

# Vegetation patterns and litterfall production dynamics during post-agricultural succession in tropical lowland ecosystems: A case study in Manokwari, West Papua, Indonesia

Original Article

## Abstract:

In West Papua, Indonesia, shifting cultivation relies on long-term natural fallow to restore soil fertility. Understanding the ecological processes underlying this practice, such as vegetation succession patterns and litterfall dynamics, is crucial for promoting sustainable agriculture and conserving natural resources in the region. This study examined changes in vegetation composition, structure, diversity, and litterfall production in 5-year, 10-year, and 15-year fallows in post-agricultural lowlands. Vegetation profiles were analyzed using nested plots, while litterfall production was measured using litter traps over six months. A general linear model (GLM) analysis of variance (ANOVA) followed by Tukey's HSD test ( $p < 0.05$ ) and non-metric multidimensional scaling (NMDS) analysis were used to compare the three fallow ages. The results showed distinct differences in vegetation structure and composition, with older fallows exhibiting a more diverse and complex vegetation structure. Total litterfall production differed significantly between the 5-year fallow and the 10- and 15-year fallows, but not between the latter two. NMDS analysis revealed a clear separation between the 5-year fallow and the 10- and 15-year fallows, with 82.5% of the variability in data attributes explained by the differences in fallow age. Our findings suggest that maintaining fallow periods of 10 years or more can enhance vegetation diversity and structure, as well as increase organic matter input through litterfall production.

## Key words:

lowlands fallow, *Piper aduncum*, shifting cultivation, vegetation analysis

## Apstrakt:

**Obrasci vegetacije i dinamika produkcije biljnog otpada tokom postpoljoprivredne sukcesije u tropskim nizijskim ekosistemima: studija slučaja u Manokwariju, Zapadna Papua, Indonezija**

U Zapadnoj Papui, Indonezija, premeštajuća poljoprivreda zasniva se na dugotrajnom neobrađivanju zemljišta, kako bi se obnovila njihova plodnost. Razumevanje ekoloških procesa koji leže u osnovi ove prakse, kao što su obrasci sukcesije vegetacije i dinamika nakupljanja biljnog otpada, ključno je za promovisanje održive poljoprivrede i očuvanje prirodnih resursa u regionu. Ova studija je ispitala promene u sastavu, strukturi i raznovrsnosti vegetacije, kao i proizvodnju biljnog otpada na nizijskim zemljištima neobrađenim 5, 10 i 15 godina. Profili vegetacije analizirani su korišćenjem potparcela, dok je proizvodnja biljnog otpada merena pomoću zamki za biljni otpad tokom šest meseci. Analiza varijanse pomoću generalnog linearnog modela (GLM ANOVA), praćena Tukey-jevom HSD testom ( $p < 0,05$ ) i analiza nemetrickeog multidimenzionalnog skaliranja (NMDS) korišćene su za poređenje zemljišta koja su neobrađena tokom tri vremenska perioda. Rezultati su pokazali izražene razlike u strukturi i sastavu vegetacije, pri čemu duže neobrađena zemljišta pokazuju raznovrsniju i složeniju strukturu vegetacije. Ukupna proizvodnja biljnog otpada značajno se razlikovala između zemljišta neobrađivanog 5 godina i onih koji su se oporavljala 10 i 15 godina, dok razlika između dva poslednja zemljišta nije bila značajna. NMDS analiza je pokazala jasnu separaciju između zemljišta neobrađivanog 5 godina i onih koja nisu obrađivana 10 i 15 godina, pri čemu je 82,5% varijabilnosti u atributima podataka objašnjeno razlikom u dužini oporavka. Naši nalazi sugerišu da oporavak zemljišta u periodu od 10 godina i više može poboljšati raznovrsnost i strukturu vegetacije i povećati unos organske materije kroz proizvodnju biljnog otpada.

## Ključne reči:

utrine, *Piper aduncum*, premeštajuća poljoprivreda, analiza vegetacije

Slamet Arif Susanto

Department Biology, Faculty Mathematics and Natural Science, Universitas Papua, Jalan Gunung Salju Amban, Manokwari, Papua Barat, Indonesia 98314

*s.susanto@unipa.ac.id* (corresponding author)

Ibnul Qayim

Department Biology, Faculty Mathematics and Natural Science, IPB University, Jalan Agatis Kampus IPB Dramaga, Bogor Telp (0251) 8622833, Bogor, Jawa Barat, Indonesia 16680

Triadiati Triadiati

Department Biology, Faculty Mathematics and Natural Science, IPB University, Jalan Agatis Kampus IPB Dramaga, Bogor Telp (0251) 8622833, Bogor, Jawa Barat, Indonesia 16680

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## Introduction

Traditional farming systems in Papua differ from those in other regions. In Papua, traditional agriculture focuses on cultivating staple crops such as sweet potato (*Ipomoea batatas*), cassava (*Manihot esculenta*), taro (*Colocasia esculenta*), papaya (*Carica papaya*), and banana (*Musa paradisiaca*) (Indow et al., 2021), as well as peanuts (*Arachis hypogaea*), corn (*Zea mays*), chili (*Capsicum annuum*), and various vegetables (Tuturop et al., 2022) on small-scale farms. This traditional farming practice leads to declining soil fertility after three to four cropping seasons (Hartemink, 2004; Wapongnungsang et al., 2021), prompting farmers to abandon the land and clear new areas through forest clearance. The abandoned land then undergoes natural fallow.

Fallow systems are an integral part of the shifting cultivation cycle characteristic of traditional farming in Papua. The primary purpose of fallow is to restore soil fertility, allowing local Papuans to re-clear the land for cultivation after several years. During the fallow period, changes in vegetation types occur, potentially altering the physical and chemical properties of the soil through the return of organic matter. However, due to limited land resources and a growing population, fallow periods have shortened in Papua, Indonesia, as well as in other tropical regions (Hepp et al., 2018; Mertz et al., 2021). This trend is consistent with previous findings in Papua New Guinea (Hartemink, 2003), highlighting the need to study vegetation succession and organic matter production to understand soil fertility dynamics.

Understanding vegetation composition during fallow periods is essential due to its strong correlation with organic matter production. Litterfall production significantly influences the amount of organic matter returned to the soil (Feng et al., 2019; Sayer et al., 2024). As fallow periods progress, increases in stem diameter and tree density can enhance litterfall production (Souza et al., 2019; Williams-Linera et al., 2021) and carbon sequestration (Chan et al., 2016). Additionally, plant species in fallow lands can alter soil conditions, and the canopy structure of trees can create a unique microclimate (Kukla et al., 2019). While previous studies have explored related topics, such as using tree diameter distribution to estimate fallow age (Susanto, 2019), long-term vegetation changes in Papua New Guinea (Whitfeld et al., 2014), and forest regeneration in 20-year-old fallows (Gonçalves et al., 2018), further research is needed to comprehensively understand the dynamics of vegetation succession and organic matter production in fallow systems.

Changes in vegetation types during succession

are closely linked to the quantity of organic matter produced through litterfall production (Teixeira et al., 2020). However, the relationship between fallow regeneration processes and litterfall production remains understudied in West Papua, Indonesia. Previous research has explored litterfall production in various ecosystems, including comparisons of production and decomposition rates along altitudinal gradients (Sari et al., 2016), differences in litterfall production across agroforestry land uses (Sari et al., 2022; Verma et al., 2022), and the impact of forest land clearing on litterfall production (Tsfay et al., 2020). Additionally, studies have shown that removing litter from the soil surface can significantly reduce soil carbon (Xu et al., 2021). These findings highlight the importance of understanding the relationship between vegetation components and litterfall production, particularly in the context of vegetation changes during succession on fallow land.

A preliminary study on litterfall production was conducted by Susanto et al. (2020) in 15-year-old fallow land in Manokwari, focusing only on dominant tree species such as *Pometia pinnata*, *Octomeles sumatrana*, and *Dracontomelon dao*, without considering other tree species. Consequently, a comprehensive understanding of litterfall production remains lacking. Given the prevalence and varying ages of fallows in West Papua, Indonesia, further research is needed to compare vegetation structure, composition, and organic matter production through litterfall production across different fallow ages.

