Dynamics of litter production and its quality in relation to climatic factors in a super wet tropical rain forest, West Sumatra, Indonesia

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ABSTRACT In order to clarify the detailed dynamics of litter production and its nutrient characteristics in a super wet tropical rainforest, a study was conducted using twelve litter traps installed in a one ha study plot at Pinang-Pinang, in West Sumatra, Indonesia. The trapped litter was collected monthly in two different years (December 1997 to November 1998 and December 1999 to November 2000). The annual mean litter production in 1997/98 was 12.2 Mg ha^{-1} and in 1999/2000 was 11.8 Mg ha^{-1}. The contribution of leaf litter to the total litterfall was significantly greater (64.8%) than that of the other components i.e., twigs, branches and fruits. The total litterfall and leaf litter production ranged from 0.16 to 1.98 and from 0.10 to 1.30 Mg ha^{-1}month^{-1}, respectively, during the two observation periods. The seasonal pattern of leaf litter production showed a strong positive correlation with mean monthly temperature. Since the mean monthly temperature showed a negative correlation to monthly precipitation, the monthly leaf litter production also showed a negative correlation to the monthly precipitation. The negative correlation between leaf litter production and monthly precipitation was, however, less significant than the positive correlation of leaf litter production to temperature. This finding suggests that, although the mechanism is unknown, leaf litter production is strongly regulated by slight fluctuations in monthly mean temperature, within the range of 25-28 ℃ in this super wet tropical rainforest. A positive correlation between temperature and litter production was also observed for the total litter and for the other litter components. However, the correlation was less significant for these other litter categories than for leaf litter. Among the litter components (leaf, twigs, branches and fruit), leaf litter showed the highest concentration of nitrogen (N), magnesium (Mg) and sulfur (S). The reproductive structure (fruit) had a significantly higher concentration of P and K than leaf litter, but the fruit's concentration of Ca was lower than those of the other components of the litter. The concentrations of Ca in leaf litter showed a positive correlation to rainfall and a negative correlation to temperature, while the concentration of K in leaf litter showed the reverse trend. The trend of N concentration in leaf litter was somewhat similar to Ca. These trends might be due to the effect of dilution on Ca and N, remobilization on N, and the leaching by rainfall on K.

Key words: litterfall dynamics, leaf litter production, rainfall effect, super wet tropical rain forest, temperature effect, West Sumatra

Litterfall is the first phase of the biogeochemical cycle (Lebret *et al.*, 2001) and a major mechanism for nutrient cycling in forest ecosystems (Proctor *et al.*, 1983; Spain, 1984; Vitousek and Sanford, 1986). Many studies have been done on the litterfall and nutrient dynamics of tropical rainforests in various regions (Jordan 1985; Vitousek, 1982, 1984). However, there have been very few studies on litterfall and its nutrient dynamics in the super wet tropical rainforest in West Sumatra, Indonesia (Richard, 1996).

Hotta and Ogino (1984, 1986) established various plots for long-term ecological research along the slopes of G. Gadut, in West Sumatra. This study plot has an annual precipitation of more than 5,000 mm

(Hotta, 1984) and no dry season. Masunaga *et al.* (1998) showed the extremely diverse nature of nutritional characteristics of mineral elements in tree species and Kubota *et al.* (1998, 2000) suggested a possible interrelationship between extremely high tree species diversity and diversity of nutritional characteristics of plant species. The diverse nutritional characteristics of plant species may contribute to the creation of heterogeneous soil characteristics through nutrient cycling via litterfall in the super wet tropical rainforest in West Sumatra.

Considering these previous ecological studies, the aim of our study is to quantify the interaction between nutrient flux dynamics through litterfall and heterogeneous local soil chemical properties in subplots with an area of 10-30 m x 10-30 m, in relation to tree species composition in a super wet tropical rainforest. Although our second paper (Hermansah *et al.*, in review) described such spatial micro areal heterogeneity, this paper describes the details of the dynamics of litterfall and its nutrient composition in relation to the seasonal fluctuation of both rainfall and temperature with regards to tree species diversity within a one-ha study plot at Pinang-Pinang in West Sumatra, Indonesia.

MATERIALS AND METHODS

Study Site

The study was carried out on a one-hectare plot of primary forest in a tropical rain forest at Pinang-Pinang on the foothill of mount Gadut in West Sumatra, Indonesia. The plot was established by Hotta and Ogino (Hotta, 1984, 1986). It is located at an altitude of 460 - 550 m above mean sea level (Fig.

