

# GROWTH AND PHOTOSYNTHETIC RESPONSE OF FOUR MALAYSIAN INDIGENOUS TREE SPECIES UNDER DIFFERENT LIGHT CONDITIONS

T Kenzo<sup>1</sup>\*, R Yoneda<sup>1</sup>, Y Matsumoto<sup>1</sup>, A Mohamad Azani<sup>2</sup> & M Nik Majid<sup>2</sup>

<sup>1</sup>Forestry and Forest Products Research Institute, Tsukuba, Ibaraki 305-8687, Japan

<sup>2</sup>Faculty of Forestry, Universiti Putra Malaysia, 43400 Serdang Darul Ehsan, Selangor, Malaysia

Received June 2010

**KENZO T, YONEDA R, MATSUMOTO Y, MOHAMAD AZANI A & NIK MAJID M. 2011. Growth and photosynthetic response of four Malaysian indigenous tree species under different light conditions.** Growth and photosynthetic response of four indigenous tree seedlings, i.e. *Dyera costulata*, *Dipterocarpus baudii*, *Neobalanocarpus heimii* and *Gonystylus affinis* were studied under different light conditions in a degraded secondary forest. Maximum photosynthesis ( $A_{max}$ ) was measured at 2 and 12 months after planting. The ratio of variable to maximum fluorescence ( $F_v/F_m$ ) was determined. Leaves measured at 2 and 12 months after planting were old leaves present on the seedlings and new leaves that had expanded after planting respectively. Seedling growth was measured over four years. Changes in the growth rate and  $A_{max}$  with canopy openness were categorised into two groups. The growth and  $A_{max}$  of the first group (*D. costulata* and *D. baudii*) were maximum at 30–40% canopy openness. This group may be suitable for planting under large canopy gaps. The second group (*G. affinis* and *N. heimii*) showed maximum growth and  $A_{max}$  at relatively low canopy openness (less than 20%). Leaves in the second group suffered chronic photoinhibition under large gap. These species were suitable to be planted under low light conditions.

Keywords: Dipterocarp, chengal, jelutong, enrichment planting, rehabilitation, wood density, degraded forest

**KENZO T, YONEDA R, MATSUMOTO Y, MOHAMAD AZANI A & NIK MAJID M. 2011. Pertumbuhan dan gerak balas fotosintesis empat spesies pokok asli di Malaysia terhadap keadaan cahaya yang berlainan.** Pertumbuhan dan gerak balas fotosintesis empat spesies pokok asli iaitu *Dyera costulata*, *Dipterocarpus baudii*, *Neobalanocarpus heimii* dan *Gonystylus affinis* terhadap keadaan cahaya yang berlainan di hutan sekunder tersusut nilai dikaji. Fotosintesis maksimum ( $A_{max}$ ) disukat pada 2 dan 12 bulan selepas penanaman. Nisbah kependafluoran boleh ubah kepada kependafluoran maksimum ( $F_v / F_m$ ) ditentukan. Daun yang disukat pada usia 2 bulan dan 12 bulan selepas penanaman ialah masing-masing daun tua yang terdapat pada anak benih dan daun baharu yang berkembang selepas penanaman. Pertumbuhan anak pokok disukat selama empat tahun. Perubahan kadar pertumbuhan dan  $A_{max}$  dengan keterbukaan kanopi dikategorikan kepada dua kumpulan. Pertumbuhan dan  $A_{max}$  untuk kumpulan pertama (*D. costulata* dan *D. baudii*) mencapai tahap maksimum pada 30%–40% keterbukaan kanopi. Kumpulan ini mungkin sesuai ditanam di bawah ruang hutan yang besar. Kumpulan kedua (*G. affinis* dan *N. heimii*) menunjukkan pertumbuhan dan  $A_{max}$  yang maksimum pada keterbukaan kanopi yang agak kecil (kurang daripada 20%). Daun dalam kumpulan kedua mengalami fotorencat yang kronik di bawah ruang hutan yang besar. Spesies ini lebih sesuai ditanam di bawah keadaan cahaya yang rendah.

## INTRODUCTION

Large areas of tropical rainforest in South-East Asia have been logged and degraded to secondary forest. As a result, 63% of the total forest cover has been changed to secondary forest (Wright 2005, Kettle 2010). In particular, canopy trees such as Dipterocarpaceae in the lowland rainforests of South-East Asia are often heavily logged for

commercial timber (Whitmore 1998, Kenzo et al. 2009a). These remnant secondary forests usually show significantly lower aboveground biomass, species richness and forest products compared with late-successional tropical rainforests (Brown & Lugo 1990, Christensen 2002, Kenzo et al. 2009b, 2010). Therefore, appropriate

\* E-mail: mona@affrc.go.jp

rehabilitation or reforestation techniques are required in these forests (Kobayashi 2004, Lamb et al. 2005).

Enrichment planting promises to be highly effective in rehabilitating or reforesting degraded forests, especially with the use of dipterocarp and other indigenous tree species that provide benefits such as timber, food and medical products (Wyatt-Smith 1963, Appanah & Weinland 1993, Adjers et al. 1995, Lamb et al. 2005). However, the rate of growth and survival of planted seedlings in a degraded forest usually differ among species even in the same taxonomic group (Suzuki & Jacalne 1986, Kenzo et al. 2007, Hattori et al. 2009). A better understanding of ecological traits such as high light tolerance and growth performance of target species could bring improved techniques for enrichment planting in tropical secondary forests (Appanah & Weinland 1993, Krishnapillay 2002, Kenzo et al. 2007). In particular, leaf ecophysiological traits related to photosynthesis could be useful indicators for plant ecological traits such as growth and light acclimation ability. This is because leaf photosynthesis is essential to carbon assimilation and environmental adaptation (Larcher 2003, Kenzo et al. 2007, 2008).

Growth and leaf ecophysiological traits of planted seedlings are closely related to the light environment (Sasaki & Mori 1981, Turner & Newton 1990, Kenzo et al. 2007, Hattori et al. 2009) although various environmental factors exist in the forest. In addition, seedling growth and leaf ecophysiological traits also correlate not only to the light environment but also to species-specific ecological traits such as wood density and successional status (Suzuki & Jacalne 1986, Popma & Bongers 1988, Ishida et al. 2008, Kenzo et al. 2008, Chave et al. 2009). In fact, many early-successional trees with low wood density showed faster growth rates than late-successional trees with high wood density in tropical regions (Whitmore 1998, Yamashita et al. 2000).

It is necessary to consider species-specific favourable light conditions for effective enrichment planting in degraded secondary forests. However, various light conditions from strong light conditions in large canopy gaps to dark under canopy conditions usually exist in degraded tropical secondary forests (Whitmore 1998). Moreover, the response to the light environment differs significantly between species (Sasaki & Mori 1981, Kenzo et al. 2007) and little information is available about growth and

leaf photosynthetic responses to different light conditions in degraded secondary forests (Kenzo et al. 2008).

