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Micro spatial distribution pattern of litterfall and nutrient flux in relation to soil chemical properties in a super wet tropical rain forest plot, West Sumatra, Indonesia

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ABSTRACT The micro spatial distribution of the litterfall and nutrient flux in relation to tree composition and soil chemical properties was investigated within a one-hectare study plot with 115 subplots (10 m x 10 m) in a super wet tropical rain forest in West Sumatra, Indonesia. Litterfall production and its nutrient flux throughout a one-year period were determined using 63 circular litter traps installed in 63 subplots among the 115 subplots. The aim of this study was to qualify the micro spatial distribution of the litterfall production and nutrient flux in relation to tree composition and soil chemical properties among the 63 subplots within the study plot. To characterize the relationship among the micro spatial distribution of the litterfall, nutrient flux and tree composition and/or soil chemical properties, the correlation coefficients and omega index of Iwao (1977) were determined. The mean litterfall was 11.4 Mg ha^{-1} y^{-1} and the litterfall varied among the 63 subplots within the range of 7.4 - 16.3 Mg ha^{-1} y^{-1}. The variations in litterfall were positively correlated ($P = 0.01$) to tree density and the number of tree species in the subplots. Based on the nutrient contents and the production of leaf litter, the nutrient fluxes in the 63 subplots were calculated, and were found to vary significantly within the subplots as follows: N, 54-140; P, 1.4-4.5; K, 8.8-27.5; Ca, 71-207; Mg, 6.2-17.7; Al, 3.2-26.4; Fe, 0.7-3.5; and S, 6.2-16.4 (kg $ha^{-1}y^{-1}$). The amount of each nutrient flux was strongly affected by the amount of litterfall production, and was, in turn, positively correlated with tree density and the number of tree species in each subplot. The micro spatial distributions of nutrient flux showed significant positive correlations with the soil chemical properties of total N and 0.1 M HCl extractable K at the surface (0-5 cm) soil of each subplot. However, for the other major elements such as Ca and Mg, no correlation was shown. The micro spatial tree species diversity, i.e., the number of species per subplot, showed a significant positive correlation to tree density, litterfall production and N and Ca flux. However, as Kubota *et al.*(2000) and results in this paper, show, the micro spatial distribution of soil fertility parameters, except for the 0.1 M HCl extractable Fe in topsoil, had a negative correlation to the number of tree species. These results suggest that in this super wet tropical rain forest, tree species diversity with diverse tree nutritional characteristics may contribute to create the diversity of an edaphic niche, rather than increase the soil fertility level through nutrient cycling via litterfall.

Key words: micro spatial litterfall distribution, nutrient fluxes of N, P, K and Ca, soil chemical property, super wet tropical rain forest, West Sumatra

As Hotta described (1984, 1986, 1989), the Pinang-Pinang plot, a super wet tropical rain forest in West Sumatra, is very rich in tree species that have highly diverse nutritional characteristics (Masunaga *et al.*, 1997, 1998). Yoneda *et al.* (1994) and Yoneda (1997) reported a wide horizontal variance of stand and productivity and decomposition of litter in the same study plot. Seasonal leaf litter production within the plot was positively correlated with small temperature fluctuations and was negatively correlated with

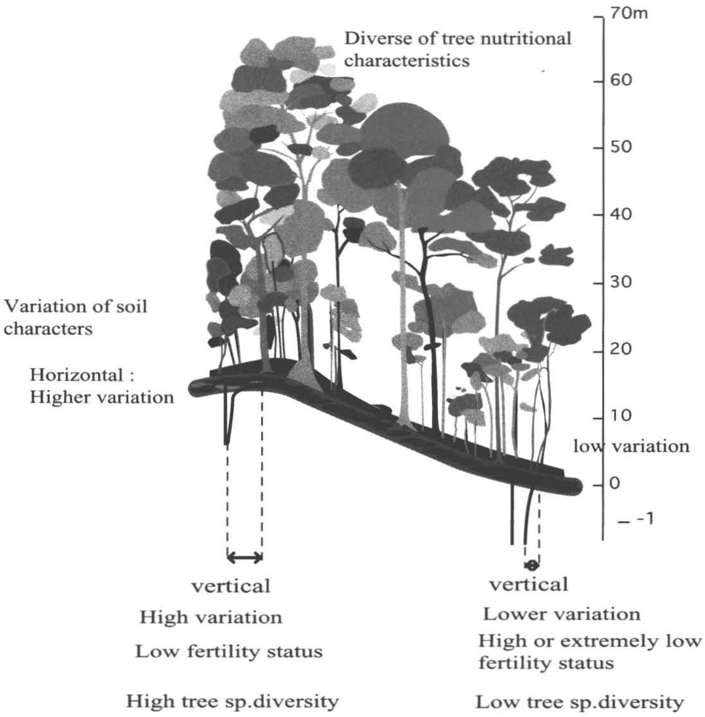


Fig. 1. Interrelation among extremely high tree species diversity, diverse nutritional characteristics of tree species and heterogeneous soil (Kubota et al., 2000).

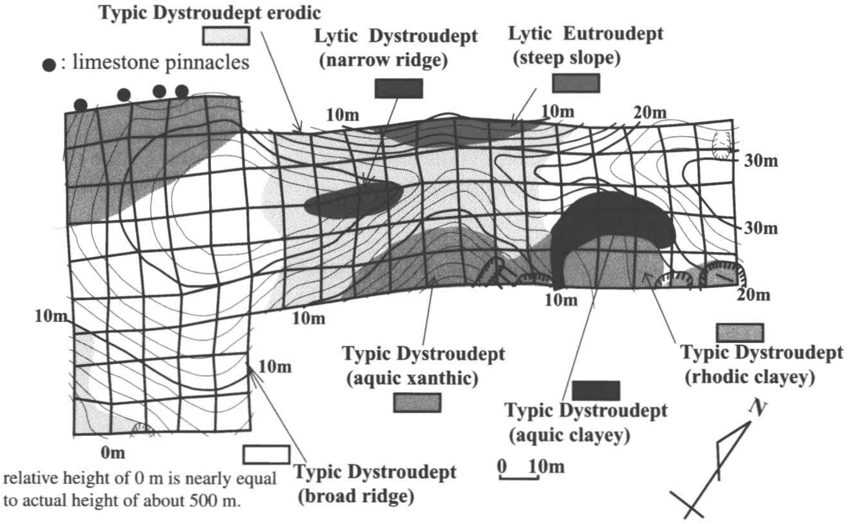


Fig. 2. Soil and topographical map of Pinang-Pinang plot (Cited from Wakatsuki et al., 1986. Soil classification was updated based on Soil Taxonomy 1999)

the amount of rainfall (Hermansah *et al.*, in review). In this study such relationships between litterfall and temperature or rainfall were also observed in most of the subplots where the litter traps were installed, even though the amount of leaf litterfall varied among the subplots.

