

**Ecological Study on Interrelation Between Litter  
Production, Decomposition Rate, and the Development of  
Three Secondary Forests in Maros, South Sulawesi**



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**Ecological Study on Interrelation Between Litter  
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Three Secondary Forests in Maros, South Sulawesi**

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Prepared and submitted by

Putu Supadma Putra

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# ENDORSEMENT PAGE

## DISSERTATION

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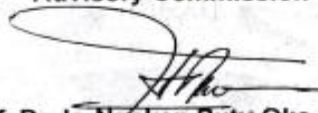
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## DISSERTATION AUTHENTICITY STATEMENT AND COPYRIGHT OWNERSHIP

I hereby declare that the dissertation entitled "Ecological Study on Interrelation Between Litter Productivity, Decomposition Rate, and the Development of Three Secondary Forests in Maros, South Sulawesi" is my work with directions from the supervisory committee (Prof. Dr. Ir. Ngakan Putu Oka, M.Sc., Prof. Dr. Ir. Amran Achmad, M.Sc. and Prof. Dr. Toshihiro Yamada). This scientific work has not been submitted in any form to any university. Sources of information cited from published and unpublished works by other authors have been mentioned in the text and listed in the bibliography of this dissertation. Several chapters of this dissertation have been published as follows: the journal (Biodiversitas, Vol. 24, 852-860, and DOI:10.13057/biodiv/d240222) under the title "Seasonal Litter Production Patterns in Three Tropical Forests in Sulawesi, Indonesia: Implications for Secondary Forest Management"; the journal (International Journal of Forestry Research, Vol. 2023, Article ID 9677809, 14 pages and <https://doi.org/10.1155/2023/9677809>) under the title "Seasonal Decomposition Rates of Broadleaf and Conifer Wood Litter in Far Eastern Tropical Forest Communities"; the proceeding (IOP Conference Series: Earth and Environmental Science, Vol. 1230, 012059, and DOI:10.1088/1755-1315/1230/1/012059) under the title "Seasonal diversity and distribution of decomposing macrofungi in three forest communities: why do they differ?"; and the journal (Biodiversitas, Vol. 24, 5065-5073, and DOI: 10.13057/biodiv/d240950) under the title "Differences in the vegetation dynamic patterns of three tropical secondary forests in South Sulawesi, Indonesia."

I hereby transfer the copyright of my scientific work in the form of this dissertation to Hasanuddin University.

Makassar, 16/01/2024



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Putu Supadma Putra

## ABSTRACT

Putu Supadma Putra. **Ecological study on interrelation between litter production, decomposition rate, and the development of three secondary forests in Maros, South Sulawesi** (supervised by Ngakan Putu Oka, Amran Achmad dan Toshihiro Yamada).

We studied differences in the seasonal patterns of litter production, decomposition rates and vegetation dynamics related to forest type, age, species composition and environmental factors in three tropical forests (Karst, Lowland and Pine forests) on Sulawesi Island, Indonesia. Permanent plots were established in each forest: 0.75 ha, 1 ha and 0.40 ha. Thirty-six litter traps, with a surface area of 1 m<sup>2</sup>, were installed to collect litterfall. For the decomposition rate experiments, 60 containing tusam leaves and 60 containing ebony leaves were placed to observe the ex-situ decomposition process, 24 quadrats (1 m x 1 m) were set up on the forest ground to observe the in-situ decomposition process, and 600 jabon and 600 tusam wood planks were placed on the ground to observe the decomposition rate. The diversity of decomposing agents, soil properties, and chemical content of wood and leaf samples were analysed. We also observed the dynamics of forest vegetation. The results showed that the Karst forest, which has much lower total litter production than the Lowland and Pine forests, shows a higher k-value of the decomposition rate. The highest basal area growth rate was also found in the Karst forest with the lowest in the Pine forest, however, this does not align with the soil fertility indicator, which was higher in the Lowland forest than in the Karst forest and lowest in the Pine forest. Age and dominance of tree species could be the cause of this mismatch. This study explains that the rate of decomposition does not always have to be directly or inversely proportional to litter production. Depending on the combined influence of the intrinsic and extrinsic factors, the litter production and decomposition rates can vary between forest communities which in turn influences the development of forest communities.

**Keyword:** Decomposition rate, Dynamics, Litter Production, Karst, Lowland, Pine

## EXECUTIVE SUMMARY

Litter is the main component of terrestrial ecosystems that regulates the accumulation of organic matter, nutrient cycles and the development of forest communities. However, studies on litter produced by a forest stand, the speed of the process of litter decomposition and the factors involved in the production and decomposition processes of litter have generally been carried out in subtropical and temperate climates; only a few studies relating to litter production and decomposition rates have been carried out in the Far Eastern tropical region. Tropical regions have a warm climate, varied climate types (from seasonal to wet) and a very diverse tree species composition, which has consequences for the chemical quality of the litter produced, and this in turn, determines the high diversity of the decomposing agents when compared to temperate and subtropical areas. Therefore, a profound understanding of production processes and litter decomposition rates is vital for tropical forest communities in the Far East. In addition, the high diversity of ecosystems in tropical regions means that the results of studies on one ecosystem do not always apply to other ecosystems.

This research is one of the few studies on the relationship between litter production, decomposition rates and forest dynamics in tropical regions. In this study, the seasonal patterns of litter production, decomposition rates and vegetation dynamics related to forest type, age, species composition and environmental factors were analysed in three tropical forests (Karst, Lowland and Pine forests) on Sulawesi Island, Indonesia. Permanent plots of varying sizes were established in each forest community (type): 0.75 ha (50 m x 150 m) in the Karst forest, 1 ha (100 m x 100 m) in the Lowland forest and 0.40 ha (50 m x 80 m) in the Pine forest. Thirty-six litter traps, with a surface area of 1 m<sup>2</sup>, were installed in the three plots to collect litterfall. For the decomposition rate experiments, 120 litter bags (60 containing tusam leaves and 60 containing ebony leaves) were placed to observe the ex-situ decomposition process and 24 quadrats, each sized 1 m x 1 m, were set up on the forest ground to observe the in-situ decomposition process. In addition, 1,200 wooden planks (600 jabon logs, 600 tusam logs) measuring 10 cm x 10 cm x 1.5 cm were placed on the ground to observe the decomposition rate. Through PCR analyses, the diversity and abundance of the decomposing agents (micro and macro) were identified, and the physical and chemical properties of four soil samples taken from each permanent plot were also analysed. The diameter of

the trees in each plot was measured annually to observe the dynamics of the species composition, population and tree dominance in each plot. Except for these annual tree measurements, all of the other works were carried out in both the dry and wet seasons.

The results of the study on litter production showed that the greatest litter production was found in the Lowland forest (1,607.21 g/m<sup>2</sup>/year), followed by the Pine forest (1,288.24 g/m<sup>2</sup>/year) and then the Karst forest (1,099.83 g/m<sup>2</sup>/year). Leaves were the most abundant litter component produced by the three forest communities (869.39, 738.28 and 677.59 g/m<sup>2</sup>/year, respectively, in the Lowland, Karst and Pine forests), followed by reproductive organs (447.11 g/m<sup>2</sup>/year in the Lowland forest and 455.80 g/m<sup>2</sup>/year in the Pine forest) and twigs (290.72 g/m<sup>2</sup>/year in the Lowland forest and 154.86 g/m<sup>2</sup>/year in the Pine forest); however, in the Karst forest, the twig component (293.79 g/m<sup>2</sup>/year) was more abundant than reproductive organs (67.75 g/m<sup>2</sup>/year). Litter production was greater in the dry season in the Karst and Pine forests, but there was no inter-seasonal difference in the Lowland forest. Rainfall was the only environmental factor that differed between seasons. Differences in the phenological seasonal adaptation between the pioneer and climax species found within each forest likely account for the observed differences in the litter production patterns.

