

Leaf physiological and morphological responses of seven dipterocarp seedlings to degraded forest environments in Sarawak, Malaysia: A case study of forest rehabilitation practice

Tanaka KENZO¹, Tomoaki ICHIE², Tomoko OZAWA³, Seiichi KASHIMURA³, Daisuke HATTORI⁴, Kazuo O. IRINO⁴, Joseph Jawa KENDAWANG⁵, Katsutoshi SAKURAI² and Ikuo NINOMIYA³

¹ Forestry and Forest Products Research Institute, Tsukuba, 305-8687, Japan.

² Faculty of Agriculture, Kochi University, Nankoku, 783-8502, Japan.

³ Faculty of Agriculture, Ehime University, Matsuyama, 790-8566, Japan.

⁴ United Graduate School of Agricultural Sciences, Ehime University, Matsuyama, 790-8566, Japan.

⁵ Forest Department Sarawak, Kuching, 93660, Malaysia.

Tel: +81-29-873-3211, Fax: +81-29-874-3797, E-mail: mona@affrc.go.jp

ABSTRACT Leaf physiological and morphological responses were studied in seedlings of seven dipterocarp species planted in three degraded forest environments: grassland, logged remnant forest and secondary forest. *Dryobalanops beccarii*, *Parashorea macrophylla*, *Shorea macrophylla*, *S. ovata*, *S. parvifolia*, *S. seminis* and *S. virescens* were used as study species. The leaf photosynthetic rate at light saturation (A_{max}), the dark respiration rate (R_d), light compensation point (I_c), leaf mass per area (LMA) and SPAD value were measured during the 38 months after planting. Water loss by detached leaves was also determined at 13 months after planting. In the grassland, LMA and A_{max} increased from three months after planting in all species except *S. ovata*. The time by which 50% of total leaf water content had been lost from detached leaves was positively correlated with LMA, suggesting that species with high LMA (*D. beccarii*, *S. ovata* and *S. parvifolia*) have high tolerance to desiccation in the grassland. The positive correlation found between LMA and A_{max} indicates that LMA accelerated the photosynthetic rate, although those species with higher A_{max} /LMA (*P. macrophylla*, *S. macrophylla* and *S. seminis*) had low tolerance of desiccation in the grassland. The seedlings planted in the remnant forest had lower leaf R_d and higher SPAD values than in the other environments. Large increase in SPAD value and decrease of I_c in *P. macrophylla* and *S. virescens* suggest that both species have acclimation ability to the remnant forest. The lowest mortality and I_c in the remnant forest was in *S. seminis* and suggests high shade tolerance in this species. In contrast,

S. ovata, which maintained the highest I_c over the measurement period, may suffer greatest mortality in the remnant forest. In the secondary forest, the leaf A_{max} , LMA and SPAD value were intermediate in value between the other two environments. We conclude that leaf ecophysiological traits in dipterocarp seedlings differ significantly between species. This is information needed for enrichment planting in degraded tropical rainforest areas in Southeast Asia.

Keywords: Dipterocarpaceae, photosynthesis, Sarawak, sifting cultivation, tropical degraded forest

INTRODUCTION

Deforestation rates in the lowland rainforest of Southeast Asia have increased significantly, especially over the last 50 years (Hansen and DeFries, 2004; Wright, 2005). In particular, the dominant Dipterocarpaceae family in the lowland rainforest of Southeast Asia is often heavily logged for commercial timber (Whitmore, 1998). Following disturbance, various types of degraded forest remain in this area, because of differences in the type of disturbance, environmental conditions, time elapsed since the disturbance, and the original vegetation type. These degraded forests can be broadly divided into three types of degraded vegetation, namely grassland after burning, remnant forest after logging, and secondary forest. Appropriate rehabilitation or reforestation techniques are required in each case. Enrichment planting in degraded forest promises to be highly effective in rehabilitating or reforesting degraded forest, especially using Dipterocarpaceae and other endemic late-successional

tree species; these provide benefits such as timber, food and medical products (Schulze et al. 1994; Kuusipalo et al. 1996; Alias et al. 1998; Kobayashi, 2004; Lamb et al. 2005). Growth and survival of the planted seedlings in degraded forest may differ among species, however (Suzuki and Jacalne, 1986; Maruyama et al. 1997a). A better understanding of environmental responses in possible planting species would greatly enhance enrichment planting in forest environments (Appanah & Weinland, 1993; Krishnapillay, 2002). Leaf ecophysiological traits should provide valuable information, since leaf photosynthesis and water use are essential to carbon assimilation and link directly to plant growth, survival and environmental acclimation. However, we know little about the leaf environmental responses of late-successional tree species to degraded forest conditions.

Leaf ecophysiological properties related to photosynthesis and water use generally depend on both leaf physiological and morphological traits, and are strongly related to the light environment (Kramer, 1983; Lee et al. 1996; Lambers et al. 1998; Larcher, 2003; Shimizu et al. 2005). Leaves in strong light and drought conditions (sun leaves) have greater leaf mass per area (LMA), corresponding to a higher photosynthetic rate and higher dehydration tolerance, than leaves in limited light conditions (shade leaves). Shade leaves have higher leaf chlorophyll content and are thinner, so as to maintain the dark respiration rate and light compensation point; these are lower than in sun leaves (Koike et al. 2001; Lambers et al. 1998). Shade leaves also suffer excessive leaf water loss when shade-adapted seedlings are transplanted into strong light conditions (Maruyama et al. 1997b). However, these responses of leaves to the environment differ significantly between species even in the same taxonomic group, especially under strong light conditions as in the forest canopy (Kenzo et al. 2004) and may influence differences in seedling performance after planting (Maruyama et al. 2005). For instance, under degraded conditions, growth and survival of the planted seedlings may be strongly related to the light environment (Ådjers et al. 1995; McNamara et al. 2006). Grassland after forest burning usually experiences very high light intensity, and some planted late-successional tree seedlings, including dipterocarp species, had lower growth and survival rate (Norisada et al. 2005; Yoneda et al. 2005). On the other hand, seedling survival and growth rate in some late-successional tree species under very dark conditions, as in late-successional and logged over closed remnant forest, was also significantly suppressed, especially when growth light conditions

were less than 3% of the relative light intensity (Suzuki and Jacalne, 1986; Ashton et al. 2006). Therefore we can assume that leaf physiological and morphological traits of the planted seedlings differ greatly between the three vegetations, and strongly influence the adaptability of the planted seedlings to the conditions.

In this study we measured leaf morphological and physiological properties before and after planting, in order to demonstrate interspecific acclimation ability in the three types of typical degraded forest (logged over remnant forest, secondary forest and grassland after burning) in seven endemic dipterocarp species. All seven species are popular enrichment planting species in east Malaysia.

MATERIALS AND METHODS

Study site

Our study was carried out in the Niah Forest Reserve, Sarawak, Malaysia (3°39'N, 113°42'E). The area has a humid tropical climate, with weak seasonal changes in rainfall and temperature (Kato et al. 1995). Annual rainfall and average temperature are about 2800 mm and 27°C (Hattori et al. 2005). The original vegetation was lowland mixed dipterocarp forest. The soil at the study site mainly comprised moderately soft gray mud stones and shales (Baillie, 1972). It was classified into Typic Kandihumults, and showed a light clay (LiC) texture (Irimo et al. 2004, 2005; Hattori et al. 2005). There were no large differences in total nitrogen and carbon, cation exchange capacity, particle distribution between the three vegetation types, although soil exchangeable bases and pH tended to be higher in the grassland because of shifting cultivation practice (Hattori et al. 2005).

The planting area (about 70ha) consists of the three kinds of degraded forest vegetation specified above (see Hattori et al. 2005). The first is grassland, which established itself after sifting cultivation. The vegetation is a few years old, since the last burning, and is covered by tall grasses of height 1–2 m, and young pioneer trees such as genus *Trema*. The relative light intensity (RLI) was approximately 77%. The second type of degraded vegetation is remnant forest, which formed after selective logging from mixed dipterocarp rainforest. The forest was logged selectively in the 1980s, but the forest canopy is now almost closed, and the forest floor is as dark as in natural rainforest. The RLI of the forest was approximately 4%, similar to late-successional tropical rain forest (Whitmore, 1998). Tree species in this forest are diverse, and include many dipterocarp species such

as genus *Dryobalanops* and *Shorea*. The stand density and basal area (diameter at the breast height > 3 cm) in the forest were approximately 1990 trees ha⁻¹ and 21m² ha⁻¹ (according to our preliminary survey). Some large trees were 40 m high. The last habitat is secondary forest, also established after sifting cultivation. This forest most recently experienced fire about 15 years ago. Trees are mainly pioneer species such as genus *Macaranga*, *Artocarpus* and *Ficus*. Tree height varies from 15 to 25 m. The forest floor is less dark, and sunflecks commonly penetrate. The RLI was approximately 8% in the forest. These post-fired forests are widely distributed around tropical Asia, particularly in Borneo Island (Dennis et al. 2001), and the forest under study is a typical post fired secondary forest in its species composition (Whitmore, 1998; Mori, 2000). These three vegetation patterns are distributed patchily throughout the study area.