In this paper, we hypothesise that the characteristics of leaf ecophysiological traits in planted indigenous tree seedlings associate with both light conditions and their ecological traits such as wood density under different light conditions in degraded tropical secondary forests. We tested our prediction by monitoring seedling growth traits from just after planting to four years after planting under different sizes of artificial gaps (large gap, small gap and closed canopy conditions) in a degraded secondary forest. We also focused on changes to leaf ecophysiological traits from old leaves found on tree just after planting to new leaves flushed at 12 months after planting. From these results, we proposed favourable planting light conditions for the studied indigenous tree species.

## MATERIALS AND METHODS

### Study site

The study was carried out at the Ayer Hitam Forest Reserve (1248 ha, 3° 00' N, 101° 38' E), Selangor, Malaysia. The area has humid tropical climate with weak seasonal changes in rainfall. Monthly rainfall fluctuates from approximately 100 to 400 mm and a relatively large amount of rainfall occurs from October till March (R Yoneda, personal communication). Annual rainfall and average temperature are 2700 mm and 25.3 °C respectively (Kenzo et al. 2008).

The enrichment planting area (about 1 ha) was a typical degraded secondary forest after commercial logging. The area consisted mainly of pioneer trees such as genera *Endospermum*, *Macaranga*, *Artocarpus* and *Ficus* (Kenzo et al. 2008). Tree heights varied from 15 to 25 m. The soil was generally a combination of alluvium–colluvium soil and had sandy loam soil texture (Faridah-Hanum & Philip 2006). The forest floor was less dark compared with a primary forest and sun flecks commonly penetrated the canopy. The relative light intensity was approximately 10% of full sun in the forest. Different sizes of artificial canopy gaps were created in the secondary forest by cutting down canopy trees in September 2005 (Kenzo et al. 2008).

## Plant materials and canopy openness

The species planted were *Dyera costulata* (Apocynaceae), *Dipterocarpus baudii* (Dipterocarpaceae), *Neobalanocarpus heimii* (Dipterocarpaceae) and *Gonystylus affinis* (Thymelaeaceae). All species are usually distributed in the lowland dipterocarp forest in Malaysia. Two of the dipterocarp tree species in this study are canopy species that produce useful timber (Ashton 1982, Symington 2004). The other two species are also useful as timber and *D. costulata* produces latex, an ingredient in chewing gum (Yap 1980). *Dyera costulata* is preferably planted under a canopy gap. It is a fast-growing species (Aminuddin 1982). Its wood density is also the lowest among the species studied (Table 1). *Dipterocarpus baudii* is a relatively fast-growing mid-successional species and has medium wood density compared with the other species studied (Appanah & Weinland 1993, Symington 2004). In contrast, *N. heimii* is a slow-growing late-successional species and has high wood density (Appanah & Weinland 1993). *Gonystylus affinis* also shows high wood density and late-successional traits (Whitmore 1972). It is a medium-sized tree, reaching 33 m in height and 90 cm in bole diameter.

Seeds were collected from a natural rainforest in Peninsular Malaysia and planted in plastic pots (diameter 15 cm, height 20 cm). The seedlings were tended in a nursery for approximately 12 months under light conditions equal to 35% full sunlight. Initial seedling height varied from 62 to 126 cm (Table 1). The seedlings were transplanted to the degraded secondary forest in September 2005. Before planting, various sizes of artificial canopy gaps were created by cutting the canopy trees in the secondary forest. We conducted random species planting with 2 × 2 m intervals at the site. Maintenance of the

planted seedlings was carried out three times a year. Climbers were removed from the seedling stems, and grass and pioneer tree seedlings were slashed. From the planted seedlings grown under various light conditions, 12 to 13 individuals per species were randomly selected for the study (Table 1). All of the studied seedlings survived the first year after transplantation. The seedling diameter at the base and height were measured from just after planting to four years after planting. The relative growth rate (RGR) of diameter and height during the period was also calculated using the following formula:

$$\text{RGR} = (\ln D_1 - \ln D_0) / T$$

where  $D_0$  and  $D_1$  were the initial and final plant sizes respectively and  $T$  was the respective time interval (King 1991, Feeley et al. 2007).

Canopy openness above the seedlings was estimated from a hemispherical photograph E9. Openness was calculated using LIA32 image analysis freeware for Windows (Yamamoto 2000). The data on canopy openness was roughly divided into three categories of planted conditions: closed canopy (less than 15% canopy openness), small gap (15% to 35%) and large gap (greater than 35%).

## Measurement of leaf photosynthetic traits

The leaf photosynthetic rate at light saturation was measured at 2 and 12 months after planting. Leaves measured at two months after planting were old leaves that had acclimated to the light conditions before planting. Leaves measured at 12 months after planting were new leaves that had expanded after planting. We used a portable photosynthesis meter to measure the leaf gas exchange rate. All measurements took place in the morning from 0800 to 1100 hours to avoid midday

**Table 1** Ecological characteristics, seedling number and initial height of studied species

Family	Species	Wood density (kg m <sup>-3</sup> )	Successional status	Seedling number	Height (cm)
Apocynaceae	<i>Dyera costulata</i>	415–495	Gap	12	64.7
Dipterocarpaceae	<i>Dipterocarpus baudii</i>	610–800	Mid	12	126.1
	<i>Neobalanocarpus heimii</i>	915–981	Late	12	62.0
Thymelaeaceae	<i>Gonystylus affinis</i>	730–780	Late	13	104.1

Wood density and successional status based on Burgess (1966), Soerianegara & Lemmens (1994), Gan & Lim (2004) and Symington (2004).

photosynthesis depression (Kenzo et al. 2007). The relationship between the photon flux density and carbon assimilation rate was determined for fully expanded leaves and apparent non-senescent leaves. The measured light intensities were 0, 25, 50, 100, 700 and 1500  $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ , and the temperature was approximately 30 °C (Kenzo et al. 2004, 2006). The  $\text{CO}_2$  concentration and air humidity in the leaf chamber were maintained at 360 ppm and approximately 60% respectively. The photosynthetic rate at light saturation ( $A_{\text{max}}$ ) and light compensation point ( $I_c$ ) was calculated from these measurements (Kenzo et al. 2004).  $A_{\text{max}}$  and RGR against the canopy openness curve were drawn using the distance-weighted least squares smoothing method (Vincent 2001) provided in the statistical package (Origin Ver. 7.0).

After the completion of gas exchange measurement, the leaves were collected and the SPAD value was measured. The SPAD value, which is an index of leaf chlorophyll content (Ichie et al. 2002), was determined using a SPAD-502 meter.

