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Article Secondary Succession after Slash-and-Burn Cultivation in Papuan Lowland Forest, Indonesia

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Abstract: Papuan forests have been subjected to shifting cultivation for centuries by indigenous people affecting the ecological processes therein; during secondary succession, fallow forests recover naturally. However, the information on ecological succession after swidden practices remains poorly understood in Papuan lowland forests. This study aimed to examine the plant species richness and density of different plant lifeforms in fallows of increasing time after slash-and-burn cultivation along with basic edaphic factors. We performed data collection in the northern part of the lowland evergreen tropical forest near Manokwari, West Papua, Indonesia. The sampling consisted of 26 plots distributed in the primary forest (n = 6) and in secondary/fallow forests 2-, 4-, 7-, and 9-years after cultivation (n = 5 for each age class). The plant community in primary forest clearly differed from the secondary forests. The plant species richness was about twice as high in primary compared to secondary forests. The density of trees and shrubs increased during succession whereas that of lianas declined. The soil fertility declined in secondary forests, although soil organic matter was greatest two years after swidden and then decreased gradually over time. This research underlined that indigenous swidden practices alter ecological conditions and that secondary forests will take a long time to fully recover to resemble primary forest. Hence, the monitoring of vegetation during the process is necessary to inform conservation programs.

Keywords: lifeforms; New Guinea; species richness; swidden; tropical secondary forest

1. Introduction

Indonesian New Guinea is part of the largest tropical island containing some of the world's greatest floristic richness [1]. Forests of New Guinea have contributed to people's livelihoods and provided ecosystem services for many centuries [2–5]. However, the tropical forest area is being reduced over time as a result of anthropogenic factors such as agriculture, road expansion, and land-use conversion [6]. Of the human activities in tropical forests of this island, traditional agriculture has been conducted by indigenous people, and has been part of their culture, for generations [3,7,8]. This agricultural system is generally subsistence in nature and is mostly done by slashing-and-burning vegetation and subsequently cultivating the area [9–11]. The processes involved in this practice include site selection, cutting, clearing, burning, planting, and harvesting, and the fields are generally only cultivated for one or a few years. The ex-cultivation areas are left to recuperate naturally through secondary succession, and, in many cases, local people return to these fallow forests to implement the next farming cycle after a given fallow period. They apply traditional indicators such as the density of vegetation and the presence of certain



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). species in the former areas of cultivation in order to determine when the area is ready to be recut [12]. Many researchers from around the world have shown the effect of shifting cultivation on species richness and diversity and the projection that recovery processes to reach mature forests would take decades or even centuries depending upon the disturbance intensity and other ecological conditions [13–16]. During slash-and-burn cultivation (a.k.a. swidden), the burning of vegetation adds nutrients to the soil via ash deposition which is used by the crops. Soil fertility then recovers during the fallow phase [17]. Some authors consider that shifting cultivation in New Guinea is less perturbing to soils due to the low intensity cultivation [18] when compared to other localities but there is little data to test this assertion.

Ecological studies related to the impact of slash-and-burn cultivation in Papua are infrequent although there are some studies on secondary forests regrowing after cultivation [19–21]. Thereby, we collected data in the western part of Papua to contribute to our understanding of the ecological changes post-slash-and-burn cultivation. Here, we hypothesize that plant species richness and density in fallow forests would differ from primary forests but would increase over time since cultivation due to the greater amount of time for the accumulation of species. Moreover, we hypothesize that soil properties would be also altered during the successional process with a general increase in soil fertility during secondary succession as nutrients are returned to the soil from regrowing vegetation.

2. Materials and Methods

2.1. Study Area

The research was conducted in the northern part of lowland evergreen tropical forest in Manokwari, West Papua province, Indonesia (0°44′ S and 133°54′ E; Figure 1). While areas away from the coast are largely primary forest with species composition typical of the region [2,22,23], some areas relatively close to coastal villages are used for traditional farming, mainly shifting cultivation, by local communities. Most cultivated areas are found in flat locations with an elevation below 50 m a.s.l. (Figure 2). The annual precipitation is 2640 mm with 235 rainy days per year and at least 100 mm precipitation every month [24]. The soil types are characterized as Entisols, Inceptisols, and Ultisols. The soils in shifting cultivation areas have not had fertilizers applied, so the nutrient inputs are largely derived from decomposition of vegetation debris.