The Sidey District in Manokwari, West Papua, Indonesia, is characterized by widespread natural vegetation changes due to the prevalent fallow system. Local Papuan communities, specifically the Arfak Tribe, practice nomadic land use for cultivation (BPS-Statistics West Papua Province, 2024). Villages in the lowlands of Sidey District, such as Womnowi, Kasi, and Kaironi, have fallow lands with ages ranging from 1 to 30 years. Notably, Kaironi Village, with an area of 23.29 km<sup>2</sup> and an average altitude of 107 asl (BPS-Statistics of Manokwari Regency, 2019, 2024), exhibits a diverse ecosystem, including coastal areas and hills. The local Meyah Tribe, part of the Arfak Tribe, has practiced shifting cultivation with a fallow system for generations, resulting in the formation of fallow lands around the village.

Fallow lands in Sidey District, Manokwari, West Papua, Indonesia, play a crucial role in enhancing soil fertility naturally, resembling forest ecosystems due to shifting cultivation practices. Local communities, particularly the Arfak Tribe, exhibit a high dependence on shifting cultivation systems, exceeding that of other Indonesian regions

(Yuminarti & Darwanto, 2018; Indrawati et al., 2022). This study investigates the importance of soil fertility in fallow lands, influenced by vegetation changes and litterfall production during succession. Specifically, it addresses three research questions: (1) How do vegetation structure and composition differ among 5-, 10-, and 15-year-old fallows in Kaironi Village? (2) What are the differences in litterfall production among these fallow ages? (3) What determination model can be applied to biotic and abiotic factors in these fallows over a short period?

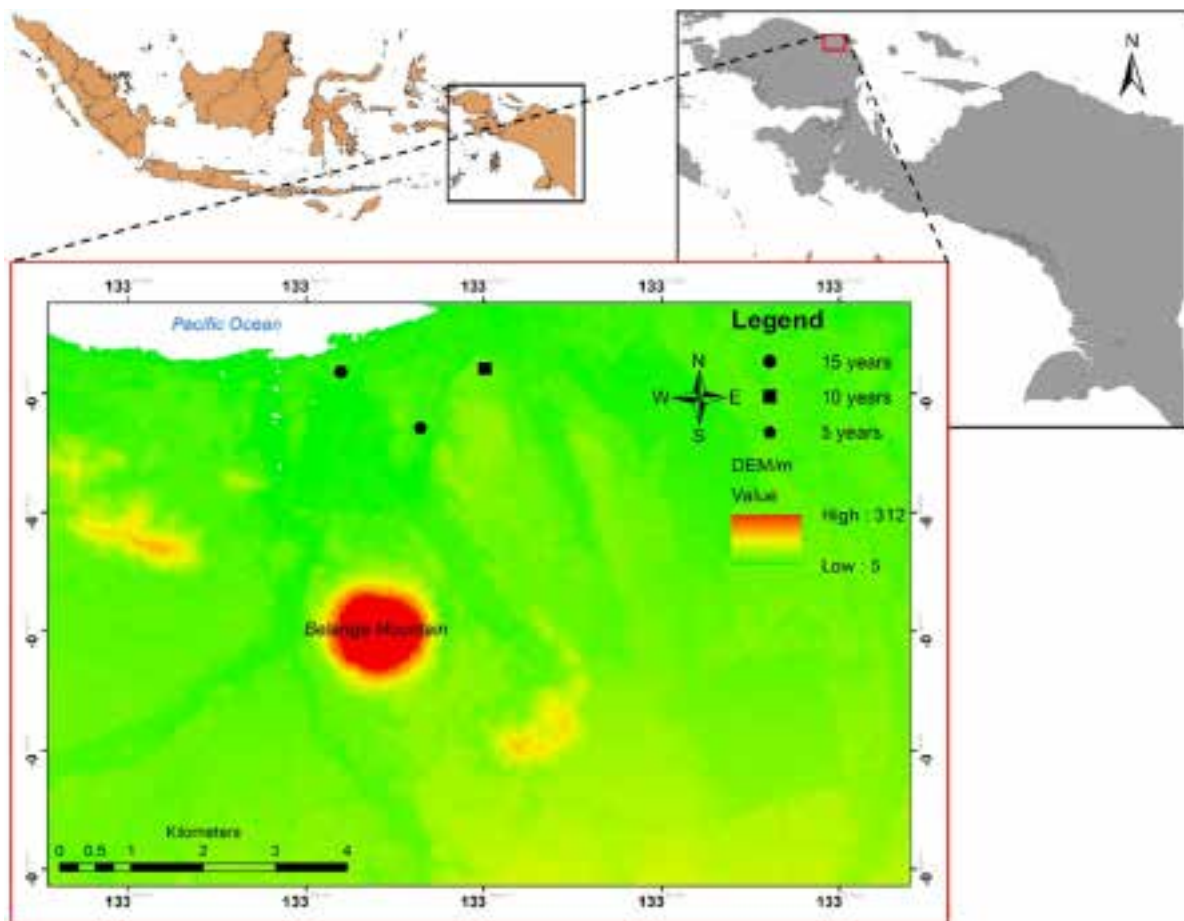
## Materials and Methods

### Description of study site

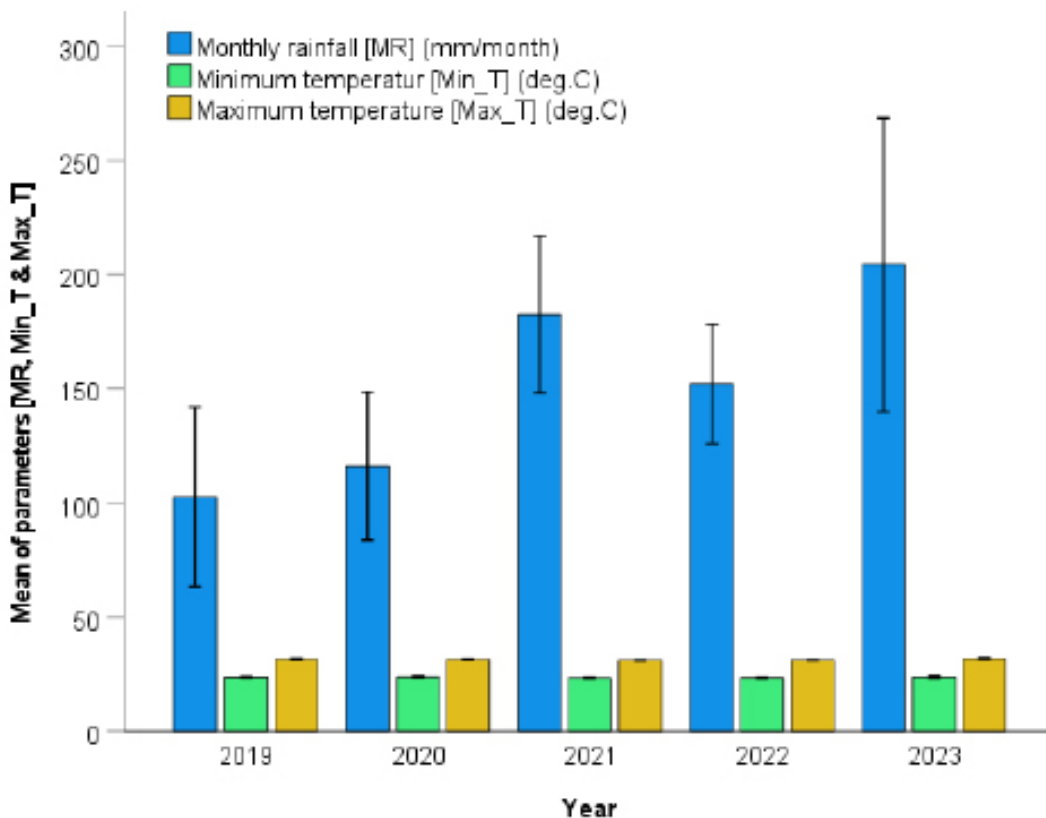
The study was conducted in the lowlands of Sidey District, Manokwari Regency, West Papua Province, Indonesia (0°45'0"S, 133°33'32.4"E). The study area has an altitude of 5–312 meters above sea level (masl), where the location of fallow lands ranges from 65–75 m asl (Fig. 1). The northern side

of the study area (15-year fallow) is very close to the Pacific Ocean ( $\pm 5$  km), while many hills exist to the south and southwest of the study area. One of the most iconic hills in the Sidey District is ‘Gunung Belanga’ because, when viewed from any side, it has the same shape (see DEM maps in Fig. 1).

