTEN (1994). The model consists of modules describing the processes of rainfall interception, transpiration, soil evaporation, infiltration into the soil and the redistribution of water in the soil. The atmospheric parameters required for the model were collected at the Tropenbos Meteorological station about 3 km north of the present research site. Soil physical characteristics were determined as in

JETTEN (1994) and vegetation parameters were mainly derived from other research in the Amazon region (see JETTEN, 1994 for details).

3.4 Soil Water Chemistry

Ceramic cup suction soil water samplers were used to collect soil water. The samplers were installed at an angle of 30 degrees from the vertical to avoid surface disturbance immediately above the porous cup. In total 36 samplers were installed and about 800 samples were extracted and analysed over a period of almost three years. Most of the samplers were used for the evaluation of the chemistry of percolating water at 120 cm depth, which was considered to be essentially below the rooting zone (EERNISSE, 1993). It is assumed that at this depth in sandy soils the effect of macropores is smoothed. Eight samplers were used to extract soil water from a depth of 15 cm, which is in the zone having the highest root density (PRINSEN and STRAATSMA, 1992).

The soil water samplers were brought to a suction of 35 kPa about 48 hours before sample collection. Immediately after sampling the electrical conductivity and pH of the samples were determined. Subsequently the samples were filtered through a 0.45 μm filter and two aliquots of the samples were taken. To one aliquot 25% HNO_3 was added (4% of the total sample volume), to the other 5% H_2SO_4 was added (4% of the total sample volume). The samples were stored at 4 $^{\circ}\text{C}$ and within three months shipped to the laboratory of Physical Geography of Utrecht University, The Netherlands for analysis. The HNO_3 -acidified samples were analysed for Al, Ca, Fe, K, Mg, Mn, Na, Si and SO_4 on an ICP-AES. The H_2SO_4 -acidified samples were analysed colorimetrically on a Skalar autoanalyzer for NH_4 , Cl and NO_3 .

Leaching of nutrients was calculated by multiplying the average soil water nutrient concentration per zone with the corresponding water percolation as simulated by the SOAP model.

4. RESULTS

4.1 Decomposition

Dry weight loss of the leaf material in the litterbags was significantly influenced by leaf type and location (two way ANOVA). The weight loss of brown leaves was significantly lower than the weight loss of green leaves, and brown leaves in the open area had significantly lower weight loss than brown leaves in the closed forest (both $p<0.05$, Scheffé test). Green leaves in the crown zone had a tendency to decompose faster than green leaves in the closed forest, however this difference was not significant.

(Table 2)

The initial contents of N, P and K were higher in the green leaves than in the brown leaves. The initial Mg content did not differ and the initial Ca content was slightly higher in the brown leaves (table 2).

The dry weight loss with time and the release of the individual nutrients are shown in figure 1. In the brown leaves P was retained and after a year there was no net release of this element. In the green leaves P was released at similar rates as the dry weight loss (crown zone) or slightly slower (closed canopy forest). N was also released at a similar rate as dry weight loss (brown leaves in open area) or slightly slower (other treatments). Na, K and Mg were rapidly released in all treatments. After two months about 50 % of the initially present K and Mg and 80% of the Na were released in all treatments. The rate of Ca release was slightly faster than the overall weight loss. The initial nutrient content of the leaves, the percentage remaining of the original nutrient content after one year of decomposition and the amount of nutrients released per gram of leaf material during the year are shown in table 2.

(Figure 1)

After a year of decomposition far more P and K had been released from green leaves than from brown leaves, which is mainly because of the differences in original concentration. A similar trend could be observed for N and Na albeit less pronounced. Ca tended to be released at higher rates in the closed canopy forest than in the gap.

4.2 Water Fluxes

The SOAP water balance model was tested against tensiometer readings over two periods: a relatively dry period in 1992 and a relatively wet period in 1993. The results of the tensiometer readings at 120 cm depth and the SOAP simulated soil water tension and percolation at the same depth are shown in figure 2 for CCF and the skidder zones of the gaps from February to April 1992.

(Figure 2)

It appears that the soils in the gaps were consistently wetter than in the CCF, especially during dry periods. Although direct evaporation from the soil surface was higher in the gap, this was apparently not enough to compensate the decreased transpiration due to the removal of the trees. Simulations by SOAP indicated that the percolation of water in the gaps immediately after logging was

75% of the incoming rainfall versus 43% in closed canopy forest (JETTEN, 1994). Because of the sandy nature of the soil, overland flow did not occur, despite soil compaction. Over a period of 652 days the simulated percolation in the skidder zone of the gap areas was 2787 mm, compared to 1797 mm in the CCF.

4.3 Soil Moisture Chemistry and Nutrient Leaching.

Nutrient concentrations in the soil moisture at 120 cm depth were generally higher in the gaps than in the CCF. The concentrations of NO_3 , Mg, Ca, K and Na started to rise within the first month after logging (figure 3) and reached a maximum after approximately five months, except for Na which reached its peak level earlier. High levels of nutrient concentrations in subsoil water were maintained for another seven months. Between 12 and 15 months after logging concentrations started to decrease, but they remained relatively stable after about 16 months (figure 3).

(Figure 3)

The average composition of the soil water at 120 cm depth is presented in table 3 for two periods: 1) the first 15 months after logging and 2) the period from 16 to 34 months after logging. The concentrations in the deep soil water for each zone in the two gaps were tested against the concentrations under CCF during the same period. In the first 15 months after logging most element concentrations were significantly higher in the gaps, except for NH_4 , Si and SO_4 . Compared to the closed canopy forest NO_3 concentrations showed the largest increase (more than 15 times higher in the large gap). Mg, Ca and K concentrations were 1.5 to 10 times higher in the gaps. The pH was significantly lower in the soil water of the gaps, except in the undisturbed zone of the small gap. Consistently low pH values ($\text{pH} < 4.2$) were found from July 1992 to July 1993 in the skidder zones of both gaps. Element concentrations in deep soil water were higher in the large gap than in comparable zones of the small gap. The soil moisture composition in the undisturbed zones of the gaps resembled the CCF soil moisture more than the skidder and crown zones of the gaps (table 3).

(Table 3)

In the second period the nutrient concentrations of the soil moisture at 120 cm depth were lower compared to the first period. However, NO_3 , Mg, Ca, Mn and Al concentrations were still significantly higher in the gaps than in the CCF for most zones (table 3).

The temporal variation of the soil water composition at 15 cm depth was larger than at 120 cm depth, especially during the first year after logging (data not

shown here). Again, most elements showed higher levels in the gaps than in the CCF. There was a negative relationship between soil moisture content and element concentrations, but it was not very pronounced.

The calculated nutrient exports are presented in table 4. The largest nutrient losses occurred within the first 652 days. However as the results of the period between 652 and 1030 days indicate, leaching losses continued to be higher in the gaps. The values for the undisturbed and crown zones in the small gap approached the values for the CCF.

(Table 4)

5. DISCUSSION

Brown leaves decomposed significantly slower in the skidder zone of the gap compared to the CCF (table 2). Despite the generally wetter conditions in the soils of the gaps, the litter layer got rapidly desiccated by the high direct solar radiation received at the soil surface. This led to decreased activity of decomposer organisms and the relatively slow decomposition of leaves in this centrally positioned zone of the gap.

Green leaves had higher initial nutrient concentrations and larger weight loss than brown leaves during the first year of decomposition (table 2). The highest amounts of released N, K and Na per unit weight of leaves were found in the crown zone of the gap. This, combined with the addition of large quantities of leaves to the soil surface in this zone during a logging operation creates high nutrient inputs in the topsoil during the first year after logging and therefore, theoretically, a high potential for nutrient leaching. The difference in release per unit weight of leaf between brown and green leaves was less for Ca and Mg (table 2).

In this study increased percolation was found in the gaps (2787 mm in the skidder zone) compared to the CCF (1797 mm) over the first 652 days after logging. It has been shown before that large gaps have a higher soil moisture level than surrounding forest especially in dry periods (PARKER, 1985, BAUHUS and BARTHEL, 1995). PARKER (1985), working in the high rainfall zone of Costa Rica on soils derived from volcanic material, reported a percolation of 2110 mm in a large clearing compared to 1252 mm in CCF over a 404 day period. This finding corroborates the results of the present study.

UHL et al. (1988) and PARKER (1985) found little effect on soil moisture composition by single treefall gaps ($47-164 m^2$). However, an increase in soil moisture nutrient concentrations after more intensive disturbance (multiple treefall gaps, large clearings or clearing followed by burning) of a forest has been reported by a number of authors (HERRERA et al., 1981, PARKER, 1985, UHL

and JORDAN, 1984, UHL et al., 1982, BAUHUS and BARTHEL, 1995). UHL and JORDAN (1984) reported a distinct increase of K, Mg and $\text{NO}_3\text{-N}$ concentrations in soil leachate after cutting and burning one-hectare forest plots on a Venezuelan oxisol. Ca concentrations did not change significantly. UHL et al. (1982) collected soil water with zero-tension lysimeters at 40 cm depth after cutting Amazon caatinga forest growing on seasonally water-logged white sand soils. After cutting, K concentrations were very high, Mg and Ca showed a slight increase and $\text{NO}_3\text{-N}$ did not respond. BAUHUS and BARTHEL (1995) evaluated soil water composition changes after gap creation (diameter 30 meter) in a temperate forest on acid soil. They found levels of $\text{NO}_3\text{-N}$ in soil water at 80 cm depth changing from 0 in an intact forest stand to about 15 mg/l in the gaps. The main accompanying cation appeared to be Al, although Ca and Mg also increased.

Arguably, the study that is most comparable to this study is that of PARKER (1985) in Costa Rica. Here two clearings, sized 50*10 and 50*50 meter, were made in a forest stand on a relatively fertile clayey ultisol. Calculated nutrient leaching at 70 cm from the large clearing during the first 404 days was 115 kg/ha $\text{NO}_3\text{-N}$, 57/ha kg Na, 8 kg/ha K, 22 kg/ha Mg and 22 kg/ha of Ca. The calculated losses in the small clearing were very similar. Parker assumed, based on electrical conductivity measurements, that nutrient levels in the leachate had returned to their original values after 534 days, so some additional leaching losses are to be expected. The calculated leaching losses in Parkers' study are in the same order of magnitude as the present data, with the exception of K and Na, which were lost in higher amounts at the Guyanese site. Surprisingly, the difference between the large and the small gap is pronounced in this study, especially for the crown zone and the undisturbed zone contrary to the results in Costa Rica, at least according to Parker. Parker concludes, based on his calculations, that "water and solute budgets appear to react to increasing disturbance intensity with a threshold for response and a maximal response at higher levels of disturbance, with a probable sharp transition in between", and, "the threshold is likely to be less than 500 m^2 of forest cut and may be related to the extent that living roots from unaffected areas are present in the disturbed areas". The area (canopy opening) of the small gap in this study was about 730 m^2 and round shaped, but in this area the soil water did show distinctly lower nutrient concentrations than soil water in the large gap. It seems clear that the extent of living roots from surrounding vegetation does play a decisive role in preventing high leaching rates. In that respect it is surprising that in the rather narrow (10 m) clear-cut strip of Parker, the calculated leaching losses were comparable with the large clearing. In fact, it even seems unlikely, since both soil water content (PARKER, 1985: p 76) as well as e.g. $\text{NO}_3\text{-N}$ concentrations (PARKER, 1985: p 92) are clearly higher in the large clearing. Further work is necessary on hydrological and nutrient gradients from the gap centre to CCF.

The most dramatic change in soil water composition after selective logging concerned N. When released from organic compounds it is usually in the form of NH_4^+ , which is not very mobile in the soil. In the presence of nitrifying bacteria NH_4^+ can be transformed into NO_3^- , releasing two protons (nitrification). If the

NO_3^- is not taken up by plants this will cause a drop in soil pH, which in acid soils will lead to an increased solubility of Al^{3+} . The Al ions or the protons in the soil solution displace exchangeable bases from the soil exchange complex into the soil solution, or prevent that bases released by decomposition are held by the soil exchange complex. Contrary to NH_4^+ , NO_3^- is very mobile in the soil. If excess NO_3^- is leached downward in the soil profile it needs to be accompanied by a cation and this may therefore lead to an increased leaching of bases (CAHN et al., 1993, FREIESLEBEN and RASMUSSEN, 1986).

Increased Al solubility may also have other, more direct effects. It is well known that Al in the soil solution can be toxic to plants, especially if $\text{pH} < 5$ (GUNDERSEN and RASMUSSEN, 1987, WOLT, 1990). Al toxicity is generally visible in the root morphology of plants. High Al levels in the soil often interferes with P and Ca nutrition in plants (LATHWELL and GROVE, 1986, RAAIMAKERS, 1994). Because different species do have different tolerance to Al in the soil environment (WOLT, 1990), the soil acidification following selective logging might have a selective influence in the natural re-growth of species, and in this way influence future species composition.

It was shown above that nutrient inputs by decomposition were highest in the crown zone, both due to the quantity of material and the rapid release of nutrients, and that nutrient inputs by decomposition in the skidder zone were even lower than in CCF due to retarded decomposition. This was not reflected in the soil solution concentrations and the leached amounts, except for Na and Cl which were higher in the soil solution of the crown zone. The following explanation of the differences between the skidder and crown zone is hypothetical but may be tested in future research.

In the skidder zone nutrient release is mainly from soil organic matter. Very few living roots are present because of the absence of nearby trees and the damage to the top soil by the skidder. Nitrification occurs, the pH goes down, bases are exchanged from the soil exchange complex and the bases leach downward in the profile with the NO_3^- . Because there is not much fresh material and exchangeable bases were already low, the bases available for leaching become depleted, and N mineralisation rates become lower. With a new vegetation establishing, the uptake of nutrients increases and leaching rates will approach background values. In the crown zone similar processes will occur but at different intensity. Because of the minimal disruption of the soil and the proximity of undamaged trees, part of the root system will remain intact (UHL et al., 1988). The large inputs of nutrients by the decomposition of the debris will therefore partly be captured by those roots, perhaps except for elements which are in relatively abundant supply in this forest system (Na, Cl). The lowering of the pH as caused by the nitrification process will partly be buffered by the release of cations from the decomposing slash. Because there is much fresh decomposing debris from which nutrients are released and successional vegetation has difficulties to establish in the debris, the leaching of nutrients extends for a relatively long period.

Making a direct comparison between leaching losses in the gap areas and the CCF, it appears that N losses are 16.6 times higher in the large gap than in the CCF over a period of 1030 days. For Mg, Ca and K this is respectively 9.9, 4.7 and 3.9 times. In the small gap the losses are about 50% of the losses in the large gap for N, Mg and K, but of similar magnitude for Ca.

In an ecosystem with extremely low weatherable minerals in the soil, replenishment of nutrients will mainly depend on atmospheric inputs, except perhaps for N. Estimates on the time required to compensate extra nutrient losses due to leaching by atmospheric inputs are 71 years for N, 25 years for Mg, 17 years for K and 11 years for Ca (BROUWER, 1995). This does not include compensation for nutrients exported in timber.

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Table 1: Chemical characteristics of the soil at various depths.

depth	texture	pH H ₂ O	pH KCl	Org. C (%)	total N (%)	total P mg/kg	P-Bray mg/kg	CEC cmol+/kg	Ca	K	Mg	Na	Al
0-20 cm	LS	4.7	4.2	0.9	0.07	69	3	4.1	0.02	0.01	0.02	0.02	0.82
20-50 cm	SL	5.1	4.5	0.5	0.04	67	0.8	3.8	0.02	0.01	0.01	0.01	0.62
50-100 cm	SL	5.2	4.6	0.3	0.02	53	0.3	3.5	0.01	0.00	0.01	0.01	0.46

Table 2: The original concentration, the percentage of the original nutrient quantity still present in the leaf tissue after one year of decomposition and the amount of nutrients released per gram of original leaf material after a year. CCF = closed canopy forest, LGS = Large Gap Skidder zone, LGC = Large Gap Crown zone. Letters indicate differences in dry weights between groups ($p<0.05$, Scheffé test).

	treatment	dry weight	Ca	K	Mg	Na	P	N
original concentration (mg/g)	green leaves	2.65	2.45	3.23	3.00	0.39	19.1	
	brown leaves	3.04	0.77	3.10	2.62	0.14	15.8	
% remaining after one year of decomposition	brown leaves CCF	56.6 ^b	24.5	32.3	11.0	5.4	90.5	78.8
	green leaves CCF	48.6 ^a	13.1		6.6	3.7	44.8	67.6
	brown leaves LGS	63.0 ^c	38.0		7.1	5.8	97.3	67.4
	green leaves LGC	42.2 ^a	34.9	14.6	16.7	4.0	55.5	52.1
quantity released (mg-nutrient/g-leaf)	brown leaves CCF	2.27	0.57	2.66	2.48	0.01	3.4	
	green leaves CCF	2.37	>1.84	3.14	2.76	0.21	6.2	
after one year of decomposition	brown leaves LGS	1.93	>0.45	3.02	2.49	0.00	5.1	
	green leaves LGC	1.65	2.37	2.57	3.00	0.18	9.2	

Table 3: Average concentrations in soil moisture at 120 cm depth during two periods: the top half of the table represents the concentrations from February 1992 - April 1993 and the bottom half represents the concentrations from May 1993 to December 1994. Highlighted concentrations are significantly different (t-test, **= p< 0.01, * = p<0.05) from the concentrations measured in the closed canopy forest during the same period. Average n=31, all n>18 except for NH₄. Abbreviations: CCF = Closed Canopy Forest, L= Large, S = Small, G = Gap, C = Crown zone, S = Skidder zone, U = Undisturbed zone

zone	EC μS/cm	pH	Al mg/l	Ca mg/l	K mg/l	Mg mg/l	Mn mg/l	Na mg/l	Si mg/l	SO ₄ mg/l	NH ₄ mg/l	Cl mg/l	NO ₃ -N mg/l
CCF	22.9	5.3	0.14	0.43	0.51	0.15	0.01	3.07	3.76	1.23	0.19	3.71	0.45
LGC	111.2**	5.1*	0.54**	1.32**	2.46**	1.18**	0.04**	13.90**	4.99**	4.40	0.24	15.21**	7.68**
LGS	120.7**	4.7**	1.81**	1.66**	2.46**	1.60**	0.05**	8.97**	4.26	1.58	0.27	7.36**	9.64**
LGU	75.0**	4.7**	1.13**	1.22**	1.15**	0.76**	0.03**	6.64**	4.03	2.46**	0.42	8.83**	6.90**
SGC	40.1**	5.1*	0.10	0.91**	0.76**	0.29**	0.02**	5.27**	3.85	1.72*	0.30	9.47**	2.22**
SGS	76.5**	4.7**	1.20**	1.57**	1.27**	0.96**	0.05**	5.51*	3.66	1.38	0.28	5.07	7.18**
SGU	45.7**	5.3	0.18	1.19**	0.92**	0.46**	0.02**	5.31**	4.24	1.57	0.33	10.83**	1.49**
CCF	15.9	4.9	0.07	0.14	0.37	0.09	0.00	2.31	3.23	0.71	0.12	1.64	0.27
LGC	43.0**	4.9	0.21**	0.43**	1.12**	0.60**	0.01**	5.18**	4.69**	4.15**	0.13	2.54	2.47**
LGS	30.5**	4.5**	0.80**	0.47**	0.41	0.38**	0.01**	1.19**	3.65	0.82	0.11	1.24*	2.13**
LGU	35.3**	4.4**	0.94**	0.23**	0.44	0.30**	0.01**	1.92*	3.73*	0.96	0.21	1.85	2.43**
SGC	20.7*	5.1	0.06	0.23**	0.57	0.14	0.00	2.73	3.50	1.02	0.18	1.31*	1.11**
SGS	39.3**	4.2**	0.88**	0.56**	0.45	0.36**	0.02**	1.85	4.01**	0.34**	0.21	1.14*	3.30**
SGU	19.7	4.9	0.13	0.29**	0.42	0.17*	0.01**	2.31	3.34	0.76	0.12	2.13	0.75**

Table 4: Calculated amounts of elements (kg/ha/yr) leached to a depth greater than 120 cm. Quantities are calculated by multiplying the measured chemical composition of soil water at 120 cm depth with the percolated amount of water over the period in between two samplings as calculated with the SOAP water balance model. For the calculation of the 1994 leaching amounts (652-1030 days) percolation is calculated using 1993 rainfall data. Abbreviations: CCF = Closed Canopy Forest, L= Large, S = Small, G = Gap, C = Crown zone, S = Skidder zone, U = Undisturbed zone

zone	period	Al	Ca	Fe	K	Mg	Mn	Na	Si	Cl	NH ₄ -N	NO ₃ -N	N-total
		kg/ha	kg/ha	kg/ha									
CCF	0-652 days	1.8	5.1	0.7	8.5	2.2	0.1	50.5	62.2	54.2	1.7	7.2	8.8
	652-1030 days	0.9	1.2	0.2	4.5	1.2	0.0	17.3	31.0	17.1	0.4	2.2	2.6
	0-1030 days	2.7	6.3	0.9	13.0	3.4	0.1	67.8	93.1	71.3	2.1	9.3	11.4
LGS	0-652 days	49.6	34.9	0.9	60.1	40.3	1.3	167.9	109.0	144.3	3.2	232.9	236.1
	652-1030 days	8.5	5.4	0.5	5.5	4.9	0.1	15.9	45.7	14.9	0.3	21.2	21.6
	0-1030 days	58.2	40.4	1.4	65.6	45.1	1.4	183.8	154.8	159.2	3.5	254.2	257.7
LGC	0-652 days	15.3	24.6	1.3	50.7	27.8	0.9	248.8	118.4	248.3	4.3	154.8	159.1
	652-1030 days	2.4	4.4	0.3	8.5	6.9	0.1	52.5	54.4	32.2	0.5	13.3	13.8
	0-1030 days	17.7	29.0	1.6	59.2	34.8	1.0	301.3	172.7	280.5	4.8	168.1	172.9
LGU	0-652 days	28.6	18.2	0.8	23.3	18.8	0.6	114.4	97.0	134.7	5.2	118.6	123.8
	652-1030 days	8.5	2.2	0.3	4.1	2.3	0.0	13.8	41.3	20.3	0.4	14.0	14.4
	0-1030 days	37.2	20.4	1.0	27.4	21.1	0.6	128.2	138.3	155.0	5.6	132.6	138.2
SGS	0-652 days	29.8	37.7	0.8	31.6	29.5	1.3	101.5	104.5	112.0	4.4	152.9	157.3
	652-1030 days	2.3	3.6	0.4	2.7	1.9	0.1	31.4	53.2	15.0	0.1	17.0	17.1
	0-1030 days	32.2	41.3	1.2	34.3	31.4	1.4	132.9	157.6	127.0	4.6	169.9	174.5
SGC	0-652 days	2.1	13.5	0.8	16.0	5.9	0.3	138.8	89.4	169.0	2.7	47.4	50.1
	652-1030 days	0.4	2.6	0.4	7.1	1.6	0.0	21.2	40.2	11.7	0.4	5.1	5.4
	0-1030 days	2.6	16.1	1.1	23.1	7.4	0.4	160.0	129.6	180.7	3.1	52.5	55.6
SGU	0-652 days	3.0	17.9	0.5	16.8	8.3	0.4	117.3	90.4	165.8	4.6	29.0	33.6
	652-1030 days	0.8	3.0	0.5	4.4	1.7	0.0	22.9	38.2	20.7	0.3	4.0	4.3
	0-1030 days	3.8	20.9	1.0	21.1	10.0	0.4	140.2	128.6	186.5	4.9	32.9	37.8

Figure 1: Percentage of original dry mass, N, P, Ca, K, Mg and Na remaining with time for green and brown leaves of *Chlorocardium rodiei* leaves in Closed Canopy Forest, Large Gap Skidder zone and Large Gap Crown zone.

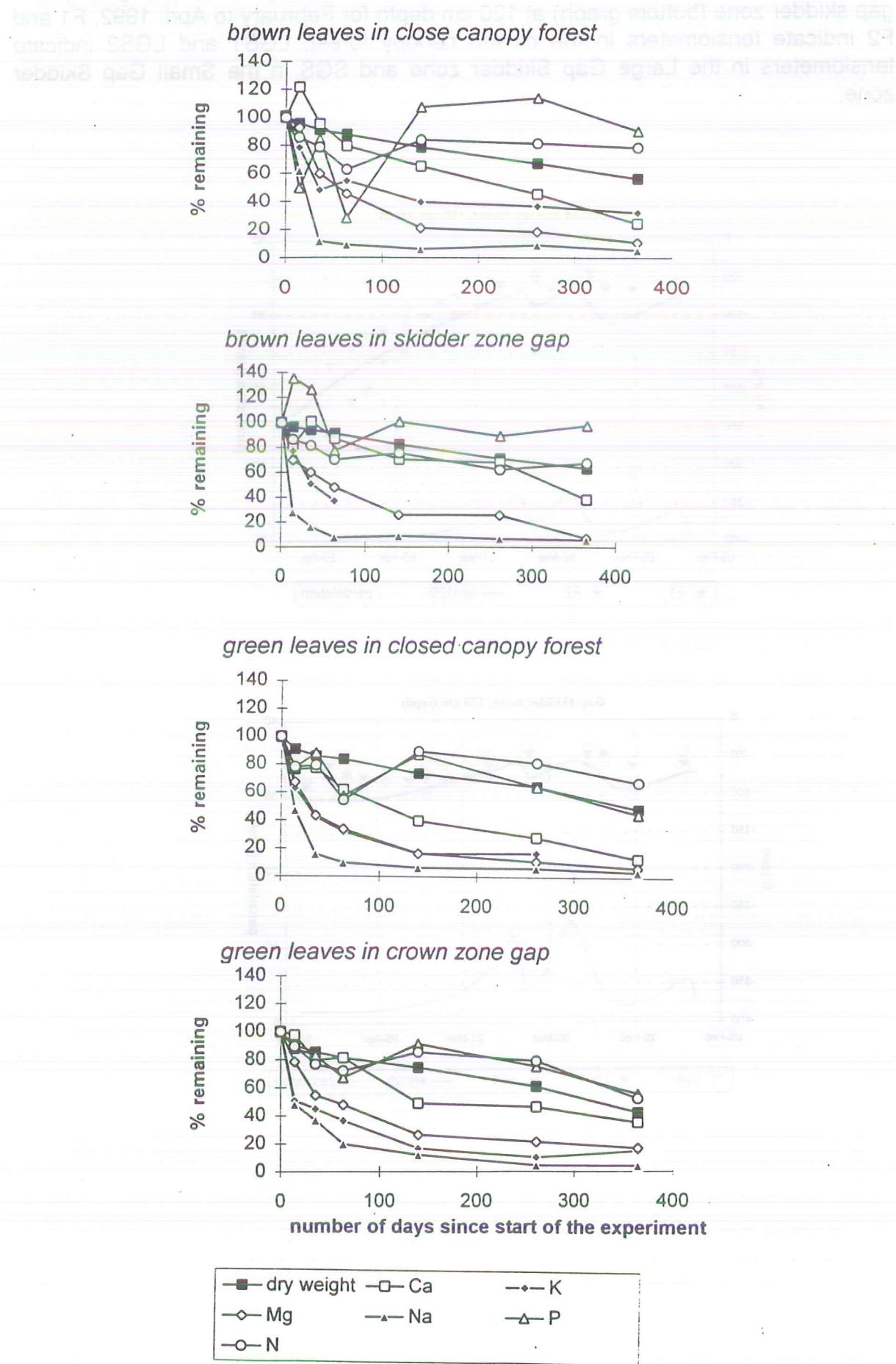


Figure 2: Measured soil water tension, soil water tension as simulated by SOAP and the corresponding calculated percolation in closed canopy forest (top graph) and gap skidder zone (bottom graph) at 120 cm depth for February to April 1992. F1 and F2 indicate tensiometers in the closed canopy forest, LGS1 and LGS2 indicate tensiometers in the Large Gap Skidder zone and SGS in the Small Gap Skidder zone.

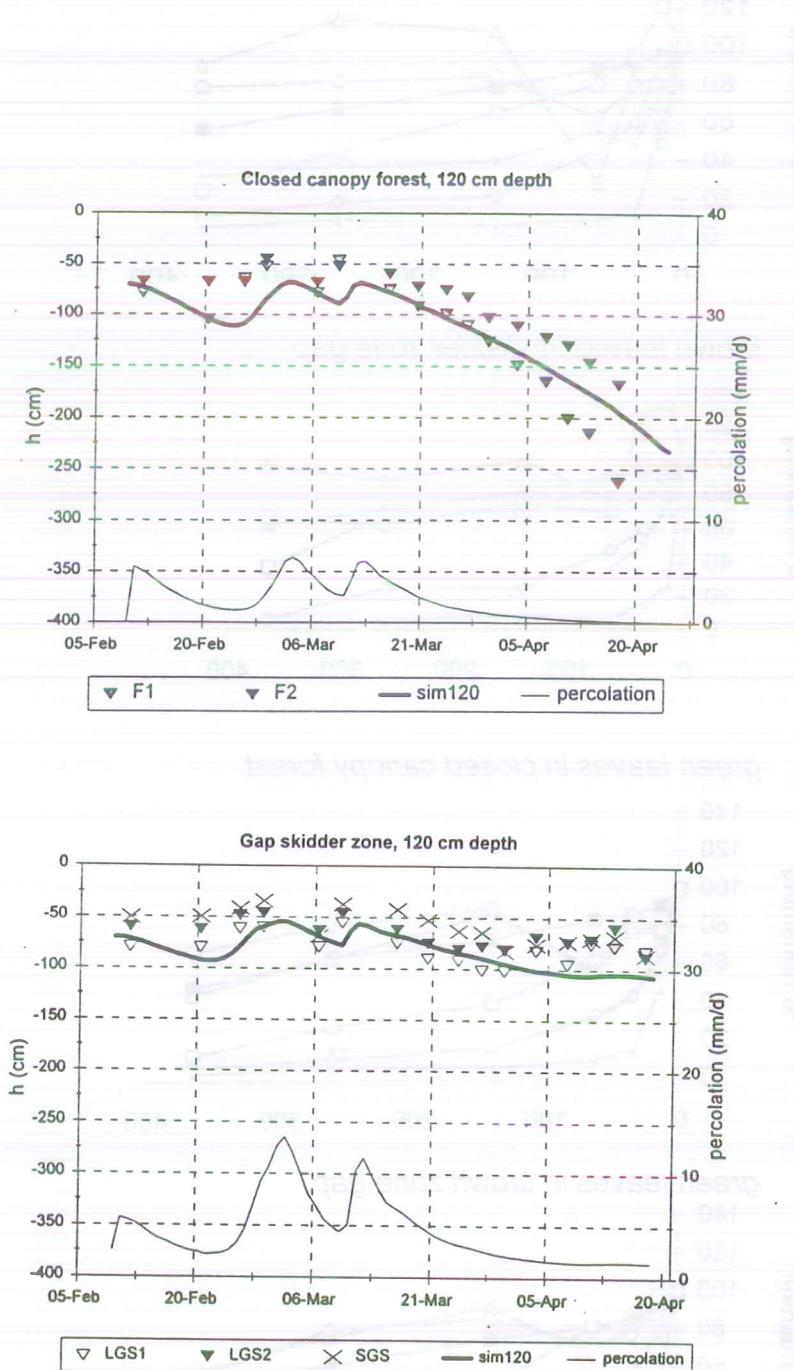
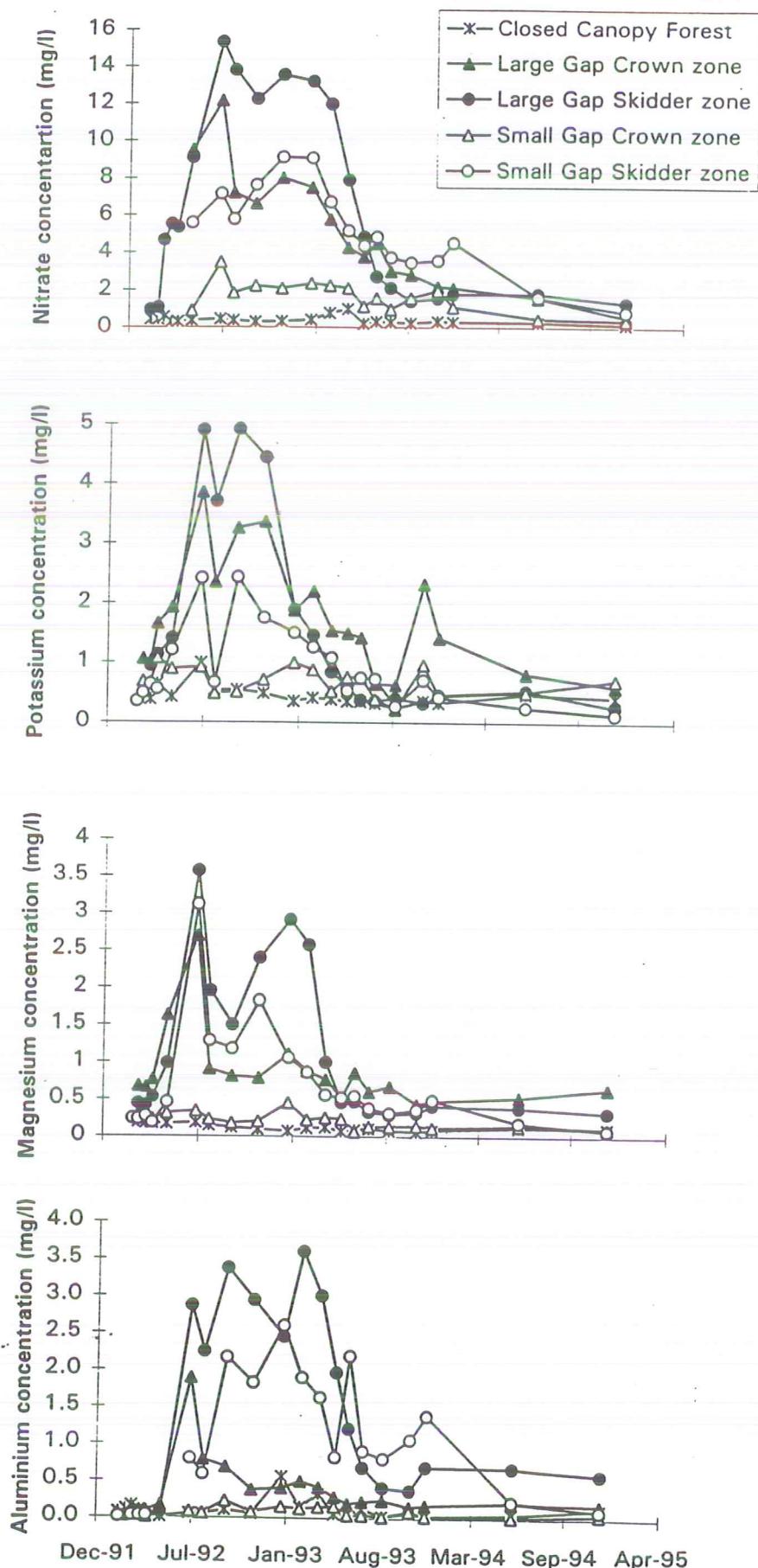


Figure 3: Concentration (mg/l) of $\text{NO}_3\text{-N}$, K, Mg and Al in soil water at 120 cm in closed canopy forest, the large gap skidder and crown zone and the small gap skidder and crown zone over a period of three years after selective logging.



SERIOUS LACK OF CALCIUM IN A TROPICAL RAINFOREST ECOSYSTEM IN SABAH, MALAYSIA

Nils Nykvist¹

ABSTRACT

Chemical analysis of total calcium in soil samples from Mendolong research area revealed that they had a very low calcium content. This finding was not expected based on earlier results of analyses of foliar contents and contents of exchangeable calcium in the soil. The content was so low that the harvesting of stemwood and stembark from all trees larger than 20 cm DBH should result in the loss of about 19 % of the calcium in the ecosystem down to 50 cm depth.

Almost half of the calcium in the ecosystem is stored in the above- and below-ground biomass. This result seems to support the common notion that in tropical rainforests most calcium tends to be tied up in the biomass, with very little left in the soil.

