



Effect of selective logging on canopy and stand structure and tree species composition in a lowland dipterocarp forest in peninsular Malaysia

Toshinori Okuda^{a,*}, Mariko Suzuki^a, Naoki Adachi^b, Eng Seng Quah^c,
Nor Azman Hussein^c, N. Manokaran^c

^aNational Institute for Environmental Studies, 16-2 Onogawa, Tsukuba 305-0053, Japan

^bJapan Science and Technology Corporation, Kawaguchi 332-0012, Japan

^cForest Research Institute Malaysia, Kepong 52109, Malaysia

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Abstract

The authors compared tropical rain forest canopy structure and tree species composition in two forests southeast of Kuala Lumpur, Malaysia: a primary forest and a regenerating forest that was selectively logged in 1958. For each of the forests, the study plots were set out and all trees of ≥ 1 cm in DBH (diameter at breast height) were mapped and measured. Canopy heights were measured in the two study plots based upon aerial triangulation using aerial photographs taken over the forests in 1997. Using this data, digital elevation models of the canopy were then constructed. The mean canopy height was greater in the primary forest (27.4 m versus 24.8 m), as was the variance in height and the number of emergent canopy trees >40 m height. The mean canopy surface area in the primary forest was nearly 1.5 times the value in the regenerating forest, and the mean crown size of canopy layer trees in the primary forest was more than twice that in the regenerating forest. The species diversity index (Fisher's α) differed for the two forests, indicating that tree species diversity had been affected by the logging. Both forests had the same five families with the greatest stem density (stems ha^{-1}), but the 50 most abundant species, in terms of both stem density and basal area, differed greatly between the two forests. Stem densities and basal areas were similar, but the number of stems per hectare and the basal areas of medium-sized trees (10–30 cm in DBH) were distinctly higher in the regenerating forest. These results suggest that average basal area and stem density in the regenerating forest that had been selectively logged 41 years earlier had recovered to levels similar to those in the primary forest; however, the regenerating forest had a more monotonic canopy structure comprised of medium-sized trees growing at high density. These findings also imply that structural development takes a long time to manifest in a regenerating forest as a result of the time taken for the development of emergent and canopy trees and the formation of gaps; structural development might also be delayed by the high density of medium-sized trees in the canopy layer.

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1. Introduction

Many investigators have studied the structural and compositional aspects of tropical forests (e.g.,

* Corresponding author. Tel.: +81-298-50-2426;

fax: +81-298-50-2483.

E-mail address: okuda@nies.go.jp (T. Okuda).

Richards, 1952; Brunig, 1970; Holdridge et al., 1971; Walter, 1971; Whitmore, 1984), but few studies have focused on the forest's dynamic features, which may change in response to logging, burning, clearing, and other human impacts. Selective logging is the most popular and most widely employed approach for commercial timber production in southeast Asia, and its impacts on forest structure, composition, and regeneration dynamics are large; this has concerned forest managers and forest ecologists greatly. Although district forest department offices undertake periodic censuses after logging operations to investigate regeneration of the forest and determine the proper logging intervals (Wyatt-Smith, 1963; Thang, 1987), most censuses focus on commercial timber species; as a result, they neglect changes in compositional and structural aspects of other species. To provide the fundamental knowledge required to undertake sustainable management of the forests, both silviculturally and ecologically, more precise studies are needed to clarify the effects of logging on stand structure, floristic composition, and species diversity, including those of non-timber species (Shugart and West, 1981; Favrichon, 1998). In addition, since canopy structure determines and is determined by the species present in a forest, the dynamic features of the forest after logging provide a good indicator for predicting the ecological soundness of logging and the sustainability of the operation (Clark et al., 1996).

In peninsular Malaysia, a selective logging regime named the "Malaysian Uniform System" (MUS) was commonly used from the 1950s to the 1970s. A part of the Pasoh Forest Reserve was originally logged under this system from 1954 to 1959. A tree census conducted in 1989 in the reserve and its vicinity (Manokaran, 1996) indicated that, under the MUS, there was considerable regeneration of commercial timber species (e.g., Dipterocarpaceae) in the regenerating secondary forest even 34 years after logging. However, the stand structure and the species composition of major tree families (≥ 10 cm in DBH—diameter at breast height) in the logged forest differed distinctly from those observed in the primary forest. Such differences have also been reported in the African, South American, and Central American tropical regions (Crow, 1980; Chapman and Chapman, 1997; Webb, 1997; Whitman et al., 1997; Panfil and Gullison, 1998; Finegan and Camacho, 1999).

However, few studies have examined the changes in canopy surface structure after logging. Before beginning the present study, we acquired satellite (LANDSAT) images of the study area taken in 1988, and found that the surface texture of the canopy in regenerating forests logged in the 1950s differed dramatically from that of primary forest (Fig. 1). We suspected that the observed differences arose primarily from changes in stand structure, stem density, individual crown size of canopy trees, species composition, and other functional aspects of the forest as a result of the logging. For this reason, it was desirable to study differences in the floristics, stand structure, and canopy structure of the unlogged and logged forests. With the help of aerial photographs and tree census data, we analyzed how these functional aspects of the forest had been altered by the selective logging. We hypothesized that the impacts of logging on the forest remained visible in the form of delayed structural development in the regenerating forest.

2. Methods and study area

2.1. Study area and logging history

The site where we conducted the present study was an old-growth lowland dipterocarp forest within the Pasoh Forest Reserve (latitude $2^{\circ}59'N$, longitude $102^{\circ}18'E$), which is located in the state of Negeri Sembilan, about 70 km southeast of Kuala Lumpur, Malaysia. The mean annual rainfall from 1974 to 1992 at Pasoh-Dua (latitude $2^{\circ}56'N$, longitude $102^{\circ}18'E$), 6 km south of the reserve, was 1842 mm, with distinct peaks in April–May and November–December (data provided by the Malaysian Meteorological Service). The soil type of the study area is Bungor-Malacca Association Type (data provided by the Malaysian Soil Science Division), which develops mainly from shale, granite, and fluvialite granite alluvium parent materials (Allbrook, 1973). The topography consists mainly of flat alluvial areas, with smaller expanses of swales, riverine areas, and gently rolling hills with slopes of between 3° and 10° .

The overall vegetation type in the reserve is lowland dipterocarp forest, which is characterized by a high proportion of species in family Dipterocarpaceae (Symington, 1943; Wyatt-Smith, 1961, 1964). Based

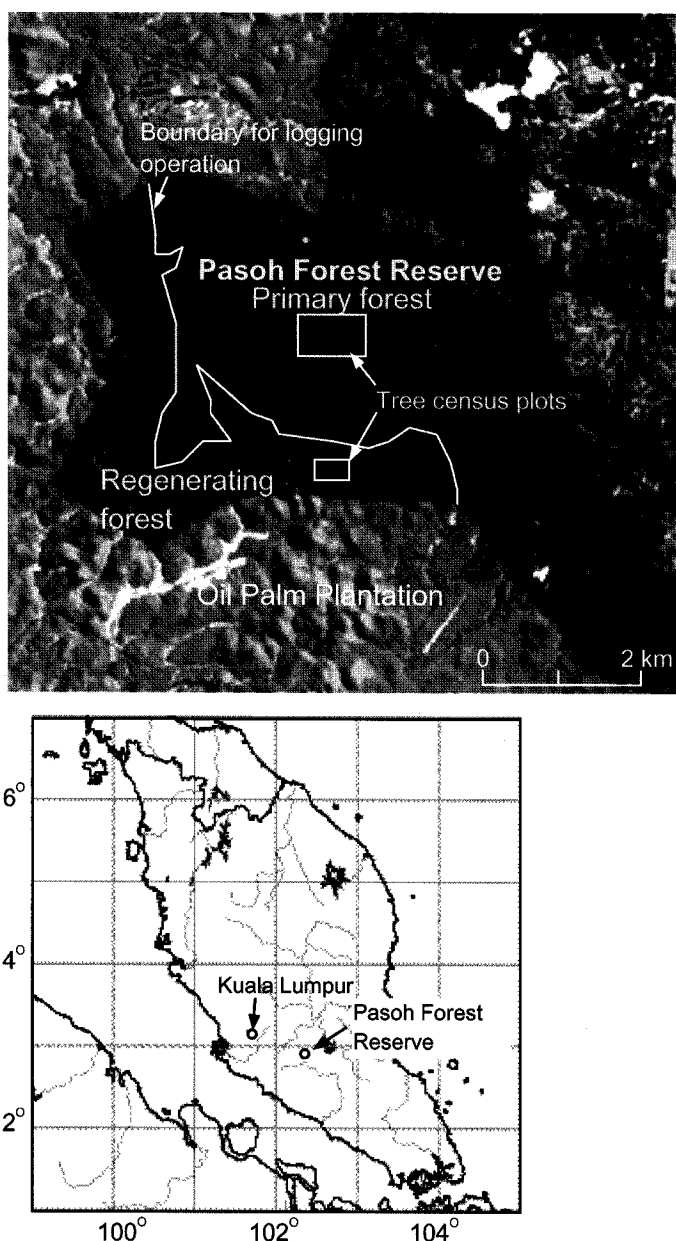


Fig. 1. A map of the study area, showing the location of the tree census plots in the primary and regenerating forests of the Pasoh Forest Reserve, Negeri Sembilan, Malaysia. The photograph is a LANDSAT image taken in 1988. The regenerating forest was logged between 1955 and 1959 under the MUS. The differences in canopy texture between the two forest types are visible.

on floristic evidence, the core area of the primary forest in the study area was generally homogeneous, with no evidence of major disturbance, and appeared to be a representative example of the lowland forest of the south-central Malay Peninsula (Kochummen et al.,

1990; Manokaran and LaFrankie, 1990). Lowland dipterocarp forest is one of the most species-rich communities in the world, with more than 200 tree species per hectare. Approximately, 25% of the total number of tree and shrub species (3197) recorded in the Malay

Peninsula were found within the study plots (Kochummen et al., 1990). In contrast, the southern and eastern edges of the reserve had been selectively logged from the mid-1950s until the early 1970s (Fig. 1).