The site of study has a tropical rainforest climate (Af type) based on the Köppen-Geiger climate classification (Peel et al., 2007), with annual average rainfall exceeding 1200 mm/year. Information on monthly rainfall, minimum temperature, and maximum air temperature for the last 5 years derived from climate data of the Climatology Station of West Papua Province (BMKG, 2024) with coordinates 1°28'12"S, 134°11'24"E and elevation 20 m asl is summarized in Fig. 2. The average monthly rainfall is consistently above 100 mm/month, with minimal monthly temperature variations. The average minimum temperature is 23.5 °C, and the maximum temperature is 31.3 °C. Over the last five years, the lowest rainfall was recorded in 2019 (1,229 mm/year), while the highest was in 2023 (2,451 mm/



**Fig. 1.** Map of the study site in Sidey District, Manokwari Regency, West Papua, Indonesia. The Digital Elevation Model (DEM) provides elevation information for the study area with a spatial resolution of 8.1 meters (Ina-Geoportal, 2024). The labels “5 years,” “10 years,” and “15 years” indicate the locations of the 5-, 10-, and 15-year fallow sites, respectively



**Fig. 2.** Monthly rainfall information and 5-year average minimum and maximum temperatures in Manokwari, West Papua. Bars indicate the standard error ( $\pm$ SE) of means

year).

Soils in the Doberai Region, including Manokwari Regency, West Papua, are generally of the order Ferrasols (FAO-UNESCO, 1979), while the soils at the studied sites are included in District Fluvisols (Jd10-2/3a) associated with District Cambisols, including Humic Gleysols and District Regosols (FAO, 1976). There is a diversity of soil textures in the three research locations, where the clay fraction dominates the 5-year fallow land, and the 10- and 15-year fallow lands are dominated by the sand fraction (Susanto et al., 2021). The study sites were also influenced by the Circum-Australian Orogenic System, with the vegetation region comprising tropical lowland evergreen rainforest (FAO-UNESCO, 1979).

**Plot design**

The first stage involves observing the fallow land based on the results of interviews with fallow landowners. The initial observation aimed to assess the most representative land with an age of 5 years, 10 years, or 15 years. The next stage involved designing research plots within the fallows, where we created three plots, each measuring 20 m  $\times$  20 m, for each age of the fallow. The three plots for each fallow were selected by purposive sampling; we

assumed three plots as replicates. Within the plots, we recorded all woody vegetation (excluding lianas and palms) and measured litterfall production for six consecutive months. During the fallow period, no cultivation activities were carried out by local communities on the land area under study.

**Vegetation survey**

In July and August 2020, we collected data on vegetation, which included mature trees and tree juveniles. A plot method of vegetation analysis was employed in this study, specifically the nested plot technique (Guariguata et al., 1997), with a main plot measuring 20 m  $\times$  20 m to record mature trees. Inside the main plot, 10 m  $\times$  10 m plots were made to record young trees (poles), and 5 m  $\times$  5 m and 2 m  $\times$  2 m plots were made to record sapling and seedling phases, respectively. The assumption used is that different ages of fallow land have different proportions of seedlings and saplings; therefore, the nested plot method is expected to reduce the bias in vegetation data resulting from the number of seedlings and saplings for each age of fallow land. Vegetation structure and composition were observed, and the ecological role of plant species was calculated using the importance value index.

The determination of each growth phase in plant

vegetation analysis is done by referring to Widiyatno et al. (2017) and Murdjoko et al. (2021), where the seedling phase is recorded when tree juveniles reach  $\leq 1.5$  m in height. The sapling phase refers to young trees that are  $\geq 1.5$  m tall and have a diameter of less than 10 cm. Meanwhile, data collection for the pole phase is conducted on tree emergence with diameters ranging from 10 cm to 20 cm. If the diameter size of the plant recorded is  $\geq 20$  cm, it is included in the tree phase category. Measurements of the sapling, pole, and tree phases were made at a stem diameter of 1.30 m above ground level (diameter at breast height/dbh) because stem diameter growth at these heights is stable. All stem diameter data  $\geq 5$  cm were used to determine the distribution of tree diameter classes at each fallow age (Whitfeld et al., 2014).

### Measurement of litterfall production

Litterfall production was measured using the 1 m  $\times$  1 m nylon mesh litter trap method (Feng et al., 2019) for six consecutive months (August 2020–January 2021). Litter traps were set  $\sim 1$  m above the ground to prevent loss of litter weight due to decomposition (Nakagawa et al., 2019), as well as to reduce wildlife disturbances, such as those caused by wild pigs. The litter traps were stretched out in a square shape and supported by four wooden sticks, with the center of the trap curved to trap the litterfall efficiently (modified from Tesfay et al. (2020)). A total of 3 litter traps were installed in a 20 m  $\times$  20 m plot, so nine litter traps were used in one fallow season. All litter traps installed in the 5, 10, and 15-year fallow plots were labelled to simplify the calculation of litterfall production conversion per year.

All litter traps were deliberately placed within 20 m  $\times$  20 m plots, following the guideline that traps should not be positioned in canopy gaps (Huang et al., 2018; Martin et al., 2018). In the case of 5-year fallow plots, which contained numerous canopy gaps, traps were strategically placed near saplings, young trees, or mature trees. Litterfall accumulated in the traps was collected on the same date each month (Morffi-Mestre et al., 2020). The collected litter from each trap was manually sorted into leaves, branches (diameter  $\geq 2$  cm), twigs (diameter  $\leq 2$  cm), and flowers and fruits (including buds). The sorted litter was then oven-dried at 80 °C to a constant weight (Souza et al., 2019). Monthly dry weights were measured using a scale with a precision of 0.01 g, and subsequently converted to mg/ha/year (Rodriguez et al., 2023).

### Environmental parameter measurements

Environmental parameters were measured at biweekly intervals for six consecutive months in each fallow land. The measured factors included

air temperature, soil temperature, air humidity, soil moisture, and soil pH. These parameters were assessed using a 4-in-1 Environmental Meter (Krisbow KW0600291) with a temperature measuring accuracy of  $\pm 2$  °C for temperature and  $\pm 5\%$  for humidity and a soil tester (Takemura DM-15) with an accuracy of 0.1 for temperature, humidity, and soil pH. The collected data were used to determine the impact of fallow age on changes in vegetation structure and litterfall production through a non-metric multidimensional scaling (NMDS) model or a suitable non-metric analysis approach.

### Data analysis

To analyze the vegetation data, we calculated the importance value index (IVI) for each identified plant species, which indicates the ecological role and existence of species in each fallow age (Curtis & McIntosh, 1951). Furthermore, we calculated the summed dominance ratio (SDR) to determine the dominant species by comparing the IVI of the most dominant species with the total IVI of each growth phase (Numata, 1982; Patel et al., 2022). For seedlings and saplings, the SDR was calculated by dividing the IVI of the dominant species by 200 (the sum of relative density and relative frequency). For poles and trees, the SDR was calculated by dividing the IVI of the dominant species by 300 (the sum of relative density, relative frequency, and relative dominance).

The diversity index was calculated separately for each growth phase (seedling, sapling, pole, and tree) in each plot, resulting in three diversity index values for each fallow age. The Shannon diversity index ( $H'$ ) was calculated using the equation  $H' = -\sum p_i \times \ln(p_i)$  (Shannon, 1948), where  $p_i$  represents the proportion of individuals of the  $i$ -th species to the total number of individuals of all species in each plot. Additionally, stem diameter distributions were analyzed using histograms and normal curves to estimate changes in vegetation structure over the fallow period and to characterize land age (Stride et al., 2018).

