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Seasonal litter production patterns in three tropical forests in Sulawesi, Indonesia: Implications for managing secondary forests

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Abstract. *Putra PS, Achmad A, Yamada T, Ngakan PO. 2023. Seasonal litter production patterns in three tropical forests in Sulawesi, Indonesia: Implications for managing secondary forests. Biodiversitas 24: 852-860.* We studied the seasonal patterns of litter production in three tropical forests (Karst, Lowland, and Pine) on the Indonesian island of Sulawesi and measured environmental factors related to litter production from June 2019 to May 2020. Permanent plots of 0.4 ha to 1.0 ha were established in each forest to analyze forest structure and species composition. Thirty-six traps with a surface area of 1 m^2 were installed to collect litterfall. The results showed the highest species diversity in the Karst forest, the highest tree density in the Lowland forest, and the largest basal area in the Pine forest. The greatest litter production was in the Lowland forest (1,607.21 g/m^2/year), followed by the Pine forest (1,288.24 g/m^2/year) and Karst forest (1,099.83 g/m^2/year). Litter production was greater in the dry season in Karst and Pine forests, but there was no inter-seasonal difference in Lowland forest. Rainfall was the only environmental factor that differed between seasons. Differences in phenological adaptation between pioneer and climax species that comprise each forest likely account for the observed differences in litter production patterns.

Keywords: Karst forest, litter component, Lowland forest, Pine forest, season\

INTRODUCTION

Litter plays a vital role in the soil nutrient cycle in forest soils, serving as a major source of organic matter (León and Osorio 2014; Chakravarty et al. 2019). Litter found on the forest floor is generally dominated by components of plant origin (Krishna and Mohan 2017), with limited contributions (approximately 1%) from animal-derived litter (Carter et al. 2007). Therefore, the amount of litter produced by plants contributes to the nutrient cycle processes for the development of forest ecosystems (González et al. 2020).

Plant litter production is defined as the amount of vegetative and reproductive organs shed at a particular time and place (Bisht et al. 2014). The rate of the litter biodegradation process to return nutrients to the forest soil is determined by the species composition and the components of the plant litter (Marler and Cruz 2022). This is because litter of different species compositions and tree components may consist of different chemical compounds (e.g., cellulose, hemicellulose, tannin, lignin), which, in turn, determine their retention in the decomposition process (Krishna and Mohan 2017). Therefore, apart from understanding the level of litter productivity, knowing its species composition and tree components is also crucial (Berg and Meentemeyer 2001).

Forest litter production has been frequently reported from studies in temperate and subtropical regions (Berg and Meentemeyer 2001; Fekete et al. 2016; Huang et al. 2018; Nonghuloo et al. 2020). However, reports on litter production in the tropics are limited, with most studies conducted in the Neotropics (e.g., Capellesso et al. 2016; González-Rodríguez et al. 2019) and South Asia (Bisht et al. 2014; Ahirwal et al. 2021). Little to no information is available from the tropics of the Far East. This study helps fill this gap in knowledge by examining litter production in tropical forests on the Indonesian island of Sulawesi.

Forests growing under different climates in the tropics will consist of different tree species (Toledo et al. 2012). As each species synchronizes its phenology with seasonal patterns in different ways, forests with different species compositions will differ in annual litter production patterns (Huang et al. 2018; Nickmans et al. 2019). Knowledge of litter production patterns from various forest ecosystems in the Far East tropical region is needed as a reference in accelerating the succession process of degraded forests and critical lands that currently dominate the area tropics (Chokkalingam and De Jong 2001), especially for selecting tree species for reforestation.

Forests on the island of Sulawesi naturally consist of broadleaf trees. However, since the late 1960s, *Pinus merkusii* Jungh. et de Vriese (Sumatran pine), which is native to the island of Sumatra, has been widely introduced in Sulawesi as a reforestation tree to accelerate the reforestation process of critical lands. However, coniferous litter is not readily biodegradable (Rodríguez et al. 2019) and, therefore, has the potential to increase soil acidity (Burgess-Conforti et al. 2019) and trigger forest fires

(Busse and Gerrard 2020). However, no studies have attempted to compare litter production between natural secondary broadleaf forests and introduced *P. merkusii* plantation forest in the Far East tropics.