The *k*-value of the in-situ experiment – the litter decomposition observed on the forest ground where it was produced – was highest in the Karst forest (0.0921 g/1 m<sup>2</sup>), followed by the Lowland forest (0.0700 g/1 m<sup>2</sup>) and then the Pine forest (0.0277 g/1 m<sup>2</sup>). This relates to the diversity and abundance of decomposing agents, such as the microbes (bacteria and microscopic fungi), macroscopic fungi, macrofauna on the soil surface and macrofauna in the soil, which were significantly higher in the Karst and Lowland forests than in the Pine forest. During the dry season, the mean *k*-value of the tusam leaves was faster than that of the ebony leaves in the Karst and Lowland forests, but it was slower in the Pine forest. During the wet season, there was no significant difference between the mean *k*-value of the tusam leaves compared to the ebony leaves in the Karst and Lowland forests, but in the Pine forest, the mean *k*-value of the tusam leaves was significantly slower than that of the ebony leaves. The tusam leaf litter decomposed faster than the ebony leaf litter in the mixed broadleaf forests, which relates to the lower content of secondary metabolites, such as phenolics, tannins and resins, in the tusam leaf litter compared to the ebony leaf litter. Although the tusam leaf litter had a higher



lignin content, which can directly inhibit the decomposition process, this may not have had much of an impact, considering that many more bacterial and microfungus species were found in the mixed broadleaf forests than in the Pine forest, with most of these species being lignin-degrading species. Extrinsic factors, including chemical, physical and biological factors that influence each other, create conditions in which mixed broadleaf forests are able to support a higher diversity and abundance of decomposing agent organisms. The higher soil concentrations of pH and C and the soil moisture in the mixed broadleaf forests compared to the Pine forest provide a suitable environment for many species of both microorganisms and macrofauna decomposing agents to thrive. This study shows that the decomposition process of leaf litter is species-specific and is controlled by a combination of factors. Extrinsic factors play a more critical role than intrinsic factors in determining the *k*-value.

In the wood plank decomposition experiments, this study shows that the value of the decomposition rate constant (the *k*-value) of jabon wood (a broadleaf) was higher in the dry season than in the wet season, while the opposite trend was noted for tusam (coniferous) wood. The high abundance of *Odontotermes* sp. in the dry season showed a significant association with the mean *k*-value of jabon wood in the same season (WPJ1-6). Tusam wood, meanwhile, distinctly contains more hemicellulose (9.68%) than jabon wood (3.97%). Hemicellulose significantly increases the water absorption behaviour and wettability of wood to potentially reduce its resistance to microorganisms. This study showed a significant positive correlation between the number of bacterial species and the mean *k*-value of the one-year decomposition experiments of tusam wood that began at the onset of the wet season (WPT2-12). The data that are not normally distributed and the insignificant difference between the mean *k*-values of the 12-month experiments that began at the onset of the dry season and at the onset of the wet season, for the tusam wood samples in particular, implies that the difference in the initial conditions of the decomposition process does not affect the process throughout the year. Wood that begins with a faster decomposition process in the dry season does not decompose faster in the following wet season, and wood that begins with a slower decomposition process in the wet season does not decompose more slowly in the following dry season. The presence of a suitable decomposing agent seems to have a more significant effect on the rate of decomposition than the environmental conditions at the start of the wood decomposition process. The

results of this study also show that the *k*-value of both wood samples was higher in the broadleaf forest than in the Pine forest. Similar to temperate climates, the rate of litter decomposition in Pine forests in tropical areas is also slower than in broadleaf forests. The differences in the mean *k*-value between forest communities are proportional to the differences in the number of microbial species, especially macrofungi, between forest communities. In addition, among the soil's chemical properties, the pH and C were significantly lower in the Pine forest than in the Karst and Lowland forests. These findings indicate that the decomposition processes in tropical forests vary at the microsite scale due to the high diversity of the decomposing agents and their complex reciprocal association.

In total, 130 species of macrofungi were found from 38 families across forest communities, with 81 species recorded in the wet season, 22 species recorded in the dry season and 27 other species recorded in both the wet and dry seasons. The highest number of macrofungi species was found in the Lowland forest (67 species), followed by the Karst forest (65 species) and then the Pine forest (42 species). Most of the macrofungal species found in this study were saprophytic and growing on litter or soil substrate, but some of the species were ectomycorrhizal fungi. Litter was the substrate that best supported the growth of macrofungal species (81 species), followed by soil (46 species), weathered wood (25 species) and living trees (17 species); one species was found to grow on cow dung. Some species were specialists in specific forest communities. Given that most macrofungal species are monophagous and were found to only degrade litter from a single tree species, the difference in the diversity of macrofungi among forest communities is likely related to the difference in the diversity of tree species among forest communities. In addition, the microhabitat conditions were found to be in line with the inter-seasonal and inter-forest diversity of macrofungal species.

The species composition of the three forest communities studied were different. Among the ten most dominant species in each plot, only one species was found in all three forest communities, while the rest were exclusive to a single forest community. During the four years of study, 25 out of a total of 90 species in the Karst forest, 27 of 68 species in the Lowland forest and 12 of 43 species in the Pine forest experienced dynamics in the form of an increase or decrease in population. The tree density decreased in the Karst plot and fluctuated slightly in the Lowland and Pine forest plots, while the basal area cover continued to increase in all plots during the four years of observation. The highest basal area growth rate

was found in the Karst forests with the lowest in the Pine forests, which does not align with the soil fertility indicators such as C, N and CEC, which were higher in the Lowland forest than in the Karst forest and lowest in Pine forest. Given that the *k*-value of decomposition rate was found to be the highest in the Karst forest, followed by the Lowland forest, and lowest in the Pine forest. The mismatch in decomposition rates, soil fertility levels (C, N, C/N, and CEC) and basal area growth between the three forests does not mean that the decomposition rates and soil fertility do not affect forest growth. Rather, the difference in the dominant species between the young broadleaf secondary forest (Karst) and the old broadleaf secondary forest (Lowland) could be the cause of this mismatch. Pioneer species, fast-growing species that dominate the Karst forest, such as *Kleinhovia hospita*, *Cananga odorata* and *Pterospermum celebicum*, grow faster than primary species, such as *Palaquium obovatum*, *Diospyros celebica* and *Areca catecu* (palm species), which dominate the Lowland forest. In addition, Older forests experience a longer process of returning nutrients than younger forests. This could be another reason why the C and CEC values in the Lowland forest are higher than those in the Karst forest. The Pine forest is the oldest of the three forests; however, based on the soil fertility indicators, it has the lowest C, N, C/N and CEC values. This appears to be related to the low rate of litter decomposition in the Pine forest community. As a result, the growth rate of the basal area in the Pine forest is also slower than in the other two forest communities.

# TABLE OF CONTENTS

<b>ENDORSEMENT PAGE</b> .....	<b>ii</b>
<b>DISSERTATION AUTHENTICITY STATEMENT AND COPYRIGHT OWNERSHIP</b> .....	<b>iii</b>
<b>ACKNOWLEDGEMENT</b> .....	<b>iii</b>
<b>ABSTRACT</b> .....	<b>v</b>
<b>EXECUTIVE SUMMARY</b> .....	<b>vi</b>
<b>TABLE OF CONTENTS</b> .....	<b>xi</b>
<b>LIST OF TABLES</b> .....	<b>i</b>
<b>LIST OF FIGURES</b> .....	<b>ii</b>
<b>CHAPTER 1</b> .....	<b>1</b>
<b>GENERAL INTRODUCTION</b> .....	<b>1</b>
1.1 BACKGROUND .....	2
1.2 STATEMENT OF ISSUES .....	6
1.3 OBJECTIVES AND USES .....	7
1.4 RESEARCH SCOPE.....	8
1.5 RESEARCH NOVELTY .....	9
1.6 CONCEPTUAL FRAMEWORK AND HYPOTHESIS .....	9
1.7 REFERENCES .....	11
<b>CHAPTER 2</b> .....	<b>17</b>
<b>SEASONAL LITTER PRODUCTION PATTERNS IN THREE TROPICAL FORESTS IN SULAWESI, INDONESIA: IMPLICATIONS FOR SECONDARY FOREST MANAGEMENT</b> .....	<b>17</b>
2.1 ABSTRACT.....	18
2.2 INTRODUCTION .....	18
2.3 MATERIAL AND METHODS.....	20
2.3.1 Study Site.....	20
2.3.2 Vegetation Analysis.....	22
2.3.3 Litter Production .....	23
2.3.4 Climate Elements and Soil Moisture .....	23
2.3.5 Data Analysis .....	23
2.4 RESULTS .....	24
2.4.1 Species Composition and Forest Structure .....	24
2.4.2 Inter-Seasonal Litter Production Within Each Forest Type .....	26
2.4.3 Comparison of Litter Production Across the Forest Types .....	27
2.4.4 Rainfall, Wind Velocity, Soil Moisture, and Temperature .....	30
2.5 DISCUSSION.....	31