Comparable figures for total calcium contents in the soil are not available from other areas. They have therefore been calculated by multiplying literature values for concentrations of total calcium in tropical rainforest soils by soil weights from corresponding depths in Mendolong. The total calcium contents in the mineral soil to 50 cm depth varied from more than 20 000 kg ha⁻¹ in Chile to less than 200 kg ha⁻¹ in Brazil. This great variation indicates that not all tropical rainforests have low contents of calcium in their mineral soil. However, low contents can be found in certain areas which can be rather widespread in the humid tropics. In such areas, sustainable forestry is not possible without fertilization.

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1. INTRODUCTION

The most commonly determined plant-nutrient variables in soils are total nitrogen and plant-available phosphorus as well as exchangeable potassium, calcium and magnesium. Such analyses made on bare soil provide essential information when evaluating soil productivity or developing guidelines for fertilization before growing agricultural crops.

These analyses have also become the most common ones used in forest soils. Several soil scientists have stressed that such analyses underestimate the amounts of nutrients that are actually taken up by the plants, but few attempts to develop better methods have been made.

In this paper some methods of estimating the amounts of calcium in rainforest ecosystems are discussed, with examples taken from the Mendolong research area and from the literature.

2. STUDY AREA

The study area was situated at an altitude of 650-750 m about 35 km southeast of Sipitang at the Brunei Bay in Sabah, Malaysia. The bedrock consisted of interbedded sandstones, siltstones and shales on top of which Orthic Acrisols or Podzols were formed depending on the type of bedrock. The lowland hill dipterocarp forest growing in the area had been lightly selectively logged in 1981.

3. SAMPLING AND CHEMICAL ANALYSES

Twenty sample trees representing different diameter classes larger than 20 cm DBH were harvested. Ground vegetation and trees smaller than 20 cm DBH were harvested from ten 10x10 m sample plots. A more detailed description of the forest and biomass sampling procedures is given in Sim and Nykvist (1990).

The mineral soil used for analysis of exchangeable calcium was sampled with an auger (area 13.8 cm²) before clear-felling the forest. For the total analysis of calcium, the soil was sampled from ten plots four years after clear-felling in the *Acacia mangium* plantation. From each plot, two cylinder samples (height 5 cm, diameter 7.2 cm) were taken from each 5-cm layer of the mineral soil down to 50 cm.

Concentrations of exchangeable cations were determined by ICP-technique after extraction with 1N ammonium acetate at pH 7 and filtration of the solution. Total analysis of cations were determined with the same technique after digesting the

soil samples with perchloric and hydrofluoric acids. A more detailed description of the methods can be found in Emteryd (1989).

4. FOLIAR ANALYSIS

Foliar analysis is commonly used to determine whether any deficiency of plant nutrients exists in crops. Since the concentration of nutrients in the leaves varies with their age, the leaves must be sampled under pre-defined conditions to be comparable. The method is most commonly used in agriculture.

Concentrations of calcium in leaves from the rainforest in Mendolong before clear-felling and in the following plantation of *Acacia mangium* are given in Table 1.

(Table 1)

4.1 Foliar Calcium in Tropical Rainforests

Concentrations of calcium in trees from different rainforest areas are shown in Table 2. In 9 out of 15 investigations, the concentration of foliar calcium was lower than in Mendolong. Ovington and Olson (1970) reported a minimum value of 0.23 and a maximum of 2.92 % for foliar calcium among trees in a montane rainforest in Puerto Rico. The lowest figure obtained for the rainforest in Mendolong was 0.48 % which is not indicative of any serious lack of calcium in the ecosystem.

(Table 2)

4.2 Foliar Calcium in *Acacia mangium* Plantations

The concentration of calcium in the leaves of *Acacia mangium* was lower than that in the leaves of rainforest trees from the same site before clear-felling. However, calcium concentrations in *Acacia mangium* leaves did not reach the critical level of 0.2 %, below which growth is suppressed, according to Mead, who studied *Acacia mangium* plantations in Sabah (Unpublished. From Srivastava 1993). Using standard sampling procedures, Simpson (1992) studied the relationship between plant growth and concentrations of plant nutrients in leaves of *Acacia mangium* in Kalimantan (Fig. 1). No relationship between growth and the foliar concentration of calcium seemed to exist.

(Figure 1)

5. CONCENTRATION OF CALCIUM IN THE ABOVE-GROUND BIOMASS OF TROPICAL RAINFORESTS

A great amount of calcium is stored in the stems. Thus, the concentration of calcium in the total above-ground biomass provides a better indication of any lack of this element compared with values obtained in foliar analysis. The concentration of calcium in the above-ground biomass of the tropical rainforest in Mendolong was 0.25 %. In 21 other stands for which concentrations of calcium in the above-ground biomass of tropical rainforests could be calculated based on published data, the concentration was lower in eight, most of which were situated in Brazil and Venezuela (Tab. 1).

6. AMOUNTS OF EXCHANGEABLE CALCIUM IN THE SOIL

Amounts of exchangeable calcium in the Mendolong soil and amounts reported in 17 other investigations of tropical rainforest soils are given in Table 1. In five of the other investigations, the calcium amounts were found to be lower than those in the Mendolong soil. Before planting *Acacia mangium* in Mendolong, there was 21 kg ha⁻¹ exchangeable calcium in the uppermost 30-cm layer of mineral soil. Calcium amounts in the above-ground biomass of *Acacia mangium* after 18 and 45 months were 47 and 152 kg ha⁻¹, respectively. The amount of calcium utilized by the plants greatly exceeded the storage of exchangeable calcium (Nykvist and Wong, unpublished).

7. AMOUNTS OF TOTAL CALCIUM IN THE SOIL

Exchangeable calcium is only a minor part of the total storage of calcium in a soil. Most is bound in organic compounds, calcium-containing silicates (e.g. augite, hornblende and anorthite) and carbonates. Thus, to estimate the total content of calcium in a soil, one must do more than just oxidize the organic substances in the soil and extract the soil samples in acids. Such treatments will bring calcium in organic substances and carbonates into solution but not that in silicates. Unfortunately, reported contents of cations such as potassium, calcium and magnesium in the soil are misleading in some investigations in which the "total analysis" of mineral soils only includes extractions with acids. To determine the total contents of these cations, the silicates must be completely dissolved before the chemical analyses of the different elements are carried out. The most common method is digestion in perchloric and hydrofluoric acids in which volatile SiF₄ is formed and lost; thus bringing all cations in solution.

The amount of total calcium in the mineral soil to 50 cm depth in Mendolong research area was 730 ± 110 kg ha⁻¹ which is about 35 % of the total calcium in the ecosystem (Nykvist, unpublished). The loss of calcium when harvesting

stemwood from rainforest trees larger than 20 cm DBH was about 126 kg ha^{-1} . If stemwood and stembark from all trees larger than 20 cm DBH would have been harvested, the loss of calcium would have been almost 400 kg ha^{-1} which is about 19 % of the total calcium in the ecosystem and almost 55 % of the storage of total calcium in the soil.

Low contents of total calcium in the mineral soil were also found outside the research area in Mendolong. In a surrounding area covering about 46 000 hectares, the content of total calcium in the mineral soil to 100 cm depth was $790 \pm 440 \text{ kg ha}^{-1}$. The soil was sampled at random from 23 sampling plots.

Fertilization with wood ash or chemical fertilizers is obviously necessary to compensate for nutrient losses associated with any further utilization of the forest resources in the area. Fertilization experiments are now under way at Sabah Forest Industries.

The low amounts of exchangeable calcium in soils from other parts of the world (Tab. 1) indicate that the calcium content of the soil can be a critical factor influencing forest production in other rainforest areas as well.

To my knowledge, there are no other investigations of tropical rainforest ecosystems in which the amounts of total calcium, magnesium and potassium have been investigated in both soils and biomass. In the excellent book "The soils of Sabah", the concentrations of total nitrogen, phosphorus, potassium and magnesium are given for a great number of rainforest soils but, for some unknown reason, concentrations of calcium are not presented.

However, figures for concentrations of total calcium can be found in the "FAO-UNESCO. Soil Map of the World" and in papers by Stark (1970, 1971) and Waterloo (1994). Since the concentration figures are from different soil depths, they are not comparable. To get them comparable, the amounts have been calculated by multiplying the concentrations by soil weights from corresponding depths in the Mendolong research area and then summing them to a soil depth of 50 cm. Even though the bulk density varied among the different soils, the variation in mineral soils is very small compared with the great differences in amounts from different areas (Fig. 2). Amounts of calcium from Peru, Brazil and Suriname were calculated from mean figures of concentrations from only two or three soil depths multiplied by the total dry weight of the Mendolong soil to 50 cm depth. These figures are less accurate than the others; nevertheless, the very low amounts of calcium in the investigated soils from Brazil are alarming.

(Figure 2)

8. DISCUSSION

Analysis of total calcium has shown that the amounts of this element in the mineral soil at Mendolong are so low that any further removal of calcium from the ecosystem would probably result in reduced forest production. The seriousness of the situation was not appreciated earlier when analyses were limited to determining concentrations of calcium in leaves or above-ground biomass and amounts of exchangeable calcium in the soil.

Calcium is one of the most important plant nutrients. If the total calcium content in the soil is low, the amount supplied to plants through chemical weathering will also be low, which, in combination with low atmospheric input, will restrict the buildup of plant biomass in the ecosystem. However, as a result of the efficient nutrient-conserving mechanisms in nutrient-poor ecosystems, the biomass and its content of calcium in such ecosystems increases gradually when the only cause of calcium losses is leaching.

In the tropical rainforest ecosystem at Mendolong, calcium has accumulated to a level high enough to support comparatively good growth of the rainforest. Even in the *Acacia mangium* plantation, planted after the clear-felling and harvesting of stemwood containing a calcium amount of about 126 kg ha^{-1} , the foliar concentration was above the critical level for calcium in *Acacia mangium* plantations.

The mean annual volume increment for the 35-month-old *Acacia mangium* plantation for the tractor-harvested and burnt catchment on Orthic Acrisol and Podzol was 45 and $25 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$, respectively (Nykvist, Sim and Malmer, unpublished). However, such high growth figures will not be obtained in following generations as the storage of calcium gradually decreases with each harvest. A similar decline in forest production can also be expected in response to selective logging.

The main reason for the low content of total calcium in the Mendolong soil is that the bedrock consists of interbedded sandstones, siltstones and shales with low calcium contents. Concentrations of calcium in sandstone and shale were 0.007 and 0.022 % , respectively (Malmer, personal communication). The soil is formed from weathering *in situ*; thus bedrock composition is a much better indicator of soil fertility in such areas than in temperate areas where the soil contains minerals from different bedrock types mixed by the inland ice. A deficiency of any plant nutrient, except nitrogen, would therefore be more pronounced in tropical areas than in most temperate areas. However, the real fertility of the soil has long been concealed by an accumulation of plant nutrients in the biomass without any losses due to harvesting. In addition, the most productive soils have been utilized for growing cash crops.

The accumulation of plant nutrients, even on very poor soils, combined with *in situ* weathering in the tropics could explain why such calcium-poor soils have not been described from temperate forest soils.

Almost half of the total calcium in the ecosystem is stored in the above- and below-ground biomass (Nykvist, unpublished). This result seems to support the common notion that in tropical rainforests most plant nutrients tend to be tied up in the biomass, with very little left in the soil. Figure 2 shows that this is not a general characteristic for all tropical rainforests but specific for certain areas which, however, can be rather widespread in the humid tropics. In such areas sustainable forestry is not possible without fertilization.

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Table 1. Foliar calcium in catchments W4 and W5 in Mendolong research area for trees larger and smaller than 20 cm DBH and for *Acacia mangium*. Mean figures (in per cent) with 95 % confidence intervals. Sample size (n) varies from 3 to 10.

Rainforest				<i>Acacia mangium</i>			
Trees > 20 cm		Trees < 20 cm		Age 1 year		Age 3.7 years	
W4	W5	W4	W5	W4	W5	W4	W5
0.48 ±0.22	0.79 ±0.31	0.64 ±0.36	0.66 ±0.44	0.35 ±0.01	0.46 ±0.29	0.42 ±0.09	0.41 ±0.10
n=10	n=10	n=5	n=5	n=3	n=3	n=5	n=5

Table 2: Concentrations of calcium in leaves and above-ground biomass, and amounts of exchangeable calcium in soils from different tropical rainforest areas. Limestone areas are excluded.

Source	Concentration of calcium In leaves %	In above- ground biomass %	Amounts of exchange- able calcium Kgha ⁻¹
Malaysia, Mendelong Sam & Nykvist, 1990 Soil depth 0-50 cm	0.64	0.25	37
Indonesia, Kalimantan Ruhiyat, 1989 Soil depth 0-50 cm	0.79	0.30	60
Papua New Guinea Montane Edwards & Grubb, 1982 Grubb & Edwards, 1982 Soil depth 0-30 cm	1.50	0.41	3750
Ghana Greenland & Kowal, 1960 Soil depth 0-30 cm	1.54	0.75	2580
Ivory Coast, Banco Bernhard-Reversat et al., 1978 Soil depth 0-50 cm		0.27	150
Ivory Coast, Yapo Bernhard-Reversat et al., 1978 Soil depth 0-50 cm		0.51	170
Surinam Poels, 1987 Soil depth 0-60 cm	0.54	0.57	170
Brazil, Manaus Klinge, 1976 Soil depth 0-30 cm	0.21	0.10	0
Brazil, Jari Florestal Russell, 1983 Soil depth 0-50 cm ¹	0.23	0.23	40
Venezuela, San Carlos Oxisol Jordan, 1989 Soil depth 0-30 cm	0.13	0.08	7

Venezuela, San Carlos Tall caatinga forest Herrera 1979. From Medina & Cuevas, 1989 Soil depth 0-40 cm		0.13	130
Venezuela, San Carlos Guaco forest Buschbacher, 1984. From Medina & Cuevas, 1989 Soil depth 0-30 cm ¹	0.16	0.08	3
Venezuela, Western Llanos Hase & Fölster, 1982 Soil depth 0-50 cm	1.50	0.85	1680
Venezuela, San Eusebio Montane Grimm & Fassbender 1981 Soil depth 0-40 cm	0.46	0.21	200
Colombia, Terrace Fölster et al., 1976 Soil depth 0-50 cm	0.50	0.23	30
Colombia, Slope Fölster et al., 1976 Soil depth 0-50 cm	0.50	0.25	1780
Jamaica, Mull ridge Montane Tanner, 1985 Soil depth 0-40 cm	0.93	0.28	240
Jamaica, Mor ridge Montane Tanner, 1985 Soil depth 0-45 cm	0.59	0.17	30

1. Cations extracted with double acid solution.

Figure 1: Calcium levels in foliar samples of *Acacia mangium* in relation to stand health.

Source: Simpson (1992). From Srivastava (1993).

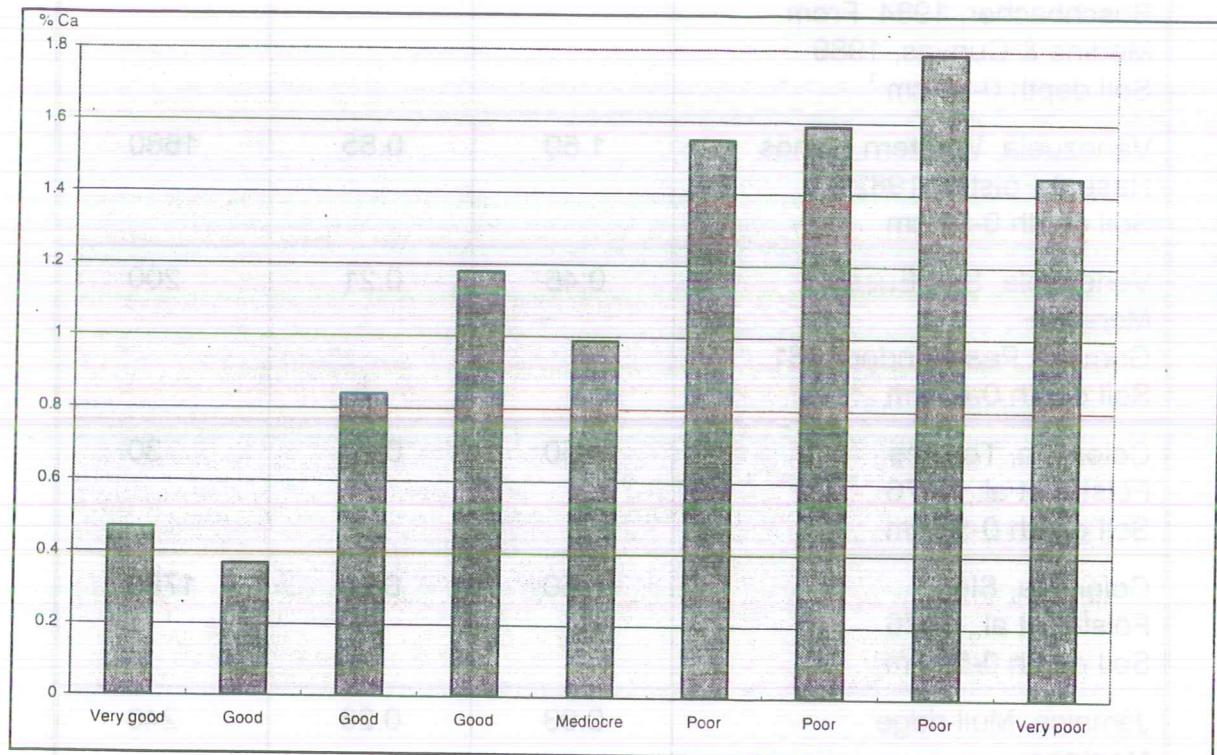
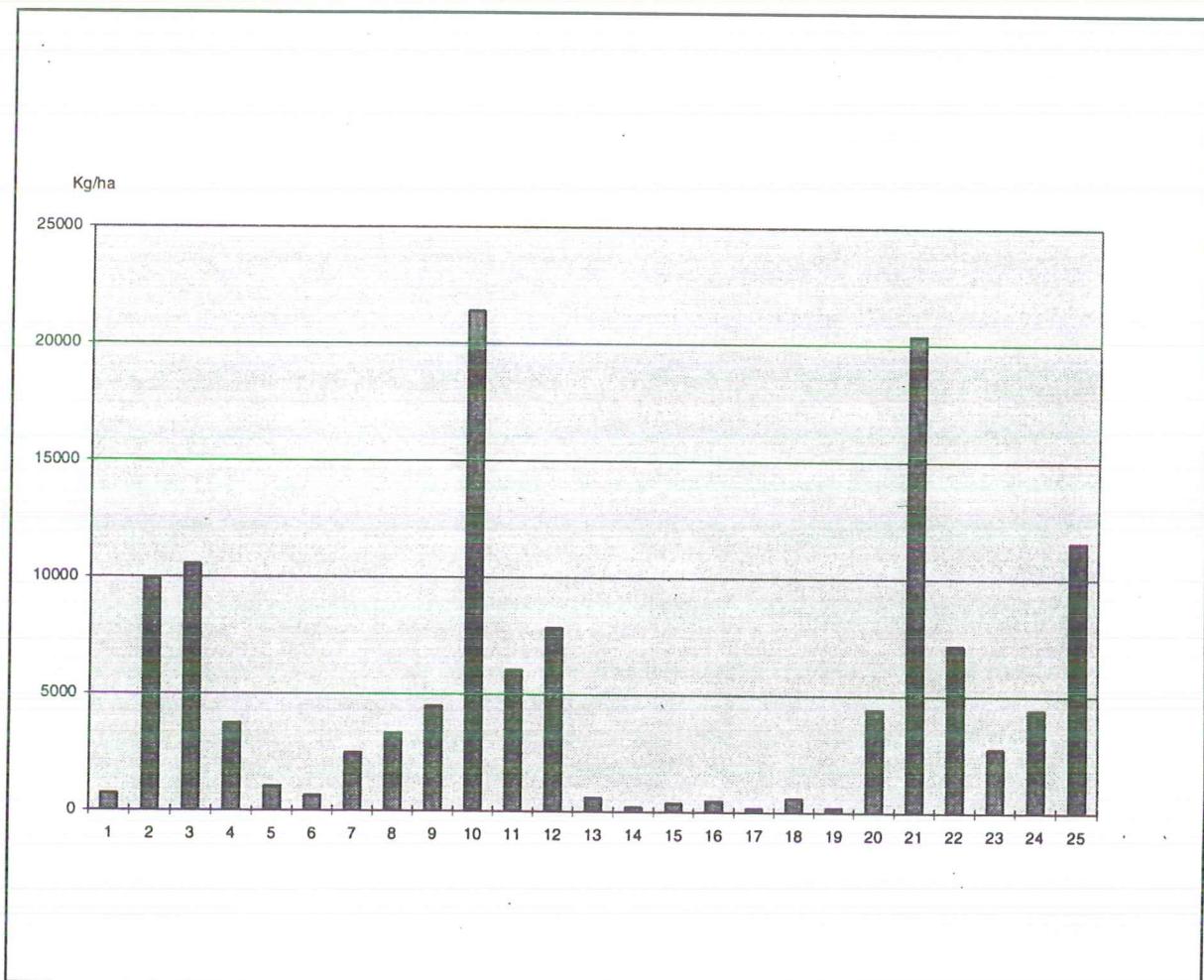


Figure 2. Amounts of total calcium in mineral soil to 50 cm depth. Amounts were calculated taking concentrations found in the FAO-UNESCO Soil map of the world, Stark (1970, 1971) and Waterloo (1994) and multiplying them by soil weights from corresponding depths at the Mendolong research area. Limestone areas are excluded.

- 1: This study.
- 2-4: Fiji. From Waterloo, M.J. (1994).
- 5: Hawai. From FAO-UNESCO. Soil map of the world. Volume X. Australasia.
- 6-8: Madagaskar. From FAO-UNESCO. Soil map of the world. Volume VI. Africa.
- 9: Sierra Leone. From FAO-UNESCO. Soil map of the world. Volume VI. Africa.
- 10: Chile. From FAO-UNESCO. Soil map of the world. Volume IV. South America.
- 11: India. From FAO-UNESCO. Soil map of the world. Volume VII. South Asia.
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- 13-15: Brazil. From Stark, N. (1971). Amounts calculated from mean figures for soil depths 0-4, 20-22 and 60-62 cm.
- 16-18: Brazil. From Stark, N. (1971). Amounts calculated from mean figures for soil depths 0-4 and 20-22 cm.
- 19-25: Surinam. From Stark, N. (1970). Amounts calculated from mean figures for soil depths 0-3 and 60-62 cm.



SAMPLING STRATEGIES FOR TROPICAL FOREST NUTRIENT CYCLING STUDIES: A BRAZILIAN CASE STUDY

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1. ABSTRACT

Sampling of soil, biological or micro climatic attributes in tropical forests, which are characterized by a high diversity of species and large spatial variability is a difficult task. In spite of this fact, there are few basic studies to guide sampling procedures. The objective of this study was to define the best sampling strategy and data analysis for some parameters frequently used in nutrient cycling studies, i. e., litter composition (Ca, Mg, K, N and P) and its quantity of nutrients and soil attributes at three depths (organic matter, phosphorous content, cation exchange capacity and base saturation). A natural forest remnant in the West of São Paulo State (Brazil) was selected as study area. The total quantity of litter and its nutrient quantities had a very high spatially independent variance. Conversely, litter nutrient contents had a lower and peculiar to each nutrient spatially dependent variance. Therefore the sampling strategies for the estimation of litter quantity and its nutrient content should be different, i.e., quantity estimations do not need to be spatially referenced and a large number of determinations are needed otherwise, nutrient content estimation should consider a smaller quantity of spatially referenced samples. Sampling for soil attributes determination has to be different according to its depths. Overall, surface samples (0-50 mm) showed a very high short distances spatially dependent variance, whereas, subsurface samples exhibited spatial dependency in longer distances. Short transects with sampling interval of 5-10 m can be recommended for surface sampling. Subsurface samples must also be spatially referenced, but with transects or grids with longer distance between sampling points covering the whole area. Composed soil samples would not allow the complete understanding of the relation between soil properties and surface dynamic processes or landscape aspects. Phosphorous was the attribute showing more difficulties for its precise distribution estimation in the area.

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2. INTRODUCTION

Tropical forests are known to have a high number of species organized in a very heterogeneous and complex ecosystem. Due to the interaction between the aboveground biota and the soil via nutrient cycling processes and a very intense pedogenesis some of this heterogeneity may be transferred to the soil. As the nutrients behave differently in pedogenesis and cycling processes, differences in variability for distinct nutrients and for other associated soil properties may be awaited. Therefore, if the same sampling and data analysis procedure is used for all parameters, some of them may be well estimated while others may be incorrectly evaluated. The unworthy is when parameters determined with extremely different accuracy or detail are compared in nutrient cycling calculations or other modeling procedures as if they were similar. Therefore it is necessary to develop guidelines for sampling and data analysis for this kind of situation. The objective of this study was to develop such guidelines for commonly analyzed parameters in nutrient cycling studies, in order to help a gathering of a reliable data set with similar degree of precision. A more detailed report of this study can be found in SPAROVEK (1993).

3. MATERIAL AND METHODS

The study was carried out at the Agronomic Institute Research Station located in Pindorama, São Paulo, Brazil ($48^{\circ}55'W$ e $21^{\circ}13'S$). The climate, according to Köppen's classification, is Aw, with mean annual precipitation of 1,259 mm. The soils within the 5.0 ha research plot are Typic Kandiudalf at the midslope and Plinthic Paleudult at the footslope near the drainage lines (LEPSCH and VALADARES, 1976). The tropical semideciduous forest has an irregular 15-20 m high canopy with emergent trees of 25-30 m. Approximately 20% of the species are deciduous in the dry winter season. The area has not been disturbed for at least 50 years.

Sixty four sampling points were chosen randomly in the core area of the forest remnant to provide levels organized by a distance hierarchy (7, 25 and 80 m) covering 16 parcels of 62.5 to 100 m (Figure 1).

(Figure 1)

The coordinates of these points were previously selected to avoid any sampling bias during field work. In each point litter was collected using a squared frame of 0.25 m^2 . The material was then oven dried (60°C), separated in coarse ($> 2.0\text{ mm}$) and fine ($< 2.0\text{ mm}$) fractions, weighed and analyzed for total N, P and K contents. By multiplying litter quantity of each point by its nutrient content, nutrient quantities were calculated. At the same points soil samples were

collected at 0-50, 50-250 and 600-800 mm depth. The air dried soil samples were sieved and analyzed for organic matter and resin extractable phosphorous (P). Cation exchange capacity (CEC) based on the sum of exchangeable cations and pH 7.0 extractable hydrogen and base saturation (BS) were calculated.

The statistical analysis included measurements of the mean, coefficient of variation, and the number of samples needed to estimate the mean value for a given percentage of error. In addition hierarchical analysis of variance and the semivariograms were also computed. The statistical parameters were computed following the procedures described by VIEIRA et al. (1983) and WEBSTER and OLIVER (1991).

4. RESULTS AND DISCUSSION

4.1 Litter

The average values of nutrient contents in the litter fractions, the coefficient of variation and the number of samples necessary to estimate average values within 5 and 10% of error are given in Table 1. In Table 2 are presented the same parameters for litter quantity and its nutrient quantities.

(Table 1)

(Table 2)

Nutrient contents and the coefficients of variation were higher in the litter's coarse fraction than in the fine one. Litter quantities and nutrient quantities in litter coefficients of variation were very high varying from 67% for total litter to 142% for K quantity. The number of samples to estimate the average with 10% of error was much higher for nutrient quantities (average of 209 samples) than for nutrient contents (average of 34 samples). The spatial dependency of the variance and the accumulated variance according to the distance levels are presented in Figure 2 for P and in Figure 3 for Ca.

(Figure 2)

(Figure 3)

Total quantities of litter as well as N and K quantities and contents did not show spatially dependent variance. Conversely, the P contents resulted in linear semivariograms with very low variance at small distances. Differently the Ca

contents presented exponential semivariograms with a smaller distance of spatial dependency. The same trend was observed in relation to Mg contents. Total nutrient quantities did not reveal spatial dependency. Therefore, sampling aiming nutrient content estimation in litter should not be done in the same way as for quantities estimation.

As a result of the very high variance and lack of spatial dependency, quantity estimations do not need to be spatially referenced and a larger number of determinations are needed. In this study, more than 200 samples would be needed to estimate the average within 10% of error. Conversely, estimation of nutrient contents could be done with a smaller quantity of spatially referenced samples. However, the variance spatial dependency is different for each nutrient. In order to combine the difference in litter's nutrient contents and quantities variability in a unique sampling approach the following strategy can be recommended: a) previous definition of a grid or transect with small sampling intervals covering the whole study area; b) collection of samples for litter quantity estimation in all positions and examination of some of them for nutrient content estimation; c) nutrient contents extrapolations should consider the calculated semivariogram. The number of samples needed to obtain reliable semivariograms may be different for each nutrient. A matching procedure analyzing some sampling positions followed by the evaluation of the results in order to define more specific sampling points for analysis until obtaining desired results certainly is a very time and cost saving procedure. This can also avoid oversampling and misevaluation easily occurring if all parameters are sampled in the same way.

4.2. Soil

The average values of soil organic matter content, resin extractable P content, soil cation exchange capacity and base saturation for three depths are shown on Table 3. Coefficients of variation and the number of samples necessary to estimate average values within error limits are also provided. Base saturation was used instead of the single exchangeable cations (Ca, Mg and K) because in this experiment the base saturation illustrates the overall trend of the individual cations.

(Table 3)

The absolute values of the organic matter contents, extractable phosphorous and CEC were much higher for the surface layer of 0-50 mm than in the deeper ones. Base saturation were more homogenous in the deeper layers. This may indicate the necessity to consider a thin layer in soil sampling for nutrient cycling studies, thinner than the 0-200 mm layer usually sampled for soil fertility studies or the first pedological A horizon that can be down to 1,000 mm. This phenomenon is caused by the interaction between the litter and the surface mineral soil layer, not allowing most of the nutrients to leach deeply into the profile. The non

consideration of this thin surface layer apart from the remaining mineral soil may induce in misunderstanding of this relationship. Overall, the coefficients of variation were higher in the 0-50 mm layer than in the deeper ones. The trend is reversed for base saturation what may be due to nutrient cycling, considering that the parent material of the soils is rich in Ca and Mg which are the main base saturation components. The high variability in the subsoil for this attribute may be related to pedogenic factors, since different soil classes occur in the area (Typic Kandiudalf at the midslope and Plinthic Paleudult at the footslope). The number of samples necessary to estimate the average of soil nutrient parameters within 10% error was highly variable. Base saturation at the 0-50 mm layer may be estimated with 2 samples whereas 812 samples would be necessary for P. The spatial dependency of the variance and the accumulated variance according to the distance levels for the three sampling depths are illustrated for soil organic matter in Figure 4, cation exchange capacity in Figure 5 and base saturation in Figure 6.

(Figure 4)

(Figure 5)

(Figure 6)

The variance of P content did not vary with distance. The organic matter variance was different with depth. Surface samples had a very low variance at short sampling intervals. However increased sharply with distance, achieving total variance at 25 m. For the 600-800 mm depth, the variance increased slowly with distance and the semivariogram is almost linear. Similar trend was observed for CEC, probably due to the sharp relation between CEC and organic matter in these tropical soils.

Thus, it is not recommended to sample for determination of all soil attributes in the same way at all depths. Usually the variance and consequently the number of samples needed to estimate the average, is higher at the surface than at the subsurface. Similarly the variance relation with distance is short (< 25 m). Therefore for soil surface, the position of sampling points should be related with trees or groups of trees rather than soil morphology, taxonomic class or landscape positions. Conversely, the subsurface samples showed a lower variance with a long distance dependent variance. Here the relation to pedological attributes should be strong. Nevertheless some parameters may have a distinct behavior, such as base saturation or the P content which showed an extremely high variance.

5. CONCLUSIONS

The variability of the litter and the measured soil attributes were different, justifying a distinct sampling and data analysis procedures for each case. The lack of consideration of the systematic spatial variability and the underestimation of the casual variability may compromise the accuracy of cycling studies in tropical forests.

6. ACKNOWLEDGMENTS

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Table 1: Nutrient contents from litter fractions average values, coefficients of variation and number of samples necessary to estimate the average (NS) with 10 and 5% of error

Nutrient	Litter Fract.	Average	Coeff. Var.	NS	
				10% of error	5% of error
Ca	> 2.0 mm	24.8	21	12	18
Ca	< 2.0 mm	12.5	49	67	95
Mg	> 2.0 mm	2.5	21	12	17
Mg	< 2.0 mm	1.6	35	34	49
K	> 2.0 mm	2.1	40	45	65
K	< 2.0 mm	1.2	34	33	47
N	> 2.0 mm	18.2	14	6	8
N	< 2.0 mm	12.4	36	35	51
P	> 2.0 mm	0.7	26	19	27
P	< 2.0 mm	0.6	47	62	89

Table 2: Litter quantity and its nutrient quantities average values, coefficients of variation and number of samples necessary to estimate the average (NS) with 10 and 5% of error

Parameter	Average	Coeff. Var.	NS	
			10% of error	5% of error
Coarse Litter (> 2.0 mm)	5,900	81	184	264
Fine Litter (< 2.0 mm)	9,000	69	131	188
Total Litter	15,000	67	127	182
Total Ca quantity	309	79	173	249
Total Mg quantity	32	78	170	244
Total K quantity	27	142	560	803
Total N quantity	241	71	142	204
Total P quantity	10	82	186	267

Table 3: Soil attributes in three depths average values, coefficient of variation and number of samples to estimate the average (NS) with 10 and 5% of error

Parameter	Depth	Average see unit below	Coeff. Var. %	NS	
				10% of error	5% of error
OM ⁽¹⁾	0-50	58	45	57	81
OM	50-250	22	23	15	22
OM	600-800	12	22	14	20
P ⁽²⁾	0-50	11	171	812	1164
P	50-250	3	75	157	226
P	600-800	1	126	444	636
CEC ⁽³⁾	0-50	170	58	93	133
CEC	50-250	70	34	32	46
CEC	600-800	50	32	28	40
BS ⁽⁴⁾	0-50	89	9	2	3
BS	50-250	75	19	10	14
BS	600-800	60	28	22	31

⁽¹⁾ OM = Total soil organic mater (g/kg) oxidized by H_2SO_4 and quantified by colorimetry. ⁽²⁾ P = Phosphorus (mg/dm³) extracted by an exchange resin and quantified by colorimetry. ⁽³⁾ CEC = cation exchange capacity (mmol_ckg⁻¹), based on the sum of exchangeable cations and pH 7.0 extractable hydrogen. ⁽⁴⁾ BS = base saturation (%), CEC occupied with Ca^{+2} , Mg^{+2} and K^+ .

Figure 1. Sample collecting procedure in the study area and topographic profile. Dots are sampling points.

