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ОРИГИНАЛЬНЫЕ СТАТЬИ

Litter Production and Decomposition in Dry Forests of East Nusa Tenggara, Indonesia

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This 12-month long study explores the litterfall production and decomposition at four different sites in tropical dry forests of East Nusa Tenggara, Indonesia. The total litterfall, leaf litter and branch litter production values were found to be significantly different ($p < 0.05$) at all sites. The production of total litterfall, leaf litter, and branch litter was greater in Binafun (2778.125 g·m^{-2}·year^{-1} and 2453.125 g·m^{-2}·yr^{-1}) and Bonmuti (300.437 g·m^{-2}·yr^{-1}). The annual mean litterfall decomposition rate followed the order of Binafun < Letkole < Bonmuti < Oelbanu ($p < 0.05$), which positively correlated with the monthly mean precipitation, mean humidity, and mean temperature. The turnover rate calculation indicated that the forest floor was replaced every year with a turnover time of 1.083 years.

Keyword: decomposition, dry forest, litterfall, turnover.
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Analysis of litterfall production and decomposition is important for understanding the cycling of nutrients in forest ecosystems (Giweta, 2020). All natural forest ecosystems depend on the cycling of nutrients to meet nutritional demands of growing plants (Grierson, Adams, 1999; Chakravarty et al., 2019). The nutrients are primarily transferred as leaves and other plant parts fall to the ground as litter, where they are subsequently leached by percolating water and decomposed by live organisms (Eaton et al., 1973). Litterfall represents the key process of transferring nutrients from aboveground biomass to the soil. The changes in litter nutrient concentration over time decisively affect plant nutrition (Vitousek, 1984). Litterfall is a large transitional nutrient bank that may interfere with the species composition, structure, and dynamics in communities and plays a key role in transfer of energy among trophic levels (Facelli, Pickett, 1991).

According to Aber et al. (1991) and González et al. (2020), litter production and decomposition are fundamental ecosystem processes and play key roles in the cycling of nutrients, in particular the turnover of carbon and nutrients in terrestrial ecosystems. Litter accumulation has profound implications in the cycling of nutrients at plantations. The fertility of soils under plantations can only be maintained or sustained for fairly long periods due to the plantations' capacity of recycling nutrients back into the soil via litterfall production and decomposition (Muoghalu, Odiwe, 2011).

In tropical forest ecosystems with nutrient-poor soils, litterfall production and decomposition processes are particularly important for the nutrient budget (Sundarapandian, Swamy, 1999). Determining the decomposition rate makes it possible to assess the humification process that involves conversion of biomass into humic substances that are relatively resistant to microbial decomposition and have a long turnover time. This is one of the pedogenic processes in carbon sequestration (Lal et al., 2003). Several studies have compared the litterfall in monocultures to the litterfall in natural forests (Yang et al., 2004), temperate and subtropical regions (Fekete et al., 2016; Huang et al., 2018; Nonghuloo et al., 2020), in the Neotropics (Capellesso et al. 2016, González-Rodríguez et al. 2019) and South Asia (Ahirwal et al. 2021). However, natural forests generally have a more complex stand structure and differ in demographic dynamics, so it is difficult to infer effects of tree species richness by comparison with planted monocultures alone (Yang and Luo 2011).

How these processes work in tropical dry forests is relatively poorly known; in particular, there are no known published studies on litterfall production and decomposition in the tropical forests of East Nusa Tenggara, Indonesia. This study helps to address this gap by providing an analysis of litterfall production and decomposition rates at 4 sites of Mutis Timau Protected Forest Management Unit, a region representative of Mutis mountain conditions. Therefore, the present study is aimed at: (1) investigating the monthly variations of litter production in a tropical dry forest in the province of East Nusa Tenggara, Indonesia; (2) understanding the variations of litter decomposition; and (3) analyzing the litter decomposition rates of total litterfall, leaf litter, and branch litter of Mutis Timau Protected Forest Management Unit in East Nusa Tenggara, Indonesia.

MATERIAL AND METHODS

The study was carried out at the Mutis Timau Protected Forest Management Unit (Mutis Timau PFMU) which is covered by Kupang regency, Timor Tengah Selatan regency, and Timor Tengah Utara regency (90°20'00" – 90°45'10" S and 123°42'30" – 124°20'00" E) in Eastern Indonesia (Fig. 1). The data for this study was collected from 4 dry forest research sites named Binafun, Bonmuti, Letkole, and Oelbanu; each research site consists of two 10.000 m² plots. A detailed description of the research sites is shown in Table 1.