The MUS logging regime involved removing the mature crop in a single harvest of all trees ≥ 45 cm DBH (all species) and releasing selected natural regeneration of various ages, most of which were light-demanding, medium- and light density hardwood species (Thang, 1987, 1997). Wyatt-Smith (1963) described MUS as felling of the upper canopy (which consists of the economic crop), followed immediately by girdling the remaining large unmerchantable canopy trees using herbicide. This treatment was extended to all smaller trees and saplings with a DBH ≥ 15 cm, other than economically valuable species of sound form. Thus, the MUS was a system for converting the virgin tropical lowland rain forest (a rich, complex, multi-species and multi-aged forest) into a more or less even-aged forest that would contain a greater proportion of commercially valuable species (Wyatt-Smith, 1963).

2.2. Tree census in the study plots

Two study plots were established within the reserve: one 50 ha plot (1000 m \times 500 m) lay in the primary forest towards the center of the reserve, and a second 6 ha plot (300 m \times 200 m) lay in a part of regenerating forest in which MUS had been practiced in 1958. The sites for the two plots were chosen to have the same soil types (Bungor-Malacca Association Type) and similar topographic features, consisting of flat alluvial areas and gently rolling hillslopes, thereby minimizing the confounding effects of these factors.

We considered that a 6 ha plot was large enough to investigate the canopy height and structure in the regenerating forest, since, prior to the present study, we had examined the canopy surfaces from a 52 m tower on the boundary between the two forests (regenerating and primary) and had found that the canopy structure was mostly monotonous throughout the regenerating forest. In addition, the cumulative number of species in areas ≤ 6 ha was approximately 85% of the total number of species in the 50 ha plot in the Pasoh Forest (Okuda, unpublished data). Furthermore, most inventory studies conducted in mixed dipterocarp forests have used plots of between 1 and 6 ha (e.g., Manokaran, 1996;

Niiyama et al., 1999). In contrast, the primary forest had a highly heterogeneous canopy structure. Therefore, we used the tree demography data taken for the full 50 ha area of the plot in the primary forest, which had been established prior to the present study.

The tree census (diameter measurement and mapping) in the regenerating forest plot was undertaken in October 1997 and completed in February 1999. The methodology for establishing the plot and the tree census followed the sampling regime described by Manokaran et al. (1990). This approach had been previously employed in 1985 to establish the 50 ha plot in the primary forest. In both plots, all woody plants ≥ 1 cm DBH were identified, measured, and tagged (using consecutive numbers), and their positions were mapped to the nearest 10 cm. The census of the primary forest was based on the second 5-year re-census of the forest, which began in November 1995 and was completed in November 1997 (Manokaran et al., 1999). The Forest Research Institute of Malaysia (FRIM) and the Smithsonian Institute had established the initial census in 1985. In the present study, the most up-to-date re-census data (1995–1997) were compared with the tree census data from the plot in the regenerating forest.

2.3. Aerial photographs of the canopy's surface structure

Aerial photographs of the center of the Pasoh Forest Reserve were taken at a 1:6000 scale in February 1997, and covered the entire extent of both plots. To produce a photogrammetric map with sub-meter accuracy, four 1 m \times 1 m markers used as ground control points (GCPs) were set in place before beginning the aerial photography. Two of the markers were hung between canopy trees at the northern corners of the 50 ha plot; the other two markers were set on the ground outside the forest, where the forest had been converted into an oil palm plantation in the early 1970s. No tall vegetation obstructed an aerial view of the markers within 50 m of the markers in the cleared area of the oil palm plantation. The visibility of all four markers was confirmed from the aircraft before taking the aerial photographs. The 6 ha plot in the regenerating forest was established beneath the flight lines that connected the markers outside and inside the forest. The positions of these markers were surveyed using GPS receivers, and traverses were performed with EDM (electronic

distance measurement) instruments, which measure distances using electromagnetic waves. In addition to the four GCPs, four reference points were placed inside each plot to calibrate elevations and coordinates. The final coordinates and elevations were linked with the Malaysian Rectified Skew Orthomorphic (MRSO) system and height datum.

Based on these aerial photographs and the GCPs, we carried out aerial triangulation to establish the necessary minor photographic control points for stereo digitizing. A digital elevation model of the canopy surface (CDEM) was developed using an analytical stereo-plotter. Only the center position of each stereo model was used in order to achieve relatively reliable stereo interpretation and measurement. The digitization used a grid pattern with 2.5 m intervals. The precision of the height measurement was better than 0.5 m for well-defined and clear surface objects (e.g., the canopy tower near the study area, the 1 m × 1 m markers in the canopy and on cleared areas of ground, and the roads or trails in the oil palm plantation). The grid data for ground elevation heights (GEHs) were again interpolated at 2.5 m intervals in order to match the array in the CDEM sub-grid system. Canopy height (CHT) was then obtained by subtracting the GEH from the CDEM height for every 2.5 m interval. On the basis of the digital elevation models determined by CHT, we created TIN (triangulated irregular network) digital terrain models (Richbourg and Stone, 1997; Walker, 1999) for each forest plot using Arc View GIS software (version 3.1) (Environmental System Research Institute, Inc., Redland, USA), and obtained the canopy's surface area for every perpendicularly mapped subplot (2.5 m × 2.5 m). The crowns of the canopy trees were mapped in both plots using stereoscopes to measure the aerial photographs and determine the projected area for each individual canopy tree.

2.4. Data analysis

It is known that the species composition and structural aspects of a forest are sometimes spatially autocorrelated when plots are subdivided into smaller subplots (Thomson et al., 1996; Nicotra et al., 1999), and that the smaller the subplot, the greater the expected degree of autocorrelation among the subplots. Clark et al. (1996) discussed how to determine the optimal size of subplots, and found that sizes greater than

50 m × 50 m minimized the amount of autocorrelation. They proposed that this finding could be applied to old-growth tropical forests. Thus, we chose the subplot size of 50 m × 50 m to test the statistical differences in stem density and basal area between the two forests for every DBH class. Fisher's α (Fisher et al., 1943) was also calculated in every one of these subplots in order to compare the tree species diversity of the two forests.

For the comparison of stand structure, species composition, stem density, and other vegetational aspects between the primary and regenerating forests, the species recorded in both forests were classified into five species groups ("layer groups") based on similarities in the species' ecological characteristics, and in particular, the layer they occupied within the overall forest structure: emergent (E), canopy (C), understory (U), treelet (T), and shrub (S). These classifications were based on empirical knowledge reported in the literature (Symington, 1943; Whitmore, 1972a,b; Ng, 1978; Kochummen, 1979) and were used to detect general trends in the response of the tree species to logging, as well as to overcome the problem of most species being represented by small populations (Manokaran and Swaine, 1994). These classifications are described in detail in the literature (Manokaran, 1996; Manokaran and Swaine, 1994; Okuda et al., 1997, in press). Note that these layer classes (emergent, canopy, etc.) were not based on the heights of individual trees, but refer to groups of species that are categorized as "emergent", "canopy", or other layer groups. Thus, even "emergent" includes juvenile trees as well as large, mature trees. As for tree size classes, unless otherwise specified, they were defined according to DBH as follows: ≤ 2 cm, saplings; 2–6 cm, small trees; 6–10 cm, semi-medium-sized trees; 10–30 cm, medium-sized trees; and ≥ 30 cm, large trees. Species with a typical successional status were grouped into the following three groups based on the personal experience of researchers in this field (Peter S. Ashton, Harvard University) and on results from other studies (Ng, 1978; Whitmore, 1972a,b): shade-tolerant climax species, late-successional species, and early-successional pioneer species.

The statistical differences mentioned hereafter are based upon the ANOVA results, unless otherwise specified. For those cases with unequal variance, we employed a non-parametric analysis (Mann-Whitney *U*-test). All statistical analyses were undertaken using StatView (version 5.0, SAS Institute, Inc., Cary, NC).

3. Results

3.1. Canopy surface structure (canopy height, canopy surface area, crown size)

The mean canopy height in the primary forest was 27.4 m, and this value was significantly (Mann–Whitney *U*-test, $P < 0.001$) higher than the mean of 24.8 m in the regenerating forest (Fig. 2). The mean height of the tallest canopy within the extended subplot was 46.5 m in the primary forest, versus 41.1 m in the regenerating forest, and this difference was also statistically significant (Mann–Whitney *U*-test, $P < 0.001$). In addition, the variance of canopy height in the primary forest ($\sigma^2 = 99.92$) was more than double the value in the regenerating forest ($\sigma^2 = 44.63$), and the difference was statistically significant (based on *F*-test to examine equal variance, $P < 0.0001$). The coefficient of variation was also higher in the primary forest (CV = 0.365) than in the regenerating forest (CV = 0.270). The proportion of low canopy (<15 m) in the primary forest was 10.1% of the total ($n = 80,601$), versus 5.3% in the regenerating forest ($n = 9801$). In contrast, the proportion of higher canopy (≥ 40 m) was substantially higher in the primary forest (12.8% versus 1.7%). The tallest canopy trees in the primary forest reached heights of 62.6 m versus 47.0 m in the regenerating forest. These

findings suggest that there are more mature trees of emergent and canopy species in the primary forest than in the regenerating forest. The complexity of the canopy in terms of height was also much greater in the primary forest than in the regenerating forest as shown by the variance in canopy height.