Figure 1. Location of the research in lowland evergreen primary forest (PF) and two- to nine-years-old post-swidden fallow forests in coastal areas of north Manokwari, West Papua, Indonesia.



Figure 2. Typical field used for swidden cultivation in coastal areas of north Manokwari, West Papua, Indonesia, with a four-year-old fallow forest in the background (photo credit: Dony A. Djitmau).

2.2. Sampling and Data Collection

The secondary forest ages were identified by interviewing the local people who were directly engaged in the swidden practices and by checking satellite images via Google Earth Pro to analyze land cover changes by jumping backward in time through the Historical Imagery menu. All secondary forests were in areas that had only been cultivated once (according to local informants). These were compared with forest that had been relatively undisturbed for decades due to its inaccessibility with no reports of ever being under cultivation as it was in an inappropriate location; we hence call this primary forest. In all forests, we recorded the number of individuals and lifeforms of a range of plant taxa using a series of nested plots. The data on large trees (≥ 20 cm dbh) were collected from 20×30 m plots (plot A), Inside the plot A's, there were subplots of 10×10 m (plot B) for tree poles (\geq 10 cm dbh), of 5 × 5 m for tree saplings (<10 cm dbh, \geq 1.5 m tall), lianas, ferns, herbs, shrubs, and palms/screw palms (plot C), and of 2×2 m for tree seedlings (<1.5 m tall) (plot D) [20]. We placed the plots randomly in each forest type with a minimum distance among plots of at least 25 m. In the primary forest, n = 6 plots; and in fallow forests cultivated 2, 4, 7, and 9 years before sampling, n = 5 for each fallow age. The vouchers for identification were sent to Herbarium Papuaense of Balai Penelitian dan Pengembangan Lingkungan Hidup dan Kehutanan (BP2LHK) Manokwari and Herbarium Manokwariense (MAN) Pusat Penelitian Keanekaragaman Hayati Universitas Papua (PPKH-UNIPA), Manokwari. Specimens were identified to species in 63% of taxa; those that could not be confidently identified as a named species were assigned as having an affinity to another species (3.9%) or as a morphospecies within a genus (26%) or family (2.6%) with 4.6% of taxa only identified to lifeform. Conservation status of each species was based on The International Union for Conservation of Nature's Red List of Threatened Species (https://www.iucnredlist.org/ accessed on 5 October 2021). A soil sample was collected from each corner and the middle of each of the plot A's and those were mixed to create a composite sample. The soil analyses were conducted in the laboratory of Balai Pengkajian Teknologi Pertanian Yogyakarta, Indonesia where soil organic matter (SOM) was determined by loss-on-ignition and nitrogen (N) by the Kjeldahl method.

2.3. Data Analysis

We implemented a species abundance curve or Whittaker plot by plotting the abundance of each species (log-transformed) against its rank following a descending order. The species accumulation was analyzed using sample rarefaction (Mao's tau) [25]. These analyses were conducted using PAST (PAleontological STatistics) version 4.03 [26]. The dendrogram analysis was executed to compare the vegetation communities among contrasting forest ages using the 'vegan' package in R version 3.5.3 [27] in which all lifeforms were grouped together and plant density in smaller plots multiplied appropriately to give the equivalent area sampled for each lifeform (i.e., Plot B's × 6, Plot C's × 24, and Plot D's × 150). To determine differences between primary forest and fallow forests, analyses of variance (ANOVA) with subsequent Tukey's tests were performed with *p* < 0.05 as the threshold using SPSS 16.0.

