

## ORIGINAL ARTICLE

# Spatiotemporal changes in biomass after selective logging in a lowland tropical rainforest in Peninsular Malaysia

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**ABSTRACT** We studied biomass changes in a lowland tropical rain forest in the Pasoh Forest Reserve of Peninsular Malaysia after selective logging in 1958. A tree census was undertaken every 2 years from 1998 to 2012 in a 6-ha logged forest plot. Total aboveground biomass (AGB) was 72 % of that in a primary forest plot within the same reserve in 1998, but reached 87 % in 2012. AGB regrowth was spatially variable within the logged forest plot and was much less in swampy areas than in upland areas. The overall annual growth rate of AGB in the logged forest throughout the study period was 1.5 % and slowed (to 0.6 %) in a dry period (2004-2006). The biomass of large trees (DBH  $\geq$  50 cm) increased by 56 % during the study period, but amounted to only 58 % of the biomass of the corresponding size class in the primary forest, suggesting that stand structure is still recovering from logging. Spatiotemporal variation in AGB recovery after logging needs to be taken into account for logging and subsequent management of the tropical lowland forest biome.

**Key words:** Forest regeneration, Lowland dipterocarp forest, Stand structure, Annual rainfall, Topography

## INTRODUCTION

Given the intensive use of natural resources at global and local scales, combined with global population growth, the sustainable use of resources must be the principle behind any natural resource utilization or exploitation. This is particularly significant in the tropics, where deforestation rates averaged  $14.2 \times 10^6$  ha  $y^{-1}$  from 1990 to 2000 (FAO 2001). A more recent survey (FAO 2010) reported that net deforestation in tropical countries slowed somewhat, to  $8.1 \times 10^6$  ha  $y^{-1}$ , between 2000 and 2010, but these values may underestimate the actual extent of carbon losses, because the “deforested area” does not take into account forest degradation caused by illegal or unsustainable logging and intensive use of forests for fuelwood production (e.g., Deutscher et al. 2013, Magdon and Kleinn 2013, Mitchard et al. 2013). Furthermore, large uncertainties exist in carbon

sequestration by forests because information on the long-term recovery processes after logging is limited (Bicknell et al. 2010, Edwards et al. 2014b, Lussetti et al. 2019). The harvest cycle, even for legal logging operations, is based on the assumption that the forest recovers steadily and homogeneously and does not account for spatial heterogeneity in recovery (e.g. in relation to topography). Thus, if the biomass recovery is heterogeneous, the biomass depression after logging would be even greater than the estimated values that are often used in mitigation programs, as current knowledge of regeneration in timber production is based on optimal growth of trees, regardless of environmental conditions. Thus, as timber cropping schemes are based on the premise of homogeneous environments, slow recovery from logging might have contributed to recent rapid increases in ambient CO<sub>2</sub> (Fanin and van der Werf 2015, Fearnside et al. 2009, Gibbs et al. 2007, van der Werf and

Peterson 2009).

In this context, logging operations and subsequent forest management must be improved to promote recovery of forest structure and biodiversity (Chapman and Chapman 1997, Edwards et al. 2014a, Okuda et al. 2003a, 2004b, Panfil and Gullison 1998).

To move toward this goal, it is necessary to understand the regeneration processes that occur after selective logging and the ecological consequences, including the spatio-temporal variation of forest biomass in response to variation in environmental parameters such as climate (e.g., the effects of drought) and topography (e.g., dry uplands and swampy areas) (Busch et al. 2011, Minang and van Noordwijk 2013, Pasgaard 2013, Sangermano et al. 2012). Improving our knowledge of these factors will provide insights into the complexity of biomass changes, including whether forests regenerate steadily, with a simple linear growth rate, or show more complex trends. Despite the importance of such information, the amount of information based on field surveys and tree censuses is limited (Pinard et al. 2000, Putz et al. 2008, 2012, Poorter et al. 2016).

The objective of this study was to provide some of the missing basic information on forest growth and postharvest regrowth in a tropical rain forest. We studied the spatio-temporal changes in biomass of a naturally growing forest in the Pasoh Forest Reserve, Peninsular Malaysia, where some compartments were selectively logged in the 1950s under a uniform shelterwood forest management system called the Malayan (later Malaysian) Uniform System (MUS) (Wyatt-Smith 1963, Thang 1987, 1997). Forests in the reserve develop on undulating rolling hills and small valleys and suffer from sporadic droughts and storms. We hypothesized that biomass recovery varies with topography and precipitation, and thus cropping (timber harvest) needs to account for spatiotemporal heterogeneity even at the local scale.

## MATERIALS AND METHODS

### *Study area*

The study was conducted in a lowland dipterocarp forest within the Pasoh Forest Reserve (2°57'40"–3°00'20" N, 102°17'–102°20'E), in the state of Negeri Sembilan, about 70 km southeast of Kuala Lumpur, Malaysia (Fig. 1). The mean annual rainfall over the 18 years from 1996 to 2013 measured at the research station in the reserve (Fig. 1) was 1807.5 mm, with distinct rainfall peaks in March–May and October–December. Before our initial tree census in

1998, the study area experienced a dry spell in 1997, with extremely low precipitation (1182 mm). Rainfall that was more than 8 % below the annual average was also recorded in 1998, 2004–2005, 2009, and 2012 (Fig. 2).

The dominant soil is a silty loam from the Bungor–Malacca Association Type that develops mainly from shale, granite, and fluvialite granite alluvium parent materials in lowland alluvial areas (Allbrook 1973). Within these flat alluvial areas, the topography consists mainly of small expanses of swales, riverine areas, and gently rolling hills (Manokaran et al. 2004, Okuda et al. 2004a). The swales and swampy riverine areas usually consist of poorly drained soils, whereas the upper parts of gently rolling hills (i.e., hereafter, upland areas) have well-drained, fine sandy clay soils (Okuda et al. 2004a).

The overall vegetation type in the reserve is a lowland dipterocarp forest characterized by a high proportion of species in the Dipterocarpaceae (Symington 1943, Wyatt-Smith 1961), and is one of the most species-rich communities in the world (Whitmore 1984). Floristic evidence shows that the primary forest in the study area has no evidence of major disturbance, and therefore appears to be representative of the lowland forest of the south-central Malay Peninsula (Kochummen et al. 1990, Manokaran and LaFrankie 1990).