Masunaga *et al.* (1998) and Kubota *et al.* (1998) suggested a possible interrelationship between extremely high tree species diversity and the diverse nutritional characteristics of the plant species. The diverse nutritional characteristics of the plant species may contribute to the creation of heterogeneous soil characteristics through mineral cycling via litterfall in the super wet tropical rainforest in West Sumatra.

A detailed study of nutrient cycling and flow in relation to tree species diversity and soil chemical properties, however, has not yet been conducted. In our previous work, we hypothesized that the high horizontal and vertical variation of soil nutritional status was related to tree species diversity (Kubota *et al.*, 2000). As Fig. 1 shows, the subplots with high tree species number had soil that had a high variation of soil nutrient characteristics on both the vertical micro scale of 1-2 m, and the horizontal micro scale of 10-30 m. Also, as Fig.1 shows, the subplots with high tree species number were located at the ridge, where soil fertility was generally lower than in the subplots that were located at lower topographical positions. The lower subplots had lower tree species number than the subplots on the ridge. This result leads to the question of how such variations in soil nutritional status were created and maintained. Nutrient cycling through litterfall probably plays a role in the creation of such variations. We therefore hypothesized that a high variation of soil nutritional status among the subplots in the study plot supported high tree species diversity, and at the same time was created and maintained through mineral cycling and fluxes via litterfall by not only the large number of different tree species, but also by the wide range of nutritional characteristics among those tree species.

In order to evaluate the effect of mineral cycling in the creation of such micro spatial soil heterogeneity, in this study we quantitatively evaluated the micro spatial distribution of litterfall production and its nutrient flux. These data will ultimately contribute to a discussion of how these factors affect the variation of soil nutritional status.

MATERIALS AND METHODS

Study Sites

This study was conducted on a one hectare (ha) plot of tropical rain forest in Pinang-Pinang in West Sumatra, Indonesia. This site has been used for other long-term ecological research (Hotta 1984, 1986, 1989; Masunaga *et al.*, 1997; Kubota *et al.*, 1998; Hermansah *et al.*, 2002). The plot is located on the hilltop with a partly narrow and partly broad ridge at about 500 m above sea level. The area has very high rainfall, exceeding 5,000 mm per year, and no real defined dry season (Hotta, 1984). The soil is a relatively young Typic Dystroudept developed from andesite and limestone (Fig. 2, Wakatsuki *et al.*, 1986). A prominent red color, strong acidity, and relatively rich in carbon, nitrogen and exchangeable bases, particularly exchangeable Ca, characterize this soil (Wakatsuki *et al.*, 1986). Although the total area was only one ha, the soils were extremely heterogeneous. Three different soil groups, Typic Dystroudept, Lithic Dystroudept and Lithic Eutroudept were recognized, and they were further subdivided into seven families as shown in Fig. 2. Based on soil morphology (Wakatsuki *et al.*, 1986), the soil classified as Typic Dystroudept rhodic clay may have originated as limestone, whereas the major parent materials might be Andesite. In terms of the soil chemical properties (Table 2) Ca was highly variable within the site.

Sampling Methods

Since Kubota *et al.*, (2000) characterized the variation of the soil's physico-chemical nature in relation to tree species diversity in this study plot, we followed their methodology for data processing. In order to analyze the coefficient variation statistically, the nine 10 m x 10 m subplots were grouped into large subplots (30 m x 30 m) as shown in Fig 3, since, according to the crown projection, the biggest tree, *Swintonia schwenki,* occupied the biggest area, about 30 m x 30 m (Hotta, 1984). Litterfall was collected at the center of each of the 63 subplots (Fig.3). The basal area, tree density and number of species (both identified and unidentified sp.) of each subplot were calculated using the mean values of the nine consecutive subplots (total area was 30 m x 30 m). To characterize the horizontal soil variations, we collected 115 composite samples of topsoil from all the subplots (10 m x 10 m) at 0-5 cm depth, excluding the litter layer, and 115 composite samples at 5-15 cm depth. One composite sample consisted of 100-cc volume sampling from each of the four points in each 10 m x 10 m subplot (Fig.3, Kubota *et al.*, 2000). The mean values of the soil properties of each subplot were used to determine correlation coefficients between soil and litterfall, nutrient flux and tree composition.

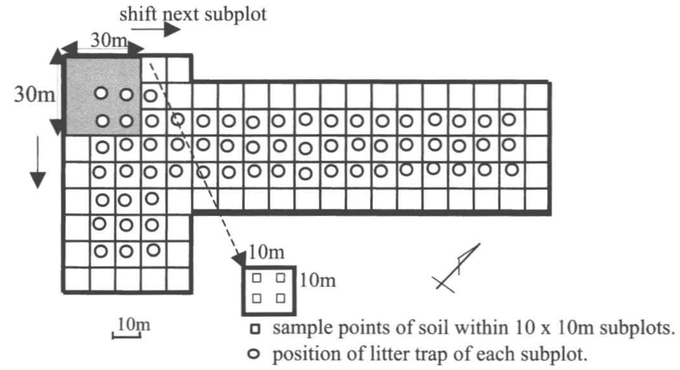


Fig.3. Trap position and soil sampling method within the study plot.

Laboratory Methods and Data Analyses

The trapped litter, which was collected every month, was sorted into leaves, wood, flowers, fruits and other litter debris. All of the litter materials were dried at 60 ℃ to a constant weight in an oven for 48 hours, and the dry weights were recorded. Leaf litterfall was then ground into a powder using a tungsten carbide vibrating mixer mill (Mitamura, Retch 18-34) and digested with nitric acid in a high pressure Teflon Vessel (Quaker *et al.*, 1970; Koyama and Sutoh, 1987). The Ca, Mg, K, Na, P, S, Al and Fe of the topsoil (0-5 and 5-15 cm) were extracted with 0.1 M hydrochloric acid (the soil-to-solvent ratio was 1:10). The concentrations of digested and extracted Ca, Mg, P, Al, Fe and S in the plants and soil were determined by an Inductive Coupled Plasma Atomic Emission Spectrometer (ICPS-2000; Shimadzu, Japan). Potassium (K) and sodium (Na) were determined by an Atomic Absorption Emission Spectrophotometer (AA-680; Shimadzu). Total C and N were determined by the dry combustion method with a highly sensitive N-C analyzer (N-C 80; Sumigraph, Sumitomo).

Monthly litterfall production data over the period of litter collection and the nutrient composition of the leaf litter in each subplot in each month were used for the estimation of nutrient flux.