This study aims to identify the seasonal pattern of litter production in three different secondary tropical forests on Sulawesi Island, Indonesia, and to analyze the factors that could influence the observed differences. The three secondary forests studied were karst, lowland, and *P. merkusii* plantation forests. Previous studies in temperate climates revealed that climatic elements such as rainfall, temperature, humidity, and wind velocity are extrinsic factors linked to seasonal dynamics in litter production (Berg and Meentemeyer 2001; Fekete et al. 2016). Meanwhile, species composition, vegetation structure, and age of the forest are intrinsic factors that have the potential to determine litter production (Souza et al. 2019). Variation in litter production patterns and masses across forest types is also potentially influenced by several other environmental factors such as altitude, topography (de Sousa-Neto et al. 2017), and elevation (Becker et al. 2015).

To adapt to reduced soil moisture during the dry season, tree species shed their leaves to reduce transpiration (Giweta 2020). Therefore, we predicted more leaf litter to fall in the dry season than in the wet season. The three types of forests studied grew in different soil types and had different ages, so the species composition and structure will differ (Whitmore 1984), potentially leading to differences in litter production. Given that each tree species exhibits distinct seasonal phenological patterns, we predicted that the inter-seasonal pattern of litter production within each forest type and the amount of annual litter production would vary across the three forest types. The results of this study will contribute to our understanding of litter production patterns in the three monsoon tropical forests and become a valuable reference for managing secondary forests in the Far East tropics.

MATERIALS AND METHODS

Study sites

We conducted the research in three secondary forests located on the Indonesian island of Sulawesi: (a) secondary karst forest (Karst forest hereafter), (b) secondary lowland forest (Lowland forest hereafter), and (c) plantation *P. merkusii* forest (Pine forest hereafter). The Karst forest is a 45-year-old broadleaf secondary forest in Bantimurung Bulusaraung National Park (119º44'14.9" E, 05º01'46.8" S) that grows in shallow Rendzina soil on limestone. The Lowland forest is a 54-year-old broadleaf secondary forest that grows on Cambisol soil in Hasanuddin University Educational Forest (119º46’35.0” E, 04º58’06.9” S). Meanwhile, the Pine forest is a 58-year-old plantation forest of *P. merkusii* that grows on Luvisol soil, also located in Hasanuddin University Educational Forest (119º45’56.7” E, 05º00’17.3” S) (Center for Agricultural Land Resources 2017 for soil types of all forest types) (Figure 1).

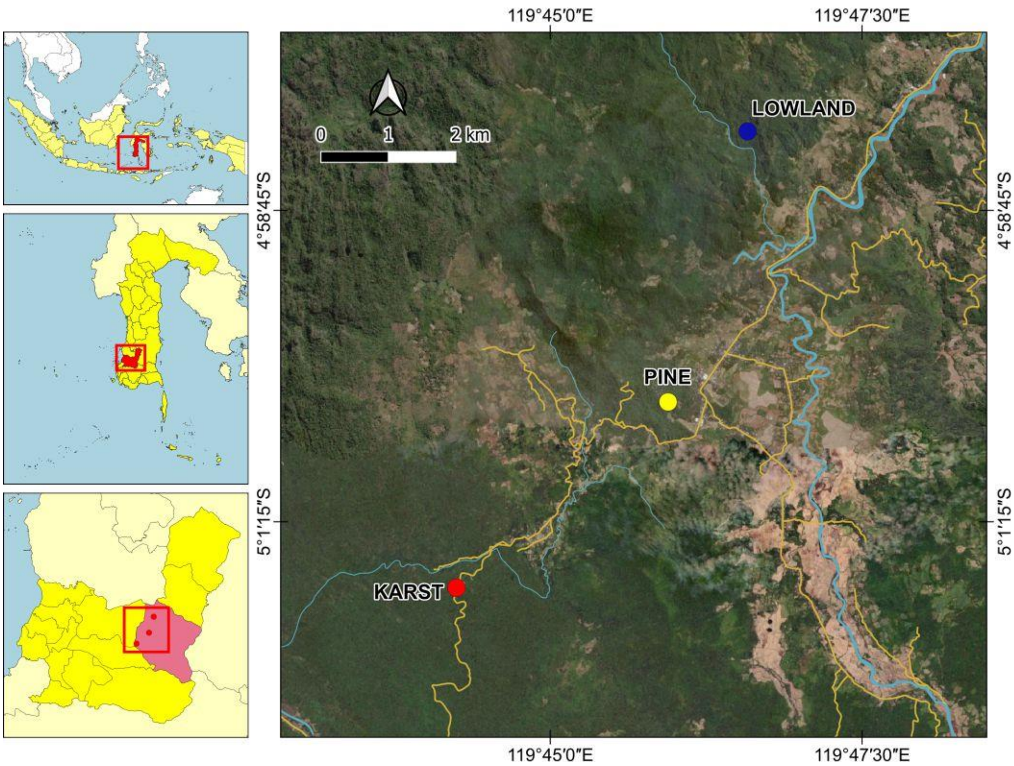

Figure 1. Map showing the locations of the three forest types studied. This map was produced using QGIS 3.10.9 - A Coruna (A Free and Open Source Geographic Information System) based on three data sources: Citra SPOT 6 & 7 2019, Point location (measured using Garmin GPSMAP 60CSx), and RBI (Indonesian Topographical Map) 1: 50000