2.6 CONCLUSION .....	33
2.7 REFERENCES .....	34
<b>CHAPTER 3 .....</b>	<b>39</b>
<b>CLARIFYING THE SLOW RATE OF <i>Pinus merkusii</i> LITTER DECOMPOSITION UNDER ITS MOTHER TREE STAND .....</b>	<b>39</b>
3.1 ABSTRACT.....	40
3.2 INTRODUCTION .....	40
3.3 MATERIAL AND METHODS.....	42
3.3.1 Study Site.....	42
3.3.2 Litterfall Observation .....	43
3.3.3 In Situ Decomposition Experiment.....	43
3.3.4 Decomposition Rate of Tusam and Ebony Leaves Under and Outside Their Stand Origin .....	44
3.3.5 Chemical Analysis of Tusam and Ebony Leaves .....	45
3.3.6 Decomposing Agent.....	46
3.3.7 Soil Chemical Properties .....	48
3.3.8 Climate and Soil Moisture .....	48
3.3.9 Data Analyses .....	49
3.4 RESULTS .....	50
3.4.1 Litterfall and In-Situ Decomposition Rate Among the Forest Communities.....	50
3.4.2 Tusam and Ebony Leaf Decomposition Rates Under and Outside Its Stand Origin .....	50
3.4.3 Chemical Composition of Leaf Litter .....	52
3.4.4 Macrofungi .....	52
3.4.5 Macrofauna .....	53
3.4.6 Soil Chemical Properties .....	54
3.4.7 Soil Moisture and Maximum and Minimum Temperature .....	55
3.5 DISCUSSION.....	56
3.6 CONCLUSION .....	59
3.7 REFERENCES .....	59
<b>CHAPTER 4 .....</b>	<b>64</b>
<b>SEASONAL DECOMPOSITION RATES OF BROADLEAF AND CONIFER WOOD LITTER IN FAR EASTERN TROPICAL FOREST COMMUNITIES.....</b>	<b>64</b>
4.1 ABSTRACT.....	65
4.2 INTRODUCTION .....	65
4.3 MATERIAL AND METHODS.....	67
4.3.1 Study Site.....	67
4.3.2 Wood Decomposition Experiments.....	69

4.3.3 Chemical Analysis of Wooden Planks .....	72
4.3.4 Decomposing Agent: Bacteria and Microscopic Fungi.....	72
4.3.5 Decomposing Agent: Macrofungi.....	73
4.3.6 Decomposing Agent: Macrofauna in the Soil.....	73
4.3.7 Decomposing Agent: Macrofauna on the Forest Floor.....	74
4.3.8 Soil Properties.....	74
4.3.9 Maximum Minimum Temperature.....	74
4.3.10 Data Analyses .....	75
<b>4.4 RESULTS .....</b>	<b>75</b>
4.4.1 Comparison in Decomposition Rate Between Seasons and Between Forests.....	75
4.4.2 Decomposition Rate Constants Between Different Sample Materials	77
4.4.3 Chemical Traits of Sample Wood Experiment .....	78
4.4.4 Diversity of Decomposing Bacteria and Fungi vs Decomposition Rate Constant .....	79
4.4.5 Decomposing Agent Macrofauna vs. Decomposition Rate Constant .	82
4.4.6 Soil Properties vs Decomposition Rate Constant .....	84
4.5 DISCUSSION.....	85
4.6 CONCLUSION .....	88
4.7 REFERENCES .....	88
<b>CHAPTER 5 .....</b>	<b>95</b>
<b>SEASONAL DIVERSITY AND DISTRIBUTION OF DECOMPOSING MACROFUNGI IN THREE FOREST COMMUNITIES: WHY DO THEY DIFFER?</b>	<b>95</b>
.....	<b>95</b>
5.1 ABSTRACT.....	96
5.2 INTRODUCTION .....	96
5.3 MATERIAL AND METHODS.....	98
5.3.1 Study Site.....	98
5.3.2 Climate and Environmental Factors.....	100
5.3.3 Macrofungal Diversity and Distribution .....	100
5.3.4 Data Analysis .....	101
5.4 RESULTS AND DISCUSSION.....	102
5.4.1 Environmental Conditions During the Wet Season and Dry Season	102
5.4.2 Seasonal Diversity of Macrofungi in the Three Forest Communities	103
5.5 CONCLUSION .....	114
5.6 REFERENCES .....	114
<b>CHAPTER 6 .....</b>	<b>120</b>
<b>DIFFERENCES IN THE VEGETATION DYNAMIC PATTERNS OF THREE TROPICAL SECONDARY FORESTS IN SOUTH SULAWESI, INDONESIA ..</b>	<b>120</b>

6.1 ABSTRACT.....	121
6.2 INTRODUCTION .....	121
6.3 MATERIAL AND METHODS.....	123
6.3.1 Study Site.....	123
6.3.2 Vegetation Analyses.....	124
6.3.3 The Dynamics of Forest Structure and Species Composition .....	126
6.3.4 Data Analysis .....	127
6.4 RESULTS .....	127
6.4.1 Dominant Species Composition and Structure .....	127
6.4.2 Dynamics of BA and Density of the Karst Forest .....	128
6.4.3 Dynamics of BA and Density of the Lowland Forest .....	129
6.4.4 Dynamics of BA and Density of the Pine Forest .....	130
6.4.5 Population Dynamics.....	131
6.5 DISCUSSION.....	132
6.6 CONCLUSION .....	135
6.7 REFERENCES .....	136
<b>CHAPTER 7 .....</b>	<b>140</b>
<b>GENERAL DISCUSSION AND CONCLUSIONS .....</b>	<b>140</b>
7.1 DISCUSSION.....	141
7.2 CONCLUSIONS.....	147
7.3 REFERENCES .....	149

## LIST OF TABLES

<b>Table 2.1.</b> Description of the three forest types. ....	24
<b>Table 2.2.</b> Basal area of the top five dominant tree species (> 5 cm in diameter) in each forest type. ....	25
<b>Table 2.3.</b> Comparison of the amount of litter produced across the three forest types during the dry and wet seasons.....	29
<b>Table 3.1.</b> Diversity of microscopic decomposing agents in three forest communities (Putra et al., 2023b).....	4747
<b>Table 3.2.</b> Comparison of the abundance of soil macrofauna in the forest communities. ....	5454
<b>Table 3.3.</b> Chemical properties of the soil in the permanent plots in the three forest communities during the dry season and wet season.....	5555
<b>Table 4.1.</b> Plot Description (Adapted from Putra et al., 2023).....	68
<b>Table 4.2.</b> Experimental time period. ....	71
<b>Table 4.3.</b> Chemical compound content of wood samples. ....	79
<b>Table 4.4.</b> Existence of microscopic decomposing agents in the three forest communities ( $\sqrt{}$ = exist). ....	81
<b>Table 4.5.</b> Mean abundance of soil macrofauna in three forest communities....	83
<b>Table 4.6.</b> Chemical properties of soil in permanent plots at three research sites during the dry season and wet season. ....	84
<b>Table 5.1.</b> Description of the research location.....	99
<b>Table 5.2.</b> Microhabitat conditions in the three forest communities.....	103
<b>Table 5.3.</b> Number of species and cover area of macrofungi in the wet and dry seasons.....	106
<b>Table 6.1.</b> Differences in the determinants of succession that potentially determine forest structure and species composition.....	124
<b>Table 6.2.</b> Basal area of each plot's top ten dominant tree species ( $\geq$ 5 cm in diameter). ....	128



## LIST OF FIGURES

<b>Figure 1.1.</b>	Research Conceptual Framework .....	10
<b>Figure 2.1.</b>	Map showing the locations of the three forest communities 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. ....	21
<b>Figure 2.2.</b>	Monthly total rainfall and maximum wind velocity during the study period (Source: Meteorology Climatology and Geophysics Council (BMKG) of the Republic of Indonesia). ....	22
<b>Figure 2.3.</b>	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). ....	27
<b>Figure 2.4.</b>	Percentage of leaves, twigs, and reproductive organs in the litter collected in each of the forest types. ....	28
<b>Figure 2.5.</b>	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. ....	30
<b>Figure 3.1.</b>	Monthly total rainfall during the study period (Source: BMKG [Meteorology, Climatology and Geophysics Agency] of the Republic of Indonesia 2019-2021). ....	4343
<b>Figure 3.2.</b>	Mean litter production, mean unbiodegradable litter and mean in-situ decomposition rate in the three forest communities. ....	5050
<b>Figure 3.3.</b>	The mean decomposition rate constant of the tusam leaves and ebony leaves over six months in the dry season and four months in the wet season. The lowercase letters to the left of the slash above each bar indicate a significant difference between the leaf samples in a forest community (a–b for Karst, c–d for Lowland and e–f for Pine), while the uppercase letters to the right of the slash above each bar indicate a significant difference among the forest communities for the same leaf sample (A–C for tusam leaf samples and X–Z for ebony leaf samples). The bars indicate the standard error. ....	5151
<b>Figure 3.4.</b>	The content of the chemical compounds in the sample leaves. .	5252