The research sites represent the dry forests of East Nusa Tenggara, Indonesia, whereas the surrounding areas are the wettest areas on the island of Timor where it rains almost every month with the highest frequency of rainfall occurring from November to July, temperatures ranging between 14–29°C with possible decrease of up to 9°C under extreme conditions. High-speed winds occur from November to March. About 71% area are hilly (15–30% slope) to mountainous (>30% slope). The high-intensity rainfall (2000–3000 mm·yr^{-1}) can be observed during the rainy season (Fisher et al., 1999; Kuswanto et al., 2021).

Eight traps were placed at every site in Binafun, Bonmuti, Letkole, and Oelbanu. Litterfall was collected every month from all traps in the course of a year. Litterfall was sorted into two categories: leaf litter and branch litter. The monthly litter production (g·m^{-2}) was calculated for every plot. Branch and leaf litter decomposition was studied using the standard litter-bag technique (Falconer et al., 1933). One hundred grams of dry mass consisting of leaf and branch litter were collected in litter bags and randomly placed on the soil surface. In total, we collected 48 bags of leaf litter and 48 bags of branch litter. Four litter bags per month were brought back to the laboratory. To get the constant weight, the collected litter was oven-dried at 80°C for 48 hours.

The annual decomposition quotient (KL) was calculated for leaf and branch litter using the formula (1):

$$KL = \frac{l}{X}, \quad (1)$$

where l means the annual litter input to the forest floor and X means the average standing crop of litter (Olson, 1963).

The decomposition constant of each species' leaf litter was calculated using the formula (2):

$$K_t = -\ln \frac{X_t}{X_0}, \quad (2)$$

where K_t means a constant of overall fractional loss rate, X_0 means the original mass, and X_t means the mass remaining at time t (Olson, 1963).

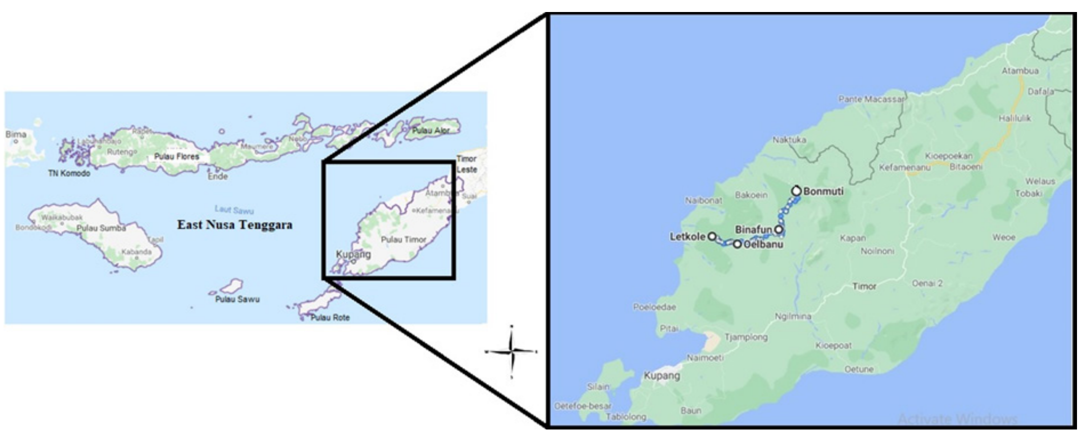

Fig. 1. Research site location.