Annual litterfall production was estimated based on 6 months of litterfall collection data using a model adapted from Morffi-Mestre et al. (2020), with the following modified equation:

$$LP = \frac{\bar{x} \text{ LPT} \times 12 \times 10000}{1000}$$

where LP is litterfall production (Mg/ha/year) and  $\bar{x}$  LPT is the average litterfall production from 9 litter traps per month per fallow age (kg). Our estimate of annual litterfall production, based on 6 months of

measurement, relies on the assumption that tropical rainforest ecosystems (Af type) experience minimal seasonal climate variation (Doughty et al., 2023) and lack a distinct dry season (Borchert, 1998). Given this, we believe that the impact on annual litterfall production is negligible, making 6 months of measurement representative of annual litterfall production.

### Statistical analysis

This study assumed that fallow age was the primary factor influencing vegetation structure, composition, plant diversity, and litterfall production. Therefore, a General Linear Model (GLM) univariate analysis of variance (ANOVA) was conducted at  $p < 0.05$  to compare plant diversity and litterfall production across different fallow ages (Triadiati et al., 2011). Post-hoc comparisons were performed using Tukey's HSD test, with significance set at  $p < 0.05$ . For non-parametric spatiotemporal analysis, non-metric multidimensional scaling (NMDS) based on the Bray-Curtis dissimilarity index with square root transformation was applied (Chen et al., 2020; Ferreira et al., 2021). The study employed a temporal pseudoreplication approach (Hurlbert, 1984), utilizing data collected over six consecutive months. All statistical analyses and visualizations were performed using IBM SPSS Statistics (v. 27) and PAST (v. 4.03) software.

## Results and discussion

### Composition, structure, and diversity patterns of vegetation

Our results show that the SDR values of dominant species in the 5-year fallow exceeded 50% across all growth stages. In contrast, SDR values in the seedling and sapling stages of the 10-year fallow and all growth stages in the 15-year fallow were below 50% (Table 1). The highest dominance was observed in the tree stage of the 5-year fallow, with an SDR value of 100%, while the lowest dominance was found in the sapling stage of the 15-year fallow, with an SDR value of 21.03%. This study indicates that the pole and tree stages ( $\text{dbh} \geq 10$  cm) tend to exhibit a higher degree of dominance compared to the seedling and sapling stages.

This study shows that the vegetation composition in each fallow land is dominated by specific species that grow naturally, supporting the practice of natural fallowing in the lowlands of Sidey, Manokwari. The fallow lands are predominantly inhabited by plant species from the Piperaceae, Euphorbiaceae, Malvaceae, Meliaceae, and Moraceae families (Table 1). Notably, 5-year-old fallow lands are characterized by the dominance of Piperaceae and

Euphorbiaceae, particularly *Piper aduncum*, which is consistent with previous research in Papua New Guinea that identified this species as dominant during the initial stages of fallow periods (3-5 years) (Hartemink, 2001). Similarly, in East Kalimantan, *Ficus* sp. and *P. aduncum* are considered indicator plants for the onset of fallow periods (Hashimoto et al., 2007). Interestingly, *P. aduncum* can thrive in nutrient-poor soils (Hapsari et al., 2020) and accumulate significant biomass, reaching 48 tons/ha in just 5 months, with an average growth rate of 69 kg/ha under high rainfall conditions (Hartemink, 2001). In the context of ecological implications for soil fertilization, leaf litterfall from *P. aduncum* has been reported to produce 222 kg N, 50 kg P, 686 kg K, 255 kg Ca, 75 kg Mg, and 24 kg S per hectare over two years (Hartemink, 2001). Therefore, the presence of this species in the early stages of fallow plays a crucial role in increasing the soil's content of essential nutrients.

The seedling and sapling phases in the 5-year fallow were dominated by only two families, Piperaceae (*P. aduncum*) and Euphorbiaceae (*Mallotus* sp1 and *Macaranga aleuritoides*). In addition, at the pole and tree phases, more than 50% of the important values of plant species were dominated by the Euphorbiaceae family (*M. aleuritoides*, *Mallotus* sp1, and *Homalanthus novoguineensis*) (see Table 1).

The dominance of *Macaranga* spp. in 5- and 10-year fallows (Table 1) suggests that these areas were initially open lands without a canopy. This finding is consistent with previous studies that have identified *Macaranga* spp. as dominant pioneer species in open canopy areas, such as post-forest fire areas in East Kalimantan (Sakai et al., 2022). Similarly, *Macaranga* spp. have been reported to dominate the seedling and sapling stages in 5-year fallows in Sarawak, Malaysia (Karyati et al., 2018). In East Kalimantan, *Macaranga triloba* has been identified as an indicator species of young secondary forests on former shifting cultivation lands (Susanto et al., 2016). Furthermore, in Papua New Guinea, *Macaranga aleuritoides* and *Piper aduncum* have been found to act as pioneer species during the early stages of succession in secondary forests (Lepš et al., 2002). The dominance of *Macaranga tanarius* in 10-year fallow land may be associated with the soil texture, which is dominated by sandy fractions, allowing for faster root growth and a vertical root distribution reaching 60 cm (Lee et al., 2020). Overall, the presence of *Macaranga* spp. in these fallow lands confirms that they are likely former shifting cultivation areas (Slik et al., 2003).

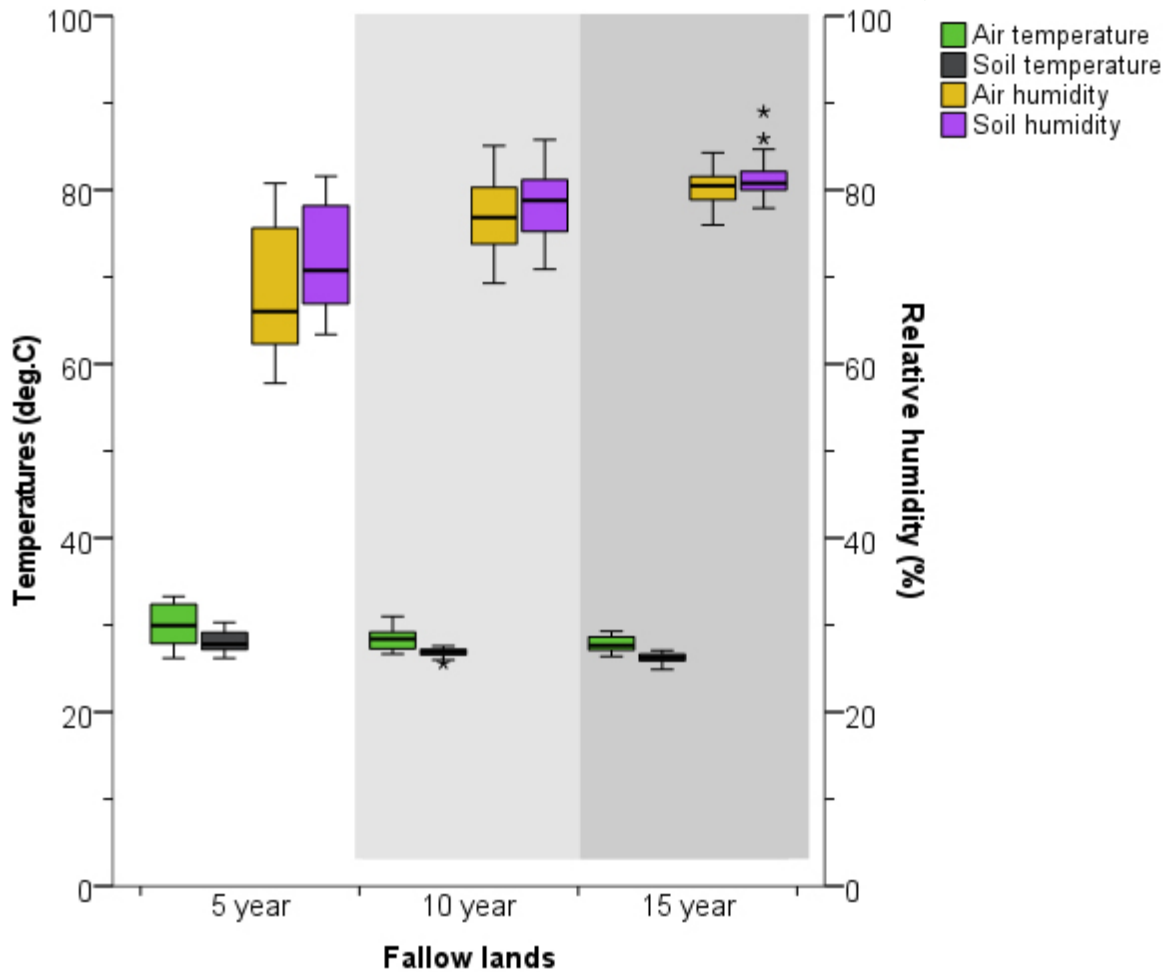
The high dominance of *P. aduncum* in 5-year-old fallows can be attributed to intensive sun-