Plant materials and planting methods

The planted species were *Dryobalanops beccarii* Dyer, *Parashorea macrophylla* Wyatt-Sm. ex P. S. Ashton, *Shorea macrophylla* (de Vriese) P. S. Ashton, *S. ovata* Dyer ex Brandis, *S. parvifolia* Dyer, *S. seminis* (de Vriese) Slooten and *S. virescens* Parijs. All are Dipterocarpaceae, and usually grow in the lowland dipterocarp forest in Sarawak (Ashton, 2004). Dipterocarpaceae dominate in the tropical rainforest in Southeast Asia, and often make up the upper canopy layer (Whitmore, 1998; Symington, 2004). This family also includes many important commercial timber species (Ashton, 2004). The tree species chosen in this study are canopy tree species that produce useful timber. Seeds of *S. macrophylla* also contain a high-fat oil and are exported commercially. These trees are therefore good species for enrichment planting and forest rehabilitation in the region (Kendawang, 1992).

The planted seedlings were fostered in a nursery for three months to one year after germination at about 40% RLI (before planting). In May 2000 the seedlings were planted in remnant forest, in secondary forest and in grassland. An island corridor planting system was used for the planting (Ninomiya et al. 2000). The planting density in the system was approximately 370 trees per hectare.

Measurement of leaf gas exchange rate and leaf characteristics

To measure the leaf gas exchange rate, we used a portable photosynthesis meter (LI-6400, Li-Cor, Lincoln, NE). To avoid the midday photosynthesis depression, measurements were made from 0800 to 1100 in the

morning (Hiromi et al. 1999; Kenzo et al. 2003). The relation between photon flux density and carbon assimilation rate was determined for fully expanded leaves of five individuals in each plot. The measured light intensity varied from 0 to 1800 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$, and the temperature was about 30°C (Kenzo et al. 2004, 2006). The CO₂ concentration, vapor pressure deficits (VPD) and air humidity in the chamber were approximately 370 ppm, 1.7 to 2.0 kPa and 60%. The photosynthetic rate at light saturation (A_{max}), light compensation point (I_c) and the dark respiration rate (R_d) were calculated from the measurements (Kenzo et al. 2003, 2006). Stomatal conductance at A_{max} (g_{Smax}) was also recorded, and the water use efficiency (WUE), which is the ratio of A_{max} to g_{Smax} ($A_{\text{max}}/g_{\text{Smax}}$), was calculated. After the gas exchange measurements, the leaf mass per unit area (LMA) and SPAD value were measured. The SPAD value was determined using a SPAD-502 (Konica Minolta Holdings Co. Ltd., Tokyo, Japan). This value is an index for the chlorophyll content in the leaf (Ichie et al. 2002). The measurements were carried out at the nursery before planting, and then at 3, 13, 25 and 38 months after planting. We used fully expanded and apparently non-senescent leaves. To mitigate the effects of variable leaf age, the age of the leaves was estimated from the position on the branch, leaf texture, and particularly the leaf color (Sobrado and Medina, 1980; Kenzo et al. 2006). Leaf color was measured by the SPAD-502.

Measurement of water loss by detached leaves

Water loss by detached leaves was determined by gravimetric methods at 13 months after planting (Kaul and Kramer, 1965; Slavík, 1974). Mature leaves of five individuals of each species were detached from freshly collected shoots, and were placed with the petiole in water for one night in a saturated atmosphere to allow them to become fully saturated (Peace and Macdonald, 1981). The water loss from a leaf was measured periodically for about 12 hours at approximately 35°C and 40% relative humidity. The leaf water loss generally decreases exponentially with time (Hygen, 1951; Slavík, 1974). We calculated the 'half life' after which 50% of the total leaf water content was left (Hygen, 1951).

Statistical analysis

We performed two-way analysis of variance (ANOVA) on the leaf physiological and morphological properties from transplantation to 38 months after planting (Socal and Rohlf, 1995). The significance of the difference was determined using Tukey's test ($P < 0.05$).

Scatter plots of LMA with leaf physiological properties were analyzed by linear regression. Differences in leaf properties between species were tested by analysis of covariance (ANCOVA), with species as main factor and LMA as covariable (Sokal and Rohlf, 1995). All statistical analyses were conducted using SPSS ver. 11.5 for Windows (SPSS Japan Inc., Tokyo, Japan).

RESULTS

Changes in leaf properties after planting

The photosynthetic rate at light saturation (A_{\max}) increased after planting in grassland in all species except *S. ovata*, and the rates varied by a factor of two between species (Fig. 1). *S. macrophylla* exhibited the highest

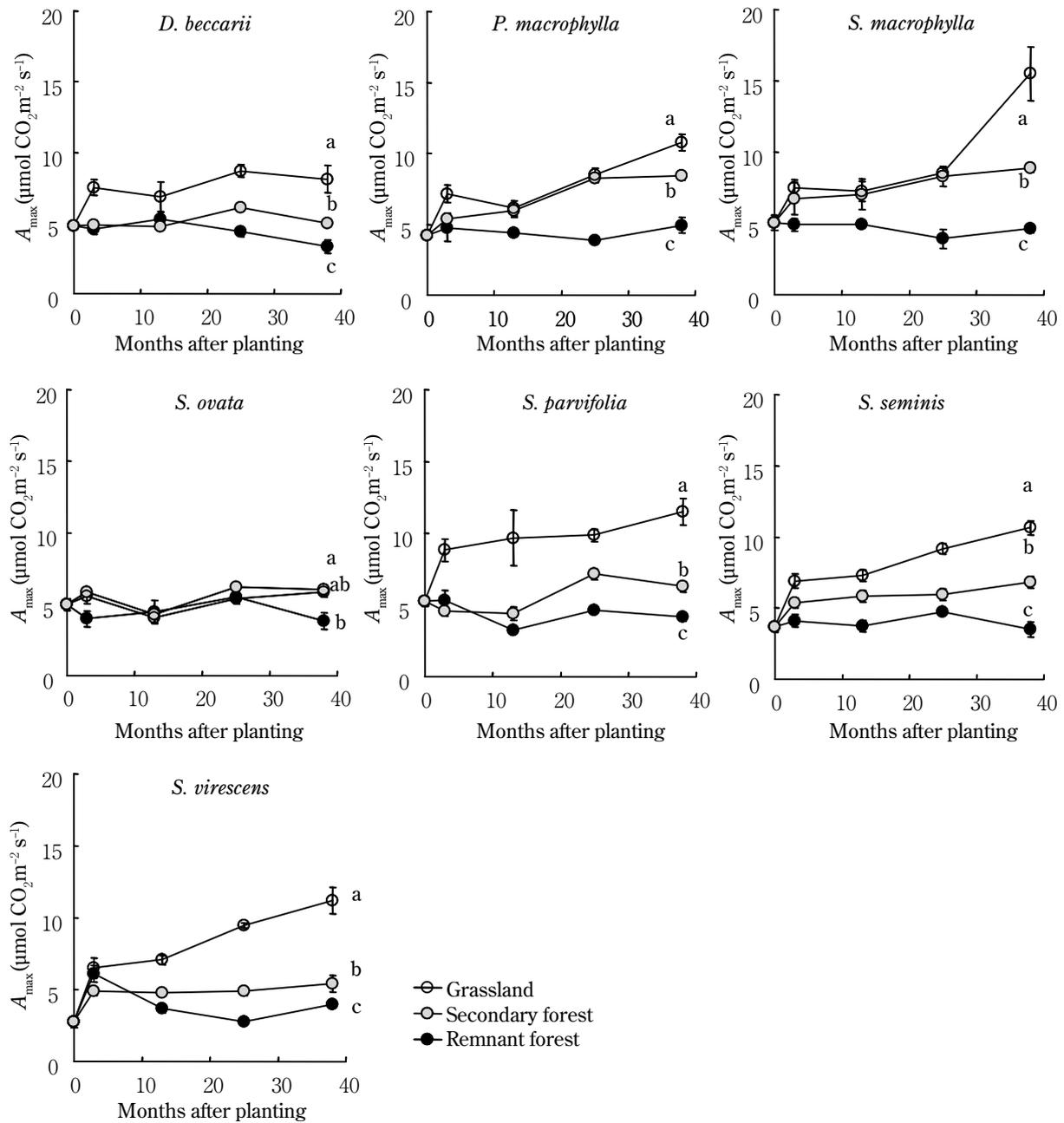


Fig. 1. Changes in photosynthetic rate at light saturation (A_{\max}) after planting. Different letters indicate a significant difference across the measurement period ($P < 0.05$, ANOVA). Bars indicate the standard error ($n=5$ for each species).