Table 1. Research site description

Indicator	Village			
	Binafun	**Bonmuti**	**Letkole**	**Oelbanu**
District	Amfoang Tengah	Amfoang Tengah	Amfoang Barat Daya	Amfoang Selatan
Long S	09°39'12.22"	09°37'46.50"	09°41'02.62"	09°42'28.59"
Latitude E	124°01'421.16"	124°91'27.92"	123°48'	123°53'04.82"
Geology[a]	Mixed volcanic and limestone rock	Mixed volcanic and limestone rock	Mixed volcanic and limestone rock	Mixed volcanic and limestone rock
Rainfall[b], mm·yr^{-1}	1301	1405	1203	1254
Temperature[b], °C	24.1	21.4	26.4	25.3
Slope, °	0–14	0–26	0–10	0–12
Elevation, m	513–635	631–1007	122–125	310–636
Driest month[b]	September (5 mm)	August (12 mm)	September (3 mm)	September (4 mm)
Wettest month[b]	January (280 mm)	January (263 mm)	January (307 mm)	January (301 mm)
Highest temperature[b]	25.4°C (November)	22.7°C (November)	27.6°C (November)	26.6°C (November)
Lowest temperature[b]	22.6°C (July)	19.7°C (July)	25.0°C (July)	23.9°C (July)
Dry periods	June–October	June–September	May–October	May–October
Rain periods	December–May	October–May	September–April	December–April
Density, stem·ha^{-1}	285.5	249	524.5	355.5
Basal area, m^2·ha^{-1}	27.53	12.295	21.135	18.93
Species richness	7.995	4.655	9.995	4.935
Number of species based on DBH size:				
4.5–11.5 cm	22	16	36	36
11.5–18.5 cm	19	15	22	22
18.5–25.5 cm	30	33	53	74
25.5 cm	11	6	18	23

Note: [a] Fisher et al. (1999), [b] BPS (2016).

The turnover rate (K) of litter was calculated indirectly according to Olson (1963) using the formula (3):

$$K = \frac{A}{A+F}, \quad (3)$$

where: A is the annual increment of litter, i.e. annual litterfall and F is the annual averages across months.

Turnover time (t) is the reciprocal of the turnover rate $t = \frac{1}{K}$.

The monthly total litterfall, leaf litter and branch litter production, annual variation of litter production, and the weight of litter remaining for twelve months at the research sites were analyzed using a one-way ANOVA, and the means were compared with the Tukey HSD test at a 5% probability level.

RESULTS AND DISCUSSION

In this study, litterfall production at the research sites varied from 360 to 2778.125 g·m^{-2}·yr^{-1} (Figs. 2–5). Monthly total litterfall, leaf litter and branch litter production values were significantly different ($p < 0.05$) at all sites. The greatest total litterfall, leaf litter and branch litter production values were recorded in Binafun (2778.125 g·m^{-2}·yr^{-1} and 2453.125 g·m^{-2}·yr^{-1}) and Bonmuti (300.437 g·m^{-2}·yr^{-1}) whereas the lowest total litterfall, leaf litter and branch litter production values of 360 g·m^{-2}·yr^{-1}, 229.687 g·m^{-2}·yr^{-1} and 102 g·m^{-2}·yr^{-1} were recorded in Letkole and Bonmuti.

The litterfall occurred throughout the year; most of the litter fell between June and October with only

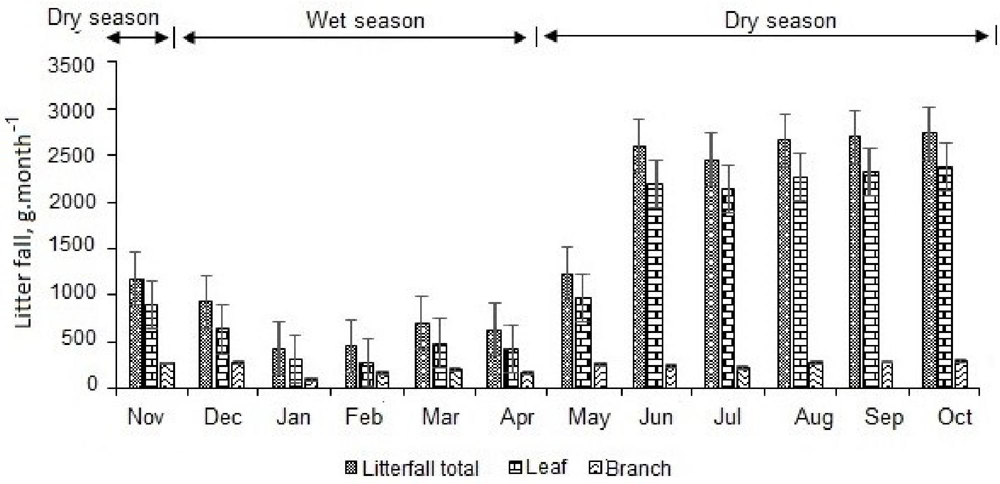

Fig. 2. Monthly litterfall in the dry forest of Binafun.