Southern and eastern edges of the reserve had been selectively logged during the mid- to late 1950s (Fig. 1) under the MUS, and at the time of this study, it represented regenerating forest (Okuda et al. 2003a). Under the MUS, only commercially valuable timber (with a lower cutting limit of 45 cm in diameter at breast height: DBH) was extracted. MUS was a more moderate operation than the selective forest logging regimes (termed “conventional logging”) that were used after MUS until the 1990s, in which heavy equipment such as tractors and bulldozers were used for timber extraction (Manokaran 1998 and pers. comm., Thang 1987, 1997). Such equipment (for timber extraction) can seriously delay subsequent regeneration, cause erosion, and damage the forest floor and non-target trees during the creation of logging roads and extraction of wood using mechanized equipment such as skidders (Burgess 1968, 1971).

The MUS was discontinued in the 1970s when the potentially valuable tracts of lowland dipterocarp forest were converted into oil palm plantations, leading to loss of most of the native forest in the lowland area (Manokaran 1998). By the time the MUS was implemented at our study site, the logging operations had shifted to the hill dipterocarp forests, as the monocyclic approach was advocated under the MUS, which allows only one harvest until the site

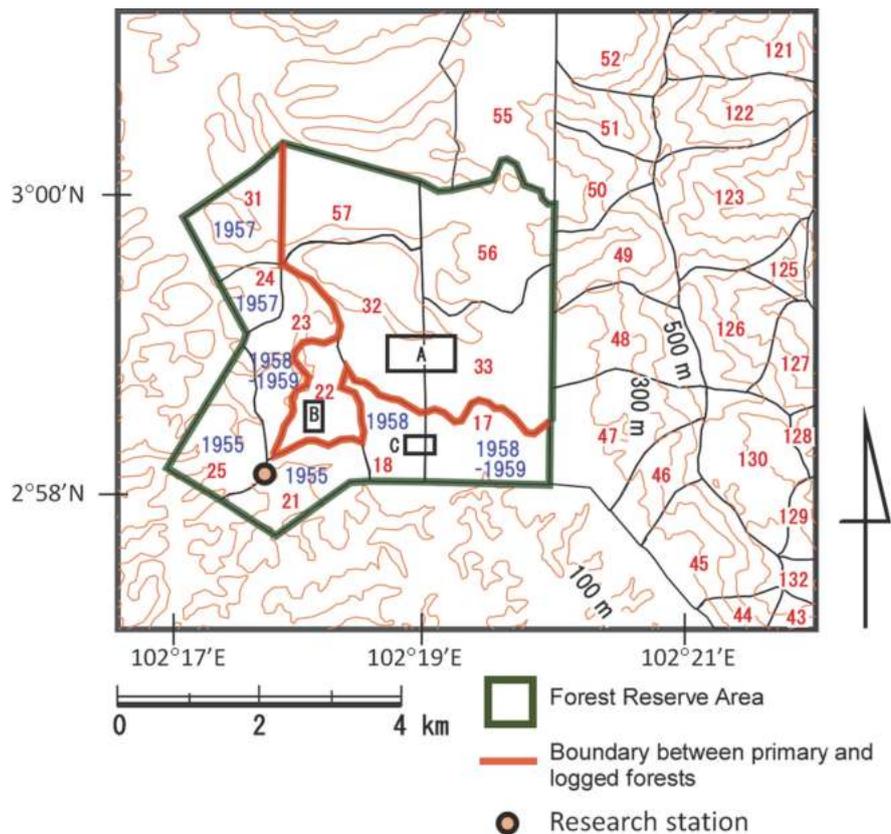


Fig. 1. The study plots in the Pasoh Forest Reserve. Blue dates represent the years when logging was carried out under the Malaysian Uniform System; red numbers represent the forest compartments. The logged forest plot (C) was in the southern part of the reserve. The primary forest plot (B) was in the southwestern part of the primary forest, near the boundary between the primary and secondary forests. A 50-ha plot (A) was established in the central part of the reserve and has been maintained as pristine (primary) forest. The map is modified from Okuda et al. (2003b). Part of the logged forest plot was located in compartment 17, where selective logging was implemented from 1958 to 1959, so the “logging operation year” for this plot was regarded as “1958”.

has recovered completely, predicted to take  $>70$  years (Kurpick et al. 1997). Such an approach proved unsuccessful in the hill-dipterocarp forests owing to their uneven stocking, preventing the MUS operations from being economically attractive to the forestry sector (Thang 1997). Under the MUS, large unmerchantable trees were supposed to be felled by poison girdling in order to encourage the growth of merchantable trees, but many big canopy trees had been left untouched (Okuda et al. 2003b). This suggests that the MUS had not been completely implemented at the study site.

### *Tree censuses in the study plots*

Two 6-ha study plots of equal size ( $300\text{ m} \times 200\text{ m}$ ) were established within the southern part of the reserve: one in the primary forest, near the southern edge of the reserve (the “primary forest plot”; Plot B in Fig. 1), and the other

in an area of forest that had been selectively logged in 1958 following the MUS (Thang 1987, 1997, Wyatt-Smith 1963) (the “logged forest plot”; Plot C in Fig. 1). We compared the total aboveground biomass (AGB) in these plots. To provide an additional comparison with the AGB of the primary forest, we used tree census data acquired in another primary forest plot (50 ha; Plot A in Fig. 1).

Although the Pasoh Forest Reserve is located in a relatively flat lowland area, the topography within the study plots includes low rolling hills, with taller hills in the east, near the boundary with an adjacent oil palm plantation, and slopes descending toward the south and southwest. The maximum slope angle was  $<15^\circ$  in the logged forest plot. The northeastern and northwestern corners of this plot are swampy areas, and the rest of the plot comprises upland areas (Fig. 3). The tree density and AGB were lower in the swampy areas than in the upland areas, which do not flood during the rainy season (Okuda et al. 2004b). In our analyses of AGB and its spatiotemporal changes, we