light exposure, which elevates air and soil temperatures compared to 10- and 15-year-old fallows (Fig. 3). In Papua New Guinea, this species has been reported to be an invasive species that dominates fallows less than 5 years old (Hartemink, 2001; Lepš et al., 2002). However, *P. aduncum* can also act as a facilitator species due to its high potassium content in litter (Hartemink, 2004). Notably, this species exhibits resilience in relatively humid conditions, with germination pos-

sible up to temperatures of 70 °C (Wen et al., 2015) and a germination percentage exceeding 90% within 17-25 days (Susanto et al., 2018). Furthermore, its photosynthetic activity increases significantly under 100% irradiation (Pacheco et al., 2013). These findings suggest that *P. aduncum*'s habitat preference aligns with the biophysical conditions of 5-year-old fallow land, characterized by higher average air and soil temperatures compared to older fallows (Fig. 3), thereby enabling its dominance.

**Table 1.** Dominant plant species based on summed dominance ratio (SDR) in fallow lands of different ages in the Sidey lowlands, Manokwari, West Papua

Age of fallow	Phase	Summed dominance ratio (SDR) (%)			Cumulative SDR (%)
		First	Second	Third	
5 year	Seedling	<i>Piper aduncum</i> (22.30)	<i>Mallotus</i> sp. (21.57)	<i>Macaranga aleuritoides</i> (14.94)	58.81
	Sapling	<i>Mallotus</i> sp. (29.83)	<i>Piper aduncum</i> (20.55)	<i>Macaranga aleuritoides</i> (11.27)	61.65
	Pole	<i>Macaranga aleuritoides</i> (34.20)	<i>Mallotus</i> sp. (17.22)	<i>Premna tomentosa</i> (10.45)	61.87
	Tree	<i>Macaranga aleuritoides</i> (34.83)	<i>Homalanthus novoguineensis</i> (34.05)	<i>Octomeles sumatrana</i> (31.13)	100.0
	Seedling	<i>Syzigium</i> sp. (15.97)	<i>Mangifera odorata</i> (15.97)	<i>Intsia bijuga</i> (11.48)	43.42
	Sapling	<i>Kleinhovia hospita</i> (14.82)	<i>Intsia bijuga</i> (13.89)	<i>Pimelodendron amboinicum</i> (12.97)	41.68
10 year	Pole	<i>Macaranga tanarius</i> (32.24)	<i>Kleinhovia hospita</i> (20.44)	<i>Alstonia scholaris</i> (8.75)	61.43
	Tree	<i>Macaranga tanarius</i> (27.03)	<i>Kleinhovia hospita</i> (18.18)	<i>Mangifera odorata</i> (13.86)	59.07
	Seedling	<i>Sterculia shillinglawii</i> (16.35)	<i>Artocarpus altilis</i> (14.63)	<i>Ficus ampelas</i> (11.51)	42.49
15 year	Sapling	<i>Aglaia spectabilis</i> (8.60)	<i>Ficus</i> sp. (6.66)	<i>Ficus nodosa</i> (5.77)	21.03
	Pole	<i>Aglaia spectabilis</i> (21.11)	<i>Ficus nodosa</i> (15.38)	<i>Macaranga tanarius</i> (10.85)	47.34
	Tree	<i>Ficus nodosa</i> (25.43)	<i>Alstonia scholaris</i> (10.99)	<i>Macaranga tanarius</i> (10.98)	47.4



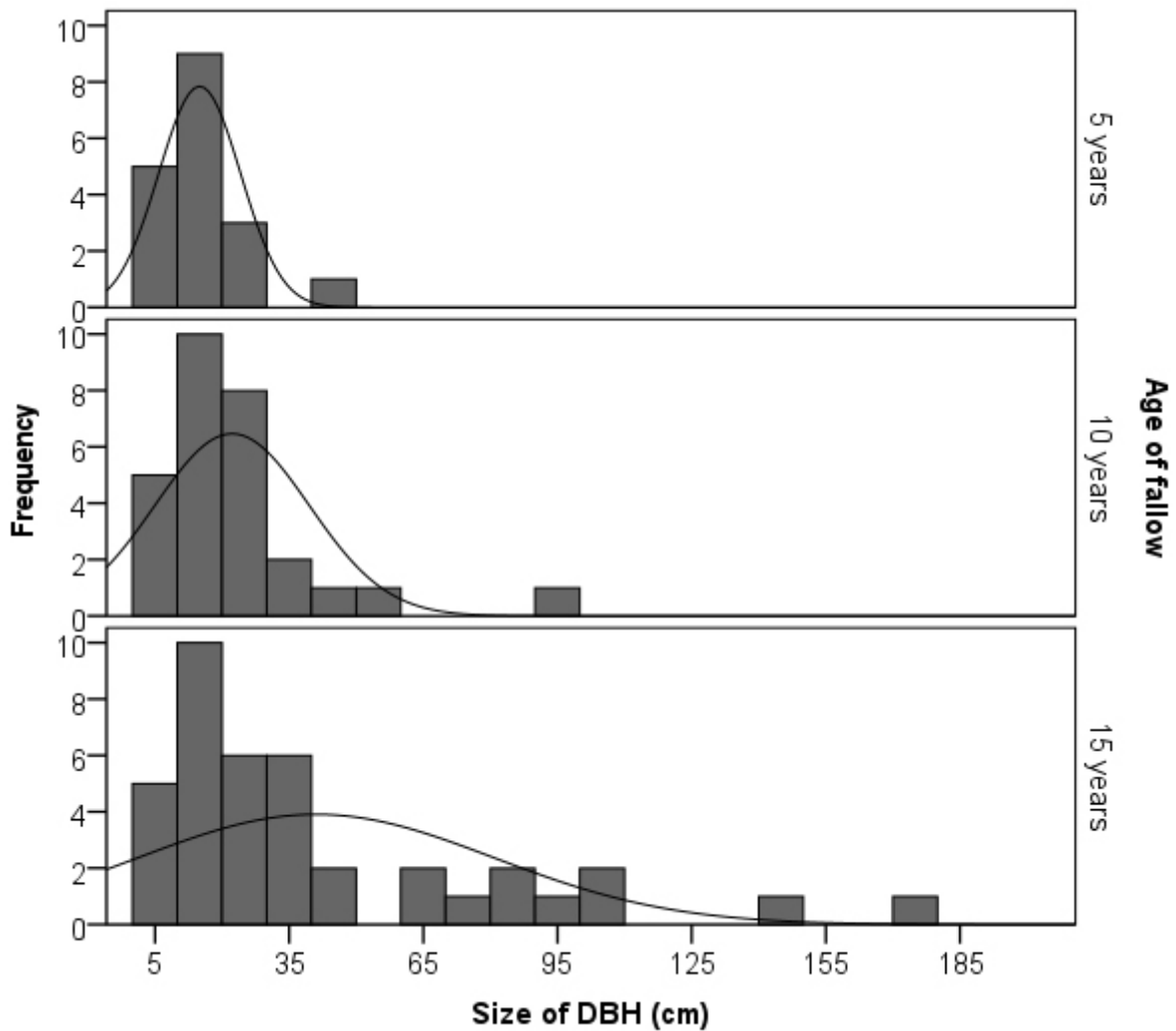
**Fig. 3.** Box-plot of variations in air and soil temperature and humidity in 5-, 10-, and 15-year fallows during 6 months of measurements (2-week measurement interval). The asterisks indicate data outliers

In the 10-year fallow, no strong dominance was observed in the seedling and sapling phases, with only one family, Fabaceae (*Intsia bijuga*), accounting for 25%. However, the pole and tree phases were dominated by the Euphorbiaceae (*Macaranga tanarius*) and Malvaceae (*Kleinhovia hospita*) families, comprising 52.68% and 45.21%, respectively (**Tab. 1**). Although no single species exhibited strong dominance in the seedling and sapling phases of the 15-year fallow, the Moraceae family (including *Artocarpus altilis*, *Ficus ampelas*, *Ficus* sp., and *Ficus nodosa*) was dominant, alongside the Meliaceae (*Aglaiia spectabilis*) and Euphorbiaceae (*Macaranga tanarius*) families.