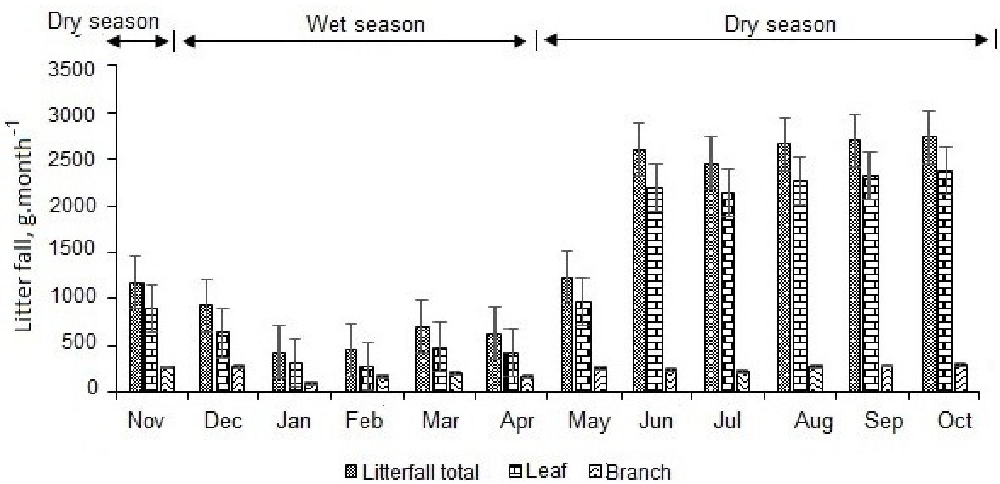

Fig. 3. Monthly litterfall in the dry forest of Bonmuti.

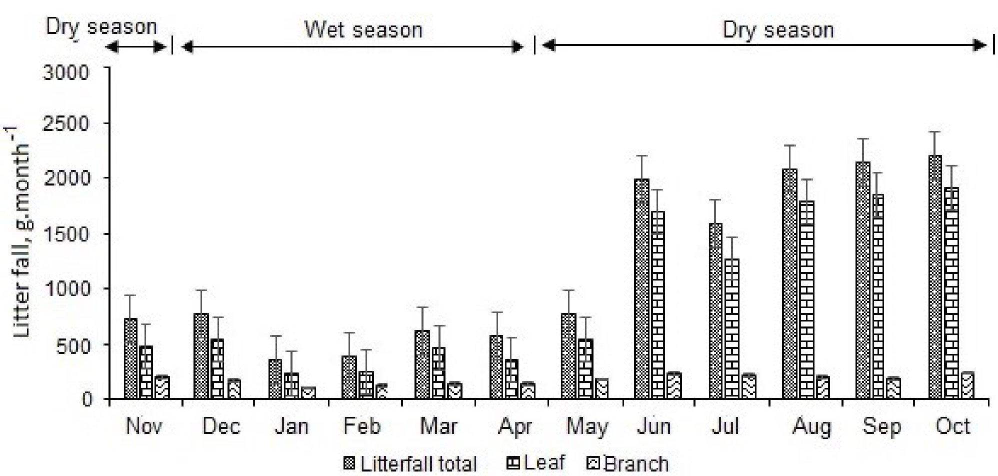

Fig. 4. Monthly litterfall in the dry forest of Letkole.

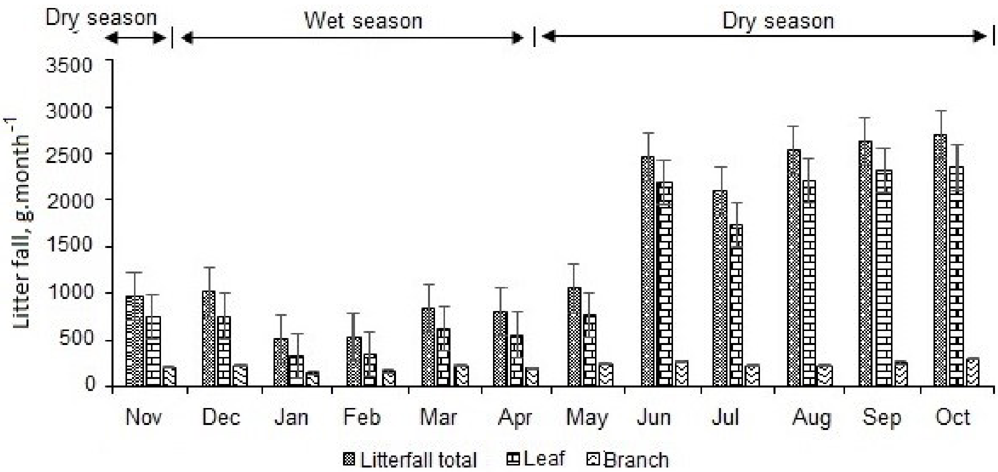

Fig. 5. Monthly litterfall in the dry forest of Oelbanu.

a small fraction of it falling between November and May for each research site. At all research sites, the higher peak occurred in the dry season (September – October) and the minor peak also occurred in the middle-late rain season (January – February). Leaf litter and branch litter values showed similar seasonal patterns compared to the total litterfall (Figs. 2–5).