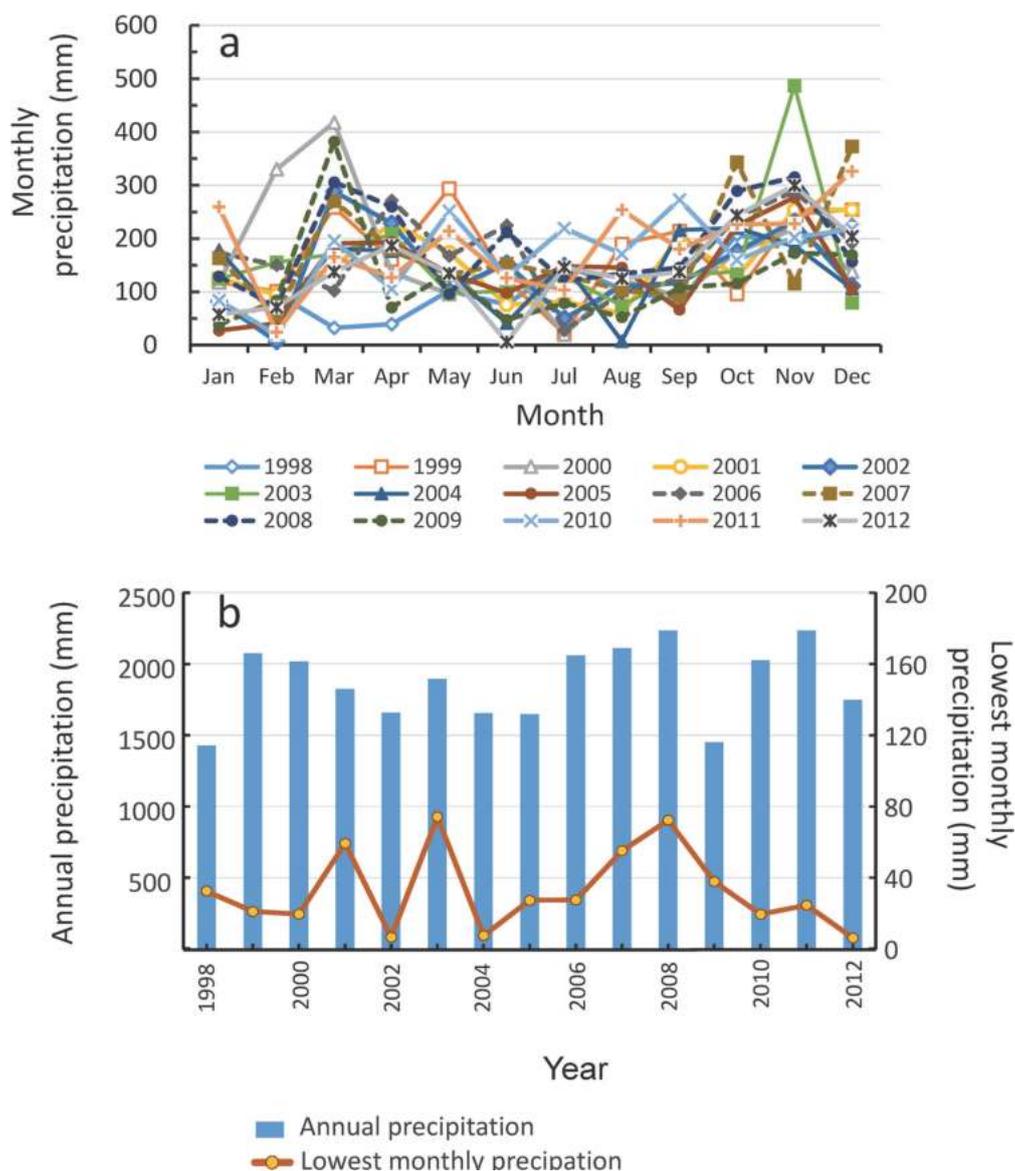


Fig. 2. (a) Monthly precipitation, (b, left axis) annual precipitation, and (b, right axis) lowest monthly precipitation measured at a research station 0.5 km southwest of the 6-ha primary forest plot (Fig. 1) in the Pasoh Forest Reserve, from 1998 to 2012. The range bars in the monthly values represent  $\pm 1$  SE. The mean annual rainfall measured in this period was 1870.9 mm (see text). Monthly precipitation was lowest in either January–March or June–August.

distinguished between the swampy and upland areas to account for the effects of topography (Fig. 3).

In plot C, a permanent plot within the logged forest, we surveyed the tree growth from 1998 to 2012. The initial tree census in the logged forest plot was conducted between October 1997 and February 1999 following the methods of Manokaran et al. (1990). This census was regarded as the 1998 data. The tree census was repeated every 2 years to generate census data in 2000, 2002, 2004, 2006, 2008, 2010, and 2012. (Each census took about 6 to 12 months to complete, so the stated census year represents the start of

the 2-year measurement period.). We used the same methodology for establishing and surveying the study plots that had been used in plot A (Manokaran and LaFrankie 1990, Manokaran et al. 1990, 1999). In the logged forest plot, all woody plants  $\geq 1$  cm in DBH were identified, tagged, and measured for DBH, and their positions were mapped to the nearest 10 cm (Manokaran et al. 1990).

Plot B, the primary forest plot chosen for comparison with the logged forest, was established 2 km southwest of the 6-ha logged forest plot (Fig. 1). In part of this old-growth forest, all trees  $\geq 5$  cm in DBH were mapped and

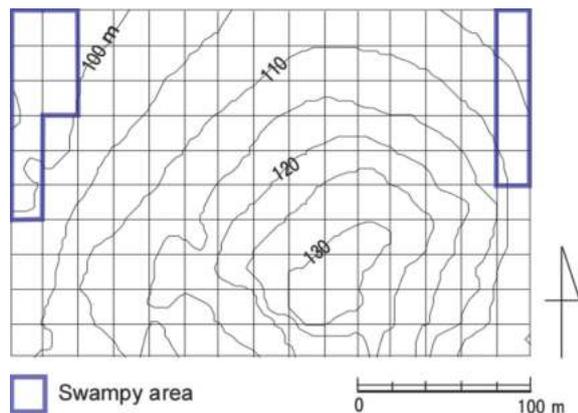


Fig. 3. Map of the logged forest plot (C). The grid is marked at 20-m intervals to divide the plot into subplots (20 m × 20 m).

subsequently measured every 2 years since 1994 (Niiyama et al. 2003). The plot was established in the upland area, and unlike the logged plot, did not include any swampy areas. The species composition, stand structure, and other aspects of the vegetation have been monitored since the early 1990s. We used tree census data ( $\geq 5$  cm in DBH) taken every 2 years from 1994 to 2006 in plot B and from 1998 to 2012 in plot C to compare AGB.

AGB and stem density were determined for six DBH size classes:  $< 10$  cm ( $5 \text{ cm} \leq \text{DBH} < 10$  cm), 10 to 20 cm ( $10 \text{ cm} \leq \text{DBH} < 20$  cm), 20 to 30 cm, 30 to 40 cm, 40 to 50 cm, and  $\geq 50$  cm. We grouped the trees into four size ranges to analyze how the stand structure recovered during the census period: small ( $5 \text{ cm} \leq \text{DBH} < 20$  cm), medium ( $20 \text{ cm} \leq \text{DBH} < 40$  cm), and semi-large ( $40 \text{ cm} \leq \text{DBH} < 50$  cm) and large trees ( $\text{DBH} \geq 50$  cm).