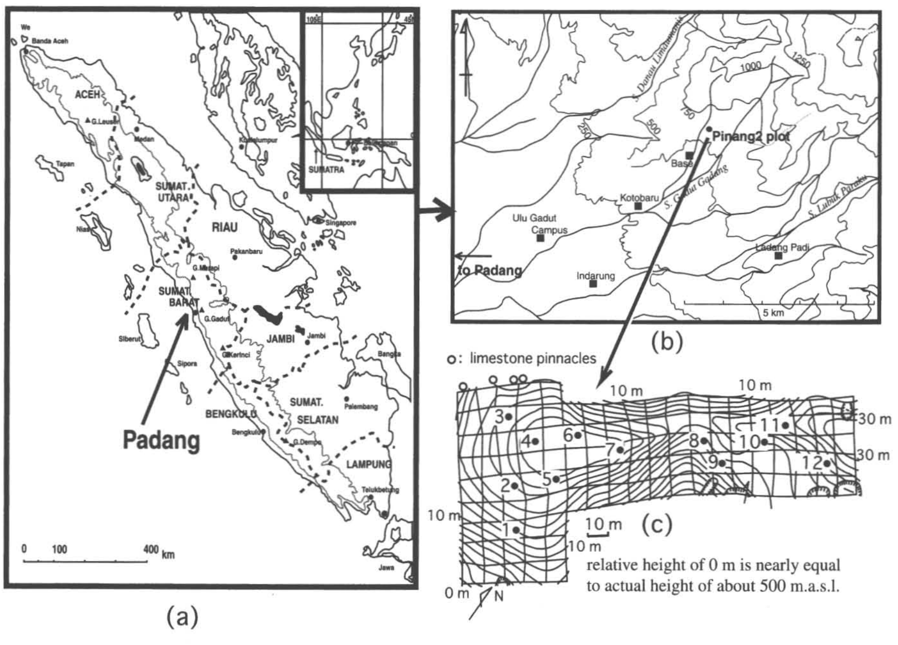


Fig.1. Study site in West Sumatra, Indoneisa. (a)Sumatra map, (b)topographical map of Gadut Mountain, and (c) the 12 litter trap positions and contour lines were drawn in 2 m height intervals.

1a,b). The plot has been divided into 115, 10 m x 10 m subplots (Fig.1c). Within this 1 ha plot, 892 trees with a diameter at breast height (DBH) greater than 8 cm were recorded by Hotta and Ogino in 1984 (Hotta, 1984). Those trees include 231 identified species and 241 unidentified species (Masunaga *et al.*, 1997). The structure of this primary forest was illustrated as emergent tree stratum, prominent tree stratum and subprominent tree stratum with an average height of 50, 35 and 20 m for each stratum, respectively (Hotta, 1984). The annual rainfall exceeds 5,000 mm and there is no dry season (Hotta 1984, 1986, 1989). According to Wakatsuki et al. (1986), soils in this plot are unmatured Dystropepts and Eutropepts developed mainly from limestone and andesite. However, the recent *Soil Taxonomy* report (Soil Survey Staff, 1999) designated these soils as Dystroudepts and Eutroudepts.

Sample Collection

Twelve litter traps (collection area 0.32 m^2) were installed in twelve different subplots in December 1997 (Fig. 1c). The traps were positioned in the center of each subplot at 1 m above ground level. The traps were constructed in the shape of a funnel using a nylon net of 1.0 mm mesh size supported by a frame of perpendicular wooden poles. The tree population and species number of each subplot were determined using the previous data recorded by Hotta and Yoneda (Kubota *et al.*, 2000). The basal area of each subplot was calculated based on the DBH size.

To observe monthly fluctuations of litterfall, litter was collected monthly from December 1997 to November 1998 and from December 1999 to November 2000. The contents of each trap were sorted into leaves, wood (twigs and branches), flowers, fruits and other litter debris. Separation of litter components by species was not done, mainly because of technical difficulty. Therefore these results indicate only overall litterfall dynamics. More detailed litterfall characterization, based on species composition, including phenological behavior, will be the subject of future research.

Laboratory Methods and Data Analyses

All litter material was dried at 60℃ to a constant weight in an oven for 48 hours, and the dry weights were recorded. The leaf litter, twigs, branches and fruits were then ground into 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 concentrations of elements, Ca, Mg, Al, Fe, S and P, were determined by an Inductive Coupled Plasma Atomic Emission Spectrometer (ICPS-2000; Shimadzu, Japan). Potassium was determined by an Atomic Absorption Emission Spectrophotometer, (AA-680; Shimadzu, Japan). Total N was determined by the dry combustion method in a highly sensitive N-C analyzer (Sumigraph N-C 80; Sumitomo, Japan). The climatic data of monthly rainfall and temperature during the monitoring period of litterfall production were taken from the records of Tabing Airport, Padang, which is about 17 km west of the study plot. Since the alluvial plains stretch uninterruptedly between the study plot and Tabing Airport, we assumed that the temperature and rainfall fluctuation were similar.

To analyze the relationships between the seasonal variations in litter production, nutrient composition and either rainfall or temperature, correlation coefficients were determined. To clarify the effects of site-specific environmental factors such as forest structure, topography, and soil chemical property factors on the litterfall-rainfall relationship, the litterfall-temperature relationship and the relationship between the nutrient composition of leaf litter and rainfall or temperature, the correlation coefficients of each of the 12 subplots were calculated separately.

The presence of significant correlations were determined by comparing the values of correlation coefficients, which were calculated using Microsoft Excel, Office 2000, to r table in Nyumon Tokei Kaisekihou "Introduction to Statistical Analysis" (Nagata, 1992). If the calculated values of the correlation coefficients are higher than the r table values at certain probability levels, the relationship between the parameters is significant. The r table values were calculated using the following formula: $r=2.576/\sqrt{\Phi+3}$ and $r=1.960/\sqrt{\Phi+1}$, for 1% and 5 % significant level, respectively. The symbol Φ represent the number of samples. The mean values of nutrient concentration over the two years were compared with t-test; and to establish the differences of means concentration among the litter components, ANOVA, continued with Least Significant Difference (LSD) ($p<0.05$), was applied.