3. Results

Species Richness of Vegetation

We grouped the vegetation lifeforms (lianas, ferns, herbs, shrubs, palms/screw palms, tree seedlings, tree saplings, tree poles, and large trees) for the following analyses. In total, we recorded 152 taxa (Table A1) across all the plots that had an area of 1.84 ha. We analyzed species richness using rank-abundance (Figure 3a) and species accumulation (Figure 3b) curves which showed the species number per 0.30 ha (0.36 ha for primary forest) as 100 for the primary forest, 39 for two-year-old, 55 for four-year-old, 35 for seven-year-old, and 47 for nine-year-old fallow forests. Sixty-one species were only found in the primary forest (0.36 ha), 48 were only found in the fallow forests (1.5 ha), and 43 were shared between them. The results of vegetation classification revealed that there were two clear groups of plant communities based on the cluster dendrogram, i.e., the primary forest and the fallow forests resulting from swidden activity (Figure 4).



Figure 3. (a) The rank abundance curve or Whittaker plot implemented by plotting the logtransformed species abundance against species rank for all vegetation lifeforms. (b) Species accumulation curve for all vegetation lifeforms using sample rarefaction (Mao's tau) in fallow forests between two- and nine-years-old and primary forest (PF) in coastal areas of north Manokwari, West Papua, Indonesia.

The density of individuals of each lifeform was compared among the forest types. Tree seedlings were the most abundant lifeform; their density was lowest after swidden agriculture, but then increased over time with increasing age of the fallow forest. The stem density of shrubs, seedlings, saplings, poles, and large trees in the primary forest was significantly greater than in fallow forests while lianas were more abundant in 2-year-old fallow forest than in most other forest ages. The density of herbs and palms/screw palms did not change during succession and that of ferns peaked in older fallows (Figure 5).



Figure 4. Grouping of plots in the primary forest (PF) and fallow forests between two- and nine-yearsold in coastal areas of north Manokwari, West Papua, Indonesia. All vegetation lifeforms are grouped together and plant density in smaller plots is multiplied accordingly to give the equivalent area sampled for each lifeform. The number before the dash is the age of the fallow (2 for two-year-old, 4 for four-year-old, 7 for seven-year-old, and 9 for nine-year-old) while the number after the dash is a label for each plot.



abc

а

ab

Large trees

Figure 5. The mean density of vegetation lifeforms in fallow forests between two- and nine-years-old and primary forest (PF) in coastal areas of north Manokwari, West Papua, Indonesia. Plant density in smaller plots is multiplied accordingly to give the equivalent area sampled for each lifeform. For clarity, error bars are omitted. Different lowercase letters in the table show the differences according to ANOVAs and Tukey's tests with p < 0.05.

с

d

<0.001

Two species were found with Near Threatened (NT) Red List status (*Cryptocarya massoy* (Oken) Kosterm. and *Intsia bijuga* (Colebr.) Kuntze) and a further three species were classified as Vulnerable (VU) (*Aglaia brassii* Merr. & L.M.Perry, *Anisoptera thurifera* (Blanco) Blume and *Neonauclea acuminata* Ridsdale). Seven species were found that were endemic to New Guinea (according to Cámara-Leret et al. [1]) along with a further three that were found in New Guinea and the Solomon Islands only (according to POWO [28]).

This study also compared the edaphic conditions among forest ages by means of soil organic matter (SOM) and nitrogen (N) as predictor of soil 'fertility'. The SOM was greatest in 2-year-old fallow forest and primary forest while the lowest SOM was found in the 9-year-old fallow forest (Table 1). The total N showed a similar pattern and was greater in the primary forest than in fallow forests while the 9-year-old fallow forest had the lowest total N among the forest types (Table 1).

Table 1. Mean (\pm standard error) soil organic matter (SOM) and total nitrogen (N) in fallow forests between two- and nine-years-old, and primary forest (PF) in coastal areas of north Manokwari, West Papua, Indonesia. Different lowercase letters show the differences according to Tukey's tests with p < 0.05.