To determine the relationship of the micro spatial distribution pattern to litterfall production, tree composition, nutrient flux and soil chemical properties, we calculated the correlation coefficients among those parameters. In order to clarify the detailed relationship and overlap among the micro spatial distribution of leaf litterfall production, nutrient flux and local soil chemical properties within the plot we also calculated the ω index of Iwao (1977) (Khoyama *et al.*, 1994; Kubota *et al.*, 1998). Our previous results (Kubota *et al.*, 2000) regarding the relationship between tree species diversity and soil physico-chemical characteristics were also discussed on the basis of the ω. The ω index is zero for a mutually independent distribution variation, +1 for a strong positive correlation, and −1 for a strong negative correlation. For the calculation of the ω index, data including tree population, species number, leaf litter production, nutrient flux and soil nutrient contents of each element were classified into four classes as $3 \geq \text{mean} + \text{SD} > 2 \geq \text{mean} > 1 \geq \text{mean} - \text{SD} > 0$. Correlation coefficients were also calculated and compared to the ω index. The significance of those relationships was determined by comparing the values of correlation coefficients, calculated by Microsoft Excel, Office 2000, to r table in Nyumon Tokei Kaisekihou "Introduction to Statistical Analyses" (Nagata, 1992). If the calculated values of correlation coefficients are higher than the r table at certain probability levels, the relationship between the parameters is significant. The r table values were calculated by the following formula, $r=2.576/\sqrt{\Phi+3}$ and $r=1.960/\sqrt{\Phi+1}$, for 1 % and 5 % significance, respectively. The symbol Φ represents the number of samples.

RESULTS AND DISCUSSION

Nutrient Composition of Litterfall

Among the 8 elements analyzed, Ca showed the highest mean concentration in leaf litterfall collected over one year in the 63 traps (Table 1). This finding is not unusual, as Ca is a very immobile element in the plant vascular system and is believed to be recycled by means of leaf litterfall (Vitousek, 1982, 1984; Cuevas and Medina, 1988). For purposes of comparison, the previously reported nutrient concentrations in leaf litterfall from a wet tropical forest growing on infertile Oxisols-Ultisols in Malaysia (Burghouts, 1993) are also shown in Table 1. The present study plot showed a considerably

Table 1. Nutrient concentrations in leaf litterfall and living leaves within the study plot and leaf litterfall of wet tropical rain forest, Malaysia.

	g kg^{-1}								
	N	P	K	Ca	Mg	Al	Fe	S	C/N
Leaf litterfall									
mean (n=63)	13.1	0.4	2.4	17.7	1.6	1.4	0.2	1.5	36.4
min	10.1	0.3	1.5	13.8	1.2	0.5	0.1	1.2	31.1
max	16.1	0.5	3.8	21.3	2.5	3.8	0.4	2.5	44.7
SD	1.1	0.1	0.3	1.8	0.2	0.7	0.1	0.2	2.7
Living leaves (Masunaga,1997)									
mean (n=608)	18.1	1.0	9.4	16.9	2.6	2.0	0.2	2.8	
Leaf litterfall of wet tropical rain forest, Malaysia (Burghouts, 1993)									
	13.8	0.4	4.8	5.5	2.4				

Table 2. Mean chemical property of soils of 63 subplots within the site.

	pH *		Total			Exchangeable ***					Extractable***			
	H_2O	KCl	N	C	C/N	Al**	Ca	Mg	K	Na	P	S	Al	Fe
			(g kg^{-1})			c mol(+) kg^{-1}					mg kg^{-1}			
0 - 5 cm														
mean (n=63)	4.4	4.3	4.7	62.0	13.2	4.0	9.60	0.68	0.27	0.12	5.56	3.89	1519	92
SD			0.95	11.66	0.82		4.02	0.32	0.08	0.05	1.32	1.04	322	65
5 - 15 cm														
mean (n=63)	4.3	3.9	3.3	33.0	10.1	6.5	2.26	0.31	0.15	0.04	5.27	8.80	1251	121
SD			0.62	6.77	2.61		1.53	0.16	0.07	0.01	2.27	4.63	265	31

* Soil : water or 1N-KCl = 1:2.5 ** Wakatsuki et al. (1986). *** Soil : 1 M-HCl = 1 : 10

higher Ca concentration in the leaf litterfall than that in the Malaysian tropical forest. The other elements in leaf litter, such as N and P, were present at comparable levels with the tropical forest in Malaysia. Masunaga *et al.* (1998) also reported that the Ca concentration in living leaves at the same site was higher than that in a Malaysian tropical forest in Lambir Malaysia (Gerhard *et al.*, 1996). The significant difference in nutrient concentrations in living leaves between these two sites was attributed to the different levels of exchangeable Ca in the soil (Masunaga *et al.*, 1998). The soil in the present study plot has been categorized as unmatured inceptisols developed mainly from limestone and andesite, and was high in exchangeable Ca (Table 2). As Table 2 shows, exchangeable Al and extractable Al were also very high. Relatively rich exchangeable bases, especially exchangeable Ca, and high exchange acidity characterize the soil in this study plot (Wakatsuki *et al.*, 1986). Probably because of these soil characteristics, leaf litterfall at this study plot had a noticeable concentration of Al, which showed larger variations than those of the other elements. This result was probably also due to the various Al accumulator plant species that are distributed throughout this plot (Masunaga *et al.*,1997). However, the K concentrations in the leaf litterfall in this study plot were relatively low compared to those in the litterfall in Malaysia (Table 1). This finding was presumably due to the leaching of K both from the canopy and at the litter traps by the very high rainfall in this forest area.

Micro Spatial Distribution of Litterfall and Nutrient Flux in Relation to Tree Composition.

The average litterfall production of the study plot was estimated as 11.4 Mg ha^{-1} y^{-1}, with a range of 7.4 to 16.3 Mg ha^{-1} y^{-1} (Table 3). The annual litter fall and nutrient fluxes in this study plot were found to vary significantly within the 63 study subplots (Fig. 4 and Table 4). Compared to the nutrient fluxes in other tropical rain forests, the mean P flux of this study plot was comparable to that in lowland rain forest in Malaysia, and was higher than those in both Dipterocarp forests in Malaysia and Mixed forests in French Guyana Table 4). This study plot also showed a considerably higher Ca flux than that in

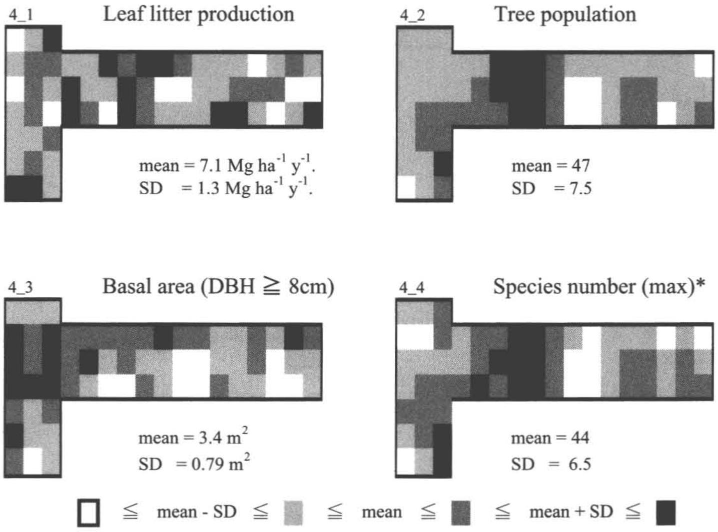
Table 3. Mean and range of annual litterfall in 63 subplots within the study site.