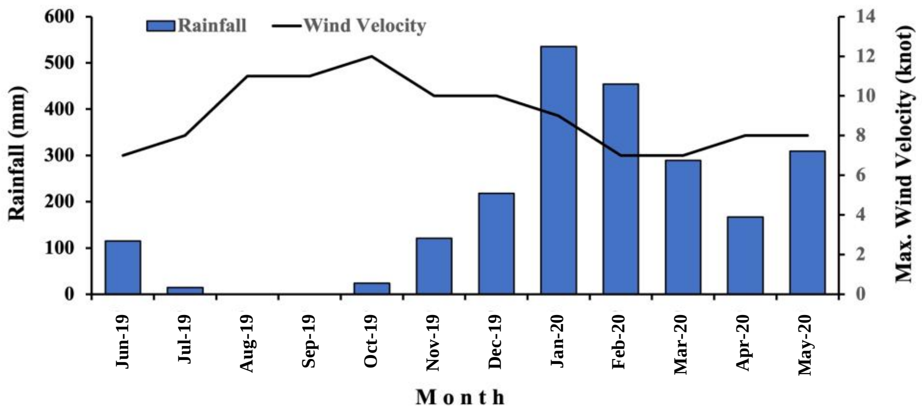

Figure 2. Monthly total rainfall and maximum wind velocity during the study period (Source: Meteorology Climatology and Geophysics Council (BMKG) of the Republic of Indonesia)

The three types of forest are located approximately 3 km from each other, and all adhere to the same climate type C according to climate classification by Schmidt and Ferguson (1951). This climate type is characterized as seasonal, with two distinct seasons, wet and dry, per year. During this study, the dry season occurred from June to November 2019, and the wet season occurred from December 2019 to May 2020 (Figure 2).

Vegetation analysis

To measure the species composition and structure of the forest, plots of 0.75, 1.00, and 0.40 ha were established in Karst, Lowland, and Pine forests. Plot size variation was due to the inherent features of the study site. In the Karst forest, limestone towers impeded our ability to find a compact area to construct a 1 ha plot. We consider the plot size of 0.4 ha is large enough to represent the diversity of *P. merkusii* monoculture plantations. Therefore, the density and basal area values were converted into a unit area of 1 ha. According to the Nested Plot Technique for determining minimum patch sizes (Mueller-Dombois and Ellenberg 1974), these plot sizes are large enough to study the structure and composition of secondary tropical rainforests.

To collect vegetation data in each plot, we first divided each plot into 10 m x 10 m subplots. Each tree with a diameter $\geq$ 5 cm in each subplot was numbered sequentially with an aluminum number tag at 150 cm above the ground. The girth of each tree was measured at 130 cm above the ground. Trees that branch at less than 130 cm in height were measured the girth of each trunk, but for density, we treated them as a single trunk. Next, we collected herbarium samples from each tree species for identification at the Bogoriense Herbarium in Bogor, Indonesia.

Litter production

We assessed plant litter production in the three forest types by installing 12 litter traps within each plot (36 litter traps in total) under the forest canopy that best represents species composition, canopy cover, and tree distribution. Litter traps were made of 0.75-inch PVC pipe with a circular surface and a surface area of 1 m^2 and mounted on three support poles made of 1-inch PVC pipe at a height of 1 m above the ground. The nets used for litter traps were made of nylon material with a mesh size of 2 mm. We installed the litter traps on June 1, 2019, and subsequently collected the litter captured on the 1st to 2nd day of each following month until May 2020.

The trapped litters were placed in separate vinyl bags for each litter trap and taken to the Forest Conservation Laboratory at Hasanuddin University. We first air-dried all litter samples in a plastic basin and then oven-dried them at 60^{o}C. We then sorted and weighed specific components of the oven-dried litter samples (i.e., leaves, twigs, and reproductive organs) for each litter trap.

Climate elements and soil moisture

We obtained rainfall and wind velocity data from the nearest climatic station of Indonesia's Meteorology Climatology and Geophysics Council (BMKG). In addition, local maximum and minimum temperatures were measured monthly by installing a maximum-minimum thermometer in each plot. We mounted the thermometers on the trunk of a tree near the center of each plot at 1 m above the ground. We measured soil surface moisture around each litter trap every month using the Takemura Soil pH and Humidity Tester Dm-5.