The canopy surface area per perpendicularly mapped subplot (2.5 m \times 2.5 m) averaged 17.4 m² (27,845 m² ha⁻¹) in the primary forest. This was almost 1.5 times the value in the regenerating forest (12.0 m² per subplot, 19,272 m² ha⁻¹) (Fig. 3). The canopy surface structures also could be compared by the number of horizontal planes in the TIN models of the two forests. We defined “horizontal planes” to be the triangular planes created by the TIN model whose size was no more than 5% greater than the original size of the perpendicularly mapped planes. Such horizontal planes amounted to 2.9% of the total in the primary forest versus 4.3% in the regenerating forest, and the average number of such planes per 50 m \times 50 m subplot was significantly higher ($P < 0.0001$) in the regenerating forest than in the primary forest. The remaining surfaces were all slanted to a greater extent, which suggests that almost all of the canopy surface is either convex or concave, and represents gaps within or between tree crowns. In addition, the “horizontal planes” were generally scattered throughout the forests,

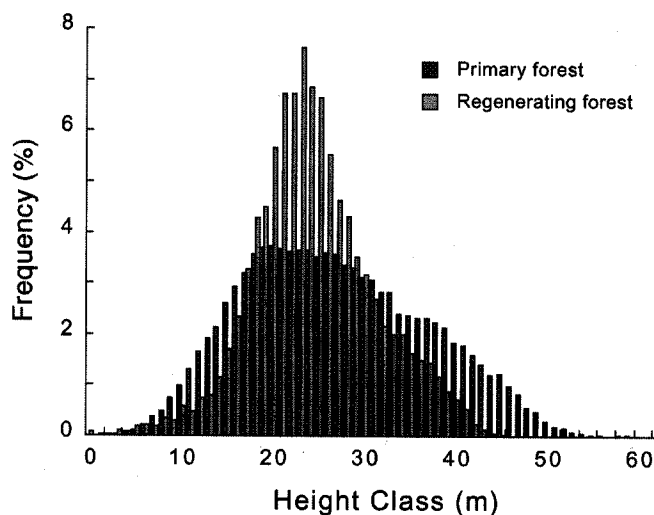


Fig. 2. The canopy's height class distribution in the primary and regenerating forests. The Y-axis represents the relative frequency (%) in each height class as a function of the total number of grid points where canopy height was measured ($n = 80,601$ in the primary forest plot; $n = 9801$ in the regenerating forest plot). The average height in the primary forest (27.4 m) was significantly higher ($P < 0.001$) than that in the regenerating forest (24.8 m).

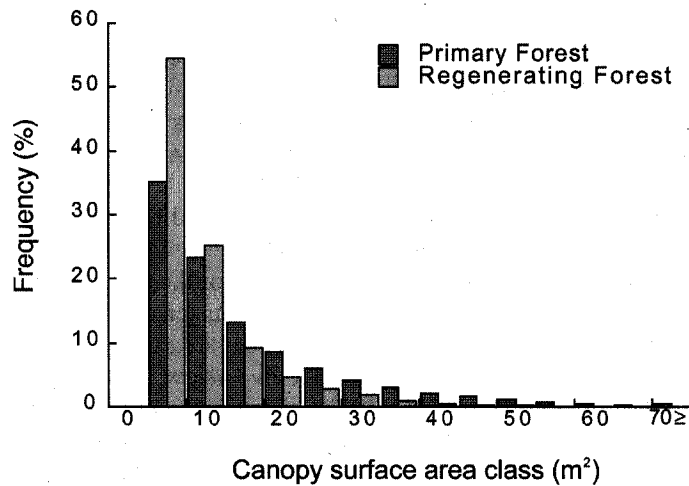


Fig. 3. The distribution of the canopy surface area classes in the primary and regenerating forests. The Y-axis represents the relative frequency (%) when each of the study plots was subdivided into 2.5 m × 2.5 m subplots (the total number equal to that in Fig. 2).

although the proportion of areas with more than two consecutive horizontal planes per 50 m × 50 m subplot was significantly higher ($P < 0.0001$) in the regenerating forest than in the primary forest. Therefore, the reduced complexity of the canopy surface in the regenerating forest did not arise from the existence of a large proportion of horizontal planes, such as can be seen in the continuous dwarf form of the canopy that characterizes the coastal vegetation and Kerangas forest in Borneo; instead, it arose primarily from the lack of an emergent layer above the main canopy.

The crown sizes of individual canopy trees were also significantly larger in the primary forest than in the regenerating forest (Mann–Whitney U -test, $P < 0.0001$) (Fig. 4). Crown sizes in the primary forest ranged from 3.7 to 886.8 m², with a mean of 94.5 m² versus 3.3–402.5 m² and a mean of 42.9 m² in the regenerating forest. The coefficient of variation in the primary forest ($CV = 0.93$) was larger than that in the regenerating forest ($CV = 0.83$), and the variance of crown size was significantly different between the two forests (based on F -test to examine equality of

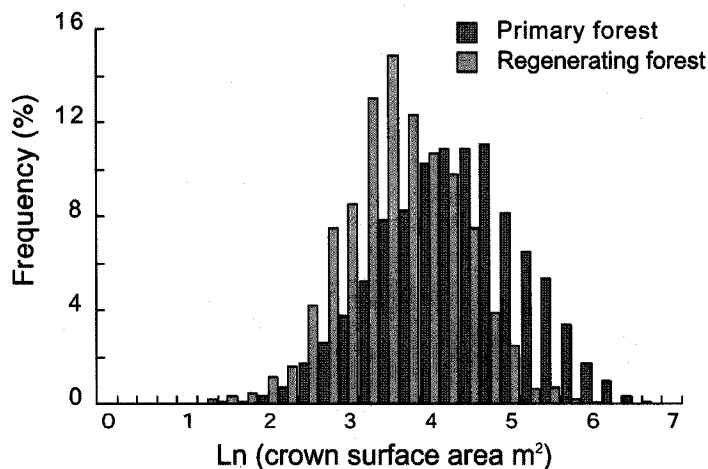


Fig. 4. Crown size distribution in the primary and regenerating forests. The Y-axis indicates the relative frequency (%) of trees within a given crown size class as a function of the total number of trees ($n = 3671$ in the primary forest; $n = 1136$ in the regenerating forest).

variances, $P < 0.0001$). The number of trees with a crown size of $\geq 300 \text{ m}^2$ (about 20 m in diameter) averaged 2.6 ha^{-1} in the primary forest and 0.5 ha^{-1} in the regenerating forest. In contrast, the number of trees with smaller crowns ($\leq 100 \text{ m}^2$, about 11 m in diameter) averaged 49.5 ha^{-1} in the primary forest and 177.5 ha^{-1} in the regenerating forest. Trees with a crown size of less than 80 m^2 (about 10 m in diameter) comprised 57% of the total in the primary forest versus 89% in the regenerating forest. In contrast, trees with a crown size $\geq 80 \text{ m}^2$ accounted for 75% of the total projected crown area in the primary forest versus only 30% in the regenerating forest.

3.2. Stand structure

The stem densities were measured in every extended subplot ($50 \text{ m} \times 50 \text{ m}$) and were averaged to provide an estimate for each plot as a whole. Although stem densities were higher for all tree size classes combined

in the primary forest ($6418 \text{ stems ha}^{-1}$) than in the regenerating forest ($6067 \text{ stems ha}^{-1}$), the difference was not significant ($P > 0.05$; Table 1). The stem densities of small regenerating trees ($< 10 \text{ cm DBH}$) were higher in the primary forest than in the regenerating forest ($P < 0.05$), but it was not the case for the medium-sized trees ($10\text{--}30 \text{ cm DBH}$).

We compared the stand structures of the two forests in terms of the five different layer groups (emergent, canopy, understory, treelet and shrub species). Note that trees are categorized by species group into one of the five layers, so that “emergent”, e.g., includes all tree size classes from small saplings to adults, as described in the study methods. The distribution of stem densities in the canopy layer group as a function of size class generally followed the same trend as that for all layer groups combined (Fig. 5); i.e., tree density in the range from the semi-medium to medium size classes ($6\text{--}30 \text{ cm DBH}$) was significantly higher in the regenerating forest than in the primary forest, but was

Table 1
Comparison of stem density and basal area between the primary and regenerating forests

DBH size class (cm)	Stem density (trees/50 m × 50 m subplot)				Basal area ($\text{cm}^2/50 \text{ m} \times 50 \text{ m}$ subplot)			
	Primary forest		Regenerating forest		Primary forest		Regenerating forest	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
(1,10]	1458.13	19.31	1335.92	46.09*	14820.27	139.75	16559.41	346.82**
(10,20]	101.03	0.94	128.58	2.67**	15139.11	149.14	19457.59	515.28**
(20,30]	25.30	0.39	31.17	1.71**	11597.98	177.33	14229.93	823.66**
(30,40]	9.52	0.21	11.21	1.02*	8786.31	199.76	10030.23	924.20
(40,50]	4.18	0.13	4.21	0.40	6454.22	207.40	6575.85	656.46
(50,60]	2.70	0.12	2.92	0.45	6260.28	270.15	6777.68	1021.14
(60,70]	1.43	0.09	1.46	0.31	4639.59	298.35	4652.26	989.07
(70,80]	0.82	0.06	0.50	0.14	3567.16	264.72	2171.62	590.32
(80,90]	0.56	0.05	0.54	0.12	3138.29	289.98	3044.84	670.99
(90,100]	0.35	0.04	0.08	0.06*	2463.94	299.56	593.08	411.39*
(100,110]	0.22	0.03	0.00	0.00*	1858.00	295.65	0.00	0.00*
(110,120]	0.12	0.03	0.08	0.08	1185.78	255.69	860.13	860.13
(120,130]	0.09	0.02	0.00	0.00	1090.73	289.05	0.00	0.00
(130,140]	0.05	0.02	0.00	0.00	637.74	208.45	0.00	0.00
(140,150]	0.01	0.01	0.00	0.00	163.57	115.37	0.00	0.00
(150,160]	0.02	0.01	0.00	0.00	371.62	184.53	0.00	0.00
(160,170]	0.02	0.01	0.00	0.00	313.92	180.37	0.00	0.00
(170,180]	0.01	0.01	0.00	0.00	124.78	124.78	0.00	0.00
(180,190]	0.01	0.01	0.00	0.00	129.30	129.30	0.00	0.00
(190,200]	0.01	0.01	0.00	0.00	152.02	152.02	0.00	0.00
All size classes	1604.52	19.49	1516.67	44.58	82894.58	864.34	84952.61	2251.00

* $P < 0.05$.