	total litterfall	leaf litterfall	other litterfall
		Mg ha^{-1} y^{-1}	
mean	11.4	7.1	4.3
min	7.4	4.3	0.6
max	16.3	10.4	19.9
SD	2.1	1.3	3.7
CV(%)	18.5	19.0	86.1

Table 4. Annual nutrient flux through leaf litterfall within the site and in the other site of tropical forest.

	kg ha^{-1} y^{-1}							
	N	P	Ca	Mg	K	Al	Fe	S
mean (n=63)	92.5	2.6	125.3	11.7	17.2	9.7	1.4	10.7
min	54.2	1.5	70.6	6.2	8.8	3.2	0.7	6.2
max	139.8	4.5	206.7	17.7	27.5	26.4	3.5	16.4
SD	19.6	0.6	28.0	2.9	4.0	5.3	0.6	2.4
CV(%)	21.2	24.3	22.3	24.8	23.2	54.3	39.7	22.0
other site								
Mixed [a)]	73.2	1.1	22.7					
Dipterocarp forest [b)]	81.0	1.2	13.0					
Lowland rain forest [c)]	100.0	2.8	70.0					

a) Brouwer, 1997, French Guyana, b) Proctor, 1983, Sarawak Malaysia and c) Lim, 1978, Pasoh Malysia.



* constitute of identified and unidentified tree sp.

Fig.4. Micro spatial distribution pattern of leaf litter production, tree population, number of species and basal area within the site.

Dipterocarp forests and Lowland rain forests in Malaysia (Table 4).

To clarify the relationships among the micro spatial distribution pattern of various parameters, including leaf litter production, tree density, number of tree species, basal area and various available/extractable elements in soil, correlation coefficients and the ω index were calculated (Tables 5 and 6). The correlation coefficients and ω index generally showed the same trend shown in Tables 5 and 6, and Fig.7. For a quick understanding of the similarities between correlation coefficients and the ω index, both Tables 5 and 6 show pattern drawings based on the criteria of significance to the relationship between the parameters. The correlation coefficients in Table 5 and the ω index in Table 6 were significantly and positively correlated (Fig.7). As shown in Fig. 7, the correlation coefficients of

0.32 (1 % level of positive significance) were equivalent to the ω index of 0.46. Correlation coefficients of 0.24 (5 % level of positive significance) and 0.20 (10 % level of positive significance) were equivalent to indices of 0.38 and 0.34, respectively. The negative values of correlation coefficients of −0.32, −0.24 and −0.20 (1%, 5 % and 10 % level of negative significance) were equivalent to the negative indices of ω index of −0.17, −0.09 and −0.05, respectively. Those values were used for the pattern drawing in Table 6. Since our previous research was based on the ω index (Kubota *et al.*, 1998, 2000), we used the ω index in the present study too, although either the correlation coefficient or the ω index is sufficient to show the relationship between the parameters in Tables 5 and 6.

Leaf litterfall production was significantly and positively correlated with tree density (r=0.34 and ω =0.56) and species number (r=0.35 and ω =0.50). Its correlation with basal area was low (r=0.10 and

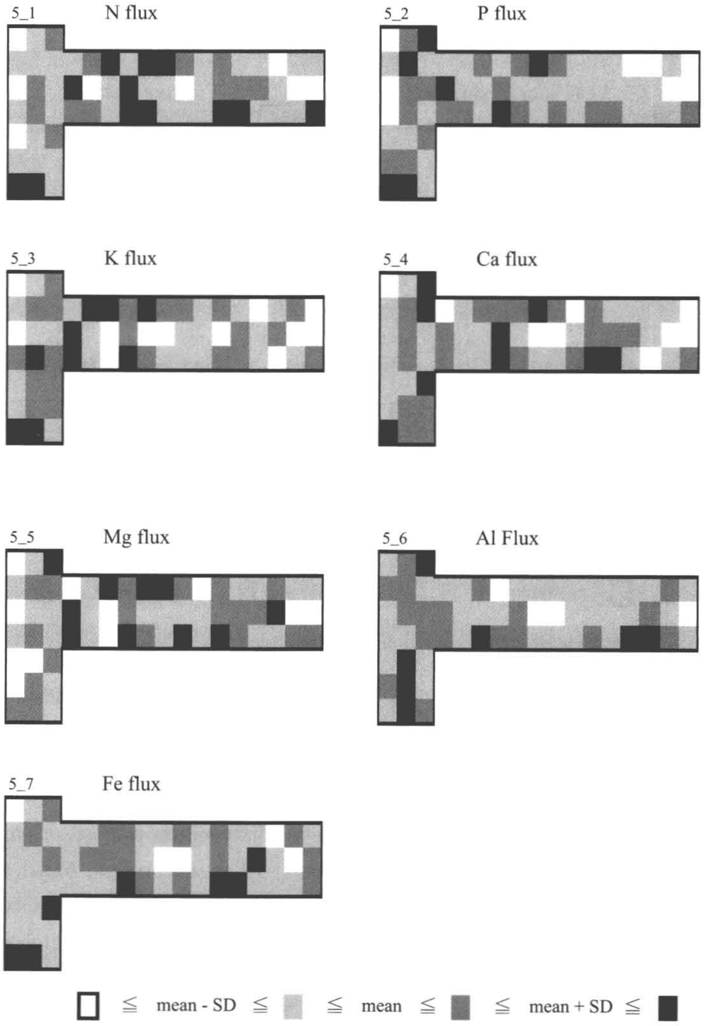
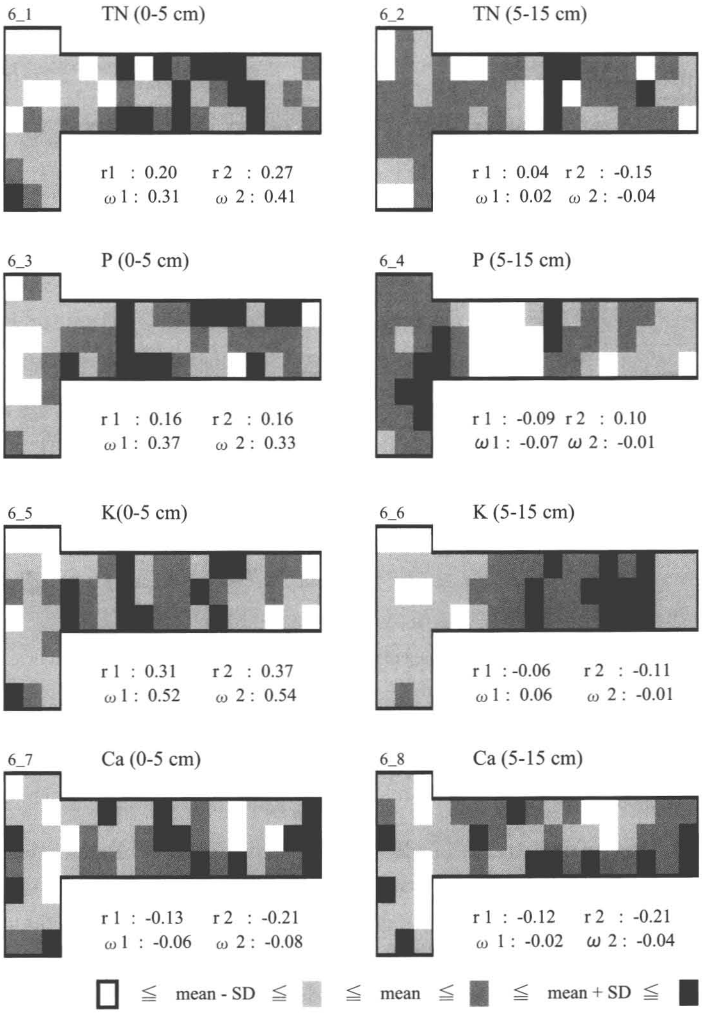