Variable			Forest Type		
	2-Year-Old	4-Year-Old	7-Year-Old	9-Year-Old	PF
SOM (%)	$\begin{array}{c} 18.40 \pm 4.82 \\ \text{b} \end{array}$	8.05 ± 3.15 ab	9.38 ± 2.77 ab	$\begin{array}{c} 3.35\pm0.36\\ a\end{array}$	$\begin{array}{c} 10.00 \pm 0.81 \\ b \end{array}$
Total N (%)	$\begin{array}{c} 0.47 \pm 0.05 \\ \text{ab} \end{array}$	$\begin{array}{c} 0.41 \pm 0.07 \\ ab \end{array}$	$\begin{array}{c} 0.54\pm 0.05 \\ b \end{array}$	$\begin{array}{c} 0.32\pm0.03\\ a\end{array}$	$\begin{array}{c} 0.84 \pm 0.02 \\ c \end{array}$

4. Discussion

The swidden practice was conducted by local people in Papua where they allow forest recovery after cultivation during secondary succession as investigated in other studies in New Guinea [7,18,29,30] as well as numerous other tropical regions around the world [10,16,31–39]. In our study, the dendrogram revealed two main groups containing the primary forest plots in the first group and the fallow forest plots in the other group indicating the similarity of species composition among the fallows. We did not see a particularly clear pattern of change in the forests with age, perhaps due to the generally young age of the fallows studied. The forest fallows were more dynamic as the re-colonization of certain pioneer species was rapid due to the more open canopy increasing light availability. Increasing light and temperature will also increase the rate of seed germination in this area [38]. In addition, the fallow forests are very near, or surrounded by, either primary forest or older/denser fallow forests allowing colonization of individuals coming from both of these forest types [39,40]. Some ruderal species could be permanently present in the successional stages up to the climax phase, but others will be suppressed by the growth of other vegetation during succession [41–45]. Those species in this research such as *Piper* sp., Macaranga species, Premna corymbosa, Rottler and Monstera sp. tended to occupy fallow forests as early successional species.

The change in the vertical structure of the forest also leads to changes in the relative importance of certain lifeforms. For example, lianas take advantage of the reduction in canopy layers, so they grow aggressively by overlaying other vegetation. For this reason, lianas were more abundant in the fallow forest, and particularly the youngest, most open forests, where this lifeform has the ability to grow not only in vertical but also horizontal directions. The increase in stem density during succession was largely comprised by trees, and larger trees at later stages of succession. The successional process in fallow forests is highly dynamic compared to primary forests in which the species composition and vertical structure are more static upon reaching the climax stage of succession. However, the time for fallow forests to reach a stable state resembling primary forest will take decades, if not longer [13,37,46]. It is also worth considering that there are alternative pathways in succession due to the influence of factors such as previous agriculture practices, the species

present in surrounding forests, and edaphic conditions [47]. It is also important to study a large number of primary forest stands due to high heterogeneity in structure and diversity influenced, at least partly, by the intensity and frequency of disturbances.

The swidden practice changed the vertical structure of vegetation particularly the understory, but in some settings, large trees were left to grow ('remnant trees') because the cutting was conducted using traditional tools and usually by a single family that were not able to remove such large stems. Therefore, in some of the fallow forests, larger remnant trees were recorded, as found in other locations globally [13,48]. These remnant trees will contribute to species richness and carbon stocks in the fallows. The larger trees within fallow forest also play a significant role as putative parent trees to supply seeds which are important in the distribution of seeds into fallow areas [49]. The variety of crops could impact the size and type of area cleared as revealed in other studies [33,36] and, in this study, most local people planted agricultural products such as cassava (Manihot esculenta Crantz) and sweet potato (*Ipomoea batatas* (L.) Lam.) which do not require the forest to be totally cleared. Certain species growing in the fallow forests were from cultivation activity such as turmeric (Curcuma zanthorrhiza Roxb.), bananas (Musa sp.), and pineapple (Ananas comosus (L.) Merr.) although these comprised only a small contribution as local people only used certain cultivated plants. Additionally, fruit trees will have been planted in the fallows such as cempedak (Artocarpus integer (Thunb.) Merr.), durian (Durio zibethinus L.), mango (Mangifera indica L.), and rambutan (Nephelium lappaceum L.). The fallows additionally contained introduced and potentially invasive species such as Ageratum conyzoides (L.) L. and Imperata cylindrica (L.) Raeusch. as well as Piper aduncum L. that was also found in primary forest from which it has rarely been reported before [42,50].