<b>Figure 3.5.</b>	Mean number of species of macrofungi in the forest communities. ....	5353
<b>Figure 3.6.</b>	Differences between seasons and among forest communities in terms of soil moisture (left), maximum temperature (centre) and minimum temperature (right). The lowercase letters to the left of the slash above each bar indicate a significant difference between the seasons in each forest community. The uppercase letters to the right of the slash above each bar indicate significant differences in the soil moisture (left), maximum temperature (middle) and minimum temperature (right) among the forest communities. The bars indicate the standard error.....	5555
<b>Figure 4.1.</b>	The dynamic of climate elements during the study period (Data for this graph were obtained from the Meteorology Climatology and Geophysics Council of the Republic of Indonesia). ....	68s
<b>Figure 4.2.</b>	The mean DR constant of wood samples for six months of the experiment (top row) and 12 months of the experiment (bottom row). Different lowercase letters to the left of the slash above each bar indicate inter-season intra-forest community significant differences (a-b for Karst, c-d for Lowland, and e-f for Pine), while different uppercase letters to the right of the slash above each bar indicate between forest community significant differences in the dry sea-son (A-B-C) and in the wet season (X-Y-Z). The bars indicate the standard of error. ....	76
<b>Figure 4.3.</b>	The mean value of k between different sample materials. Different letters on the stem in each forest type indicate a significant difference between the two wood sample materials. ....	78
<b>Figure 4.4.</b>	Macroscopic fungal species diversity by season (left) and habitat specialization (right). ....	80
<b>Figure 5.1.</b>	Monthly total rainfall during the study period (Source: Indonesian Agency for Meteorology, Climatology, and Geophysics in Maros City).....	100
<b>Figure 5.2.</b>	The number of species of each macrofungal family found in the three forest communities. ....	105
<b>Figure 6.1.</b>	Map showing the locations of the three forest types studied. (Source: Putra et al. 2023).....	124
<b>Figure 6.2.</b>	Sketch of the steps for setting a permanent plot.....	126
<b>Figure 6.3.</b>	The dynamics of forest structure based on total density (left) and total basal area (right) in the Karst forest over four years (2019 to 2022). ....	129
<b>Figure 6.4.</b>	The dynamics of forest structure based on total density (left) and total basal area (right) in the Lowland forest over four years (2019 to 2022). ....	130
<b>Figure 6.5.</b>	The dynamics of forest structure based on total density (left) and total basal area (right) in the Pine forest over four years (2019 to 2022). ....	130

# **CHAPTER 1**

## **GENERAL INTRODUCTION**

## 1.1 BACKGROUND

While forest trees need nutrients from the soil for their growth, through the process of photosynthesis, they produce large amounts of organic matter in the form of litter (Munawar et al., 2011; Baltzinger et al., 2012). Plant litter production is defined as the amount of vegetative and reproductive organs shed in a given area and period (Bisht et al., 2014). Litter consists of various dead plant organs (e.g. leaves, woods, barks, flowers, and fruits) that fall and accumulate on the forest ground (Krishna and Mohan, 2017). As organic matter, litter is the main component of terrestrial ecosystems in an ecological sense, where litter plays a vital role in soil biological processes such as decomposition and nutrient cycling to maintain balance and develop forest ecosystems (Ge et al., 2013; Szefer et al., 2017).

The process of litter decomposition, which is also known as the process of litter mineralization, refers to the physical, chemical, and biological processes involved in breaking down litter into simpler chemical elements (Krishna and Mohan, 2017). Therefore, decomposition is a major determinant of the nutrient cycling of most terrestrial ecosystems (Whitford and Wade, 2002; Austin and Ballaré, 2010; Szefer et al., 2017). Litter production and the rate of its decomposition will determine the quantity and speed with which nutrients return to the soil to be reused by trees for their growth process (Heilman and Gessel, 1963; Yang et al., 2004).

Litter production and its decomposition rate are essential factors in controlling the growth of forest stands (Grime, 1979). The forest ecosystems that grow well usually have a high rate of litter production and a high rate of decomposition (Yu-Sheng et al., 2003). Such forest ecosystems are usually characterized by a soil surface with a thick layer of humus on the forest floor so that nutrients in the soil are always available. Meanwhile, forest ecosystems with high litter production but low decomposition rate will experience worse growth due to low nutrient content in the soil (Musyafa, 2005; Rai et al., 2016). Such forest ecosystems are usually characterized by a thick litter layer on the forest floor, which can develop to become peat. There are also forest ecosystems that have low litter production and low decomposition rates (Carvalho et al., 2019).

In relation to the important role of litter as the main source of nutrients to restore forest soil fertility, several essential things to note are: how much litter is

produced by a forest stand, how fast the litter is decomposed, and what factors are involved in the process of production and decomposition of litter (Munawar et al., 2011; Paudel et al., 2015). The amount and composition of litter produced vary among forest communities and are affected by several internal factors, such as structure, age, and species composition of the forest community (Chen et al., 2002; Ruiz-Benito et al., 2014; Giweta, 2020; Wongprom et al., 2022). In addition to the internal factors, the production of litter in a forest stand can also be influenced by several external factors, such as climate, season, and substrate quality (Zhang et al., 2014; Seta and Zerihun, 2018; Giweta, 2020). The type and age of the forest (e.g. rainforest, monsoon forest, young secondary forest, old secondary forest, or primary forest) will determine the level of species diversity or composition (Naidu and Kumar, 2016), and this, in turn, will determine how much litter can be produced in a given period. Apart from being related to species composition, forest age is also related to several forest structure parameters, such as density, diameter, and the number of forest canopy layers. Older forest stands will have higher densities, larger tree diameters, more canopy layers, and therefore a larger overall basal area. Our prediction is that the older the forest stands, the wider the total basal area and the higher the production of litter.

Forest stands with different species compositions will produce litter with different chemical compositions, which will determine how quickly it can be decomposed by decomposing agents (Gnankambary et al., 2008; Vivanco and Austin, 2008; Aponte et al., 2012). For example, the litter of coniferous species, such as pine, is reported to contain allelopathic chemical compounds that make it less biodegradable (Johansson, 1995; Isidorov et al., 2010). Research on litter production and decomposition of coniferous forests, as well as comparisons with broadleaf forests, is generally carried out in temperate climates (MacLean and Wein, 1978; Prescott et al., 2000; Lorenz et al., 2004; Lin et al., 2013) because the species mostly grows in the region. On the other hand, in tropical regions such as Indonesia, research on this topic is still rarely carried out, considering that the natural forests in this region are primarily composed of broad-leaved tree species.

One species of Pinus, namely *Pinus merkusii* Jungh. et de Vriese (*P. merkusii*), is present in the tropics of the Far East (Imanuddin et al., 2020). In Indonesia, this species spreads naturally only on the island of Sumatra. It is very adaptable to new habitat conditions; therefore, since the 1960s, it has been widely planted in reforestation programs throughout the Indonesian archipelago,

particularly in South Sulawesi. Because of its superiority in terms of growth speed compared to local broadleaf tree species, and its use as a resin producer with economic value, *P. merkusii* is still the most desirable tree species for reforestation to date.

Each tree species that is part of a forest stand usually has a different phenological cycle, and this influences the seasonal dynamic of litter production. The decomposition process is also dynamic following litter production and the local macro and microclimate (Bisht et al., 2014; Kuruvilla et al., 2014; Kumar et al., 2016). Based on the data collected in Queensland, Australia, Sangha et al. (2006) reported that there are tree species with a high litter production and high rate of litter decomposition in the wet season; conversely, there are also tree species with low litter production and low decomposition rate in the wet season. The dynamics of litter production related to the season will, of course, vary in areas with different climate types because they will grow forests with different species compositions.