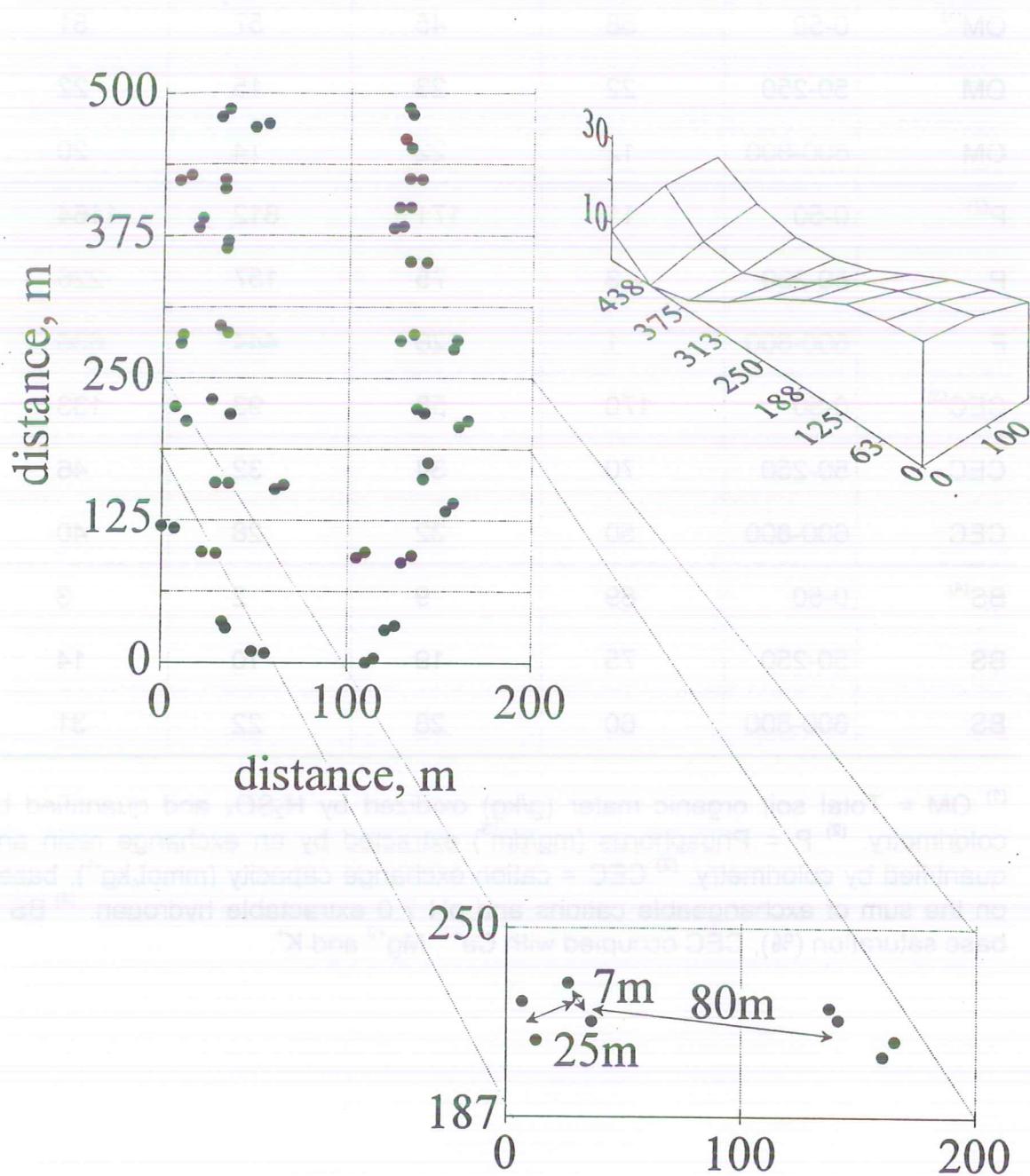


Figure 2. Normalized semivariance (dots) and accumulated variance (vertical lines) as related to distance for P content in the fine and coarse litter and its total quantity

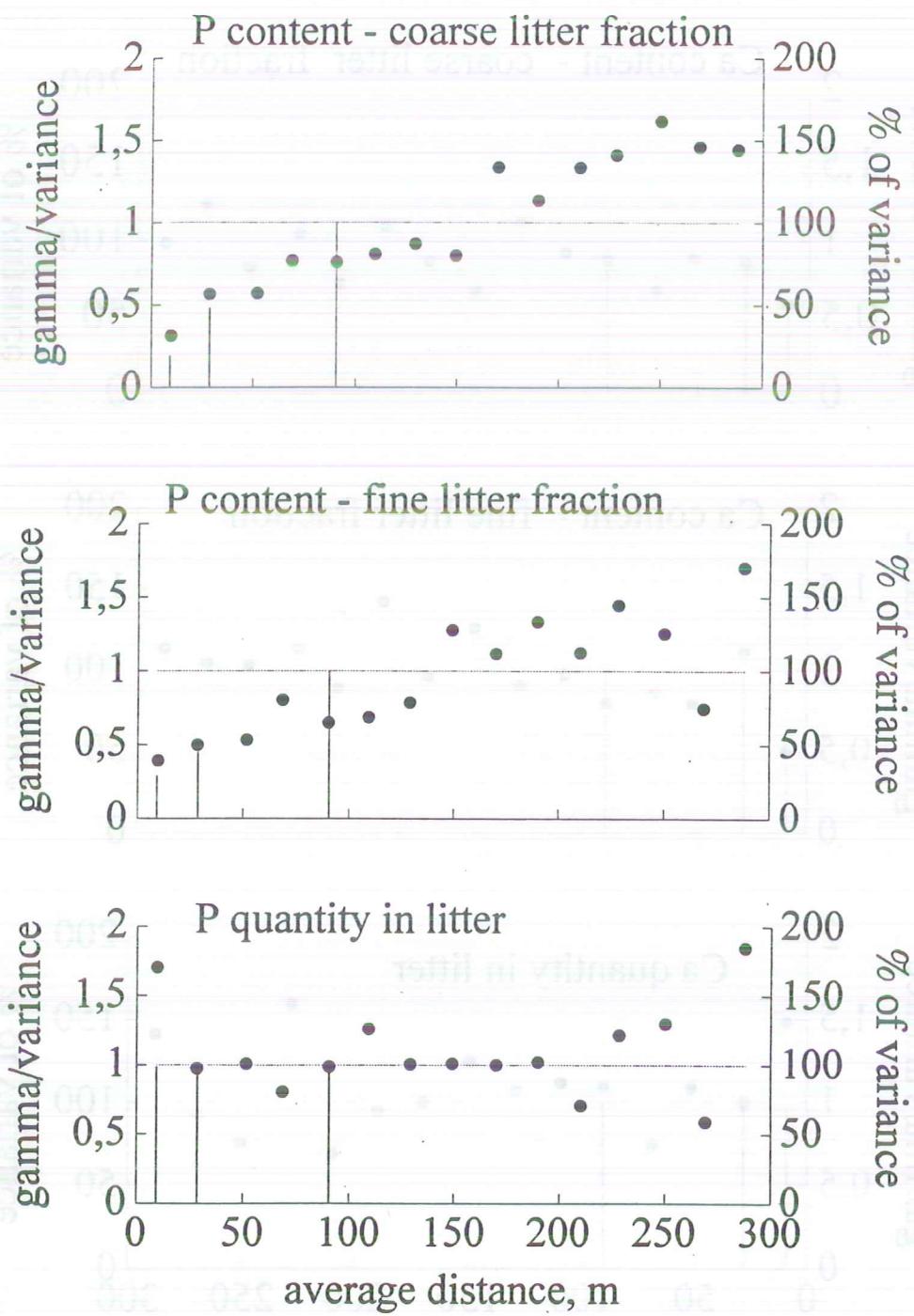


Figure 3. Normalized semivariance (dots) and accumulated variance (vertical lines) as related to distance for Ca content in fine and coarse litter and its total quantity

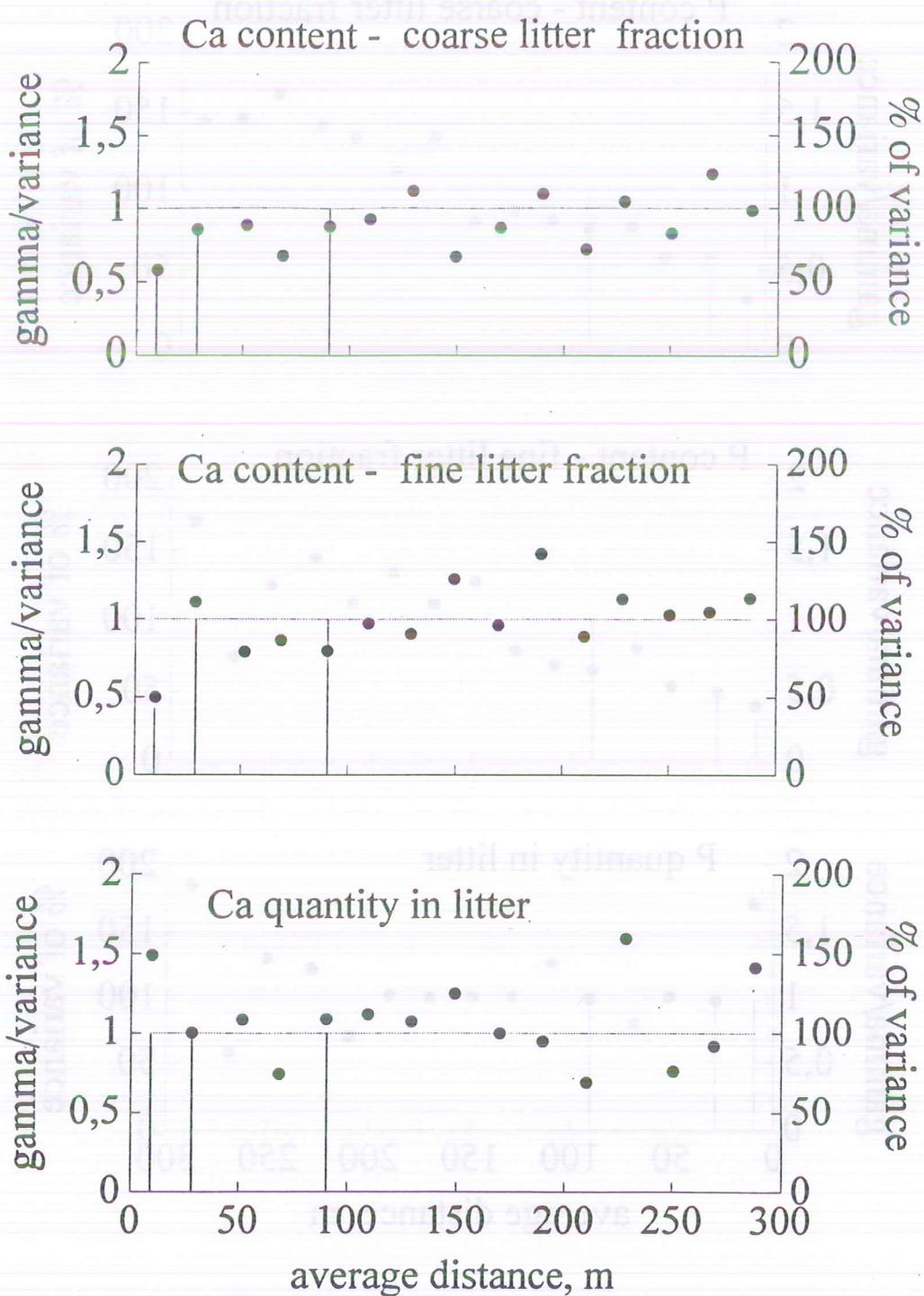


Figure 4. Normalized semivariance (dots) and accumulated variance (vertical lines) as related to distance for organic matter (OM) content according to three soil depths

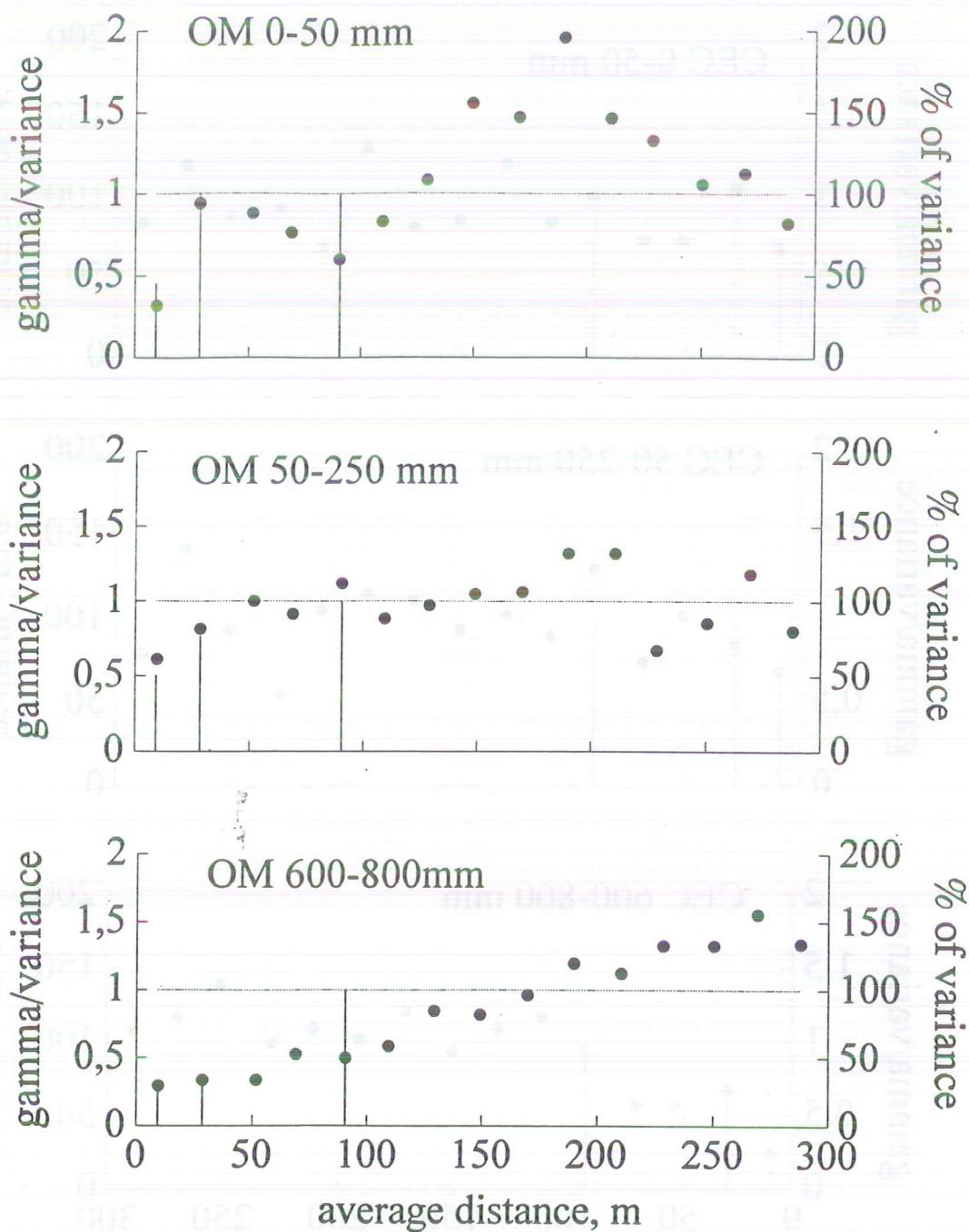


Figure 5. Normalized semivariance (dots) and accumulated variance (vertical lines) as related to distance for soil cation exchange capacity (CEC) according to three soil depths

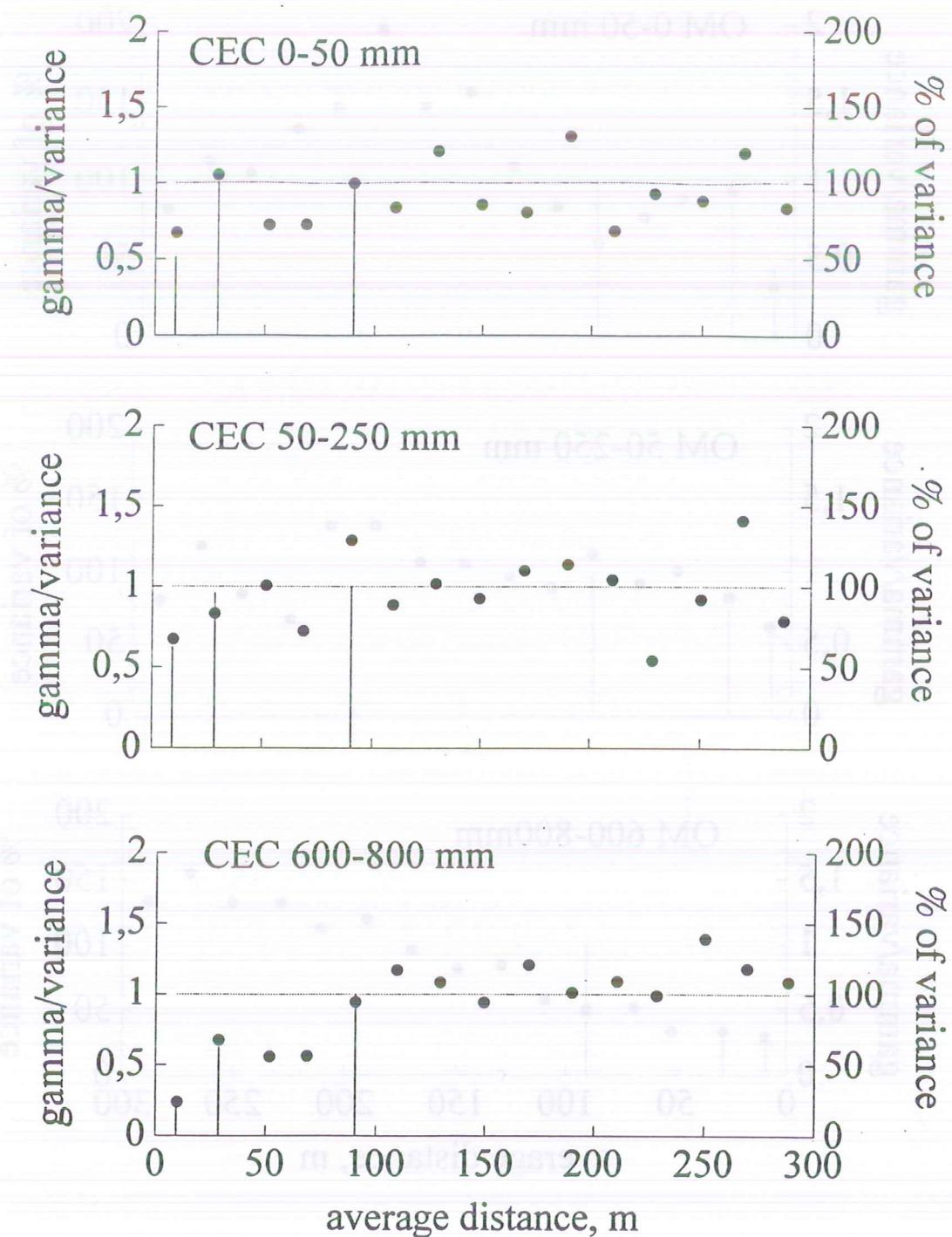
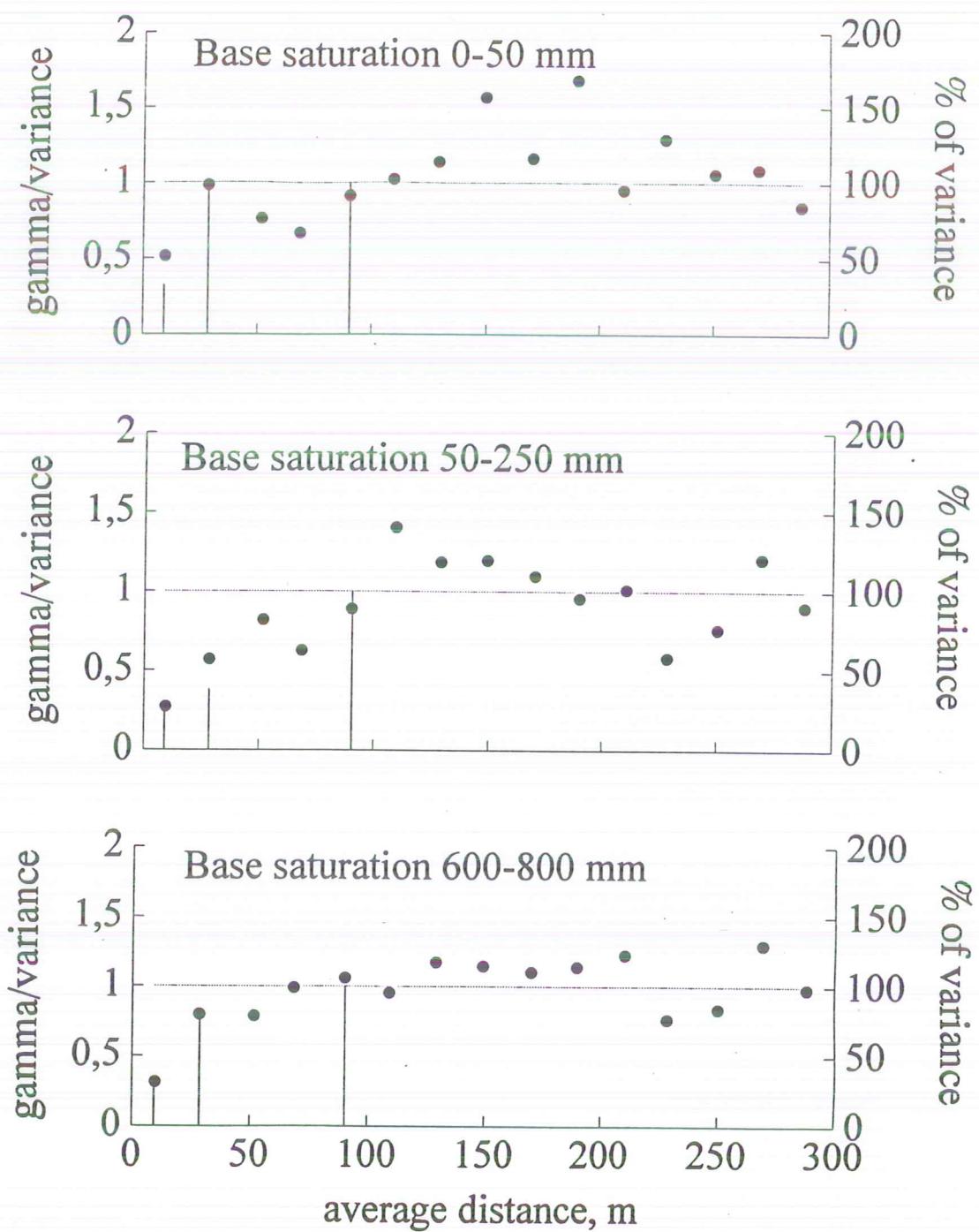


Figure 6. Normalized semivariance (dots) and accumulated variance (vertical lines) as related to distance for soil base saturation according to three soil depths



THE FLOW OF NUTRIENTS IN A PINE FOREST PLANTATION IN CENTRAL JAVA AFFECTED BY VOLCANIC EMISSIONS

B. Gunadi¹

ABSTRACT

The volume, pH and nutrient concentrations (SO_4^{2-} , NH_4^+ , NO_3^- , Cl^- , K^+ , Ca^{2+} , Mg^{2+} , and Al^{3+}) in rainfall and throughfall (as collected by funnels), and litter percolate (as collected by vacuum tube lysimeters) were studied during the wet season between October 1990 and April 1991 in two plots of a pine forest plantation (800 and 600 m a.s.l.) along the slope of an active stratovolcano, Mount Merapi (2911 m a.s.l.) in Central Java, Indonesia. After an eruption in February 1992, water collections were repeated in March 1992. The high concentration of SO_4^{2-} and Cl^- in rainfall differed distinctly from anthropogenically influenced acid rain which usually contains NO_3^- , NH_4^+ in addition to SO_4^{2-} . For most of the elements the mean concentrations tended to increase from rainfall to litter percolate.

There was no negative correlation between SO_4^{2-} -pH or Cl^- - pH. Before the eruption, input of elements tended to be similar for the high and the low plot. After the eruption, the concentration of SO_4^{2-} -S and Cl^- was higher in the low plot than in the high plot. Unexpectedly, the pH of rainfall in the low plot was higher than in the high plot. NH_4^+ -N and Cl^- input in rainfall in both plots tended to be higher than before eruption. Annual input of SO_4^{2-} -S, Cl^- , K^+ , Ca^{2+} , Mg^{2+} in rainfall (i.e. 122.1, 355.4, 164.2, 58.6, 16.6 kg ha^{-1} , respectively) is much higher than input data for other tropical forest plantations. NH_4^+ -N input of 19.1 kg ha^{-1} , year $^{-1}$ in rainfall is comparable with anthropogenic pollution in western European countries. There is no indication that high elemental input decrease the vitality of the vegetation.

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INTRODUCTION

There are different ways to study nutrient flow in terrestrial ecosystems e.g. by quantifying input of nutrients into ecosystems, loss of nutrients from ecosystems, turnover of nutrients in ecosystems, and uptake of nutrients from soils by plants (HARRISON et al., 1990). Recently, input of nutrients via rain water into forests has been studied intensively both as a result of anthropogenic influences (BRASELL and SINCLAIR, 1983, CORE et al., 1992, WRIGHT et al., 1992), and due to natural pollution from volcanoes in natural tropical rain forests (JOHNSON and PARNELL, 1986, VENEKLAAS, 1990) and in forest plantations (BRUIJNZEEL, 1989, RIEKERK and KORHNAK, 1992).

Like other pine forest plantations, those in Central Java grow without artificial fertilizer. Decomposition of pine needles in Central Java has been studied by GUNADI and VERHOEF (1993) and it was found that seasonal effects (e.g. rainfall) had more impact on decomposition than litter quality. High precipitation retarded decomposition. Furthermore, it is well known that rain water also has an important role in transferring water, nutrients and pollutants from tree canopies (McCUNE and BOYCE, 1992). Although pine forest plantations in Java usually grow along the slope of volcanoes on supposedly relatively fertile soils, nutrient losses from the forest plantations via leaching are relatively high. This makes these soils relatively poor in nutrients (BRUIJNZEEL, 1984). Input of nutrients via rain water becomes then important, especially in the event of an active volcano.

In the present paper the nutrient fluxes are studied in two plots along the slope of the active stratovolcano Mount Merapi at different distances from the crater. Over a period of 7 months (wet season) volume, pH, and nutrient concentrations (SO_4^{2-} , NH_4^+ , NO_3^- , Cl^- , K^+ , Ca^{2+} , Mg^{2+} , and Al^{3+}) of rain water and throughfall have been determined, in addition to percolate extracted from mesocosms by vacuum lysimetry.

FIELD SITES

Two 2,000 m² plots referred to as "high plot" (800 m a.s.l.) and "low plot" (600 m a.s.l.) within a 32-year-old pine forest plantation (*Pinus merkusii* Jungh. & De Vries) on the south-western slope of Mount Merapi, Central Java, Indonesia were selected. The distance between the two plots is about 1.5 km. Some site characteristics were described by GUNADI (1993). The

trees in the high plot are less dense (200 trees ha^{-1}) than those in the low plot (395 trees ha^{-1})

Annual rainfall was measured using Telemetri systems at a nearby meteorological station situated at about 825 m a.s.l. along the same slope. Annual rainfall between 1987 and 1991 were 3135, 3992, 3901, 3400, 3474 mm, respectively. Rainfall in the area is rather seasonal with the study plots belonging to rainfall climate type B of SCHMIDT and FERGUSON (1951), which means less than 3 dry months (monthly rainfall < 60 mm) per year. The temperature of the organic layers were measured using Data Logger systems at 1.5 hours intervals. The mean temperature within the L and F layers inside and out side the mesocosms were similar between both plots i.e. about 23 °C.

The two study plots had a similar undergrowth vegetation, dominated by grasses (*Centotheca lappacea* (L.) Desv. and *Paspalum conjugatum* Berg.), herbs (*Eupatorium riparium* Reg.), and shrubs (*Lantana camara* L.).

METHODS

The study was conducted during the wet season between October 1990 and April 1991, during which period 15 series of water samples were collected. After an eruption of Mount Merapi in February 1992, the water collection was done once more in March 1992. Collections were made every 1 to 2 weeks depending on the intensity of the rainfall.

Within each plot twelve rain collectors of 13 cm diameter and 225 mm capacity were used. Two collectors were located outside the plot in an open area to collect rainfall and ten were located randomly inside the plot to collect throughfall. Throughfall was collected 1 m above ground level, below the undergrowth. Filters of fine-mesh (200 μm) made from nylon gauze were placed in the plastic funnels of the collectors in order to prevent contamination by debris. The accumulated litter was removed and the filters were cleaned weekly. The water containers were covered by black plastic bags to minimize algal growth. Every week the volume of throughfall was determined using a measuring cylinder and samples were taken for chemical analysis.

Soil water percolate was collected from mesocosms by vacuum tube lysimeter. The cup is porous all over with pore size 1 - 2 μm , 2 cm in outer diameter, and 5 cm in length (P80, Staathliche Porcelän Manufaktur, Berlin, Germany). Before installation in the field, each ceramic cup was

washed with 0.1 M HCl and subsequently 3 times with distilled water. The mesocosm is constructed of dark grey PVC the same diameter as the rain collectors (: 13 cm diameter), 30 cm height, 0.5 cm thick, open at the top and covered by 200 μm nylon gauze, with a closed bottom, and connected with well closed dark glass bottle with a capacity of 225 mm. Mesocosms were filled with an undisturbed soil column, including the litter and fragmented layers, using a soil core and were put randomly in the soil in such a way that the soil surface of the column was on a level with the surrounding soil surface. Soil animals could enter and leave the mesocosms via 6 holes in the upper part of the tube. Each hole had a 3 cm diameter and was covered by 4 and 2 mm nylon gauze for the L and F layer, respectively. All mesocosms were installed randomly, below understorey vegetation with 8 replicates in each plot. The tension inside the glass bottle was set at -0.4 bar in order to suck the percolate. Therefore, a vacuum pump was used weekly.

All water samples were filtered through paper filters. A 80 ml subsample of each sample was acidified with HNO₃ to pH < 2 for NH₄, K, Ca, Mg, and Al measurements. The remaining 20 ml subsample was used for NO₃, SO₄, and Cl measurements. Both were frozen at -5 °C until they were flown to The Netherlands. Before measurement, the samples were stored in a dark room at 5 °C.

The pH of the rainfall, throughfall and percolate was measured using a Consort P907 pH meter in the laboratory on the day of collection. SO₄, NH₄, NO₃ and Cl were measured using an autoanalyser (Skalar SA-40). K, Ca, and Mg were measured using a flame atomic absorption spectrophotometer (Perkin-Elmer 1100). Total Al was measured using inductively coupled plasma atomic emissions (Perkin-Elmer 6500 XR). All concentrations were expressed in $\mu\text{mol l}^{-1}$. Nutrient fluxes were calculated by multiplication of nutrient concentrations by the volume measured in that week, and the average for the whole period were shown to compare the fluxes in rainfall, throughfall and litter percolate before and after the eruption. Estimation of annual fluxes was done using 3 years of rainfall data observation.

Bartlett test for homogeneity of group variance was used and the data that showed inhomogeneous variance were log-transformed before data analyses. Three-way ANOVA was used to compare the effects of 3 factors i.e. plot (2 levels: high and low plot), compartment (2 levels: throughfall and percolate), and time (15 levels: series of 15 collections) on pH and nutrients (SO₄, NH₄, NO₃, Cl, K, Ca, and Mg). Comparisons between rainfall and throughfall or rainfall and percolate could not be made because rainfall

data were collected with only 2 replicates per plot. The correlations between pH and each nutrient was analysed by Pearson correlation. All analyses were performed using computer software available in SYSTAT version 5.0.

RESULTS

Volumes of rainfall, throughfall, and percolate

Volumes of rainfall, throughfall, and percolate are shown in Figure 1. The pattern of volumes of rainfall and throughfall were the same throughout the study period. Rainfall interception for the high and low plots were also similar i.e. 19 and 18% of incident precipitation. Maximum rainfall and throughfall occurred in the middle of the wet season (early December 1990 and January 1991), about 300 mm per two weeks. Amounts of rainfall for series 4, 5, 7, and 8, during which occasions the rainfall collectors overflowed, were estimated by inserting the corresponding amounts recorded at the nearby Telemetry station. Associated amounts of throughfall were estimated at 82% of incident rainfall, i.e. the overall average proportion.

Volumes of percolate were more constant in time compared to those of rain water inputs. The two plots also showed a similar pattern. On most occasions volumes of percolate were about half of those for rainfall or throughfall (i.e. about 100 mm per two weeks). Because effects of additional interception by understorey vegetation (i.e. below the throughfall gauges) and the gauze lids of the mesocosms will be small, the reduced volumes of percolate may reflect enhanced evaporation from the litter in the mesocosms associated with the removal of surrounding ground vegetation during instalment. In general the spatial variation in percolate volumes was higher than that of the throughfall volumes.

pH and nutrient concentrations in rainfall

pH and concentrations of SO_4 , NH_4 , NO_3 , Cl , K , Ca , and Mg in rain water fluctuated more or less in the same manner in both plots (Figure 2). There was a tendency for the pH to increase during the study period from 6 till 7. Between October and December the SO_4 concentration was low (about $10 \mu\text{mol l}^{-1}$); then it increased to a value of $400 \mu\text{mol l}^{-1}$ in February, followed by strong fluctuations until the end of the observations. These

fluctuations probably bear a close relation to the volcanic activity of Mount Merapi.

NH_4 concentrations in both plots started with about $40 \mu\text{mol l}^{-1}$ and then increased till about $175 \mu\text{mol l}^{-1}$ in the second measurement. It then decreased gradually till about $10 \mu\text{mol l}^{-1}$ at the end of the measurements. Initial NO_3 concentrations in both plots were about $18 \mu\text{mol l}^{-1}$ but strongly decreased to fluctuate around $5 \mu\text{mol l}^{-1}$. The initially high concentrations of NO_3 and NH_4 were observed during a relatively dry spell at the start of the wet season in October 1990.

The Cl , K and Ca concentration patterns differed between the plots. Cl concentrations fluctuated for both plots around $100 \mu\text{mol l}^{-1}$. There were two peaks in Cl concentrations in the high plot of about 300 and $700 \mu\text{mol l}^{-1}$ in December and February 1991, respectively. In the low plot only one such a peak of about $1000 \mu\text{mol l}^{-1}$ occurred in February. K concentrations for both plots were relatively low: about $0 - 50 \mu\text{mol l}^{-1}$. In the high plot there were two peaks of about 250 and $800 \mu\text{mol l}^{-1}$. In the low plot there was only one peak of about $1250 \mu\text{mol l}^{-1}$. The peaks in K concentrations occurred in the same period as the peak in Cl concentrations. These high input phenomena may be of maritime or volcanic origin. In the high plot Ca concentrations were stable during the study period (: about $20 \mu\text{mol l}^{-1}$) and lower than those in the low plot. In the low plot the highest Ca concentrations was in the middle of December 1990 and early January 1991 (: about $55 \mu\text{mol l}^{-1}$). Mg concentrations fluctuated but on the whole showed a downward trend during the study period from about $20 \mu\text{mol l}^{-1}$ to about $5 \mu\text{mol l}^{-1}$. Concentrations at the low plot tended to be slightly higher than at the high plot. Al concentrations were very low in both plots, 0.40 and $0.74 \mu\text{mol l}^{-1}$ for the high and low plots, and are not presented in the figure.

pH and nutrient concentrations in throughfall and percolate

The dynamics of pH and nutrient concentrations in throughfall and percolate are shown in Figure 3 for the high plot and in Figure 4 for the low plot. The pHs of throughfall and percolate in both plots were slowly increasing like in rainfall. The pH of percolate was always higher than that in throughfall. This is due to the fact that mineral soil is relatively alkaline although the organic matter developed from the pine needles is relatively acid. According to statistical testing using 3-way ANOVA (Table 1), there was significant difference in the patterns of the pH between throughfall and

percolate between the two plots during this study (plot*compartment*series; F -value = 2.140).

As in rainfall, SO_4 concentrations in throughfall and percolate at both plots were low and stable from October to middle December (: about 40 and $100 \mu\text{mol l}^{-1}$, respectively; Figures 3 and 4). Then SO_4 concentrations started to fluctuate in throughfall and percolate in both plots as in rainfall. It is shown in Table 1 that significant differences were found for the pattern of SO_4 between both plots and between throughfall and percolate during this study (F -value = 3.727).

Patterns of NH_4 concentrations in throughfall and percolate were similar in both plots (Figures 3 and 4). The pattern of NH_4 concentrations in throughfall and percolate in the high plot followed that in rainfall (Figure 2). The pattern of NH_4 between both plots and between throughfall and percolate slightly differed during this study (F -value = 2.064)

In both plots the NO_3 , Ca and Mg concentrations in throughfall were always lower and the S.E. smaller than those in percolate (Figures 3 and 4). According to Table 1, the pattern of NO_3 and Mg did not differ (F -values 1.650 and 1.692) between both plots and between throughfall and percolate, and the pattern of Ca slightly differed during this study (F -value = 1.949).

As conservative elements, Cl and K have more or less the same pattern during this study. In most of the measurements, Cl and K concentrations in throughfall were lower than those in percolate (Figures 3 and 4). In some occasions the concentrations of Cl and K were much higher than those in percolate if concentrations of both elements were also high in rainfall. This is shown in series 5 and 10 in the high plot and series 10 in the low plot (Figure 2). It was clear in the high plot that those two peaks were followed by higher concentrations in percolate in series 6 and 10 (Figure 3). According to Table 1, differences of Cl and K patterns were significant between both plots and throughfall and percolate (F -values 26.642 and 3.547).