In addition to vegetation changes, soil properties were also impacted by the agricultural practices. The soil nutrients two years after swidden activity were generally similar to primary forest but differed from the rest of the fallow forests. This is likely due to the minimal impact of agricultural practices that conserved soil organic matter and the low-intensity fires (due to moist conditions) prior to agriculture with some cultivators not using fire [21]. The high C:N ratio of the soils in the youngest fallows (38 vs. 16 as mean of all other ages) suggests this was likely due to input of incompletely burned decomposing wood/logs into the soils. The decline in SOM in the 9-year-old fallows also supports this as this wood will have more fully decomposed but the forest has not grown back sufficiently for large inputs of carbon via leaf litter production. Soil nutrient loss could also occur from surface runoff because the fallow forests have less dense canopies, and the forest floor vegetation was not as developed. As reported by many studies, the vegetation cover has an inverse relationship with surface runoff whereby nutrients would be removed from the fallow forests over time [51].

Species richness declined in fallows compared to primary forest in line with other studies conducted in New Guinea and more broadly. We found that there were about twice as many species (all taxa) in primary forest as compared to secondary forests. This is similar to other studies in New Guinea [30] that showed there were two to three times more tree species in primary forest than younger (<9-year-old) secondary forest. The difference in diversity between the two forest types with respect to tree size was greater for the larger trees. When we re-examined our data for trees ≥ 10 cm dbh only, the pattern was more marked than for all taxa together with about four times as many tree species in primary forests (data not shown). Supporting this, another study [21] showed greater richness of trees in primary forest sites compared to formerly cultivated sites but not of non-tree plant lifeforms. It is also important to bear in mind that species richness recovers more rapidly than species composition [35] due to the slow growth of many late-successional primary forest specialist trees.

Although species richness in fallow forests is lower than primary forests, they play a crucial role in local livelihoods. Local people applied the traditional techniques and tools, and the main purpose of their cultivation was to supply food for themselves. This traditional swidden practice has been performed for centuries around the world including in New Guinea [9,52]. Local people also implemented their traditional knowledge that supports the sustainability of the swidden practice, for example, swiddens are not placed close to rivers. They only clear dense forest for cultivation, but the density of vegetation especially larger trees and presence of particular species are traditional indicators of an area ready for re-cultivation. Furthermore, there are certain areas of primary forests that were purposefully left to grow naturally without disturbance because local people hold the traditional belief that if these primary forests are disturbed, some disaster will happen in this area, therefore, they have traditional zones reserved especially for livelihood activities including their swidden practice.

Among Red-Listed plant species, four were only found in primary forest and two were found in both primary forest and fallows. Five out of the seven species endemic to New Guinea (and 7 out of the 10 endemic to New Guinea and the Solomon Islands) were only found in the primary forest. Therefore, although primary forests are more valuable in terms of species richness and contain rarer species, fallow forests have some role to play in conservation as some Red-Listed species and endemic species are still found within them. We identified about two-thirds of the taxa found to species which is comparable to other tropical studies [13,53]. Nevertheless, about 5% could not be identified even to species. Many New Guinea tree genera are in need of taxonomic revision [1,54] with herbarium collections that are critical to supporting this work being fewer in Indonesian Papua compared to Papua New Guinea [1]. Future work should focus on additional collecting effort to support such revisions as well as capacity-building for Indonesian taxonomists [1]. Overall, of the taxa we identified to species level, only 55% have been assessed for the IUCN Red List indicating that there is still considerable work to be done for such assessments as well.