The annual variation of litter production during the 1-year period was different among the four forest sites (Table 2). The lowest annual mean leaf and branch litter value was found in Letkole (950.4 $g \cdot ha^{-1} \cdot yr^{-1}$ and 181.4 $g \cdot ha^{-1} \cdot yr^{-1}$) (Table 2). Correspondingly, the ratio of maximum to minimum leaf litter and total litter over the 1-year period showed the same order of Binafun (9.3 and 6.7) > Bonmuti (8.3 and 6.4) > Letkole (8.3 and 6.4) > Oelbanu (7.0 and 5.0), and Bonmuti (2.9) > Letkole (2.2) > Binafun (2.1) > Oelbanu (2.0) for branch litter. The annual variation of litterfall components varied among the research sites. The greatest coefficient of variation for leaf litter (69.5%), branch litter (24.3%), and total litter (61.4%) was found in Letkole, Bonmuti, and Letkole, respectively (Table 2).

The litter weight remaining during the 12-month incubation had a significantly different pattern among research sites ($p < 0.05$). The decrease rate of the mass remaining in Oelbanu was faster than in Binafun, Bonmuti, and Letkole during the time, particularly in December, January, February, April, May, June, September, and October (Fig. 6).

The rates of total litterfall, leaf litter and branch litter decomposition ranged between 0.5 and 43.1 $g \cdot month^{-1}$, with the highest (leaf) and lowest (branch) litter decomposition in Oelbanu. In general, leaf litter showed the higher average decomposition rate than branch litter (Table 3).

In the present study, monthly mean litter decomposition components positively correlated

Table 2. Annual mean litterfall and its components ($g \cdot ha^{-1} \cdot yr^{-1}$) averaged over the 12-month study period

Research sites and indicators	Leaf	Branch	Total
Binafun			
Mean, $g \cdot ha^{-1} \cdot yr^{-1}$	1 258.4	218.6	1 477.0
Fraction, %	88.9	11.1	100
Coefficients of variation, %	67.8	19.9	59.7
Ratio (max/min)	9.4	2.1	6.8
Bonmuti			
Mean, $g \cdot ha^{-1} \cdot yr^{-1}$	1 275.4	231.2	1 506.7
Fraction, %	88.8	11.2	100
Coefficients of variation, %	67.1	24.3	59.3
Ratio (max/min)	8.4	2.9	6.5
Letkole			
Mean, $g \cdot ha^{-1} \cdot yr^{-1}$	950.4	181.4	1 131.8
Fraction, %	88.8	11.2	100
Coefficients of variation, %	69.5	22.9	61.4
Ratio (max/min)	8.3	2.3	6.4
Oelbanu			
Mean, $g \cdot ha^{-1} \cdot yr^{-1}$	1 243.1	222.5	1 465.6
Fraction, %	88.8	11.2	100
Coefficients of variation, %	64.0	18.2	56.5
Ratio (max/min)	7.0	2.0	5.5

