CANOPY GAP DYNAMICS OF TWO DIFFERENT FOREST STANDS IN A MALAYSIAN LOWLAND RAIN FOREST

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NUMATA, S., YASUDA, M., OKUDA, T., KACHI, N. & NUR SUPARDI, M. N. 2006. Canopy gap dynamics of two different forest stands in a Malaysian lowland rain forest. The forest structure, canopy gap dynamics and light environment in the understorey of an unlogged primary forest and a regenerating forest that had been selectively logged in the 1950s in the Pasoh Forest Reserve, Negri Sembilan, Peninsular Malaysia were studied. Eight years' observation showed that a higher frequency and larger size of canopy gaps occurred in the primary forest compared with the regenerating forest. The lack of large trees in the regenerating forest was responsible for the lower frequency and size of canopy gaps. Most of the forest floor was under closed canopy in both forests. However, the light availability to the forest understorey was significantly higher in the regenerating forest compared with that of the primary forest in closed canopy areas. This may be because of the lesser stratification of canopy layers in the regenerating forest. These changes in the light condition in the regenerating forest may have impacts on the regeneration of tropical tree species.

Keywords: Forest structure, light environment, logging, long-term effect, Pasoh Forest Reserve, regeneration

NUMATA, S., YASUDA, M., OKUDA, T., KACHI, N. & NUR SUPARDI, M. N. 2006. Dinamik pembukaan silara bagi dua dirian hutan berlainan di dalam hutan hujan tanah pamah di Malaysia. Struktur hutan, dinamik pembukaan silara dan kehadiran cahaya di tingkat bawah kanopi hutan primer yang tidak dibalak dan hutan terpulih yang dibalak pada tahun 1950an di Hutan Simpan Pasoh, Negeri Sembilan dikaji. Pemerhatian selama lapan tahun menunjukkan bahawa hutan primer mempunyai pembukaan silara yang lebih besar dan pada frekuensi yang lebih tinggi daripada hutan pulih. Kekurangan pokok bersaiz besar di dalam hutan terpulih ialah punca utama pembukaan silara yang kecil pada kadar yang rendah. Kebanyakan lantai hutan dinaungi silara. Namun kehadiran cahaya adalah lebih ketara di dalam hutan terpulih. Ini mungkin disebabkan oleh berkurangnya lapisan silara di dalam hutan terpulih. Perubahan keadaan cahaya di dalam hutan terpulih mungkin boleh mempengaruhi pemulihan spesies pokok tropika.

INTRODUCTION

Tropical rain forests are characterized by a complex vertical structure that creates spatial and temporal heterogeneity in environmental factors such as light level (Whitmore 1984). The spatial and temporal heterogeneity of forest structure depends on the rate of canopy gap production as well as on canopy gap sizes, shapes, locations and species composition.

Canopy gaps play an important role in the regeneration of forest by providing habitat for regenerating seedlings and saplings in the forest floor (Hubbell & Foster 1986). In shaded understorey of forests, many suppressed seedlings and saplings wait for many years for the appearance of a canopy gap (Hubbell & Foster 1986, Forget 1997, Ashton 1998, van der Meer *et al.* 1998, Denslow & Guzman 2000). Therefore, forest regeneration processes frequently depend on the natural disturbance regimes (Whitmore 1984).

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Tropical rain forests are facing rapid human impacts. In South-East Asia, selective logging is a widely employed approach for commercial timber production. Selective logging is therefore a common form of forest structural alteration. For example, the canopy and stand structures differ distinctly between primary forest and regenerating forest after selective logging (Okuda *et al.* 2003) and many studies have shown direct damage to residual forest stands after logging. Many studies have investigated the potential effects of logging on forest regeneration (Cannon *et al.* 1994, Panfil & Gullison 1998), but few studies have shown long-term effects of logging on the internal light condition of a forest.

If canopy structures significantly differ between primary and regenerating forests, logging may affect the growth cycle of a forest and lead to changes in the internal light environment (Chapman & Chapman 1997, Dupuy & Chazdon 1998, Fredericksen & Mostacedo 2000). In addition, if gap dynamics may provide stage of origins and maintenance of species diversity (Hubbell & Foster 1986, Chazdon *et al.* 1999, Hubbel *et al.* 1999), effects of human disturbance on canopy gap dynamics would be the key for species richness and diversity of lowland rain forests. Therefore, we hypothesized that changes in forest structure following logging remain as changes in the light environment of tree seedlings. We focused on forests after selective logging and compared the frequency of canopy gaps and light availability on the forest floor of an unlogged primary forest and a regenerating forest after selective logging.