** $P < 0.0001$.

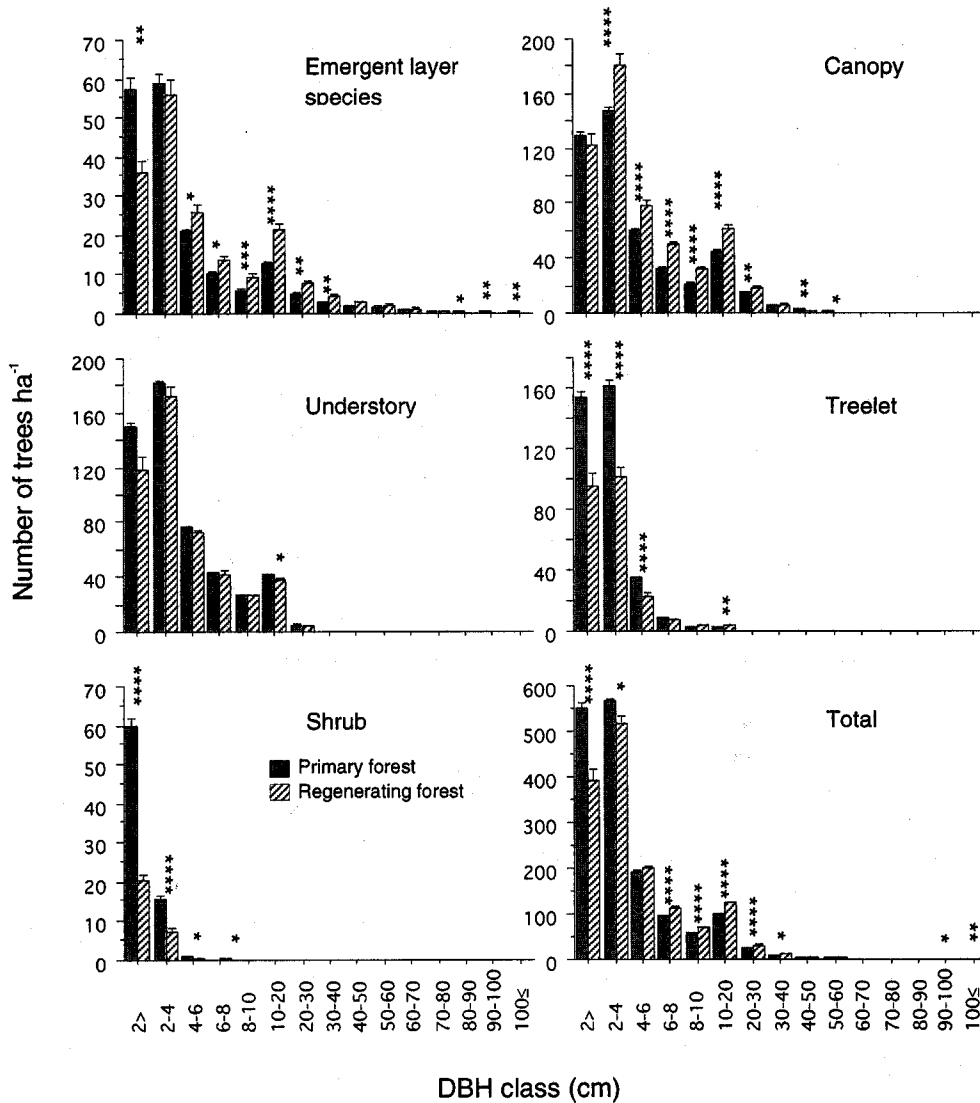


Fig. 5. Stand structures of the primary and regenerating forests in terms of five different layer groups (emergent, canopy, understory, treelet and shrub) and for all layer groups as a whole (“total”). Asterisks indicate the level of significance of the differences in the number of trees per hectare between the primary and regenerating forests: (****) $P < 0.001$, (***) $P < 0.005$, (**) $P < 0.01$, (*) $P < 0.05$. The stem density in the two size classes (90–100 cm DBH, ≥ 100 cm DBH) shown in the “total” graph was larger in the primary forest than in the regenerating forest, although the bars are not visible in the graph.

lower in the larger (40–60 cm DBH) size classes. This trend was also evident in the emergent layer groups, but not as apparent as that for the canopy layer groups, particularly in the classes ranging from 4 to 8 cm DBH. The trend became less distinct in the understory layers. However, the stem densities of smaller trees (≤ 4 cm DBH) in the treelet and shrub layers were

much higher in the primary forest than in the regenerating forest. Higher densities of smaller trees in the combined layers (described as “total” in Fig. 5) resulted largely from this trend in the lower layers.

The basal area for all DBH classes combined was around $33.1 \text{ m}^2 \text{ ha}^{-1}$ in the primary forest versus $34.0 \text{ m}^2 \text{ ha}^{-1}$ in the regenerating forest. This difference

Table 2
Comparison of tree density (stems ha⁻¹) for the five most abundant families in the primary and regenerating forests

Family name	Primary forest		Regenerating forest	
	Density (stems ha ⁻¹)	Percentage of total density	Density (stems ha ⁻¹)	Percentage of total density
Euphorbiaceae	906.8	14.1	1013.7	16.7
Dipterocarpaceae	587.4	9.2	638.3	10.5
Annonaceae	470.8	7.3	287.8	4.7
Rubiaceae	381.8	5.9	283.2	4.7
Burseraceae	341.0	5.3	454.5	7.5
All five families	2687.7	41.8	2677.5	44.1

was not significant ($P > 0.05$). The basal area for all size classes <30 cm DBH, which accounted for just above 50% of the total, was always significantly ($P < 0.0001$) higher in the regenerating forests than in the primary forest. However, when these size classes were broken down into smaller divisions, the basal area in the tree size classes <3 cm DBH were significantly ($P < 0.001$) higher in the primary forest than in the regenerating forest. In the tree size classes ≥ 70 cm DBH, the basal area was always higher in the primary forest than in the regenerating forest, but, as was the case for stem density, these differences were significant ($P < 0.05$) for only two size classes (90–100 and 100–110 cm DBH) (Table 1). No trees of more than 116 cm DBH were found in the regenerating forest, whereas the largest tree in the primary forest was a *Neobalanocarpus heimii* with DBH of 196.3 cm.

These findings suggested that most of the regeneration that arose after logging is now clustered in the medium size classes rather than in the larger or sapling classes, even though the total basal area in the two forests was the same. It is obvious that the aggregation of medium-sized trees which occurred in the regenerating forest developed mainly because of the high density of canopy or emergent applicants that had originally been remnant cohorts after logging.

3.3. Species composition and diversity

The most recent re-census in the 50 ha plot in the primary forest counted 320,903 individuals in 77 families, 298 genera, and 822 species. In the 6 ha regenerating forest plot, 36,401 individuals were recorded in 76 families, 254 genera, and 672 species. The total number of species that occurred in either or both plots was 866. Of these species, 44 were found only in the regenerating

forest, 194 were only found in the primary forest, and 628 species were common to both forests.

The five most abundant families in terms of stem density for trees ≥ 1 cm DBH did not differ between the primary and regenerating forests; the most common family was the Euphorbiaceae, followed by the Dipterocarpaceae in both forests (Table 2). The top five families ranked in terms of their basal area per hectare showed a slightly different trend, with different families accounting for more of the basal area; e.g., the Leguminosae became more important in both forests than was indicated by stem density alone (Table 3).

There was a large gap between the Dipterocarpaceae and the next most abundant family, which accounted for less than 10% of the total in both forests (Table 3). Note that trees ≥ 1 cm DBH in the Dipterocarpaceae accounted for 27.3% of the total basal area in the primary forest and 30.8% in the regenerating forest. The Dipterocarpaceae did not account for such a large proportion of the total stem density (Table 2); this suggests that, compared with other families, this family is represented by relatively few, large trees. Although the basal area of dipterocarps of all sizes and their proportion of the total basal area did not differ significantly ($P > 0.05$) between the primary and regenerating forests, the values in the size classes ranging from 10 to 60 cm in DBH were significantly greater ($P < 0.001$) in the regenerating forest than in the primary forest.

It is notable that the Moraceae and Rubiaceae, both rich in successional species, were ranked within the 10 most abundant families in the regenerating forest but were absent from the top 10 families in the primary forest. The mean basal area of the Leguminosae was significantly higher ($P < 0.01$) in the primary forest than in the regenerating forest, whereas the basal areas of the Euphorbiaceae and the Fagaceae were higher in

Table 3
Comparison of tree basal area per hectare for the 10 most abundant families in the primary and regenerating forests

Family	Basal area (m ² ha ⁻¹)	Percentage of total basal area
<i>Primary forest</i>		
Dipterocarpaceae ^a	9.1	27.3
Leguminosae ^a	2.8	8.5
Euphorbiaceae ^a	2.4	7.4
Burseraceae ^a	2.0	6.1
Myrtaceae	1.1	3.4
Annonaceae ^a	1.1	3.4
Fagaceae ^a	1.1	3.3
Anacardiaceae ^a	0.9	2.8
Myristicaceae ^a	0.9	2.8
Sapindaceae	0.9	2.7
All ten families	22.4	67.7
<i>Regenerating forest</i>		
Dipterocarpaceae ^a	10.5	30.8
Euphorbiaceae ^a	3.4	10.0
Burseraceae ^a	2.3	6.7
Fagaceae ^a	1.8	5.4
Leguminosae ^a	1.5	4.4
Annonaceae ^a	1.4	4.1
Moraceae	1.3	3.7
Rubiaceae	1.1	3.2
Myristicaceae ^a	1.0	3.0
Anacardiaceae ^a	0.7	2.1
All ten families	24.9	73.4

^a Abundant in both the primary and the regenerating forests.

the regenerating forest. The basal area of the Annonaceae was also larger in the regenerating forest than in the primary forest, but the difference was marginal ($P < 0.05$). Others of the 10 most abundant families did not differ significantly between the two forests.