We recognize that our sampling design is pseudo-replicated, thereby limiting the conclusions that can be drawn. Nevertheless, our study has value in presenting data from a very understudied tropical region that is coming under increasing pressure [1,6,55]. Furthermore, the inclusion of lifeforms that are less often included in traditional inventories of tropical forests (e.g., herbs, ferns) is of value. Generally, the fallows studied here are of a younger age (<10-years-old) and incorporation of mid- to late-age fallows across a broader landscape (avoiding pseudo-replication) and in larger plots would allow us to determine the trajectory of succession at later stages more effectively.

Government intervention is necessary to support the implementation of traditional knowledge in sustainable forest management [2,56] and the local government should legally concede the traditional zones designed by local people for livelihood activity and delineate customary forests [57]. Whilst the farming method in this area disturbs small areas of forest, these disturbed forests will recuperate over time, but at least they are still covered by vegetation and the land is not converted to other functions such as settlements. Moreover, it is crucial to carry out further anthropological research to document the swidden practice in the context of local traditions. It is also essential to monitor the vegetation in the disturbed forests to record the species diversity and recovery in permanent plots [58]. Both of these would clearly support conservation programs in tropical forests of New Guinea.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Plant species list in fallow forests between two- and nine-years-old and primary forest (PF) in coastal areas of north Manokwari, West Papua, Indonesia. The presence of species is symbolized using $\sqrt{}$. The seven species in **bold text** are endemic to New Guinea according to Cámara-Leret et al. [1].

	Forest Type					
Species	2-Year-Old 4-Year-Old 7-Year-Old 9-Year-Old					
Actinodaphne nitida Teschner						
Ageratum conyzoides (L.) L.					·	
Aglaia spectabilis (Miq.)	·				/	
S.S.Jain and S.Bennet					\checkmark	
Aglaia brassii Merr. and		/			,	
L.M.Perry		\checkmark			\checkmark	
Alpinia galanga (Ĺ.) Willd.						
Alpinia sp.			·			
Alstonia scholaris (L.) R.Br.		\checkmark	\checkmark			
Ananas comosus (L.) Merr.	·			·	•	
Anisoptera thurifera			•		/	
(Blanco) Blume					\checkmark	
Antiaris toxicaria					,	
(J.F.Gmel.) Lesch.						
Archidendron pachycarpum					,	
(Warb.) Dewit					\checkmark	
Archidendron		/		,	,	
parviflorum Pulle		\checkmark		\checkmark	\checkmark	
Archidendron sp.						
Areca catechu Ĺ.		\checkmark			•	
Artocarpus altilis (Parkinson ex	/	•	/	·	,	
F.A.Zorn) Fosberg	\checkmark	\checkmark	\checkmark		\checkmark	
Artocarpus integer				/		
(Thunb.) Merr.				\checkmark		
<i>Baccaurea</i> sp.						
Bidens pilosa L.						
Blechnum patersonii				/		
(R.Br.) Mett.				\checkmark		
Bubbia sp.		\checkmark				
Buchanania arborescens					/	
(Blume) Blume					\checkmark	
Calophyllum inophyllum L.						
Campnosperma coriaceum (Jack)					. ,	
Hallier f.					\checkmark	
<i>Cananga odorata</i> (Lam.) Hook.f.		/	/	/	/	
and Thomson		\checkmark	\checkmark	\checkmark	\checkmark	
Canarium hirsutum Willd.						
Celtis latifolia (Blume) Planch.						
Ceodes umbellifera J.R.Forst.					. /	
and G.Forst.					\checkmark	
Cerbera floribunda K.Schum.						
Chionanthus aff.	/				•	
macrocarpus Blume	\checkmark					
Chionanthus sp.						
Chisocheton ceramicus					•	
(Miq.) C.DC.					\checkmark	
Cocos nucifera L.	\checkmark		\checkmark			
Coffea sp.	•		·			

 Table A1. Cont.