MATERIALS AND METHODS

The study was conducted in a lowland rain forest in Pasoh Forest Reserve, Negeri Sembilan State, Peninsular Malaysia (latitude 2° 59' N, longitude 102° 19' E). In this region, there are generally two weak dry seasons (July and January) each year and the average annual rainfall is approximately 2000 mm (Numata *et al.* 2003). The reserve has a total area of 2450 ha (Figure 1a). The core area (200 ha) is surrounded by regenerating forests that were logged and silviculturally treated between 1955 and 1959 under the Malaysian Uniform System (MUS) approach (Manokaran & Swaine 1994).

The main part of the reserve consists of a lowland dipterocarp forest of the Keruing–Meranti type (Wyatt-Smith 1987), and there are no considerable differences in altitude (105–130 m), topography or soil type (Bugor–Mallacca association). A 10 ha plot including different profiles near the entrance to the reserve was established. The study plot consisted of unlogged primary forest stand (77.6%) and forest that has been regenerating since selective logging under MUS in 1958 (22.4%) (Yasuda 1998; see Figure 1). The primary forest stand shows various stages of maturity, from canopy gaps to climax forest topped by emergent trees with heights of 50 to 60 m. A part (34.4%) of the primary forest stand was seasonally swampy; so accordingly the swampy area was excluded from analyses owing to differences in vegetation and forest structure between the swampy area and the rest of the primary forest (Okuda *et al.* 2004). This area is inundated generally in April–May and November–December.

Tree size distribution was observed in the primary and regenerating forest stands by vegetation survey. For small trees (diameter at breast height [dbh] ≥ 5 cm), five 20 × 20 m sub-quadrats were randomly established in each forest and dbh was measured. For large trees (dbh > 60 cm), dbh of all trees was measured in the entire 10 ha plot.

A canopy gap survey was conducted in the 10 ha plot each year from August 1992 till January 2000. For the survey, the plot was divided into 5 × 5 m sub-plots (n = 400). A canopy gap was visually defined as open where open sky (≥ 25 m^2) could be seen over the investigator's head (1.7 m above the ground) at the centre of each sub-plot. Although canopy gaps are defined in terms of canopy height (Adachi *et al.* 1999, Birnbaum 2001), canopy gap was recorded by direct observation. To determine the canopy gap dynamics in each plot, a gap ratio was calculated as the total number of canopy gap patches found in each forest type. Gap size was calculated by the number of canopy gap patches connecting the adjacencies. The gap size was calculated for each isolated canopy gap: total number of sub-plots aggregated on the grids of the 10 ha plot.

To determine the light availability in the forest understorey, 121 points (11 points/line × 11 points/line) were placed in each 1 ha area of