The compositions of the most abundant species in the two forests (in terms of stem density) differed greatly. The 50 most abundant species in the primary forest and the 50 most abundant species in the regenerating forests were drawn from a total of 76 species; however, only 24 species (31.6%) were included in the 50 most abundant species in both forests (Appendix A). *Shorea maxwelliana* and *S. acuminata*, which are commercial timber species, ranked within the 50 most abundant species in each forest. However, *N. heimii*, another highly valued timber species that was common in the primary forest (66.7 stems ha⁻¹) was quite uncommon in the regenerating forest (10.8 stems ha⁻¹). In contrast with the species abundance based on stem densities, 10

dipterocarp species were among the 50 most abundant species in terms of basal area in both the primary and the regenerating forests (Appendix B).

It is notable that climax or late-successional species (e.g., *Cynometra malaccensis*, *Sarcotheca griffithii*, *Millettia atropurpurea*, *Intsia palembanica*, *Shorea ovalis*, *Ochanostachys amentacea*, *Pentaspadon motleyi* and *Mesua ferrea*) were all ranked in the 50 most abundant species in the primary forest in terms of basal area per hectare, but this was not the case in the regenerating forest (Appendix B). In contrast, the early successional species *Endospermum malaccense*, *Porterandia anisophylla* and *Croton argyratus* were among the 50 most abundant species in the regenerating forest, but their abundance (in terms of basal area per hectare) was relatively small in the primary forest, so they were not ranked among the 50 most abundant species there.

The mean value of Fisher's α was 122.1 in the primary forest—significantly higher ($P < 0.0001$) than the value of 110.1 in the regenerating forest. These findings suggest that there were differences in the species diversity or heterogeneity of the two forest types.

4. Discussion

4.1. Canopy height and surface structure

The effects of selective logging using the MUS approach on canopy and stand structure and on tree species composition were extensive, and remained evident even 41 years after the logging operation. Such differences in canopy height between primary and regenerating forests can be seen both within the study area (as shown in the satellite image in Fig. 1) and in many other places in the tropics (Knight, 1975; Foster and Brokaw, 1982; Lang and Knight, 1983). In addition to the height difference, the variations in canopy height were much smaller in the regenerating forest than in the primary forest. This may have been due primarily to the fact that most of the growth arose immediately after logging in the regenerating forest, whereas regeneration in the primary forest occurred intermittently via gap formation. The low frequency of gap formation in the canopy of the younger regenerating forest might have led in turn to a uniform structure of even-aged cohorts of canopy-forming trees. Low frequencies of gap formation in logged or regenerating forests have been

reported elsewhere in the tropics (e.g., Chapman and Chapman, 1997). Moreover, gaps tend to be smaller and less frequent in young forests, but increase in frequency as the forest ages (Knight, 1975; Brokaw, 1982; Lang and Knight, 1983). Although, the present study did not examine the difference in gap formation rate between the two study plots (regenerating versus primary forest), a study conducted elsewhere in the Pasoh Forest revealed that the proportion of regenerating patches that resulted from gap formation was higher and the average gap size was larger in the primary forest than in the regenerating forest (Yasuda, 1998). According to this study, the proportion of gap area increased from 4.3 to 14.6% in the primary forest after a strong storm occurred in mid-1995 in the Pasoh region, while the value changed from 2.0% to only 3.1% in the regenerating forest. These facts imply that the structure of the regenerating forest is not yet mature and the probability of gap formation is higher in the primary forest.

The present study showed that the average size of canopy crowns was much smaller in the regenerating forest than in the primary forest, whereas the number of canopy trees identified by aerial photography was much lower in the primary forest than in the regenerating forest. Some short trees with small crowns in the primary forest were not visible, and their outlines could not be identified from the aerial photographs because they were concealed by taller canopy trees with large crowns. These “invisible” trees were not considered in the crown mapping. Thus, the density of canopy trees identified in the aerial photography did not necessarily represent the actual density of stems in the emergent, canopy, and sub-canopy layers; this number can be derived from tree census data. Furthermore, the “crowns” of trees in the top layer that we identified by aerial photography might have comprised more than one individual. These are reasons why the density of canopy trees calculated from the aerial photographs was much less in the primary forest (73.4 stems ha^{-1}) than in the regenerating forest (189.3 stems ha^{-1}). Nevertheless, the canopy layer in the regenerating forest was densely packed with many trees with small crowns, whereas the canopy of the primary forest was characterized by unevenness in crown size and high convexity (i.e., there were many emergent crowns). The complexity and heterogeneity of the canopy surface structure that was evident in the primary forest has not yet completely recovered in the regenerating forest.

4.2. Stand structure and species composition

The present study showed an aggregation of medium-sized trees within the stand structure of the regenerating forest, and this aggregation was apparent in the species that formed the canopy and emergent layers (Table 1, Fig. 5). The high density of canopy or emergent applicants is predicted to have originated from remnant cohorts after logging; these trees had not reached the minimum size for harvesting, but had been left unharvested because they were regarded both as commercial species and as having sound form at the time of the logging operations. Supardi (1999) analyzed stem density in study plots elsewhere in the Pasoh region and demonstrated that there was a higher density of medium-sized trees in the regenerating forest than in the primary forest. Thus, aggregation of medium-sized trees within the stand structure may be commonly found throughout the regenerating forests of the study site.

The average annual increase in DBH of canopy trees measured in the 50 ha plot of primary forest from 1985 to 1995 was 1.1 cm per year for the most rapidly growing 10% of the trees (at 40–50 cm DBH). The growth rate increased to 1.6 cm per year as stem DBH increased (Okuda, unpublished data). The values measured by dendrometer elsewhere in our study site were even higher, ranging from 1.2 to 2.2 cm per year in the canopy-forming dipterocarp trees (e.g. *Shorea leprosula*) (Toma et al., 1994). Although tree growth data were unavailable for the area of regenerating forest where the present study was conducted, the trees in the regenerating forest that survived the logging operations in the 1950s—the most sound and healthy commercial timber species with high growth rates, originally <45 cm in DBH—are most likely to have formed the canopy layer later on. If the highest growth rate of canopy trees in the primary forest is applied to the trees in the regenerating forest, these surviving trees would have possibly reached DBHs of more than 90 cm. (The larger trees might have even enjoyed much higher growth rates where competitors were removed, as the MUS suggests.) However, both the stem density and basal area in these size classes were significantly ($P < 0.05$) lower in the regenerating forest. In contrast, the stem densities in the medium size classes (10–30 cm DBH) were much higher in the regenerating forest.

Nevertheless, because stem growth varies greatly by species, season, edaphic conditions, and size of trees

(Clark and Clark, 1996, 1999; Ong and Kleine, 1996), the lack of big canopy trees in the regenerating forest may simply imply that it takes more than 40 years after logging for emergent species to grow tall enough to penetrate the canopy layers. We also cannot exclude the hypothesis that large 'remnant trees', which had nearly reached the lower size limit for harvesting (45 cm in DBH), were illegally logged, and that only the small canopy trees were left behind during the logging operation. Thus, the development of the canopy structure would have been slower than it otherwise would have been.

The present study was unable to show a proportional difference in the abundance of climax or early-successional tree species between the primary and regenerating forests, since not all species could be identified in terms of their successional status. However, typical early-successional species (e.g., *P. anisophylla*, *C. argyratus* and *E. malaccense*) were more common or abundant in the regenerating forest than in the primary forest, and their total basal area was significantly higher. The study plot in the regenerating forest lay close to an oil palm plantation (Fig. 1), so we cannot completely eliminate the possibility that some of these early-successional/pioneer species invaded the plot during the regeneration process after the logging was complete. However, medium or larger trees (10–60 cm DBH) of these species were also found in the regenerating forest, so it appears likely that these early-successional/pioneer species became established immediately after the logging and remain dominant in the regenerating forest. Statistical differences in Fisher's α revealed that selective logging may have reduced species diversity. However, we do not completely exclude the possibility that these differences can be attributed to differences in the pre-logging status and background of the two forest sites.

4.3. Effects of the MUS approach and implications for sustainable management

In the present study, it was shown that some dipterocarp species which are mostly commercial timbers, maintained or even increased their level of stem density and basal area in the regenerating forest. In the largest size class group in the regenerating forest (trees ≥ 60 cm DBH), the basal area per hectare for dipterocarps accounted for 40–80% of the total basal area; these proportions were significantly higher than those

in the same size classes in the primary forest (20–60%). In this sense, changes in tree species composition seen in the regenerating forest is exactly what the MUS approach was originally designed to produce.