A_{\max} at 38 months after planting in the grassland, of $15 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. In contrast, A_{\max} in the remnant forest maintained a stable value for 38 months in all species. In the secondary forest, A_{\max} was intermediate between values in remnant and grassland (Fig. 1). The dark respiration rate (R_d) in the grassland increased in all species after planting (Fig. 2). In particular, R_d at three

months after planting was 2–3 times higher than at other measurement times. In the remnant forest, R_d continued to decline throughout the 38 months after planting in all species. The rate at 38 months after planting was 1/2–1/3 of the rate before the seedlings were planted (Fig. 2).

Leaf mass per area (LMA) increased after planting in the grassland in all species except *S. ovata* (Fig. 3). *S.*

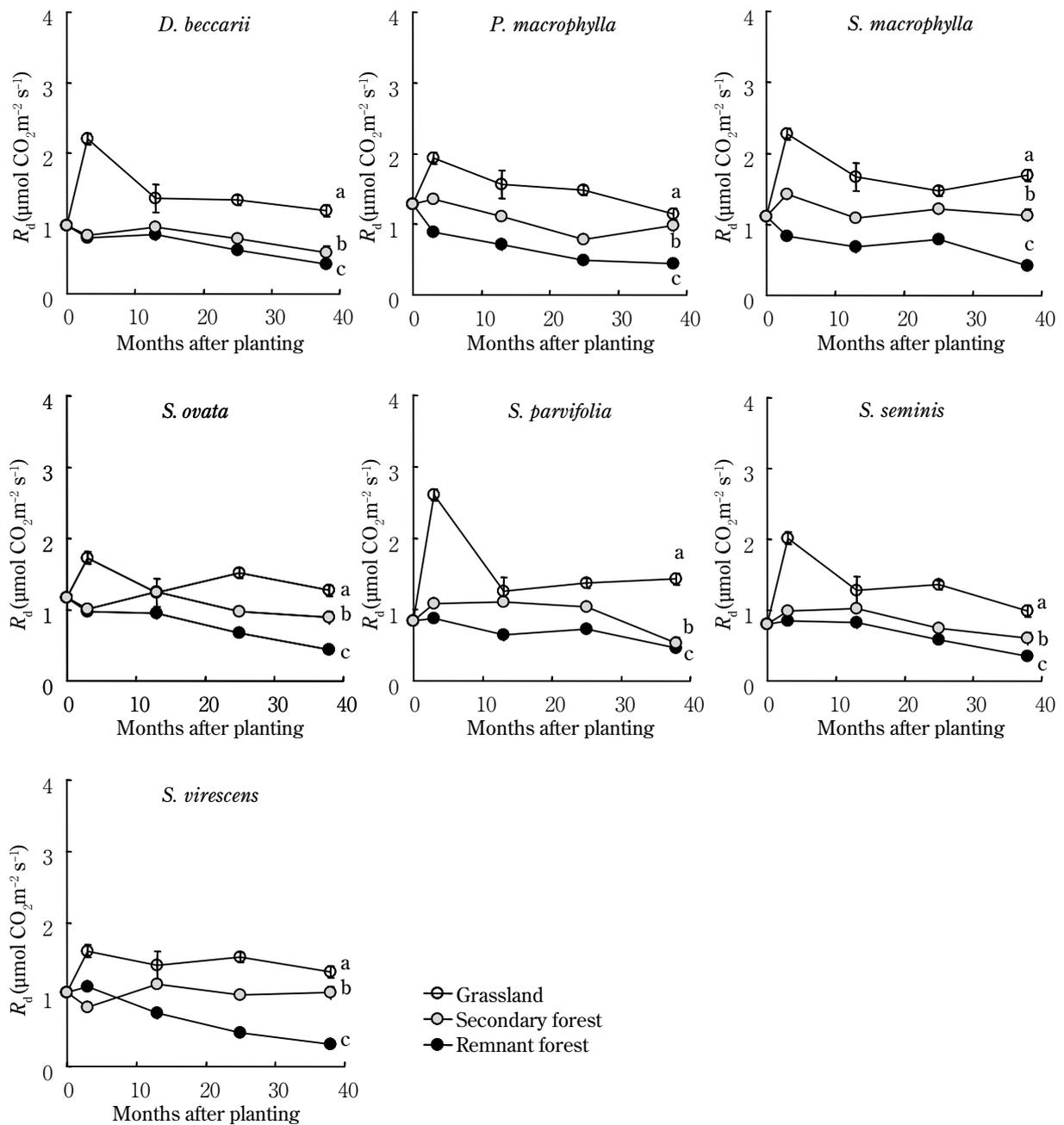


Fig. 2. Changes in dark respiration rate (R_d) after planting. Different letters indicate a significant difference across the measurement period ($P < 0.05$, ANOVA). Bars indicate the standard error ($n=5$ for each species).

ovata maintained almost the same LMA throughout the measurement period. In contrast, the LMA in the remnant forest decreased after planting in all species. The SPAD value, which indicates the chlorophyll content in the leaf, increased at three months after planting in all species in the remnant and secondary forest (Fig. 4). Thereafter, the value rose gently until 38 months after planting. The SPAD value in the grassland also increased slightly, but the value in some species, such as *S. macrophylla*, dropped at three months after planting.

The light compensation point (I_c) at 36 months after planting in the remnant forest was lower than in the nursery for all species (Fig. 5). The pattern of the changes after planting was different between the species, however. *S. ovata* maintained a higher I_c value than the other species after planting ($P < 0.05$, ANOVA). In contrast, *S. seminis* had the lowest I_c value ($P < 0.05$, ANOVA). *Parashorea macrophylla* and *S. virescens* had relatively high I_c value in the nursery, but the value dropped at three months after planting. We calculated the degree of variance of the SPAD and I_c values from nursery to three months after planting in the remnant forest. A negative relation was observed between both degrees of variance in the remnant forest (Fig. 6). SPAD and I_c values of *S. ovata* showed little change from nursery to three months after planting. In contrast, the SPAD value of *P. macrophylla* and *S. virescens* approximately doubled, and the I_c value fell by more than 20 to 30% from the nursery to three months after planting.

Relation between leaf photosynthetic rate (A_{\max}) and LMA

The leaf photosynthetic rate (A_{\max}) is positively correlated with LMA in all species ($P < 0.05$; Fig. 7). Differences were found between species by statistical analysis (ANCOVA; $P < 0.05$). The analysis divided the studied species into three groups. For instance, *P. macrophylla* and *S. seminis* had higher photosynthetic rates at lower LMA. *D. beccarii*, *S. macrophylla*, *S. parvifolia* and *S. virescens* belonged to the same group. The regression slope, which refers to the photosynthetic rate per LMA (A_{\max}/LMA ; $\mu\text{mol CO}_2 \text{ s}^{-1} \text{ g}^{-1}$), was significantly smaller in *S. ovata* than in other species.

Leaf desiccation traits and water use efficiency (WUE)

The time after which half of the total leaf water had left the detached leaf (50% water loss time) was also positively correlated with LMA in grassland ($P < 0.05$; Fig. 8). *Parashorea macrophylla*, *S. macrophylla* and *S. seminis*,

which had lower LMA, had shorter 50% water loss times than higher LMA species such as *D. beccarii*, *S. parvifolia* and *S. ovata* in the grassland. In contrast, there was no significant correlation between the 50% water loss time and LMA in the secondary and remnant forest.

Water loss time in the grassland was also in negative relation to the photosynthetic rate per LMA (A_{\max}/LMA ; Fig. 9). Some species, which had longer water loss time (*D. beccarii*, *S. parvifolia* and *S. ovata*), showed lower A_{\max}/LMA than shorter species such as *P. macrophylla* and *S. macrophylla*.

Changes of water use efficiency (WUE) differed significantly between species in the grassland (Fig. 10). The highest WUE over the measurement period was in *D. beccarii* ($P < 0.05$, ANOVA). Although *S. parvifolia* had low WUE in nursery conditions, WUE in this species increased after planting and showed relatively higher WUE compared with other species. In contrast, *S. macrophylla* had high WUE in nursery conditions, but the value decreased after planting and showed the lowest WUE over the measurement period ($P < 0.05$, ANOVA).

DISCUSSION

Leaf acclimation to the grassland environment

Most of the dipterocarp seedlings studied acclimated to the grassland condition, which experiences strong sunlight and drought, by changing their LMA. However, their acclimation abilities to the grassland differed significantly between species.