Fig.5. Micro spatial distribution pattern of various nutrient fluxes through leaf litterfall within the site.

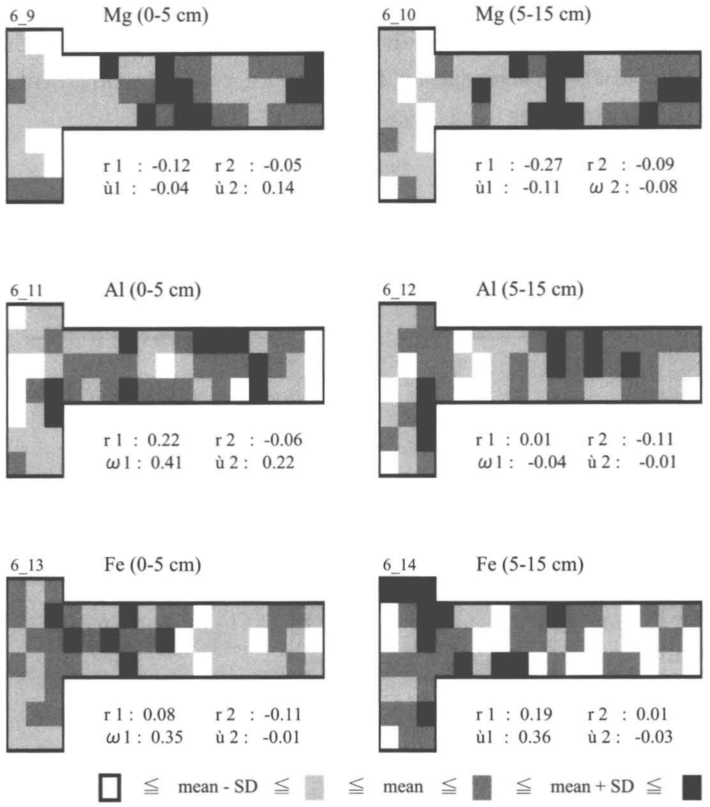
$\omega = 0.43$). In terms of nutrient flux, since the nutrient flux was calculated by multiplying the amount of leaf litterfall production by the nutrient concentration, the amount of each nutrient flux was strongly affected by the amount of leaf litterfall production. It was, in turn, positively correlated with tree density and species number, as seen in Tables 5 and 6 as well as in Figs. 4 and 5.



r 1, ω1: correlation coeficients and omega index between leaf litterfall and each soil chemical property.

r 2, ω2: correlation coefficients and omega index between nutrient flux of litterfall and each soil chemical property.

Fig.6. Micro spatial distribution pattern of TN, extractable P, K, Ca, Mg, Al and Fe in topsoil (0-5 cm and 5-15 cm) depth within the site.

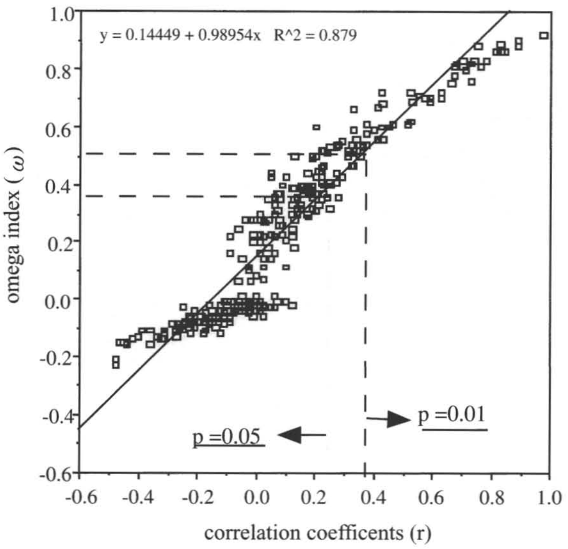


r 1, ω 1: correlation coeficients and omega index between leaf litterfall and each soil chemical property.
r 2, ω2: correlation coefficients and omega index between nutrient flux of litterfall and each soil chemical property.

Fig.6. Continued.

Micro Spatial Distribution of Litterfall in Relation to Soil Chemical Properties

In relation to soil chemical properties, the micro spatial distribution of leaf litter production was significantly and positively correlated with the distribution of some elements in the top soils (0-5 cm), namely 0.1 M extractable K ($r= 0.31$, $\omega = 0.52$) and Al ($r=0.22$, $\omega = 0.41$). The relationship of litterfall production to the total N ($r=0.20$, $\omega = 0.31$ equivalent 10 % significant level) and extractable P ($r=0.16$, $\omega =0.37$ equivalent 10 % level), in soil were relatively low (Tables 5 and 6). High leaf litter production might contribute to the increase in the total N, extractable P, K, Al, and Fe in the surface soil (0-5 cm). The degree of overlap of those actual micro spatial distributions on the study plot was determined by comparing the micro spatial distribution pattern of leaf litterfall production in Fig. 4-1 and the distribution patterns of various soil chemical properties in Fig 6. The positive interactions between leaf litter production and soil nutrient distribution, particularly the distribution of total N and available P, although not very strong were likely due to either a direct increase in the absolute amounts of these nutrients in the soil or the indirect effect of organic matter contributing to an increase in soil