The high Species Dominance Ratio (SDR) value in 5-year-old fallow land indicates that certain species play a significant role in shaping community composition and acting as pioneer species during succession (**Tab. 1**). This finding is consistent with previous research showing that dominant species in post-mining succession areas exhibit high SDR values (You-Bao et al., 2004). The higher SDR values

in the pole and tree phases compared to the seedling and sapling phases across all fallow ages suggest that the dominant species in these phases have a greater impact on the environment. A high SDR value can influence the surrounding environment, particularly through basal area dominance, which in turn increases organic matter input through litterfall (Bhaskar et al., 2018; Williams-Linera et al., 2021). Consequently, young and mature trees play a crucial role in restoring soil fertility during the fallow period.

The histogram in **Fig. 4** represents 325 individual plant data (dbh ≥ 5 cm), comprising 79, 121, and 125 individuals for 5-, 10-, and 15-year fallows, respectively. Despite differences in the number of individuals contributing to the stem diameter distribution at each fallow age, the findings indicate that the normal curve tends to shift in accordance with fallow age. All fallows exhibited a stem diameter distribution of trees accumulating below 30 cm. The normal curve patterns formed at each fallow age were distinct (**Fig. 4**). Specifically, the



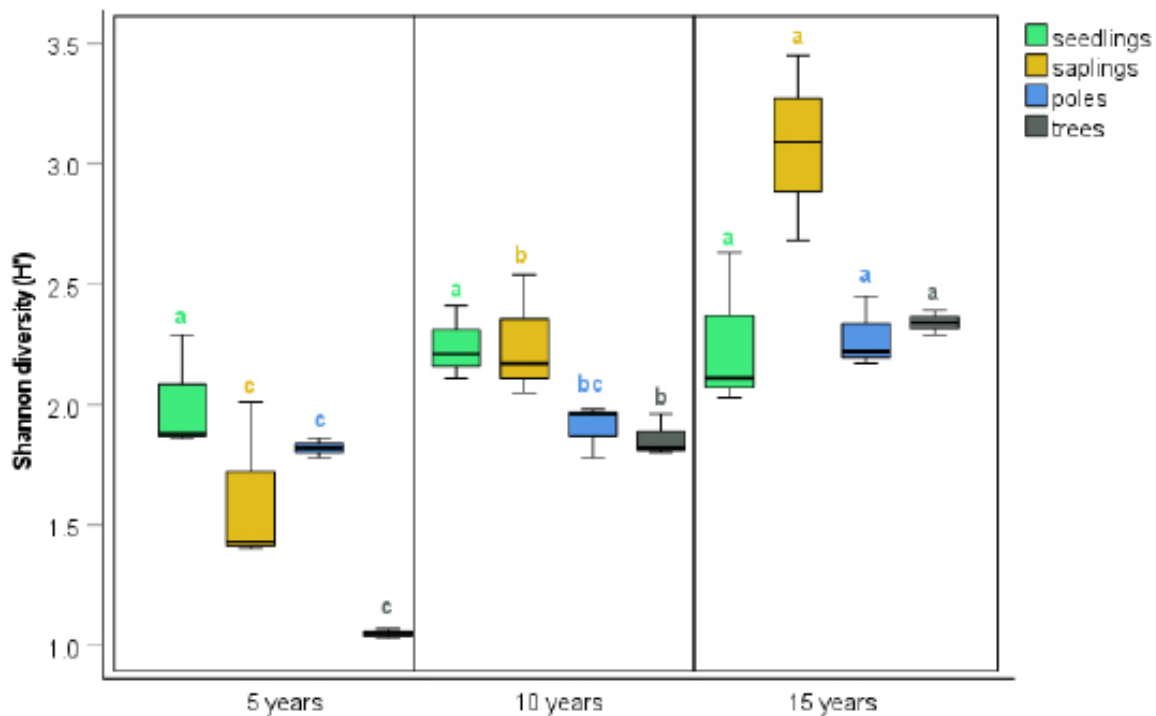
**Fig. 4.** Stem size distribution patterns (dbh ≥ 5 cm) in fallow lands of different ages in the Manokwari lowlands of West Papua

5-year fallow land displayed a more concentrated distribution of tree stem diameters in specific classes compared to the 10- and 15-year fallow lands.

The normal curve, which trends towards a more even slope in the 15-year fallow compared to the 5- and 10-year fallows (**Fig. 4**), may indicate a more stable succession process. The distribution of tree diameters varied across fallows, with a trend towards increasing diameter size as the fallow period lengthened, with the majority of trees accumulating in the class below 30 cm. This pattern is consistent with natural forest regeneration in Papua New Guinea, where tree diameter distribution is predominantly below 30 cm in forests aged ≤ 15 years (Whitfeld et al., 2014). In contrast to studies in Burkina Faso, Africa, where selective logging led to a decline in tree numbers in fallows aged 15 years and above (Kindt et al., 2008), the natural fallow model in Papua, Indonesia, suggests that succession

occurs without human interference, allowing tree diameter size to increase with fallow age. This natural fallow model shows promise for future tree conservation efforts.

This study successfully visualized that the shift of the normal curve to the right (**Fig. 4**), demonstrates changes in tree diameter structure during the succession process in fallow land. The further to the right, the more trees with larger diameters. The ecological implication is that fallow lands aged 5-15 years still exhibit distinct differences in diameter structure (dbh), suggesting continuous changes in structure and composition every 5 years. This finding is consistent with Ohtsuka et al.'s (2025) study, which showed a similar rightward shift in tree diameter distribution over 23 years of succession in a cool-temperate secondary deciduous forest, correlating with increased ecosystem net primary production (NPP). Thus, our study confirms that the



**Fig. 5.** Box-plot of plant diversity pattern in Manokwari lowland fallow, West Papua. Different letters above bars of the same colour indicate significant differences based on Tukey HSD test  $p < 0.05$

fallow lands investigated accurately represent the actual age of the land.

Our results showed that the plant diversity index of the seedling phase did not differ significantly among the three fallow ages ( $F_{2,6}=0.92$ ;  $p > 0.4$ ). In contrast, diversity indices for the sapling ( $F_{2,6}=14.52$ ;  $p < 0.005$ ), pole ( $F_{2,6}=14.92$ ;  $p < 0.005$ ), and tree ( $F_{2,6}=64.37$ ;  $p < 0.001$ ) phases differed significantly between the 5-year fallow and the 10- and 15-year fallows (**Fig. 5**). Furthermore, overall diversity ( $p < 0.05$ ) between the 5-year fallow and the 15-year fallow was significantly different.