However, this is not the case as for other compositional aspects. For example, the stem density of small (<6 cm DBH) trees of many dipterocarp species (e.g. *Dipterocarpus cornutus*, *N. heimii*, *Shorea acuminata*, *S. bracteolata*, *S. guiso*, *S. leprosula*, *S. lepidota*, *S. ovalis*, *S. parvifolia*, *S. pauciflora*), most of which are categorized as highly commercial species, was significantly lower ($P < 0.01$) in the regenerating forest than in the primary forest. When the MUS approach was originally formulated, the seedlings and saplings of non-commercial tree species were supposed to have been killed by repeated girdling with poison in order to provide the open space for the seedlings and saplings of commercial timber species. However, if these operations had been effective, the present sapling stocks of commercial timber species in the regenerating forest would be expected to be higher than those in the primary forest. Because of the indistinct increases, or even decreases, in abundance of sapling stocks in the regenerating forest, we suspect that the competition-control aspect of the MUS approach was not performed adequately, and to this extent, the strategy failed to accomplish some of its goals in our study area.

The MUS approach would have required regular thinning at 20, 35 and 55 years after logging (Wyatt-Smith, 1963), but such thinning operations were never practiced in the Pasoh Forest Reserve (Manokaran, 1996). Instead, the vast, potentially valuable tracts of lowland dipterocarp forest were cleared after the 1970s when the first of the thinnings should have occurred; these cleared plots were converted into oil palm plantations rather than being maintained as secondary forest for timber production by selective logging (Manokaran, 1996). Most selective logging subsequently shifted to the hill dipterocarp forests with the goal of producing timber under a logging regime called the Selective Management System (SMS). As a result, little forest was left that could have been managed by the MUS approach, and this approach was abandoned in the lowland forests.

The incomplete MUS operation in the study area in turn resulted in the large amounts of tree regeneration in medium-sized trees and minimal damage to the forest floor that were observed in the regenerating

forest in the present study. In the regenerating forest plot (6 ha), we found only 15 stumps of large trees, whereas the current logging regime being employed in the hill forests near the study area extracted more than 20 trees per hectare. The remaining stumps do not necessarily represent the actual number of trees felled or poison-girdled, but the similarity in the properties of the residual trees at the Pasoh study site is unlikely to have resulted from factors such as logging damage, excessive timber extraction, and soil disturbance from logging operations, which can affect as much as 80% of the timber resources and other ecological values of a forest (Manokaran, 1996).

Nevertheless, even moderate logging resulted in distinct changes in the fauna of the regenerating forest. The insect species composition (understory butterflies and soil micro-arthropods) was found to differ between the primary and regenerating forests (Fukuyama et al., 1998). Based on automatic photography (i.e., cameras that were left unattended and that were triggered by an infrared beam interrupted by animal motion nearby) and live trapping, the species composition of medium-sized and small mammals and birds were also found to differ between the two types of forest (Miura and Ratnam, 1998; Nagata et al., 1998; Yasuda et al., 1998). Wild boar (*Sus scrofa*), pig-tail monkey (*Macaca nemestrina*) were more often seen in the regenerating forest than in the remaining primary forest, while dusky leaf monkey (*Presbytis obscura*) and white-handed gibbon (*Hylobates lar*), which spend most of their time in the canopy layer, were less frequently observed in the regenerating forest. The observed changes in the canopy structure and lack of an emergent layer may have been responsible for these changes in the animal composition and distribution. These facts suggest that the structural aspects of the canopy layers may in turn be diagnostic indicators not only for assessing the dynamics and regenerative status of a forest, but also for assessing species richness and distribution of wildlife. This will be of benefit to forest managers and silviculturists who have been looking for a rapid and simple assessment of the ecological and productive potentials of a forest before and after logging (Moravie et al., 1999).

Apart from the fact that the MUS approach to logging seems not to have been fully practiced in the study area, secondary effects on the biodiversity and forest microclimate were apparent. These effects could be expected

to be greater in the current logging regime (SMS), which is being conducted with a shorter felling cycle and greater level of timber extraction. Although the 70-year felling rotation suggested by the MUS approach may be a sustainable silvicultural system in the lowland dipterocarp forest, the present logging cycle (25–30 years) is too short to expect a healthy stocking of regeneration (Manokaran, 1996; Kurpick et al., 1997). In addition, reproduction of the major canopy-forming species takes place synchronously, with mass fruiting events (“masting”) occurring at intervals of 2–10 years (e.g., Appanah, 1985, 1993; Ashton et al., 1988). These and other phenological characteristics must be taken into account when planning the logging cycle. Second and third harvests may not produce as much timber as in the first harvest, and the decreased density of parent trees could easily lead to inbreeding depression (Bawa and Krugman, 1991) and, ultimately, low genetic diversity and low adaptive potential in the offspring (Konuma et al., 2000).

4.4. Requirements for further study

Some final points remain in need of further study and analysis. In the present study, it was found that stem density in small-sized trees (<4 cm DBH) was significantly lower in the regenerating forest than in the primary forest. The trend was more distinct in the treelet and shrub layer species than in the upper story species (emergent and canopy species) (Fig. 5). In contrast to these results, however, the light intensity values measured at 1 m above the ground under the closed canopy in the regenerating forest were generally 5–10% of the levels measured in a completely open area, whereas the corresponding values in the primary forest, with a tall and multi-layered canopy, were less than 1–2% (Okuda, unpublished data). Therefore, despite higher light intensity at the forest floor than in the primary forest, the lower stem density of sapling size trees in the regenerating forest may be due to the fact that after logging operations the residual adult trees did not produce as many juveniles as the adult trees in the primary forest did, or the original vegetation in treelet and shrub layers of the regenerating forest has not yet fully recovered from logging impacts.

For these points, further experimental research is needed to study physiological responses of juvenile and small trees under different light intensities and qualities, since each tree species has an optimal range

of light intensity and wavelength for growth (e.g. Lee et al., 1997; Terborgh and Mathews, 1999) and they might have had different responses to the light available and light spectrum in the primary forest and that in the regenerating forest.

As well, tree species composition and canopy height are altered by edaphic factors (topography and soil type) (Newbery, 1991; Ashton and Hall, 1992; Okuda et al., in press). These factors cannot be neglected in any consideration of niche separation among the species in the tropical rain forest. The sites for the two plots in the present study were chosen because they had similar topographic and soil conditions. However, small-scale changes in micro-edaphic factors sometimes resulted in structural and compositional differences, and such comparisons should be redone to better account for differences in the topographic and soil types of each subplot.

5. Conclusions

The present study demonstrated that in the regenerating forest, canopy height was lower and the canopy's surface structure was more monotonic than in the primary forest. As well, the stand structure, species composition, and basal area of the major species differed between the two forests. Other investigators have also reported increased tree density, reduced basal area, a lower canopy height, and a more even (homogeneous) canopy structure in younger forests (Knight, 1975; Foster and Brokaw, 1982; Lang and Knight, 1983; Chapman and Chapman, 1997). In contrast, Pélissier et al. (1998) studied the impacts of selective logging, 10–15 years after harvest, on the dynamics of moist evergreen forest in south India; they report that species composition was not greatly altered and that growing stocks (density and basal area) will gradually recover to become similar to that of unlogged forest. However, they warn that repetition of selective logging might not be sustainable in terms of forest structure and composition. In the present study, we also observed that the forest structure had not completely recovered from the changes or begun to resemble the primary forest even 41 years after logging. The present 25–30-year logging cycle needs to be reconsidered not only from the goal of sustaining timber production, but also particularly from the goal of ecologically sustainable forest management.

Both of these goals can be achieved by maintaining the high complexity of the structural aspects of the forest. Thinning the forest by artificially removing canopy trees stuck in a state that shows no signs of evolving towards maturity may be required with minimum damages on forest floor in order to recreate the complexity of the canopy structure and the heterogeneity of the forest-floor light environment that exist in the primary forest. These conditions would, in turn, promote highly diverse regeneration, including regeneration of gap (pioneer) species (e.g., Denslow, 1980; Denslow et al., 1990).

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Appendix A. (Continued)