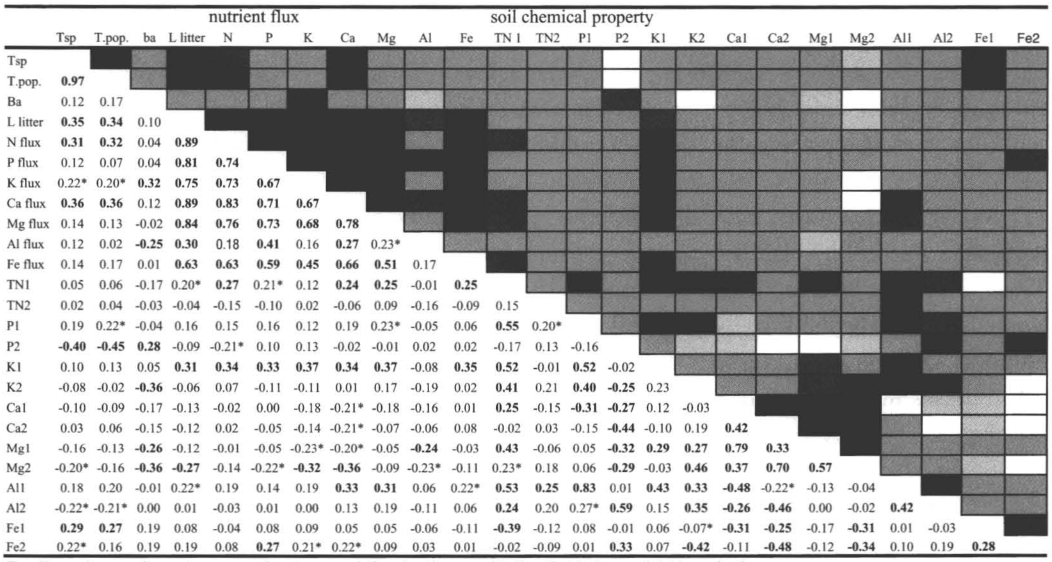
p =0.01 : r= 0.32 , ω = 0.46 p =0.01 : r= -0.32 , ω = -0.17

p =0.05 : r= 0.24 , ω = 0.38 p =0.05 : r= -0.24 , ω = -0.09

p =0.10 : r= 0.20 , ω = 0.34 p =0.10 : r= -0.20 , ω = -0.05

Fig.7. Relationship between correlation coefficients in Table 5 and omega index in Table 6 for all the parameters which were analyzed for this study.

Table 5. Correlation coefficients matrix of tree composition, litterfall, nutrient flux and soil chemical property within the study site.



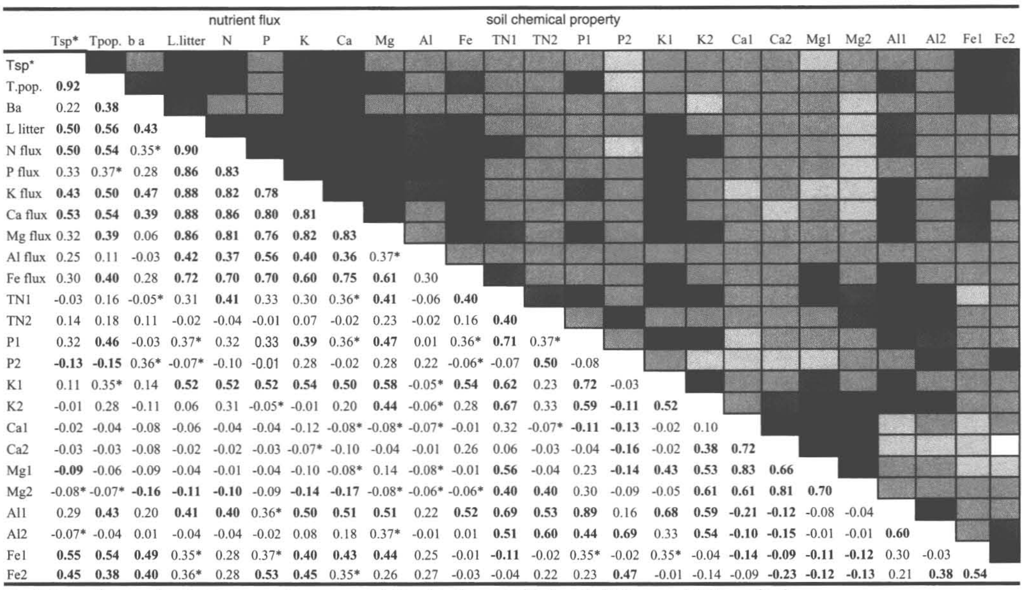
					nutrient flux							soil chemical property													
	Tsp	T.pop.	ba	L litter	N	P	K	Ca	Mg	Al	Fe	TN 1	TN2	P1	P2	K1	K2	Ca1	Ca2	Mg1	Mg2	Al1	Al2	Fe1	Fe2
Tsp																									
T.pop.	**0.97**																								
Ba	0.12	0.17																							
L litter	**0.35**	**0.34**	0.10																						
N flux	**0.31**	**0.32**	0.04	**0.89**																					
P flux	0.12	0.07	0.04	**0.81**	**0.74**																				
K flux	0.22*	0.20*	**0.32**	**0.75**	**0.73**	**0.67**																			
Ca flux	**0.36**	**0.36**	0.12	**0.89**	**0.83**	**0.71**	**0.67**																		
Mg flux	0.14	0.13	-0.02	**0.84**	**0.76**	**0.73**	**0.68**	**0.78**																	
Al flux	0.12	0.02	**-0.25**	**0.30**	0.18	**0.41**	0.16	**0.27**	0.23*																
Fe flux	0.14	0.17	0.01	**0.63**	**0.63**	**0.59**	**0.45**	**0.66**	**0.51**	0.17															
TN1	0.05	0.06	-0.17	0.20*	**0.27**	0.21*	0.12	**0.24**	**0.25**	-0.01	**0.25**														
TN2	0.02	0.04	-0.03	-0.04	-0.15	-0.10	0.02	-0.06	0.09	-0.16	-0.09	0.15													
P1	0.19	0.22*	-0.04	0.16	0.15	0.16	0.12	0.19	0.23*	-0.05	0.06	**0.55**	0.20*												
P2	**-0.40**	**-0.45**	**0.28**	-0.09	-0.21*	0.10	0.13	-0.02	-0.01	0.02	0.02	-0.17	0.13	-0.16											
K1	0.10	0.13	0.05	**0.31**	**0.34**	**0.33**	**0.37**	**0.34**	**0.37**	-0.08	**0.35**	**0.52**	-0.01	**0.52**	-0.02										
K2	-0.08	-0.02	**-0.36**	-0.06	0.07	-0.11	-0.11	0.01	0.17	-0.19	0.02	**0.41**	0.21	**0.40**	**-0.25**	0.23									
Ca1	-0.10	-0.09	-0.17	-0.13	-0.02	0.00	-0.18	-0.21*	-0.18	-0.16	0.01	**0.25**	-0.15	**-0.31**	**-0.27**	0.12	-0.03								
Ca2	0.03	0.06	-0.15	-0.12	0.02	-0.05	-0.14	-0.21*	-0.07	-0.06	0.08	-0.02	0.03	-0.15	**-0.44**	-0.10	0.19	**0.42**							
Mg1	-0.16	-0.13	**-0.26**	-0.12	-0.01	-0.05	-0.23*	-0.20*	-0.05	**-0.24**	-0.03	**0.43**	-0.06	0.05	**-0.32**	**0.29**	**0.27**	**0.79**	**0.33**						
Mg2	-0.20*	-0.16	**-0.36**	**-0.27**	-0.14	-0.22*	**-0.32**	**-0.36**	-0.09	-0.23*	-0.11	0.23*	0.18	0.06	**-0.29**	-0.03	**0.46**	**0.37**	**0.70**	**0.57**					
Al1	0.18	0.20	-0.01	0.22*	0.19	0.14	0.19	**0.33**	**0.31**	0.06	0.22*	**0.53**	**0.25**	**0.83**	0.01	**0.43**	**0.33**	**-0.48**	-0.22*	-0.13	-0.04				
Al2	-0.22*	-0.21*	0.00	0.01	-0.03	0.01	0.00	0.13	0.19	-0.11	0.06	**0.24**	0.20	0.27*	**0.59**	0.15	**0.35**	**-0.26**	**-0.46**	0.00	-0.02	**0.42**			
Fe1	**0.29**	**0.27**	0.19	0.08	-0.04	0.08	0.09	0.05	0.05	-0.06	-0.11	**-0.39**	-0.12	0.08	-0.01	0.06	-0.07*	**-0.31**	**-0.25**	-0.17	**-0.31**	0.01	-0.03		
Fe2	0.22*	0.16	0.19	0.19	0.08	**0.27**	0.21*	0.22*	0.09	0.03	0.01	-0.02	-0.09	0.01	**0.33**	0.07	**-0.42**	-0.11	**-0.48**	-0.12	**-0.34**	0.10	0.19	**0.28**	