Leaf light acclimation to the grassland appeared in LMA and A_{\max} in most of these species from just after planting. Tree seedlings transplanted to strong light conditions display a higher rate of photosynthesis and LMA than in low light conditions (Bazzaz, 1979; Givnish, 1988; Ashton and Berlyn, 1992). The high A_{\max} values of the species studied here, apart from *S. ovata*, show that they have relatively rapid acclimation ability to grassland conditions. In particular, *P. macrophylla*, *S. macrophylla* and *S. seminis*, which showed high photosynthetic rate per LMA (A_{\max}/LMA , Fig. 7), may have high plasticity on the A_{\max} to the different light condition by changing LMA. However, the disproportionately large increase in dark respiration rate just after planting, contrasted with the increase in A_{\max} in all species (Figs. 1, 2), reflect the high cost of maintaining the photosynthetic apparatus, and the cost of increased investment in photo-protective mechanisms in grassland conditions (Demming-Adams and Adams, 1992; Clearwater et al. 1999). The increased respiration rate also reduces the benefits of high

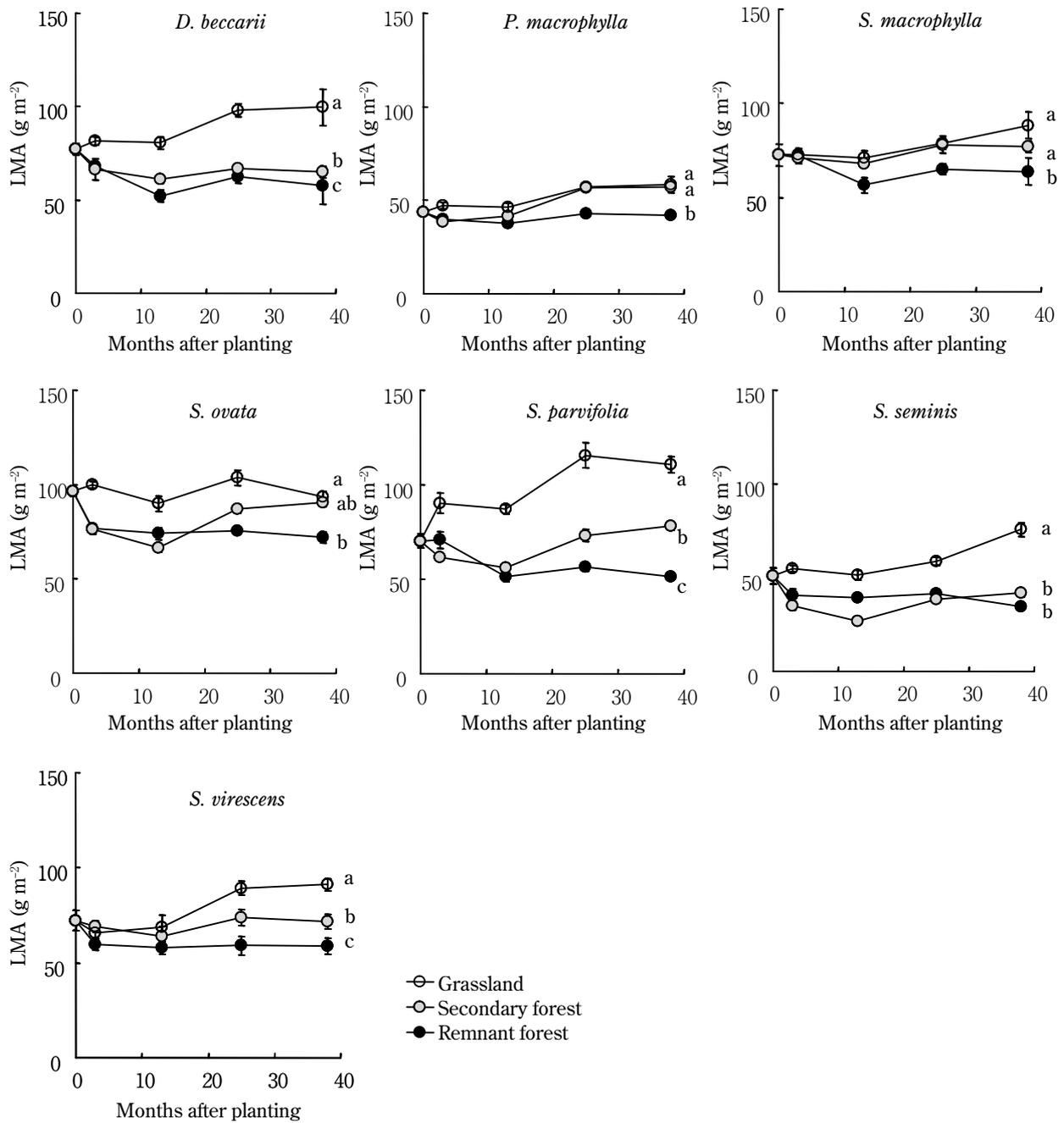


Fig. 3. Changes in leaf mass per area (LMA) after planting. Different letters indicate a significant difference across the measurement period ($P < 0.05$, ANOVA). Bars indicate the standard error ($n=5$ for each species).

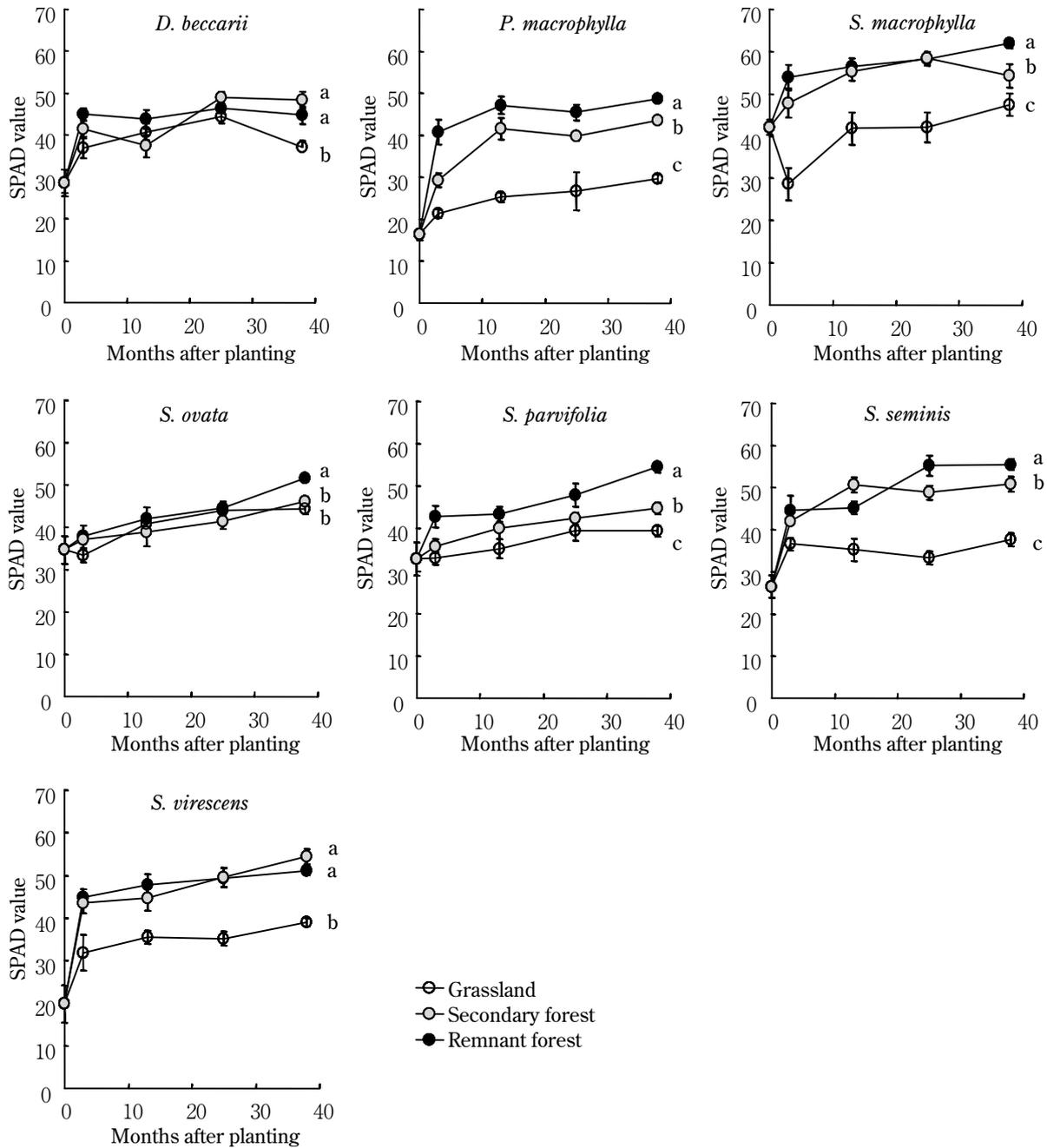


Fig. 4. Changes in SPAD value after planting. Different letters indicate a significant difference across the measurement period ($P < 0.05$, ANOVA). Bars indicate the standard error (n=5 for each species).