RESULTS AND DISCUSSION

Climate

The annual rainfall recorded in Tabing Airport, Padang was 1776, 5664, 4489 and 4133 mm in 1997, 1998, 1999 and 2000, respectively. The annual mean temperature was 26.2, 26.8, 24.2 and 26.3 ℃ for 1997, 1998, 1999 and 2000, respectively. Figure 2 shows the monthly distribution of rainfall and temperature (mean, maximum and minimum) from December 1997 to November 2000. Over the observation year of December 1997 to November 1998, the period of lowest rainfall was observed from February to May, after which the rainfall increased until September, then declined again between September and October. From December 1999 to November 2000, the low rainfall period was from February to March, after which rainfall increased gradually until November. During the observation period, temperature and rainfall were clearly negatively correlated ($r=-0.40$), (Fig.3). In the year prior to the start of the first study period, (January to March 1997) and again from June to November 1997, there were unusually long periods of dryness. Although we were unable to collect data during this El-nino year, we began our monitoring immediately after November 1997. This means that the first batch of our monitoring, December 1997 to November 1998, might have been influenced by the El-nino of the

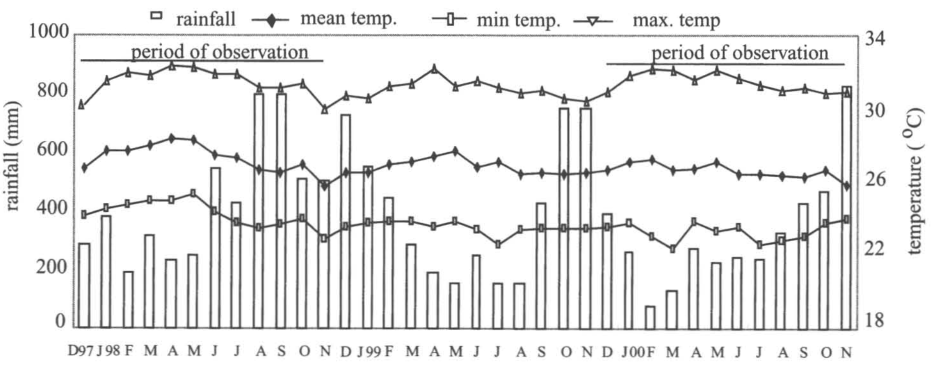


Fig. 2. Rainfall and temperature (min, mean, max) during the litterfall 2-years observation period(Dec. 1997 to Nov.2000) recorded from Tabing Airport meteorological station, Padang.

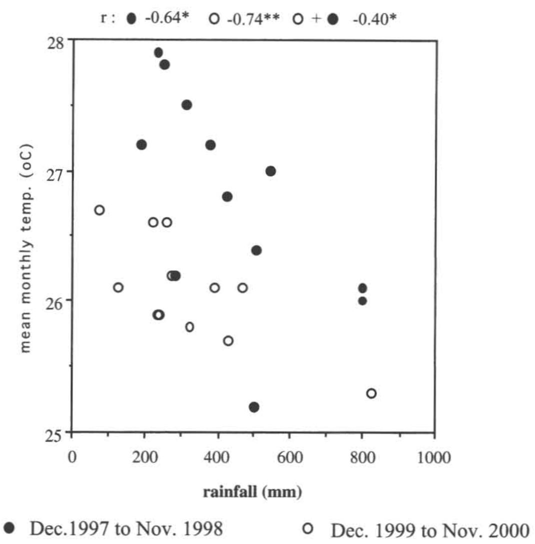


Fig. 3. Rainfall and temperature relationship during the litterfall 2-year observation period (Dec. 1997 to No.1998 and Dec. 1999 to Nov. 2000). * and **, significant at 5 and 1 % level, respectively.

previous year. The effects of the dry climate induced by El-nino on the litterfall dynamics in the secondary forest in this region have been reported (Yoneda *et al.*, 2000).

Litter Production

The average annual litter production from December 1997 to November 1998 at the study site was estimated to be 12.2 Mg ha^{-1}, while it was estimated to be 11.8 Mg ha^{-1} from December 1999 to November 2000 (Table 1). The amounts of litterfall were comparable between the two years, and they were also comparable with those of other tropical forest sites in Venezuela (10.3 Mg ha^{-1} y^{-1}) as reported by Cuevas and Mediana (1986). However, they were slightly higher than that recorded by Luizao (1989) in Brazil (8.2 Mg ha^{-1} y^{-1}). During the observation period, the litterfall components were

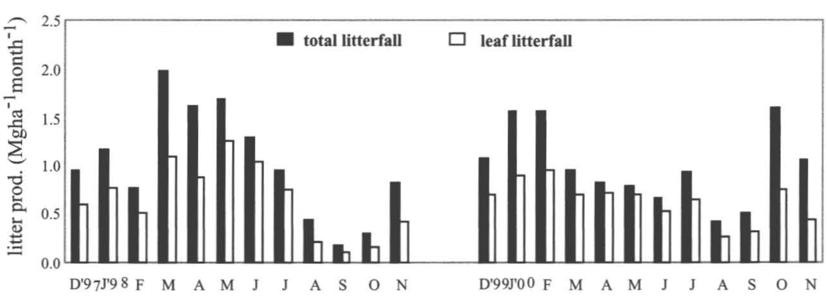


Fig. 4. Litterfall pattern during two years (Dec.1997 to Nov 1998 and Dec.1999 to Nov. 2000) of obervation in the Pinang-Pinang study plot.

composed primarily of leaf litter (64.8%), followed by wood (twigs and branches, 32.2 %), fruits (0.9%), flowers (0.3%) and other litter debris (1.8 %). The proportion of leaf litter to the total litterfall was comparable to that in other tropical rain forests in Malaysia (71 %; Lim, 1978), Brazil (66%; Luizao, 1989), and Venezuela (74%; Cuevas and Medina, 1986).