Several factors affect the rate of decomposition of litter produced by a forest stand (Schoor, 2001; Ott et al., 2012; Szefer et al., 2017). These factors are biotic (Ristok et al., 2019; Zhou, 2019) and abiotic (Berg and Matzner, 1997; Cisneros-Dosal et al., 2007; Powers et al., 2009) and originate from external environmental influences on the forest ecosystem and internal factors in term of the quality of the litter itself (Giweta, 2020). The biotic factors include the diversity and abundance of decomposer communities, consisting of macrofauna and microorganisms, that inhabit the soil surface (Höfer et al., 2000; Schmidt et al., 2008). The abiotic factors are generally in the form of environmental influences and, among others, are related to climate elements such as rainfall, humidity, temperature, and soil properties such as pH, NH<sub>4</sub>-N, slope, and topography (Setälä and McLean, 2004; Giweta, 2020; Qu et al., 2020). Several studies in temperate regions indicate that physical properties of soil, such as temperature and humidity, indirectly influence the rate of the litter decomposition process through the decomposing organism activity (Devi and Yadav, 2007; Tripathi et al., 2009). Although the mechanism is still being debated (Giweta, 2020), a number of studies conducted in India confirmed that the decomposition process is more effective during the rainy season (Pant and Tiwari, 1992; Kumar et al., 2010). In the tropics, altitude is related to temperature and rainfall, so it can indirectly influence the decomposition rate by inhibiting the activity of microorganisms.

As an intrinsic factor, litter quality can be determined by the presence of chemical compounds, such as lignin, tannin, cellulose, and hemicellulose (Hopkins et al., 1990; Austin and Vitousek, 2000; Sjöberg et al., 2004; Austin and Ballaré, 2010; Zhang et al., 2011) or allopathic substances, which are often reported to be found in pine leaves. Litter containing more lignin is hard to degrade due to its complex structure and heterogenous bonds with cellulose, and hemicellulose in the tissues (Orth et al., 1993; Cornwell et al., 2008; Austin and Ballaré, 2010). Based on a study of coniferous litter in Scandinavia, Johansson (1995) suggested that the contents of elements, such as Nitrogen (N), Phosphor (P), Potassium (K), Calcium (Ca), Magnesium (Mg), and Manganese (Mn), from the litter also determine the rate of decomposition.

Currently, the ecological aspects of secondary forest growth have become an essential issue in forest management, especially in Indonesia. This is because most of the forest areas that still exist in Indonesia are secondary forests. The linkages between components in the succession process will determine the growth rate of the secondary forest ecosystem (Guariguata and Ostertag, 2001); the components include vegetation type, age (successional stage), species diversity, litter production, and litter decomposition rate. To reveal the interrelationship between these components, each has to be investigated in depth, and this takes a very long time, year after year; therefore, only a few researchers are interested in conducting research on this topic (Waring and Schlesinger, 1985). Particularly for tropical forest ecosystems in Indonesia, no literature thoroughly examines the relationship between vegetation types, forest age, species composition, litter production, litter decomposition rates, and the factors influencing their interaction. Information is needed regarding the ecological interconnectivity in the development of forest ecosystems in order to plan secondary natural forest management so that past forest management failures, especially natural forest management, are not repeated.

As a result of reforestation activities on several islands in Indonesia in the 1960s and 1970s, especially Sulawesi Island, there are many areas with *P. merkusii* plantation forests. Various ecological issues related to *P. merkusii* plantation forests are often discussed, including litter production and decomposition rates, which are believed to be more difficult to resolve than for broadleaf species. However, until now, there have been no in-depth research results in Indonesia that report whether the litter produced by *P. merkusii* plantation

forests is also challenging to decompose, as is common in temperate climates. If pine forest litter in Indonesia decomposes slowly, as is typical in temperate climates, it is important to determine whether the cause is the same, considering the environment is different. Knowing the cause is critical before considering what actions to take to speed up the decomposition rate.

In connection with several problems described in the previous paragraphs, this research aims to: (a) reveal and analyse differences in seasonal litter production between three secondary forest communities that each grow on a different microhabitat type, succession stage, and restoration history, (b) compare, study, and analyse seasonal decomposition rates of *P. merkusii* needleleaf litter and *Diospyros celebica* Bakh. broadleaf litter, (c) examine and analyse the differences in the seasonal wood decomposition rate between the three forest communities, and (d) understand the dynamic of the three forest communities in relation to litter production and decomposition. All intrinsic and extrinsic factors that could potentially affect litter production, decomposition rates, and forest growth were investigated and analysed, including the diversity of each forest community, climate, soil chemical and physical properties, microorganism decomposing agents, macrofungal decomposing agents, macrofauna, and the chemical composition of the litter.

The three forest communities studied were: secondary natural forest in the karst ecosystem in the Karaenta forest complex of Bantimurung Bulusaraung National Park (hereinafter referred to as the Karst forest), lowland secondary tropical natural forest located in the Palanro forest complex of Hasanuddin University Educational Forest (hereinafter referred to as the Lowland forest), and the *P. merkusii* plantation forest located in the Hasanuddin University Educational Forest (hereinafter referred to as the Pine forest). The Karst forest and Lowland forest both represent secondary natural broadleaf forests but have different habitat characteristics and ages, while the Pine forest represents a forest dominated by conifers, *P. merkusii*.

## **1.2 STATEMENT OF ISSUES**

It is essential to understand the factors that play a role in the development of forest ecosystems in order to speed up the development of secondary forest ecosystems and achieve the expected conditions in a shorter period of time.



Forests of different ages and habitats will differ in litter production, as they do not have the same species composition, tree density, and basal area. Although there is still a debate among plant ecologists, many believe that the ecological processes in forest stands dominated by pine, such as *P. merkusii* plantations, are poor compared to those in natural broadleaf forests. Therefore, several research questions are posed that relate to the processes of litter production, litter decomposition, and forest stand growth, as well as the factors that influence these processes in various forest communities, as follows:

1. What are the differences in seasonal litter production between forest stands with different habitats, ages, and species compositions, and why do they differ? (Chapter II)
2. What are the differences in the processes and rates of broadleaf and coniferous leaf litter decomposition between forest stands with different habitats, ages, and species compositions, and why do they differ? (Chapter III)
3. What are the differences in the processes and rates of broadleaf and coniferous wood litter decomposition between forest stands with different habitats, ages, and species compositions, and why do they differ? (Chapter IV)
4. What are the differences in the seasonal diversity and distribution of macrofungal decomposing agents in the two broadleaf secondary forests and *P. merkusii* plantation forest and their host specialisation? (Chapter V)
5. What is the dynamic of the secondary forests in relation to litter production and decomposition? (Chapter VI)

### **1.3 OBJECTIVES AND USES**

Based on the statement of issues as described previously, the objectives of this study are:

1. To uncover and analyse the differences in seasonal litter production among three forest communities growing in different habitats and at different ages (45-year-old secondary forest in the karst ecosystem, 54-year-old lowland secondary forest, and 58-year-old *P. Merkusii* plantation forest), therefore differing in species composition and structure (Chapter II).

2. To examine and analyse the differences in the process and rate of decomposition of leaf litter of broadleaf trees and coniferous trees (*P. merkusii*) between that which decomposes under the parent tree stand (in-situ: coniferous leaves under the coniferous tree stand) and that which does not decompose under the parent tree stand (ex-situ: coniferous leaves under broadleaf stands) (Chapter III).
3. To examine and analyse the differences in the decomposition processes and rates of broadleaf and coniferous wood litter between forest communities with different habitats, ages, and species compositions (broad-leaved trees and conifers) (Chapter IV).
4. To reveal and analyse the seasonal diversity and distribution of macrofungal decomposing agents in the two secondary broadleaf forests and the *P. merkusii* plantation forest (Chapter V).
5. To analyse the dynamic of the secondary forests in relation to litter production and decomposition (Chapter VI).

The results of this study are useful as a basis for preparing management plans for secondary natural forests that currently dominate forest areas in Indonesia, thereby significantly accelerating the soil nutrient cycle and, at the same time, encouraging the rate of forest growth.

#### **1.4 RESEARCH SCOPE**

This is an ecological study that covers the process of litter production and litter decomposition along with the factors involved in it, which occur in three secondary forest communities: Karst forest, Lowland forest, and Pine forest. Furthermore, this research analyses the relationship between litter production, decomposition rate, and soil fertility level and their relationship to growth dynamics. This study focuses primarily on differences in seasonal litter production and decomposition rates in the three secondary forest communities, and specifically the intrinsic and extrinsic factors that play a role in determining these differences. In addition, this study also analyses the effect of production and decomposition rates on the growth of the three forest communities. Research was conducted in Hasanuddin University Educational Forest and the Karaenta forest complex of Bantimurung Bulusaraung National Park.