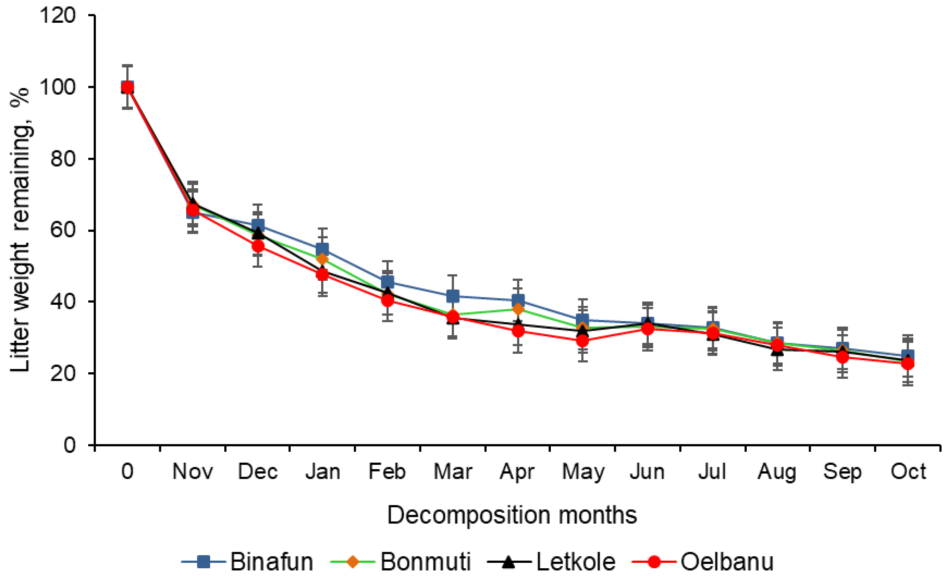

Fig. 6. Percentage of litterfall mass remaining.

Table 3. Litter decomposition rate (g·month^{-1}) at all research sites and litter components

Research site and litter components	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
Binafun												
Leaf	41.9	20.6	12.4	7.8	5.7	4.6	3.5	3.0	2.5	1.9	1.7	1.5
Branch	23.1	9.2	3.0	2.0	2.6	2.1	1.5	1.3	1.1	0.9	0.8	0.6
Total	65.0	29.8	15.4	9.8	8.3	6.7	5	4.3	3.6	2.8	2.5	2.1
Bonmuti												
Leaf	42.5	19.5	11.7	7.8	5.0	4.2	3.3	2.9	2.5	2.0	1.7	1.4
Branch	24.5	9.6	3.1	1.7	2.3	2.1	1.4	1.2	1.1	0.9	0.7	0.6
Total	67.0	29.1	14.8	9.5	7.3	6.3	4.7	4.1	3.6	2.9	2.4	2.0
Letkole												
Leaf	42.9	19.1	11.2	7.4	4.9	3.8	3.1	2.9	2.4	1.8	1.7	1.4
Branch	21.7	8.4	1.3	1.1	2.1	1.8	1.4	1.3	1.1	0.9	0.7	0.6
Total	64.6	27.5	12.5	8.5	7.0	5.6	4.5	4.2	3.5	2.7	2.4	2.0
Oelbanu												
Leaf	43.1	18.5	10.7	7.4	5.0	3.5	2.6	2.7	2.3	1.9	1.6	1.4
Branch	21.0	9.0	2.4	1.6	2.0	1.8	1.6	1.4	1.1	0.9	0.7	0.5
Total	64.1	27.5	13.1	9.0	7.0	5.3	4.2	4.1	3.4	2.8	2.3	1.9

The annual mean decomposition quotient (*KL*) of the leaf and branch litter in Oelbanu (1.4 ± 0.8 and 1.5 ± 0.8) was significantly higher than that of the leaf and branch litter at other sites (Table 4). The turnover rate calculation indicated that about 75.2% (Binafun), 76.5 % (Bonmuti), 76.3% (Letkole) and 77.2% (Oelbanu) of the forest floor was replaced every year with a turnover time of 1.08 years.

Table 4. Annual decomposition quotient (KL) for leaf, branch, and total litter components

Litter components	Annual decomposition quotient			
	Binafun	Bonmuti	Letkole	Oelbanu
Leaf	1.3 ± 0.8	1.3 ± 0.8	1.3 ± 0.8	1.4 ± 0.8
Branch	1.5 ± 0.7	1.5 ± 0.7	1.5 ± 0.7	1.5 ± 0.8
Total	2.8 ± 1.6	2.8 ± 1.6	2.8 ± 1.6	2.8 ± 1.5

Table 5. Pearson's correlation coefficient (*r*) between coefficients of mean climatic variables and monthly mean litter decomposition components measured at all research sites

Research sites and indicators	Monthly mean precipitation, mm	Monthly mean humidity, %	Monthly mean temperature, °C
Binafun			
Leaf	0.603**	0.611**	0.489*
Branch	0.496*	0.511*	0.494*
Total	0.565*	0.576*	0.493*
Bonmuti			
Leaf	0.570*	0.537*	0.441*
Branch	0.357*	0.352*	0.499*
Total	0.492*	0.470*	0.468*
Letkole			
Leaf	0.525*	0.510*	0.474*
Branch	0.345*	0.394*	0.469*
Total	0.458*	0.468*	0.475*
Oelbanu			
Leaf	0.508*	0.493*	0.454*
Branch	0.331*	0.361*	0.438*
Total	0.451*	0.452*	0.454*

Note: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ns > 0.05 (not significant).

with the monthly mean precipitation, monthly mean humidity, and monthly mean temperature (Table 5). Specifically, leaf litter in Binafun showed strong positive correlations with monthly mean precipitation (0.603) and monthly mean humidity (0.611).