Name	Layer group	Successional group	Family	Primary forest			Regenerating forest									
				Ranking	<10 cm (DBH)	Total	Ranking	<10 cm (DBH)	10–30	30–50	≥50	Total				
<i>Lepisanthes senegalensis</i>	U		Sapindaceae	36	33.8	0.9	0.0	0.0	0.0	34.7	25	40.8	0.8	0.0	0.2	41.8
<i>Aporosa prainiana</i>	U		Euphorbiaceae	40	31.1	1.2	0.0	0.0	0.0	32.3	18	48.2	0.2	0.2	0.0	48.5
<i>Mesua comeri</i>	T		Guttiferae	43	31.4	0.1	0.0	0.0	0.0	31.5	43	28.2	0.3	0.2	0.0	28.7
<i>Shorea macroptera</i>	E	L	Dipterocarpaceae	48	25.6	3.5	0.7	0.3	0.3	30.2	6	91.0	13.3	3.0	2.2	109.7
Group B																
<i>Rinorea anguifera</i>	T	C	Violaceae	2	154.4	0.0	0.0	0.0	0.0	154.4	67	22.2	0.0	0.0	0.0	22.2
<i>Anaxagorea javanica</i>	T	L	Annonaceae	3	150.9	0.1	0.0	0.0	0.0	150.9	79	20.2	0.0	0.0	0.0	20.2
<i>Ardisia crassa</i>	T		Myrsinaceae	4	136.1	0.0	0.0	0.0	0.0	136.1		0.0	0.0	0.0	0.0	0.0
<i>Barringtonia macrostachya</i>	U	E/L	Lecythidaceae	10	64.5	7.2	0.0	0.0	0.0	71.7	372	2.5	0.0	0.0	0.0	2.5
<i>N. heimii</i>	E	C	Dipterocarpaceae	12	62.9	2.2	0.5	1.1	1.1	66.7	158	8.7	1.3	0.8	0.0	10.8
<i>Diospyros scortechinii</i>	T		Ebenaceae	14	62.1	0.2	0.0	0.0	0.0	62.3	198	7.7	0.2	0.0	0.0	7.8
<i>Aidia wallichiana</i>	U	L	Rubiaceae	17	43.8	7.3	0.0	0.0	0.0	51.2	211	6.2	1.0	0.0	0.0	7.2
<i>Shorea pauciflora</i>	E	C	Dipterocarpaceae	20	44.3	3.1	0.6	1.1	1.1	49.1	61	18.5	3.8	0.3	0.8	23.5
<i>Lepisanthes tetraphylla</i>	S		Sapindaceae	22	46.9	0.0	0.0	0.0	0.0	46.9	324	3.5	0.0	0.0	0.0	3.5
<i>S. leprosula</i>	E	E/L	Dipterocarpaceae	25	33.6	6.1	1.3	2.1	2.1	43.1	122	5.2	6.0	2.8	0.0	14.0
<i>Macaranga lowii</i>	U	L	Euphorbiaceae	26	38.8	3.3	0.0	0.0	0.0	42.1	148	11.2	0.2	0.0	0.2	11.5
<i>Memecylon minutiflorum</i>	U	C	Melastomataceae	27	38.8	1.8	0.0	0.0	0.0	40.5	56	23.3	1.0	0.0	0.0	24.3
<i>Xanthophyllum eurhynchum</i>	C		Polygalaceae	28	34.0	6.3	0.1	0.0	0.0	40.4	85	18.5	0.2	0.0	0.0	18.7
<i>Oncodostigma monosperma</i>	U		Annonaceae	31	34.6	4.5	0.0	0.0	0.0	39.0	125	13.7	0.2	0.0	0.0	13.8
<i>M. ferrea</i>	C	C	Guttiferae	35	29.8	4.7	0.8	0.0	0.0	35.3	143	10.2	1.8	0.0	0.0	12.0
<i>Urophyllum glabrum</i>	T		Rubiaceae	37	33.8	0.1	0.0	0.0	0.0	33.9	240	6.0	0.0	0.0	0.0	6.0
<i>Ardisia species 2</i>	S		Myrsinaceae	38	33.3	0.0	0.0	0.0	0.0	33.3	81	19.5	0.0	0.0	0.0	19.5
<i>M. atropurpurea</i>	C	C	Leguminosae	39	26.0	5.0	1.1	0.2	0.2	32.3	312	3.0	0.7	0.0	0.0	3.7
<i>Lithocarpus curtisii</i>	C	L	Fagaceae	41	27.3	4.5	0.1	0.0	0.0	31.9	331	1.7	1.2	0.5	0.0	3.3
<i>Ardisia kunstleri</i>	T		Myrsinaceae	42	31.7	0.0	0.0	0.0	0.0	31.7	327	3.5	0.0	0.0	0.0	3.5
<i>D. cornutus</i>	E		Dipterocarpaceae	44	25.7	3.3	0.8	1.3	1.3	31.1	272	3.7	0.7	0.3	0.3	5.0
<i>Canarium littorale</i>	C		Burseraceae	45	27.3	2.7	0.6	0.1	0.1	30.7	93	13.7	3.2	0.2	0.0	17.0
var. <i>Rufum</i>																
<i>Payena lucida</i>	U		Sapotaceae	46	25.1	5.6	0.0	0.0	0.0	30.7	102	11.7	4.0	0.0	0.0	15.7
<i>Vatica bella</i>	C	C	Dipterocarpaceae	47	27.7	2.7	0.1	0.0	0.0	30.5	69	20.5	1.2	0.0	0.0	21.7
<i>Diospyros apiculata</i>	U	C	Ebenaceae	49	27.2	2.9	0.0	0.0	0.0	30.1	53	23.0	1.8	0.0	0.0	24.8
<i>Rothmannia macrophylla</i>	S	L	Rubiaceae	50	30.0	0.0	0.0	0.0	0.0	30.0	155	10.8	0.0	0.0	0.0	10.8

Appendix B

The 50 most abundant species (in terms of basal area per hectare) in the tree census plots of the primary and regenerating forests. The figure listed in the table were summed basal area (cm²) in each diameter class. The species in Group A were ranked within the top 50 in both plots. Group B represents species ranked within the top 50 in the primary forest, but not in the regenerating forest. Group C represents species ranked within the top 50 in the regenerating forest, but not in the primary forest. The following layer groups were used: E, emergent; C, canopy; U, understory; T, treelet; and S, shrub. The species with typical successional status were grouped with following characters: C, climax (shade tolerant); L, late successional; E, pioneer/early successional. Ranking was not shown if no trees were found in the plot.

Name	Layer group	Successional group	Family	Primary forest			Regenerating forest			Total					
				Ranking	<10 cm	10–30	30–50	Ranking	<10 cm		10–30	30–50			
					(DBH)				(DBH)						
Group A															
<i>S. leprosula</i>	E	E/L	Dipterocarpaceae	1	395	1332	1458	8256	11442	13	114	1984	2759	0	4857
<i>S. maxwelliana</i>	E	C	Dipterocarpaceae	2	965	1984	1840	6093	10882	2	1545	2097	4356	6718	14717
<i>N. heimii</i>	E	C	Dipterocarpaceae	3	591	433	577	7759	9360	41	200	286	1080	0	1566
<i>Shorea pauciflora</i>	E	L/C	Dipterocarpaceae	4	384	699	774	6566	8423	11	269	874	475	4252	5870
<i>S. acuminata</i>	E	L	Dipterocarpaceae	5	337	534	1032	5794	7696	3	493	4243	5295	3772	13803
<i>D. cornutus</i>	E	E	Dipterocarpaceae	6	292	894	844	5663	7694	44	64	99	512	824	1498
<i>Shorea lepidota</i>	E	L	Dipterocarpaceae	7	138	610	834	5932	7514	10	55	2663	2297	1852	6868
<i>Koompassia malaccensis</i>	E	E	Leguminosae	8	115	636	1097	5230	7078	16	311	626	327	2493	3758
<i>Shorea parvifolia</i>	E	L	Dipterocarpaceae	10	214	935	1473	2381	5003	1	56	2328	4510	9565	16460
<i>Xerospermum noronhianum</i>	C	C	Sapindaceae	13	975	2468	424	0	3867	28	1191	949	203	0	2343
<i>Scaphium macropodum</i>	C	L	Sterculiaceae	18	142	752	1121	1157	3172	38	490	1035	122	0	1646
<i>Shorea macroptera</i>	E	L	Dipterocarpaceae	19	264	849	815	1233	3161	4	1012	3151	3830	5529	13522
<i>Pimelodendron griffithianum</i>	C	C	Euphorbiaceae	20	558	1561	741	129	2988	14	1381	2746	153	0	4280
<i>Dipterocarpus crinitus</i>	E	E	Dipterocarpaceae	23	54	59	129	2421	2663	17	399	1422	657	1271	3749
<i>Dyera costulata</i>	E	E/L	Apocynaceae	25	62	398	356	1811	2626	27	43	162	222	2079	2507
<i>Santiria laevigata</i>	C	C	Bursaceae	29	127	359	372	1294	2152	23	343	1269	678	748	3037
<i>Castanopsis schefferiana</i>	C	C	Fagaceae	34	88	440	894	502	1925	7	169	3654	2865	1011	7699
<i>Monocarpia marginalis</i>	C	C	Annonaceae	37	211	1097	555	0	1863	30	229	1678	271	0	2177
<i>Gironniera parvifolia</i>	U	C	Ulmaceae	38	1358	475	0	0	1834	26	2129	299	225	0	2654
<i>Heritiera simplicifolia</i>	E	E	Sterculiaceae	41	121	483	290	767	1661	25	98	410	935	1261	2704
<i>Dacryodes rostrata</i>	C	C	Bursaceae	42	618	826	167	0	1611	35	1090	815	0	0	1906
<i>Parkia speciosa</i>	C	L	Leguminosae	45	127	306	597	485	1515	12	82	2586	2208	0	4876
<i>Archidendron bubalinum</i>	U	U	Leguminosae	46	426	1006	80	0	1512	33	868	1147	0	0	2015

Appendix B. (Continued)