The turnover time of leaves in this site was estimated to be 0.90/yr, and was calculated as the living leaf biomass of 6.9 Mg ha^{-1} (Yoneda *et al.*, 1994) divided by the average annual leaf litter production over the two years of litter collection (7.7 Mg ha^{-1}). The turnover time of leaves in this site was comparable to that of a moist forest in Panama (0.9/yr) (Golley *et al.*, 1975). However, the turnover time at this study site was shorter than the turnover time of leaves in Dipterocarp Forest Pasoh, Malaysia (1.3/yr) (Ogawa, 1978).

Monthly total litter and leaf litter production fluctuated more in 1997-1998 than in 1999-2000 (Fig.4). The difference between the minimum and maximum values of monthly leaf litter and total litter (Table 1) was wider in 1997-1998 than in 1999-2000, being a 13-fold *versus* a 3-fold difference for leaf litterfall and a 9-fold *versus* a 4-fold difference for total litterfall. This suggests that there were some unknown after effects of the El-nino of previous year of 1997-1998. The seasonal variation of litter production varied among the litter components. The coefficients of variation (CV) of the total, leaf, wood, including twig, branch and other debris and fruit including flower litterfall were 55.7, 59.1, 71.4 and 172.2, respectively from 1997 to 1998; and were 39.9, 33.4, 73.9, and 112.7 from 1999 to 2000, respectively. Leaf litter showed a smaller seasonal variation than the other litter components during the observation period. In terms of the annual litter production of the 12 subplots, leaf litter also showed a smaller spatial variation than the sum of the other litter components (Table1). Since wood litter fall may need relatively strong wind and fruit litter fall may be related to an unknown phonological event, leaf litter was thought to be the best component to analyze the relationship between litter production and climatic factors. For this reason, and due to the fact that leaf litter was the main component of total litterfall, our discussion of the seasonal variation in relation to climatic factors such as rainfall and temperature focused on leaf litter.

Table 1. Variation of monthly and annual litterfall production in the study plot for two years.

	monthly litterfall (Mg $ha^{-1}month^{-1}$)			annual litterfall (Mg $ha^{-1}y^{-1}$)		
	n= 144			n= 12		
1997-1998	total	leaf	other[1)]	total	leaf	other[1)]
mean	1.0	0.7	0.4	12.2	7.8	4.4
min	0.2	0.1	0.1	6.1	4.6	1.5
max	1.9	1.3	0.9	23.0	11.7	11.4
CV (%)	55.7	59.1	64.5	39.1	29.2	66.5
1999-2000						
mean	1.0	0.6	0.4	11.8	7.6	4.3
min	0.4	0.3	0.1	10.0	6.1	2.6
max	1.6	0.9	0.8	15.2	9.2	6.4
CV (%)	39.9	33.4	70.5	12.7	14.4	23.2

1) other: wood, fruits, flowers and other debris.

Leaf litter production varied seasonally, as shown in Figure 4. The leaf litter production ranged from 0.1 to 1.3 Mg ha^{-1}month^{-1} from December 1997 to November 1998 and from 0.3 to 0.9 Mg ha^{-1} month^{-1} from December 1999 to November 2000. The leaf litter production from December 1997 to April 1998 did not show any specific trend. However, from May 1998 to September 1998, leaf litter production decreased gradually, while an increasing trend in rainfall was observed during the same period (Fig.2). The leaf litter production then increased again from September until November 1998. In the period from December 1999 to November 2000, leaf litter production decreased gradually between February 2000 and August 2000. In both observation periods the trend of leaf litterfall was the reverse trend of that of rainfall.

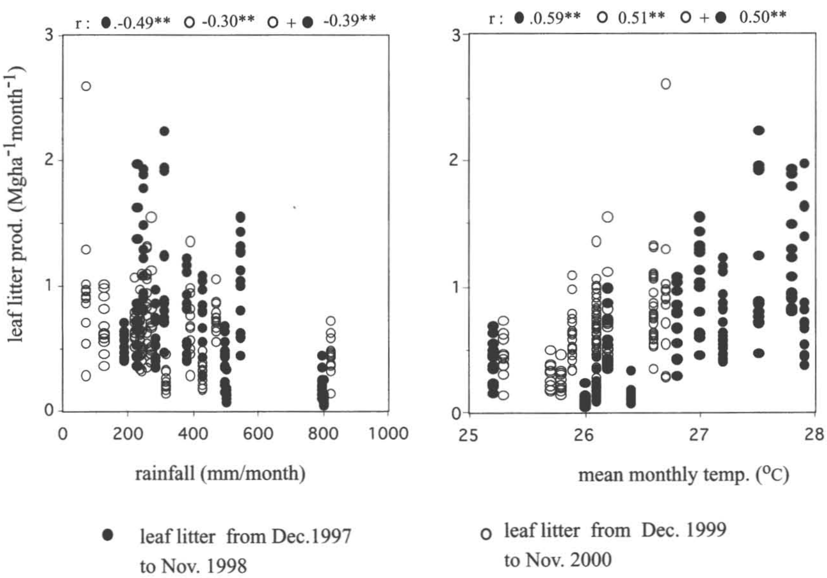


Fig. 5. Relationship between leaf litter production and rainfall and leaf litter production and mean temperature at two different times in the study site. **, significant at 1 % level.

Figure 5 shows the relationship between monthly leaf litter production and monthly rainfall and mean temperatures. Leaf litter production was negatively correlated (r=−0.39 in two years) with rainfall. The correlation coefficients between rainfall and leaf litter production was -0.49 in Dec. 1997-Nov. 1998 and was −0.30 in Dec. 1999-Nov. 2000. The results in Dec. 1997-Nov. 1998 may have been affected by the 1997 El-nino. However, these correlations were not as strong as the correlation between temperature and leaf litter production (r=0.50 for Dec, 1997-1998, 0.59 for Dec. 1999-2000 and 0.51 for the two years combined). This finding suggests that seasonal litterfall variation is not strongly regulated by rainfall, except during special years, such as ones El-nino. The observed findings concurr with the results of former studies (Vitousek, 1984), showing that water availability does not affect the seasonal changes of litter production at sites having an annual rainfall greater than 2,000 mm.