Correlations between elements

Pearson rank correlation was used to analyse correlation between all variables (Table 2). The data used to estimated correlations, originated from all plots, compartments and sampling times. Positive significant correlations exist between $\text{pH} - \text{SO}_4$, $\text{pH} - \text{NO}_3$, $\text{pH} - \text{Ca}$, $\text{pH} - \text{Mg}$, $\text{SO}_4 - \text{NO}_3$,

$\text{SO}_4 - \text{Cl}$, $\text{SO}_4 - \text{Ca}$, $\text{SO}_4 - \text{Mg}$, $\text{NH}_4 - \text{Mg}$, $\text{NO}_3 - \text{Cl}$, $\text{NO}_3 - \text{Ca}$, $\text{NO}_3 - \text{Mg}$, $\text{Cl} - \text{K}$, $\text{Cl} - \text{Ca}$, $\text{Cl} - \text{Mg}$, and $\text{Ca} - \text{Mg}$ (all at $p < 0.001$, except $\text{SO}_4 - \text{Mg}$ at $p < 0.01$). Negative significant correlations exist between $\text{pH} - \text{NH}_4$ and $\text{SO}_4 - \text{NH}_4$ only (at $p < 0.001$ and $p < 0.01$).

Comparison between pH and element concentrations in rainfall, throughfall, and percolate

Mean concentrations of elements in rainfall, throughfall, and percolate before the eruption of Mount Merapi (October 1990 - April 1991) are shown in Table 3. During this study pH of percolate was significantly different from that in throughfall (Table 1; F -value 649.314). According to Table 3, mean pH in the high plot was 6.44 in throughfall and 6.98 in percolate, and in the low plot 6.33 and 7.01, respectively. The pH of throughfall in both plots tended to be lower than that in rainfall.

According to Table 1, mean SO_4 concentrations in throughfall and percolate were significantly different (F -value = 66.426). Mean SO_4 concentrations in the high plot was 93.71 in throughfall and 109.10 in percolate, and in the low plot 137.16 and $146.78 \mu\text{mol l}^{-1}$, respectively. SO_4 concentrations in rainfall in the high plot ($136.21 \mu\text{mol l}^{-1}$) tended to be higher than that in throughfall and percolate. On the contrary, in the low plot there was a tendency that concentrations in rainfall ($112.77 \mu\text{mol l}^{-1}$) were lower than that in throughfall and percolate (Table 3).

Mean NH_4 concentrations in throughfall and percolate did not differ significantly (Table 1) and the mean concentrations in rainfall were comparable with that in throughfall and percolate (: all about $40 \mu\text{mol l}^{-1}$; Table 3).

Mean NO_3 concentrations in throughfall and percolate differed significantly (F -value = 216.944). Mean NO_3 concentrations in rainfall were relatively low in both plots and comparable with those concentration in throughfall. The relatively high concentrations in percolate (48.72 and 61.61 $\mu\text{mol l}^{-1}$, respectively) may be due to nitrification in the mesocosms.

Mean Cl concentrations in throughfall and percolate differed significantly (F -value = 117.949). Mean Cl concentrations in rainfall in both plots seem to be lower than those in throughfall and percolate.

Mean K concentrations in throughfall and percolate did not differ significantly. As in Cl , mean K concentrations in rainfall in both plots also were lower than that in throughfall and percolate. It is shown in Table 3,

the S.E. of both elements in rainfall, throughfall, and percolate in both plots was relatively high.

Mean Ca concentrations in throughfall and percolate differed significantly (F -value = 381.158). Mean Ca concentrations in percolate in both plots were much higher than those in throughfall or in rainfall.

Mean Mg concentrations in throughfall and percolate differed significantly (F -value = 337.526). As in Ca, mean Mg concentrations in percolate in both plots were higher than that in throughfall or in rainfall.

There is no ANOVA test for Al because measurements were done only once in the middle of February 1991. According to Table 3, mean Al concentrations in rainfall were very low and much lower than that in percolate.

After eruption condition

Mean concentrations of elements in rainfall, throughfall, and percolate after the eruption of Mount Merapi are shown in Table 4, and are compared with those before the eruption (Table 3). pH of percolate in both plots tended to be higher than that of throughfall and rainfall, as was found before the eruption of Mount Merapi.

Unexpectedly, after the eruption SO_4 concentrations in rainfall, throughfall, and percolate in both plots were lower than those before eruption. After eruption SO_4 concentrations in rainfall in the high plot tended to be lower than that in the low plot.

NH_4 concentrations in rainfall after the eruption seem to be higher than those before the eruption. Following NH_4 concentrations in rainfall after the eruption, in throughfall they became slightly lower, and in percolate much lower. Before the eruption these concentrations were all similar.

After the eruption NO_3 concentrations in rainfall, throughfall and percolate were similar. Before the eruption NO_3 concentrations in percolate were 2 or 3 times higher than after the eruption.

Of all elements measured in rainfall, only Cl concentrations showed much higher (2 times) concentrations after eruption than before the eruption. However, Cl concentrations in throughfall and percolate were about twice lower after eruption than before the eruption. This may be due to the fact that after the eruption collection had been done only once and Cl had not reach the percolate fraction. It has been shown earlier, before the eruption, for the dynamics of Cl, that Cl concentrations in percolate

increase two weeks after Cl peaks in rainfall or throughfall (Figures 2 and 3).

K concentrations in rainfall after the eruption were higher in the high plot than that in the low plot. The K concentrations in throughfall and percolate differed strongly between both plots. In the high plot the concentrations in throughfall increased till 154.38 and decreased till $42.80 \mu\text{mol l}^{-1}$ in percolate. In the low plot the concentrations in throughfall and percolate increased from 269.40 to $553.20 \mu\text{mol l}^{-1}$. It can be presumed that the high K concentrations in throughfall and percolate in the low plot were caused by the high input in rainfall prior to the collection period.

Ca concentrations in rainfall in the high plot after the eruption were more than twice before the eruption, whereas in the low plot, Ca concentrations in rainfall were similar. After the eruption Ca concentrations in percolate were lower than before the eruption.

Mg concentrations were comparable before and after the eruption. Mg concentrations tended to increase from rainfall to percolate in both plots.

Al concentrations in rainfall after the eruption were about 5 times higher than that before eruption i.e. $2.50 \mu\text{mol l}^{-1}$ in both plots.

Nutrient fluxes in rainfall, throughfall, and percolate ($\text{kg ha}^{-1} \text{ week}^{-1}$) of both plots before and after the eruption are shown in Table 5. All elements in rainfall before eruption tended to be similar between high and low plots. After the eruption in March 1992, only Cl and Al input in rainfall may have increased in both plots. SO₄ input in rainfall appeared to decrease after eruption.

The input of elements in throughfall before the eruption were similar in both plots compared to rainfall. Only Cl and K were higher in the high plot than that in the low plot. After the eruption, Cl input in throughfall was lower in both plots compared to in rainfall. As usual K input in both plots increased from rainfall to throughfall i.e. 3.25 and $5.28 \text{ kg ha}^{-1} \text{ week}^{-1}$ for the high plot, and 0.76 and $7.58 \text{ kg ha}^{-1} \text{ week}^{-1}$ for the low plot. In case of throughfall fluxes was much higher than percolate that for the conservative element Cl, we assumed that this was caused by interception. This of course then also applies for the other elements, which means that an equivalent lower amount enters the mesocosms. This should be taken into account in interpreting the comparison throughfall - percolate.

After the eruption most amounts of elements in percolate in both plots were lower than before eruption except for Ca, Mg and Al. This is due to the fact that after eruption, the vacuum tube lysimeters were installed only for

a short period (7 days), were not fully equilibrated with the soil conditions, causing relatively low amounts of elements.

DISCUSSION

Rainfall interception in this study was 19 and 18% of incident rainfall and was lower compared to the results calculated by BONS in BRUIJNZEEL (1988) for a 31-year-old *Pinus merkusii* forest plantation in West Java (25 - 28%). This may be due to the fact that although the trees at the Merapi site had about the same age, the thinning of branches by local people before the start of the study reduced the canopy biomass and made the interception lower. Another reason may be the fact that rainfall intensities and total rainfall for the sites in West Java were considerably lower (BONS, personal communication).

Element concentrations in rainfall, throughfall, and percolate in the wetter period (November 1990 - February 1991, with a monthly rainfall of about 250 mm) were comparable with the drier period (October - November 1990 and February - April 1991, with a monthly rainfall of about 150 mm). This is probably because the study took place in the wet season (October - April). It is well known that due to volcanic activity HCl and H₂SO₄ concentrations in rain water may increase (DARZI and WINCHESTER, 1982, SMITH et al., 1982). The dominance of HCl in volcanic "acid rain" makes it distinctly different from anthropogenic acid rain which usually contains HNO₃, H₂SO₄ and (NH₄)₂SO₄ (JOHNSON and PARNELL, 1986, VAN BREEMEN and VAN DIJK, 1988). Comparison of element concentrations with other research in the tropics (Table 6) shows that the high concentrations in rainfall and throughfall of Cl in this study were similar to the results from the slope of the Masaya volcano in Nicaragua. The SO₄ concentrations in rainfall in this study were about 4 times higher than the former results. SO₄ and Cl concentrations in rainfall in this study were much higher than other researches done by BRUIJNZEEL (1989) in a Javanese plantation forest or by VENEKLAAS (1990) in a Colombian montane rain forest. Both studies were carried out in upland volcanic terrain with active vulcanism, although the volcanoes were not as close to the sampling sites as in the present study. Moreover, contrary to these two examples, the present study was done on the slope of a continuously active volcano.

There was no negative correlation between SO_4 - pH or Cl - pH as shown in other studies (JOHNSON and PARNELL, 1986, VENEKLAAS, 1990). On the other hand, cation concentrations, especially K, were high in rainfall and may have neutralized the pH. Also there were significant positive correlations between Ca - pH and Mg - pH. Following the high concentrations of SO_4 and Cl in rainfall in this study, the concentrations of both elements in throughfall increased as reported by the authors mentioned in Table 6, except for SO_4 in the high plot. This might be caused by a heterogeneous input of SO_4 via rainfall; local input following the wind direction may have influenced the distribution of SO_4 on the canopy in the high plot. The very high percolate data on SO_4 , NO_3 , Cl , K, Ca, and Mg of JOHNSON and PARNELL (1986) are difficult to compare with these results as they do not mention clearly the kind of lysimeter used in their research; the porous cup alundum lysimeter they use may have lead to differences with vacuum tube lysimeter used in this study. However, the strong element accumulation in the soil surface of Masaya volcano may be a possible reason.

The relatively high inputs of SO_4 , Cl and K in rainfall in both plots before eruption (Table 5) had a close relation with the volcanic activity. Since Mount Merapi is one of the most active volcanos in Indonesia its continuous activity causes a high input of elements via rainfall into the forest plantation. In this case the evidence that elemental input through rainfall may decrease with increasing altitude as found in Hawaii (ERIKSSON, 1957) is rejected. It was reported by KELLMAN et al. (1982), that volcanic activity appeared to be the most likely explanation for the high input of cations recorded in a rainfall study, although their research was far away from the volcano; the nearest volcano Volcan Fuego is located near Guatemala City, approximately 300 km west of the research location at Siguatepeque, Honduras.

After the eruption, the input of SO_4 and Cl in rainfall was higher in the low plot than in the high plot. Since K input (as major cation) at that time was much lower than in the high plot, pH of rainfall is expected to be more acid in the low plot than that in the high plot. However, as shown in Table 4, pH of rainfall in the low plot was higher than that in the high plot (6.60 vs 5.75). This may be caused by the relatively high input of NH_4 or the maritime input of Na from the Indian Ocean with a nearest distance from the low plot of approximately 75 km.

As in literature most data on elemental input are presented as $\text{kg ha}^{-1} \text{ year}^{-1}$ instead of $\text{kg ha}^{-1} \text{ week}^{-1}$, the comparison with other research is calculated on annual basis. For Table 7 average values of rainfall and throughfall data within 3 years in the high and low plots before and after the eruption of Mount Merapi have been used. Two comparisons will be made. Firstly, that with elemental input from other research in tropical pine forest plantations. Secondly, that with other research focused on anthropogenic influences. As shown in Table 7, the average elemental input by rainfall and throughfall in this study is much higher compared to research in the tropical pine forest plantations in Sumedang, West Java (BONS in prep.) or in Korokula, Fiji (WATERLOO in prep.). This can be explained by the fact that studies in West Java and Fiji were not done along the slope of an active volcano. The cyclone influences in Fiji caused a high Cl input from the ocean by throughfall till about $150 \text{ kg ha}^{-1} \text{ year}^{-1}$. Still, this amount is half the Cl input in this study. In the following, comparisons are made with anthropogenic pollution as it gives information to evaluate the vulnerability of ecosystems. Compared with anthropogenic pollution, it can be said that volcanic activity is a kind of natural pollution to forests. In The Netherlands the estimated atmospheric input of NH_x and NO_x by industrial and agricultural practices is amongst the highest in the world (VAN BREEMEN and VAN DIJK 1988). In a *Pinus sylvestris* forest plantation in Wekerom (BERG et al. in prep.) $\text{NH}_4\text{-N}$ input by rainfall was comparable with this study (i.e. 23.7 and $19.1 \text{ kg ha}^{-1} \text{ year}^{-1}$); however, NO_3 input was higher than this study (i.e. 13.7 and $3.4 \text{ kg ha}^{-1} \text{ year}^{-1}$). NH_4 and NO_3 input by throughfall were higher compared to this study i.e. 38.0 vs 15.2 for NH_4 and 11.7 vs $3.4 \text{ kg ha}^{-1} \text{ year}^{-1}$ for NO_3 (Table 7). The high input of NH_4 and NO_3 is an important reason for the decrease in vitality of both coniferous and deciduous forests in Europe (VAN BREEMEN and VAN DIJK 1988). Most other elements especially SO_4 , Cl and K were much higher in this study compared to the anthropogenic pollution in The Netherlands. However, there is no indication that high elemental input (SO_4 , NH_4 , Cl, K, Ca and Mg) decreased the vitality of natural vegetation in the area as was also noticed by SIEFFERMANN (unpublished data). A plausible explanation for this phenomenon may be that the vegetation on the slope of Mount Merapi is already adapted to this natural pollution since along time. The first eruption of Mount Merapi was recorded in 1006 (KARTODIRDJO et al., 1975 in TRIYOGA, 1991).

Time scale of only about 20 years for the vegetation in Europe to adapt to the anthropogenic pollution, including the acid rain, is too short. Although the chemical agents in this type of atmospheric deposition are the same, forest decline by means of man-made pollution is more dangerous than natural pollution because in the former case the vegetation is not adapted to that situation. The fact that our 32-year-old pine forest plantations did not appear to suffer from the continuous volcanic activity is remarkable.

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Figure 1: Volumes of rainfall, throughfall (\pm S.E.), and percolate (\pm S.E.) in the high and low plots. The x axis is divided into 15 series collections.

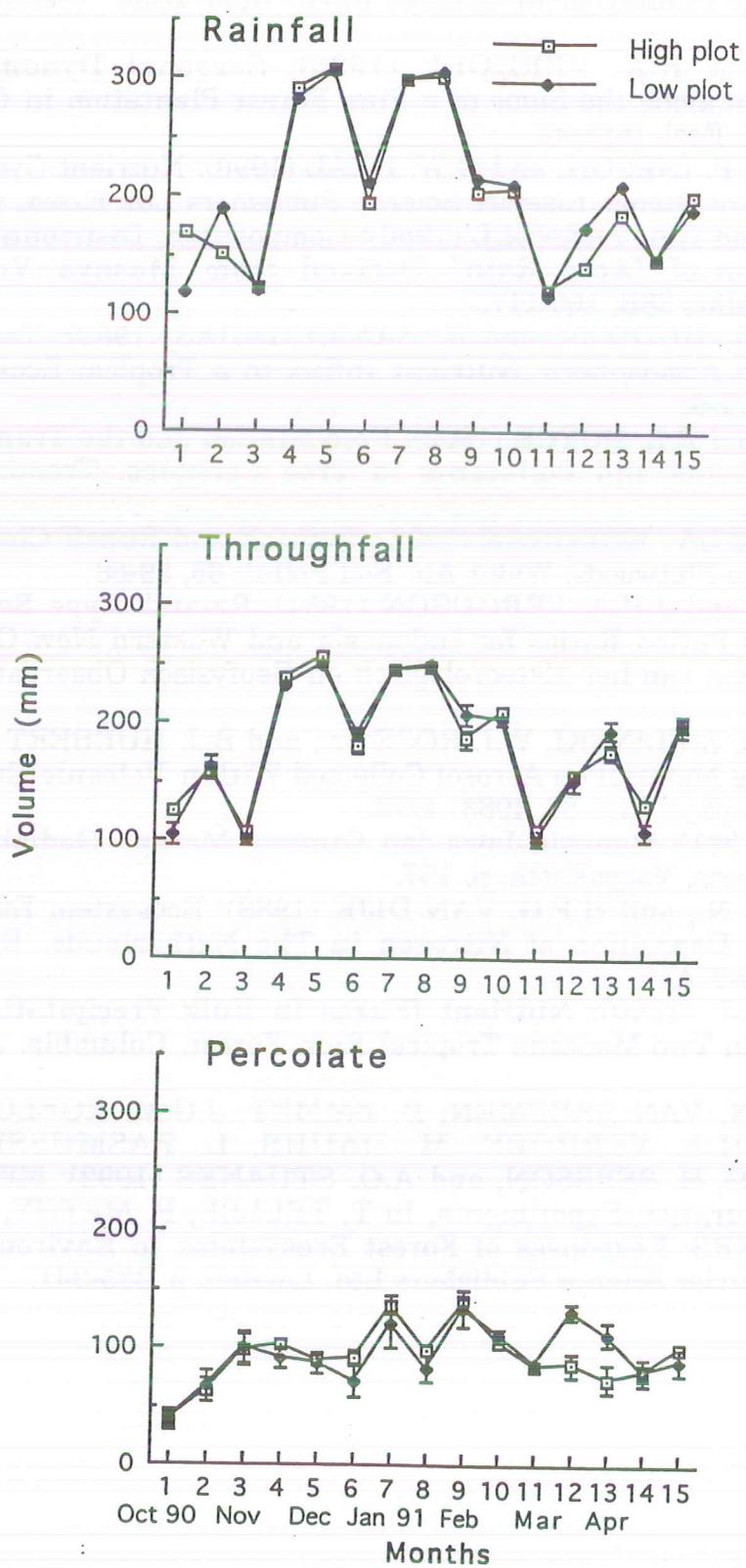


Figure 2: Dynamics of pH and element concentrations in rainfall in both plots.

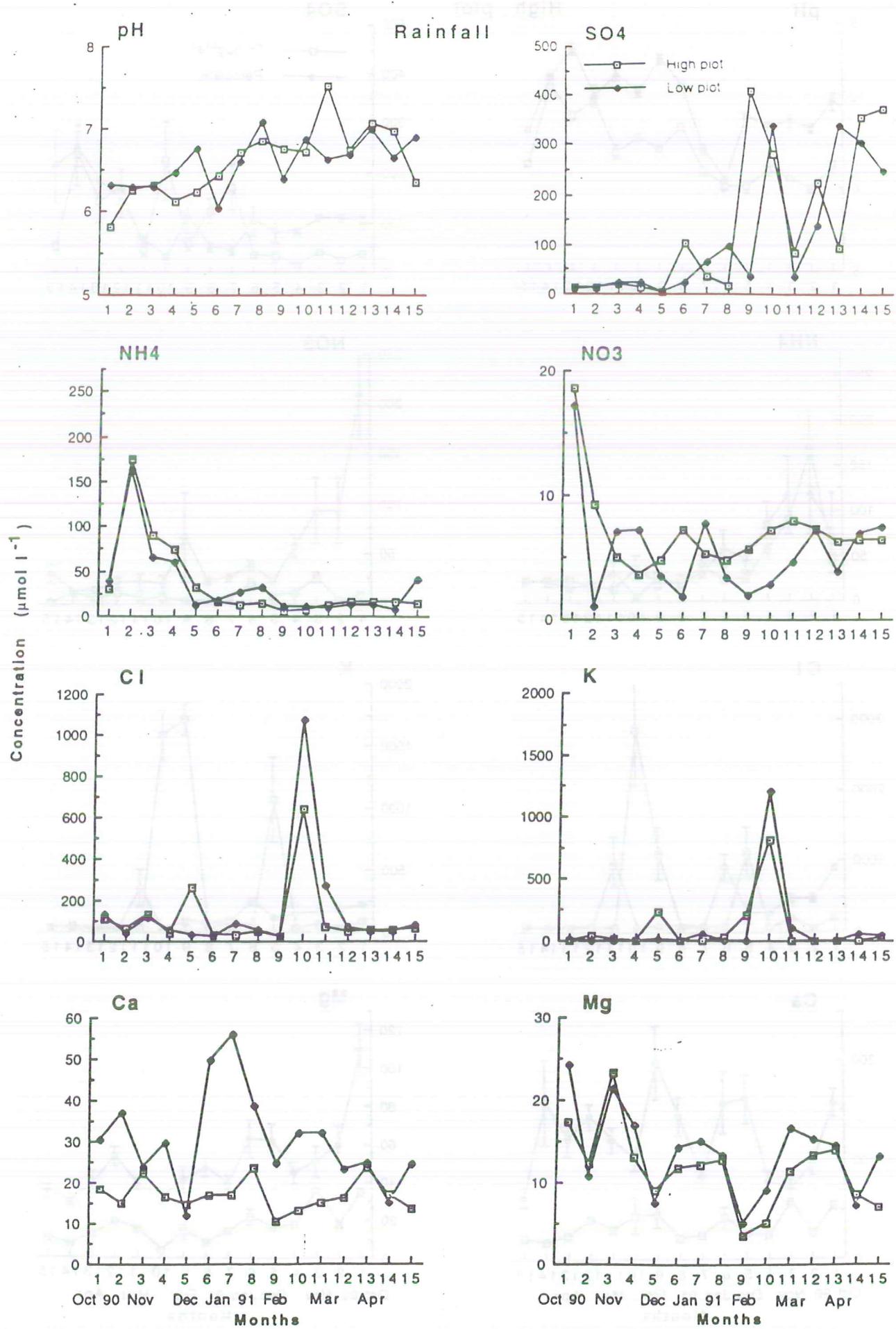


Figure 3: Dynamics of pH and element concentrations in throughfall and percolate in the high plot. The results are \pm S.E.

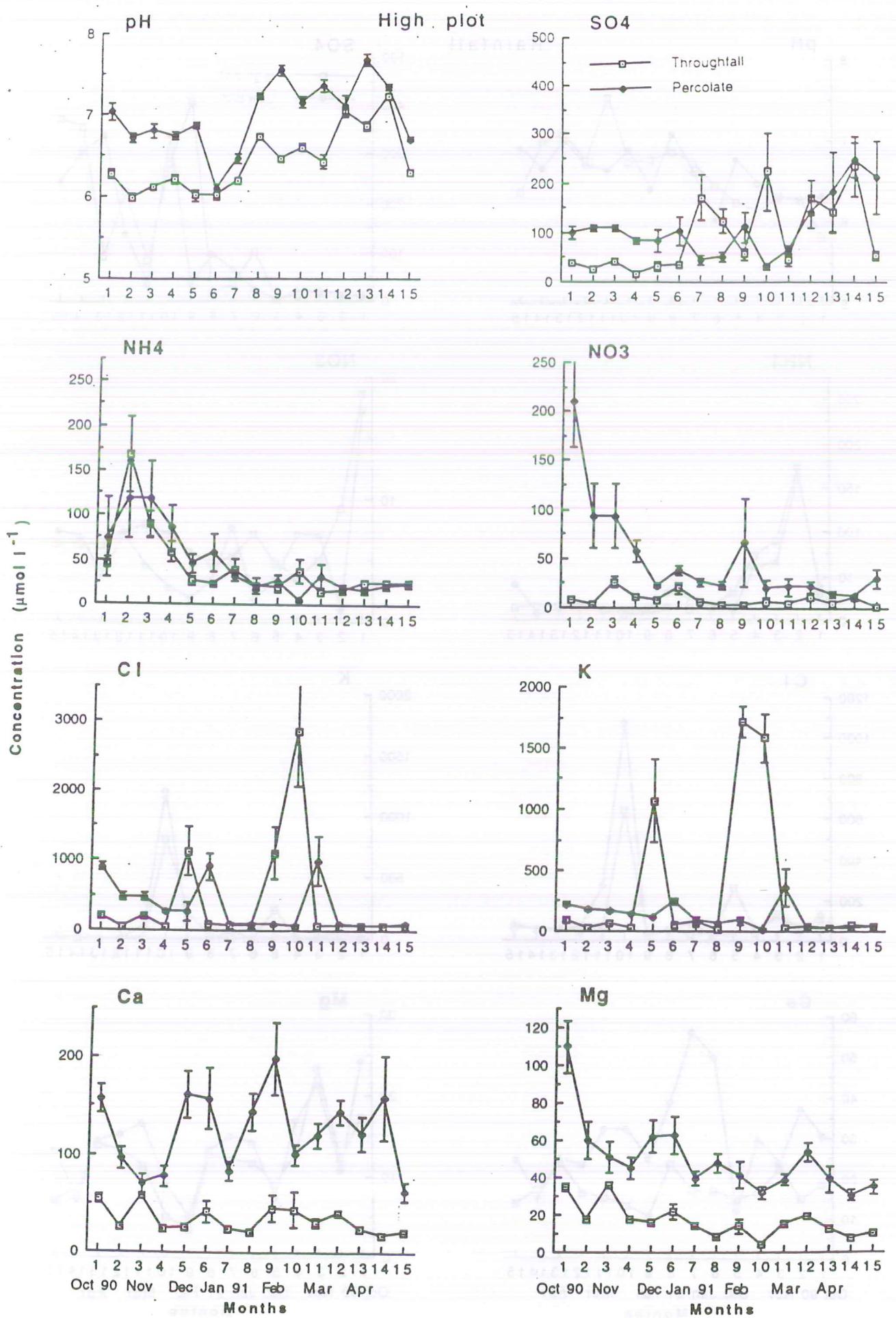


Figure 4: Dynamics of pH and element concentrations in throughfall and percolate in the low plot. The results are \pm S.E.

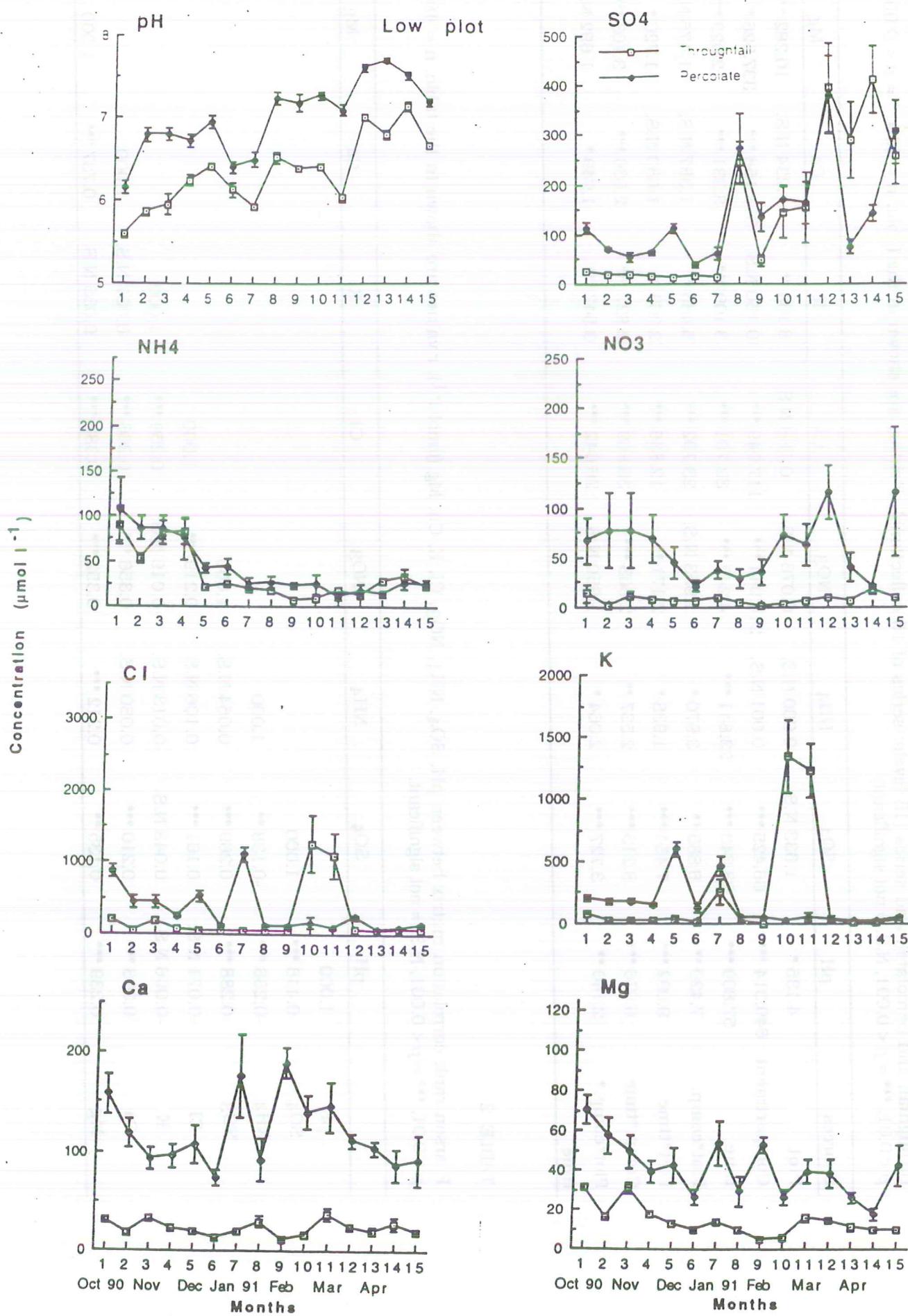


TABLE 1

ANOVA results of the pH, SO₄, NH₄, NO₃, Cl, K, Ca, Mg ($\mu\text{mol l}^{-1}$) against plot (2 levels: high and low), compartment (2 levels: throughfall and percolate), and series (15 levels: series of 15 collections). F-ratios are shown in the table. n = 480, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, N.S. = not significant.

Sources	pH	SO ₄	NH ₄	NO ₃	Cl	K	Ca	Mg
Plot	4.135 *	1.633 N.S.	0.060 N.S.	0.076 N.S.	0.188 N.S.	8.168 **	1.234 N.S.	10.282 ***
Compartment	649.314 ***	66.425 ***	0.001 N.S.	216.944 ***	117.949 ***	0.150 N.S.	381.158 ***	337.526 ***
time	57.809 ***	23.343 ***	23.841 ***	4.242 ***	32.701 ***	3.109 ***	3.331 ***	12.023 ***
Plot*comp.	7.420 **	6.885 **	3.970 *	1.953 N.S.	23.792 ***	5.485 *	1.387 N.S.	1.475 N.S.
Plot*time	9.092 ***	7.454 ***	1.938 *	2.171 **	12.836 ***	2.363 **	1.683 N.S.	1.726 *
Comp.*time	6.026 ***	8.213 ***	2.537 **	2.963 ***	35.860 ***	2.827 ***	2.636 ***	3.103 ***
Plot*comp.* time	2.140 **	3.727 ***	2.064 *	1.650 N.S.	26.642 ***	3.547 ***	1.949 *	1.692 N.S.

TABLE 2

Pearson rank correlation matrix between pH, SO₄, NH₄, NO₃, Cl, K, Ca, Mg ($\mu\text{mol l}^{-1}$). r values are shown in the table. n = 480, ** = $p < 0.01$, *** = $p < 0.001$, N.S. = not significant.

	pH	SO ₄	NH ₄	NO ₃	Cl	K	Ca	Mg
pH	1.000							
SO ₄	0.448 ***	1.000						
NH ₄	-0.266 ***	-0.138 **	1.000					
NO ₃	0.288 ***	0.269 ***	0.054 N.S.	1.000				
Cl	-0.071 N.S.	0.161 ***	0.106 N.S.	0.219 ***	1.000			
K	-0.096 N.S.	0.048 N.S.	-0.013 N.S.	-0.019 N.S.	0.259 ***	1.000		
Ca	0.396 ***	0.210 ***	0.080 N.S.	0.356 ***	0.266 ***	0.037 N.S.	1.000	
Mg	0.239 ***	0.135 **	0.212 ***	0.352 ***	0.383 ***	0.035 N.S.	0.737 ***	1.000

TABLE 3

Mean (\pm S.E.) concentrations of elements ($\mu\text{mol l}^{-1}$, except for pH) in rainfall, throughfall, and percolate of both plots before the eruption of Mount Merapi (October 1990 - April 1991).

Element	High plot			Low plot		
	Rainfall	Throughfall	Percolate	Rainfall	Throughfall	Percolate
pH	6.58 \pm 0.11	6.44 \pm 0.10	6.98 \pm 0.11	6.59 \pm 0.08	6.33 \pm 0.11	7.01 \pm 0.11
SO ₄	136.21 \pm 38.66	93.71 \pm 19.60	109.10 \pm 16.04	112.77 \pm 33.01	137.16 \pm 37.71	146.78 \pm 25.97
NH ₄	35.66 \pm 12.50	42.17 \pm 10.34	46.48 \pm 11.15	33.94 \pm 10.42	34.71 \pm 7.28	42.78 \pm 8.05
NO ₃	7.04 \pm 0.90	8.69 \pm 1.75	48.72 \pm 13.14	5.61 \pm 1.03	7.50 \pm 1.14	61.91 \pm 8.91
Cl	110.73 \pm 40.72	410.34 \pm 198.63	306.86 \pm 89.90	142.26 \pm 68.29	244.91 \pm 116.49	313.31 \pm 80.58
K	96.43 \pm 56.31	330.43 \pm 156.79	119.52 \pm 25.98	98.80 \pm 79.06	269.11 \pm 154.01	148.31 \pm 43.83
Ca	16.87 \pm 0.98	32.95 \pm 3.38	123.52 \pm 10.48	28.08 \pm 3.12	25.99 \pm 4.44	118.82 \pm 9.06
Mg	11.59 \pm 1.26	16.36 \pm 2.30	49.74 \pm 5.07	13.59 \pm 1.37	14.09 \pm 2.02	40.80 \pm 3.69
Al	0.40	6.80 \pm 0.20	7.46 \pm 0.10	0.74	1.11 \pm 0.30	6.90 \pm 0.20

TABLE 4

Mean (\pm S.E.) concentrations of elements ($\mu\text{mol l}^{-1}$, except for pH) in rainfall, throughfall, and percolate of both plots after the eruption of Mount Merapi in February 1992.

Element	High plot			Low plot		
	Rainfall	Throughfall	Percolate	Rainfall	Throughfall	Percolate
pH	5.73	5.94 \pm 0.06	7.07 \pm 0.08	6.60	6.71 \pm 0.15	7.04 \pm 0.01
SO ₄	12.13	10.05 \pm 0.87	15.96 \pm 2.50	40.66	29.37 \pm 10.34	15.20 \pm 3.45
NH ₄	50.36	38.27 \pm 3.36	17.50 \pm 1.31	82.39	78.34 \pm 13.24	27.15 \pm 1.53
NO ₃	10.52	10.79 \pm 0.78	21.85 \pm 8.76	13.48	14.52 \pm 0.75	21.93 \pm 7.24
Cl	202.92	171.54 \pm 21.17	128.52 \pm 19.43	244.91	182.90 \pm 58.76	164.44 \pm 28.57
K	82.00	154.38 \pm 15.12	42.80 \pm 9.66	21.00	269.40 \pm 11.15	553.20 \pm 6.79
Ca	43.50	36.50 \pm 7.14	55.80 \pm 5.37	25.50	51.40 \pm 10.73	69.00 \pm 3.38
Mg	13.85	17.01 \pm 1.65	47.00 \pm 7.30	13.50	22.20 \pm 5.11	64.84 \pm 6.16
Al	2.50	3.25 \pm 0.20	3.20 \pm 0.70	2.50	2.80 \pm 0.40	7.80 \pm 1.00

TABLE 5

Nutrient fluxes in rainfall, throughfall, and percolate ($\text{kg ha}^{-1} \text{ week}^{-1}$) of both plots before and after the eruption in February 1992.