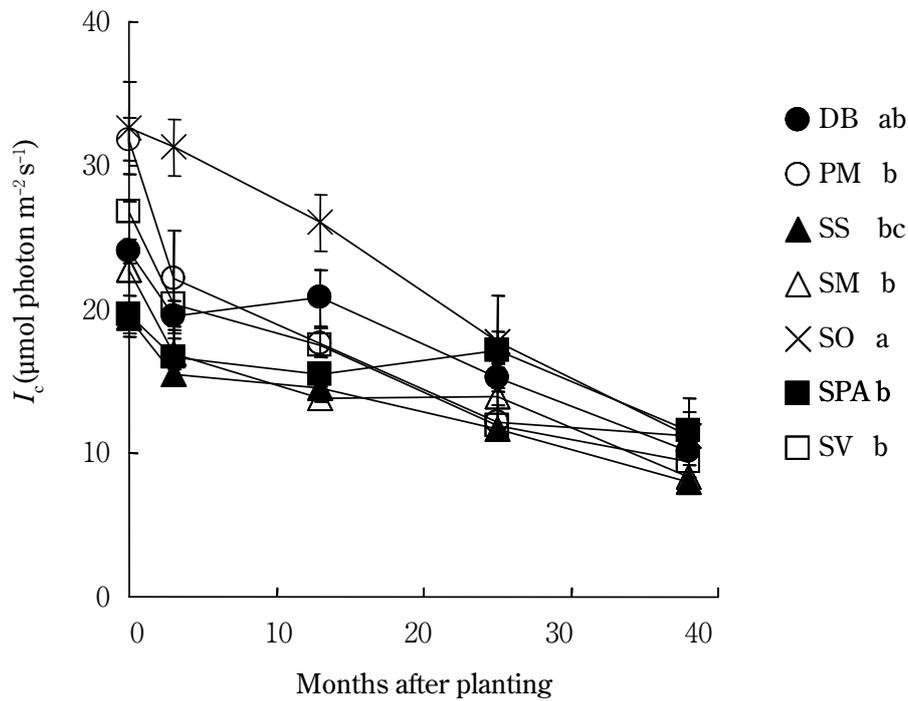


Fig. 5. Changes in light compensation point (I_c) in the remnant forest after planting. Different letters indicate a significant difference across the measurement period ($P < 0.05$, ANOVA). Bars indicate the standard error ($n=5$ for each species).

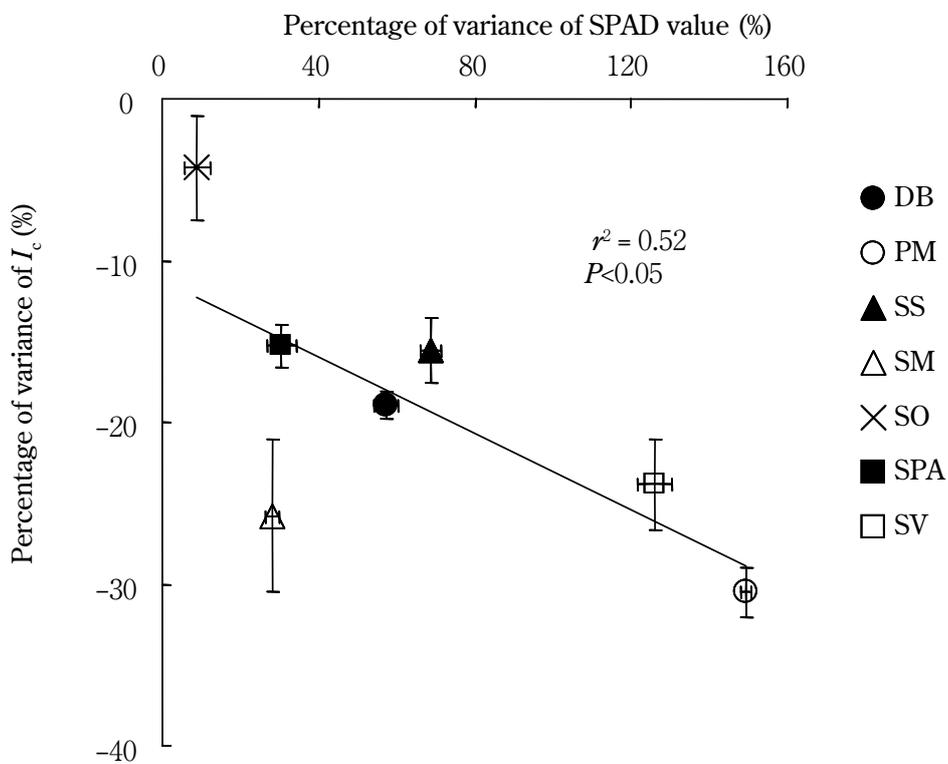


Fig. 6. Relation between degree of variance of SPAD and I_c value from nursery to 3 months after planting in the remnant forest. Bars indicate the standard error ($n=5$ for each species).

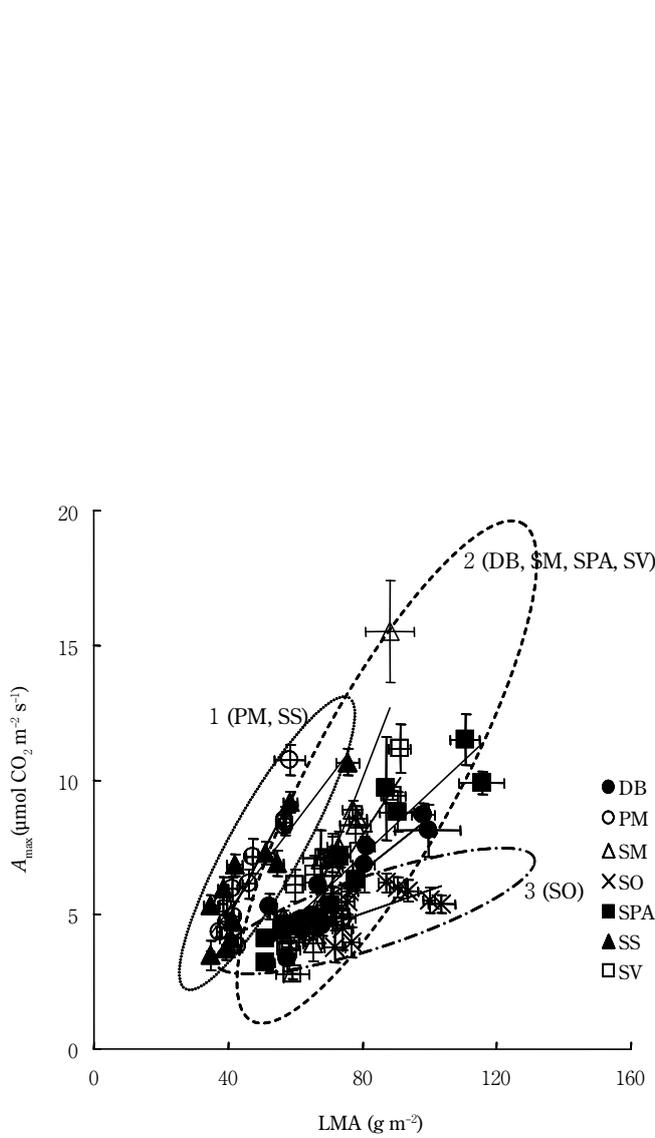


Fig. 7. Relationships between LMA and photosynthetic rate at light saturation (A_{max}) for three vegetations. Values are means for each measurement period across all replicate individuals ($n=5$ for each species). The numbers and ellipses (dotted lines) in the figure indicate three groups for the relation between LMA and A_{max} , distinguished by ANCOVA analysis ($P < 0.05$). The regression lines are: *D. beccarii*, $y = -1.26 + 0.10x$; $r^2 = 0.81$, $P < 0.001$. *P. macrophylla*, $y = -4.64 + 0.24x$; $r^2 = 0.84$, $P < 0.001$. *S. macrophylla*, $y = -15.87 + 0.32x$; $r^2 = 0.75$, $P < 0.001$. *S. ovata*, $y = -1.59 + 0.04x$; $r^2 = 0.37$, $P < 0.05$. *S. parvifolia*, $y = -2.19 + 0.12x$; $r^2 = 0.90$, $P < 0.001$. *S. seminis*, $y = -1.41 + 0.16x$; $r^2 = 0.81$, $P < 0.001$. *S. virescens*, $y = -7.13 + 0.19x$; $r^2 = 0.76$, $P < 0.001$.