The litterfall in this study was the highest from June to October, and about 70% of total litterfall occurred during said period. The same marked seasonality in the amount of litterfall that was the highest during the dry season and lowest during the rainy season, which was reported for *T. cacao* plantations in Malaysia (Ling, 1986) and India (Sreekala et al. 2001), a secondary rain forest in Nigeria (Odiwe, Muoghalu, 2003), West Africa tropical rain forests (John, 1973) and three types of land in the Bengkulu protection forest in Indonesia (Apriyanto et al., 2021).

In Letkole, our results do not correlate with the conclusion drawn by Stohlgren (1988), Starr et al. (2005), Goma-Tchimbakala and Bernhard-Reversat (2006). According to Stohlgren (1988), the annual litterfall can be predicted by a function derived from the individual tree basal area and live crown ratio. Litterfall production in natural forests is strongly influenced by the stand basal area, age structure, stem volume, latitude, season, and climatic factor (Starr et al., 2005; Goma-Tchimbakala, Bernhard-Reversat, 2006). Litterfall production in natural forests (13.67 $t \cdot ha^{-1} \cdot yr^{-1}$) is higher than in primary forests of Ghana (8 $t \cdot ha^{-1} \cdot yr^{-1}$) (Owusu-Sekyere et al., 2006).

The present results can be explained by annual cycles of moisture and temperature. Leaf litter would occur to avoid seasonal moisture and temperature stress during the dry season (Hardiwinoto et al., 1996). As mentioned above, the annual litterfall in the dry dipterocarp forest occurred in the dry season because trees had to adapt to the dry air by shedding their leaves to reduce evaporation, so the amount of litterfall in this period is high. Pascal (1988) also reported that heavy leaf litter occurred during the dry season in the evergreen forests of Attappadi, Western Ghats, and India. This pattern can be explained by annual cycles of moisture and temperature. In the wet period which has high moisture content in the air, the trees do not need to reduce evaporation, so the amount of litterfall is low (Hanpattanakit, Chidthaisong, 2012). In addition, water stress could cause the production of abscisic acid in the foliage of plants which could stimulate senescence of leaves and other parts (Landsberg, Gower, 1997).

Previous studies have shown that several factors, such as nutrient availability and temperature, may affect litter decomposition (Webster, Benfield, 1986). Our results are similar to those previously found. Many authors have concluded that decomposition rates vary as a function of temperature, moisture, and quality of litterfall material, as indicated by nutrient concentration and lignin content in the structural tissues (Garkoti, Singh, 1995). Studies have shown that litter decomposition positively correlated with high N and P concentrations and negatively correlated with high lignin and tannins levels in the litter (Aerts, 1997). High nutrient concentrations positively affect fungal and bacterial colonization, while lignin and tannins inhibit microbial growth (Webster, Benfield, 1986). The high cellulose and lignin content contribute to reducing the rate of litter decomposition because of the difficulty of breaking down the carbon bonds (Fioretto et al., 2005). Litter decomposition is often negatively related to its initial lignin content (Vivanco, Austin, 2008).

The turnover time of litter mass in the present study (1.08 years) is higher than in tropical broadleaf semi-deciduous forests (0.37 years), tropical broadleaf deciduous forests (0.94 years) (Brown, Lugo, 1982) but much lower than that in tropical broadleaf evergreen forests (2.41 years) (Vogt et al., 1986). The decomposition rates obtained in our study (0.54–1.46) are relatively low yet fall within the upper range of decomposition rates previously recorded for tropical rainforests (1.0–3.3) (Anderson, Swift, 1983).

CONCLUSION

It can be concluded that the Binafun forest had the higher litterfall production than Bonmuti, Letkole, and Oelbanu forests. The litterfall production at the research sites were influenced by climatic factors. Leaf litter showed a major contribution to the total litterfall, as found by many authors for tropical forests. Decomposition rates were strongly affected by precipitation, humidity, and temperature, which may be driven by decomposers being more active at high temperatures.

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