The initial ( $F_o$ ) and maximum fluorescence ( $F_m$ ) of the same leaves used for photosynthesis measurement were determined after 12 months using a portable fluorometer with a saturating light for  $F_m$  (Kitao et al. 2006). The ratio of variable to maximum fluorescence ( $F_v/F_m$  where  $F_v = F_m - F_o$ ) after overnight dark adaptation, which represented the maximum photochemical efficiency of photosystem II (PSII), was also determined (Kitao et al. 2006). Overnight dark adaptation was achieved by covering the leaves with aluminium foil before sundown and  $F_v/F_m$  was measured early the next morning after an additional 15 min of dark adaptation using dark leaf clips.

## RESULTS AND DISCUSSION

### Growth performance of seedlings under different light conditions

The height and diameter growth rates of the studied species differed significantly between species and light environment, and could be roughly divided into two tree groups according to their growth patterns (Figures 1 and 2). The first group showed relatively high growth performance under bright conditions such as that provided by large canopy gaps (greater

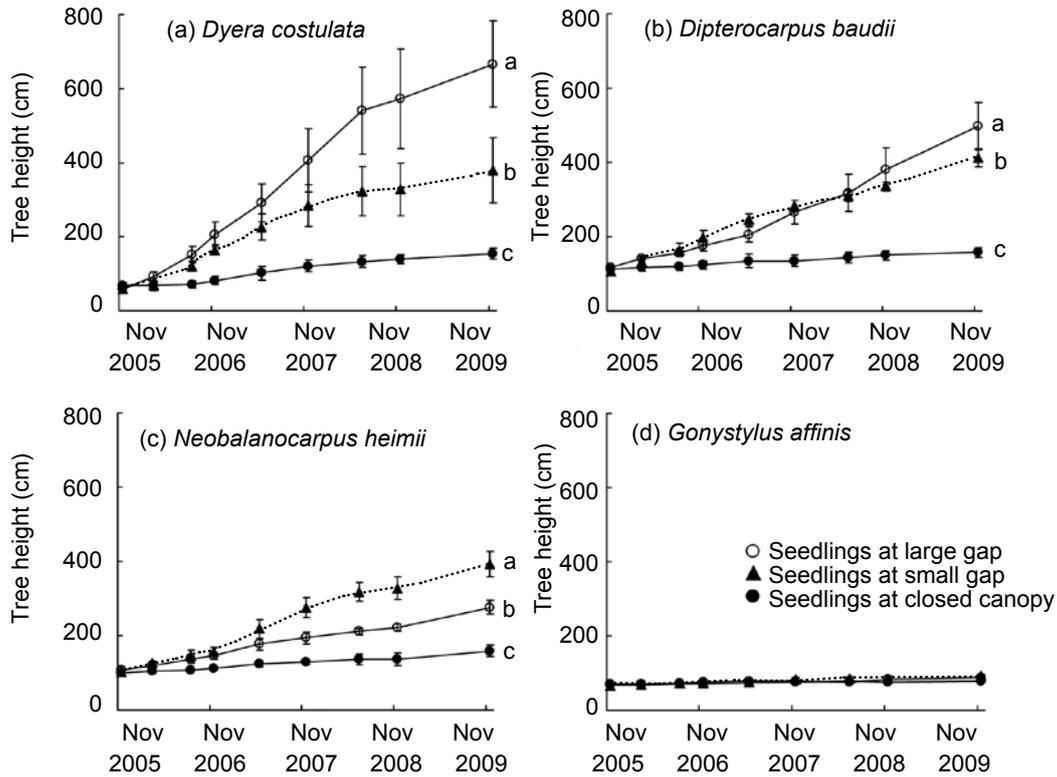
than 35% of canopy openness). Seedlings of *D. costulata* planted in an area with large gaps showed the highest growth, reaching a maximum height of 6.7 m and diameter of 8.0 cm four years after planting (Figures 1a and 2a). The height and diameter of *D. baudi* were higher under large gap conditions, reaching 5.0 m and 5.0 cm respectively (Figures 1b and 2b). These values were higher than those of other dipterocarp species, which averaged about 3 to 4 m in height three to four years after being planted under high light conditions (Ådjers et al. 1996, Alias et al. 1998, Hattori et al. 2009).

In contrast, the second group (*N. heimii* and *G. affinis*) showed relatively small growth performance under bright conditions, although height growth was greater under relatively shaded conditions. The height of *N. heimii* was greater under small gap conditions of 15 to 35% canopy openness, compared with that under large and/or closed canopy conditions (Figure 1c). The maximum seedling height reached 3.9 m under small gap conditions while the diameter, 3.0 cm under large gap conditions, although the height was only 2.5 m under large gap conditions four years after planting. Several researchers have reported that increasing the gap size had a negative effect on height growth for some dipterocarp seedlings including *N. heimii* (Nicholson 1960, Ådjers et al. 1995, Tuomela et al. 1996, Ueda et al. 1997).

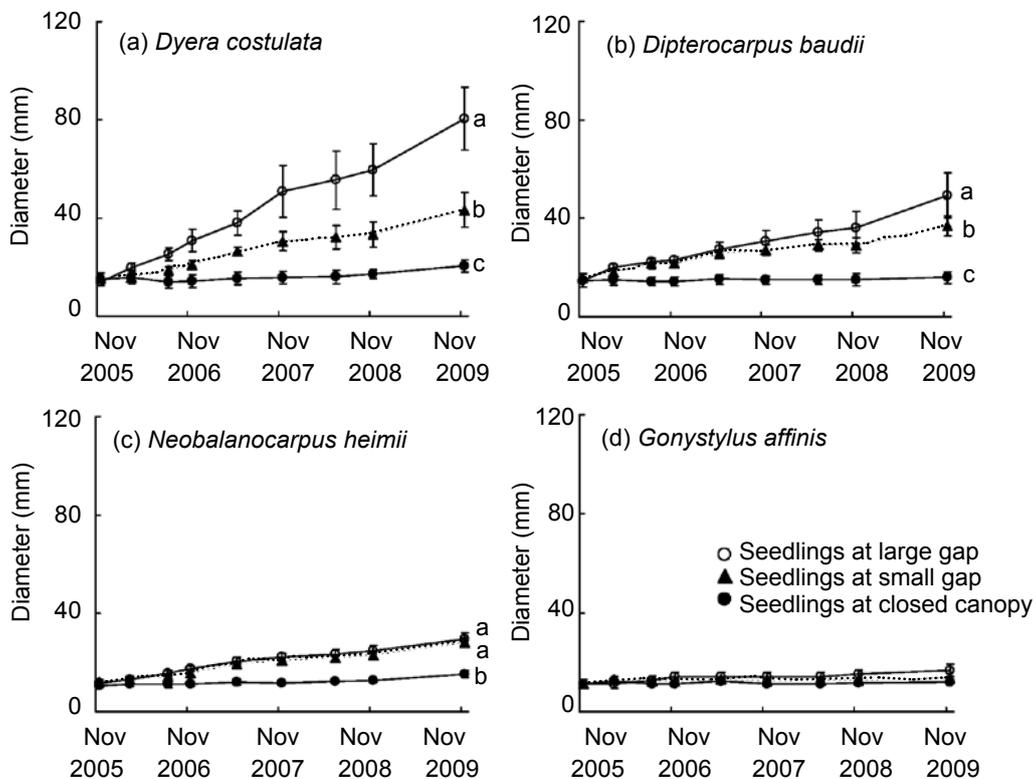
*Gonystylus affinis* showed the smallest height and diameter growth among all the species studied (Figures 1d and 2d). Most *G. affinis* seedlings were less than 1 m in height and 2 cm in diameter even after four years.