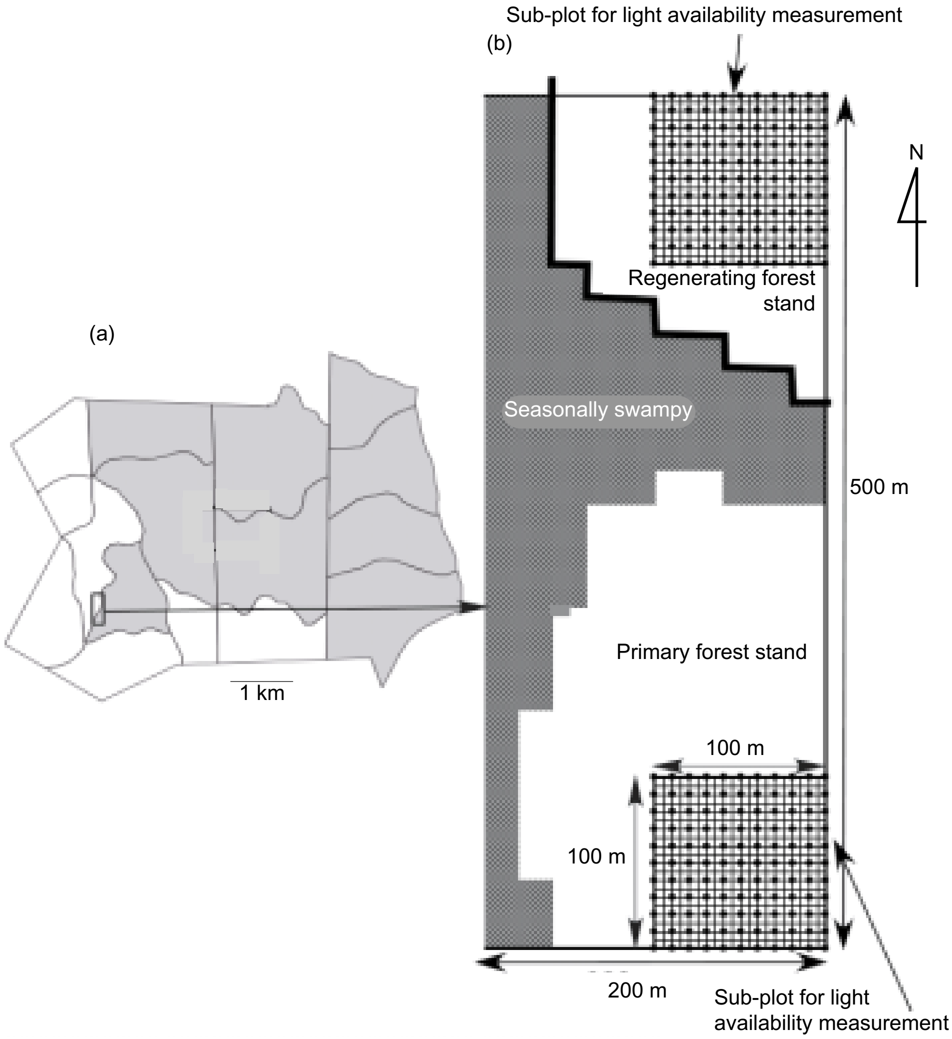

Figure 1 (a) Map of Pasoh Forest Reserve showing primary forest stands (shaded) and regenerating forest stands (open) and (b) Two plots for light availability measurement (both 100 × 100 m) in the primary and regenerating forests

forest type at regular intervals in the two most extreme corners of the forest block under investigation (Figure 1). Hemispherical photographs were taken in May 2001 from 0.5 m above the ground at regular intervals of 10 m inside the plots through a fisheye converter (FC-E8, Nikon, Japan) mounted on a digital camera (Cool Pix 950, Nikon). Two light environment variables—direct site factor (DSF) and indirect site factor (ISF)—in each subplot were estimated by Hemiview software (Delta-T Devices Ltd, UK). DSF is the percentage of the maximum potential direct radiation that reaches the photo site and is a measure of the total possible sunfleck availability. ISF is the fraction of incident diffuse radiation transmitted by holes in the canopy (Pearcy 1989).

All statistical analyses were conducted with StatView (ver. 5.0, SAS Institute, Inc., USA). Comparisons of the primary and regenerating forests were generally done by Student's *t*-test. For comparisons of variables among size classes and years, two-way ANOVA was used. Post-hoc multiple comparisons of these variables were performed by using Scheffé's post-hoc test.

RESULTS

Forest structure

Overall, there were clear differences in forest structure between the primary and regenerating forest stands. The density of trees (> 5 cm in dbh) was 1415 ha^{-1} in the primary forest stand and 1740

ha^{-1} in the regenerating forest stand. The mean basal area of trees (> 5 cm in dbh) was 32.3 m^2 ha^{-1} in the primary forest stand and 44.0 m^2 ha^{-1} in the regenerating forest stand, but the mean dbh of trees did not differ significantly between forest (df = 629, F = -0.44, p = 0.66).

The distribution of tree size classes of small trees (dbh < 30 cm) differed between two forest stands (Figure 2a). The density was higher in the regenerating forest stand but the difference was significant in only one size class (10–15 cm; df = 64, F = -2489, p < 0.05). No distinct differences in the densities of medium-sized trees (35–60 cm) were found between the two forest stands. On the other hand, the density of large trees (dbh > 70 cm) was higher in the primary forest stand while tree density of the class (60–70 cm in dbh) was lower in the primary forest stand (Figure 2b). No large trees (dbh > 130 cm) were found in the regenerating forest stand.

Canopy gap dynamics

Differences in canopy gap dynamics were observed between the primary and regenerating forest stands. Many trees had died of trunk-snapping or uprooting during a windstorm in 1995 and 1996, and some large gap creations were observed in this region. However, an increase in the gap ratio was distinctive only in the primary forest. Inter-annual changes in the gap ratio differed between the two forest stands (Figures 3a, c). The gap ratio varied from 0.045 (1992) to 0.160 (1995) in the primary forest stand, and from 0.007 (1994) to 0.043 (1998) in the regenerating forest stand. The frequency of canopy gaps was higher in the primary forest stand than in the regenerating forest stand in each year (df = 7, F = 5.45, p < 0.001).