Tsp, T pop.,ba., maximum tree sp. number, tree population, basal area and 1, 2, soil at 0-5 cm and 5-15 cm depth.

bold letter, significant at 5 and 1 % level 1% 5% 5% 1%

*, significant at 10 % levels. ☐ ≦ **-0.32** ≦ ▨ ≦ **-0.24** ≦ ▨ ≦ **0.24** ≦ ■ ≦ **0.32** ≦ ■

Table 6. Omega index matrix of tree composition, litterfall, nutrient flux and soil chemical property within the study site.



					nutrient flux							soil chemical property													
	Tsp*	Tpop.	b a	L.litter	N	P	K	Ca	Mg	Al	Fe	TN1	TN2	P1	P2	K1	K2	Ca1	Ca2	Mg1	Mg2	Al1	Al2	Fe1	Fe2
Tsp*																									
T.pop.	**0.92**																								
Ba	0.22	**0.38**																							
L litter	**0.50**	**0.56**	**0.43**																						
N flux	**0.50**	**0.54**	0.35*	**0.90**																					
P flux	0.33	0.37*	0.28	**0.86**	**0.83**																				
K flux	**0.43**	**0.50**	**0.47**	**0.88**	**0.82**	**0.78**																			
Ca flux	**0.53**	**0.54**	**0.39**	**0.88**	**0.86**	**0.80**	**0.81**																		
Mg flux	0.32	**0.39**	0.06	**0.86**	**0.81**	**0.76**	**0.82**	**0.83**																	
Al flux	0.25	0.11	-0.03	**0.42**	**0.37**	**0.56**	**0.40**	**0.36**	0.37*																
Fe flux	0.30	**0.40**	0.28	**0.72**	**0.70**	**0.70**	**0.60**	**0.75**	**0.61**	0.30															
TN1	-0.03	0.16	-0.05*	0.31	**0.41**	0.33	0.30	0.36*	**0.41**	-0.06	**0.40**														
TN2	0.14	0.18	0.11	-0.02	-0.04	-0.01	0.07	-0.02	0.23	-0.02	0.16	**0.40**													
P1	0.32	**0.46**	-0.03	0.37*	0.32	0.33	**0.39**	0.36*	**0.47**	0.01	0.36*	**0.71**	0.37*												
P2	**-0.13**	**-0.15**	0.36*	-0.07*	-0.10	-0.01	0.28	-0.02	0.28	0.22	-0.06*	-0.07	**0.50**	-0.08											
K1	0.11	0.35*	0.14	**0.52**	**0.52**	**0.52**	**0.54**	**0.50**	**0.58**	-0.05*	**0.54**	**0.62**	0.23	**0.72**	-0.03										
K2	-0.01	0.28	-0.11	0.06	0.31	-0.05*	-0.01	0.20	**0.44**	-0.06*	0.28	**0.67**	0.33	**0.59**	**-0.11**	**0.52**									
Ca1	-0.02	-0.04	-0.08	-0.06	-0.04	-0.04	-0.12	-0.08*	-0.08*	-0.07*	-0.01	0.32	-0.07*	**-0.11**	**-0.13**	-0.02	0.10								
Ca2	-0.03	-0.03	-0.08	-0.02	-0.02	-0.03	-0.07*	-0.10	-0.04	-0.01	0.26	0.06	-0.03	-0.04	**-0.16**	-0.02	**0.38**	**0.72**							
Mg1	**-0.09**	-0.06	-0.09	-0.04	-0.01	-0.04	-0.10	-0.08*	0.14	-0.08*	-0.01	**0.56**	-0.04	0.23	**-0.14**	**0.43**	**0.53**	**0.83**	**0.66**						
Mg2	-0.08*	-0.07*	**-0.16**	**-0.11**	**-0.10**	-0.09	**-0.14**	**-0.17**	-0.08*	-0.06*	-0.06*	**0.40**	**0.40**	0.30	-0.09	-0.05	**0.61**	**0.61**	**0.81**	**0.70**					
Al1	0.29	**0.43**	0.20	**0.41**	**0.40**	0.36*	**0.50**	**0.51**	**0.51**	0.22	**0.52**	**0.69**	**0.53**	**0.89**	0.16	**0.68**	**0.59**	**-0.21**	**-0.12**	-0.08	-0.04				
Al2	-0.07*	-0.04	0.01	-0.04	-0.04	-0.02	0.08	0.18	0.37*	-0.01	0.01	**0.51**	**0.60**	**0.44**	**0.69**	0.33	**0.54**	**-0.10**	**-0.15**	-0.01	-0.01	**0.60**			
Fe1	**0.55**	**0.54**	**0.49**	0.35*	0.28	0.37*	**0.40**	**0.43**	**0.44**	0.25	-0.01	**-0.11**	-0.02	0.35*	-0.02	0.35*	-0.04	**-0.14**	**-0.09**	**-0.11**	**-0.12**	0.30	-0.03		
Fe2	**0.45**	**0.38**	**0.40**	0.36*	0.28	**0.53**	**0.45**	0.35*	0.26	0.27	-0.03	-0.04	0.22	0.23	**0.47**	-0.01	-0.14	-0.09	**-0.23**	**-0.12**	**-0.13**	0.21	**0.38**	**0.54**	