We also classified the tree species recorded in both logged and primary forest plots (plots B and C) into five structural component categories (emergent, canopy, understory, treelet and shrub component), regardless of their size, in accord to their predicted category at maturity based on the “life form category list” of Manokaran et al. (1990). This grouping was done to see how structural recovery progressed from the perspective of the structural role of each species. We omitted the result of shrub category from this paper because it accounted for a small proportion to AGB ( $< 3\%$ ). These component categories were based on a floristic and tree census survey conducted in plot A (Fig. 1), where the species composition differs somewhat from those in plot B (primary forest) and plot C (logged forest), thus doesn't perfectly describe the two present study plots.

To provide additional AGB reference data for comparison with plot C, we used the estimated value of AGB based on tree census data obtained from plot A (Okuda et al.

2004b). The western side of this plot includes a swampy area that floods during the rainy season. Thus, the topographic features of this plot resemble those of plot C. Plot A was established in 1985, when all trees  $\geq 1$  cm in DBH were mapped, and they have been measured every 5 years since then.

### Estimation of AGB

To estimate AGB, we estimated the individual tree biomass using a simple regression model based on an improved version ( $R^2 = 0.736$ ,  $P < 0.001$ ; Okuda et al. 2004b) of an older allometric relationship between DBH and tree height (Kato et al. 1978). To identify significant differences in AGB between plots B and C and between swampy and upland areas within plot C, we subdivided each plot into 150 subplots of 0.04 ha (20 m × 20 m); in Plot C, 14 subplots were in swampy areas and 136 were in uplands. The rate of temporal variation in AGB (AGB growth rate) was expressed as the annual change in AGB between surveys:

$$\begin{aligned} \text{AGB growth rate (y}^{-1}\text{, \%)} \\ = (\text{AGB}_{t_1} - \text{AGB}_{t_0}) / (t_1 - t_0) / \text{AGB}_{t_0} \times 100, \end{aligned}$$

where  $\text{AGB}_{t_1}$  and  $\text{AGB}_{t_0}$  are AGB in tree census years  $t_1$  and  $t_0$ . This included negative values (a reduction of AGB) caused by tree death between censuses.

To examine the significance of differences in AGB within the logged plot (swampy vs. upland area) and between the plots (logged plot vs. primary forest plot), we converted the average AGB per plot and per subplot into a value per hectare, and then employed one-way ANOVA using the Bell Curve add-in package (SSRI, Tokyo, Japan) for Excel 2013 (Microsoft Inc., Redmond, WA, USA). Before performing the ANOVA, we used Levene's test (Levene 1960) to confirm homogeneity of variance of the AGB values.

Similarly, we analyzed the difference in AGB growth rate ( $\text{y}^{-1}$ , %) between the swampy and upland areas and between the consecutive tree census periods (e.g., 2002–2004 vs. 2004–2006) on a subplot basis within the logged forest plot.

If either sample to be compared had a heterogeneous (unequal) variance, we instead used the Brown–Forsythe test, which can reveal differences in mean values between samples with heterogeneous variance. Hereafter, we state which test (ANOVA or Brown–Forsythe test) was used in the analysis.

## RESULTS

### Overall and spatiotemporal biomass changes in the logged forest plot

AGB increased by 1.5% annually in the logged forest over the 14-year period from 1998 to 2012, but by only 0.6% annually after dry years (2004–2006), and by 0.8% after low rainfall in 2009 (Fig. 4). In contrast, it increased by only 0.01% annually in the primary forest from 1994 to 2006, the net result of a 1.12% annual decrease from 1994 to 2002, followed by a 2.50% annual increase from 2002 to 2006 (Fig. 4). Initially, the AGB of the logged forest plot was 261 t ha<sup>-1</sup> in 1998 tree census. By the 2012 census, however, AGB had reached 315 t/ha in the whole plot area, which was 87% of the average value of 363 t/ha from 1994 to 2006 in the 6-ha primary forest plot.

Average AGB per subplot was significantly lower in the upland areas of the logged forest plot than in the primary forest plot in the same years (1994–2006) (Brown–Forsythe test,  $P < 0.01$ ; Fig. 4). However, AGB in 2012 was 328 t/ha, and was no longer significantly different from that in the primary forest plot in 2006 (Brown–Forsythe test,  $F_{1,207.4} = 3.96$ ,  $P = 0.0478$ ; Fig. 4), indicating that AGB had recovered to the same level as in the primary forest plot in an area with similar topography. Moreover, the average total AGB in the whole area of logged forest (315 t/ha) was comparable to the average value of 310 t/ha estimated in the 50-ha primary forest plot (Plot A Fig. 1).

Within the logged forest plot, the average AGB in the swampy subplots was 55% to 60% of that in upland areas

(Fig. 4). The average during the 14 years ranged from 165.0 to 187.5 t/ha in the swampy areas versus 272.5 to 327.5 t/ha in the upland areas (Fig. 4). The difference between areas was significant at all tree censuses (ANOVA,  $P < 0.001$ ).

AGB decreased sharply in the swampy area from 2004 to 2006 (Fig. 4), with a growth rate of  $-3.3\% \text{ y}^{-1}$  (Fig. 5), which was significantly lower than in the previous tree census period of 2002 to 2004 (ANOVA,  $P < 0.01$ ). Similarly, AGB stopped the growth in the upland area during 2002 to 2004, with a growth rate of  $0.2\% \text{ y}^{-1}$ , but this reduction was not significant compared with the previous census period (ANOVA,  $P > 0.05$ ). The AGB growth rate in the swampy area recovered to  $4.8\% \text{ y}^{-1}$  in 2006–2008 and was significantly higher (ANOVA,  $P < 0.001$ ) than that in the upland area (Fig. 5). However, the overall AGB growth rate throughout the census period was not significantly different (ANOVA,  $P > 0.05$ ) between the two areas.