Element	High plot			Low plot		
	Rainfall	Throughfall	Percolate	Rainfall	Throughfall	Percolate
Before eruption						
SO ₄ -S	4.16	2.35	1.66	3.64	3.84	2.43
NH ₄ -N	0.46	0.48	0.29	0.46	0.41	0.27
NO ₃ -N	0.09	0.11	0.26	0.07	0.09	0.44
Cl	6.81	16.82	4.58	5.21	9.45	9.20
K	4.43	15.12	2.16	4.19	9.11	2.77
Ca	0.72	1.31	2.43	1.26	0.93	2.43
Mg	0.30	0.40	0.56	0.35	0.36	0.49
Al	0.02	0.08	0.03	0.04	0.02	0.08
After eruption						
SO ₄ -S	0.39	0.28	0.14	1.20	0.68	0.09
NH ₄ -N	0.71	0.47	0.07	1.07	0.79	0.07
NO ₃ -N	0.15	0.13	0.08	0.17	0.15	0.06
Cl	7.29	5.32	1.25	8.03	4.67	1.05
K	3.25	5.28	0.46	0.76	7.58	3.90
Ca	1.77	1.28	0.61	0.95	1.48	0.50
Mg	0.34	0.36	0.31	0.29	0.39	0.28
Al	0.07	0.08	0.02	0.06	0.05	0.04

TABLE 6

Comparison of pH and mean elemental concentrations ($\mu\text{mol l}^{-1}$) in rainfall, throughfall, and percolate with other research in the tropics.

Location	Annual rainfall (mm)	pH	SO ₄	NH ₄	NO ₃	Cl	K	Ca	Mg
Central Java ¹									
Altitude 800 m	3400								
Rainfall		6.6	136.2	35.7	7.0	110.7	96.4	16.9	11.6
Throughfall		6.4	93.7	42.2	8.7	410.3	330.4	33.0	16.4
Percolate		7.0	109.1	46.5	48.7	306.9	119.5	123.5	49.7
Altitude 600 m	3400								
Rainfall		6.6	112.8	34.0	5.6	142.3	98.8	28.1	13.6
Throughfall		6.3	137.2	34.7	7.5	244.9	269.1	26.0	14.1
Percolate		7.0	146.8	42.8	61.9	313.3	148.3	118.8	40.8
Nicaragua ²									
Rainfall		4.5	33.3	2.2	1.6	228.5	5.2	34.9	2.5
Throughfall		6.5	125.0	6.1	3.2	313.1	227.6	180.6	94.6
Percolate		5.8	377.1	2.8	2940.8	1689.6	935.6	1442.6	549.3
South central Java ³									
Altitude 560 m	4670								
Rainfall		6.4	8.1	10.0	4.3	17.8	4.1	4.0	3.3
Colombia ⁴									
Altitude 2550 m	2115								
Rainfall		4.4	38.6	61.7	-	25.8	9.6	11.2	6.3
Throughfall		5.6	68.8	82.6	-	55.3	131.4	36.5	23.7
Altitude 3370 m	1453								
Rainfall		4.4	36.2	55.2	-	26.4	12.2	12.6	7.0
Throughfall		4.4	83.3	69.9	-	46.9	71.1	39.6	24.2
Australia ⁵									
Altitude 760 m	2256								
Rainfall		-	-	-	-	-	45.3	33.2	36.5
Throughfall		-	-	-	-	-	1655.7	646.0	532.7

¹Present study; ²Johnson and Parnell (1986), Masaya volcano, vegetation *Malanthora*; ³Bruijnzeel (1989), *Agathis dammara* plantation; ⁴Veneklaas (1990), montane rainforest; ⁵Brasell et al. (1980), Brasell and Sinclair (1983), rainforest. - = no information.

TABLE 7

Comparison of pH and elements input (kg ha⁻¹ year⁻¹) by rainfall and throughfall with other research in pine forest plantations.

Location	pH	SO ₄ -S	NH ₄ -N	NO ₃ -N	Cl	K	Ca	Mg
Central Java¹								
Rainfall	6.6	66.5	19.1	3.4	193.5	89.4	31.9	9.0
Throughfall	6.4	50.6	15.2	3.4	256.6	262.5	35.4	10.7
West Java²								
Rainfall	5.8	5.2	8.1	4.2	12.4	9.7	13.6	1.8
Throughfall	5.9	7.2	5.2	1.7	25.1	40.3	13.9	4.9
Fiji³								
Rainfall	5.5	8.7	5.3	5.5	13.5	1.7	0.8	0.5
Throughfall	5.7	28.7	2.3	1.7	156.4	13.5	5.7	11.5
The Netherlands⁴								
Rainfall	5.1	21.0	23.7	13.7	5.0	4.7	4.9	4.4
Throughfall	4.2	28.6	38.0	11.7	53.3	15.2	5.5	6.4

¹Present study; ²Bons (in prep.) 31-year-old *Pinus merkusii* forest plantation; ³Waterloo (in prep.) 11-year-old *Pinus caribaea* forest plantation; ⁴Berg et al. (in prep.) 35-year-old *Pinus sylvestris* forest plantation.

ROLE OF SOIL MICROARTHROPODS IN LITTER DECOMPOSITION AND NUTRIENT CYCLING IN FOREST PLANTATION ECOSYSTEMS IN INDIA

M. Vikram Reddy¹

ABSTRACT

A review of litter decomposition and mineralisation processes in relation to microarthropod abundance in different forest plantations and forests in India showed wide variation in the decomposition rate and mineral concentrations of decaying litter, depending on the abiotic and biotic environmental factors of the soil and litter system, and the physical and chemical qualities of the litter. The decomposition rate of coniferous litter was low (needle litter of pine, 40.3%) while that of deciduous litter was high (eucalyptus leaf litter, 50.4% and *Dalbergia sissoo* litter, 93%). Microarthropods — mostly Collembola and Acarina — of the soil and litter system played an indispensable role in the fragmentation and communication of litter, and their abundance showed significant correlations with mass-loss and concentrations of nutrient such as N, P, K, Ca and Mg in decaying litter. The cumulative effect of total microarthropods on mass loss and nutrient concentrations of decaying litter differed from the response of individual taxa.

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1. Introduction

Soil fertility is a determining factor in the growth and development of tropical forests and forest plantations which play a key role in global climate control, soil erosion, flood control and water quality. Soil fertility in forests, particularly natural biological fertility, depends on litter decomposition and nutrient cycling, i.e., the release of nutrients from decaying plant litter through the integrated action of soil microorganisms and soil invertebrate fauna on the forest floor. Thus, soil faunal action is one of the important biological functions that affects nutrient cycling in forest and forest plantation ecosystems. Soil and litter microarthropods, dominated by *Collembola* and *Acarina* which made up more than 95% of the total mesofauna in some cases (REDDY, 1984; GUPTA and RAJVANSI, 1988; REDDY and ALFRED, 1989), constituted a major component of the biotic environment of the forest soil and litter system. They played a significant role in litter breakdown and communiton leading to the release of mineral nutrients by microbial action and leaching. The introduction of mesofauna (mainly *Collembola*) in microcosms with deciduous forest litter increased the release of nitrogen (NO_3^- and NH_4^+) about three folds compared to that of the control without soil animals (ANDERSON et. al., 1983). Other dominant groups of such litter-feeding mesofauna as oribatid mites and small millipedes inhabiting the soils of tropical forests and forest plantations may considerably enhance such nutrient release. Soil microarthropods physically disintegrate plant litter with their mouth parts and expose a greater surface area for microbial decomposition and leaching (SWIFT et. al., 1979; REDDY, 1995). Although bacteria and fungi are responsible for most of the decomposition in tropical forests (LEE, 1974), the exclusion experiments studying the effects of soil microarthropods on litter decomposition showed that these organisms played an indispensable role in litter decomposition in forest and forest plantation ecosystems (REDDY and ALFRED, 1989; MADGE, 1965; GUPTA and RAJVANSI, 1991; REDDY, 1995). LEE (1974) has reviewed the significance of soil animals in organic matter decomposition in tropical forests. However, the role of microarthropods in litter decomposition and mineralisation in different tropical forest and forest plantation ecosystems is not adequately documented. Therefore, this review has attempted to examine the importance of soil- and litter- inhabiting microarthropods during the process of litter decomposition and humus formation across different forest and forest plantations, summarizing different studies conducted on the role of soil microarthropods in litter decomposition and mineralisation in the tropics, particularly in the Indian Subcontinent.

Three sites with different types of forest plantations --- two in northeastern and one in southcentral India --- have data sets on soil microarthropods associated with plant litter decomposition and nutrient release processes :

- i) pine (*Pinus kesiya* Royle) forest plantations at an altitude of 1150 m m.s.l. at Shillong ($25^{\circ} 34' N$; $91^{\circ} 56' E$) representing the upper montane subtropical rain forest (REDDY, 1981, 1984; REDDY and ALFRED, 1989).
- ii) fallows of the humid tropical mixed-deciduous forests at an altitude of 100 m m.s.l. at Burnihat ($26^{\circ} 0' N$; $90^{\circ} 5'E$) with red loamy lateritic soil (Oxisol) having a pH of 6-8, and such dominant weed colonizers as *Imperata cylindrica* Beauv., *Eupatorium odoratum* L., and *Borreria hispida* K.Sch. in the Khasi hills of Meghalaya in northeastern India (REDDY and TOKY, 1990). Bamboo (*Dendrocalamus hamiltonii*) and other early successional species such as *Schima wallichii* Chois., *Bauhinia purpurea* L., and *Vitex penduncularis* Wall also occur in this region.
- iii) *Eucalyptus* sp., neem (*Azadirachta indica* A. Juss) and teak (*Tectona grandis* L.) forest plantation systems at an altitude of 260 m m.s.l. with semi-arid tropical climatic conditions and sandy loam Alfisol having a pH of 7-8 at Warangal ($18^{\circ} 0' 31'' N$; $79^{\circ} 29' 5'' E$) in Andhra Pradesh (REDDY and VENKATAIAH, 1989; REDDY, 1992 and 1995).

Besides, this paper also discusses briefly the data sets of a dry deciduous forest plantation of *Dalbergia sissoo* Roxb. at an altitude of 250 m m.s.l. with old alluvium soil and sandy loam texture having a pH of 7-6 at Kurukshetra ($29^{\circ} 58' N''$; $76^{\circ} 51' E$) in northern India (GUPTA and RAJVANSHI, 1991).

2. Decomposition Rate Across Different Forest Plantations

Decomposition and mineralisation of plant litter varies from species to species and from site to site, depending on a number of abiotic and biotic environmental factors (SWIFT, et al., 1979; REDDY, 1995). Some of the plant-litters have low decay rates, while the litter of other species show faster decomposition rates. The time required for complete decomposition and disappearance of the original biomass ranged from even less than two months to more than one year. An analysis of the litter decomposition rates in different forests and forest plantations in the tropics and sub-tropics showed that the mass loss of needle litter of pine (*P. kesiya*) at Shillong in the eastern Himalayas was 72.4% after one year, the annual average being 40.3%

(REDDY, 1981). However, RAMAKRISHNAN and DAS (1983) reported it as 38%, while that of the oak-conifer forest in the western Himalayas ranged from 54 to 65% (PANDEY and SINGH 1981). TOKY and RAMAKRISHNAN (1984) and REDDY and TOKY (1989) have reported > 97% mass loss in bamboo litter in degraded forest fallows, whereas SINGH and RAMAKRISHNAN (1982) recorded 56-78% loss of litter mass in deciduous leaf litter in the humid sub-tropical forests of Meghalaya. GUPTA and RAJVANSHI (1991) reported 93% mass loss rates of *D. sissoo* litter in 5 mm mesh bags, 84% in 2 mm mesh bags and 60% in 90 μm mesh bags after 354 days. SINGH and AMBASHT (1980) reported that mass loss of teak litter near Varanasi was 90% after one year while at Thailand and Nigeria it was 95% and 100% per year (AKSORNKOAE et al., 1972; EGUNJOBI, 1974). However, mass loss of teak and eucalyptus litter was recorded as 96% and 64% after 18 months at Peechi in Kerala (SANKARAN, 1993). The mass loss of eucalyptus litter was 50.4% in coarse (5 mm) mesh bags and 44.5% in fine (1 mm) mesh bags after one year at Warangal (REDDY and VENKATAIAH, 1989). Although the decomposition rate of the Brazilian tropical lowland rain forest was 93% (KLINGE and RODRIGUES, 1968) and that of the tropical lower montane forest of Puerto Rico was 94% (WIEGERT, 1970) --- which are comparable to the rates of some plant litters in Indian forests --- relatively higher decomposition rates were reported in the lowland rain forests in Nigeria (240%) (HOPKINS, 1966) and Trinidad (164%) (CORNFORTH, 1970), and in the tropical lower montane rain forests of New Guinea (120%) (EDWARDS, 1977).

The large differences in decomposition rates at different sites were attributable to changes in some abiotic factors such as temperature and moisture, and the biotic factors such as decomposer populations (particularly the micro- and macro-arthropods including termites). It has been suggested that the variation in temperature and moisture, and their profound combined influence on the decomposer communities can explain, to a large extent, the variation in the litter decomposition rates and mineralisation (WILLIAMS and GRAY, 1974). Besides, the physical quality of litter (leaf thickness and leaf hardness or toughness) and the biochemical quality (lignin, nitrogen, and tannin contents and their ratios in the litter) influenced the decomposition rates and mineralisation (EDWARDS, 1977; MELILLO et al., 1982; TAKEDA et al., 1984). A high proportion of structural substances such as lignin and cellulose lowered the decomposition rates, while high levels of soluble components such as carbohydrates, fats, and waxes increased the decomposition rates (TAKEDA

et al., 1984). All these biotic and abiotic environmental factors could be responsible for the very little or no accumulation of litter in tropical forests and forest plantations, which could imply a fast turnover of organic matter in the soil. However, available information on tropical litter decomposition and nutrient dynamics particularly pertaining to forest and forest plantation ecosystems is very limited and not sufficient for a complete understanding of the functioning of the detritus system of the tropical forests and forest plantations (TAKEDA et al, 1984; REDDY 1995).

3. Microarthropod Populations

The estimation of population densities of microarthropods inhabiting the soil and litter systems of forest and forest plantations depends on the methods of sampling, extraction and enumeration, and published information generally showed underestimates of the natural population of microarthropods (SEASTEDT, 1984). Their densities showed a wide range of variation in the tropics depending not only on the abiotic and biotic environmental factors of the soil and litter system, but also on the physico-chemical qualities of the litter, and were influenced by both the amount and quality of detritus (WALLWORK, 1976; SEASTEDT, 1984). More information is needed on the relationship between microarthropod densities and their abiotic and biotic microenvironment, and the food resources in tropical forest plantations (REDDY, 1995).

Collembola and Acarina usually comprise a major component, representing more than 97% of the microarthropods in the soil and litter system of forest and forest plantations. Among them, isotomids and oribatids are the most abundant groups in the soils of forests and forest plantations (REDDY 1984, 1995). Other microarthropods such as prostigmatids, mesostigmatids and astigmatids in Acarina, and sminthurids, podurids and entomobryids in Collembola are rarely dominant. Collembola and Acarina, and other taxa such as micro-isopods, pseudoscorpions, diplopods (Polyxenidae, Polydesmidae, and Glomeridae), Paupropoda, Chilopoda, Symphyla, Protura, Diplura, Thysanura, Psocoptera, Isoptera, Thysanoptera, Homoptera, Hymenoptera (Formicidae), and coleopteran and dipteran larvae constitute the whole guild of microarthropods in the soil and litter system (REDDY, 1995).

Microarthropods occupy all the trophic levels within the detritus food web on the floor of forest and forest plantations (WALLWORK, 1976). Some of them such as oribatids, collembolans, isopods and diplopods have well-developed mouth parts to

fragment the litter and feed on the microflora associated with the detritus. The role of microarthropods in fragmentation and communion of litter on the forest floor is very important and indispensable in the decompositon and mineralisation processes. Such microarthropod activity creates new surface area for enhanced microbial activity and colonization. In this manner, microarthropods and microorganisms play a synergistic role during these processes. Other microarthropods such as Prostigmata and Mesostigmata have piercing mouth parts, and, being predators, along with other predatory microarthropods such as pseudoscorpions and chilopods, they regulate collembolan and nematode population densities and microbial biomass, which in turn influences the decomposition rate.

4. Decomposition Rate in Relation to Microarthropod Abundance

4.1 Coniferous litter

Population densities of microarthropods of the soil and litter system varied considerably, being influenced by abiotic environmental factors particularly moisture (REDDY, 1984, 1992). During August to January, when the population densities of microarthropods were low, the mass loss of needle litter from the litter bags was observed to be low. On the other hand, the mass loss was higher when the microarthropod populations were relatively denser during the monsoon months (Fig. 1). The mass-loss during the initial two months (May-June) was probably due to leaching of soluble organic compounds (SWIFT et al., 1979; REDDY, 1995). The fragmentation activity of the microarthropods in the needle litter was evident from the disintegrated litter recovered from the bags. The densities of Collembola, Acarina

Figure - I

and other miscellaneous groups of microarthropods showed positive correlations with mass loss. Moreover, the microarthropod densities along with such abiotic factors as rainfall, litter moisture and temperature showed significant combined influence on the mass loss of needle litter, and were responsible for 75% variation in mass loss ($R^2 = 0.75$; $P < 0.05$) (REDDY, 1989).

In an other exclusion experiment using bags of different mesh sizes (3 mm, 1 mm, and 0.3 mm), the difference in mass loss across the bags was marginal, the average mass loss being maximum (38%) in the coarse (3 mm) mesh bags and minimum (34%) in the fine (1 mm) mesh bags. The dominant microarthropods such as Collembola

and Acarina in the three types of litter bags together constituted 95.5%, 97.1% and 97.3% of the total microarthropods. In the needle litter of coarse mesh bags, the groups of Collembola, Protura, Paupropoda, Isopoda, Hemiptera and coleopteran adults and larvae, dipteran larvae and juvenile earthworms were recorded in large numbers (REDDY and ALFRED, 1989). Therefore the presence of important faunal groups with larger populations made a greater contribution to litter decomposition (SANTOS and WHITFORD, 1983).

4.2 Deciduous litter

Mass loss in bamboo (*D. hamiltonii*) and tree (*S. wallichii*) leaf litter was three and five times higher compared with the stem litter of these species at Burnihat in the fallows of tropical mixed deciduous forest (REDDY and TOKY, 1990). The mass loss of tree leaf litter gradually increased with a slight decrease during the dry winter, while that of the tree stem litter (stem with bark, stem without bark, and bark) increased steadily reaching a maximum during summer with intermittent pre-monsoon rains. Densities of microarthropods with dominance of Collembola and Acarina, were associated with all types of litter throughout the period of study (300 days), and were minimum in sole bark litter and stem litter without bark and maximum with weed (*I. cylindrica*) stem litter. The decomposition rate during the period was maximum for the weed litter and minimum in stem (with bark) litter of *S. wallichii* (Table 1). The stem litter of the weed, bamboo and tree (with bark) harboured higher densities of

Table - 1

microarthropods than their corresponding leaf litter. However the mass loss was considerably lower in the stem litter than in the leaf litter, which was probably because of the harder texture of the stem tissue. The higher mass loss of weed litter compared to the other types of litter may be attributable to the initial higher N content and narrower C:N ratio, and greater microarthropod abundance (SWIFT et al., 1979). The mass loss of bamboo leaf litter in coarse (5 mm) mesh bags was higher than in the fine (1 mm) mesh bags, and the litter in the coarse mesh bags contained higher densities of microarthropods. It showed the influence of coarse mesh size permitting access of different sizes of soil arthropods into the bags, and the greater abundance of certain taxa may have determined the communion rate.

In the case of eucalyptus forest plantations at Warangal in Andhra Pradesh, the mass-loss of leaf litter was significantly higher (50.4%) in the coarse mesh bags compared with the loss in fine mesh bags (44.5%) ($P<0.05$). The fine mesh bags

showed about six times higher litter mass-loss than in suspended bags (7.4%) ($P<0.01$) (Fig. 2). No microarthropods were recorded in the litter of suspended bags. Microarthropods were more abundant in the coarse mesh bags (REDDY and VENKATAIAH, 1989). Similarly, in the case of neem leaf litter, the percentage of

Figure - 2

mass loss in the coarse mesh bags was significantly higher than in the fine mesh bags, which may indicate higher fragmentation losses from the coarse mesh bags (REDDY, 1992). The higher decomposition rates in coarse mesh bags may be related to the high population densities of microarthropods.

Teak leaf litter was treated with insecticide (endosulfan) in order to keep away the microarthropods from the decomposition process, and its mass-loss was compared with that of normal leaf litter, i.e., without any chemical treatment, allowing access to all the microarthropods. The mass loss of the insecticide-treated teak leaf litter was significantly less (<45%) compared with that of normal leaf litter where the mass loss was more than 80% after 330 days ($P<0.01$) (Fig. 3). It indicated the significant role of microarthropods in mass loss of teak litter during the process of litter decomposition (REDDY, 1995).

Figure - 3.

The mass loss of leaf and twig litter of *D. sissoo* was higher (93.0%) in 5 mm mesh bags, 83.9% in 2 mm mesh bags, and 60.2% in 90 μm mesh bags. The mass-loss, as in the eucalyptus leaf litter (REDDY and VENKATAIAH, 1989), was minimum (27.8%) in suspended aerial bags which offered no access to microarthropods (GUPTA and RAJVANSI, 1991). Collembola and Acarina were dominant groups of microarthropods in the decaying litter in the coarse mesh bags, and their activity along with termite activity caused significant mass loss in these mesh bags.

5. Nutrient Release in Relation to Microarthropod Abundance

5.1 Coniferous needle litter

Nutrient release from the decaying litter is the net effect of changes in nutrient concentrations and litter mass. When the densities of fauna are generally high per g of litter, the fragmentation and communiton and grazing effects appear to be the dominant factors influencing nutrient dynamics. Seasonal patterns of Nitrogen (N), Phosphorus (P), Potassium (K), Calcium (Ca) and Magnesium (Mg) concentrations in the

decomposing needle litter showed much less variation than could be expected from the bimodal pattern of rainfall at Shillong. Nitrogen concentrations slowly increased throughout the first year of decay, while Mg exhibited no clear pattern (Fig. 4). Calcium exhibited a sharp decline during the initiation of the dry period, while

Figure - 4

K showed an increase in concentration during the dry period. This increase is correlated with an apparent absolute increase in litter mass (Table 2) suggesting deposition of dry particulate on the litter (SEASTEDT and CROSSLEY, 1980). Although microarthropods have often been reported to influence the net mineralisation of the chemical elements of decaying litter (SEASTEDT, 1984), there was no significant correlation between the N and Ca concentrations of the decomposed needle litter and the abundance of any of the group of microarthropods (Table 2). The lack of a relationship supports the findings of MACAULEY (1975) that microarthropods have little effect on the N concentration of the decomposed needle litter. Similarly, microarthropods have been reported to have little effect on the amount of Ca (SEASTEDT, 1984). However, ANDERSON et al. (1983) reported that *Collembola* have a considerable effect on the leaching of N from the decomposed litter than any other taxa of soil microarthropods. *Collembolan* grazing has been reported to increase the leaching of ammonium, nitrate and calcium from decomposed oak litter (INESON et al., 1982). Potassium concentration of the decomposed needle litter, while not showing any correlation with the densities of *Collembola* and *Acarina*,

Table - 2

was significantly negatively correlated with the abundance of miscellaneous groups of microarthropods. However, INESON et al. (1982) reported that the concentration of K was little affected by the microarthropods. The Mg concentrations of litter showed significant positive correlations with the abundance of *Acarina* in the litter bags (Table 2). In contrast, SEASTEDT (1984) reported that microarthropods have no consistent effect on Mg concentration of the decomposed litter.

5.2 Deciduous litter

Seasonal variation in the concentrations of N and Ca (Fig. 5) and that of P and K (Fig. 6) in the decomposed leaf litter of eucalyptus indicated that the concentration of N increased from 0.56% to 1.56%, while the increase in Ca concentration was negligible (Fig. 5). The concentration of P decreased from 0.6% to 0.2%, and that of

K from 0.18% to 0.04% over one year (Fig. 6) (REDDY and VENKATAIAH, 1989). However, there were only negligible changes in the concentration of these mineral elements in the litter of suspended bags during the period, where there was no access to microarthropods. However, the concentration of N in the litter was higher in the coarse mesh bags (1.21%) than in the fine mesh bags (1.16%) and more than double compared with the concentration in the suspended bags. The Ca concentration was

Figure - 5

identical in the litter of both the mesh bags and was slightly higher than that of the suspended bags. The concentrations of P and K were slightly lower in the coarse mesh bags than in the fine mesh bags and far lower than the concentrations in the suspended bags. The almost total absence of K leaching and changes in concentrations of other nutrients from the suspended bags suggests that the litter must be fragmented or otherwise physically altered by the fauna in order to promote nutrient leaching (REDDY and VENKATAIAH, 1989).

Figure - 6

The measurements of mass loss and elemental concentrations, and the population densities of microarthropods are consistent with the hypothesis that the abundance of microarthropods plays a significant role in the seasonal dynamics of nutrients in litter bags during the process of litter decomposition (SEASTEDT and CROSSLEY, 1980). The seasonal variation in the concentration of N in decaying eucalyptus leaf litter showed significant positive correlation with the total microarthropods in the coarse mesh bags (Table 2), which may imply that the abundance of total microarthropods contributes to the release of N (SEASTEDT, 1984). The variation in concentration of Ca and K did not show any correlation with the changes in the abundance of any of the microarthropods. The seasonal variation in the concentration of P showed positive linear correlation with the abundance of total *Collembola*, with the abundance of *Lepidocyrtus* sp. and *Sminthuridae* in both the mesh bags, and with the total microarthropods in the litter of the coarse mesh bags (Table 2). Therefore, the increase in microarthropod density appears to enhance P concentration, whereas the decrease in their abundance during winter and summer reduces its concentration in the eucalyptus leaf litter during decomposition.

In conclusion, these studies suggest that microarthropods play an indispensable role in mass loss and nutrient dynamics of coniferous and deciduous litter during decomposition. The net result of rapid mass loss with no significant increase in the

elemental concentration of the decaying needle mass indicates a very rapid mineralisation effect of the microarthropods. Both the increase and decrease in the mineral nutrients of the decomposed litter are determined by the relative balance of inputs minus the outputs (SEASTEDT and CROSSLEY, 1980). The outputs are directly increased by consumption of litter by the microarthropods and indirectly enhanced by the fragmentation and stimulation of more microflora or by other mechanisms (CROSSLEY, 1977). The various positive and negative correlations of microarthropod densities with N and P concentrations of decomposed leaf litter of eucalyptus, if not spurious, could suggest that the cumulative effect of fauna on mass loss and nutrient concentrations of decaying litter may differ from the responses of the individual groups.

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TABLE - I

Abundance of different groups of microarthropods and mass loss in different types of litter per bag (mean \pm S.E.) in a fallow of humid tropical deciduous forest ecosystem

(Numbers in the parentheses represent the minimum and maximum ranges)

Types of litter	Collembola	Acarina	Total micro-arthropods	Mass loss (%)
<i>Imperata cylindrica</i> :				
Leaf	40.8 \pm 14.8 (2 - 88)	97.3 \pm 25.6 (3 - 149)	164.5 \pm 47.2 (7 - 208)	65.7 \pm 7.0 (27.8 - 94.02)
Stem	51.5 \pm 17.5 (1 - 108)	156.8 \pm 32.9 (8 - 224)	235.6 \pm 48.8 (16 - 336)	72.1 \pm 8.4 (22.2 - 97.0)
<i>Dendrocalamus hamiltonii</i> :				
Leaf				
fine-mesh bags	16.8 \pm 5.2 (2 - 30)	49.6 \pm 8.5 (23 - 67)	72.6 \pm 8.4 (50 - 100)	59.8 \pm 4.5 (33.0 - 74.2)
Coarse-mesh bags	34.8 \pm 12.2 (1 - 82)	115.0 \pm 24.3 (60 - 218)	172.2 \pm 28.0 (115 - 284)	64.4 \pm 4.5 (46.1 - 75.4)
Stem	37.0 \pm 17.8 (4 - 65)	139.6 \pm 49.8 (1 - 197)	144.8 \pm 54.9 (1 - 226)	18.4 \pm 5.4 (3.0 - 42.1)
<i>Schima wallichii</i>				
Leaf	21.6 \pm 7.6 (1 - 56)	73.0 \pm 17.2 (33 - 151)	113.8 \pm 22.4 (35 - 184)	67.8 \pm 4.4 (41.15 - 85.80)
Stem with bark	20.6 \pm 1.5 (18-23)	63.6 \pm 10.3 (43 - 74)	124.6 \pm 32.0 (75 - 184)	4.1 \pm 6.4 (2.6 - 24.9)
Stem without bark	4.0 \pm 2.0 (0 - 7)	43.0 \pm 8.7 (27 - 57)	49.3 \pm 6.3 (37 - 59)	17.1 \pm 10.9 (1.2 - 37.7)
Bark	10.3 \pm 4.6 (1 - 15)	33.6 \pm 6.2 (27 - 46)	49.0 \pm 1.5 (47 - 52)	27.7 \pm 2.3 (23.7 - 31.6)

TABLE - 2

Linear regression equations between the abundance of different taxa of microarthropods and the mass loss and elemental concentrations (% of dry mass) of the decaying leaf litter

Microarthropod taxa	Mass loss	N	P	K	Mg
Coniferous litter (pine needle)					
Total Collembola	$y = 5.58 + 0.007x$ $t = 2.05^*$	-	-	-	-
Total Acarina	$y = 5.9 + 0.002x$ $t = 2.9^{**}$	-	-	-	$y = 0.2 + 0.004x$ $t = 2.08^*$
Miscellaneous taxa	$y = 6.17 + 0.28x$ $t = 4.0^{**}$	-	-	$y = 0.07 - 0.014x$ $t = 2.19^*$	-
Deciduous litter (eucalypt leaf)					
Fine-mesh bags					
Total Collembola	-	$y = -1.29 - 0.008x$ $t = 2.48^*$	$y = 0.31 + 0.003x$ $t = 2.57^*$	-	-
<i>Lepidocyrtus</i> sp.	-	$y = -1.29 - 0.01x$ $t = 2.43^*$	$y = 0.31 + 0.004x$ $t = 2.49^*$	-	-
Sminthuridae	-	$y = -1.27 - 0.03x$ $t = 2.28^*$	$y = 0.31 + 0.01x$ $t = 2.34^*$	-	-
Coarse-mesh bags :					
Total Collembola	-	$y = -1.36 - 0.009x$ $t = 2.81^*$	$y = 0.28 + 0.003x$ $t = 2.45^*$	-	-
<i>Lepidocyrtus</i> sp.	-	$y = -1.36 - 0.001x$ $t = 2.65^*$	$y = 0.28 + 0.004x$ $t = 2.31^*$	-	-
Sminthuridae	-	$y = -1.34 - 0.04x$ $t = 2.71^*$	$y = 0.29 + 0.001x$ $t = 2.31^*$	-	-
Total Microarthropods	-	$y = 1.61 + 0.08x$ $t = 2.55^*$	$y = 0.28 + 0.01x$ $t = 2.22^*$	-	-

* $P < 0.05$; ** $P < 0.01$

Figure 1. Temporal variations of densities of microarthropods per g of decaying needle litter in relation to litter mass-loss on a pine forest plantation floor (after REDDY, 1989).

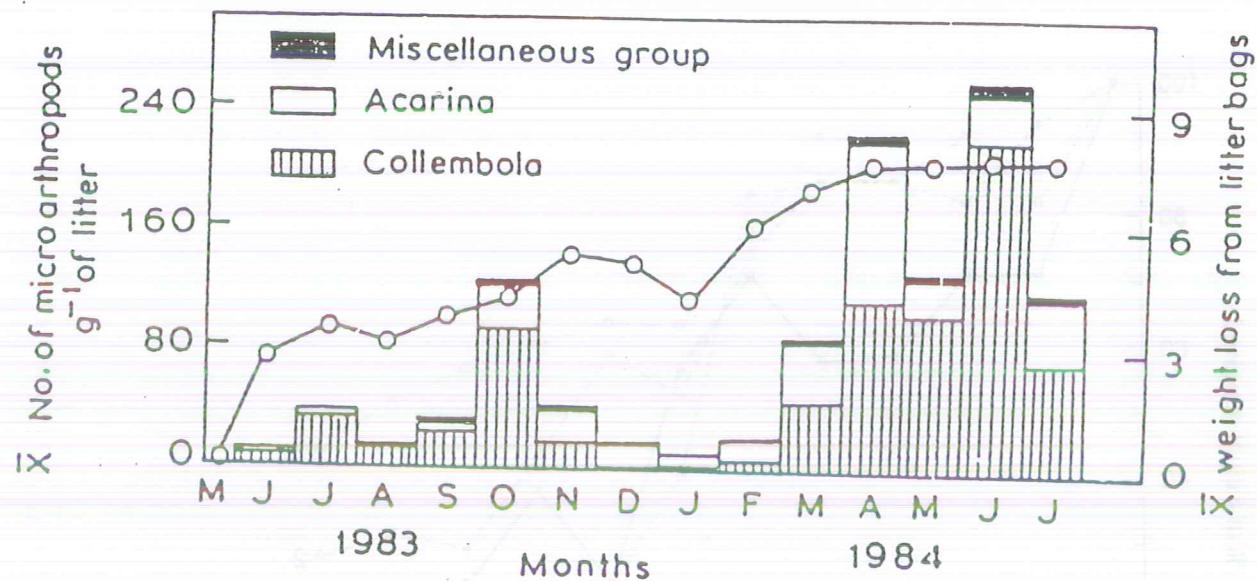


Figure 2. Temporal changes in weight loss of eucalyptus leaf litter in fine (Δ) and coarse mesh (\circ) bags and in suspended bags (\bullet) in a eucalyptus forest plantation (after REDDY and VENKATAIAH, 1989).

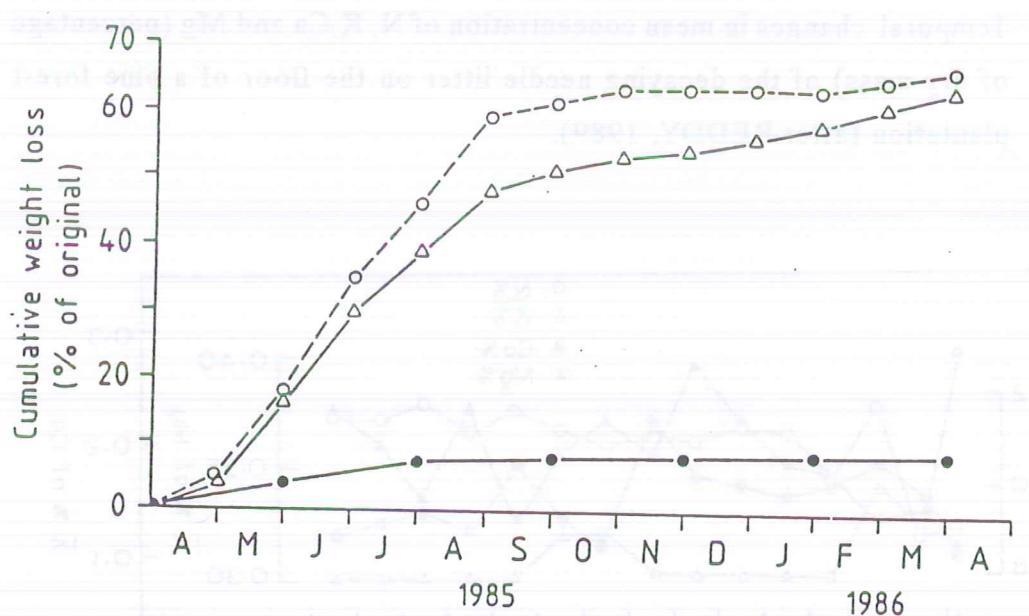


Figure 3. Percentage of mass-loss in decaying leaf litter of teak under different pesticide treatments: 1-litter with bactericide, 2-with fungicide, 3-with insecticide, and 4- without any chemical treatment in a teak forest plantation (after REDDY, 1995).