### Leaf ecophysiological response and growth under high light conditions

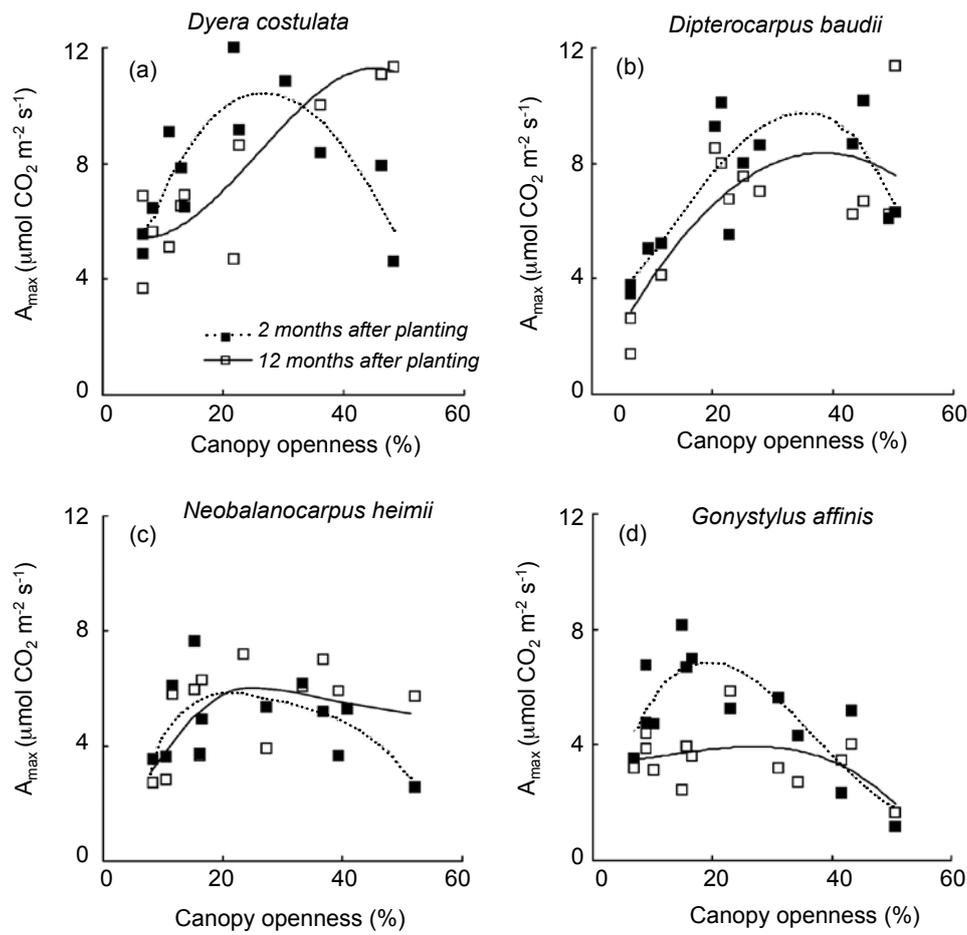
Canopy openness in relation to leaf photosynthetic properties such as  $A_{\text{max}}$  and  $F_v/F_m$  was also divided into two groups (Figures 3 and 4), and the differences in properties indicate interspecific light acclimation ability. In the first group (*D. costulata* and *D. baudi*),  $A_{\text{max}}$  was maximum at relatively higher light conditions, i.e. 30–40% canopy openness (Figures 3a and b). The RGRs of the diameter and height were also favourable under relatively high light conditions, i.e. 30–40% canopy openness for tree height (Figures 5a and b). The high growth rate in this group may correspond to the high photosynthetic



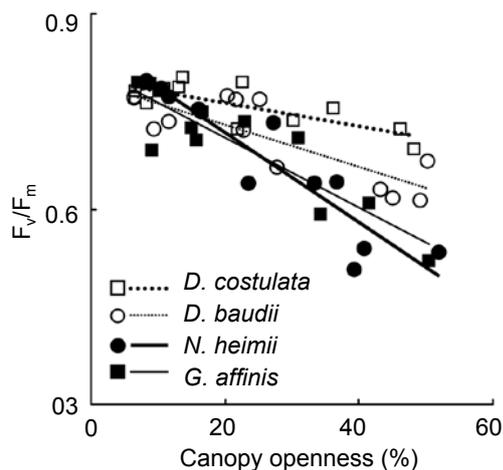
**Figure 1** Changes in tree height growth under different light conditions after planting. Different letters indicate significant difference across the measurement period ( $p < 0.05$ , ANOVA). Bars indicate standard errors. Closed canopy: less than 15 canopy openness, small gap: 15 to 35% and large gap: greater than 35%.



**Figure 2** Changes in tree diameter at the base under different light conditions after planting. Different letters indicate significant difference across the measurement period ( $p < 0.05$ , ANOVA). Bars indicate standard errors. Closed canopy: less than 15 canopy openness, small gap: 15 to 35% and large gap: greater than 35%.