Data analysis

Vegetation data from the plots were used to calculate tree density and basal area. Tree density was measured as the number of trunks per hectare. We calculated the Shannon Diversity Index (H Index) according to Spellerberg and Fedor (2003). We used the ANOVA with the Tukey HSD method to detect the differences in (i) inter-season mean litter production within each forest type, (ii) mean litter production between forest types, (iii) inter-season mean monthly rainfall and wind velocity, (iv) inter-season and within each forest type soil moisture, and (v) inter-forest type soil moisture. When data were not normally distributed, we used nonparametric equivalents (i.e., Kruskal Wallis or Mann-Whitney U for two independent samples). All statistical analyzes were performed using the R application version 4.1.2. (R Core Team 2021).

RESULTS AND DISCUSSION

Species composition and forest structure

As predicted, the species composition and structure of the three types of forest studied varied widely. Karst forest shows the highest value of the H' Index (Table 1). The density of trees $\geq$ 5 cm in diameter was highest in the Lowland forest plot (Table 1), while the total basal area was significantly largest in the Pine forest (Table 2). Three of the five species with the highest basal area in the Karst forest, *Kleinhovia hospita*, *Cananga odorata*, and *Pterospermum celebicum*, are pioneer tree species characterized by their tiny orthodox seeds, which remain dormant for a long time in the soil. *Dracontomelon dao* is a semi-pioneer species. Meanwhile, *Palaquium obovatum*, *Diospyros celebica*, and *Mangifera* cf. *longipetiolata*, as well as two species of palm, *Areca catechu*, and *Arenga pinnata*, which dominate the basal area of Lowland forest, represent species that are generally found in a primary forest. These species are characterized by fleshy fruits and large recalcitrant seeds germinating immediately after being shed from the mother tree. Most broadleaf species codominant in *P. merkusii* plantations are pioneer species.

Inter-seasonal litter production within each forest type

In the Karst forest, leaf litter and reproductive organ litter were significantly greater in the dry season (465.79 ± 18.79 g/m^2/6 month for leaf litter and 56.42 ± 13.04 g/m^2/6 month for reproductive organ litter) than in the wet season (272.49 ± 18.79 g/m^2/6 month for leaf litter and 11.33 ± 13.04 g/m^2/6 month for reproductive organ litter) (leaf: F=52.9387, P<0.001; reproductive organ: F=5.9755, P=0.0230). There was no significant difference in the amount of twig litter between the dry season (143.05 ± 28.03 g/m^2/6 month) and the wet season (150.74 ± 28.03 g/m^2/6 month) (F=0.0377, P=0.8479). The production of combined litter for all components was also significantly greater in the dry season (665.26 ± 46.44 g/m^2/6 month) compared to the wet season (434.57 ± 46.44 g/m^2/6 month) (F=12.3369, P=0.0020) (Figure 3 top row).

In the Lowland forest, leaf litter production was similar across seasons (442.88 ± 32.30 g/m^2/6 month in the dry season and 426.51 ± 32.30 g/m^2/6 month in the wet season) (F=0.1284, P=0.7235). In comparison, the production of twigs and reproductive organs litter was significantly greater in the wet season (203.94 ± 42.47 g/m^2/6 month for twig litter and 283.08 ± 49.22 g/m^2/6 month for reproductive organ litter) compared to the dry season (86.78 ± 42.47 g/m^2/6 month for twig litter and 164.03 ± 49.22 g/m^2/6 month for reproductive organ litter) (twig: W=34, P=0.0284; reproductive organ: W=32, P=0.0205). However, when the three organs were combined, litter amounts did not differ significantly between seasons (693.68 ± 89.00 g/m^2/6 month in the dry season and 913.53 ± 89.00 g/m^2/6 month in the wet season) (W=44, P=0.1135) (Figure 3 middle row).

Table 1. Description of the three forest types

Characteristics	Karst	Lowland	Pine
Plot Area (ha)	0.75	1.00	0.4
Altitude (masl.)	271	563	501
Age (years)	45	54	58
The density of trees/ha	1125	1672	1273
Number of species/plot	97	65	46
H' Index	3.43	1.62	2.61

Table 2. Basal area of the top five dominant tree species ($\geq$ 5 cm in diameter) in each forest type