## **1.5 RESEARCH NOVELTY**

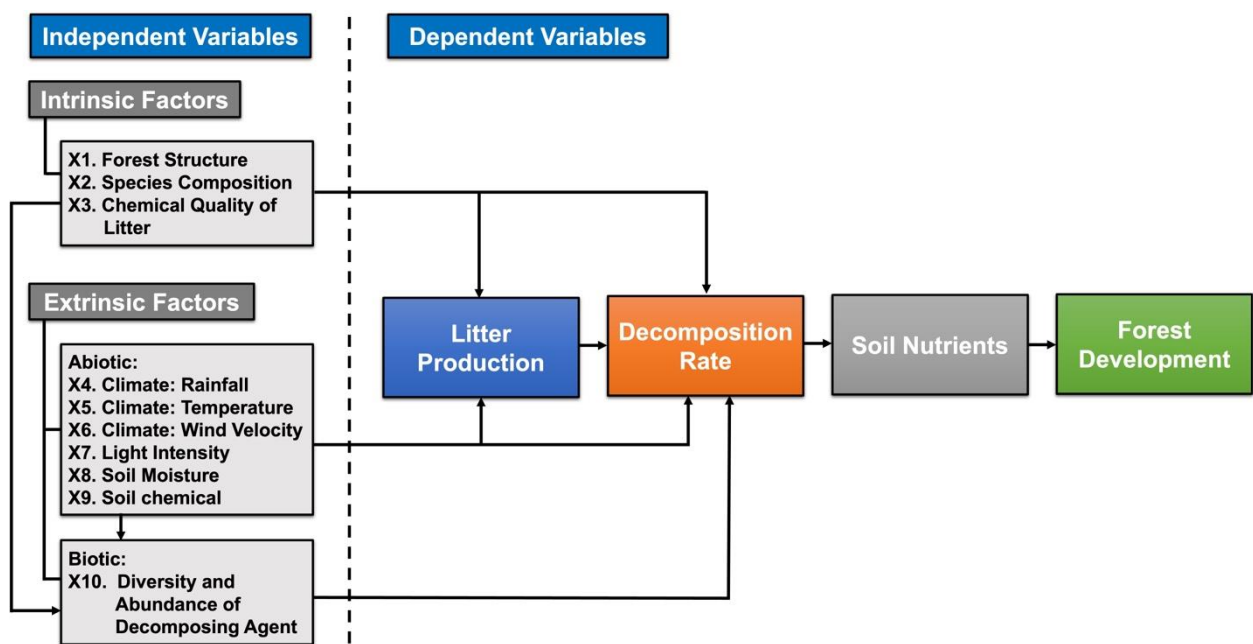
1. The existing literature shows that studies on forest litter production and decomposition rates, especially comparisons between broadleaf and coniferous forests, are generally carried out in temperate regions. This study is intended to examine whether the tropical Far East region (in particular, around the equator) will show the same results as that in the temperate region.
2. Because it takes a long time, studies on litter production and litter decomposition conducted in the tropical region so far have not assessed the role of the season, even though the season has the potential to influence litter production and decomposition, both directly and indirectly. This study was designed for both the dry season and the wet season.
3. This study examines and analyses the relationship between litter production, litter decomposition, soil fertility, and forest growth (dynamic).
4. The methods used to compare and assess the differences in decomposition rates between broadleaf forests and coniferous forests are in-situ and ex-situ experiments. The in-situ experiments were carried out by allowing the litter to decompose naturally under forest stands that produce the litter (coniferous leaf litter under coniferous forest). Meanwhile, the ex-situ experiment was carried out by allowing the litter to decompose under a stand that did not include the parent trees (coniferous leaf under broadleaf forest).

## **1.6 CONCEPTUAL FRAMEWORK AND HYPOTHESIS**

This conceptual model illustrates the expected relationship between the variables studied, provides an overview of the research plan, and explains the relationship between the independent and dependent variables. The independent variable is the variable that causes changes in the dependent variable. The purpose of this section is to clearly explain the conceptual framework that is the basis for the study of all variables, both independent and dependent, to examine the pattern of relationships or mutual influence between them. Another purpose is to outline several research hypotheses, as alleged answers to research gaps need

to be examined through this study. Therefore, the interconnectivity of all potential variables is analysed here.

The independent variables in this research study are both intrinsic and extrinsic factors. The intrinsic factors consist of forest structure, species composition of forest trees, and chemical quality of litter, while the extrinsic factors (also called environmental factors) consist of abiotic (chemical and physical) and biotic factors. Meanwhile, the dependent variables in this study are litter production, decomposition rate, soil nutrients, and forest development, which sequentially influence one another.



**Figure 1.1.** Research Conceptual Framework

Based on the conceptual framework described above, we formulate several hypotheses as initial predictions of the relationship between the variables studied, as follows:

1. Litter production in the three forest communities studied differs between seasons and between forest communities; this is influenced by the dynamics of climate elements between seasons and differences in species composition between forest communities.
2. Given that coniferous leaves are believed to have allelopathic compounds, the decomposition rate of leaf litter from the conifer *P. merkusii* (tusam) will

be slower than leaf litter from the broadleaf *D. celebica* (ebony), both in the parent tree forest stands of each species and in the parent tree forest stands of the other tree species.

3. Decomposition rates between woody litter from broadleaf tree species differ from coniferous species and differ between forest communities. The chemical composition of wood litter influences this as an intrinsic factor, and the diversity and abundance of decomposer organisms affect this as an extrinsic factor. Meanwhile, the season indirectly controls the decomposition rate of the two wood samples through the activity of decomposition agents.
4. Considering that macroscopic fungi require high humidity to grow, the diversity of these fungal types is higher in the wet season than in the dry season. Macroscopic fungal species composition varies between forest communities following the differences in tree species that dominate each forest community.
5. There is a unidirectional relationship between litter production, decomposition rate, and soil fertility, and this will have a positive impact on the development of forest stands in terms of increasing basal area.

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## **CHAPTER 2**

### **SEASONAL LITTER PRODUCTION PATTERNS IN THREE TROPICAL FORESTS IN SULAWESI, INDONESIA: IMPLICATIONS FOR SECONDARY FOREST MANAGEMENT**

## 2.1 ABSTRACT

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 analyse forest structure and species composition. Thirty-six traps with a surface area of 1 m<sup>2</sup> 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<sup>2</sup>/year), followed by the Pine forest (1,288.24 g/m<sup>2</sup>/year) and Karst forest (1,099.83 g/m<sup>2</sup>/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

## 2.2 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.,

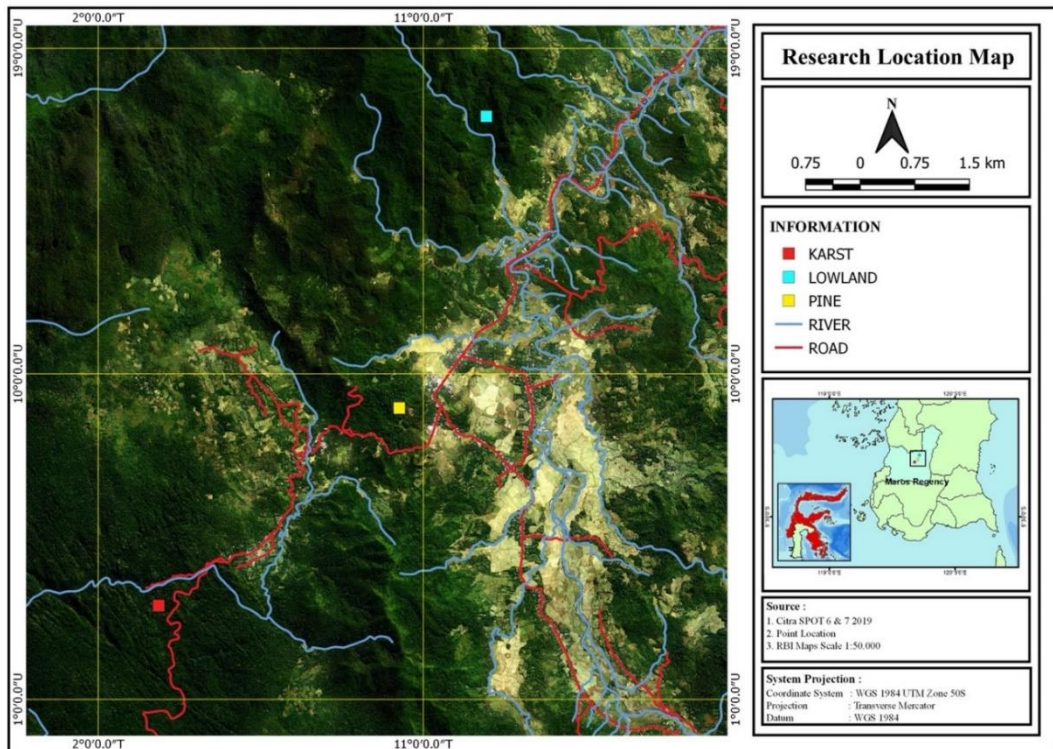
2019). Variation in litter production patterns and masses across forest types is also potentially influenced by several other environmental factors such as altitude, topography (de Sousa-Neto et al., 2017), and elevation (Becker et al., 2015).