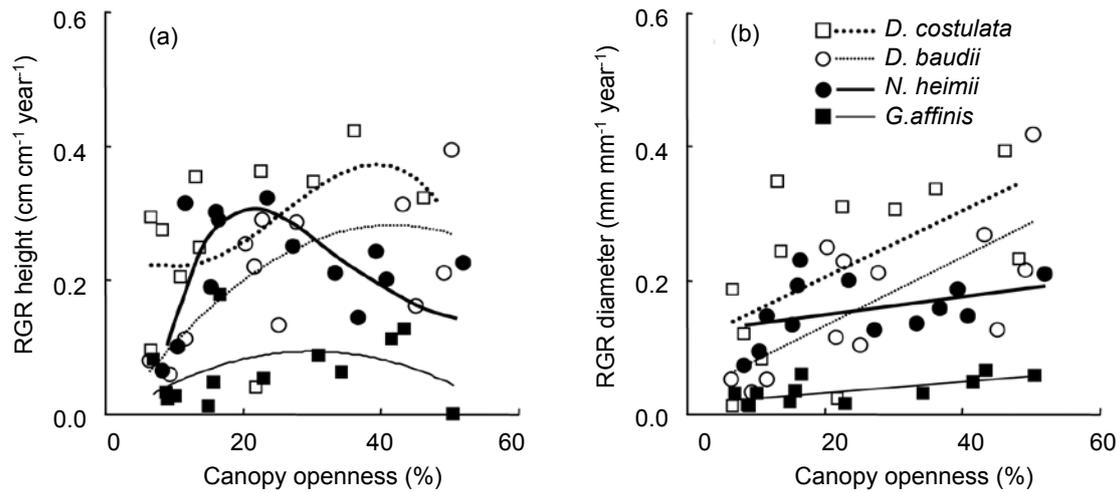
**Figure 3** Canopy openness in relation to maximum photosynthetic rate ( $A_{max}$ ) at 2 and 12 months after planting. Correlation coefficients of regression lines are (a) 2 months  $r^2 = 0.73$ , 12 months  $r^2 = 0.77$ , (b) 2 months  $r^2 = 0.60$ , 12 months  $r^2 = 0.70$ , (c) 2 months  $r^2 = 0.41$ , 12 months  $r^2 = 0.40$ , (d) 2 months  $r^2 = 0.66$ , 12 months  $r^2 = 0.26$ .



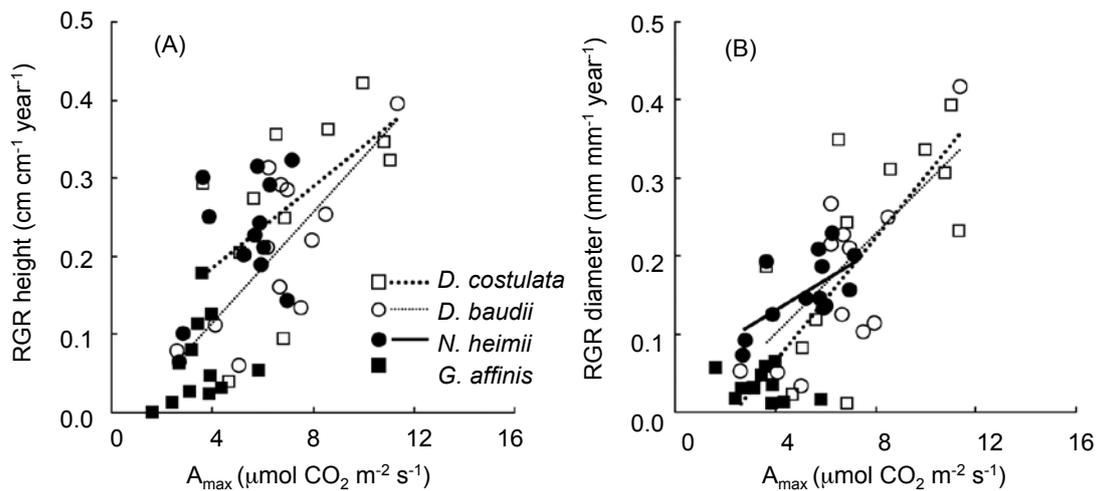
**Figure 4** Canopy openness in relation to the ratio of variable to maximum fluorescence ( $F_v/F_m$ ). The regression lines are *D. costulata*,  $y = 0.80 - 0.002x$ ,  $r^2 = 0.59$ ,  $p < 0.05$ ; *D. baudii*,  $y = 0.80 - 0.003x$ ,  $r^2 = 0.69$ ,  $p < 0.001$ ; *N. heimii*,  $y = 0.85 - 0.007x$ ,  $r^2 = 0.85$ ,  $p < 0.001$ ; *G. affinis*,  $y = 0.82 - 0.005x$ ,  $r^2 = 0.80$ ,  $p < 0.001$ .

rate and low wood density because the RGRs of the diameter and height for this group are significantly related to  $A_{max}$  (Figures 6a and b) and a negative relationship between wood density and growth rate is common among tropical trees (Ang & Maruyama 1995, Suzuki 1999, Muller-Landau 2004, Chave et al. 2009). In particular, *D. costulata*, which had the lowest wood density and the highest  $A_{max}$  and light demand showed the highest growth rate (Figure 1a).

In contrast, the second group (*N. heimii* and *G. affinis*) showed maximum  $A_{max}$  under relatively dark conditions, i.e. approximately 10% canopy openness (Figures 3c and d). The diameter and height increments for this group were also lower than for the first group (Figures 5a and b). The  $F_v/F_m$  for the second group also showed significant decrease with increasing canopy openness (Figure 4,  $p < 0.05$ ). In particular, the  $F_v/F_m$  of *N. heimii* and *G. affinis* under large canopy gap conditions was less than



**Figure 5** Canopy openness in relation to relative growth rate (RGR) in (a) height and (b) diameter. Correlation coefficients of regression lines are (a) *D. costulata*  $r^2 = 0.55$ , *D. baudii*  $r^2 = 0.17$ , *N. heimii*  $r^2 = 0.21$ , *G. affinis*  $r^2 = 0.52$  and (b) *D. costulata*  $r^2 = 0.32$ , *D. baudii*  $r^2 = 0.51$ , *N. heimii*  $r^2 = 0.17$ , *G. affinis*  $r^2 = 0.45$ .



**Figure 6** Maximum photosynthetic rate ( $A_{max}$ ) in relation to relative growth rate (RGR) in (a) height and (b) diameter. The regression lines are (a) *D. costulata*,  $y = 0.082 + 0.026x$ ,  $r^2 = 0.32$ ,  $p < 0.05$ ; *D. baudii*,  $y = -0.027 + 0.035x$ ,  $r^2 = 0.58$ ,  $p < 0.05$ ; *N. heimii*,  $y = 0.082 + 0.026x$ ,  $r^2 = 0.23$ , ns; *G. affinis*,  $y = 0.021 + 0.01x$ ,  $r^2 = 0.06$ , ns and (b) *D. costulata*,  $y = -0.023 + 0.032x$ ,  $r^2 = 0.43$ ,  $p < 0.05$ ; *D. baudii*,  $y = -0.092 + 0.040x$ ,  $r^2 = 0.60$ ,  $p < 0.05$ ; *N. heimii*,  $y = 0.053 + 0.020x$ ,  $r^2 = 0.40$ ,  $p < 0.05$ ; *G. affinis*,  $y = 0.055 - 0.006x$ ,  $r^2 = 0.38$ , ns.