A stronger positive relationship between leaf litter production and mean monthly temperature was observed in both observation periods. These results suggest that the seasonal dynamic of leaf litter production is inflenced more strongly by small temperature fluctuations than by rainfall fluctuations in the super wet tropical rainforest. Van Schaik (1986) also reported, qualitatively, that increasing monthly temperatures had an effect on the emergence of young leaves and leaf fall in a tropical rain forest in north Sumatra, Indonesia, where the annual rainfall was 3,229 mm. The results of this study constitute the first quantitative data on the effect of mean monthly temperature on monthly leaf litterfall. In the this study, the minimum and maximum temperatures showed no correlation or only weak correlation with the variation of leaf litter production. This indicates that mean monthly temperature is the best parameter for describing the relationship between temperature fluctuations and litter production.

Table 2. Correlation coefficients between litterfall production and rainfall and mean temperature at each of the 12 subplots in Pinang-Pinang.

subplot[1)]	rainfall-total litter	temperature-total litter	rainfall-leaf litter	temperature-leaf litter	rainfall-others[2)]	temperature-others[2)]
all subplots	-0.26*	0.37**	-0.39**	0.50**	-0.06	0.15
1	-0.43*	0.66**	-0.40*	0.71**	-0.26	0.21
2	-0.31	0.63**	-0.38	0.21	-0.17	0.56**
3	-0.46*	0.45*	-0.36	0.74**	0.38	0.3
4	-0.08	0.24	-0.40*	0.52**	0.16	0.04
5	-0.46*	0.38	-0.46*	0.44*	-0.23	0.08
6	-0.17	0.11	-0.64**	0.44*	0.12	-0.09
7	-0.14	0.45**	-0.42*	0.59**	0.07	0.13
8	-0.43*	0.27	-0.52**	0.44*	-0.12	0.03
9	-0.29	0.48*	-0.40*	0.67**	0.25	-0.36
10	-0.31	0.30	-0.50**	0.28	0.07	0.23
11	-0.49**	0.69**	-0.63**	0.64**	0.11	0.44*
12	-0.30	0.50**	-0.34	0.61**	0.21	0.29

**, * significant at 1 and 5 % levels. 1) for the position of 12 subplots, see Fig.1c.
2) others include wood, fruits, flowers and other litter debris.

In order to determine the micro spatial variation in the relationship between climatic factors such as rainfall and temperature and the production of total, leaf and the sum of other litter components, data were break down into each of the 12 subplots (for the position, see Fig.1c) as shown in Table 2. Among the total litter, leaf litter and the sum of the other litter components, leaf litter had the highest correlation coefficients with both rainfall and temperature (Table 2). This indicates that leaf litterfall is the best parameter for studying the effect of climatic factors in this study site. The relationship between leaf litter production and rainfall or temperature fluctuation in each subplot (Table 2) was basically the same as the general trend of the results in the whole plot scale as shown in Fig. 5. Both rainfall and mean temperature showed a significant correlation with leaf litter production in most of the subplots. Nine of the 12 subplots showed a significantly negative rainfall-leaf litter relationship, and 10 of the 12 subplots showed a significantly positive temperature-leaf litter relationship. Although statistical analyses of all of the subplots showed significant correlations between leaf litter production and both rainfall and temperature, the correlation coefficients between litter production and climatic factors (rainfall and temperature) among the 12 subplots were varied. This finding suggests that spatial variability of microclimate among the subplots or other environmental factors including soil chemical and physical characteristics or tree species composition in each subplot, could just as well influence the seasonal variation of leaf litter production.

In order to examine the effects of tree density, number of species, and size of tree on the leaf litter production at the subplot level (10 x 10 m), the correlation coefficients between leaf litter production and tree population and basal area were calculated. Although the results are not shown here, leaf litter production tended to be high but not significant ($P>0.05$) in the subplots that had a large tree population ($r=0.2$) and had a large basal area ($r=0.2$). This result simply implies that subplots with a large population and high above-ground biomass have higher litter production. The detailed studies of the micro spatial distribution of litterfall in relation to tree species composition or diversity and soil heterogeneity in this super wet tropical rain forest were described in another paper (Hermansah *et al.*, in review).

Nutrient Characteristics of Litterfall and Its Relation to Rainfall and Temperature

There were significant differences in the mean Ca, Al and Fe content in leaf litter among the two observation periods (Table 3) although the reasons for these differences were not clear. Among the litter components, leaf litter had the highest concentrations of N, Mg and S. The reproductive component, (fruit) had significantly higher K concentrations, though it had a significantly lower Ca concentration. The woody material, (twigs and branches) showed a higher concentration of Ca.

The concentrations of Ca and N in leaf litter had a significant negative correlation to the total and leaf litter production (Table 4). These trends may be due, partly, to a dilution effect, especially with Ca, and partly to the remobilization effect, especially with N. On the other hand, the concentration of K was strongly positive correlated to both total and leaf litter production (table 4).

Rainfall showed a strong positive correlation to the concentration of Ca, Fe, P, S and N in leaf litter, and a significant negative correlation to that of K in leaf litter (Table 4 and Fig. 6). There are

Table 3. Mean nutrient concentration of litterfall in the study site.