Species	Family	Basal area (cm^2 / ha)		
		Karst	Lowland	Pine
Kleinhovia hospita L.	Sterculiaceae	58689.61		
Cananga odorata (Lamk.) Hook	Annonaceae	34048.54		
Pterospermum celebicum Miq.	Sterculiaceae	17697.82		
Dracontomelon dao (Blanco) Merr. & Rofle)	Anacardiaceae	15689.87		
Diospyros celebica Bakh.	Ebenaceae	19906.25	50392.11	
Areca catechu L.	Arecaceae		106653.91	
Arenga pinnata Merr.	Arecaceae		62570.78	
Palaquium obovatum (Griff.) Engl.	Sapotaceae		48835.17	
Mangifera cf. *longipetiolata* King.	Anacardiaceae		25527.17	
Pinus merkusii Jungh. et de Vriese	Pinaceae			527626.49
Arthrophyllum diversifolium Bl.	Araliaceae			20143.15
Cinnamomum iners Reinw. Ex Bl.	Lauraceae			16534.00
Neolitsea cassiaefolia (Bl.) Merr.	Lauraceae			6359.46
Alstonia scholaris (L.) R. Br.	Apocynaceae			3600.52
Other species		149523.82	173480.49	25806.41
Total		295555.91	467459.63	600070.03

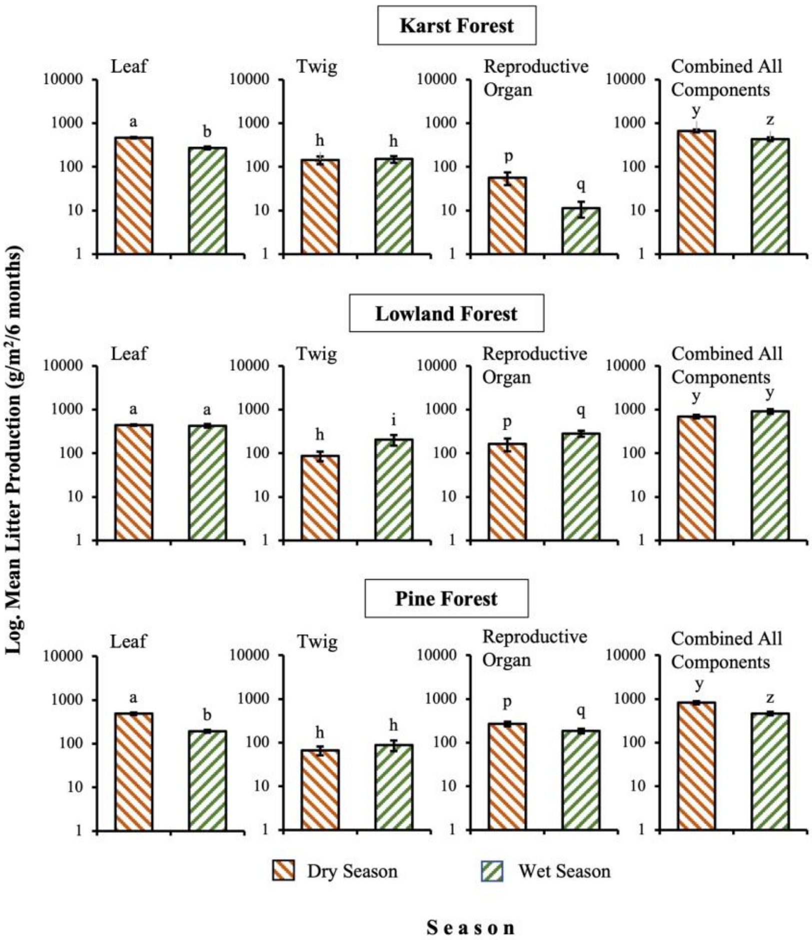

Figure 3. Mean dry weight of leaf, twig, and reproductive organ litter in Karst forest (top row), Lowland forest (middle row), and Pine forest (bottom row). A different letter above each bar indicates a significant difference between seasons (ANOVA with Tukey HSD, except for twigs, reproductive organs, and all components combined in Lowland forest, which were analyzed using Nonparametric 2 independent samples with Mann-Whitney U).

The inter-seasonal litter production pattern in the Pine forest was the same as in the Karst forest. Leaf litter and reproductive organ litter were significantly greater during the dry season (485.07 ± 24.73 g/m^2/6 month for leaf litter and 270.56 ± 28.45 g/m^2/6 month for reproductive organ litter) compared to the wet season (192.52 ± 24.73 g/m^2/6 month for leaf litter and 185.24 ± 28.45 g/m^2/6 month for reproductive organ litter) (F=69.9885, P<0.001 and F=4.4953, P=0.0455 respectively). There was no significant difference in the production of twig litter between seasons (66.18 ± 20.31 g/m^2/6 month in the dry season and 88.68 ± 20.31 g/m^2/6 month in the wet season) (F=0.6134, P=0.4418). The mean production of all components combined was significantly greater in the dry season (821.81 ± 56.31 g/m^2/6 month) compared to the wet season (466.43 ± 56.31 g/m^2/6 month) (F=19.9119, P<0.001) (Figure 3 bottom row).