### Stand structure

In contrast to the AGB results, the total number of trees ( $\geq 5$  cm in DBH) was higher in the logged forest plot than in the primary forest in all tree census years (Table 1). This can be attributed largely to the higher density of small ( $< 20$  cm in DBH) and medium (20 to 40 cm in DBH) trees in the logged plot. It is notable that the density of the large trees ( $\geq 50$  cm) was still lower in the logged plot than in the primary forest more than 50 years after the logging (24.7 trees/ha in 2012, vs. 31.5 trees/ha in 2006). The proportion of the total number of stems accounted for by this DBH

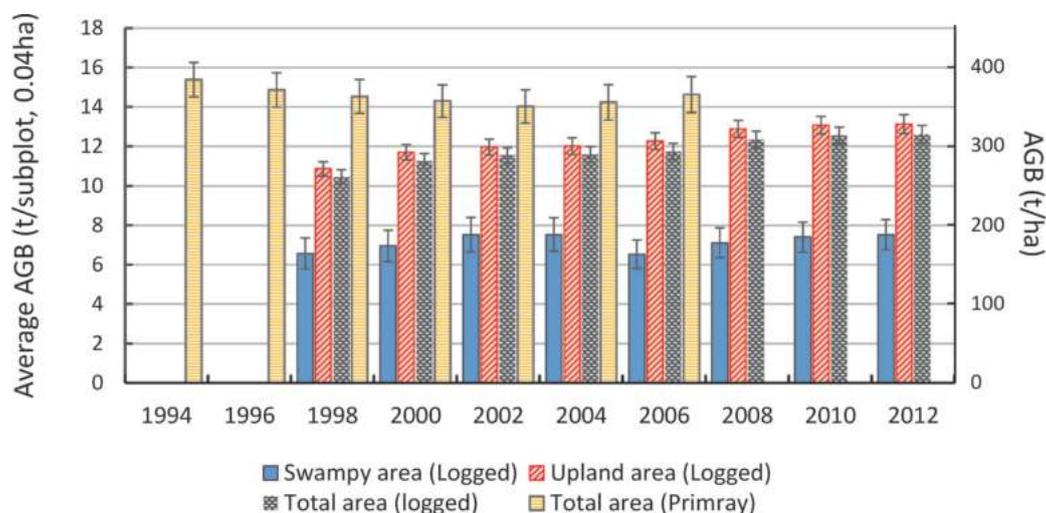


Fig. 4. Changes in the mean value of total aboveground biomass (AGB) in the 20-m  $\times$  20-m subplots from 1998 to 2012 in the logged forest plot (plot C in Fig. 1) and from 1994 to 2006 in the primary forest plot (plot B) in the Pasoh Forest Reserve. Both plots covered 6 ha. The right axis shows AGB values per hectare (t/ha). The range bars represent  $\pm 1$  SE.

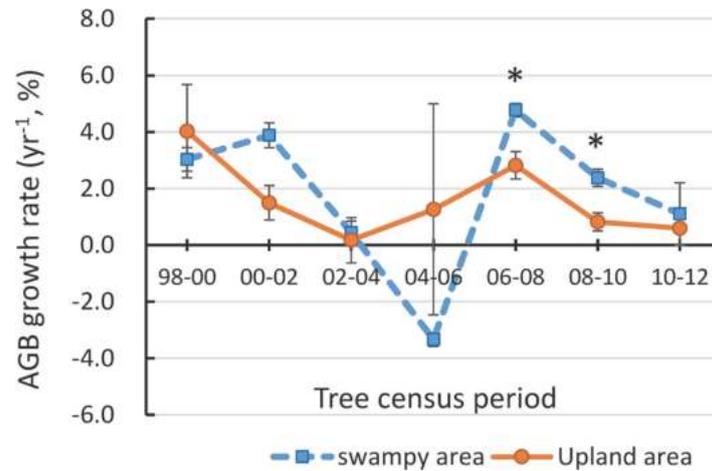


Fig. 5. Changes in average AGB growth rate (%  $y^{-1}$ ) between two consecutive tree census years in swampy and upland areas of logged forest plots. The range bars represent  $\pm 1$  SE. \*Average AGB growth rates are significantly different (ANOVA,  $P < 0.001$ ) between the swampy and upland areas.

Table 1. Stem density (number of trees/ha) for trees  $\geq 5$  cm in DBH in the logged and primary forest plots in the Pasoh Forest Reserve. The values in parentheses represent the proportion (%) of the total number of trees observed in the corresponding census year. The logged forest plot and primary forest plot correspond to plots C and B, respectively, in Fig. 1.

| Census year    | DBH class (cm) |               |               |               |               |            |        |  |  |  | Totals |
|----------------|----------------|---------------|---------------|---------------|---------------|------------|--------|--|--|--|--------|
|                | 5 ≤ DBH < 10   | 10 ≤ DBH < 20 | 20 ≤ DBH < 30 | 30 ≤ DBH < 40 | 40 ≤ DBH < 50 | DBH ≥ 50   |        |  |  |  |        |
| <b>Logged</b>  |                |               |               |               |               |            |        |  |  |  |        |
| 1998           | 1110.7 (61.3)  | 502.7 (27.7)  | 121.0 (6.7)   | 43.5 (2.4)    | 16.2 (0.9)    | 18.3 (1.0) | 1812.3 |  |  |  |        |
| 2000           | 1105.2 (60.9)  | 502.5 (27.7)  | 125.0 (6.9)   | 46.3 (2.6)    | 17.5 (1.0)    | 19.5 (1.1) | 1816.0 |  |  |  |        |
| 2002           | 1083.0 (60.2)  | 498.2 (27.7)  | 129.0 (7.2)   | 46.2 (2.6)    | 19.2 (1.1)    | 22.2 (1.2) | 1797.7 |  |  |  |        |
| 2004           | 1037.7 (59.7)  | 484.3 (27.9)  | 125.3 (7.2)   | 49.2 (2.8)    | 18.7 (1.1)    | 22.0 (1.3) | 1737.2 |  |  |  |        |
| 2006           | 1019.7 (59.5)  | 478.7 (27.9)  | 122.3 (7.1)   | 51.3 (3.0)    | 18.5 (1.1)    | 22.7 (1.3) | 1713.2 |  |  |  |        |
| 2008           | 1006.2 (59.0)  | 477.2 (28.0)  | 124.3 (7.3)   | 53.0 (3.1)    | 21.0 (1.2)    | 23.7 (1.4) | 1705.3 |  |  |  |        |
| 2010           | 980.7 (58.5)   | 475.0 (28.3)  | 118.8 (7.1)   | 53.3 (3.2)    | 23.5 (1.4)    | 24.2 (1.4) | 1675.5 |  |  |  |        |
| 2012           | 963.0 (58.7)   | 468.7 (28.6)  | 111.8 (6.8)   | 49.5 (3.0)    | 23.8 (1.5)    | 24.7 (1.5) | 1641.5 |  |  |  |        |
| <b>Primary</b> |                |               |               |               |               |            |        |  |  |  |        |
| 1994           | 858.7 (60.5)   | 370.8 (26.1)  | 99.8 (7.0)    | 37.8 (2.7)    | 22.5 (1.6)    | 29.2 (2.1) | 1418.8 |  |  |  |        |
| 1996           | 868.3 (61.3)   | 366.8 (25.9)  | 95.7 (6.8)    | 36.5 (2.6)    | 21.0 (1.5)    | 28.7 (2.0) | 1417.0 |  |  |  |        |
| 1998           | 865.5 (61.3)   | 366.7 (26.0)  | 94.3 (6.7)    | 36.0 (2.5)    | 20.3 (1.4)    | 29.2 (2.1) | 1412.0 |  |  |  |        |
| 2000           | 875.7 (61.1)   | 373.2 (26.0)  | 97.5 (6.8)    | 36.3 (2.5)    | 20.8 (1.5)    | 29.5 (2.1) | 1433.0 |  |  |  |        |
| 2002           | 852.2 (60.9)   | 369.3 (26.4)  | 92.5 (6.6)    | 34.3 (2.5)    | 21.3 (1.5)    | 28.7 (2.1) | 1398.3 |  |  |  |        |
| 2004           | 872.3 (61.2)   | 372.5 (26.1)  | 96.3 (6.8)    | 36.2 (2.5)    | 19.3 (1.4)    | 29.3 (2.1) | 1426.0 |  |  |  |        |
| 2006           | 890.7 (61.3)   | 379.3 (26.1)  | 95.3 (6.6)    | 37.3 (2.6)    | 19.2 (1.3)    | 31.5 (2.2) | 1453.3 |  |  |  |        |