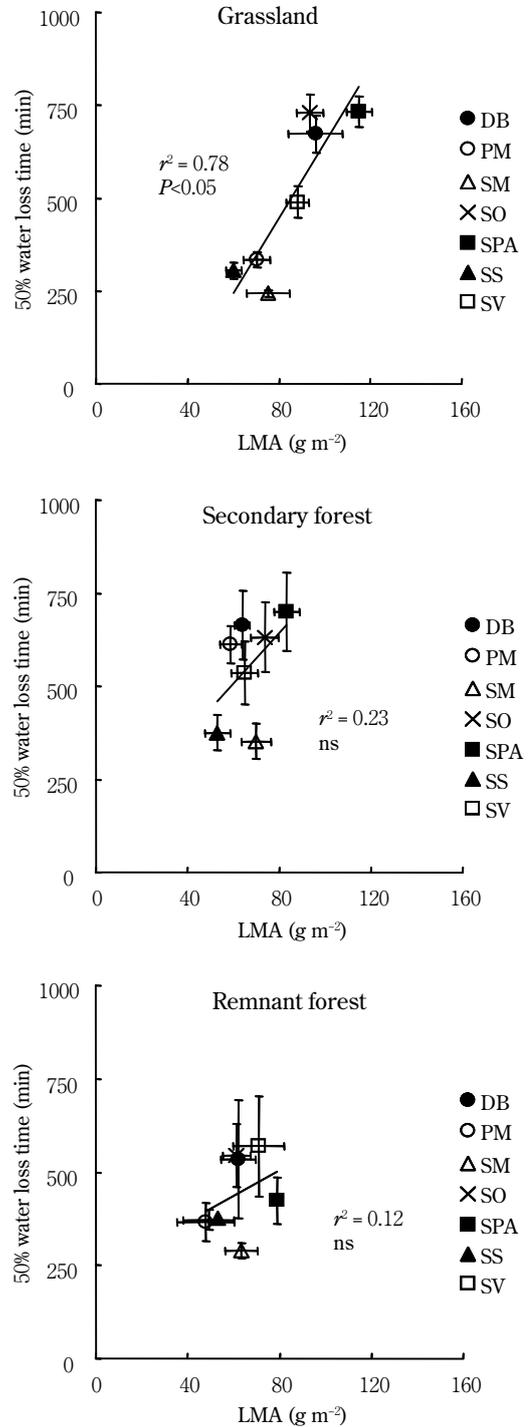


Fig. 8. Relationships between LMA and the time when 50% of total leaf water was lost from detached leaves (50% water loss time) in the three vegetations Bars indicate the standard error ($n=5$ for each species).

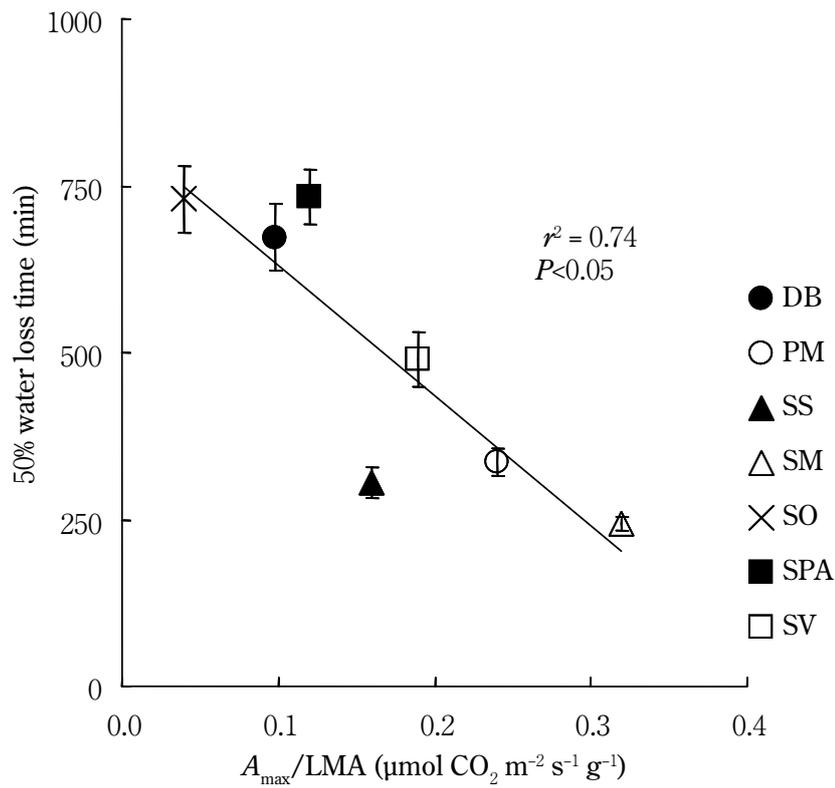


Fig. 9. Relationships between A_{max}/LMA and the time when 50% of total leaf water was lost from detached leaves (50% water loss time) in the grassland. Bars indicate the standard error (n=5 for each species).

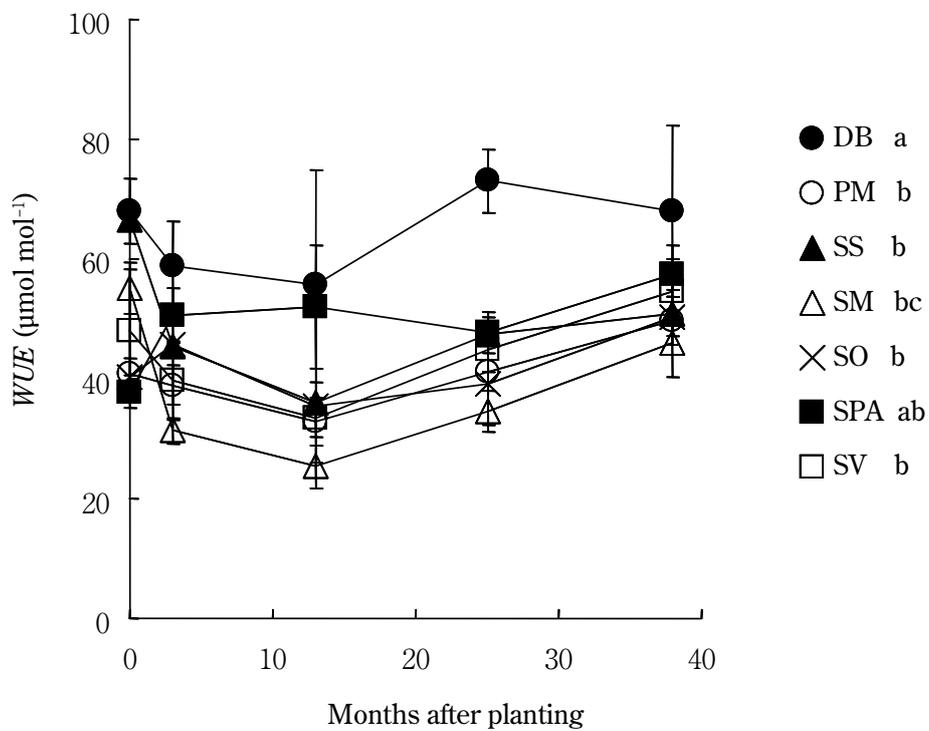


Fig. 10. Changes in water use efficiency ($WUE; A_{max}/g_{s_{max}}$) after planting in the grassland. Different letters indicate a significant difference across the measurement period ($P < 0.05$, ANOVA). Bars indicate the standard error (n=5 for each species).

photosynthetic capacity in grassland when the leaf carbon gain is calculated on a total day basis. This negative effect may be large in *D. beccarii*, *S. macrophylla*, *S. parvifolia* and *S. seminis*, because these species had higher increment ratio of R_d after planting than in the other species. In addition, the SPAD value of *S. macrophylla* dropped just after planting (Fig. 4), so that this species may be weaker at chlorophyll synthesis (Tange et al. 1998) than the other species under strong sunlight conditions. A long hardening period before planting may therefore be needed for this species.

High LMA also contributes to tolerance of desiccation in grassland after planting (Fig. 8), though there was a trade-off between desiccation tolerance and photosynthetic efficiency per unit leaf mass (A_{\max}/LMA ; Fig. 9). Species having low tolerance of desiccation, such as *P. macrophylla*, *S. macrophylla* and *S. seminis*, tended to have higher photosynthetic efficiency and lower LMA than in other species such as *D. beccarii*, *S. ovata* and *S. parvifolia*. In addition, interspecific differences in desiccation tolerance in the leaf, as indicated by the relation between LMA and 50% water loss time (Fig. 8) may be related to the original growth habitat of the species. Species with high tolerance to leaf desiccation, such as *D. beccarii*, *S. ovata* and *S. parvifolia*, usually grow at well-drained places such as narrow ridges and in sandy soil (Ashton, 2004). In contrast, species having low tolerance of desiccation, such as *P. macrophylla*, *S. macrophylla* and *S. seminis*, grow in wetter areas such as river banks and flood plains (Ashton, 2004). Species with low tolerance cannot adjust their LMA adequately in dryer habitats. Leaf water use efficiency (WUE) after planting also indicates drought tolerance (Maruyama et al. 1997a), and showed similar trends to the desiccation tolerance of the leaf in the grassland. The lowest WUE , in *S. macrophylla* which is also of low tolerance to leaf desiccation, indicates that this species requires large amounts of water to maintain a high carbon assimilation rate in grassland. Thus, this species may be weakest under drought conditions. In contrast, high WUE species such as *D. beccarii* and *S. parvifolia*, which are also high tolerance species in regard to leaf desiccation, are able to avoid excessive water loss by their leaf photosynthetic activity under drought conditions. These species maximize water conservation in high water stress conditions as in the grassland.