E modian	Forest Type					
Species	2-Year-Old 4-Year-Old 7-Year-Old 9-Year-Old				d PF	
Cryptocarya massoy					/	
(Oken) Kosterm.					\mathbf{v}	
Curcuma zanthorrhiza Roxb.				\checkmark		
Cynometra browneoides		./			./	
(Harms) Rados.		v			v	
Diospyros discolor Willd.						
Dracontomelon dao (Blanco)		./			./	
Merr. and Rolfe	v	v		V	v	
Durio zibethinus L.	,		,			
Dysoxylum mollissimum Blume	\checkmark	\checkmark	\checkmark			
Dysoxylum parasiticum					1	
(Osbeck) Kosterm.		v			v	
Elaeocarpus angustifolius Blume						
Endospermum moluccanum						
(Teijsm. and Binn.) Kurz		v		v	v	
Falcataria falcata (L.) Greuter						
and R.Rankin	/				v	
Ficus aff. annulata Blume	\checkmark				,	
Ficus benjamina L.						
Ficus drupacea Thunb.	/	/	/	/	\mathbf{v}	
Ficus macrothyrsa Corner Ficus racemifera Roxb.	\checkmark	\checkmark	\checkmark	\checkmark	,	
<i>Ficus racemigera</i> Roxb. <i>Ficus septica</i> Burm.f.		/	/	/	\mathbf{v}	
Ficus variegata Blume		$\mathbf{v}_{\mathbf{r}}$	$\mathbf{v}_{\mathbf{r}}$	$\mathbf{v}_{\mathbf{r}}$		
Ficus our regulu blume Ficus sp. 1	/	$\mathbf{v}_{\mathbf{r}}$	$\mathbf{v}_{\mathbf{r}}$	\mathbf{v}_{\prime}		
Ficus sp. 1 Ficus sp. 2	V	$\mathbf{v}_{\mathbf{r}}$	V	V	/	
Ficus sp. 2 Ficus sp. 3		V			V	
Ficus sp. 5		V			V	
Ficus sp. 4					V	
Garcinia sp. 5					V	
<i>Gmelina</i> sp.					V	
Gnetum gnemon L.		./			V	
Gonocaryum littorale		V	V	V	v	
(Blume) Sleumer						
Grass A		./				
Gymnacranthera farquhariana	V	V		V		
(Wall ex. Hook.f. and					./	
Thomson) Warb.	V				v	
Harpullia sp.					./	
Hibiscus tiliaceus L.					v	
Hibiscus sp.	v				1	
Homalium foetidum			v		v	
(Roxb.) Benth.						
Hopea sp.					./	
Horsfieldia irya (Gaertn.) Warb.		1		1	v v	
Hylodesmum repandum (Vahl)		v		v	v	
H.Ohashi and R.R.Mill		\checkmark		\checkmark		
Imperata cylindrica (L.)	,	,	,	,		
Raeusch.	\checkmark	\checkmark	\checkmark	\checkmark		
Intsia bijuga (Colebr.) Kuntze		1			1	
Koordersiodendron pinnatum		v	v	,	v	
(Blanco) Merr.		\checkmark	\checkmark	\checkmark		
Lauraceae sp.	1					
<i>Leea aculeata</i> Blume ex Spreng.	v		1		1	
Lepiniopsis ternatensis Valeton	1		v	1		
Leucaena leucocephala (Lam.)	v	,		v	v	
de Wit		\checkmark				

Table A1. Cont.