Both frequency of canopy gaps and gap size tended to be larger in the primary forest stand than in the regenerating forest stand (Figures 3b, c). The gap size varied from 1 to 58 (1995) in the primary forest stand, and from 1 to 8 (1997) in the regenerating forest stand. The gap size ratio in the primary forest stand was significantly different between the years (df = 7, F = 5.71, p < 0.0001) and was significantly higher than that in the regenerating forest stand (df = 1, F = 9.79, p = 0.0019).

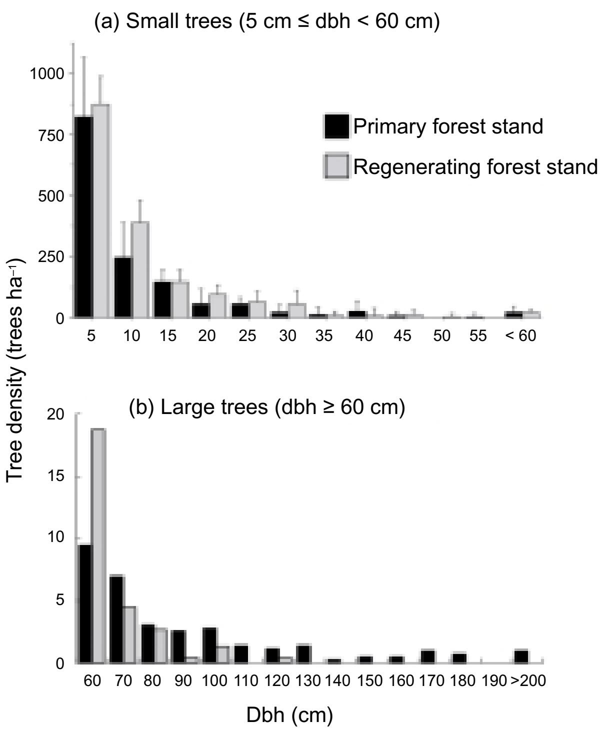

Figure 2 (a) Size distribution of small to medium trees (5 cm ≤ dbh <60cm) (b) Size distribution of large trees (dbh ≥ 60 cm) in the primary and regenerating forest stands. Bars indicate SD.

Light environment of understorey

The forest floor was generally shady in both forests, except beneath canopy gaps, but there were differences in light availability on the forest floor. ISF ranged from 0.04 to 0.10 in the primary forest stand, and from 0.06 to 0.13 in the regenerating forest stand (Figure 4a). In contrast to the canopy gap dynamics, both ISF and DSF tended to be higher in the regenerating forest stand than in the primary forest stand (Figure 4a, b). The coefficient of variation (CV) in ISF was larger in the primary forest stand (CV = 0.171) than in the regenerating forest stand (CV = 0.121), but the distribution patterns of DSF and ISF were similar between two forest stands.

DISCUSSION

Forest structures clearly differed between primary and regenerating forest stands. It may be because the incomplete MUS operation resulted in greater tree regeneration in medium-sized trees (Figure 2). The MUS was originally one cut irregular shelterwood using proper silvicultural definition (Wyatt-Smith 1963) but generally does not mean selective logging (Okuda *et al.* 2003). However, this logging regime generally involved removing the mature crop in a single operation