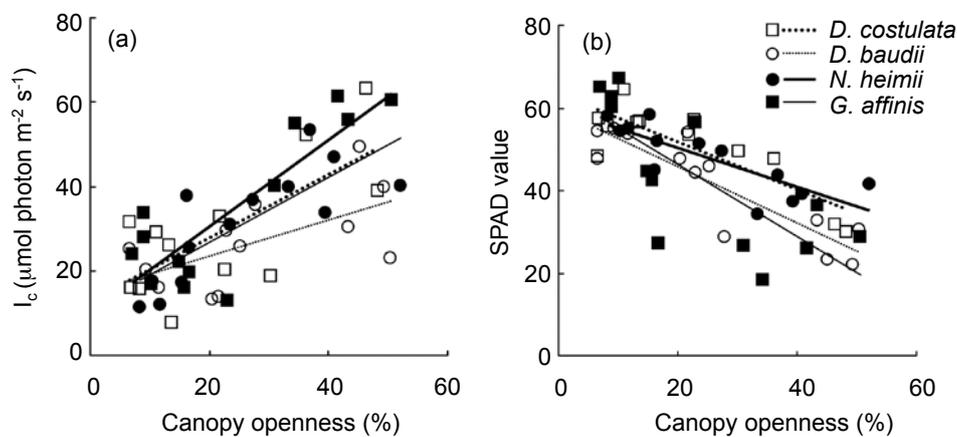
0.6. The low  $F_v/F_m$  for new leaves indicates that both species may suffer chronic photoinhibition to strong sunlight under high canopy openness (Björkman & Demmig 1987, Deming-Adams & Adams 1992, Kitao et al. 2006). In addition, the midday depression of photosynthesis may occur in *N. heimii* under large gap conditions. This depression was marked in *N. heimii* compared with other dipterocarp species under open dry conditions (Ishida et al. 1999). These responses

indicated that the second tree group (*N. heimii* and *G. affinis*) could be categorised as low producers of photosynthesis and less tolerant to photoinhibition under strong light conditions even for new leaves that had expanded after planting. Therefore, these species may need shading by nurse plants and/or artificial shading to avoid environmental stress to the leaves (Ashton et al. 1997, Norisada et al. 2005, Yoneda et al. 2005).

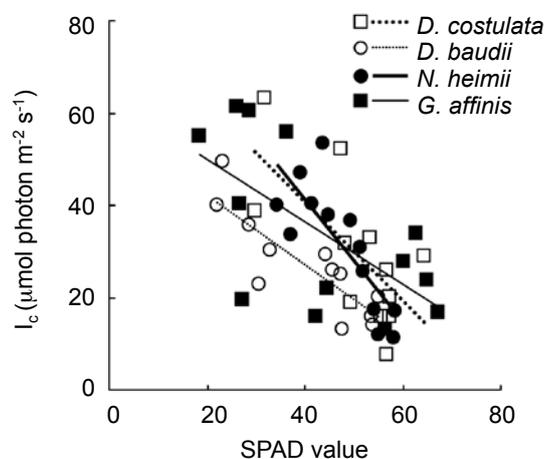
## Leaf ecophysiological response to low light conditions

The light compensation point ( $I_c$ ) decreased significantly with decreasing canopy openness in all studied species (Figure 7a,  $p < 0.05$ ), indicating that photosynthetic efficiency increased under shaded conditions (Kimura et al. 1998, Larcher 2003). Although the  $I_c$  for old leaves of *D. baudi* at two months after planting did not show significant relationship with canopy openness (Kenzo et al. 2008), that for newly expanded leaves at 12 months after planting was negatively correlated with canopy openness (Figure 7a). This indicated that shade acclimation due to change in  $I_c$  occurred in new leaves for this species.

High chlorophyll content in the leaves also facilitated acclimation under low light conditions (Kimura et al. 1998, Kull & Niinemets 1998). The SPAD value, which indicated leaf chlorophyll content (Ichie et al. 2002), increased with decreasing canopy openness in all studied species (Figure 7b). In general, high chlorophyll content in the leaves contributed to high light-capturing ability and reduced the leaf  $I_c$  value (Lambers et al. 1998, Kenzo et al. 2006). In our study, there was also negative correlation between the SPAD and  $I_c$  values for all species (Figure 8). This indicates that high chlorophyll content in the new leaves of these species contributes to the light-capturing efficiency at low light availability (Kenzo et al. 2008).



**Figure 7** Canopy openness in relation to (a) light compensation point ( $I_c$ ) and (b) SPAD value. The regression lines for (a) are *D. costulata*,  $y = 12.63 + 0.76x$ ,  $r^2 = 0.50$ ,  $p < 0.05$ ; *D. baudi*,  $y = 15.0 + 0.43x$ ,  $r^2 = 0.37$ ,  $p < 0.05$ ; *N. heimii*,  $y = 11.2 + 0.78x$ ,  $r^2 = 0.64$ ,  $p < 0.05$  and *G. affinis*,  $y = 10.0 + 1.03x$ ,  $r^2 = 0.72$ ,  $p < 0.001$ . The regression lines for (b) are *D. costulata*,  $y = 63.5 - 0.58x$ ,  $r^2 = 0.71$ ,  $p < 0.001$ ; *D. baudi*,  $y = 59.3 - 0.68x$ ,  $r^2 = 0.79$ ,  $p < 0.001$ ; *N. heimii*,  $y = 59.7 - 0.47x$ ,  $r^2 = 0.67$ ,  $p < 0.001$  and *G. affinis*,  $y = 63.9 - 0.88x$ ,  $r^2 = 0.57$ ,  $p < 0.05$ .



**Figure 8** Light compensation point ( $I_c$ ) in relation to SPAD value. The regression lines are *D. costulata*,  $y = 83.6 - 1.07x$ ,  $r^2 = 0.48$ ,  $p < 0.05$ ; *D. baudi*,  $y = 57.4 - 0.76x$ ,  $r^2 = 0.72$ ,  $p < 0.001$ ; *N. heimii*,  $y = 94.8 - 1.34x$ ,  $r^2 = 0.65$ ,  $p < 0.001$  and *G. affinis*,  $y = 63.3 - 0.67x$ ,  $r^2 = 0.41$ ,  $p < 0.05$ .

## CONCLUSIONS

The contrasting photosynthetic responses of the different species strongly predicted growth performance under a range of light environments in the degraded tropical secondary forest. *Dyera costulata* and *D. baudii*, which had relatively low wood density, showed higher photosynthesis and growth rates under high light conditions. They may be suitable for planting under large canopy gaps in the secondary forest. In contrast, *N. heimii* and *G. affinis*, which had relatively high wood density, showed lower growth rates and leaf photosynthesis to strong sunlight, even in newly flushed leaves. These species should be preferred for planting in low light conditions, i.e. small gaps of less than 20% canopy openness.