Name	Layer group	Successional group	Family	Primary forest				Regenerating forest							
				Ranking	<10 cm (DBH)	10–30	30–50 ≥50	Total	Ranking	<10 cm (DBH)	10–30	30–50 ≥50	Total		
<i>Artocarpus scortechinii</i>	C	L	Moraceae	49	97	310	526	467	1400	8	178	4264	2857	0	7299
Group B															
<i>Ixonanthes icosandra</i>	C	E/L	Ixonanthaceae	9	544	2480	2422	531	5977	89	432	356	0	0	787
<i>Quercus argentata</i>	E		Fagaceae	11	163	788	1713	2127	4790	112	20	369	244	0	633
<i>C. malaccensis</i>	E	C	Leguminosae	12	208	1041	1599	1793	4641	682	1	0	0	0	1
<i>Dacryodes rugosa</i>	C		Bursaceae	14	1247	2163	101	0	3512	86	493	319	0	0	812
<i>Dipterocarpus costulatus</i>	E	L	Dipterocarpaceae	15	115	109	42	3209	3475	60	333	154	233	410	1130
<i>S. griffithii</i>	C	L	Oxalidaceae	16	28	225	483	2739	3475	175	61	298	0	0	359
<i>M. atropurpurea</i>	C	C	Leguminosae	17	421	1187	1294	560	3462	227	70	146	0	0	216
<i>I. palembanica</i>	E	C	Leguminosae	21	58	342	1028	1461	2889		0	0	0	0	0
<i>S. ovalis</i>	E	L	Dipterocarpaceae	22	228	464	346	1766	2804	66	40	468	551	0	1059
<i>O. amenitacea</i>	C	C	Oleaceae	24	340	1621	658	42	2662	285	48	104	0	0	152
<i>P. motleyi</i>	E	L	Anacardiaceae	26	145	605	1182	581	2514	61	132	493	482	0	1108
<i>Triplaris malaccensis</i>	E	L	Bursaceae	27	83	293	565	1470	2411	83	215	642	0	0	857
<i>M. ferrea</i>	C	C	Guttiferaceae	28	328	1137	824	0	2290	147	103	368	0	0	471
<i>Shorea bracteolata</i>	E		Dipterocarpaceae	30	186	499	737	607	2029	134	21	185	298	0	504
<i>Neoscortechinia kingii</i>	C		Euphorbiaceae	31	277	1179	524	0	1980	158	242	170	0	0	413
<i>Aidia wallichiana</i>	U	L	Rubiaceae	32	681	1281	14	0	1976	237	78	126	0	0	204
<i>Pometia pinnata</i> var. <i>alnifolia</i>	C	L	Sapindaceae	33	143	803	626	366	1938	146	91	238	142	0	472
<i>Dialium platysepalum</i>	E		Leguminosae	35	181	353	617	728	1880	169	68	302	0	0	370
<i>Canarium littorale</i> var. <i>rufum</i>	C		Bursaceae	36	331	686	690	157	1863	81	199	573	118	0	889
<i>Sindora coriacea</i>	E	C	Leguminosae	39	212	221	185	1169	1787	65	191	354	519	0	1064
<i>Barringtonia macrostachya</i>	U	E/L	Lecythidaceae	40	740	994	14	0	1747	484	30	0	0	0	30
<i>Xanthophyllum eurhynchum</i>	C		Polygalaceae	43	458	1087	56	0	1601	189	292	15	0	0	308
<i>Alangium ebenaceum</i>	U		Alangiaceae	44	629	826	93	0	1548	93	386	362	0	0	748
<i>Atuna excelsa</i>	E		Rosaceae	47	66	298	641	474	1480	315	39	84	0	0	123
<i>Lithocarpus curtisii</i>	C	L	Fagaceae	48	334	996	63	49	1442	75	25	333	583	0	940
<i>Nephelium costatum</i>	C		Sapindaceae	50	301	743	316	0	1361	102	204	488	0	0	692

Appendix B. (Continued)

Name	Layer group	Successional group	Family	Primary forest				Regenerating forest							
				Ranking	<10 cm (DBH)	10–30	30–50 ≥50	Total	Ranking	<10 cm (DBH)	10–30	30–50 ≥50	Total		
<i>Artocarpus scortechinii</i>	C	L	Moraceae	49	97	310	526	467	1400	8	178	4264	2857	0	7299
Group B															
<i>Ixonanthes icosandra</i>	C	E/L	Ixonanthaceae	9	544	2480	2422	531	5977	89	432	356	0	0	787
<i>Quercus argentata</i>	E		Fagaceae	11	163	788	1713	2127	4790	112	20	369	244	0	633
<i>C. malaccensis</i>	E	C	Leguminosae	12	208	1041	1599	1793	4641	682	1	0	0	0	1
<i>Dacryodes rugosa</i>	C		Bursaceae	14	1247	2163	101	0	3512	86	493	319	0	0	812
<i>Dipterocarpus costulatus</i>	E	L	Dipterocarpaceae	15	115	109	42	3209	3475	60	333	154	233	410	1130
<i>S. griffithii</i>	C	L	Oxalidaceae	16	28	225	483	2739	3475	175	61	298	0	0	359
<i>M. atropurpurea</i>	C	C	Leguminosae	17	421	1187	1294	560	3462	227	70	146	0	0	216
<i>I. palembanica</i>	E	C	Leguminosae	21	58	342	1028	1461	2889		0	0	0	0	0
<i>S. ovalis</i>	E	L	Dipterocarpaceae	22	228	464	346	1766	2804	66	40	468	551	0	1059
<i>O. amenitacea</i>	C	C	Oleaceae	24	340	1621	658	42	2662	285	48	104	0	0	152
<i>P. motleyi</i>	E	L	Anacardiaceae	26	145	605	1182	581	2514	61	132	493	482	0	1108
<i>Triplaris malaccensis</i>	E	L	Bursaceae	27	83	293	565	1470	2411	83	215	642	0	0	857
<i>M. ferrea</i>	C	C	Guttiferaceae	28	328	1137	824	0	2290	147	103	368	0	0	471
<i>Shorea bracteolata</i>	E		Dipterocarpaceae	30	186	499	737	607	2029	134	21	185	298	0	504
<i>Neoscortechinia kingii</i>	C		Euphorbiaceae	31	277	1179	524	0	1980	158	242	170	0	0	413
<i>Aidia wallichiana</i>	U	L	Rubiaceae	32	681	1281	14	0	1976	237	78	126	0	0	204
<i>Pometia pinnata</i> var. <i>alnifolia</i>	C	L	Sapindaceae	33	143	803	626	366	1938	146	91	238	142	0	472
<i>Dialium platysepalum</i>	E		Leguminosae	35	181	353	617	728	1880	169	68	302	0	0	370
<i>Canarium littorale</i> var. <i>rufum</i>	C		Bursaceae	36	331	686	690	157	1863	81	199	573	118	0	889
<i>Sindora coriacea</i>	E	C	Leguminosae	39	212	221	185	1169	1787	65	191	354	519	0	1064
<i>Barringtonia macrostachya</i>	U	E/L	Lecythidaceae	40	740	994	14	0	1747	484	30	0	0	0	30
<i>Xanthophyllum eurhynchum</i>	C		Polygalaceae	43	458	1087	56	0	1601	189	292	15	0	0	308
<i>Alangium ebenaceum</i>	U		Alangiaceae	44	629	826	93	0	1548	93	386	362	0	0	748
<i>Atuna excelsa</i>	E		Rosaceae	47	66	298	641	474	1480	315	39	84	0	0	123
<i>Lithocarpus curtisii</i>	C	L	Fagaceae	48	334	996	63	49	1442	75	25	333	583	0	940
<i>Nephelium costatum</i>	C		Sapindaceae	50	301	743	316	0	1361	102	204	488	0	0	692

Appendix B. (Continued)

Name	Layer group	Successional group	Family	Primary forest			Regenerating forest			Total					
				Ranking	<10 cm (DBH)	10–30	30–50	≥50	Ranking		<10 cm (DBH)	10–30	30–50	≥50	
Group C															
<i>E. malaccense</i>	C	E	Euphorbiaceae	362	10	62	67	0	138	5	27	5567	5268	1097	11959
<i>Dipterocarpus sublamellatus</i>	E		Dipterocarpaceae	648	2	12	0	0	14	6	718	2042	1756	3636	8151
<i>P. amisophylla</i>	U	E	Rubiaceae	62	190	914	15	0	1119	9	398	5827	0	1048	7273
<i>Lithocarpus wallichianus</i>	C	L	Fagaceae	219	61	139	117	0	317	15	51	1939	2244	0	4234
<i>Ganua species 1</i>	C	C	Sapotaceae	225	16	122	169	0	308	18	1205	907	136	1275	3522
<i>Xylopia ferruginea</i>	C	L	Annonaceae	332	18	147	0	0	165	19	18	2413	1034	0	3465
var. <i>ferruginea</i>															
<i>Hopea mengerawan</i>	C	C	Dipterocarpaceae	117	108	269	148	78	603	20	630	748	1667	391	3437
<i>C. argyrateus</i>	U	E	Euphorbiaceae	161	269	143	0	46	458	21	923	964	0	1369	3256
<i>Anisophyllea corneri</i>	C	C	Rhizophoraceae	79	182	638	50	0	870	22	648	187	285	1986	3106
<i>Canarium patentinervium</i>	U		Burseraceae	337	38	80	0	43	161	24	654	1362	131	798	2945
<i>Artocarpus maingayi</i>	C	L	Moraceae	142	26	163	206	113	508	29	566	1387	303	0	2256
<i>Dacryodes costata</i>	C	C	Burseraceae	86	112	323	332	48	815	31	629	703	226	531	2089
<i>Lithocarpus rassa</i>	C	L	Fagaceae	100	114	360	219	42	736	32	82	1803	132	0	2017
<i>Santiria tomentosa</i>	C		Burseraceae	77	69	307	434	84	894	34	144	1248	145	469	2006
<i>Shorea multiflora</i>	C	C	Dipterocarpaceae	768	1	0	0	0	1	36	163	408	387	798	1756
<i>Artocarpus rigidus</i>	C	L	Moraceae	70	57	161	289	512	1018	37	284	715	169	561	1729
<i>Sandoricum koeijape</i>	C	C	Meliaceae	342	38	119	0	0	157	39	253	1375	0	0	1628
<i>Knema scortechinii</i>	C	C	Myristicaceae	112	187	433	28	0	648	40	314	451	0	863	1627
<i>Anisoptera laevis</i>	E	E	Dipterocarpaceae	51	25	196	65	1071	1356	42	43	56	464	973	1536
<i>Parashorea densiflora</i>	E	E	Dipterocarpaceae	75	41	131	74	673	919	43	299	377	846	0	1521
<i>Myristica maingayi</i>	E	E	Myristicaceae	137	53	161	191	110	515	45	135	343	0	1017	1495
<i>Dillenia reticulata</i>	C	E/L	Dilleniaceae	314	13	31	73	63	180	46	139	917	0	430	1486
<i>Lepisanthes senegalensis</i>	U	U	Rubiaceae	182	293	104	0	0	398	47	434	116	0	917	1467
<i>Knema patentinervia</i>	U	L	Myristicaceae	91	388	387	0	0	775	48	376	350	0	722	1448
<i>Xylopia caudata</i>	U	L	Annonaceae	205	80	245	15	0	341	49	351	733	0	358	1441
<i>Santiria apiculata</i>	C	C	Burseraceae	153	164	234	88	0	486	50	403	487	0	534	1424

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