class was also lower in the logged forest (1.5% vs. 2.2% of stems; Table 1). In the logged plot, the stem density in the smallest size class (<10 cm in DBH) decreased, whereas that in the semi-large and large size classes ( $\geq 40$  cm) increased steadily (Table 1).

From the viewpoint of biomass changes in the four size classes, structural replacement in the logged plot has proceeded: AGB increased among semi-large trees (40–50 cm) by 64% and among large trees ( $\geq 50$  cm) by 56%

from 1998 to 2012 (Fig. 6). In contrast, AGB decreased among small trees by 12% (<10 cm) and 8.9% (10–20 cm). Medium trees showed smaller changes:  $-5.1\%$  (20–30 cm) and  $+6.4\%$  (30–40 cm).

However, the biomass of the large size class ( $\geq 50$  cm) in the logged forest plot in 2012 accounted for only 58% of the AGB in the primary forest in 2006, whereas the AGB in the other size classes was greater than the corresponding values in the primary forest plot (i.e., values  $> 100\%$ ; Fig.

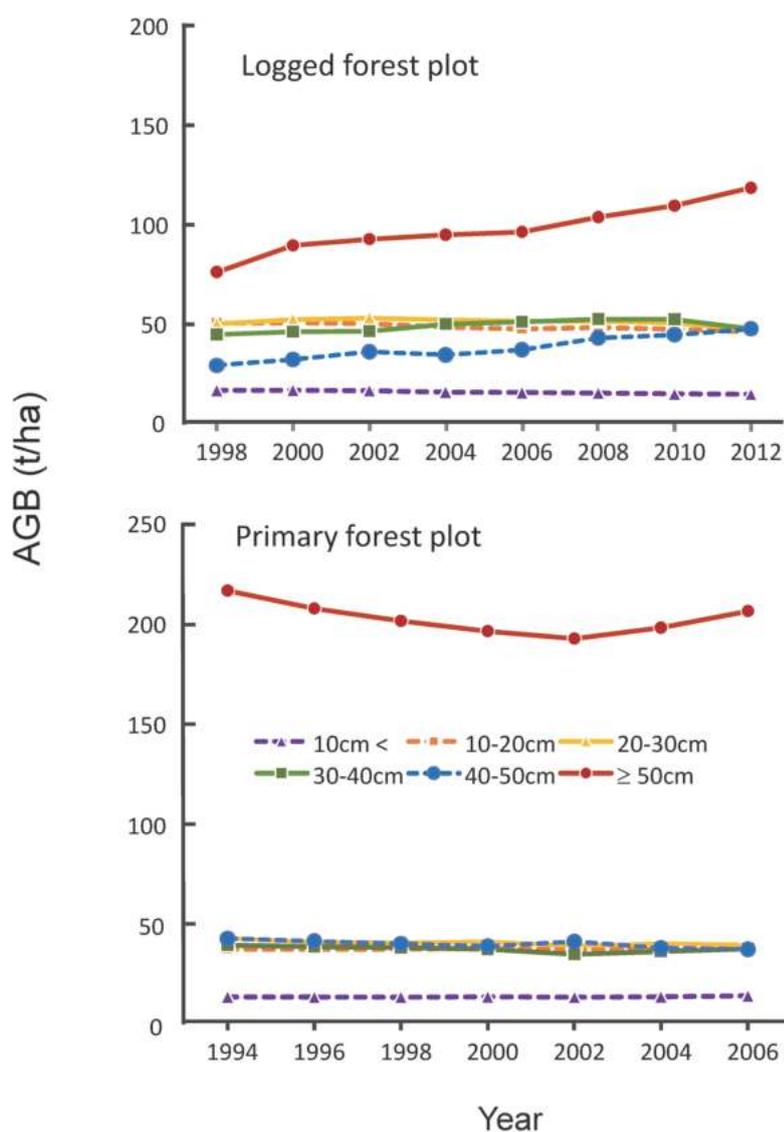


Fig. 6. Changes in the total aboveground biomass (AGB) in each DBH size class in the logged forest plot (C in Fig. 1) and the primary forest plot (B in Fig. 1).

6). Moreover, the “emergent” structural component has not reached a state similar to that in the primary forest, at only 87% of the corresponding AGB (Fig. 7); in contrast, the AGB values of the canopy and understory components have nearly caught up to the values in the primary forest, with 2012 values >95% of the primary forest values.

## DISCUSSION

### *Spatial heterogeneity in AGB*

AGB in the logged forest (plot C) recovered to a level comparable to that in the 50-ha (A) and 6-ha (B) primary forest plots 54 years after the cessation of selective logging

despite the slow growth in the swampy areas (Fig. 4). Moreover, the biomass changes resulted largely from the regeneration of large and semi-large trees (DBH ≥ 40 cm) (Fig. 6), which suggests that the forest components that would mature into individuals in these strata (large and semi-large trees; DBH ≥ 40 cm) might have been relatively undamaged during logging operations and have successfully reconstructed the canopy layer.