	($g\ kg^{-1}$)							
component	N	P	K	Ca	Mg	Al	Fe	S
Dec.1997 to Nov.1998								
leaf (n=144)	14.3 a	0.4 a	2.6 a	13.8 a	1.5 a	1.9 a	0.4 a	1.7 a
SD	0.9	0.1	0.9	1.9	0.2	0.7	0.1	0.2
Dec.1999 to Nov.2000								
leaf (n=144)	13.8 a	0.4 a	2.5 a	18.2 b	1.7 a	1.3 b	0.2 b	1.6 a
SD	1.3	1.0	0.9	2.4	0.3	0.6	0.1	0.2
mean for 2 years								
leaf	14.1	0.4	2.5	15.9	1.6	1.6	0.3	1.6
twigs	7.3	0.4	1.1	17.0	0.9	1.5	0.2	1.3
branches	3.9	0.3	0.6	21.2	0.8	1.7	0.3	1.2
fruits	13.4	0.9	4.7	7.6	1.3	0.8	0.4	1.4
LSD (0.05)	3.6	2.1	2.7	5.5	2.2	2.3	2.1	2.2

means followed by a common letter in the same column are not significantly different at the 5 % level as indicated by a t test.

Table 4. Correlation coefficients between litter production, climatic factors and nutrient concentrations in leaf litter.

	total [1]	leaf [2]	other [3]	rainfall	temp.
total [1]					
leaf [2]	0.75**				
other [3]	0.79**	0.31**			
rainfall	-0.26**	-0.39**	-0.06		
temp.	0.37**	0.50**	0.15	-0.40	
Ca	-0.16**	-0.14*	-0.16	0.17**	-0.44**
Mg	-0.04	-0.05	0.00	0.09	-0.15**
K	0.15**	0.21**	0.04	-0.26**	0.22**
Al	-0.13	-0.06	-0.13	0.11	0.03
Fe	-0.07	-0.11	-0.02	0.23**	0.18**
P	0.01	-0.07	0.12*	0.22**	0.02
S	0.04	0.06	0.00	0.13*	0.07
N	-0.13*	-0.16**	-0.07	0.14*	-0.08

** and *, significant at 1 and 5 % levels.

1) total litterfall, 2) leaf litterfall and 3) other litterfall including wood, fruits, flowers and other litter debris.

significant negative correlations between temperature and concentrations of Ca and Mg in leaf litter (Table 4 and Fig.6). The leaf litter concentration of K, however, was significantly lower during the period of higher rainfall. This may suggest that K was leached out of leaf litter by rainfall. The increase of K loss from leaf litter during the rainy season was also reported by Das and Ramakrishnan (1985). We also observed in our study site that stemflow and throughfall contributed to the K flux more than five times more than the K flux through litterfall although data are not shown. The relatively low N, P and Mg concentration in leaf litter during the period of high temperature could be partly explained by the remobilization or retranslocation of those elements from leaf to twig before leaf fall (Helmisaari, 1992 and Marschner, 1995). Remobilization is presumably more efficient in trees growing on infertile soil (Miller *et al.*, 1979). It can be assumed, therefore, that the nutrient remobilization from the senescing part of the leaf was more efficient during the highest leaf litterfall period when the temperature was high. Marschner (1995) stated that remobilization of mineral nutrients is important during the ontogenesis of a plant during seed germination, periods of insufficient supply to the roots during vegetative growth, reproductive growth and in perennials, the period before leaf fall. A lower Ca concentration during periods of lower rainfall and high temperature might be explained by the dilution effect, caused by a higher rate of leaf production. The accumulation of carbohydrates caused by a higher rate of photosynthesis might occur during leaf production at higher temperatures and lower rainfall periods thus decreasing Ca concentration. We need further research to clarify this phenomenon. The trends for the other elements such as Al, Fe and S were unclear.

To clarify the variation in the relationship between the concentration of elements in leaf litter and rainfall / temperature, the correlation coefficients of each subplot are shown in Table 5. The relationships varied according to both element and subplot. For example, the concentration of P showed significant positive correlations with rainfall only in sites 8 through 12, which were located on the east side of the study plot (Fig.1c). Such variations in the relationship between nutrient concentrations and