Comparison of litter production across the forest types

The greatestoverall mean of litter production occurred in the Lowland forest; however, this difference was only statistically significant compared to the Karst forest (F=5.8141, P=0.0069). During the dry season, there were no significant differences in the production of all litter components across the three forest types (χ^2=4.3303, P=0.1147). However, during the wet season, litter production in the Lowland forest was significantly greater than in Karst and Pine forests (F=14.5327, P<0.001) (Table 3).

No significant differences were detected for leaf and twig litter production across the three forest types in the dry season (leaf: F=0.8084, P=0.4542; twig: χ^2=4.4339, P=0.1089), but reproductive organ production differed significantly across the forest types (χ^2=16.7130, P=0.0002). Meanwhile, during the wet season, the mean production of leaf and reproductive organ litters was greater in the Lowland forest compared to the Karst and Pine forests (leaf: F=17.9863, P<0.001; reproductive organ: χ^2=24.37, P=0.000005108). On the other hand, the production of twig litter in the wet season was not significantly different across the three forest types(χ^2=5.6148, P=0.0604).

The leaf litter constituted the greatest proportion of the total litter collected in all forest types throughout the study period (Figure 4). Twig litter constituted the second-greatest proportion, and reproductive organs constituted the smallest in the Karst forest. However, in the Lowland and Pine forests, reproductive organ litter constituted the second greatest followed by twig litter.

Rainfall, wind velocity, soil moisture, and temperature

ANOVA analysis showed that the mean monthly rainfall was significantly lower in the dry season (45.83 mm) compared to the wet season (328.67 mm) (F=20.9249, P<0.001). Mean soil moisture also differed significantly between seasons in each forest type (Figure 5: F=5.3402, P=0.0434; F=6.4645, P=0.0292; F=19.9933, P=0.0012 for Karst, Lowland, and Pine forests, respectively). The mean monthly maximum wind velocity in the dry season (9.83 knots) was not significantly different from that in the wet season (8.17 knots) (F=3.2468, P=0.1017). In all forest types, the maximum and minimum temperatures were not significantly different between seasons, except for the maximum temperature in the Karst forest, which was higher in the dry season, and the minimum temperature in the Pine forest, which was lower in the dry season.

During the dry season, soil moisture in the Karst forest was not statistically different from that in the Lowland forest. However, in the Pine forest, it was significantly lower than in the Karst and Lowland forests (Figure 5 left: U-U-V (F=4.7923, P=0.0246)). Meanwhile, during the wet season, soil moisture was significantly different across the three forest types: highest in the Karst forest, followed by the Lowland forest, and then the Pine forest (Figure 5 left: X-Y-Z (F=54.8970, P<0.001)). On the other hand, the maximum temperature was not significantly different between forest types both in the dry and wet seasons (Figure 5 center: U-U-U (F=0.5051, P=0.6134 in the dry season) and X-X-X (F=1.6007, P=0.2344 in the wet season). During the dry season, the minimum temperature was significantly higher in the Karst forests; however, there was no significant difference between the last two forests (Figure 5 right: U-V-V (F=3.9263, P=0.0425)). During the wet season, the minimum temperature did not differ between forest types (Figure 5 right: X-X-X (F=0.3391, P=0.7177)).

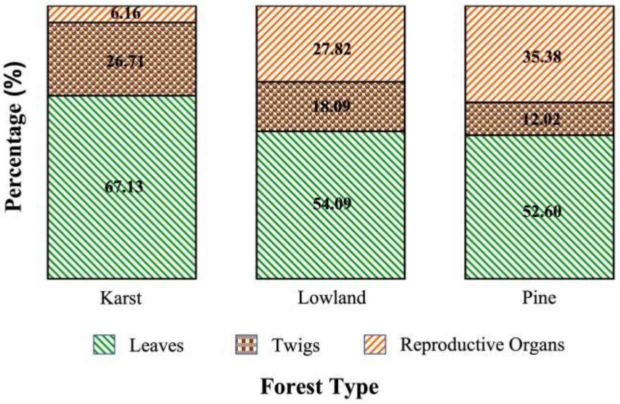

Figure 4. Percentage of leaves, twigs, and reproductive organs in the litter collected in each of the forest types