Emociat	Forest Type					
Species	2-Year-Old 4-Year-Old 7-Year-Old 9-Year-Old					
Liana A	\checkmark			\checkmark		
Liana B	·			v V		
Liana C				v		
Liana D	v			1		
Litsea ledermannii Teschner				v	1	
Litsea timoriana Span.		./		./	v v	
Litsea tuberculata		v		v	v	
(Blume) Boerl.						
Litsea sp.					. /	
Lunasia amara Blanco		. /			V	
Maasia glauca (Hassk.) Mols,		V			V	
Kessler and Rogstad						
	/	/	/	/		
<i>Macaranga</i> sp. 1	$\mathbf{v}_{\mathbf{r}}$		$\mathbf{v}_{\mathbf{r}}$			
Macaranga sp. 2	\checkmark	\checkmark	\checkmark	\checkmark		
Mallotus floribundus						
(Blume) Müll.Arg.				,	·	
Mangifera indica L.				\checkmark		
Maniltoa sp.						
Mastixiodendron pachyclados		1	1	1	1	
(K.Schum.) Melch.		v	v	v	v	
Medusanthera laxiflora					. /	
(Miers) R.A.Howard		V			V	
Melicope elleryana				/	,	
(F.Muell.) T.G.Hartley				V	V	
<i>Merremia</i> sp.				\checkmark		
Mimusops elengi L.						
Monoon polycarpum (Burck)						
B.Xue and R.M.K.Saunders					\checkmark	
<i>Monstera</i> sp.						
Mucuna novo-guineensis Scheff.	v	v	v	v	1/	
Musa sp.	v			./	v	
<i>Myristica fatua</i> Houtt.	v			v	1	
Myristica aff. gigantea King		./			v	
Myristica sp.		V			. /	
Neolamarckia cadamba					V	
(Roxb.) Bosser				\checkmark		
Neonauclea acuminata Ridsdale						
Neonauclea sp.			/	/		
Nephelium lappaceum L.	/	/	\checkmark			
Nephrolepis sp.	\checkmark	\checkmark	\checkmark	\checkmark		
Ochrosia sp.						
Octomeles sumatrana Miq.	\checkmark		\checkmark	\checkmark		
Orchidaceae sp.		\checkmark				
Ormosia calavensis Azaola						
<i>Ormosia</i> sp.						
Osmoxylon aff.	/	/				
globulare Philipson	\checkmark	\vee				
Palaquium amboinense Burck						
, Palaquium sp.		, V	\checkmark			
Pandanus tectorius Parkinson	/	·	÷	¥		
ex Du Roi	\checkmark					
Pimelodendron amboinicum		,				
Hassk.		\checkmark				
Piper aduncum L.	./	./	./	./	. /	
Piper sp.	v	v	v	v	v	
riper sp.	V					

	Forest Type					
Species	2-Year-Old	4-Year-Old	7-Year-Old	9-Year-Old	PF	
Pipturus argenteus					,	
(G.Forst.) Wedd.					\checkmark	
<i>Polyalthia</i> sp. 1						
<i>Polyalthia</i> sp. 2						
Pometia pinnata J.R.Forst.		/		/	,	
and G.Forst.		V		V	V	
Premna corymbosa Rottler	\checkmark	\checkmark	\checkmark	\checkmark		
Prunus arborea		. /			. /	
(Blume) Kalkman		V			V	
Pterygota horsfieldii				/	,	
(R.Br.) Kosterm.				V	V	
<i>Pterygota</i> sp.						
Rhus taitensis Guill.		\checkmark				
<i>Rhus</i> sp.						
Sapindaceae sp.						
Semecarpus papuanus					. /	
Lauterb.					V	
Spathiostemon javensis Blume		\checkmark	\checkmark			
Spondias dulcis Parkinson	\checkmark	\checkmark	\checkmark			
Stachytarpheta jamaicensis	./					
(L.) Vahl	V					
Sterculia aff. elongata Ridl.		\checkmark	\checkmark			
Sterculia macrophylla Vent.		\checkmark		\checkmark		
Sterculia parkinsonii F.Muell.						
Sterculia urceolata Sm.	\checkmark	\checkmark	\checkmark			
<i>Syzygium</i> sp.	\checkmark					
Tectaria aff. zollingeri	. /				. /	
(Kurz) Holttum	V				v	
Teijsmanniodendron bogoriense					./	
Koord.					V	
Thelypteridiaceae sp.		\checkmark	\checkmark	\checkmark		
<i>Timonius timon</i> (Spreng.) Merr.						
<i>Timonius</i> sp.						
Tree A	\checkmark					
Tree B	\checkmark	\checkmark	\checkmark			
<i>Uncaria</i> sp. 1						
<i>Uncaria</i> sp. 2						
Vigna trilobata L. (Verdc.)				\checkmark		
Vitex sp.		\checkmark	\checkmark	\checkmark		
Ziziphus sp.						

Table A1. Cont.

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