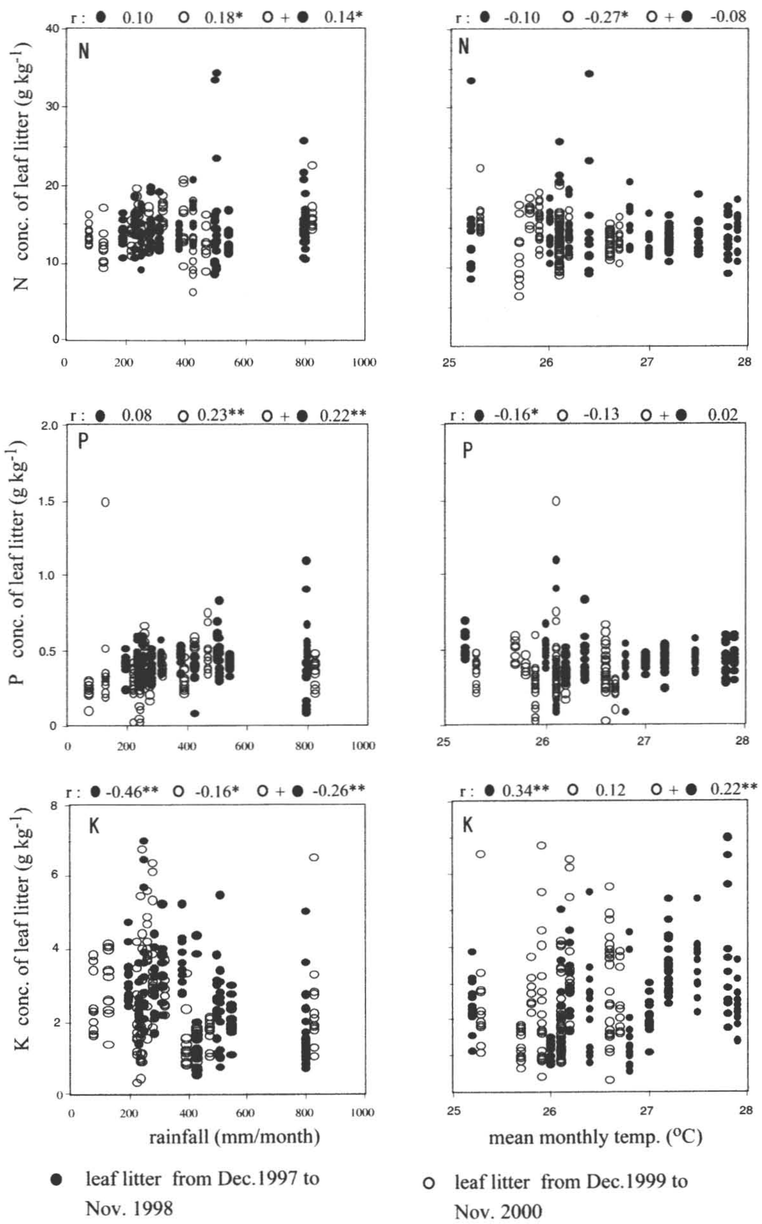
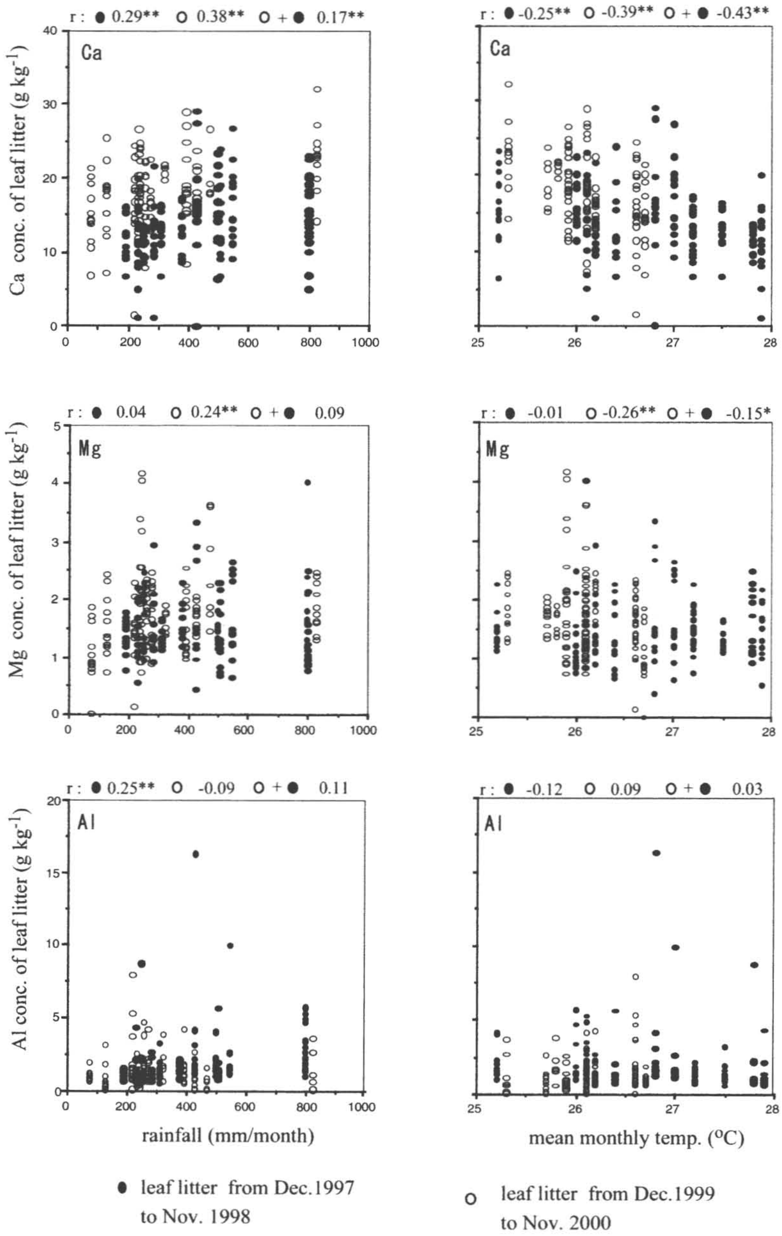


Fig. 6. Relationship between nutrient concentrations in leaf litter and climatic factors (rainfall and temperature) in the study site. * and **, significant at 5 and 1 % level, respectively.