Leaf light acclimation to the remnant forest environment

Leaves of the species studied acclimated to the remnant

forest by changing their SPAD and I_c values (Fig. 4 & 5), which contribute to efficient seedling growth and survival under shade conditions. Although there were no large differences in soil nutrient content between the three vegetation environments studied (Hattori et al. 2005), the highest leaf SPAD value indicated that a large chlorophyll content (Ichie et al. 2002) was observed in the remnant forest. A large leaf chlorophyll content helps to maintain low I_c at low light availability (Lee et al. 2000; Koike et al. 2001; Larcher, 2003). Initial acclimation ability to the shade condition, as indicated by the relation between the extent of changes in the SPAD value and I_c from the nursery to three months after planting (Fig. 6), reflects interspecific shade tolerance. Species with only small changes in SPAD value and I_c , such as *S. ovata* and *S. parvifolia*, are categorized as weak acclimatizers to shade conditions. This weak acclimation is a cause of the higher mortality in the remnant forest in these species, which was approximately 60% in *S. parvifolia* to 80% in *S. ovata* at 36 months after planting (Kenzo et al. 2005b). In contrast, the large increase in SPAD value and decrease of I_c in *P. macrophylla* and *S. virescens* indicate that these species have strong acclimation ability to the shade condition. Mortality of these species was relatively low, at approximately 40% in *S. virescens* and 50% in *P. macrophylla* at 36 months after planting (Kenzo et al. 2005b). Although the SPAD value for *S. macrophylla* did not change greatly after planting, a 25% decrease of I_c occurred, and mortality was also low (approximately 25% at 36 months after planting). Changes of I_c across the measurement period (Fig. 5) also explain the seedling mortality in the remnant forest. The lowest I_c across the measurement period was found in *S. seminis* and the mortality of this species was the lowest of these species (approximately 20% at 36 months after planting, Kenzo et al. 2005b). In contrast, *S. ovata*, which maintained the highest I_c across the measurement period, suffered the highest mortality in the remnant forest.

Leaf acclimation to the secondary forest environment

Most leaf morphological and physiological traits in the secondary forest were intermediate in value between the other two vegetation environments. Some researchers have found that seedlings of late-successional species, including dipterocarp trees, grow successfully and survive under other tree canopies in stressful environments such as severely degraded open land and semiarid land (Ashton et al. 1997; Otsamo, 1998; Tewksbury and Lloyd, 2001; Kenzo et al. 2005a). This is because the other trees

provide shade from strong sunlight, leading to only moderate light intensity, temperature and vapor pressure deficits (VPD; Norisada et al. 2005). In fact, optimal growth rate of many dipterocarp seedlings occurs under partially shaded conditions (Nicholson, 1960; Sasaki and Mori, 1981; Okauchi et al. 2000). We also found that the dark respiration rate was lower in the secondary forest than in grassland conditions in all species, suggesting that the cost of maintaining the photosynthetic apparatus and photo-protective mechanisms is reduced by the canopy covering. In contrast, the photosynthetic capacity (A_{\max}) increased from the nursery, except *S. ovata* (Fig. 1). These findings suggest that naturally regenerated secondary forest trees can be used as nurse trees for dipterocarp seedlings under degraded vegetation conditions. In addition, A_{\max} clearly increased after planting from the nursery, though light conditions decreased after planting. This combination may cause a shortage of nutrients such as nitrogen in potted soil in the nursery; the total nitrogen content in the potted soil fell from 0.14% to 0.05% with growth of dipterocarp seedlings, and this nitrogen level was significantly lower than in the soils of planted sites (Iriano et al. 2004, 2005; Hattori et al. 2005). The increase in SPAD value in the grassland is also related to nutrient shortage of the potted soil in the nursery.

CONCLUSIONS

The responses of leaf morphological and physiological traits in seven dipterocarp seedlings differed significantly between species in three distinct degraded forest environments. Based on our results, we suggest points to consider for each species when conducting enrichment planting: (1) drought intolerant species (*P. macrophylla*, *S. macrophylla* and *S. seminis*) should be planted in high soil moisture and/or clay rich soil condition to avoid serious drought; (2) species intolerant to strong sunlight just after planting (*S. macrophylla*) may need a long hardening period or planting under the crown of nurse trees; (3) shade intolerant species (*S. parvifolia* and *S. ovata*) should be planted in relatively high light conditions, perhaps created by partial removal of the crown of forest trees, to enhance the growth and survival of these seedlings. This information allows improved techniques for enrichment planting in degraded tropical rainforests.

ACKNOWLEDGEMENTS The authors thank to the Forest Department, Sarawak, and to Prof. K. Ogino, Dr.

K. Kamiya and Ms. A. Oda for their kind support of this study. This research was partly supported by Grant-in-Aid for scientific research (No. 13575038 & 18780126) from the Ministry of Education, Culture, Sports, Science and Technology, Japan.

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.
- Alias, M.A., Hamzah, M.Z., 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.
- Appanah, S. & Weinland, G. 1993. Planting quality timber trees in peninsular Malaysia. –A review. Malayan Foresters Records No. 38, Forest Research Institute Malaysia, Kuala Lumpur, Malaysia. pp 247.
- Ashton, P.S. 2004. Dipterocarpaceae. In: Soepadmo, E., Saw, L.G. & Chung, R.C.K. (eds.), *Tree flora of Sabah and Sarawak*. Pp. 63–388. FRIM., Sabah Forestry Department and Sarawak Forestry Department, Kuala Lumpur, Malaysia.
- Ashton, P.M.S. & Beryn, G.P. 1992. Leaf adaptations of some *Shorea* species to sun and shade. *New Phytologist*, **121**: 587–596.
- Ashton, P.M.S., Gamage, S., Gunatilleke, I.A.U.N. & Gunatilleke, C.V.S. 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.
- Ashton, P.M.S., Singhakumara, B.M.P. & Gamage, H.K. 2006. Interaction between light and drought affect performance of Asian tropical tree species that have differing topographic affinities. *Forest Ecology and Management*, **221**: 42–51.
- Baillie, I.C. 1972. Report on a Detailed Examination of Soils of Silvicultural Research Plot 53, Niah Forest Reserve. In: Soil Survey Research Section (Ed.). Forest Department Sarawak, Kuching, Malaysia.
- Bazzaz, F.A. 1979. The physiological ecology of plant succession. *Annual Review of Ecology and Systematics*, **10**: 351–371.
- Clearwater, M.J., Susilawaty R., Effendi, R. & van Gardingen, P.R. 1999. Rapid photosynthetic acclimation of *Shorea johorensis* seedlings after