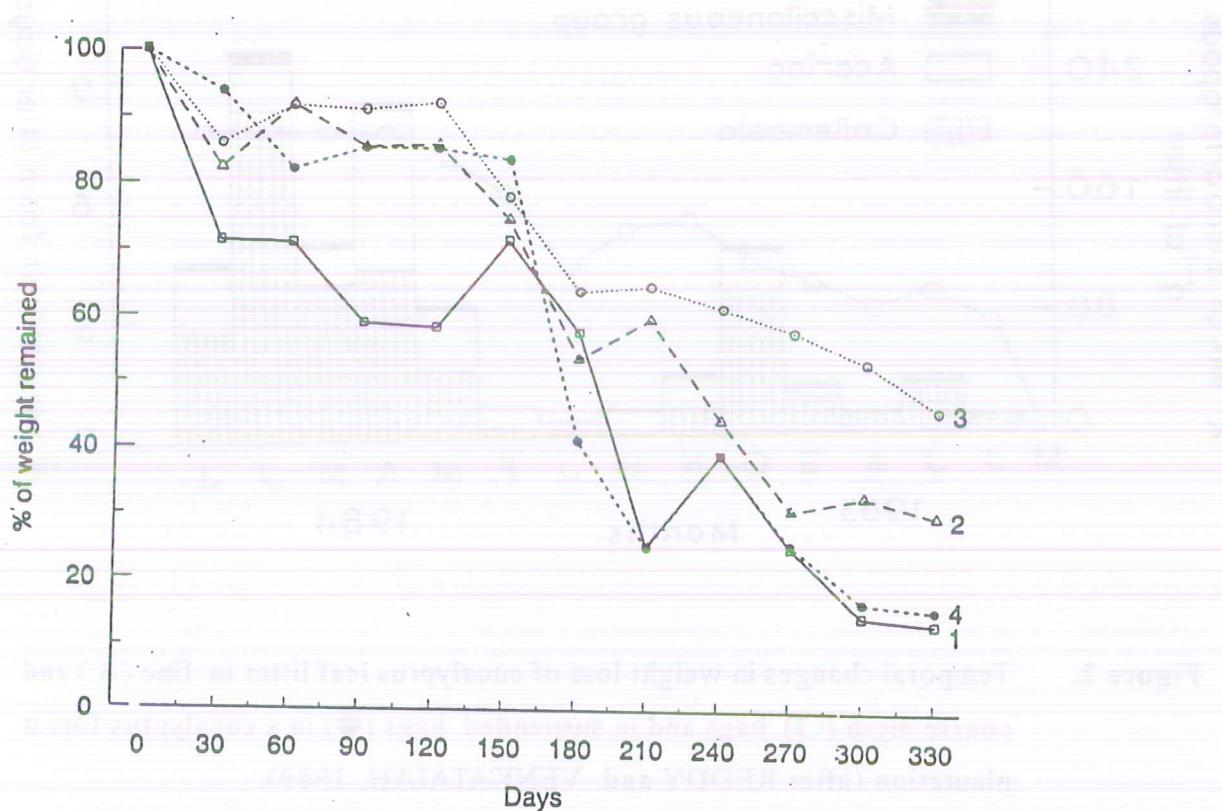


Figure 4. Temporal changes in mean concentration of N, K, Ca and Mg (percentage of dry mass) of the decaying needle litter on the floor of a pine forest plantation (after REDDY, 1989).

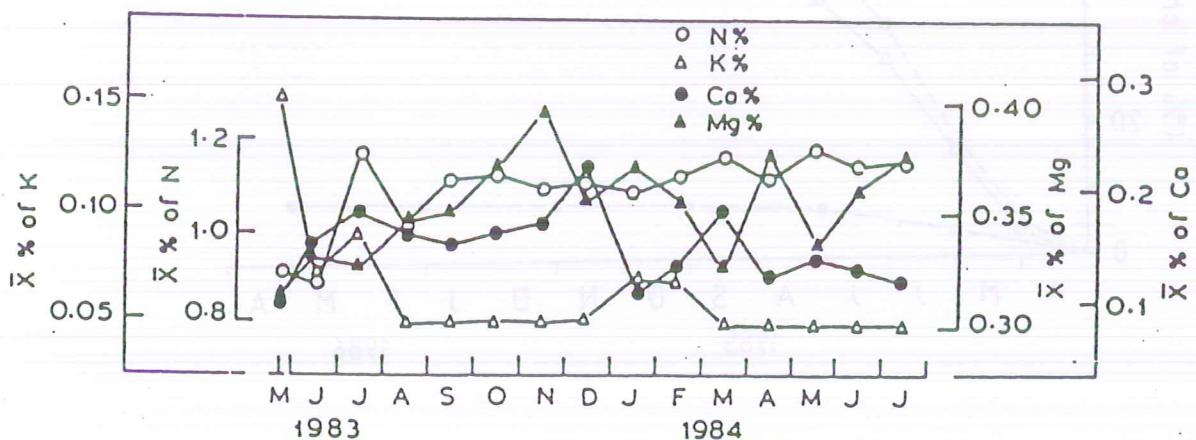


Figure 5. Temporal changes in concentration of (a) Ca and (b) N (% of dry mass) of leaf litter in fine (Δ) and coarse (\circ) mesh bags and in suspended (\bullet) bags in a eucalyptus forest plantation. (after REDDY and VENKATAIAH, 1989).

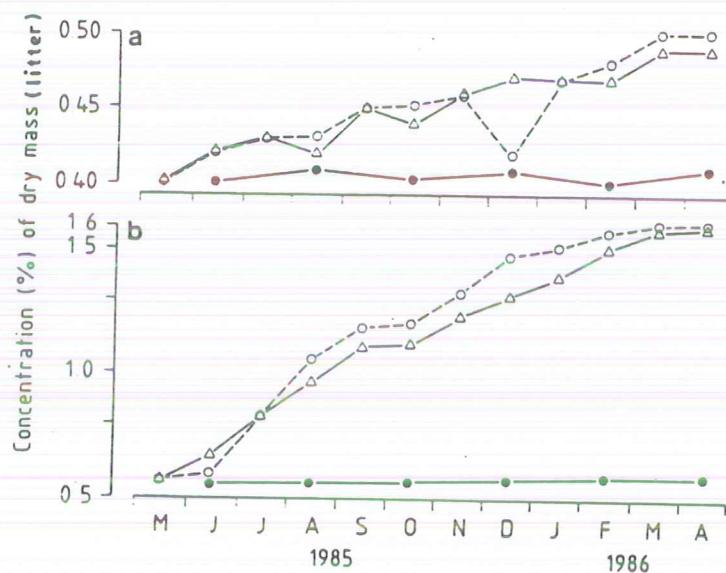
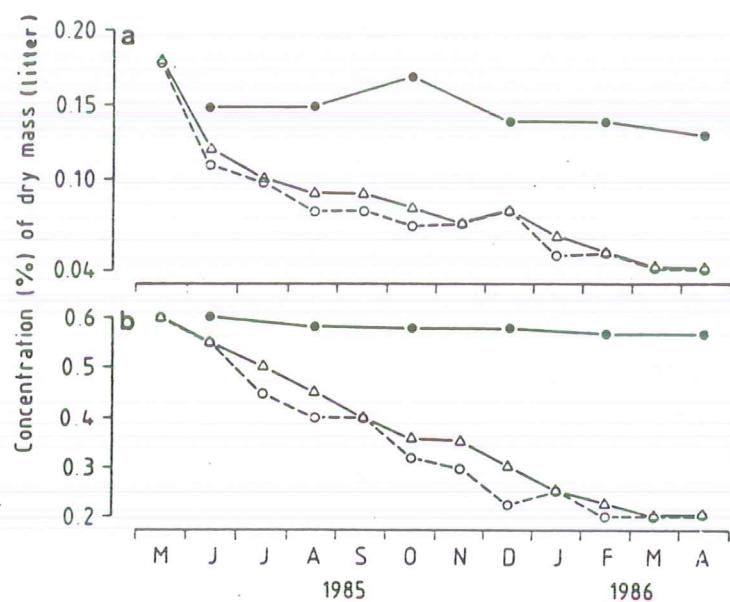


Figure 6. Temporal changes in the concentration of (a) K and (b) P (percentage of dry mass) of litter in fine (Δ) and coarse (\circ) mesh bags and in suspended (\bullet) bags in a eucalyptus forest plantation (after REDDY and VENKATAIAH, 1989).



NUTRIENT RETRANSLLOCATION DURING THE EARLY GROWTH OF TWO EXOTIC PLANTATION SPECIES

Wan Rasidah Kadir and O. Van Cleemput¹

ABSTRACT

Retranslocation of nutrients before leaf abscission is an important pathway of nutrient conservation. This article reports the extent of nutrient withdrawal by *Acacia mangium* Willd. and *Khaya ivorensis* A. Chev., before leaf fall. Our measurements, carried out based on the nutrient content in the intact green leaves and freshly fallen litter, showed that *A. mangium* confiscated back about 78 % of P compared to only 26 % by *K. ivorensis*. *A. mangium* could probably need some of these P for the N₂ fixation process beside for surviving on a soil with poor P availability. The fact that *A. mangium* took back about 22 % of N, which was far more higher than what has been taken back by *K. ivorensis*, is not fully understood as the former species has the capability to fix the atmospheric nitrogen. The withdrawal of K was about 13 % for both species and Mg was not retranslocated.

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1. INTRODUCTION

The productivity of plants can often be improved through proper manuring. In a situation where plants were not supplied with additional nutrients, they could turn to other strategies such as retranslocation to conserve sufficient amount of nutrients to overcome nutrient limitations. In a study carried out on deciduous forest species in the North America, Luxmore et al. (1981) observed a very rapid translocation of N, P, K, Ca and Mg to leaves during spring and a retranslocation back to the stem around June for N and P. This implies that internal cycling of nutrients can be very important in the forest ecosystem.

In December 1991, an experimental plot was set up in a newly established forest plantation to study the nutrient dynamics. Since our analysis carried out at different stand ages showed a considerable decline in the nutrient content in the leaf litter compared to the green leaves, this short study was conducted to quantify the percentage of nutrient retranslocation before leaf abscission.

2. MATERIALS AND METHODS

The study site, located at the Kemasul Forest Reserve ($3^{\circ} 28' N$ and $102^{\circ} 23' E$), comprised of 34-month-old *Acacia mangium* and *Khaya ivorensis* trees. A survey of the area showed that the soil belongs to the Batu Anam series (Aquoxic tropudult), developed from iron poor shales with heavy clay texture. The annual rainfall for the period of 1992 to 1995 ranged from 1521 mm to 2257 mm while the mean temperature was constant at $26^{\circ}C$.

The two species used in this study are both plantation species and are considered as fast growing. *A. mangium* is a nitrogen fixing tree, grows well on a wide range of soil. The best growth, however, was observed on a deep, fertile soil with rainfall of more than $2000 \text{ mm year}^{-1}$ (Zulkefli, 1989). This species is suitable for use in light construction applications, for board making and in the production of tannin (Chew et al., 1992). The other species studied, *K. ivorensis*, is also known as African mahogany. This species originated from the coastal area of West African rainforests. Its timber properties is only slightly inferior to the genuine mahogany. Growth performance under the Malaysian conditions is satisfactory with the height reached 26.2 m after 26 years of growth (Darus et al., 1991).

Foliar samples were collected from trees selected randomly in a 0.2 ha plot. Sampling were partitioned into three categories for *A. mangium* i.e. intact green leaves, intact yellow leaves and freshly fallen leaves. While for *K. ivorensis*, due to the limited availability of intact yellow leaves, only green leaves and freshly fallen leaves were sampled. These samples were dried, ground and extracted for the N content using Kjeldahl digestion and P, K, Mg and Ca contents using microwave digestion. Nitrogen and phosphorus were determined colorimetrically while K, Mg and Ca were quantified using inductively coupled plasma.

Nutrient withdrawal prior to leaf fall was measured based on the assumption that Ca is immobile the moment it reaches the leaves (Vitousek and Sanford, 1986). The following equation was used to estimate nutrient retranslocation.

$$\% \text{ retranslocation} = \frac{[\text{Nutrient/Ca}]_{\text{leaf litter}}}{[\text{Nutrient/Ca}]_{\text{green leaves}}} \times 100$$

3. RESULTS AND DISCUSSION

The related physical and chemical properties of the soil at various depths are presented in Table 1. pH values showed that the soil is acidic and this agrees well with the low exchangeable bases content. The overall chemical data showed that the nutrient content in this soil was rather low, particularly extractable P.

The percentages of nutrient retranslocation by *A. mangium* and *K. ivorensis* before leaf abscission were presented in Table 2. Both species have a different capacity to retranslocate nutrients. Generally, nitrogen fixing species tend to retranslocate less N due to the availability of N through biological nitrogen fixation (Cole, 1981). Measurements from this study, however, revealed the opposite. Almost half of the N present in the green leaves of *A. mangium* disappear when the leaves turn into yellow before abscission. When the leaves fall, 22 % N was estimated to be retranslocated back to the tree. On the other hand, the N content in the intact green leaves of *K. ivorensis* do not differ greatly compared with their corresponding litter. The trees retranslocated an average of 7 % of N.

The most pronounced withdrawal of all elements was found with phosphorus. This could be a strategy of these trees to survive in a soil with poor P availability. Values reported by Vitousek and Sanford (1986) were between 42 to 58 % for N and 67 to 69 % for P on an infertile Oxisol/Ultisol soils. In this study, the most distinct retranslocation was for *A. mangium*. Nearly 80 % of P in *A. mangium* was retranslocated compared to only 26 % by *K. ivorensis*. Many studies have confirmed the importance of P for biological nitrogen fixation. Sanginga et al. (1991) observed a significant increase in the nodule production by *Leucaena leucocephala* after P fertilization. In another study, P application increased the N concentration considerably in inoculated *Casuarina* but in N fertilized plants, the N concentration in the shoot decreased (Sanginga et al., 1989). *A. mangium* could have reserved some of these P for fixation besides plant growth. Why *A. mangium* retranslocates such a high amount of N is not fully understood considering the fact that it can fix nitrogen.

The other two nutrients, K and Mg, did not differ much between the two species. Both species returned back about 13 % of K, which seemed to be more important than N for *K. ivorensis*. However, Mg was not retranslocated.

4. ACKNOWLEDGEMENT

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Table 1: The properties of soil in the plantation area

Soil depth (cm)	pH	Clay (%)	C (%)	N (%)	C/N	Extr. P ($\mu\text{g g}^{-1}$)	Exch. cations			CEC ($\text{cmol}_{\text{C}} \text{ kg}^{-1}$)
							K	Ca	Mg	
0 - 5	4.60	32	0.73	0.10	7.3	1.84	.16	n.d.	.07	4.75
5 - 15	4.45	32	0.63	0.09	7.0	1.70	.16	.21	.15	3.35
15 - 30	4.47	44	0.34	0.07	4.9	1.25	.10	.07	.06	2.28
30 - 45	4.42	44	0.22	0.06	3.7	1.20	.08	.03	.02	3.62

Table 2: Selected nutrient contents (g kg^{-1}) in *Acacia mangium* and *Khaya ivorensis* leaves before and after senescence

Parameter	Types of leaves			% estimated
	Intact green	Intact yellow	Freshly fallen	
<u><i>Acacia mangium</i></u>				
Nitrogen	21.80 ± 0.69	13.61 ± 0.39	12.84 ± 0.20	22.3
Phosphorus	0.60 ± 0.05	0.18 ± 0.04	0.10 ± 0.00	78.0
Potassium	10.22 ± 0.87	6.82 ± 0.79	6.77 ± 0.82	12.6
Magnesium	1.03 ± 0.07	1.17 ± 0.15	0.92 ± 0.06	-17.8
Calcium	8.48 ± 0.51	9.32 ± 0.57	6.43 ± 0.11	
<u><i>Khaya ivorensis</i></u>				
Nitrogen	11.37 ± 1.15		10.16 ± 2.03	7.3
Phosphorus	0.35 ± 0.03		0.25 ± 0.03	25.9
Potassium	2.80 ± 0.28		2.35 ± 0.95	13.0
Magnesium	2.20 ± 0.35		2.70 ± 0.28	-27.3
Calcium	2.24 ± 0.07		2.16 ± 0.00	

(results are mean of six replicates for *Acacia mangium* and four replicates for *Khaya ivorensis*).

DISTRIBUTION CHARACTERISTICS OF MINERAL ELEMENTS IN TREES OF TROPICAL RAIN FOREST, WEST SUMATERA, INDONESIA

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ABSTRACT

Indonesia. The elemental composition of the leaves and the barks. The distribution characteristics of mineral elements in trees and soils were studied on a 1ha permanent plot at Mt. Gadut area near Padang, West Sumatera, were analysed. Most elements, such as S, K, Al, C1, Si, B and Sr, showed significant correlation between leaves and barks, suggesting that barks can also be used instead of leaves as the first approximation. The concentrations of elements in 457 barks showed quite a wide range indicating the enormous diversity of absorption characteristics of mineral elements among these tree species. The concentrations range in mg kg⁻¹ were Mn (0.1-3800), Sr (0.1-1070), Si (2-1700), Fe (0.6-4100), Al (10-46000), Mg (10-7200), Zn (0.4-290), K (60-22000), Cu (0.8-150), P (19-2540), Cl (110-9200), S (170-13600), Ca (2300-100000), B (4-70) and Na (130-700). The DBH (diameter at breast height) showed negative correlation with S, Ca, Mg, and Zn. Among the tree species, accumulators were *Mallotus glaberrimus* for S, *Evodia latifolia* for K and B, *Eurya acuminata* and *Memecylon laurinum* for Al, *Ficus ribes* for Ca and Sr, *Macaranga triloba* for Mg, *Mallotus affinis* for Si and *Aquilaaria malaccensis* for Mn and Zn. "accumulator" and "excluder" are defined as the trees which had the highest concentrations for the top and bottom 20 respectively among the 457 trees. The distribution patterns of the "accumulators" and "excluders" for S and K were influenced by available nutrient levels in soil. The spacial distributions of "excluders" and "accumulators" were exclusive for Sr, Cu and Mg. On the other hand the spacial distribution patterns of "excluder" and "accumulators" for Al, Ca and Si were complex, which need more detail examinations.

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INTRODUCTION

The diversity of tree species of tropical rain forest is high. The number of tree species often reaches over 200 per ha (HUSTON, 1994). In our study site, it is estimated to be 300 species (HOTTA, 1992). Consequently the forest stands are quite complicated and form complex tree community. There are many studies on the spacial distribution pattern of representative tree species (ITOH et al., 1995, KAJI and SUZUKI, 1994, KOHYAMA and SUZUKI et al., 1994, ERIZAL et al., 1992, SUZUKI and KOHYAMA, 1991, and HUBBELL et al., 1990).

The tree community is affected by various factors, the distribution characteristics of mineral elements in both trees and soils being the major factors. There are some reports on the dynamics of mineral nutrients in tropical rain forest (MO et al., 1994, JORDAN, 1983, ASHTON, 1982). However, there seems to be few papers on the relationship between the structure of tree community and the distribution characteristics of mineral elements in both trees and soils.

In this study we analysed the various mineral elements such as S, K, Al, Ca, Mg, Cl, Si, Na, B, Cu, Fe, Mn, P, Sr and Zn in 457 trees and 115 soils from a 1ha long-term tropical forest observation plot, Pinang Pinang, West Sumatra, Indonesia (HOTTA, 1984, 1986, 1989). Since the sampling of plant leaves are difficult in tall tropical forest trees, mainly barks were collected.

The results of mineral element distribution characteristics were discussed with the following view points; correlation between barks and leaves, comparison with temperate forest, definition of accumulator and excluder species, spacial distribution of accumulator and excluder in the plot, and the influence of available element status in soils.

MATERIALS AND METHODS

This study was conducted in a 1 ha long-term observation plot, Pinang Pinang, established by HOTTA and OGINO et al. in 1980 (HOTTA, 1984, 1986, 1989). The plot

was located at a foothill Depterocarp forest in Mt. Gadut area 18 km east of Padang, West Sumatra. The plot is divided into 115 subplots with a 10m X 10m grid. The trees with over 8 cm in diameter at breast height (DBH) were numbered and recorded. Various ecological observations, including DBH and tree height measurement were started in 1981. During 1981 to 1987, tree mortality (% per year) and recruitment (% per year) were 0.95 and 1.92. Hence turnover rate was 1.44 (PHILLIPS and GENTRY, 1994, HOTTA, 1984, 1989). The Pinang Pinang plot is on a hill top, which is partly narrow and partly broad ridge at 550 m altitude. Annual rainfall exceeds 5000 mm. Soils are relatively young Typic Dystropepts, developed from andesite and limestone. Details soil characterization were made by WAKATSUKI et al. (1986) and KUBOTA et al (1995).

SAMPLING

Leaves and barks for all trees with over 10 cm of DBH in the plot were sampled during June-July 1990 and September-October 1991. However, leaf samples could only be collected from trees lower than 10m high. Bark samples included inner and outer bark. Soil samples were collected at 5-15 cm depth from five points for each subplots. A composite sample was made for each subplot.

ANALYSIS

The leaves and the barks were analysed as follows. Samples were dried in oven at 80 °C, and then broken into powdery form by tungsten carbide vibrating mixer mill. Total elemental concentrations of S, K, Al, Ca, Mg, Si, Na, B, Cu, Fe, Mn, P, Sr and Zn were measured by inductively coupled plasma atomic emission spectrometry (ICP) using Shimazu ICPS-2000 after digestion with nitric acid in a high pressure Teflon vessel (QUAKER et al., 1970, KAYO and SOUTH, 1987). The chlorine ion concentration was measured by thiocianate method (ADRIANO, 1982). Available forms of elements in soils were extracted by 0.1N HCl (Soil to solvent ratio of 1:10), and analysed on ICPS-2000.

RESULTS AND DISCUSSIONS

Leaves and barks

Table 1 shows the mean concentrations, standard deviations, std., and correlation ranges of leaves and barks from 42 trees in the plot. The analytical results of the leaves from temperate Beech Forest in Mt. Sanbe, Japan (NASU, 1983) are also shown for comparison. The concentrations of K, Mg, Cl, Si, Na and Sr in the leaves from Beech forest were higher than those of Pinang Pinang Plot, where as Fe and Mn were lower. The levels of concentrations of the other elements were about the same.

Although the concentrations of Al, Ca and Sr in the barks were slightly higher than those in the leaves, most of the other elements were higher in the leaves. In general the leaf is considered better than the bark in studying the characteristics of mineral composition in the tree. However, in Tropical Rain Forest most trees are too tall to collect sufficient leaf samples. It will require enormous labor and skill to collect enough leaves. Therefore, in order to validate the use of bark samples instead of leaves, we calculated the correlation coefficients of elements in the barks with that of the leaves (Table 2). The concentrations of S, K, Al, Cl, Si, B and Sr showed significant correlation and Na had a negative correlation. However, Ca, Mg, Cu, Fe, Mn, P and Zn did not show any significant correlation. These results suggest, at least as our first approximation that the composition in the bark can be used for the characterization of mineral elements in tropical rain forest trees.

Mineral composition in the barks

Table 3 shows the analytical results of mineral elements in 457 bark samples. The order of the mean concentration of the elements showed that Ca was highest and B lowest, i.e., Ca > K > Al > S > Cl > Mg > Si > Mn > Na > P > Fe > Sr > Zn > Cu > B. The order of the coefficients of variation were Si > Al > Fe > Zn > Mn > Sr > P > Cu > B > Mg > S > Cl > K > Ca > Na. The concentration range in mg kg⁻¹ were Mn (0.1-3800), Sr (0.1-1070), Si (2-1700), Fe (0.6-4100), Al (10-46000), Mg (10-7200), Zn (0.4-290), K (60-22000), Cu (0.8-150), P (19-2540), Cl (110-9200), S (170-13600), Ca (2300-100000), B (4-70) and Na (130-700) respectively. The extremely high variation in the concentrations indicate the

enormous diversity of mineral element absorption characteristics in the trees even in a merely 1ha plot.

Fig.1 shows the frequency distributions of both normal and logarithmic concentration of elements in the barks. The logarithmic transformation gave shapes more similar to normal distribution pattern than those of concentrations themselves. The frequency distribution of logarithmic concentrations of Si showed 3 peaks around 3.5, 2 and less than 1. Frequency distribution of Ca also showed three peaks around 3%, 5% and 9%. Some tree species in the plot may accumulate or exclude these elements than the other trees.

Table 4 shows the correlation coefficient of elemental concentration and DBH in the barks. Correlations of Ca-Sr and B-P were extremely high. The high correlations between Ca and Sr in soils is well known (WAKATSUKI, 1978). The effect of B on P uptake at the root tips of faba bean and maize has been reported (POLLARD et al., 1977). In tropical trees also, similar physiological mechanism may apply. Phosphorus showed strong correlation with Zn, K and Cu. Potassium showed significant correlations with S, B and Mg. Correlations among Zn-Ca, Zn-Mg, Zn-B and Zn-Mn were strong. It was interesting that Al showed significant correlation with S, which is a metallothionein element. The DBH showed negative correlations with the concentrations of most elements, especially S, Ca, Mg and Zn at 1% level of significance. This negative correlation was probably due to the dilution in concentration of elements in the bark as the tree was growing.

Accumulator

An accumulator is defined as a tree which had a concentration higher than the mean + 2std. Table 5 shows the accumulator tree species which had more than two analyses in the same species. The percentages of accumulator among the same species were calculated as the quotient of accumulator in each species in Table 5. Fifteen species were picked up. Five out of the fifteen species accumulated two elements, i.e. *Mallotus glaberrimus* for S and Si, *Evodia latifolia* for K and B, *Ficus ribes* for Ca and Sr, *Grewia florida* for Mg and Zn and *Aquilaria malaccensis* for Mn and Zn. The number of accumulator trees were between 1 and 3 for all species in the 1ha plot, except for *Mallotus glaberrimus* which had 6 accumulator trees for S and 5 for Si. Most of the quotients were more than 50% in Table 5, such as

Mallotus glaberrimus for S and Si, *Evodia latifolia* for Al and B, *Memecylon laurinum* for Al, *Ficus ribes* for Ca and Sr, *Macaranga triloba* for Mg, *Meliosma lepidota* for Mg, *Mallotus affinis* for Si, and *Aquilaria malaccensis* for Mn and Zn. These tree species may be true accumulators. However since the quotients of accumulators were less than 50%, such as *Mastixia trichotoma* for Al, *Grewia florida* for Mg and Zn, *Cleistanthus glandulosus* for Fe, *Artocarpus glaucus* for Si, *Nephelium mutabile* for Mn, and *Parashorea lucida* for Sr, these trees may not be true accumulators. There may be problems for the identification of some tree species.

Table 6 shows the mean concentrations of true accumulator species. Bold-letters indicate concentrations higher than the mean + 2std. In addition to these species the following species may also be accumulators, as they had concentrations higher than the mean + 3std (even though only one bark sample of each species was used for analysis). These are *Aporusa maingayi*, *Macaranga triloba*, *Gomphandra javanica*, *Memecylon laurinum* and *Pellacalyx axillaris* for S, *Macaranga triloba*, *Barringtonia n**, *Pellacalyx axillaris*, *Grewia florida*, *Dendrocnide stimulans*, *Chisocheton macranthus* and *Aglaia n** for K, *Aporusa frutescens*, *Diospyros n**, *Cleistanthus glandulosus*, *Aporusa maingayi* and *Trema angustifolia* for Al, *Grewia florida*, *Ficus lepicarpa* and an unknown species for Ca, *Dysoxylum n**, *Aglaia n**, *Dendrocnide stimulans*, *Aglaia argentea* and an unknown species for Mg, *Barringtonia pendula*, *Urophyllum macrophyllum*, *Barringtonia n**, *Madhuca n**, *Dysoxylum n** and *Gomphandra javanica* for Cl, *Madhuca sericea*, *Swintonia schwenkii*, *Durio griffithii*, *Cleistanthus glandulosus*, *Castanopsis n**, *Streblus elongata*, *Artocarpus heterophyllus*, *Shorea n**, *Canarium n** and two unknown species for Si, *Diospyros diepenhorstii*, *Diospyros n**, *Mallotus affinis*, *Lithocarpus elegans*, *Cryptocarya scortechinii* and *Eurya acuminata* for Na, *Stychnos n**, *Eugenia opaca*, *Gonocaryum macrophyllum*, *Callicarpa arborea*, *Memecylon n**, *Ficus n**, *Dysoxylum n** and two unknown species for B, *Melanochyla n**, *Mastixia trichotoma*, *Eugenia opaca*, *Gonocaryum macrophyllum*, *Pellacalyx axillaris* and an unknown species for Cu, *Ficus lepicarpa* and an unknown species for Fe, *Garcinia parvifolia* and *Didymocheton n** for Mn, *Eugenia opaca* and *Gonocaryum macrophyllum* for P, *Swintonia schwenkii*, *Uncaria n**, *Anthocephalus*

* n = not identified

chinensis and an unknown species for Sr, *Didymocheton n**, *Gonocaryum macrophyllum*, *Eugenia opaca*, *Swintonia schwenkii*, *Cleistanthus glandulosus* and an unknown species for Zn.

Table 7 shows the correlation coefficients of elements and DBH in three accumulator species. *Mallotus glaberrimus* is an accumulator of S and Si. Sulfur correlated with K and Mg. Silicon did not show any significant correlation. The DBH had no clear correlation with S and Si. This means that accumulation of both elements may occur at any growth stage of tree. *Eurya acuminata* is an accumulator of Al. The DBH showed negative correlation with Al. This means that young active plants need more Al suggesting its characteristic nature as an essential nutrient element. *Macaranga triloba* is an accumulator of Mg. The DBH showed positive correlation with Mg.

Spacial distribution of "accumulator" and "excluder"

Fig.2a and 2b shows the spacial distribution patterns of "accumulators" and "excluders". The "accumulators" are shown in black squares and "excluders" in cross marks (Fig. 2a and 2b). The "accumulators" and "excluders" are defined as the trees which had the highest concentrations for the top and bottom 20 among the 457 trees respectively. For Si and Cu, since the number of trees with the concentrations lower than the quantitative detection limits were more than 20, these were plotted. Most of the "accumulators" of K, Ca, Sr and Cu were distributed at middle part of the plot, whereas the "excluders" were distributed at both ends. So spacial separation of "accumulator" and "excluder" is clear, especially for K, Sr and Cu. These results suggest that the absorption characteristics of mineral nutrient of trees has an influence on the spacial distribution of the trees.

Although spacial distribution of "accumulators" and "excluders" in the plot seems random for S, Al and Si, it seems an "accumulator" is surrounded by non-accumulators or "excluders" to keep some distance between "accumulators". This trend is probably to avoid competition for enough elements between trees and/or a consequence of that competition.

Fig.3 shows 0.1N HCl extractable elements in soils, 5-15 cm depth. Soils rich in available S, K, Cu and Sr seem to attract "accumulators", whereas Al, Si and Ca shows no such trend. The trend of Al, Si and Ca shows that some "accumulators" actively absorb

specific elements from the soils even in poor soils. That means there are two accumulator types, an active and a passive one. Most "excluders" of S, K, Sr and Cu were distributed at the subplots poor in these elements. This trend indicates that the distributions of "excluders" were controlled, at least partly, by the status of the available elements in the soil.

The spacial distribution of trees is decided by various factors, the resource requirements of each tree species which is mainly genetically controlled, the environmental conditions, and interactions among trees. Consequently the structure of the tree community is quite complex. No single rule can be applicable directly. The results of this study suggest some guidelines in characterizing the elements distributions of elements in trees. However, more detail studies are necessary to elucidate the ecological implications of the relationships between spacial distribution patterns of trees and the distribution characteristics of mineral elements in both trees and soils.

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Table 1. The elemental composition of leaves and barks* from Pinang Pinang plot in comparison with leaves from Beech Forest, Japan**

	%						mg kg ⁻¹									
	S	K	Al	Ca	Mg	Cl	Si	Na	B	Cu	Fe	Mn	P	Sr	Zn	
leaves*																
Mean	0.341	0.895	0.131	2.19	0.308	0.261	831	225	28.7	4.3	350	786.5	731	14.8	23.0	
Std.	0.193	0.496	0.233	0.85	0.129	0.207	2338	166	30.7	6.8	203	710.2	319	16.6	29.3	
Min	0.111	0.298	0.001	0.70	0.105	0.101	2	131	3.9	0.8	77	44.0	207	0.1	2.2	
Max	1.150	2.627	0.954	5.04	0.603	1.190	13810	674	136.1	39.8	925	3035.0	1619	80.5	167.5	
barks*																
Mean	0.182	0.520	0.182	2.89	0.135	0.140	424	165	5.5	2.0	71	201.6	87	31.2	11.9	
Std.	0.137	0.273	0.219	1.40	0.130	0.108	1477	81	3.1	3.9	57	238.9	122	35.1	27.2	
Min	0.050	0.140	0.001	0.65	0.026	0.009	2	131	3.9	0.8	2	0.1	19	0.1	0.4	
Max	0.632	1.147	0.931	5.77	0.711	0.576	8440	476	16.9	19.6	240	880.5	662	141.9	158.1	
leaves from Beech forest**																
Mean	0.28	1.78	0.08	1.70	0.67	0.73	4970	1300	-	1.2	30	339.1	1200	156.9	49.7	
Std.	0.13	0.80	0.18	0.65	0.13	0.41	7170	1030	-	1.4	35	223.9	141	82.1	57.1	
Min	0.10	0.35	0.00	0.84	0.46	0.16	100	15	-	1.0	1	2.5	900	51.0	0.5	
Max	0.75	3.99	1.16	3.48	1.16	2.10	33700	4400	-	12.0	133	1239.0	1700	371.0	260.0	

* leaves and barks, n=42

** n=102, data from NASU (1983)

Table 2. Correlation coefficient of elements between the leaves and the barks from Pinang Pinang Plot (n=42)

	S	K	Al	Ca	Mg	Cl	Si	
Corelation coefficient	0.69***	0.43**	0.80***	0.02	0.04	0.57***	0.91***	
	Na	B	Cu	Fe	Mn	P	Sr	Zn
	-0.31*	0.59***	0.11	0.03	-0.07	-0.12	0.60***	0.21

*** > 0.1% > ** > 1% > * > 5%

Table 3. The results of analyses of elements in the barks from Pinang Pinang Plot (n=457)

	% S K Al Ca Mg Cl						mg kg ⁻¹ Si Na B Cu Fe Mn P Sr Zn								
	0.144	0.410	0.201	2.69	0.116	0.124	804	168	9.3	9.7	120	301.3	139	65.9	17.1
Mean	0.126	0.289	0.478	1.50	0.109	0.100	2200	68	9.1	10.8	227	429.4	181	86.2	24.7
Std.	0.017	0.006	0.001	0.23	0.001	0.011	2	131	3.9	0.8	1	0.1	19	0.1	0.4
Min	1.358	2.212	4.589	10.03	0.724	0.922	16960	700	69.6	149.2	4126	3797.8	2540	1071.5	285.0
Max	88	70	238	56	94	81	274	40	98	111	189	143	131	131	144
Coefficient of variations*															

* (%)

Table 4. Correlation coefficient of elements and DBH in the barks from Pinang Pinang Plot (n=457)

	S	K	Al	Ca	Mg	Cl	Si	Na	B	Cu	Fe	Mn	P	Sr	Zn	DBH
S	1															
K	0.383	1														
Al	0.276	-0.034	1													
Ca	0.131	0.088	0.154	1												
Mg	0.195	0.299	-0.052	0.145	1											
Cl	0.113	0.169	-0.042	0.006	0.114	1										
Si	0.132	-0.001	-0.003	-0.103	0.016	0.034	1									
Na	0.000	0.024	0.065	0.004	0.015	-0.014	-0.036	1								
B	0.113	0.372	-0.017	0.131	0.216	0.070	0.047	0.154	1							
Cu	-0.004	0.039	-0.049	-0.034	0.093	0.022	-0.006	0.044	0.105	1						
Fe	0.108	0.094	0.106	0.142	0.120	0.163	0.102	-0.028	0.111	0.037	1					
Mn	0.100	-0.006	-0.035	0.130	0.155	0.076	0.059	0.039	0.065	-0.045	0.018	1				
P	0.153	0.332	0.176	0.122	0.222	0.059	-0.061	0.122	0.533	0.273	0.118	0.035	1			
Sr	-0.029	0.052	0.020	0.562	0.073	0.016	-0.031	-0.005	0.128	0.001	0.016	-0.002	0.072	1		
Zn	0.085	0.154	0.088	0.273	0.287	0.066	0.052	0.100	0.355	0.096	0.171	0.319	0.390	0.116	1	
DBH	-0.161	-0.113	-0.091	-0.149	-0.162	-0.057	-0.057	0.021	-0.100	-0.092	-0.066	-0.075	-0.077	-0.108	-0.140	1

Significant at 1% level are expressed by bold-letters.