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.

## **2.3 MATERIAL AND METHODS**

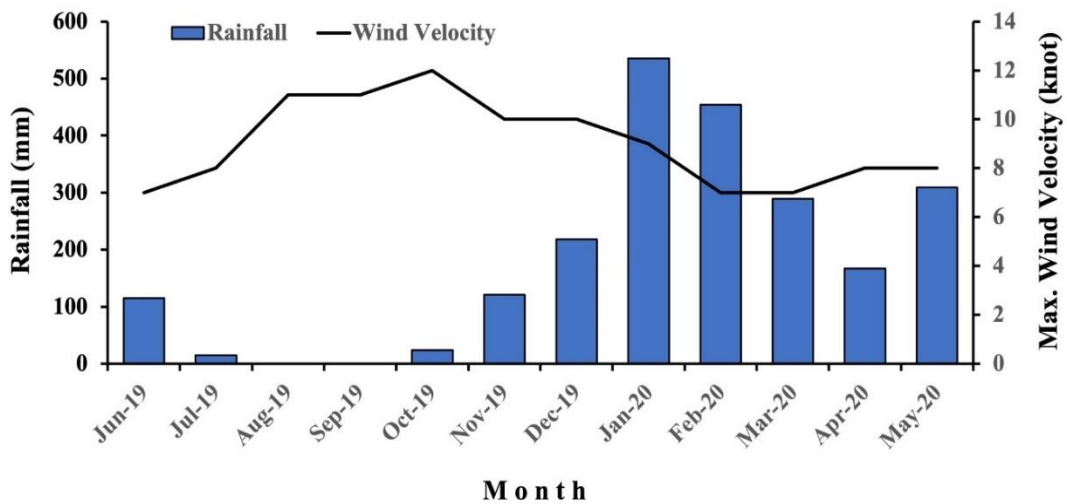
### **2.3.1 Study Site**

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 (119°44'14.9" E, 05°01'46.8" 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 (119°46'35.0" E, 04°58'06.9" 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 (119°45'56.7" E, 05°00'17.3" S) (Center for Agricultural Land Resources 2017 for soil types of all forest types) (Figure 2.1).



**Figure 2.1.** Map showing the locations of the three forest communities 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.

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 2.2).



**Figure 2.2.** Monthly total rainfall and maximum wind velocity during the study period (Source: Meteorology Climatology and Geophysics Council (BMKG) of the Republic of Indonesia).

### 2.3.2 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 >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.



### **2.3.3 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<sup>2</sup> 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 °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.

### **2.3.4 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.

### **2.3.5 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 (a) inter-season mean litter production within each forest type, (b) mean litter production between forest types, (c) inter-season mean monthly rainfall and wind velocity, (d) inter-season and within each forest type soil moisture, and

(e) 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).

## 2.4 RESULTS

### 2.4.1 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 2.1). The density of trees >5 cm in diameter was highest in the Lowland forest plot (Table 2.1), while the total basal area was significantly largest in the Pine forest (Table 2.2). 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.

**Table 2.1.** Description of the three forest types.

<b>Characteristics</b>	<b>Karst</b>	<b>Lowland</b>	<b>Pine</b>
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	90	61	42
H' Index	3.43	1.62	2.61

**Table 2.2.** Basal area of the top five dominant tree species (>5 cm in diameter) in each forest type.

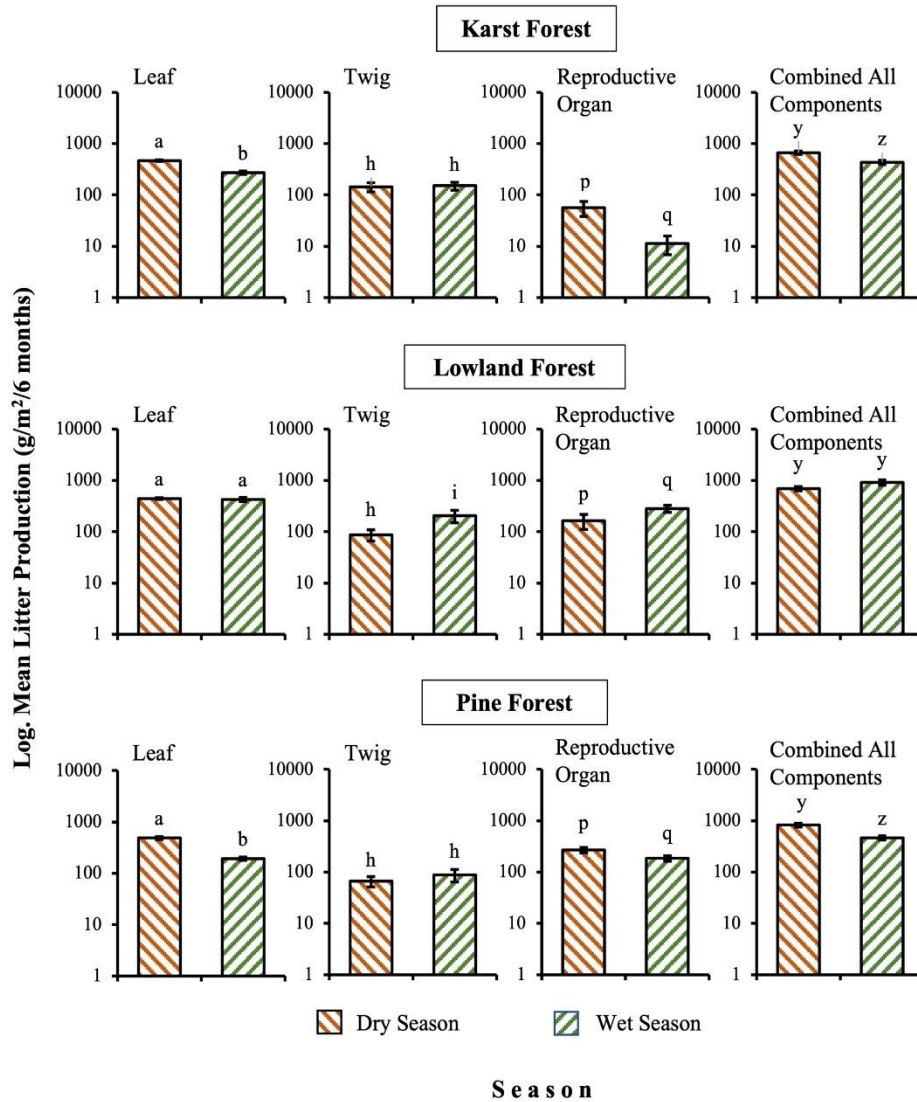
Species	Family	Basal Area (cm <sup>2</sup> / ha)		
		Karst	Lowland	Pine
<i>Kleinhovia hospita</i> L.	Sterculiaceae	58689.61		
<i>Cananga odorata</i> (Lamk.) Hook	Annonaceae	34048.54		
<i>Pterospermum celebicum</i> Miq.	Sterculiaceae	17697.82		
<i>Dracontomelon dao</i> (Blanco) Merr. & Rofle)	Anacardiaceae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

## 2.4.2 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 ( $465.79 \pm 18.79$  g/m<sup>2</sup>/6 month for leaf litter and  $56.42 \pm 13.04$  g/m<sup>2</sup>/6 month for reproductive organ litter) than in the wet season ( $272.49 \pm 18.79$  g/m<sup>2</sup>/6 month for leaf litter and  $11.33 \pm 13.04$  g/m<sup>2</sup>/6 month for reproductive organ litter) (leaf:  $P < 0.001$ ; reproductive organ:  $P = 0.0230$ ). There was no significant difference in the amount of twig litter between the dry season ( $143.05 \pm 28.03$  g/m<sup>2</sup>/6 month) and the wet season ( $150.74 \pm 28.03$  g/m<sup>2</sup>/6 month) ( $P = 0.8479$ ). The production of combined litter for all components was also significantly greater in the dry season ( $665.26 \pm 46.44$  g/m<sup>2</sup>/6 month) compared to the wet season ( $434.57 \pm 46.44$  g/m<sup>2</sup>/6 month) ( $P = 0.0020$ ) (Figure 2.3 top row).