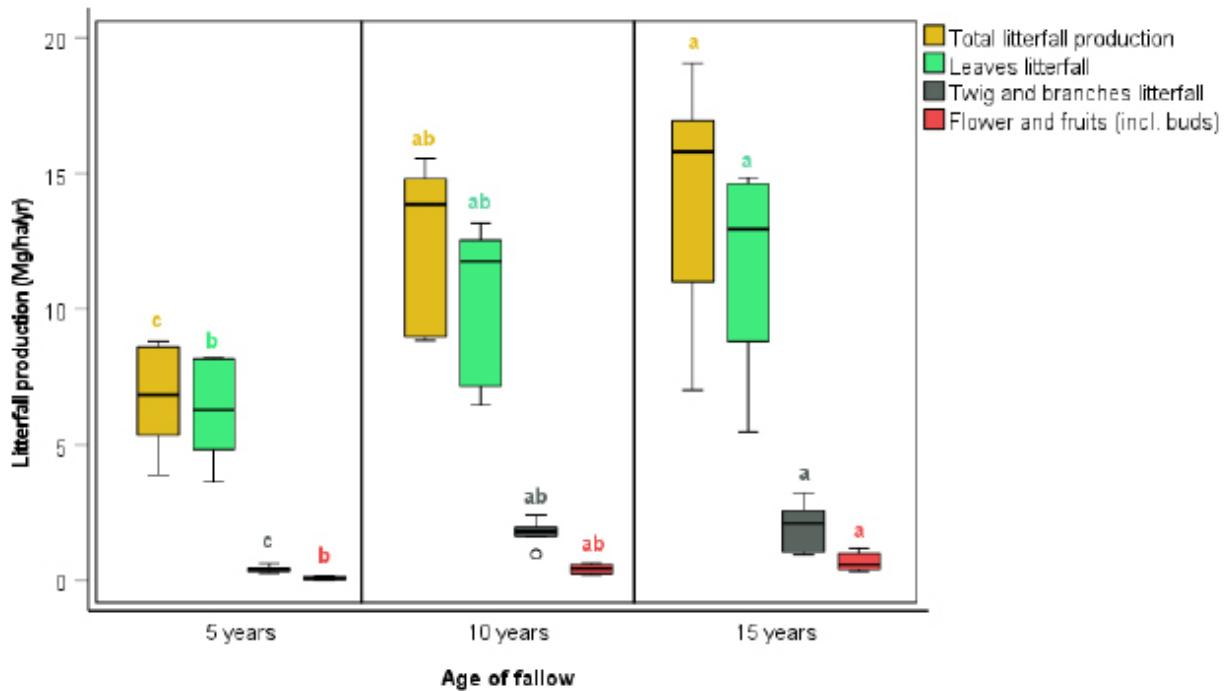
In the 5-year fallow land, the diversity index of the seedling phase is higher than that of the sapling, pole, and tree phases. The trend also occurred in the 10-year fallow period, where the highest diversity index was observed in the seedling phase compared to other phases. In contrast to the 5- and 10-year fallows, we found that the 15-year fallow had the highest diversity in the sapling phase compared to the seedling, pole, and tree phases (**Fig. 5**). Overall, the lowest diversity index was observed for the tree phase in the 5-year fallow, and the highest diversity was observed for the sapling phase in the 15-year fallow.

The Species Dominance Ratio (SDR) values of dominant species decreased with fallow land age (**Tab. 1**), corresponding to an increase in the diversity index (**Fig. 5**). This pattern is consistent with findings in Miombo, Mozambique, where increasing plant

species diversity over time was accompanied by a decline in species dominance (Montfort et al., 2021). The high density of certain pioneer species, such as *P. aduncum* and *Macaranga* spp., contributed to their dominance on 5-year fallow land. In general, species diversity increased with fallow land age, although seedling diversity remained relatively consistent across fallow ages, suggesting good seed reserve potential and viability in the early post-agricultural period. This finding is supported by studies indicating that seed viability and mortality are key indicators of forest regeneration (Wills et al., 2021; Vickers et al., 2023). The proximity of fallow lands to natural forests may contribute to the robust initial recruitment of species during the succession process.

#### Litterfall production dynamics

Results showed that total litterfall production between 5-year fallow and 10-year fallow was significantly different ( $F_{2,15}=8.74$ ;  $p < 0.018$ ), as well as total litterfall production between 5-year fallow and 15-year fallow was significantly different ( $F_{2,15}=8.74$ ;  $p < 0.003$ ). Meanwhile, fallow land with 10 years and 15 years showed no significant difference ( $F_{2,15}=8.74$ ;  $p > 0.678$ ). In general, total litterfall production increased in line with the length of fallow time (**Fig. 6**). The similarity in litterfall production between 10-year and 15-year fallow lands can be attributed to the comparable number



**Fig. 6.** Total litter production (Mg/ha/yr) and the proportional composition of litter types (leaves; stems and twigs; flowers and fruits) in lowland fallows of Manokwari, West Papua. Different letters above the bars indicate statistically significant differences based on Tukey’s HSD test ( $p < 0.05$ ). Note that comparisons are made within groups represented by the same box-plot colors

of trees (dbh±10 cm) in both areas. According to Susanto et al. (2021), 10-year fallow lands had 233 trees per hectare, while 15-year fallow lands had 253 trees per hectare, in contrast to only 42 trees per hectare in 5-year fallow lands. This is supported by studies showing a positive correlation between tree density and litterfall production in wet tropical forests (Nakagawa et al., 2019; Machado et al., 2021).

The 5-year, 10-year, and 15-year fallows produced total litterfall of  $6.72 \pm 1.89$ ,  $12.66 \pm 3.02$ , and  $14.28 \pm 4.46$  tons/ha/year, respectively. Although litterfall production increased with fallow age, the difference between 10- and 15-year fallows was not statistically significant ( $p > 0.05$ ) (Fig. 6). This finding suggests that similar fallow durations do not necessarily result in significant differences in litterfall production. Notably, early successional stages in young fallows (5-year) produced relatively little litter biomass compared to older fallows (10- and 15-year), which is consistent with the distinct vegetation composition observed in the 5-year fallow. The dominance of a few tree species in the 5-year fallow (SDR=100%) contrasts with the more diverse tree species composition in the 10- and 15-year fallows, where the three dominant species accounted for 59.07% and 47.40% of the SDR, respectively. Previous studies have reported positive correlations between tree density, canopy cover, and

plant diversity with litterfall production (Araújo et al., 2019; Machado et al., 2021). The similarity in SDR values between the 10- and 15-year fallows (Tab. 1) may contribute to the non-significant difference in litterfall production between these two fallow ages.

Leaves dominated more than 80% of litterfall production compared to stems and twigs as well as flowers and fruits (including buds), and leaf litterfall production in the 5-year fallow reached more than 90% (Fig. 6). Total leaf litterfall production was significantly different between 5- and 15-year fallows ( $F_{2,15} = 5.62$ ;  $p < 0.016$ ), but 5- and 10-year fallows and 10- and 15-year fallows were not significantly different ( $F_{2,15} = 5.62$ ;  $p > 0.059$  and  $p > 0.784$ , respectively).

This finding shows that the total litterfall production of branches and twigs has the same trend as the total litterfall production, i.e., between fallow land 5 years and 10 years, as well as between fallow land 5 years and 15 years, respectively significantly different ( $F_{2,15} = 11.97$ ;  $p < 0.04$  and  $p < 0.01$ ) (see Fig. 6). Meanwhile, fallow land with 10 years and 15 years showed no significant difference ( $F_{2,15} = 11.97$ ;  $p > 0.781$ ). The total litterfall production in the form of flowers and fruits (including buds) had the same trend as leaf litterfall production, where there was a significant difference between fallow land 5 and 15 years ( $F_{2,15} = 9.93$ ;  $p < 0.01$ ), but fallow land 5 years

with 10 years and fallow land 10 years with 15 years, respectively, did not differ significantly ( $F_{2,15}=9.93$ ;  $p>0.054$  and  $p>0.179$ ).