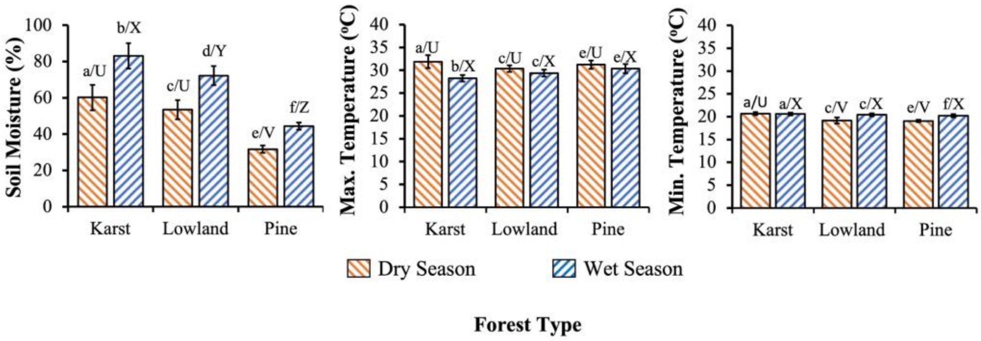

Figure 5. Differences in soil moisture (left), maximum temperature (center), and minimum temperature (right) between seasons and between the forest types. The lowercase letters to the left of the slash above each bar indicate significant differences between seasons in each forest type. The uppercase letters to the right of the slash above each bar indicate significant differences between forest types in the same season (ANOVA with Tukey HSD). The vertical line at the top of each bar indicates the inter-seasonal standard error

Table 3. Comparison of the amount of litter produced across the three forest types during the dry and wet seasons

Organ	Mean Mass Weight (g/m^2) ± SE		
	Karst Forest	**Lowland Forest**	**Pine Forest**
Dry season (June to November 2019)			
Leaves (6 months)	465.79 (± 23.49) a	442.88 (± 23.49) a	485.07 (± 23.49) a
Twigs (6 months)	143.05 (± 22.61) h	86.78 (± 22.61) h	66.18 (± 22.61) h
Reproductive organs (6 months)	56.42 (± 37.90) p	164.03 (± 37.90) q	270.56 (± 37.90) r
All components combined (6 months)	665.26 (± 62.st43) x	693.68 (± 62.43) x	821.81 (± 62.43) x
Wet season (December 2019 to May 2020)			
Leaves (6 months)	272.49 (± 28.04) a	426.51 (± 28.04) b	192.52 (± 28.04) a
Twigs (6 months)	150.74 (± 38.60) h	203.94 (± 38.60) h	88.68 (± 38.60) h
Reproductive organs (6 months)	11.33 (± 28.85) p	283.08 (± 28.85) q	185.24 (± 28.85) r
All components combined (6 months)	434.57 (± 70.25) x	913.53 (± 70.25) y	466.43 (± 70.25) x
All components and all seasons combined			
Overall mean in a year	1099.83 (±106.37) a	1607.21(±106.37) b	1288.24(± 106.37) ab

Note: A different letter after the mean weight values in a row indicates significant differences (ANOVA with Tukey HSD for normally distributed data and Nonparametric K independent sample with Kruskal Wallis for non-normally distributed data); the values after ± indicate the standard of error of the mean

Discussion

The objective of this study was to uncover variations in litter production patterns between seasons and forest types and analyze the potential environmental factors that account for that variation. A combination of environmental factors, including soil type, altitude, and formation history, could differentially affect the development of individual forests, which likely explains the differences in forest structure and species composition in the three forest types we studied. Moreover, as predicted, the results of this study show that litter production varies from one forest type to another despite being in close geographic proximity.

Leaf litter mass made the greates contribution to total litter production in all forest types. Several studies conducted in the subtropics also reported similar results (Lu and Liu 2012; Souza et al. 2019). Since the leaf is a tree organ that produces organic substances for the growth of other organs, it is not unexpected that the biomass of the leaf would be proportionally greater than the biomass of other components. The greater amount of the litter mass of reproductive organs than twigs in the Lowland and Pine forests is likely because the fruit of the climax tree species that dominate Lowland forests are usually large, fleshy, and have large seeds. The cones of *P. merkusii* in the Pine forest are also large, although the seeds are thin and light. On the other hand, the low biomass of reproductive organs in the Karst forest might be because the fruits of the pioneer tree species that dominate this forest are relatively small, fleshless, and have tiny seeds (Dalling and Hubbell 2002).

Regarding the seasonal pattern of litter production, our prediction that more litter is produced during the dry season was only evident in the Karst and Pine forests but not in the Lowland forests. The dominance of pioneer species in the Karst forest, some of which shed their entire leaves during the dry season (Ishida et al. 2013) explains this finding. Several studies have revealed that pine trees have fast transpiration rates (Swank and Douglass 1974), and they are sensitive to drought (Móricz et al. 2018), which, in turn, can lead to defoliation (Poyatos et al. 2013). When soil moisture drops during the dry season, pine trees shed most of their leaves to reduce transpiration (Jacquet et al. 2014). In addition, in the Karst and Pine forests, more trees shed their reproductive organs in the dry season than in the wet season.