## ACKNOWLEDGEMENTS

The authors thank the Universiti Putra Malaysia, M Sano and A Tanaka-Oda for support. This study was funded partly by the Global Environmental Research Fund (GERF) from the Ministry of Environment, Grant-in-Aid for Scientific Research and the Ministry of Education, Culture, Sports, Science and Technology, Japan (No. 18780126 and 20405030).

## REFERENCES

- ÅDJERS G, HADENGGANAN S, KUUSIPALO J, NURYANTO K & VESA L. 1995. Enrichment planting of dipterocarps in logged-over forests: effect of width, direction and maintenance method of planting line on selected *Shorea* species. *Forest Ecology and Management* 73: 271–277.
- ÅDJERS G, KUUSIPALO J, HADENGGANAN S, NURYANTO K & VESA L. 1996. Performance of ten dipterocarp species in restocking logged-over forest areas subjected to shifting cultivation. *Journal of Tropical Forest Science* 9: 151–160.
- ALIAS MA, HAMZAH MZ, FUJIWARA K & MEGURO S. 1998. Rehabilitation of tropical rainforests based on potential natural vegetation species for degraded areas in Sarawak, Malaysia. *Tropics* 7: 223–239.
- AMINUDDIN HM. 1982. Light requirements of *Dyera costulata* seedlings. *Malaysian Forester* 45: 203–208.
- ANG LH & MARUYAMA Y. 1995. Survival and early growth of *Shorea platyclados*, *Shorea macroptera*, *Shorea assamica* and *Hopea nervosa* in open planting. *Journal of Tropical Forest Science* 7: 541–557.
- APPANAH S & WEINLAND G. 1993. *Planting Quality Timber Trees in Peninsular Malaysia—A Review*. Malayan Forest Records No. 38. Forest Research Institute Malaysia, Kpong.
- ASHTON PS. 1982. Dipterocarpaceae. Pp 237–552 in *Flora Malesiana, Series 1 Spermatophyta*. Volume 9. Martinus Nijhoff Publishers, Dordrecht.
- ASHTON PMS, GAMAGE S, GUNATILLEKE IAUN & GUNATILLEKE CVS. 1997. Restoration of a Sri Lankan rainforest: using Caribbean pine *Pinus caribaea* as a nurse for establishing late-successional tree species. *Journal of Applied Ecology* 34: 915–925.
- BJÖRKMANN O & DEMMIG B. 1987. Photon yield of O<sub>2</sub> evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. *Planta* 170: 489–504.
- BROWN S & LUGO A. 1990. Tropical secondary forest. *Journal of Tropical Ecology* 6: 1–32.
- BURGESS PF. 1966. *Timbers of Sabah*. Forest Department, Sandakan.
- CHAVE J, COOMES D, JANSEN S, LEWIS SL, SWENSON NG & ZANNE AE. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–366.
- CHRISTENSEN H. 2002. *Ethnobotany of the Iban and the Kelabit*. A joint publication of Forest Department Sarawak, Malaysia, NEPCON, Denmark and University of Aarhus, Denmark.
- DEMING-ADAMS B & ADAMS WW. 1992. Photoprotection and other responses of plants to high light stress. *Annual Review of Plant Molecular Biology* 43: 599–626.
- FARIDAH-HANUM I & PHILIP L. 2006. Tree species composition and stand attributes of Ayer Hitam Forest Reserve, Selangor in Peninsular Malaysia. *Malaysian Forester* 69: 191–224.
- FEELEY K, WRIGHT SJ, SUPARDI MNN, KASSIM AR & DAVIES SJ. 2007. Decelerating growth in tropical forest trees. *Ecology Letters* 10: 461–469.
- GAN KS & LIM SC. 2004. *Common Commercial Timbers of Peninsular Malaysia*. Research Pamphlet No. 125. Forest Research Institute Malaysia, Kpong.
- HATTORI D, KENZO T, KENDAWANG JJ, IRINO KO, TANAKA S, ICHIE T, NINOMIYA I & SAKURAI K. 2009. Effects of light intensity and soil physico-chemical properties on seedling mortality and growth of six dipterocarp species planted for rehabilitation of degraded grassland, secondary forest and logged forest in Sarawak, Malaysia. *Japanese Journal of Forest Environment* 51: 105–115.
- ICHIE T, KITAHASHI Y, MATSUKI S, MARUYAMA Y & KOIKE T. 2002. The use of a portable non-destructive type nitrogen meter for leaves of woody plants in field studies. *Photosynthetica* 40: 289–292.
- ISHIDA A, NAKANO T, MATSUMOTO Y, SAKODA M & ANG LH. 1999. Diurnal changes in leaf gas exchange and chlorophyll fluorescence in tropical tree species with contrasting light requirements. *Ecological Research* 14: 77–88.
- ISHIDA A, NAKANO T, YAZAKI K, MATSUKI S, KOIKE N, LAUENSTEIN DL, SHIMIZU M & YAMASHITA N. 2008. Coordination between leaf and stem traits related to leaf carbon gain and hydraulics across 32 drought-tolerant. *Oecologia* 156: 193–202.
- KENZO T, FURUTANI R, HATTORI D, KENDAWANG JJ, TANAKA S, SAKURAI K & NINOMIYA I. 2009a. Allometric equations for accurate estimation of above-ground biomass in logged-over tropical rainforests in Sarawak, Malaysia. *Journal of Forest Research* 14: 365–372.