Nevertheless, AGB and its regeneration processes differed between the upland and swampy areas. This can be attributed largely to the species composition, which is probably associated with factors such as the topography and soil types (Davies et al. 2003, Manokaran et al. 2004) and the flooding and soil permeability (Yamada et al. 2010, 2013). For example, merchantable timber species (e.g., dip-

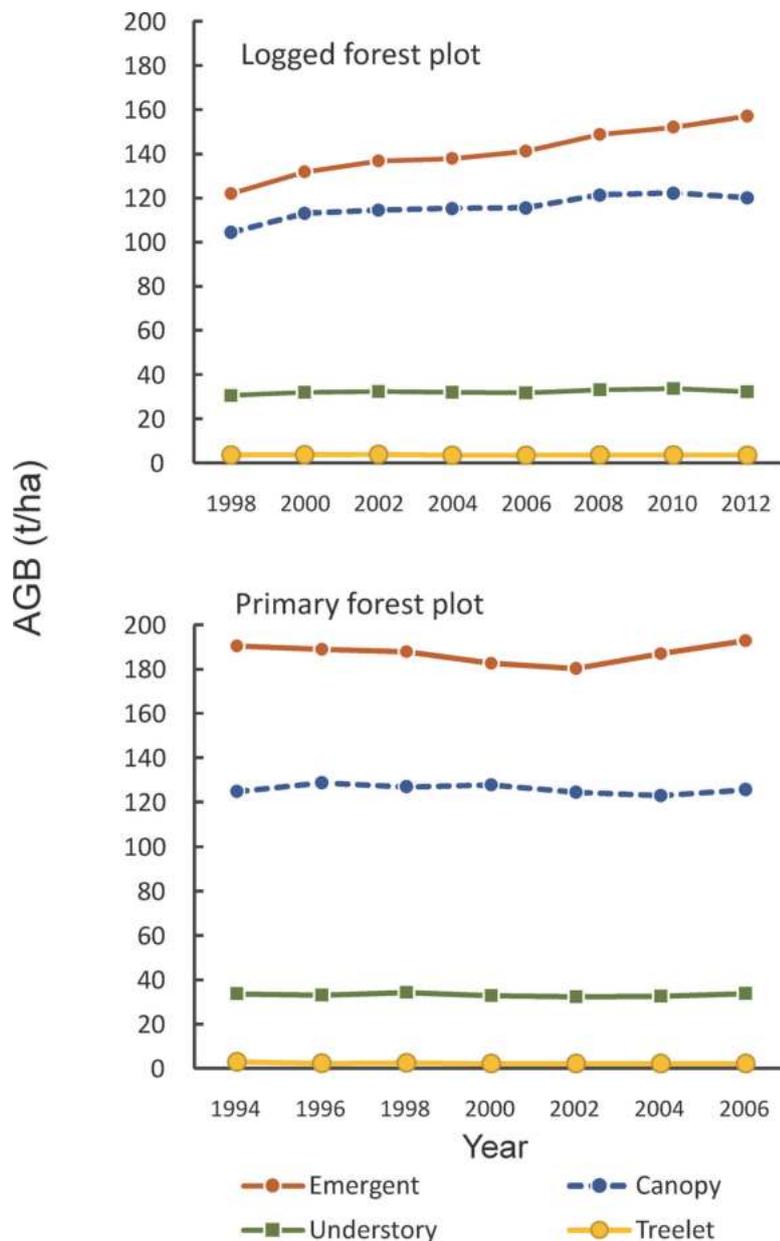


Fig. 7. Changes in the total aboveground biomass (AGB) for each of the three structural components of the logged forest plot in the logged forest and primary forest plot (plot C and B respectively in Fig. 1). The three components (emergent, canopy understory and treelet) are based on the empirical definitions of Manokaran et al. (1990), which reflect the predicted future status of the trees, not on the DBH sizes observed in each tree census.

terocarp species, canopy-layer components) remained present in the swampy area but accounted for a relatively small portion of AGB (<5.0 t/ha). *Diospyros andamanica*, *Diospyros adenophora*, *Syzygium cerasiformis*, and *Saraca declinata* were the most abundant species (based on stem density) in the swampy area. These were typical understory species, and they accounted for about 90% of the stems. In contrast, the upland subplots were dominated by large canopy-forming and commercial timber species, including *Castanopsis schefferiana*, *Dipterocarpus sublamellatus*,

and many *Shorea* species (e.g., *S. acuminata*, *S. lepidota*, *S. leprosula*, *S. maxwelliana*). These species generally contributed to a large AGB in a subplot and formed the dominant vegetation physiognomy in the upland areas.

#### *Spatiotemporal variation in AGB*

Forests can take a long time to recover to a state that resembles the pre-harvest primary forest, even after

selective logging. Nonetheless, biomass recovered to a level similar to that in the primary forest relatively quickly in the present study compared with the estimate in a previous study (Kurpick et al. 1997), which predicted that a 70-year felling rotation under the MUS approach would not be long enough to achieve sustainable timber production. The relatively rapid recovery here may have resulted primarily from the low intensity of logging that was done in the 1950s under the MUS (Manokaran 1998, Thang 1987, 1997). Therefore, the effect of the logging was likely to be lower than would be expected under a full implementation of the MUS. Moreover, we found no traces of major logging roads or skid trails within or near the logged plot. This evidence suggests very light logging effects on the plot, particularly on the forest floor.

Nevertheless, the biomass growth showed significant spatial variation within the logged plot, as can be seen in the large difference in the average AGB between the swampy and upland areas, and the temporary depression of the annual growth rate of AGB from 2004 to 2006 in the swampy areas but not the upland areas. This topographic spatial variation is similar to that found in plot A (Okuda et al. 2004a). Thus, periodic flooding and drought in the swampy parts of our study area, which enhance the dominance of understory species but suppress large species, eventually resulted in slowed biomass growth and maintained AGB at a lower level than in the upland area.

However, the effects of topography appear to be combined with the effects of other factors, such as variations in soil characteristics (Okuda et al. 2004a). These other factors should be incorporated in future analyses of the spatial variation of AGB, since these factors may have greater effects than flooding; for example, the soil in the lowland areas (corresponds to swampy area in the present study) is often clayey, with a low permeability that slows vegetation recovery (Allbrook 1973, Okuda et al. 2004a) and allows larger trees with shallow roots to be relatively easily uprooted during storms. This may also explain why trees were generally shorter in the swampy areas than in the upland areas (Okuda et al. 2004a). Given the spatiotemporal variation of AGB and the slower growth rate in the swampy areas ( $1.0\% \text{ y}^{-1}$ ) than in the upland areas ( $1.5\% \text{ y}^{-1}$ ), we suggest that the swampy areas should not be logged or used for establishing roads.