Previous studies have found that many internal and external factors influence tropical forest tree phenology (Luna-Nieves et al. 2017; Cardoso et al. 2019). For example, some studies revealed that certain tree species in the tropical monsoon begin flowering at the onset to mid of the dry season (Nanda et al. 2009; Luna-Nieves et al. 2017). This pattern may be because the soil moisture is still high at that period. At the same time, solar radiation is already high, constituting the best conditions for maximum photosynthesis rate (Girardin et al. 2016).

Depending on the species and the habitat, the duration of the fruiting phenophase ranges between 3 to 11 months (Mohandass et al. 2018). Unlike pioneer tree species that usually produce small fruit with thin seeds, climax tree species that produce large fleshy fruits with large recalcitrant seeds should take longer to grow and ripen their fruits (Susanto et al. 2016; Rungrojtrakool et al. 2021). This is because such fruits fall at the onset of the mid-wet season (Nanda et al. 2014), and their recalcitrant seeds that last only a short time (Berjak and Pammenter 2017) take advantage of wet conditions to support germination and grow further as soon as they fall (Obroucheva et al. 2016). Therefore, climax species need to maintain their leaves in the dry season, as they are still actively photosynthesizing to grow their fruit until they are ripe at the onset of the wet season (Boonkorkaew et al. 2012). This could explain our finding that why leaf litter production in the Lowland forest which dominated by climax species did not differ between the dry and wet seasons. While the reproductive organs were more likely to fall in the wet season.

Pioneer trees that dominate the Karst forest and *P. merkusii* in the Pine forest do not need to synchronize the fruit fall period with a particular season, as their orthodox seeds have the ability to remain dormant for years in the soil (Solberg et al. 2020; Matilla 2021). Therefore, the pioneer tree species may take little time to ripen their small fleshless fruit containing tiny orthodox seeds. Thus, the greater amount of reproductive organ litter during the dry season compared to the wet season in Karst forest, which is in line with leaf litter production, could possibly be because deciduous pioneer trees synchronize the maturity of their fruit with leaf senescence in the dry season (Nanda et al. 2014). That is, there is no point in the fruit persisting on the tree when the leaves have fallen entirely. This finding explains why litter production in Karst and Pine forests was significantly greater in the dry season than in the wet season. However, greater reproductive organ production in the wet season in Lowland forests did not contribute to the difference in litter production between seasons because the mass of leaf litter, which was proportionally the greatest contribution, was similar across seasons.

The vital role of litter in the nutrient cycle of forest soils has widely been accepted (León and Osorio 2014; Chakravarty et al. 2019). Forests that can produce more litter can better contribute to the restoration of soil fertility (González et al. 2020; Farooq et al. 2022). In addition, to maintain diversity and populations of decomposing agents on the forest floor, forests that can produce litter evenly throughout the year are better than those that produce litter seasonally. Our study revealed that the older (late-stage) secondary Lowland forest produced significantly more litter in an even amount throughout the year compared to the younger (middle-stage) secondary Karst forest. Thus, these findings highlight the importance of accelerating the succession rate of degraded lands and forests in tropical monsoon areas via reforestation efforts which can help accelerate the soil restoration process. A critical decision for such efforts is the tree species for reforestation. Pine leaf litter is slow to decompose (Rodríguez et al. 2019; Jugran and Tewari 2022), it accumulates on the forest floor and can trigger fires (Busse and Gerrard 2020), as is often the case at our study site. This condition supports that *P. merkusii* is not superior to broadleaf forests in producing litter. Therefore, reforestation should prioritize using local broadleaf tree species rather than pine trees.

To conclude, in line with the diversity of species composition, litter production patterns in the tropics also differ from one forest type to another. The combination of intrinsic and extrinsic factors in a complex manner determines the seasonal pattern and the amount of litter. Rainfall and soil moisture determine inter-seasonal differences in litter production patterns through the phenology of dominant trees. Regardless of habitat and growth history impacting structural and compositional differences, our results show that broadleaf lowland forest is superior in litter production, both in mass and pattern compared to younger Karst forest. Although not statistically significant, the Lowland forest, which is much smaller in basal area cover, produced more litter than the Pine forest. Therefore, in managing degraded forests in the tropics, we recommend reforestation efforts prioritizing native broadleaf species over conifers.

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