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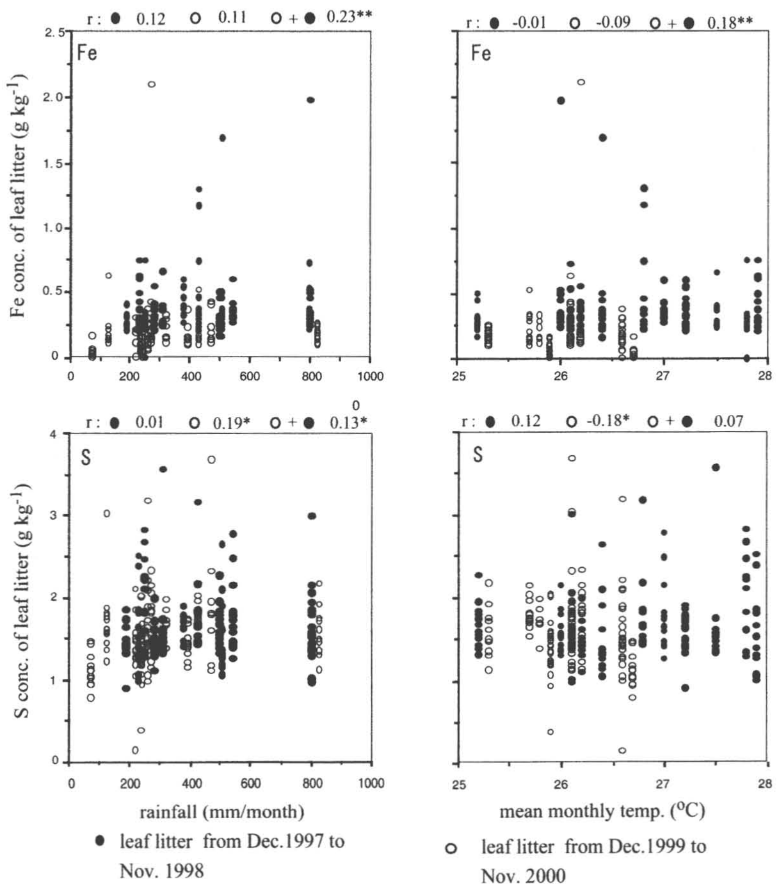

Fig. 6. Continued

climatic factors were also found for other elements such as K, Ca and Mg. These results may suggest environmental conditions vary between each subplot within the plot. Some factors, such as those related to nutrient availability, differed due to water movement or to soil chemical or physical characteristics, indicating that topographical position and soil properties might affect the relationship between the mineral concentrations in leaf litter and climatic factors (rainfall and temperature). Unlike the concentrations of N, P and Ca, that of K in leaf litter generally showed a strong negative correlation with rainfall for all subplots (Table 5). However, a like the other elements, the strength of the correlations with K among the subplot were varied. There seems to have been little inter-subplot variation in the relationships between the mineral element concentrations and rainfall and temperature.

Table 5. Correlation coefficients between nutrient concentrations of litterfall and rainfall and temperature in the study site during the 2 year observation period.

	N	P	K	Ca	Mg	Al	Fe	S
subplot	with rainfall							
all subplots	0.14*	0.22**	-0.26**	0.17**	0.09	0.11	0.23	0.13*
1	0.20	0.03	-0.34	0.27	-0.02	-0.02	0.07	0.14
2	0.27	0.01	-0.35	0.25	0.02	0.19	0.40*	-0.02
3	0.22	-0.24	-0.05	0.12	-0.04	0.29	0.13	0.42*
4	0.32	0.10	-0.52**	0.11	-0.08	0.10	0.18	-0.07
5	0.02	0.27	-0.43*	0.13	-0.10	0.09	0.15	0.21
6	0.30	-0.02	-0.23	0.36	0.07	0.21	0.25	0.05
7	0.14	0.22	-0.28	0.13	0.38*	0.17	0.36	0.15
8	-0.03	0.67**	-0.40*	0.17	0.15	0.48*	0.15	0.36
9	-0.27	0.53**	-0.39*	0.25	0.50**	-0.17	-0.19	-0.08
10	0.18	0.44*	-0.05	0.28	0.22	0.17	0.10	0.14
11	0.20	0.45*	-0.42*	0.34	0.03	0.29	0.49**	0.31
12	0.15	0.46*	-0.05	0.08	0.01	-0.04	0.37	0.05
	with temperature							
all subplots	-0.08	0.02	0.22**	-0.44**	-0.15*	0.03	0.18**	0.07
1	-0.29	0.29	0.19	-0.63**	-0.07	-0.20	0.15	0.06
2	-0.24	0.08	0.02	-0.35	-0.03	0.17	0.21	0.04
3	-0.17	0.00	0.10	-0.43*	-0.05	0.17	0.64*	0.17
4	-0.20	-0.04	0.17	-0.47*	-0.11	0.29	0.47*	0.26
5	0.07	-0.08	0.46*	-0.55**	-0.17	0.07	0.43*	-0.04
6	-0.01	0.07	-0.05	-0.67*	-0.27	-0.14	0.01	-0.29
7	0.17	0.11	0.31	-0.55*	0.38	-0.04	0.20	0.06
8	-0.11	-0.06	0.48*	-0.31	-0.04	-0.04	0.28	0.07
9	0.35	-0.10	0.33	-0.29	-0.28	0.52**	0.05	0.54**
10	-0.39*	0.05	0.57*	-0.66**	-0.38*	0.19	0.02	-0.01
11	0.00	-0.02	0.35	-0.49**	-0.01	-0.15	0.06	0.10
12	-0.23	0.09	0.35	-0.43*	-0.43*	-0.06	0.26	-0.08

** and * siginficant at 1 and 5% levels.

CONCLUSION

In this study we found that small fluctuations of 2-3 ℃ in mean monthly air temperature within the range of 25 to 28 ℃ had a strong influence on litterfall dynamics. This is probably the first finding on the effect of temperature on litterfall dynamics in a super wet tropical rainforest. Seasonal variations in the nutrient concentration composition of leaf litter was also somewhat affected by fluctuations of rainfall and temperature. Although such site variations were considered to be related to various environmental factors other than climatic factors, detailed studies of the micro-spatial distribution of litter production and its nutrient flux in relation to tree composition and soil heterogeneity are needed.

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