- KENZO T, ICHIE T, HATTORI D, ITIOKA T, HANDA C, OHKUBO T, KENDAWANG JJ, NAKAMURA M, SAKAGUCHI M, TAKAHASHI N, OKAMOTO M, TANAKA-ODA A, SAKURAI K & NINOMIYA I. 2009b. Development of allometric relationships for accurate estimation of above- and belowground biomass in tropical secondary forests in Sarawak, Malaysia. *Journal of Tropical Ecology* 25: 371–386.
- KENZO T, ICHIE T, HATTORI D, KENDAWANG JJ, SAKURAI K & NINOMIYA I. 2010. Changes in above- and belowground biomass in early successional tropical secondary forests after shifting cultivation in Sarawak, Malaysia. *Forest Ecology and Management* 260: 875–882.
- KENZO T, ICHIE T, OZAWA T, KASHIMURA S, HATTORI D, IRINO KO, KENDAWANG JJ, SAKURAI K & NINOMIYA I. 2007. Leaf physiological and morphological responses of seven dipterocarp seedlings to degraded forest environments in Sarawak, Malaysia: a case study of forest rehabilitation practice. *Tropics* 17: 1–16.
- KENZO T, ICHIE T, WATANABE Y, YONEDA R, NINOMIYA I & KOIKE T. 2006. Changes in photosynthesis and leaf characteristics with height from seedlings to mature canopy trees in five dipterocarp species in a tropical rain forest. *Tree Physiology* 26: 865–873.
- KENZO T, ICHIE T, YONEDA R, KITAHASHI Y, WATANABE Y, NINOMIYA I & KOIKE T. 2004. Interspecific variation of photosynthesis and leaf characteristics in five canopy trees of Dipterocarpaceae in a tropical rain forest. *Tree Physiology* 24: 1187–1192.
- KENZO T, YONEDA R, MATSUMOTO Y, AZANI MA & MAJID NM. 2008. Leaf photosynthetic and growth responses on four tropical tree species to different light conditions in degraded tropical secondary forest, Peninsular Malaysia. *Japan Agricultural Research Quarterly* 42: 299–306.
- KETTLE CJ. 2010. Ecological considerations for using dipterocarps for restoration of lowland rainforest in Southeast Asia. *Biological Conservation* 19: 1137–1151.
- KIMURA K, ISHIDA A, UEMURA A, MATSUMOTO Y & TERASHIMA I. 1998. Effect of current-year and previous-year PFDs on shoot gross morphology and leaf properties in *Fagus japonica*. *Tree Physiology* 18: 459–466.
- KING DA. 1991. Correlations between biomass allocation, relative growth rate and light environment in tropical forest saplings. *Functional Ecology* 5: 485–492.
- KITAO M, YONEDA R, TOBITA H, MATSUMOTO Y, MARUYAMA Y, ARIFIN A, AZANI AM & MUHAMAD MN. 2006. Susceptibility to photoinhibition in seedlings of six tropical fruit tree species native to Malaysia following transplantation to a degraded land. *Trees* 20: 601–610.
- KOBAYASHI S. 2004. Landscape rehabilitation of degraded tropical forest ecosystems. Case study of the CIFOR/ Japan project in Indonesia and Peru. *Forest Ecology and Management* 201: 13–22.
- KRISHNAPILLAY B. 2002. *A Manual for Forest Plantation Establishment in Malaysia*. Malayan Forest Records No. 45. Forest Research Institute Malaysia, Kepong.
- KULL O & NIINEMETS Ü. 1998. Distribution of leaf photosynthetic properties in tree canopies: comparison of species with different shade tolerance. *Functional Ecology* 12: 472–479.
- LAMB D, ERSKINE PD & PARROTTA JA. 2005. Restoration of degraded tropical forest landscapes. *Science* 310: 1628–1632.
- LAMBERS H, CHAPIN III FS & PONS TL. 1998. *Plant Physiological Ecology*. Springer-Verlag, New York.
- LARCHER W. 2003. *Physiological Plant Ecology*. Fourth edition. Springer-Verlag, New York.
- MULLER-LANDAU HC. 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* 36: 20–32.
- NICHOLSON DI. 1960. Light requirements of seedlings of five species of Dipterocarpaceae. *Malaysian Forester* 23: 344–356.
- NORISADA M, HITSUMA G, KURODA K, YAMANOSHITA T, MASUMORI M, TANGE T, YAGI H, NUYIM T, SASAKI S & KOJIMA K. 2005. *Acacia mangium*, a nurse tree candidate for reforestation on degraded sandy soils in the Malay peninsula. *Forest Science* 51: 498–510.
- POPMA J & BONGERS F. 1988. The effect of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia* 75: 625–632.
- SASAKI S & MORI T. 1981. Growth responses of dipterocarp seedlings to light. *Malaysian Forester* 44: 319–345.
- SOERIANEGARA & LEMMENS RHMJ. 1994. *Plant Resources of South-East Asia. No. 5(1) Timber Trees: Major Commercial Timbers*. Prosea Foundation, Bogor.
- SUZUKI E. 1999. Diversity in specific gravity and water content of wood among Bornean tropical rainforest trees. *Ecological Research* 14: 211–224.
- SUZUKI T. & JACALNE DV. 1986. Response of dipterocarp seedling to various light conditions under forest canopies. *Bulletin of Forest and Forestry Product Research Institute* 336: 19–34.
- SYMINGTON CF. 2004. *Foresters' Manual of Dipterocarps*. Second edition. Malayan Forest Records No. 16. Forest Research Institute Malaysia, Kepong.
- TUOMELA K, KUUSIPALO J, VESA L, NURYANTO K, SAGALA APS & ÅDJERS G. 1996. Growth of dipterocarp seedlings in artificial gaps: an experiment in a logged-over rainforest in south Kalimantan, Indonesia. *Forest Ecology and Management* 81: 95–100.
- TURNER IM & NEWTON AC. 1990. The initial responses of some tropical rain forest tree seedlings to a large gap environment. *Journal of Applied Ecology* 27: 605–608.
- UEDA K, SALLEH S, YUSOF MM, KIMURA K & MATSUMOTO Y. 1997. Survival and growth of three dipterocarp species line-planted under *Acacia mangium*. Pp 87–98 in *Proceedings of the Third Conference of Forestry and Forest Products Research*. Volume 2. 3–4 October 1995. Kepong.
- VINCENT G. 2001. Leaf photosynthetic capacity and nitrogen content adjustment to canopy openness in tropical forest tree seedling. *Journal of Tropical Ecology* 17: 495–509.
- WHITMORE TC. 1972. *Tree Flora of Malaya*. Volume 2. Longman, Kuala Lumpur.
- WHITMORE TC. 1998. *An Introduction to Tropical Rain Forests*. Second edition. Oxford University Press, Oxford.
- WRIGHT SJ. 2005. Tropical forests in a changing environment. *Trend Ecology and Evolution* 20: 553–560.
- WYATT-SMITH J. 1963. *Manual of Malayan Silviculture for Inland Forests*. Volume 1. Malayan Forest Records No. 23. Forest Research Institute Malaysia, Kepong.

- YAMAMOTO S. 2000. Estimation of the canopy-gap size using two photographs taken at different heights. *Ecological Research* 15: 203–208.
- YAMASHITA N, ISHIDA A, KUSHIMA H & TANAKA N. 2000. Acclimation to sudden increase in light favoring an invasive over native trees in subtropical islands, Japan. *Oecologia* 125: 412–419.
- YAP SK. 1980. Jelutong: phenology, fruit and seed biology. *Malaysian Forester* 43: 309–315.
- YONEDA R, MATSUMOTO Y, KENZO T, AZANI MA & MAJID NM. 2005. The short-term gas exchange and photoinhibition responses in planted *Dyera costulata* seedlings under artificial shading shelter in open condition. *Japanese Journal of Forest Environment* 47: 113–118.