Table 5. Accumulator tree species

Element	Species	Accumulator	Analysed	Quotient of Accumulator (%)
		n	n	
S	<i>Mallotus glaberrimus</i>	6	9	67
K	<i>Evodia latifolia</i>	2	2	100
Al	<i>Eurya acuminata</i>	3	4	75
	<i>Memecylon laurinum</i>	2	2	100
	<i>Mastixia trichotoma</i>	2	18	11
Ca	<i>Ficus ribes</i>	2	2	100
Mg	<i>Grewia florida</i>	3	15	20
	<i>Macaranga triloba</i>	3	5	60
	<i>Meliosma lepidota</i>	2	3	67
Si	<i>Mallotus affinis</i>	2	3	67
	<i>Mallotus glaberrimus</i>	5	9	56
	<i>Artocarpus glaucus</i>	2	7	29
B	<i>Evodia latifolia</i>	2	2	100
Fe	<i>Cleistanthus glandulosus</i>	2	15	13
Mn	<i>Aquilaria malaccensis</i>	2	2	100
	<i>Nephelium mutabile</i>	2	6	33
Sr	<i>Ficus ribes</i>	2	2	100
	<i>Parashorea lucida</i>	3	7	43
Zn	<i>Aquilaria malaccensis</i>	2	2	100
	<i>Grewia florida</i>	2	15	13

Table 6. Mean concentration of elements of accumulator species

Species		n	% DBH S K Al Ca Mg Cl							mg kg ⁻¹ Si Na B Cu Fe Mn P Sr Zn								
			13.9	0.488	0.512	0.150	3.93	0.192	0.065	5149	153	13.2	7.7	157	624	154	74.4	19.2
Mallotus	glaberrimus	9	41.3	0.074	1.194	0.110	2.34	0.155	0.159	2	150	47.2	11.5	102	52	496	75.4	61.3
Eurya	acuminata	4	17.4	0.374	0.189	1.670	4.15	0.108	0.155	52	252	7.9	7.6	159	248	268	78.9	17.3
Memecylon	laurinum	2	13.5	0.720	0.270	2.263	2.33	0.112	0.089	2	135	19.6	9.2	183	22	376	58.3	39.5
Ficus	ribes	2	14.8	0.141	0.747	0.205	8.23	0.081	0.326	1115	135	11.1	9.0	113	54	254	746.8	18.2
Macaranga	triloba	5	20.5	0.362	0.691	0.120	3.35	0.386	0.110	974	148	12.6	11.5	117	854	209	29.9	37.9
Meliosma	lepidota	3	13.6	0.110	0.595	0.048	1.36	0.389	0.150	257	189	17.3	11.7	117	212	172	33.3	1.4
Mallotus	affinis	3	10.1	0.122	0.236	0.065	1.58	0.137	0.155	10400	297	5.2	9.9	184	532	19	19.3	20.3
Artocarpus	glaucus	7	15.8	0.127	0.348	0.012	0.76	0.105	0.100	6415	131	14.1	5.2	119	1062	160	20.5	6.8
Aquilaria	malaccensis	2	34.8	0.121	0.669	0.155	5.39	0.129	0.308	101	226	11.7	10.3	113	3186	347	190.5	200.1
Parashorea	lucida	7	17.5	0.053	0.120	0.115	3.35	0.028	0.067	60	196	7.7	8.8	50	76	134	255.7	11.4

The bold-letters indicates tree species with concentrations greater than the mean + 2std.

Table 7. Correlation coefficient of elements and dbh for each accumulator species
Mallotus glaberrimus (n=9)

	S	K	Al	Ca	Mg	Cl	Si	Na	B	Cu	Fe	Mn	P	Sr	Zn	DBH
S	1															
K	0.851	1														
Al	0.192	0.382	1													
Ca	-0.553	-0.801	-0.668	1												
Mg	0.894	0.853	0.181	-0.729	1											
Cl	-0.041	-0.429	-0.554	0.811	-0.379	1										
Si	-0.143	-0.346	-0.486	0.504	-0.228	0.464	1									
Na	0.600	0.573	0.757	-0.736	0.558	-0.399	-0.562	1								
B	0.213	0.502	0.698	-0.806	0.422	-0.817	-0.673	0.553	1							
Cu	0.718	0.499	0.126	-0.457	0.762	-0.044	-0.342	0.543	0.313	1						
Fe	0.714	0.690	0.269	-0.549	0.639	-0.282	-0.118	0.581	0.327	0.216	1					
Mn	0.494	0.567	0.059	-0.174	0.312	0.095	0.437	-0.033	-0.165	-0.107	0.393	1				
P	0.634	0.759	0.561	-0.707	0.603	-0.502	-0.286	0.631	0.617	0.171	0.906	0.413	1			
Sr	-0.124	0.144	-0.173	0.068	-0.070	-0.024	0.126	-0.461	-0.212	-0.249	-0.432	0.468	-0.302	1		
Zn	-0.210	-0.282	-0.154	0.419	-0.213	0.133	0.217	-0.305	-0.311	-0.415	-0.073	0.056	-0.059	0.205	1	
DBH	0.064	-0.172	-0.355	0.359	-0.111	0.416	0.131	0.063	-0.629	-0.185	0.249	-0.043	-0.093	-0.207	0.308	1

Eurya acuminata (n=4)

	S	K	Al	Ca	Mg	Cl	Si	Na	B	Cu	Fe	Mn	P	Sr	Zn	DBH
S	1															
K	0.888	1														
Al	0.838	0.830	1													
Ca	0.620	0.228	0.207	1												
Mg	-0.735	-0.892	-0.490	-0.245	1											
Cl	-0.439	-0.755	-0.299	0.132	0.919	1										
Si	-0.890	-0.706	-0.927	-0.530	0.378	0.071	1									
Na	0.873	0.559	0.574	0.918	-0.458	-0.071	-0.804	1								
B	0.901	0.719	0.927	0.538	-0.399	-0.090	-1.000	0.812	1							
Cu	-0.725	-0.572	-0.923	-0.319	0.160	-0.089	0.954	-0.612	-0.947	1						
Fe	-0.571	-0.132	-0.383	-0.885	-0.051	-0.440	0.701	-0.864	-0.699	0.613	1					
Mn	-0.906	-0.714	-0.916	-0.564	0.401	0.085	0.999	-0.830	-1.000	0.939	0.716	1				
P	0.920	0.969	0.941	0.264	-0.757	-0.577	-0.847	0.619	0.855	-0.757	-0.279	-0.848	1			
Sr	-0.712	-0.901	-0.906	0.105	0.658	0.610	0.691	-0.295	-0.696	0.688	-0.026	0.679	-0.930	1		
Zn	0.064	0.133	0.589	-0.426	0.294	0.257	-0.438	-0.158	0.421	-0.681	-0.008	-0.396	0.321	-0.526	1	
DBH	0.166	-0.154	-0.360	0.823	-0.101	0.135	0.041	0.554	-0.030	0.273	-0.548	-0.001	-0.219	0.551	-0.823	1

Macaranga triloba (n=5)

	S	K	Al	Ca	Mg	Cl	Si	Na	B	Cu	Fe	Mn	P	Sr	Zn	DBH
S	1															
K	0.902	1														
Al	0.263	0.040	1													
Ca	0.113	-0.004	0.824	1												
Mg	-0.798	-0.902	-0.351	-0.210	1											
Cl	-0.710	-0.470	-0.810	-0.456	0.650	1										
Si	-0.699	-0.655	-0.097	-0.385	0.431	0.250	1									
Na	-0.107	-0.285	-0.062	-0.577	0.231	-0.176	0.683	1								
B	-0.818	-0.838	0.338	0.365	0.537	0.204	0.651	0.080	1							
Cu	0.163	0.373	-0.903	-0.733	-0.009	0.546	-0.264	-0.089	-0.696	1						
Fe	-0.643	-0.653	-0.018	-0.356	0.421	0.149	0.992	0.749	0.641	-0.329	1					
Mn	-0.669	-0.636	0.445	0.638	0.341	0.156	0.331	-0.312	0.916	-0.700	0.305	1				
P	-0.794	-0.786	0.326	0.267	0.450	0.159	0.761	0.195	0.981	-0.684	0.750	0.858	1			
Sr	-0.417	-0.565	0.751	0.776	0.241	-0.237	0.250	-0.124	0.845	-0.930	0.283	0.895	0.786	1		
Zn	-0.803	-0.718	0.276	0.444	0.430	0.309	0.504	-0.196	0.952	-0.595	0.463	0.973	0.919	0.804	1	
DBH	-0.056	-0.212	-0.547	-0.355	0.600	0.434	-0.295	0.040	-0.318	0.519	-0.284	-0.392	-0.436	-0.385	-0.382	1

Significant at 1% (for dbh at 10%) level are expressed by bold-letters.

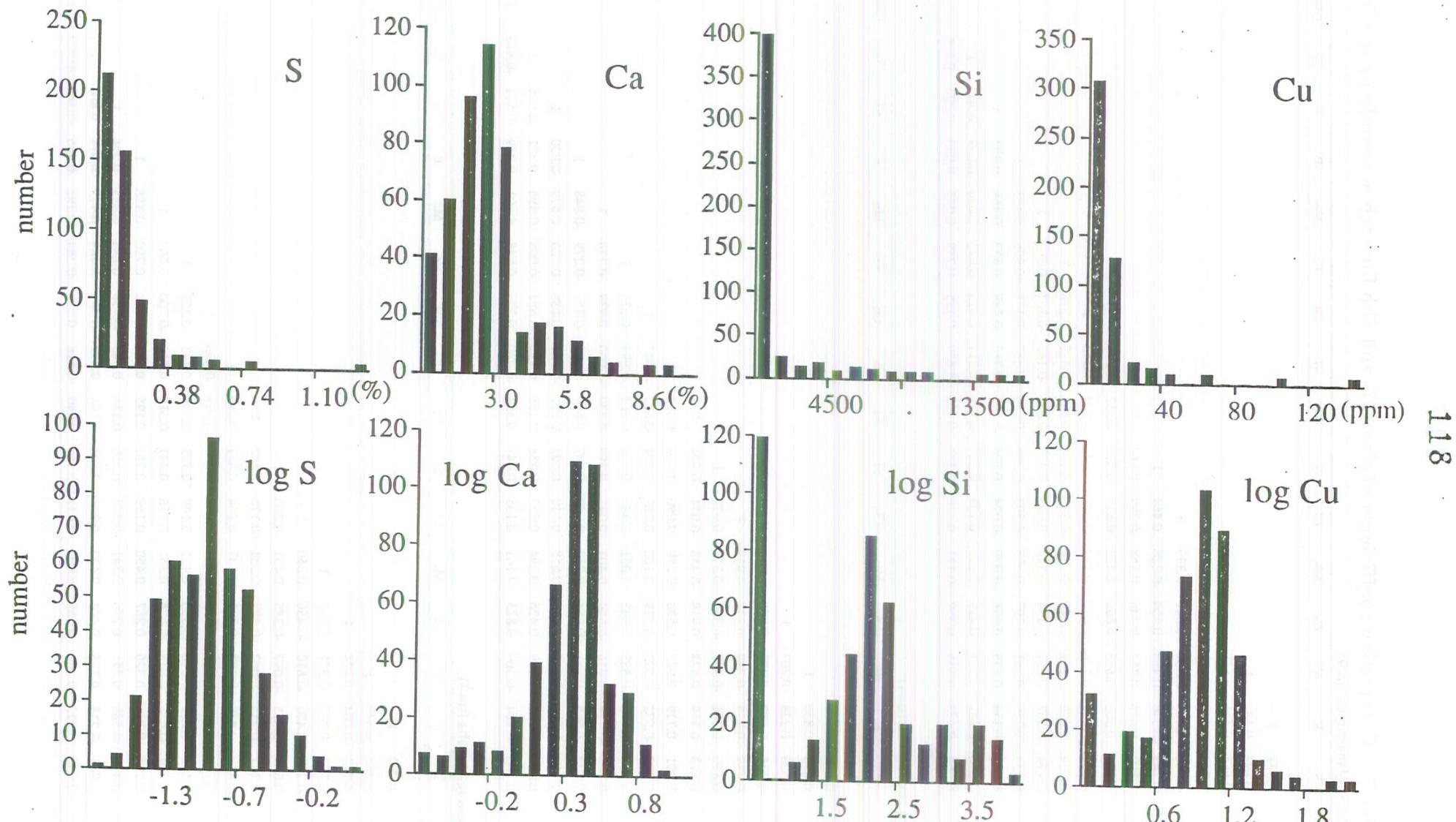
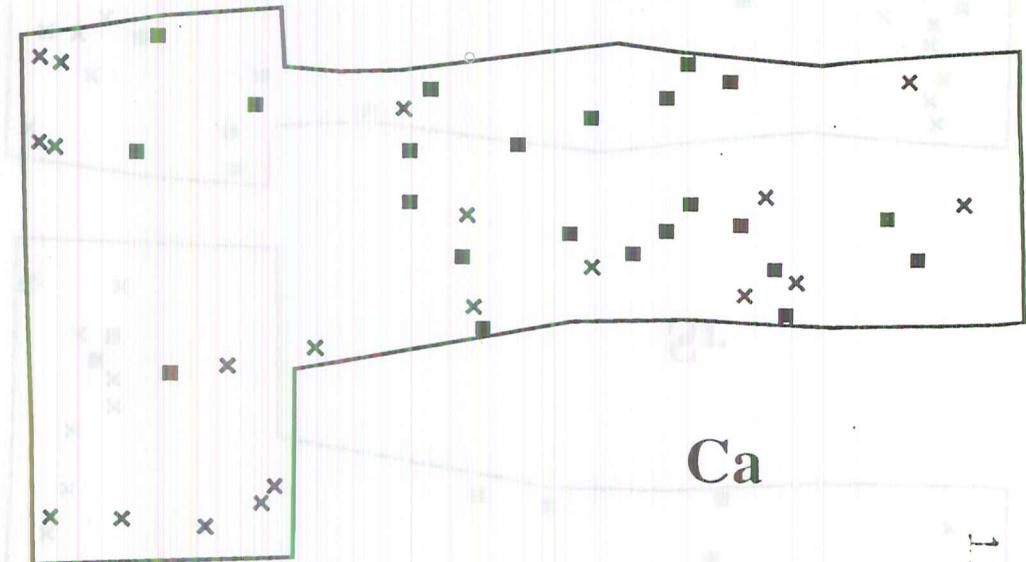
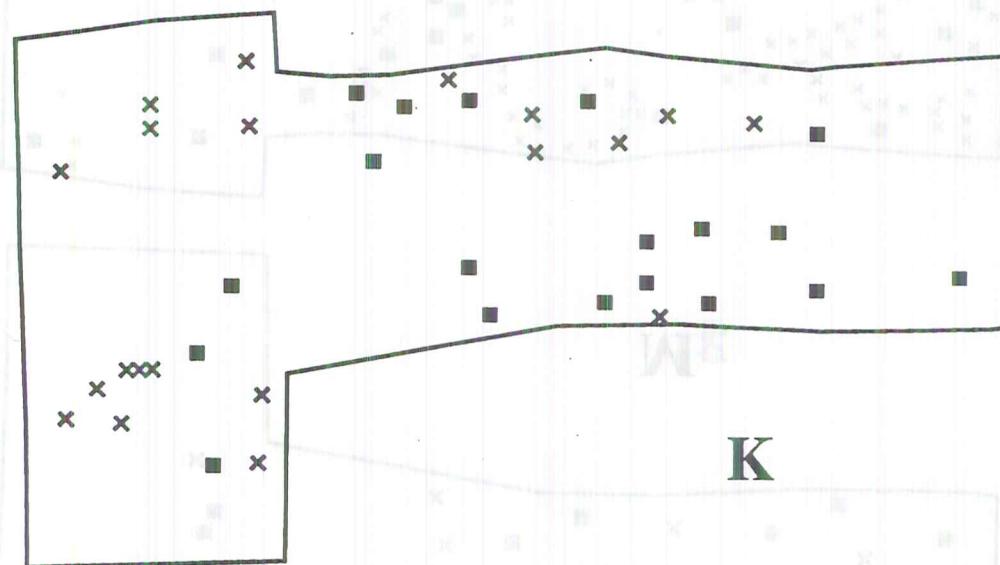
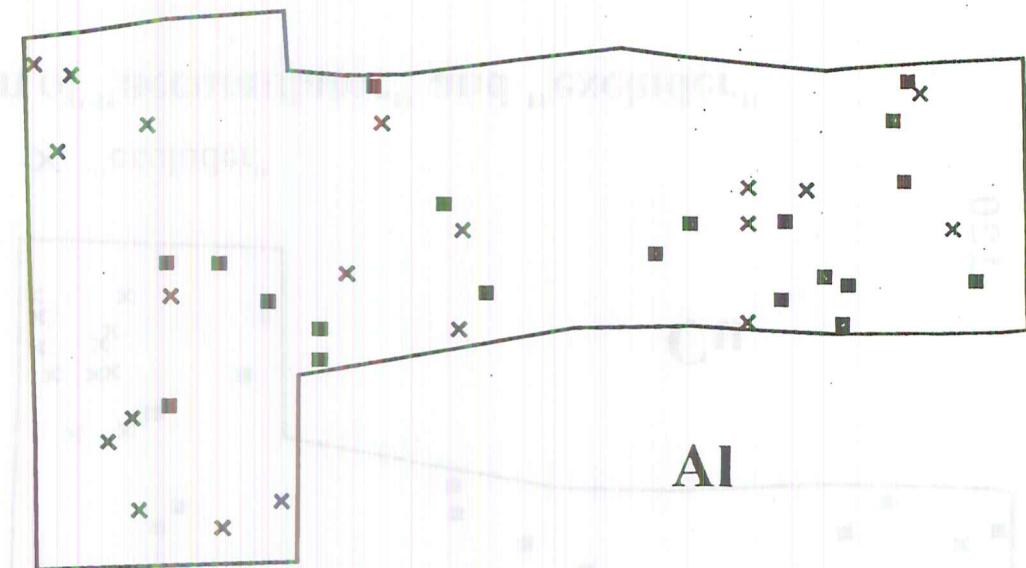
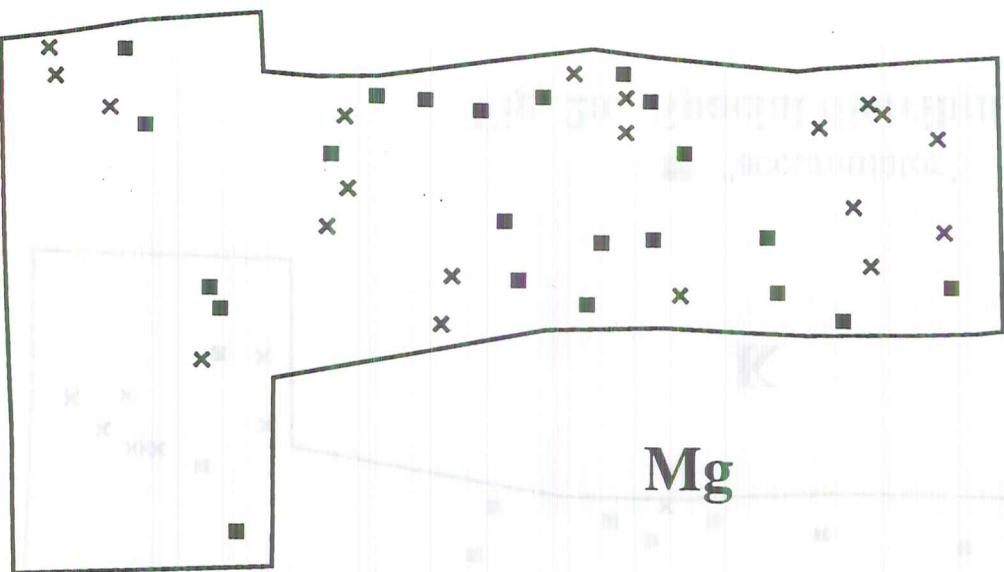


Fig. 1. Frequency distribution of mineral elements in the barks (n=457)



■ "accumulator" ✕ "excluder"

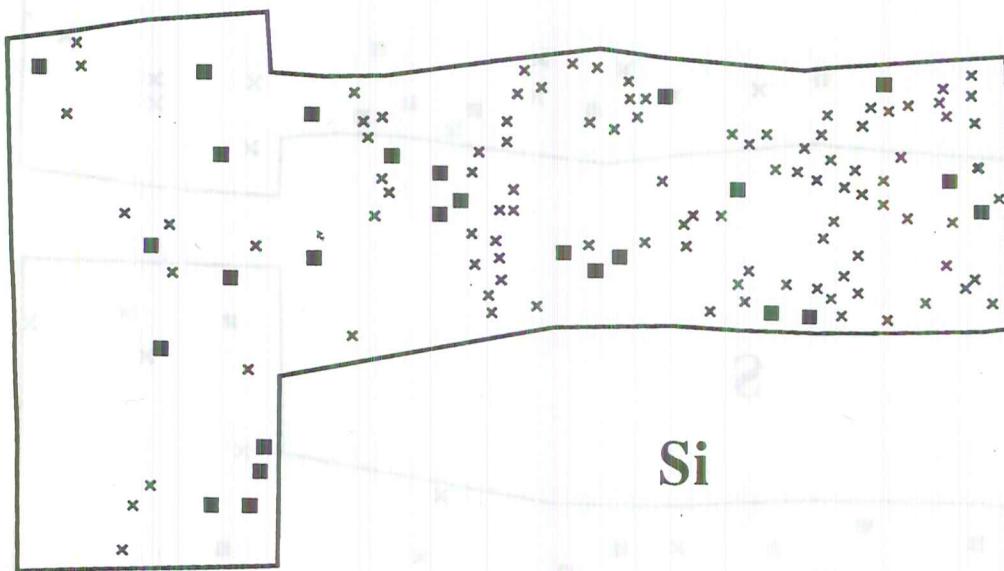
Fig. 2a. Spacial distribution of "accumulator" and "excluder"



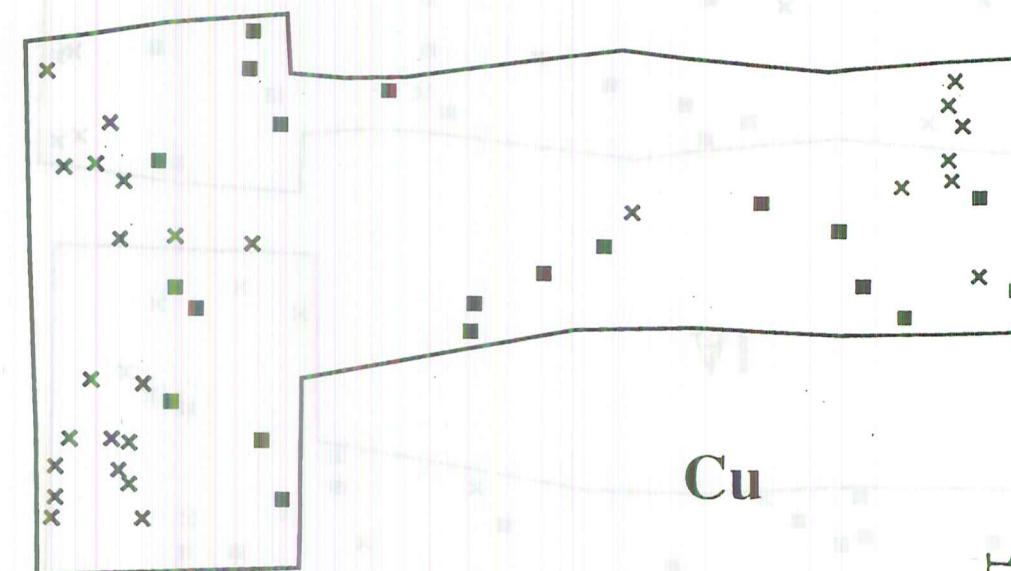
Mg



Sr



Si

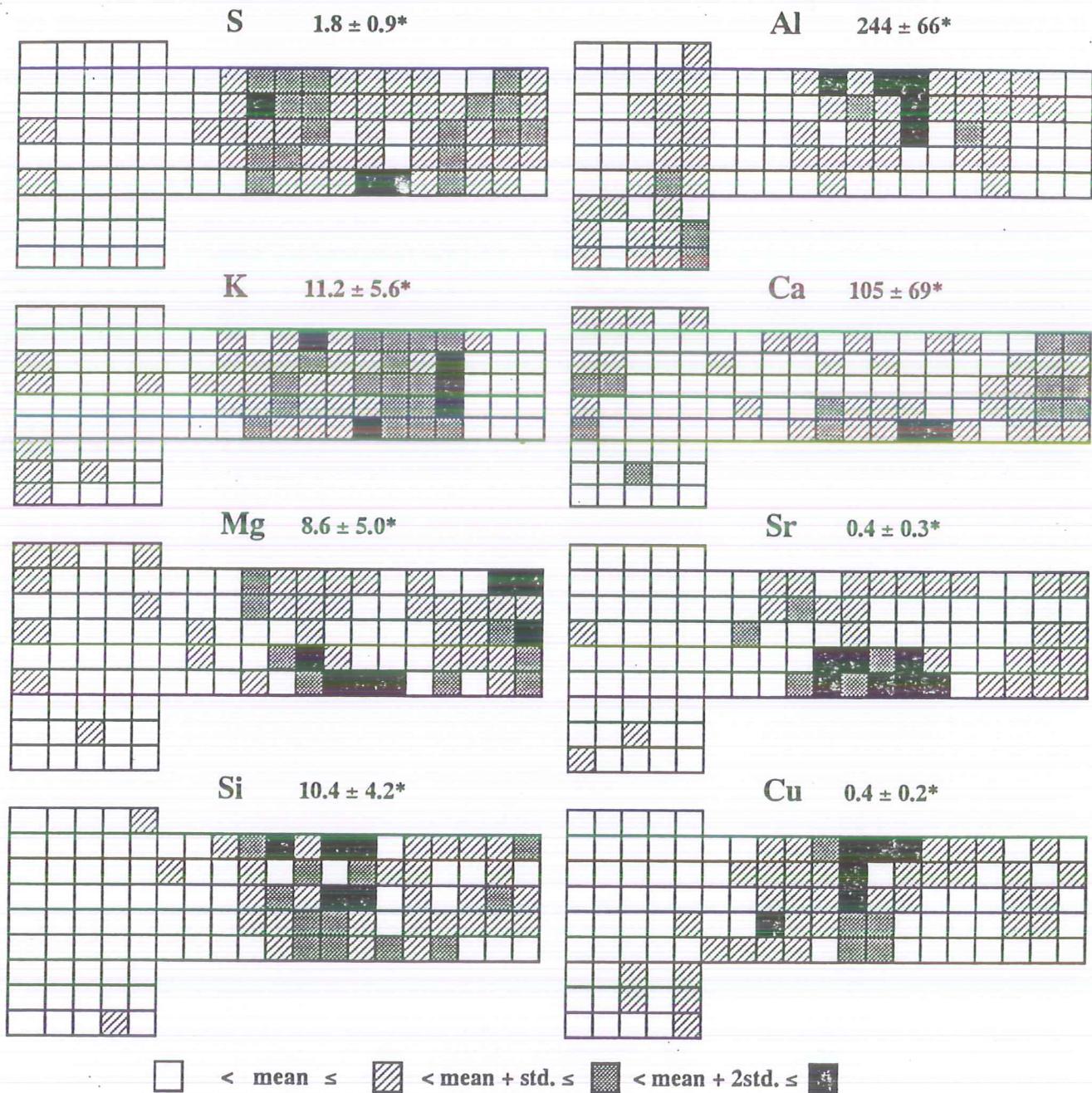


Cu

■ "accumulator"

✗ "excluder"

Fig. 2b. Spacial distribution of "accumulator" and "excluder"



*mean concentration and std. (mg kg⁻¹)

Fig. 3. Distribution pattern of the concentration of 0.1N HCl extractable form elements in soil, 5-15 cm

SOIL ENVIRONMENT AND TREE SPECIES DIVERSITY IN TROPICAL RAIN FOREST, WEST SUMATERA, INDONESIA

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ABSTRACT

Soil characteristics were examined in relation to tree species diversity of a tropical rain forest on a toposequence plot of 0.16ha and a long-term observation plot of 1.0ha. This study was conducted in Mt. Gadut area near Padang, West Sumatera, Indonesia. The study area had an annual rainfall of more than 5000 mm with no real dry season. both plots are Dipterocarp forests on a hill top (500-600m) extending to valley bottom. Soils were Typic Dystropepts developed from andesite and partly from limestone. In a toposequence plot from ridge to bottom, higher tree species diversity was observed on ridge soils which showed lower fertility. Although bottom soils were more fertile, species diversity was lower than those of ridge soils. Examination of profile distribution of Exchangeable Ca, M, T-C and T-N further revealed that ridge soils had more clear tendency of accumulation of these nutrients at the upper horizons and of dissipation at lower horizons than those of bottom soil profile. This means that both spatial and vertical variations of soil characters are important in sustaining tree species diversity. Detail characterization of 115 subplots of 1.0ha permanent plot showed that spatial and horizontal variations of soil characters were also important in supporting the tree species diversity of tropical rain forest.

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INTRODUCTION

The number of tree species greater than 10cm in diameter at breast height, DBH, found in one hectare of tropical rain forest can be over 200, as compared to 15-20 for the most diverse temperate forests (GENTRY, 1988, HUSTON, 1994, WHITMORE, 1984, WHITMORE and SIDYASA, 1986, WHITMORE et al., 1987, WHITTAKER, 1956, 1966). The enormous diversity of tropical rain forest trees is both evolutionary and ecological (HUSTON, 1994). Our present major concerns are to discover the physical and ecological characteristics, especially of soils, that are associated with high tree species diversity of the tropics. ASHTON (1982) reported the positive relationship between species diversity and soil fertility, such as magnesium content. On the other hand HOLDRIDGE et al. (1971) and HUSTON (1980) showed that soil productivity was negatively correlated with species diversity in Costa Rican tropical forest. KORNING et al. (1994) suggested that a high local species diversity in western Amazonia might be caused by local variations in soil characters.

In this report, we present detail information on vertical, horizontal and spatial variations of soil characters in relation to tree species diversity on long term forest ecology observation plots (HOTTA, 1984, 1986, 1989), on a foothill of G. Gadut, West Sumatra, Indonesia.

MATERIALS AND METHODS

STUDY SITES

We investigated the soil characters in relation to tree species diversity using two permanent plots, Pinang Pinang Plot (denoted as PIN2) and Pinang Pinang Atas Plot

(denoted as PAT), both of which are located at 500-600 m of a foothill of G. Gadut, 18km east of Padang, West Sumatra (Fig. 1). The study area has an annual rainfall of more than 5000 mm and no real dry season. The trees that existed in these plots with over 5 cm in diameter at breast height, DBH, were numbered and recorded. Total number of trees were 892 at PIN2 and 316 at PAT, and the number of species were more than 241 at PIN2 and more than 126 species at PAT. Various ecological studies, including measurement of turnover rate, DBH, tree height, spatial distribution patterns, and some nutrient dynamics, have been reported by many authors, (HOTTA, 1984, 1986, 1989, WAKATSUKI, 1986, SUZUKI and KOHYAMA, 1991, MUKHATAR et al., 1992, and PHILLIPS and GENTRY, 1994). The PIN2 Plot, 1.0ha, was divided into 115 subplots with a 10mx10m grid. This plot is located on the ridge extended from Mt. Gadut. The PAT Plot, 0.16ha, was divided into 16 subplots with the same grid size. This plot is located on the same ridge about 300m northeast from PIN2, but extends from the ridge to the valley to form a toposequence (Fig.2). Routine soil survey of PIN2 Plot was conducted, the results are shown in Fig.2 and Table 1.

SAMPLINGS

We collected 115 composite soil samples from all the subplots at 5-15cm depth from PIN2 Plot. One composite sample was a mixture of soils collected at 5 points in each subplots. In order to characterize vertical variations of soil characters, we collected soil samples at 0-5cm, 5-10, 10-25, 25-40, 40-55, 55-70, 70-85, 85-100, 100-115, 115-130, 130-145 and 145-160cm depth from three profiles dug at ridge, slope and bottom positions of PAT. The positions of the tree pits were situated at 5m from subplots No.16, No.13 and No.8 as shown in Fig.2. In order to characterize horizontal variations we divided each subplot into four sub-subplots. Soil samples, 0-5 and 5-15cm, were collected at 5 points in each 64 sub-subplots of PAT as shown in Fig.2.

ANALYSES

All soil samples were air dried, ground and passed through a 2-mm mesh sieve. Available Ca, K, Mg, Na, Al, B, Cu, Fe, Mn, Mo, P, S, Si, Sr, and Zn, were extracted with 0.1N hydrochloric acid (soil to solvent ratio of 1:10). The extracts were determined by inductively coupled plasma atomic emission spectrometry (ICP) using Shimazu ICPS-2000. For the total elemental composition, 50mg soil (powder) was digested with 1ml of 12N HCl and 0.5ml of 46% HF using high pressure Teflon vessel. After adding 6ml, 4% boric acid elemental compositions were analyzed by ICPS-2000, as described by QUAKER (1970). Total carbon and total nitrogen were measured using the dry combustion method, as described by ALLISON et al. (1965).

STATISTICS

For the correlation of spatial distribution between tree species diversity and various soil environmental factors, we calculated the ω index of IWAO (1977). The ω index is zero for mutually independent distribution, positive values up to +1 for a positive correlation, and negative values up to -1 for a negative correlation.

RESULTS AND DISCUSSIONS

1. General soil characteristics of PIN2.

Parent rocks were mainly andesite with inclusion of some limestone. The limestone pinnacles were observed at the western end of PIN2 (Fig.2). Soil map and analytical results are presented in Fig. 2 and Table 1. Although the total area is only 1.0ha, soils were extremely heterogeneous. Three different soil subgroups were recognized, which were further subdivided into seven families. The major subgroup was a Typic Dystropept. On the broad ridge, andesite formed Typic Dystropept - fine loamy clay. On the concave slope water and nutrients accumulated. On the ridge as a whole, a Typic

Dystropept with shallow soil depth was formed. At the western corner of the plot, limestone formed heavy clay and deep red soil, a Typic Dystropept, rhodic and clay. There is a clear tendency for nutrients to be distributed deeper in the soil profiles in the valleys than on the ridges. As a results, soil pH and bases increased with depth in the valley.

2. The relation between soil characters and tree species diversity in a toposequence of PAT Plot.

The number of tree species with more than 5cm in DBH, per 4 consecutive subplots of PAT Plot are shown in Fig.3. For smoothing the data, the numbers of species per plot were calculated using moving average of 4 consecutive subplots, 10x40m. The species diversity is divided into 4 levels: less than mean - standard deviation (S.D.); higher than mean - S.D. and lower than mean; higher than mean and lower than mean + S.D. and higher than mean + S.D. Fig.3 suggests that the ridge has higher diversity than the bottom in a toposequence of PAT.

Fig.4. shows the selected analytical results of surface soils, both 0-5 and 5-15cm depth, in each sub subplots in 5x5m grids. Exchangeable calcium and magnesium were higher in the bottom, an indication of higher fertility. However, the species diversity of the bottom area was lower than that of ridge area. It seems the higher the species diversity is the lower the soil fertility. There results are similar to those of Costa Rican forest where tree species diversity was negatively correlated with soil nutrient availability (HUSTON 1994). Extractable Al and Fe showed no clear relation to the species diversity. Extractable P showed intermediate distribution pattern between Extractable Al and Exchangeable Ca.

Table 1. shows the results of profile distributions of Exchangeable Ca, Mg and K, Extractable Al, Si and Fe and P, and total carbon and nitrogen contents at Upper, No.16; Middle, No.13 and Lower, No.8 positions of PAT toposequence. The profile distribution patterns of exchangeable Ca, Mg, T-N, T-C, and even extractable Al and Fe, showed

sharp decrease towards lower horizons and accumulation at top 0-5 and 5-10cm horizons. This trend was more clear in exchangeable Ca, Mg, T-C and T-N. The degree of variations, i.e. the enrichment of the upper horizons and/or dissipation to the lower horizons, were different among the three profiles. The ridge profile which had the highest species diversity showed the highest profile variations. On the other hand, the bottom profile which had the lowest species diversity showed the lowest profile variations. The difference of these trends of the profile distribution patterns of exchangeable Ca, and T-N are clearly shown in Fig.5. These results suggest that spatial variations, especially vertical profile variations of soils, are important in supporting high tree species diversity.