It is notable that the AGB growth rate in the logged plot slowed from 2004 to 2006 and became negative ( $-3.3\%$ ) in the swampy areas (Fig. 4). This depression might have resulted from the extremely low monthly precipitation (7.4 mm) observed in August 2004, much lower than the average in the dry season (120 mm in

January, 90 mm in February, 115 mm in June, 105 mm in July, 117 mm in August; Fig. 2). Similarly, the AGB growth rate was depressed in the upland area from 2002 to 2004 after the extremely low precipitation in February 2002 (6.5 mm). These results suggest that an extreme dry period in 2002 or 2004 depressed AGB in both areas. Similar trends in AGB depression were observed in plot B (Fig. 1; Hoshizaki et al. 2004, Yoneda et al. 2016) and in a rain forest in Sumatra (Yoneda et al. 2006), and were attributed to the high mortality of large trees caused by occasional severe drought.

In addition to the drought, a strong storm in 2004 with a maximum wind speed of  $18.6 \text{ m s}^{-1}$  knocked down many trees in plot A (Fig. 1) (Yoneda et al. 2017). This storm might have resulted in the abrupt AGB reduction in the swampy area from 2004 to 2006. High mortality after a strong storm in 1987 in plot A is the likely cause of many of the canopy gaps seen in the swampy area of this plot (Manokaran and LaFrankie, 1990). Such storms (gales, specifically) occur sporadically, averaging every 5.4 years at the study site, but effects on vegetation vary in relation to the topography (Yoneda et al. 2017).

It is possible, but not confirmed, that the observed temporal variation is related to an El Niño episode that possibly was resulted in the drought (Aiba and Kitayama 2002, Yoneda et al. 2017). However, the Southern Oscillation Index was not unusually low from 2004 to 2005 and therefore cannot explain our results (Meteorological Agency of Japan 2006). Also note that the AGB depression was less obvious in the upland areas, where the large canopy and emergent component trees are dominant (Fig. 4) and healthy (based on our field observations).

Considering the episodic events recorded at the study site, we posit that drought combined with strong storms caused the spatially heterogeneous tree mortalities. Nevertheless, we recorded only a few drought and storm events here, so it is difficult to clearly define their role in our study forests. Long-term observation will be required to define the effects of periodic drought on AGB growth rate.

### ***Structural changes***

Our results show apparent differences in stand structure between the primary and logged forest plots, with a lower density in the large tree size class ( $\geq 50 \text{ cm}$  in DBH) and a higher density in the medium size classes (20 to 40 cm in DBH) in the logged forest plot. This is clear if we compare biomass of the large DBH class between the primary and logged forest plots; in the logged forest, it was

only 58 % of the value in the primary forest (Fig. 6). Similarly, the biomass of the emergent component in the logged forest plot has reached only 87 % of the level in the primary forest (Fig. 7), indicating that AGB recovery has most likely resulted from the quick regrowth and high density of smaller trees (<50 cm in DBH), whereas tree species of the emergent component still remain smaller than 50 cm in DBH in the logged forest.

As 97 % of the top 30 dominant tree species (based on their biomass) were present in the emergent and canopy strata components of both the logged and primary forest plots, the logging impact appears to have been too low to eliminate most of the major emergent and canopy strata component species. Nevertheless, some emergent component species, such as *Neobalanocarpus heimii*, *Dipterocarpus sublamellatus*, *Dipterocarpus cornutus*, and *Koompassia malaccensis*, still have low biomass, with values less than 50 % of those in the primary forest plot. In contrast, several *Shorea* species (*S. maxwelliana*, *S. parvifolia*, *S. acuminata*, *S. macroptera*, *S. leprosula*, and *S. lepidota*) had higher biomass in the logged forest than in the primary forest, with a higher tree density in the large size class ( $\geq 50$  cm), as the MUS originally aimed at encouraging dominance of species in the Red Meranti group (*S. parvifolia*, *S. acuminata*, *S. macroptera*, *S. leprosula*, and *S. lepidota*) (Wyatt-Smith 1963). However, these results also suggest that structural recovery takes a long time because of the slow growth of some species that will mature into large trees in the long term.

Delay of structural recovery appears to be related to slow recovery of the canopy height (vegetation height, measured by LiDAR) observed in the same plot in the logged forest at our study site (Okuda et al. 2019). In that study, mean canopy height measured in 2011 by LiDAR was still significantly lower in the logged forest plot (25.8 m) than in the primary forest plot (30.4 m) 53 years after the logging operation. The coefficient of variation (CV) in canopy height was 0.27 in the logged forest versus 0.41 in the primary forest measured by LiDAR in 2003. CV was still lower in the logged forest (0.30) than in the primary forest (0.35) 53 years after the logging operation, which indicates that the canopy surface in the logged forest remains homogeneous.

An alternative interpretation is that the delay in structural recovery is attributable to a delay in self-thinning among the canopy and emergent components of the forest (trees that mature in these layers, not necessarily those with that status at present), i.e., high density of semi-large to large trees, as seen in the logged forest, might have depressed the growth of tree species with large maximum

height. This led to the slow recovery of forest structure, particularly in the vertically heterogeneous canopy and emergent layers.

In the selectively logged area of Pasoh Forest Reserve, unmerchantable trees that were supposed to be taken under the MUS but instead were left standing (Manokaran, 1998) might have resulted in a higher density of trees in the medium size class (20–40 cm) (Table 1) than in the primary forest plot. Nevertheless, it remains uncertain whether either the incomplete application of the MUS or the density-biomass relationship was responsible for the delay in the structural development of the logged forest, although the AGB was nearly recovered. However, the forest structure has remained homogeneous in the logged forest since the early 1990s, when we started visual monitoring from a canopy tower. The absence of the typical heterogeneous canopy surface that is seen in the primary forest may stop or suppress further AGB growth before AGB reaches a state comparable to that in the primary forest. However, large canopy gaps (>20 m in radius) due to tree fall have recently occurred within the logged plot. These gaps will increase the heterogeneity of the light environment and lead to expansion of the foliage of trees around the gaps. Thus, recovery of the stand and canopy surface structure may become visually evident within a few decades (Okuda et al. 2019).

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