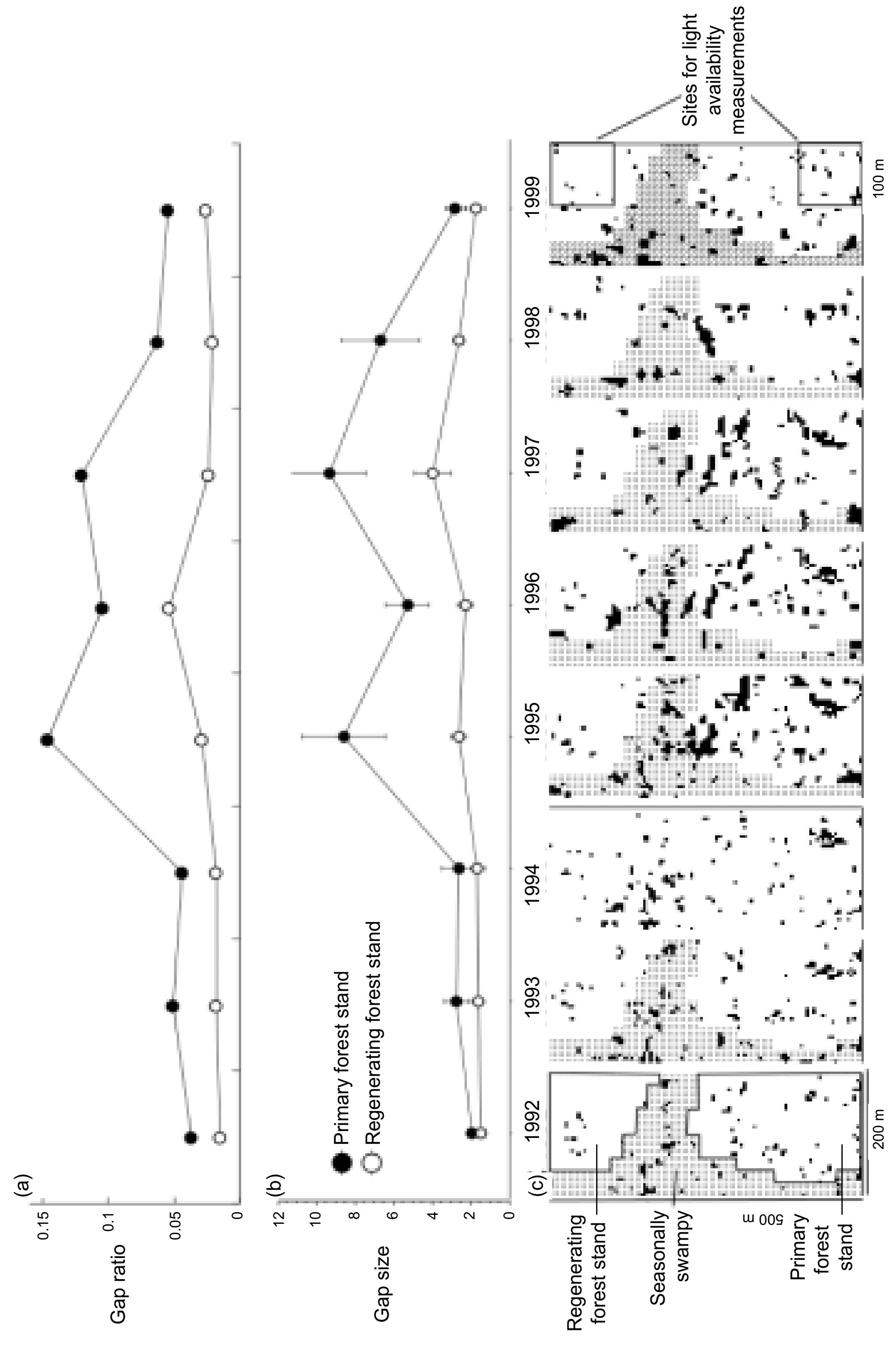

Figure 3 Annual changes in (a) canopy gap ratio and (b) gap size which means number of clustering sub-plots with canopy gaps in primary and regenerating forest stands. Bars indicate SE. (c) Location of sub-plots with canopy gaps (solid points) in the plot.

that harvested trees of all species > 45 cm in dbh in the Pasoh Forest Reserve (Manokaran 1996). High density medium-sized trees and low density large-sized trees in the 6 ha regenerating forest plot compared with the primary primary forest stand (50 ha) are suspected the result of inadequate practice of the MUS (Okuda *et al.* 2003). Canopy gap dynamics may be correlated with canopy structures nested from canopy units (Birnbaum 2001) as well as weather disturbance such as strong typhoons (Itaya *et al.* 2004). Large trees may be essential for the creation of frequent and large canopy gaps in primary forest. A high frequency and large sizes of canopy gaps were found in the