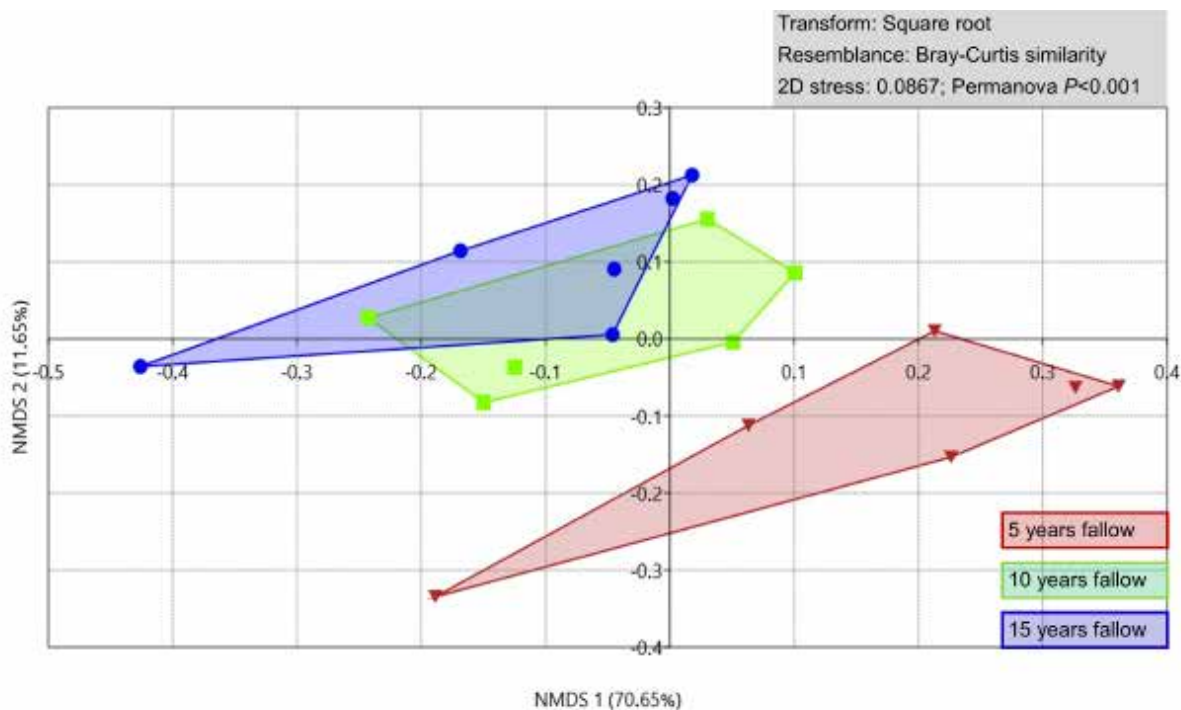
As fallow age increases, the composition of litterfall production changes, with a decrease in leaf litterfall proportion and an increase in stem, twig, and reproductive organ litterfall (Fig. 6). This trend is consistent with studies in secondary forests, where litterfall production from reproductive organs increases with succession time (da Silva et al., 2018). The high production of reproductive organ litterfall in 15-year fallows may accelerate litter decomposition and nutrient return to the soil, given the faster decomposition rate of flowers and fruits compared to leaves litterfall (de Alencar et al., 2024). Leaves litter dominates litterfall production, accounting for over 80% in 10- and 15-year fallows and over 90% in 5-year fallows. This pattern is consistent with other studies in tropical forests, where leaf litter contributes significantly to total litterfall production, although the proportion can vary between ecosystems and study durations (Nakagawa et al., 2019; Zhu et al., 2019; Liu et al., 2024).

**Environmental parameters and NMDS analyses**

Box-plots show that the 5-year fallow has greater variation in air and soil temperature than the 10- and

15-year fallows (Fig. 3). Correspondingly, variations in humidity were also higher in the 5-year fallow compared to the 10- and 15-year fallows. Overall, air and soil temperatures decreased with the age of the fallow. Meanwhile, air humidity increased with the age of the fallow. We hypothesize that there is an interaction between temperature and humidity, both in the air and in the soil, resulting in changes in vegetation structure and composition across age fallow lands. Logically, the more complex the vegetation structure, the more complex the distribution of stem sizes (Fig. 4), the higher the diversity index (Fig. 5), and most importantly, the decrease in SDR of dominant species (Tab. 1). In 5-year fallow lands, the normal curve formed is only accumulated at certain diameters, and the combined SDR value of pole and tree stages reaches more than 80%, indicating that there are dominant species in certain plots, while in other plots, plants with dbh  $\geq 10$  cm may not be found. Therefore, intensive sunlight exposure significantly affects the microclimate in 5-year fallow lands due to the low plant diversity and sparse canopy cover. Similar findings were reported by Atkins et al. (2023), who noted that changes in tree vegetation structure and composition can alter the microclimate of an area, particularly in terms of temperature and soil and air humidity.

Our NMDS plots (Fig. 7) were constructed using



**Fig. 7.** NMDS plot separating the three fallow ages based on the attributes of vegetation, litter and environmental factors. A total of 6 data symbols for each fallow age (Inverse triangle, square and dot) show temporal pseudoreplication. All computed data have been significantly different based on Permanova  $p<0.001$

10 data attributes, including litterfall production, air temperature, soil temperature, air humidity, soil humidity, soil pH, seedling and sapling diversity indices, mature tree diversity (poles and trees), stem diameter distribution, and litter decomposition data previously published by Susanto et al. (2021). Our NMDS analysis explained 82.4% of the data variability, with NMDS 1 and NMDS 2 accounting for 70.65% and 11.65% of the variation, respectively. Based on the Bray-Curtis similarity analysis, the 5-year fallows tended to be distinct from the 10- and 15-year fallows, whereas the latter two groups were more similar and slightly overlapping (Fig. 7). The 2D stress value of 0.0867 indicated that the NMDS model provided a good representation of the data.

The spatiotemporal non-metric multidimensional scaling (NMDS) analysis revealed distinct differences between 5-year fallows and 10- and 15-year fallows (Fig. 7). The 5-year fallows were characterized by the lowest litterfall production, basal area, and tree density (Susanto et al., 2021), as well as unique environmental characteristics (Fig. 3). The differences in stem diameter distribution (Fig. 4), diversity index (Fig. 5), and environmental factors (Fig. 3) among the three fallow ages likely contributed to the NMDS model. During succession, changes in vegetation structure can alter the microclimate, affecting abiotic factors such as temperature, humidity, and sunlight intensity (Gavito et al., 2021), which in turn influence nutrient return through litterfall production. Our study demonstrates that longer fallow ages are associated with increased complexity in vegetation structure and composition, higher species diversity, and greater litterfall production, all of which are important indicators of soil fertility (Feng et al., 2019; Tresch et al., 2019).

From a practical perspective, 5-year fallow lands tend to have a hotter and drier microclimate compared to 10-year and 15-year fallow lands, which are cooler and more humid. This trend can be linked to the decomposition of organic matter, where 10-year and 15-year fallow lands have a faster litter decomposition rate compared to 5-year fallow lands (Susanto et al., 2021). This suggests that increased humidity and decreased temperature may enhance the activity of decomposer communities in the soil (Krashevskaya et al., 2022), leading to faster decomposition. Another possibility is that the higher litterfall production in 10- and 15-year fallows compared to 5-year fallows may lead to increased aboveground litter accumulation, which could intercept direct sunlight, reduce soil temperature, and increase soil moisture, thereby influencing the NMDS model we developed.

## Conclusion

The vegetation structure and composition differed significantly between the three fallow ages. Notably, *Piper aduncum* serves as an early indicator of succession in Papua's lowlands, while *Macaranga* spp. and *Kleinhovia hospita* can indicate fallow age up to 10 years in sandy soils, and *Aglaia spectabilis* can indicate 15-year-old fallows. The average stem diameter distribution was below 30 cm across all fallow ages. Total litterfall production varied significantly, with 10- and 15-year fallows producing 88-112% more litterfall than 5-year fallows. The proportion of leaf litter decreased with increasing fallow age, although leaf litter remained a dominant component of total litterfall production. These findings suggest that nutrient input from leaves litterfall is substantial during early succession. Our study demonstrates that succession in fallow lands can be characterized based on vegetation structure, litterfall production, and environmental factors using the NMDS model. We recommend incorporating these data attributes into future studies to gain a better understanding of ecosystem dynamics in fallow lands.

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