In the Lowland forest, leaf litter production was similar across seasons ( $442.88 \pm 32.30$  g/m<sup>2</sup>/6 month in the dry season and  $426.51 \pm 32.30$  g/m<sup>2</sup>/6 month in the wet season) ( $P = 0.7235$ ). In comparison, the production of twigs and reproductive organs litter was significantly greater in the wet season ( $203.94 \pm 42.47$  g/m<sup>2</sup>/6 month for twig litter and  $283.08 \pm 49.22$  g/m<sup>2</sup>/6 month for reproductive organ litter) compared to the dry season ( $86.78 \pm 42.47$  g/m<sup>2</sup>/6 month for twig litter and  $164.03 \pm 49.22$  g/m<sup>2</sup>/6 month for reproductive organ litter) (twig:  $P = 0.0284$ ; reproductive organ:  $P = 0.0205$ ). However, when the three organs were combined, litter amounts did not differ significantly between seasons ( $693.68 \pm 89.00$  g/m<sup>2</sup>/6 month in the dry season and  $913.53 \pm 89.00$  g/m<sup>2</sup>/6 month in the wet season) ( $P = 0.1135$ ) (Figure 2.3 middle row).

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 ( $485.07 \pm 24.73$  g/m<sup>2</sup>/6 month for leaf litter and  $270.56 \pm 28.45$  g/m<sup>2</sup>/6 month for reproductive organ litter) compared to the wet season ( $192.52 \pm 24.73$  g/m<sup>2</sup>/6 month for leaf litter and  $185.24 \pm 28.45$  g/m<sup>2</sup>/6 month for reproductive organ litter) ( $P < 0.001$  and  $P = 0.0455$  respectively). There was no significant difference in the production of twig litter between seasons ( $66.18 \pm 20.31$  g/m<sup>2</sup>/6 month in the dry season and  $88.68 \pm 20.31$  g/m<sup>2</sup>/6 month in the wet season) ( $P = 0.4418$ ). The mean production of all components combined was significantly greater in the dry season ( $821.81 \pm 56.31$  g/m<sup>2</sup>/6 month) compared to the wet season ( $466.43 \pm 56.31$  g/m<sup>2</sup>/6 month) ( $P < 0.001$ ) (Figure 2.3 bottom row).



**Figure 2.3.** 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).

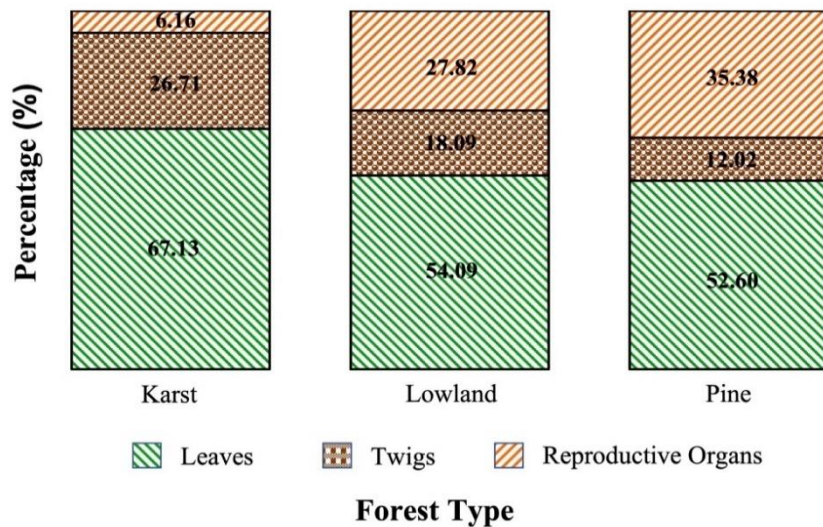
### 2.4.3 Comparison of Litter Production Across the Forest Types

The greatest overall mean of litter production occurred in the Lowland forest; however, this difference was only statistically significant compared to the Karst forest ( $P = 0.0069$ ). During the dry season, there were no significant differences in the production of all litter components across the three forest types ( $P = 0.1147$ ).

However, during the wet season, litter production in the Lowland forest was significantly greater than in Karst and Pine forests ( $P < 0.001$ ) (Table 2.3).

No significant differences were detected for leaf and twig litter production across the three forest types in the dry season (leaf:  $P = 0.4542$ ; twig:  $P = 0.1089$ ), but reproductive organ production differed significantly across the forest types ( $P < 0.001$ ). 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:  $P < 0.001$ ; reproductive organ:  $P < 0.001$ ). On the other hand, the production of twig litter in the wet season was not significantly different across the three forest types ( $P = 0.0604$ ).

The leaf litter constituted the greatest proportion of the total litter collected in all forest types throughout the study period (Figure 2.4). 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.



**Figure 2.4.** Percentage of leaves, twigs, and reproductive organs in the litter collected in each of the forest types.

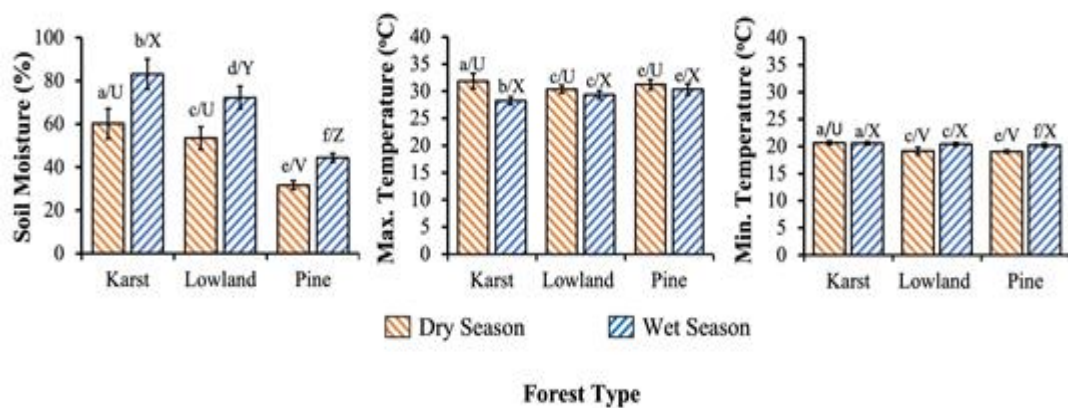
**Table 2.3.** Comparison of the amount of litter produced across the three forest types during the dry and wet seasons.

Organ	Mean Mass Weight (g/m <sup>2</sup> ) ± SE		
	Karst-Forest	Lowland-Forest	Pine-Forest
<b>Dry Season (June to November 2019)</b>			
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 (± 62.43)x	693.68 (± 62.43)x	821.81 (± 62.43)x
<b>Wet Season (December 2019 to May 2020)</b>			
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
<b>Components and All Seasons Combined</b>			
<b>Overall Mean in a Year</b>	<b>1099.83 (±106.37)a</b>	<b>1607.21(±106.37)b</b>	<b>1288.24(± 106.37)ab</b>

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.

## 2.4.4 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) ( $P < 0.001$ ). Mean soil moisture also differed significantly between seasons in each forest type (Figure 2.5:  $P = 0.0434$ ;  $P = 0.0292$ ;  $P < 0.001$  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) ( $P = 0.1017$ ). 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.



**Figure 2.5.** 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.

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 2.5 left: U-U-V ( $P = 0.0246$ )). 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 2.5 left: X-Y-Z ( $P < 0.001$ )). On the other hand, the maximum temperature was not significantly different between



forest types both in the dry and wet seasons (Figure 2.5 center: U-U-U ( $P = 0.6134$  in the dry season) and X-X-X ( $P = 0.2344$  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 2.5 right: U-V-V ( $P = 0.0425$ )). During the wet season, the minimum temperature did not differ between forest types (Figure 2.5 right: X-X-X ( $P = 0.7177$ )).

## 2.5 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 greatest 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, 2022). 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.

## **2.6 CONCLUSION**

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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