Tsp*, T pop.,ba., maximum tree sp. number, tree population, basal area and 1, 2, soil at 0-5 cm and 5-15 cm depth.
bold letter : equivalent of significant at 5 and 1% level, (based on the Fig.7)
*: significant at 10 % levels, (based on the Fig.7)

1% 5% 5% 1%
☐ ≦ **-0.17** ≦ ▒ ≦ **-0.09** ≦ ▨ ≦ **0.38** ≦ ■ ≦ **0.46** ≦ ■

nutrient availability. The weak positive relationship ($p < 0.1$) between leaf litter production and the amount of extractable Al and Fe in the soil, was presumably due to the participation of organic matter that enabled the dissolution of Al oxides and an associated reduction of Fe to form an organic complex with Fe^{2+}. One theory that has received wide attention among soil scientists is that the mobilization and transport of sesquioxide in soil may be due, at least in part, to polymeric phenols (fulvic acid) formed in the overlying litter through decay caused by microorganisms (Stevensen, 1985). As shown in Tables 1 and 4, the Al concentration in the leaf litter of this study plot was considerably high. This might at least partly cause the increase in the extractable form of Al, especially in the topsoil (0-5 cm).

Among the three most important nutrients, N, P and K, the micro spatial distribution of leaf litter production showed the highest positive correlation to the available level of K in topsoils, as seen in Tables 5 and 6 as well as Figs. 4-1 and 6-5. As shown in Table 1, the mean K concentration of living leaves in this study plot was 9.4 g kg^{-1} (Masunaga *et al.*, 1997). The mean K concentration in the leaf litter was, however, only 2.4 g kg^{-1}. This means that 75 % of the K in leaves was lost through leaching, which passes to the soil through stemflow or throughfall. On the other hand, Ca showed negligible leaching (16.9 to 17.7 g kg^{-1}) and Mg showed relatively small levels of leaching (2.60 gkg^{-1} to 1.64 g kg^{-1} for 37 % loss). If we consider the effect of leaching and compare the levels of extractable bases in soils (Table 2), we can explain why litterfall production showed a positive and significant correlation to the extractable K in topsoils. The total flux can be estimated based on the data of annual flux (Table 4) and the amount of leaching loss from litter. The total fluxes of Ca, Mg and K are estimated as 125.3 x 16.9/17.7, 11.7 x 2.64/1.64, and 17.2 x 9.44/2.44, i.e. 120, 19, and 67 kg ha^{-1} y^{-1}, respectively. The amounts of exchangeable Ca, Mg, and K in topsoil (0-5 cm), and at 5-15 cm of depth were 499 kg and 951 kg for Ca, 21 kg and 58 kg for Mg, and 27 kg and 86 kg for K, respectively. For this calculation, the mean bulk density data 0.52 kg m^{-3} for 0-5 cm and 1.0 kg m^{-3} for 5-15 cm were used (Wakatsuki *et al.*, 1986). The ratios of total flux to soil at 0-5 cm and 5-15 cm were 499/120 and 951/120 for Ca, 21/19 and 58/19 for Mg and 27/67 and 86/67 for K, respectively. The effect of litterfall production on the topsoil is much higher in K than in Mg and Ca. This result is probably the reason why the extractable/available levels of soil Ca and Mg were not related to the micro spatial distribution pattern of leaf litter production as seen in Tables 5 and 6 as well as in Fig. 4-1 and Figs. 6-7 to 6-10.

Micro Spatial Distribution of Nutrient Flux in Relation to Soil Chemical Properties and Tree Species Diversity

Our previous study (Kubota *et al.*, 2000) on soil quality characterization in relation to tree species diversity revealed a negative relationship between nutrient concentrations in soil and the diversity of tree species, with the exception of the concentrations of extractable Fe, P and Mn and exchangeable K in topsoil. Kubota *et al.* (2000) also found that, among the elements analyzed, extractable Ca of soil in particular showed a significant negative correlation with tree density and the number of tree species. This means that the areas with a high tree density and tree species number had relatively low soil Ca. The present study partly supports this previous study's findings, although exchangeable Ca content in the soil did not show a significant negative relationship to the number of tree species and tree density (Tables 5 and 6). Extractable P and Mg content in soil showed a significant negative correlation to the number of tree species and tree density although some relationships are statistically weak (Table 5 and 6).

The nutrient fluxes of N, P and K tended to show a positive relationship with the total N and extractable P and K in the topsoil (Fig. 6). A significant positive correlation between the nutrient flux of N and total N and flux of K and K in topsoil was observed. However, it was insignificant of the relationship between P flux and P in soil. The total amount of N in topsoil at 0-5 cm was estimated to be 1230 kg ha^{-1}. This amount is considerably higher than the annual N flux of 92.5 kg ha^{-1}. Since the C/N ratio of leaf litters in the forest is high (36.4) in this study, (Table 1), it is possible that some additional nitrogen might have also been fixed by microorganisms using organic matter in the litters supplied to the soil. Various soil microorganisms can fix nitrogen using carbon sources. After all, a major accumulation of N in forest soils happens in relation to the supply of litterfall to the soil. In nature, this accumulation of N is quite different than that of P, Ca, Mg and K which are mainly supplied to the soil through rock weathering. This may be the reason why soil N, especially in topsoil, has a positive correlation to litterfall production and N flux through litterfall. Although not so strong significant, the positive trend of the relationship between P flux and extractable P in soil was presumably due to the low level of extractable P in the surface soil. The addition of organic matter through litterfall increased the available P through either the addition of P from leaf litterfall material, or the indirect effect of organic matter in reducing the adsorption of P on clay minerals, and iron and aluminum oxides in soils.

CONCLUSION

These results showed that nutrient fluxes through leaf litter were positively and significantly correlated to the concentration levels of TN and K in soils. However, Ca and Mg did not show such positive correlations. These differences might relate to the ratio of the level of soil nutrients to the nutrient flux from the trees. When soil nutrient levels were low, the effects of nutrient flux through litterfall were clear. However, the micro spatial of tree species richness, i.e., the species number per subplot, showed a significant positive correlation to tree density, litterfall amount, N and Ca flux. The micro spatial soil fertility parameters, except for the extractable Fe in topsoil, had a negative correlation to the number of tree species. These results might suggest that the high diversity of tree species and the diverse nutritional characteristics of the tree species contributed to the variation of soil nutritional status and to an edaphic niche via nutrient cycling, i.e., nutrient uptake, accumulation and flux, in this super wet tropical rainforest.

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