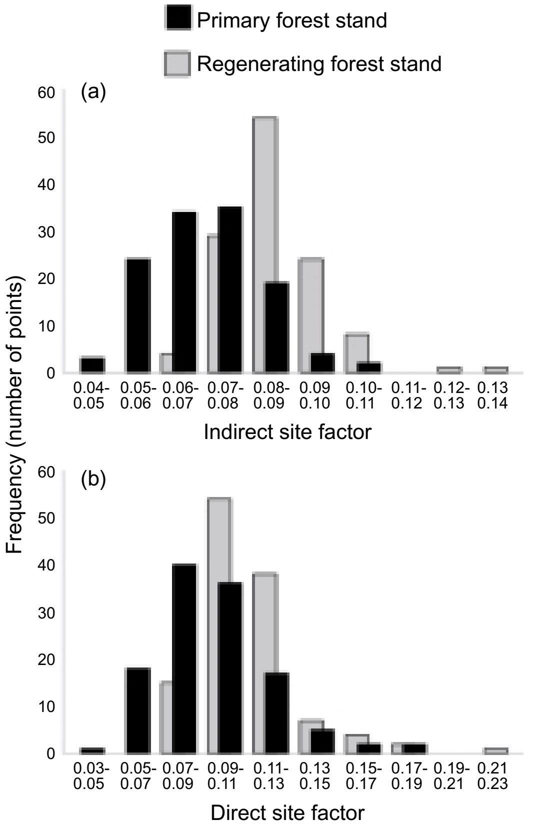

Figure 4 Frequency distributions of (a) indirect site factor and (b) direct site factor in the primary and regenerating forest stands

primary forest stand but not in the regenerating forest stand (Figure 3). These results are consistent with previous findings that old-growth forests have more large gaps than secondary-growth forests (Nicotra *et al.* 1999). All types of tree fall are found in forests among all sizes of tree (e.g. Hubbell & Foster 1986). Moreover, large canopy gaps persist longer and thus have a marked impact on canopy gap dynamics. For example, approximately 70% of small canopy gaps were closed, but most large gaps persisted for two years in a primary forest (Adachi *et al.* 1999). Although the creation of large gaps by strong windstorms may be rare, a primary forest containing large trees would have a greater potential for the maintenance of canopy gaps than a regenerating forest.

Irrespective of the frequency and size of canopy gaps, the ISF and DSF in understorey were higher in the regenerating forest stand compared with those in the primary forest stand (Figure 4). This may be because of the lesser stratification of canopy layers in the regenerating forest (Canham & Burbank 1994, Terborgh & Mathews 1999). The canopy stratification of the primary forest is characterized by unevenness of crown size and high convexity caused by the many emergent trees. Okuda *et al.* (2004) suggested that variations in canopy height are smaller in a regenerating forest stand (6 ha plot in the Pasoh Forest Reserve, see Okuda *et al.* 2003) than in a primary forest stand (50 ha plot in the Pasoh Forest Reserve). Since a larger gap size may lead to a greater proportion of open points at angles close to the zenith (Nicotra *et al.* 1999), the rich stratification of canopy in primary forest is a primary factor for the difference in light availability on the forest floor. Furthermore, light availability varies considerably within canopy gaps owing to differences in the underlayer vegetation (Canham *et al.* 1990, Chazdon 1992). A high frequency of canopy gaps, therefore, may not always increase the light availability on the forest floor.

The CV of ISF (but not DSF) was slightly higher in the primary forest compared with that in the regenerating forest. However, the distribution patterns of DSF and ISF were similar between forests (Figure 4). Small canopy gaps caused by branch falls are a primary factor in determining the temporal pattern of light availability on the forest floor. However, temporal changes in light availability should be similar in both forests because the amount of branch fall is similar in primary and regenerating forests, whereas tree falls causing canopy gaps are more common in primary forest than in regenerating forest (Hoshizaki *et al.* 2004). Therefore, heterogeneity of light availability on the forest floor is less conspicuous than that of canopy structure in the primary forest. A high density of small trees may reflect vertical heterogeneity of light availability (Canham *et al.* 1990, Terborgh & Mathews 1999).

CONCLUSIONS

There were clear differences in canopy gap dynamics and understorey light availability between the primary and regenerating forest stands. The lack of large trees in the regenerating forest stand was responsible for the static canopy gap dynamics: lower frequency and size of canopy gaps. Many tree species need to be able to persist in a suppressed condition and to cope with large differences in light availability on the forest floor. Dipterocarp tree species, which dominate South-East Asian forests, are generally regarded as climax species, but different species show different responses to canopy gaps and different strategies for regeneration in the same place. Therefore, by altering light availability, logging may have different effects on seedling and sapling establishment among species. If dynamic processes are needed for healthy natural forest cycle and maintenance of rich forest biodiversity, artificial thinning may be necessary in order to create variations in tree size and heterogeneity of light availability in regenerating forests as a possible treatment.

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