3. Spatial and horizontal variations of soil character in relation to tree species diversity in PIN2 Plot.

Horizontal distribution patterns of various soil characters at 5-15 cm depth in relation to tree species diversity in PIN2 is presented in Fig. 6. The tree species diversity was calculated using moving means of species number per 9 consecutive subplots (30mx30m). Soil characters were also shown using the moving mean of 9 consecutive subplots (30mx30m). Horizontal variations of exchangeable cations were evaluated using the values of standard deviations of 9 consecutive subplots.

The areas with higher variation (higher standard deviations) of exchangeable Ca seem to have higher species diversity. The areas with lower variation of exchangeable Ca seem to have lower species diversity. On the other hand, the areas with higher concentrations of exchangeable Ca and extractable Si showed lower species diversity. Distribution pattern of exchangeable Mg seems to have no clear relation to the species diversity.

Table 4 showed the result of calculation of ω index to quantify the degree of similarity of distribution pattern of soil characters to the tree species diversity. For the calculation of ω between higher diversity area and higher variation or higher concentration area, we gave 2 for the subplots with higher than mean + S.D., 1 for the

subplots with higher than mean but lower than mean + S.D., and 0 for all with subplots with lower than mean. On the other hand, for the calculation of ω between lower diversity area and lower variation or lower concentration areas, we gave 2 for the subplots with lower than mean - S.D., 1 for the subplots with lower than mean but higher mean - S.D., and 0 for all the subplots with higher than mean. In order to emphasized the degree of matching of distribution, bold-letters were applied for the ω values higher than 0.3, of which negative values were underlined (Table 4).

High species diversity showed higher positive ω values, i.e. higher correlation with higher spatial variations of exchangeable Ca, Mo, S and Zn. Lower species diversity showed higher positive ω values with lower spatial variations, such as exchangeable Al, B, Ca, K, Mo, Na, P and Zn. On the other hand, high species diversity showed negative ω value with higher concentration of exchangeable K, extractable Mn, Si and Zn. This indicates that higher soil fertility does not support tree species diversity. However, low species diversity showed negative ω values with lower concentrations of B, Cu, Fe, Na and Sr.

Although it is not easy to single out the soil character relating to the tree species diversity, it may be concluded from the results (Table 4) that low spatial variability of soil characters and higher soil fertility tend to decrease the diversity of tree species.

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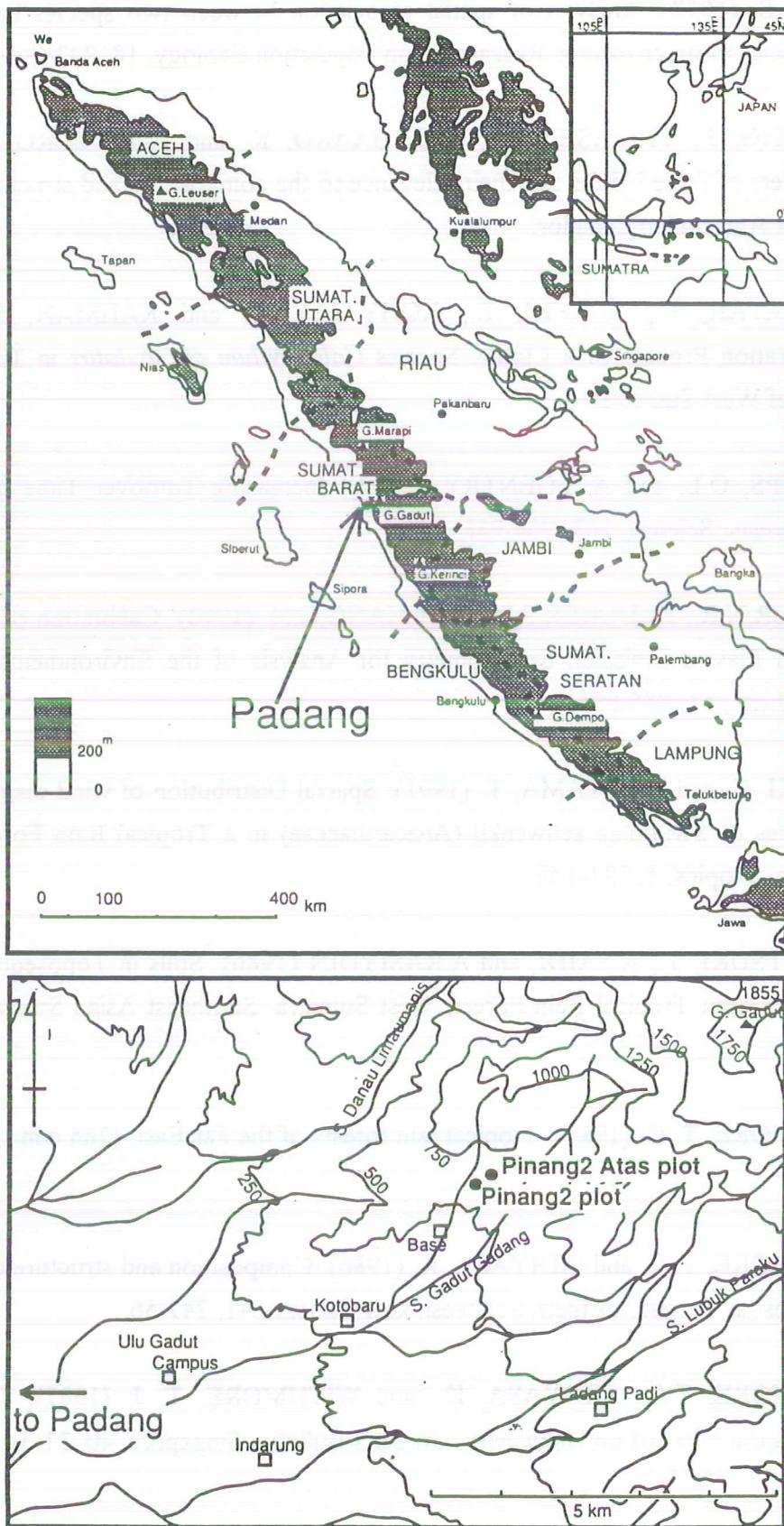


Fig. 1. Map showing the location of the study sites.

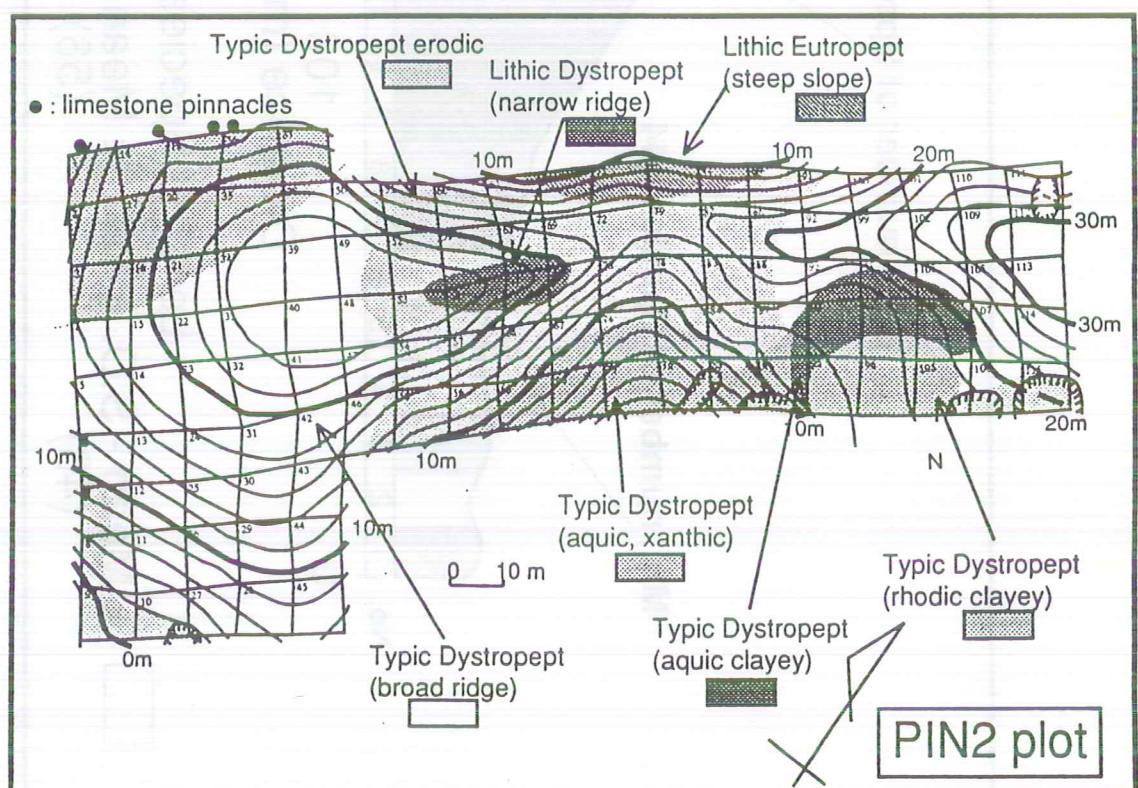
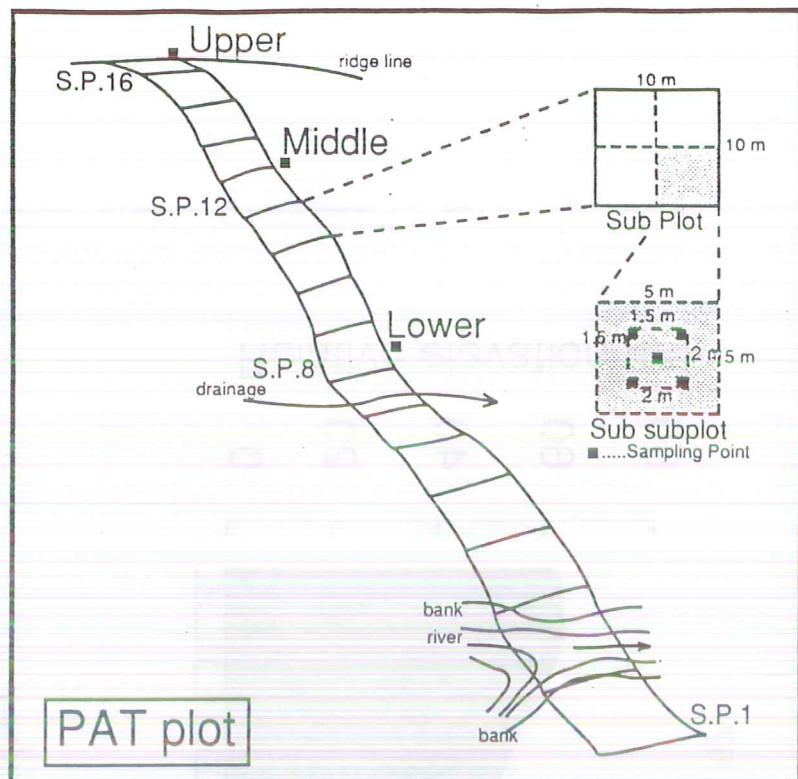


Fig. 2. Map showing the location of the study plots.
The PAT, Pinang Pinang Atas, plot is a bird's-eye view.
The PIN2, Pinang Pinang, plot shows topography and major soil distribution.

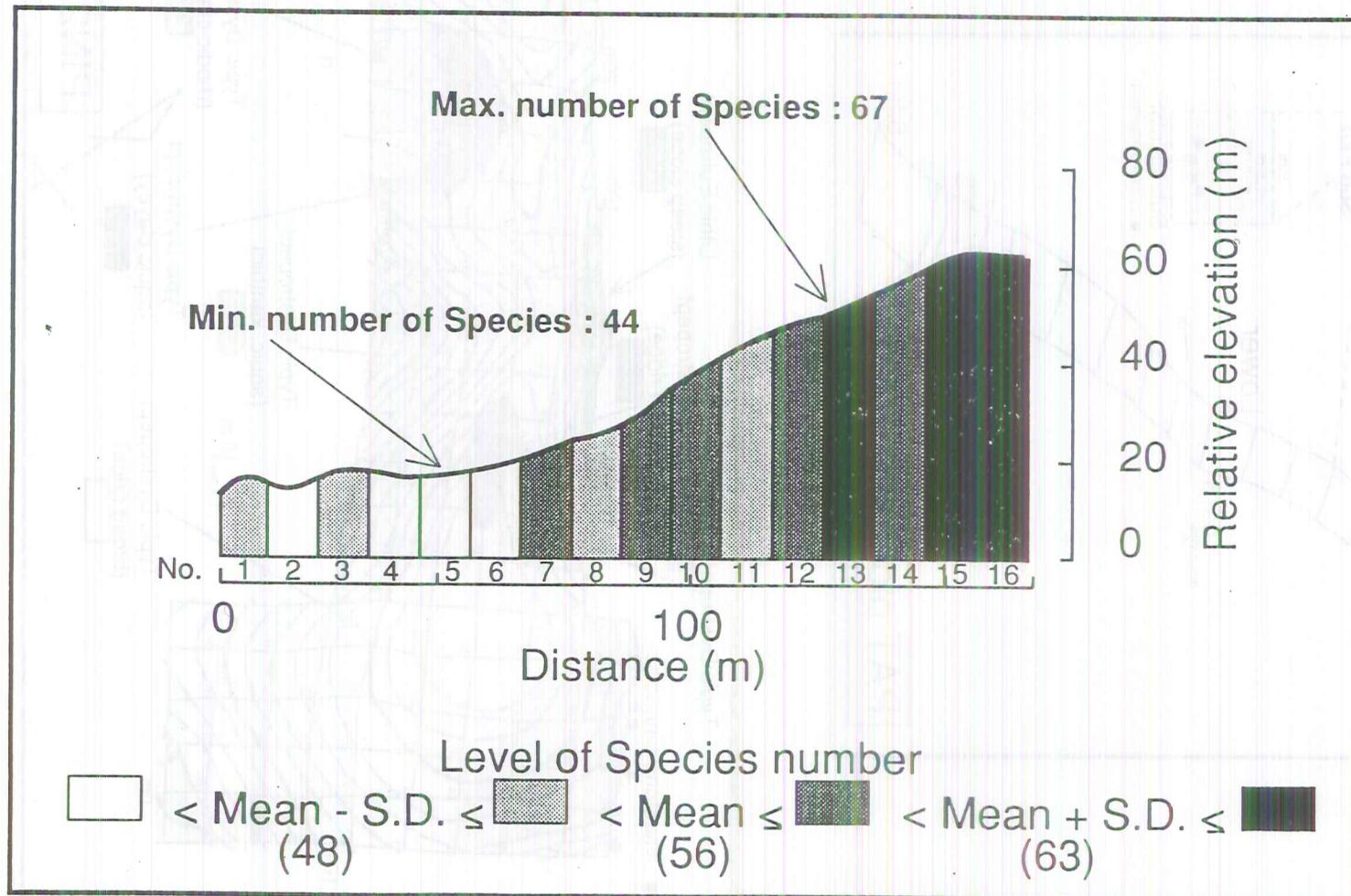


Fig. 3. Moving Mean number of species per 4 consecutive plots (10x40m) in a toposequence of PAT, Pinang Pinang Atas, plot.

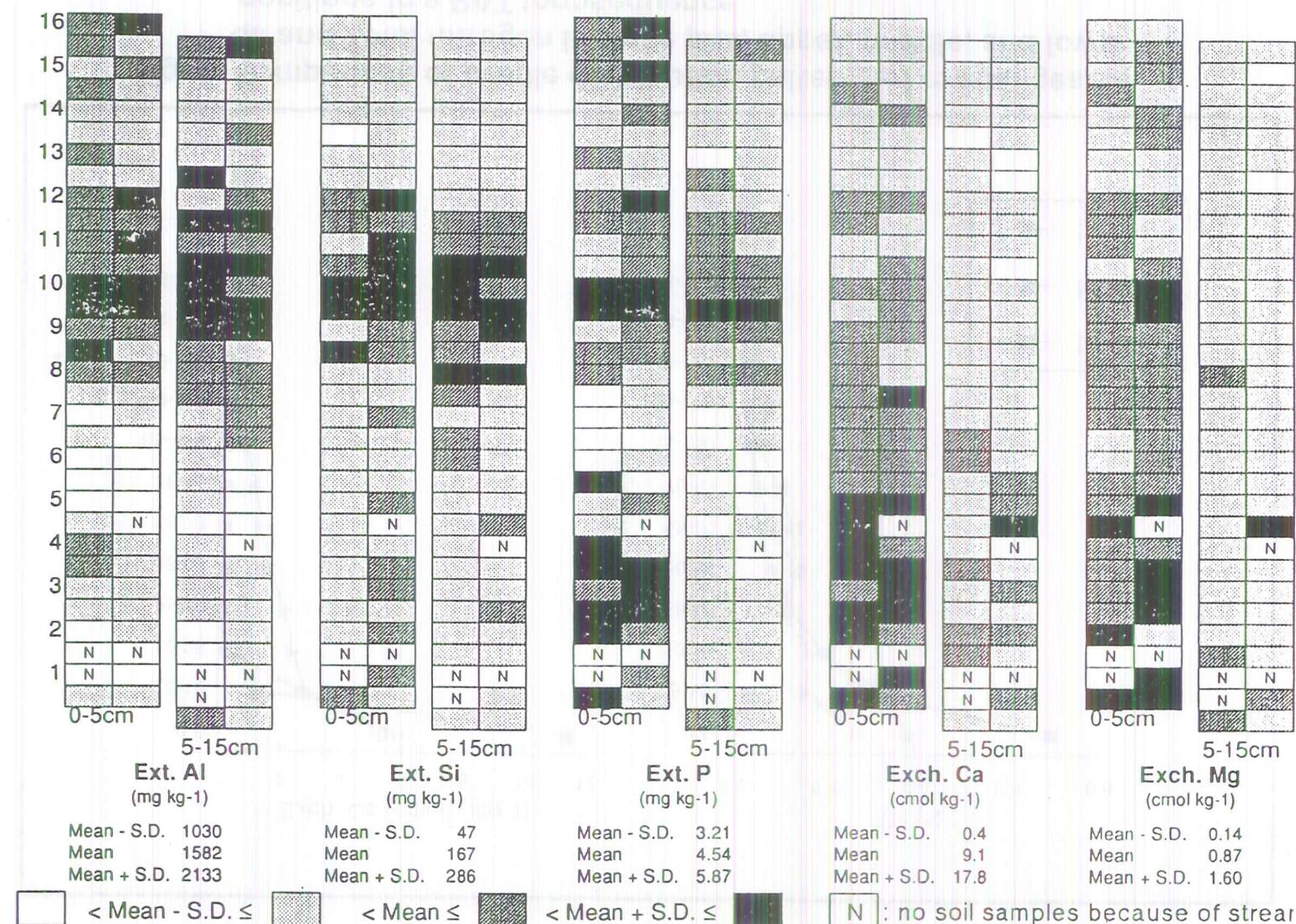


Fig. 4. The horizontal distribution patterns of Ext. Al, Si, and P, and Exch. Ca, and Mg in soils of both 0-5cm and 5-15cm depth in PAT, Pinang Pinang Atas, plot.

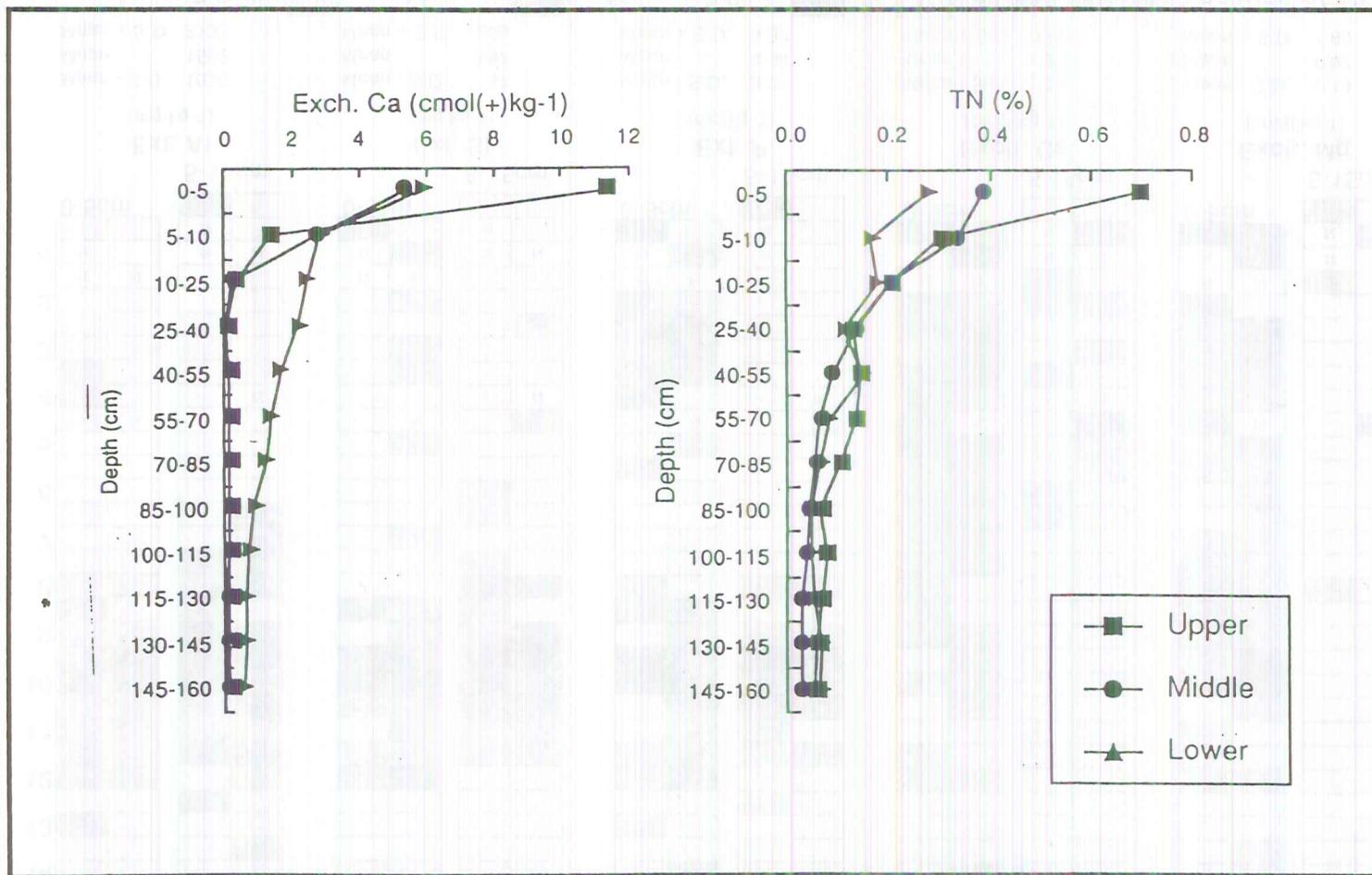


Fig. 5. Comparison of profile distribution patterns of exchangeable Ca and Total nitrogen in three pits, upper, middle, and lower positions in a PAT toposequence.

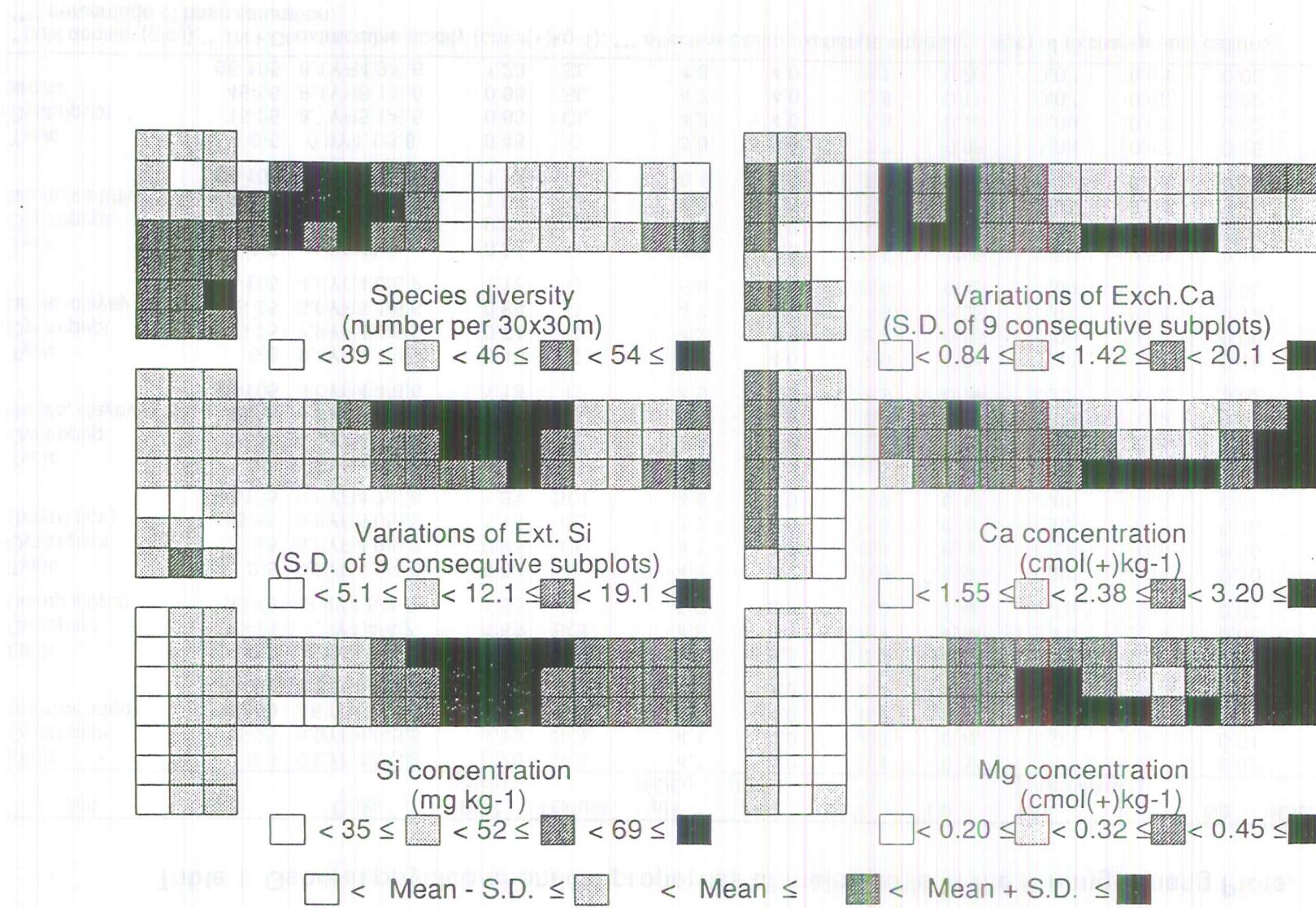


Fig. 6. The patterns of species diversity, concentrations of Exch. Ca, Mg and Ext. Si, and variations of Exch. Ca and Ext. Si.

Table 1. General physico-chemical properties of major Soils in the Pinang Pinang Plots.

Soil	Depth (cm)	Color	BD *	Texture	pH (H ₂ O)	pH (KCl)	Al **	Ca	Mg (cmol(+)kg ⁻¹)	K	Na	eCEC ***	BS **** (%)
Lithic Dystropept (narrow ridge)	0-5	9.6YR4.0/3.9	0.70	SCL	4.1	4.0	3.1	6.37	1.13	0.31	0.02	11	71.9
	15-25	8.0YR4.9/5.5	1.10	SCL	4.1	4.0	4.8	0.16	0.03	0.04	0.01	5.0	4.8
	40-50	7.6YR/5.1/7.0	1.35	SCL	4.4	4.0	6.9	0.05	0.02	0.03	0.01	7.0	1.6
	50-60	8.0YR4.8/5.5	1.25	SL	4.4	4.0	6.3	0.17	0.06	0.03	0.01	6.6	4.1
Lithic Eutropept (steep slope)	0-5	2.1Y3.7/2.3	0.50	L	5.5	5.3	0.3	14.80	3.32	0.58	0.02	19	98.4
	15-25	1.1Y4.4/4.2	1.55	SCL	4.8	3.7	6.8	4.04	5.15	0.14	0.05	16	58.0
	30-40	2.8Y4.5/3.7	1.50	SL	5.7	3.8	3.0	7.48	6.79	0.06	0.06	14	82.6
Typic Dystropept (broad ridge)	0-5	9.2YR4.5/4.6	0.52	C	4.4	4.2	5.9	8.50	0.94	0.34	0.10	16	62.8
	15-25	8.0YR4.9/6.0	0.96	CL	4.1	3.9	8.4	0.66	0.14	0.08	0.06	9.3	10.1
	45-55	6.8YR5.0/6.5	1.15	CL	4.7	4.0	7.8	0.20	0.02	0.05	0.15	8.2	5.1
	95-105	6.6YR4.7/5.8	1.31	SCL	4.8	4.0	7.9	0.17	0.06	0.06	0.04	8.2	4.0
Typic Dystropept rhodic, clayey	0-5	7.8YR3.8/3.3	0.58	C	4.8	4.7	0.7	13.6	1.46	0.35	0.05	16	95.5
	15-25	5.1YR4.7/5.9	1.00	C	4.6	4.0	5.4	2.43	0.36	0.04	0.04	8.3	34.5
	45-55	4.6YR4.6/6.2	1.10	C	4.8	4.0	5.7	0.50	0.09	0.02	0.02	6.3	10.0
	95-105	3.0YR4.4/6.8	1.18	C	4.9	3.9	7.3	0.16	0.02	0.02	0.02	7.5	2.9
Typic Dystropept aquic, clayey	0-5	9.4YR4.1/3.9	0.40	C	3.8	4.0	7.9	7.54	1.34	0.55	0.18	18	54.9
	15-25	7.9YR4.9/5.5	0.74	C	4.2	3.9	8.2	0.05	0.01	0.06	0.08	8.4	2.4
	45-55	6.6YR5.1/6.6	0.89	C	4.7	4.0	7.9	0.05	0.01	0.04	0.12	8.2	2.7
	95-105	4.6YR4.6/6.2	1.15	C	5.0	3.9	9.6	0.35	0.09	0.02	0.05	10	5.0
Typic Dystropept aquic, xanthic	0-5	1.3Y5/6	0.56	C	4.9	4.5	2.6	12.9	2.60	0.52	0.18	19	86.4
	15-25	10YR5/6	0.87	C	4.7	4.2	4.3	3.69	0.69	0.11	0.09	8.9	51.3
	45-55	8.8YR5.0/5.4	1.02	C	4.9	4.2	5.6	0.70	0.15	0.04	0.08	6.6	14.7
	95-105	8.1YR5.0/5.5	1.12	C	5.1	4.2	6.0	0.36	0.15	0.03	0.05	6.6	8.9
Typic Dystropept erodic	0-5	0.9Y4.1/3.8	0.48	C	3.9	3.8	7.7	5.08	1.08	0.47	0.05	14	46.7
	15-25	8.7YR5.1/6.5	0.83	CL	4.2	4.0	7.6	0.16	0.09	0.07	0.02	7.9	4.3
	45-55	8.1YR5.1/6.0	0.98	SL	4.7	4.0	6.8	0.13	0.07	0.02	0.02	7.0	3.4
	95-105	8.1YR4.9/5.6	1.23	SL	4.8	4.0	6.1	0.20	0.07	0.03	0.02	6.4	5.0

* bulk density (g/cc); ** 1N KCl extractable acidity (cmol(+)kg⁻¹); *** effective cation exchange capacity = sum of exchangeable cations

**** percentage of base saturation.

Table 2. The profile distributions of Exchangeable Ca, Mg, and K, T-N and T-C, and Extractable Al, Si, Fe, and P.

	Depth (cm)	(cmol kg ⁻¹)			(mg kg ⁻¹)				(\%)	
		Exch. Ca	Exch. Mg	Exch. K	Ext. Al	Ext. Si	Ext. Fe	Ext. P	TN	TC
Upper	0-5	11.3	1.22	0.49	1623	34	66	5.6	0.70	9.1
	5-10	1.3	0.28	0.05	1825	30	136	4.5	0.30	3.3
	10-25	0.3	0.11	0.05	1895	38	157	4.2	0.20	2.2
	25-40	0.1	0.05	0.02	1861	59	141	4.1	0.13	1.4
	40-55	0.1	0.06	0.04	1418	53	102	3.2	0.14	1.8
	55-70	0.1	0.06	0.05	2086	51	130	4.4	0.13	2.2
	70-85	0.1	0.04	0.04	1444	64	70	3.2	0.10	1.2
	85-100	0.1	0.05	0.05	1109	70	35	2.6	0.06	0.6
	100-115	0.1	0.04	0.05	1006	65	44	2.5	0.07	0.7
	115-130	0.1	0.11	0.09	1213	122	27	2.8	0.07	0.5
	130-145	0.1	0.06	0.08	1125	109	25	2.6	0.06	0.3
	145-160	0.1	0.04	0.07	950	87	19	2.4	0.05	0.3
Middle	0-5	5.3	0.48	0.12	1440	99	91	4.3	0.38	4.2
	5-10	2.7	0.28	0.15	1532	90	134	4.0	0.33	3.4
	10-25	0.2	0.10	0.05	1703	131	168	4.5	0.20	1.9
	25-40	0.1	0.06	0.02	1592	116	81	3.6	0.13	1.1
	40-55	0.1	0.06	0.03	1363	95	48	3.4	0.08	0.8
	55-70	0.1	0.07	0.02	1309	106	37	3.5	0.06	0.5
	70-85	0.1	0.07	0.03	1362	118	31	3.5	0.05	0.4
	85-100	0.1	0.07	0.03	1268	108	23	3.3	0.04	0.3
	100-115	0.1	0.20	0.30	1505	263	37	3.7	0.03	0.2
	115-130	0.1	0.09	0.07	1021	114	16	2.7	0.03	0.2
	130-145	0.1	0.08	0.02	1122	122	14	2.7	0.03	0.2
	145-160	0.1	0.09	0.03	1154	117	17	3.6	0.03	0.2
Lower	0-5	5.9	0.80	0.30	1048	77	11	3.3	0.28	3.0
	5-10	2.8	0.43	0.10	1054	82	28	2.7	0.16	1.4
	10-25	2.4	0.34	0.13	2087	115	26	4.7	0.18	1.7
	25-40	2.2	0.36	0.15	1836	133	89	4.2	0.11	0.9
	40-55	1.6	0.21	0.08	1744	137	106	3.8	0.14	1.4
	55-70	1.3	0.20	0.08	1464	149	115	3.3	0.08	0.6
	70-85	1.2	0.20	0.09	1323	141	81	3.0	0.06	0.5
	85-100	0.8	0.15	0.08	1052	126	42	2.5	0.04	0.3
	100-115	0.7	0.14	0.08	1085	123	38	2.5	0.04	0.3
	115-130	0.6	0.15	0.08	1435	158	69	3.2	0.05	0.4
	130-145	0.6	0.16	0.10	1414	186	70	3.2	0.07	0.5
	145-160	0.5	0.19	0.12	1531	217	90	3.3	0.06	0.4

Table 3. The results of calculation* of ω index between the areas of higher diversity and higher variations or higher concentrations and between the areas of lower diversity and lower variations or lower concentrations in Pinang Pinang Plot.

Elements	Low species diversity vs. Low variation	High species diversity vs. High variation	Low species diversity vs. Low concentration	High species diversity vs. High concentration
Al	0.39	0.24	-0.24	-0.12
B	0.43	0.05	0.39	0.33
Ca	0.50	0.60	0.20	0.40
Cu		-0.11	0.48	0.02
Fe	0.23	0.16	0.50	0.46
K	0.54	-0.05	0.11	-0.31
Mg	-0.13	-0.09	-0.16	-0.12
Mn	-0.03	0.25	0.03	-0.42
Mo	0.50	0.57	0.22	0.24
Na	0.37	0.02	0.52	0.39
P	0.36	0.25	-0.09	0.26
S	0.25	0.55	-0.27	0.12
Si	0.35	-0.26	-0.26	-0.50
Sr		0.26	0.38	0.24
Zn	0.31	0.35	-0.21	-0.57

*The calculations were made using consecutive 9 subplots, 30x30m.

Positive indices ≥ 0.30 are shown by bold-letter and negative indices ≤ -0.30 are shown by bold-letter with underlines.