- logging disturbance in Central Kalimantan. *Oecologia*, **121**: 478–488.
- Deming-Adams, B. & Adams, W.W. 1992. Photoprotection and other responses of plants to high light stress. *Annual Review of Plant Molecular Biology*, **43**: 599–626.
- Dennis, R., Hoffmann, A., Applegate, G., von Gemmingen, G. & Kartawinata, K. 2001. Large-scale fire: Creator and destroyer of secondary forests in western Indonesia. *Journal of Tropical Forest Science*, **13**: 786–799.
- Givnish, T.J. 1988. Adaptation to sun and shade, a whole-plant perspective. *Australian Journal of Plant Physiology*, **15**: 63–92.
- Hattori, D., Sabang, J., Tanaka, S., Kendawang, J.J., Ninomiya, I. & Sakurai, K. 2005. Soil characteristics under three vegetation types associated with sifting cultivation in a mixed dipterocarp forest in Sarawak, Malaysia. *Soil Science and Plant Nutrition*, **51**: 231–241.
- Hansen, M.C. & DeFries, R.S. 2004. Detecting long-term global forest change using continuous fields of tree-cover maps from 8-km Advanced Very High Resolution Radiometer (AVHRR) data for the years 1982–99. *Ecosystems*, **7**: 695–716.
- Hiromi, H., Ninomiya, I., Koike, T. & Ogino, K. 1999. Stomatal regulation of canopy trees in a tropical rain forest. *Japanese Journal of Ecology*, **49**: 68–76. (in Japanese with English summary)
- Hygen, G. 1951. Studies in plant transpiration I. *Physiologia Plantarum* **4**: 57–183.
- 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.
- Irino, K. O., Iba, Y., Ishizuka, S., Kenzo, T., Ripot, S., Kendawang, J.J., Miyashita, N., Nara, K., Hogetsu, T., Ninomiya, I., Iwasaki, K. & Sakurai, K. 2004. Effects of controlled-release fertilizer on growth and ectomycorrhizal colonization of pot-grown seedlings of the dipterocarp *Dryobalanops lanceolata* in a tropical nursery. *Soil Science and Plant Nutrition*, **50**: 747–753.
- Irino, K. O., Kang, Y., Kenzo, T., Hattori, D., Ishizuka, S., Ninomiya, I., Iwasaki, K., Kendawang, J.J. & Sakurai, K. 2005. Performance of pot-grown seedlings of the dipterocarp *Dryobalanops lanceolata* with controlled-release fertilizer after transplantation to the shifting cultivation land in Sarawak, Malaysia. *Soil Science and Plant Nutrition*, **51**: 369–377.
- Kato, M., Inoue, T., Hamid, A.A., Nagamitsu, T., Merdek, M.B., Nona, A.R., Itino, T., Yamane, S. & Yumoto, T. 1995. Seasonality and vertical structure of light-attracted insect communities in a dipterocarp forest in Sarawak. *Researches on Population Ecology*, **37**: 59–79.
- Kaul, O.N. & Kramer, P.J. 1965. Comparative drought tolerance of two woody species. *Indian Forester*, **91**: 462–469.
- Kendawang, J. 1992. Forester's perception on indigenous species for forest plantations in Sarawak. In: Ahmad, S. S., Razali, A. K., Mohd, S. H. O., Aminuddin, M., Faridah, H. I. & Hamami, M. S. (eds.), *Indigenous species for forest plantations*, pp 14–23. University Pertanian Malaysia, Serdang, Malaysia.
- Kenzo, T., Ichie, T., Ninomiya, I. & Koike, T. 2003. Photosynthetic activity in seed wings of Dipterocarpaceae in a masting year: Does wing photosynthesis contribute to reproduction? *Photosynthetica*, **41**: 551–557.
- 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., Oda, A., Ninomiya, I., Wang, L., Zhang, G., Sakamoto, K. & Yoshikawa, K. 2005a. Biomass allocation in relation to heterophylly and growth stage of seedlings on *Sabina vulgaris* Ant. in the Mu-us Desert, Inner Mongolia, China. *Journal of the Japanese Society of Revegetation Technology*, **30**: 657–661. (in Japanese with English summary)
- Kenzo, T., Ozawa, T., Hattori, D., Irino, K., Kendawang, J.J., Sakurai, K. & Ninomiya, I. 2005b. Physiological and morphological responses of leaves on seven dipterocarp seedlings to degraded forest environment in Malaysian rainforest. In: *Proceedings of International Workshop on The Landscape Level Rehabilitation of Degraded Tropical Forests*, pp 107–114. FFPRI, Tsukuba.
- Kenzo, T., Ichie, T., Yoneda, R., Watanabe, Y., 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.
- 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.

- Koike, T., Kitao, M., Maruyama, Y., Mori, S. and Lei, T.T. 2001. Leaf morphology and photosynthetic adjustments among deciduous broad-leaved trees within the vertical canopy profiles. *Tree Physiology*, **21**: 951–958.
- Kramer, P.J. 1983. Water relations of plants. Academic Press, NY, pp 489.
- Krishnapillay, B. 2002. A manual for forest plantation establishment in Malaysia. Malayan Forest Records No. 45, Forest Research Institute Malaysia, Kuala Lumpur, Malaysia. pp 286.
- Kuusipalo, J., Jafarsidik, Y., Ådjers, G. & Tuomela, K. 1996. Population dynamics of tree seedlings in a mixed dipterocarp rainforest before and after logging and crown liberation. *Forest Ecology and Management*, **81**: 85–94.
- Lamb, D., Erskine, P.D. & Parrotta J.A. 2005. Restoration of degraded tropical forest landscapes. *Science*, **310**: 1628–1632.
- Lambers, H., Chapin III, F.S. & Pons, T.L. 1998. Plant physiological ecology. Springer-Verlag, New York, pp 540.
- Larcher, W. 2003. Physiological Plant Ecology. 4th Edn. Springer-Verlag, New York, pp 513.
- Lee, D.W., Oberbauer, S.F., Johnson, P., Krishnaplay, B., Mansor, M., Mohamad, H. & Yap, S.K. 2000. Effects of irradiance and special quality on leaf structure and function in seedlings of two southeast Asian *Hopea* (Dipterocarpaceae) species. *American Journal of Botany*, **87**: 447–455.
- Maruyama, Y., Matsumoto, Y., Morikawa, Y., Ang, L.H. & Yap, S.K. 1997a. Leaf water relations of some dipterocarps. *Journal of Tropical Forest Science*, **10**: 249–255.
- Maruyama, Y., Toma, T., Ishida, A., Matsumoto, Y., Morikawa, Y., Ang, L.H., Yap, S.K. & Iwasa, M. 1997b. Leaf water relations of some dipterocarps. *Journal of Tropical Forest Science*, **9**: 434–438.
- Maruyama, Y., Nakamura, S., Marengo, R.A., Vieira, G. & Sato, A. 2005. Photosynthetic traits of seedlings of several tree species in an Amazonian forest. *Tropics*, **14**: 211–219.
- McNamara, S., Tinh, D.V., Erskine, P.D., Lamb, D., Yates, D. & Brown, S. 2006. Rehabilitating degraded forest land in central Vietnam with mixed native species plantings. *Forest Ecology and Management*, **233**: 358–365.
- Mori, T. 2000. Effect of droughts and forest fires on dipterocarp forest in East Kalimantan. In: *Rainforest Ecosystems of East Kalimantan: El Niño, Drought, Fire and Human Impacts* (eds. Guhardja, E., Fatawi, M., Sutisna, M., Mori, T., Ohta, S.), pp 29–45. Springer-Verlag, Tokyo.
- Nicholson, D.I. 1960. Light requirements of seedlings of five species of Dipterocarpaceae. *Malaysian Forester*, **23**: 344–356.
- Ninomiya, I., Sakurai, K., Harada, K., Kendawang, J.J., Lee, H.S. & Ogino, K. 2000. Island and Corridor planting system in ecosystem rehabilitation. – a proposal. In: *Proceedings of Workshop on Forest Ecosystem Rehabilitation*, pp 18–21. Forest Department Sarawak, Malaysia.
- Norisada, M., Hitsuma, G., Kuroda, K., Yamanoshita, T., Masumori, M., Tange, T., Yagi, I., Nuyum, 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.
- Okauchi, Y., Itoh, A., Tan, S., Ripot, S., Kendawang, J.J. & Yamakura, T. 2000. Effect of light on tropical tree seedling growth. In: *Proceedings of Workshop on Forest Ecosystem Rehabilitation*, pp 148–161. Forest Department Sarawak, Malaysia.
- Otsamo, R. 1998. Effect of nurse tree species on early growth of *Anisoptera marginata* Korth. (Dipterocarpaceae) on an *Imperata cylindrica* (L.) Beauv. grassland site in South Kalimantan, Indonesia. *Forest Ecology and Management*, **105**: 303–311.
- Peace, W.J.H. & Macdonald, F.D. 1981. An investigation of the leaf anatomy, foliar mineral levels, and water relations of trees of a Sarawak Forest. *Biotropica*, **13**: 100–109.
- Sasaki, S. & Mori, T. 1981. Growth responses of dipterocarp seedlings to light. *Malaysian Forester*, **44**: 319–345.
- Schulze, P.C., Leighton, M. & Peart, D.R. 1994. Enrichment planting in selectively logged rain forest: A combined ecological and economic analysis. *Ecological Applications*, **4**: 581–592.
- Shimizu, M., Ishida, A. & Hogetsu, T. 2005. Root hydraulic conductivity and whole-plant water balance in tropical saplings following a shade-to-sun transfer. *Oecologia*, **143**: 189–197.
- Slavík, B. 1974. Methods of studying plant water relations. Springer-Verlag, Berlin, pp 449.
- Sobrado, M.A. & Medina, E. 1980. General morphology, anatomical structure, and nutrient content of sclerophyllous leaves of the 'Bana' vegetation of Amazonas. *Oecologia*, **45**: 341–345.
- Sokal, R.R. & Rohlf, F.J. 1995. Biometry. The principles

- and practice of statistics in biological research. 3rd Edn. W. H. Freeman and Company, New York, pp 887.
- Suzuki, T. & Jacalne, D. V. 1986. Response of dipterocarp seedling to various light conditions under forest canopies. *Bulletin of Forestry and Forest Product Research Institute*, **336**: 19–34.
- Symington, C.F. 2004. Foresters' manual of dipterocarps. Second edition. Malayan Forest Records 16. Forest Research Institute Malaysia, Kuala Lumpur, Malaysia, pp 519.
- Tange, T., Harada, K., Kojima, K. & Sasaki, S. 1998. Response of three dipterocarp species to light regime. *Proceedings of the Japan Academy. Ser. B, Physical and biological sciences*, **74**: 206–209.
- Tewksbury, J.J. & Lloyd, J.D. 2001. Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia*, **127**: 425–434.
- Whitmore, T.C. 1998. An introduction to tropical rain forests. 2nd edition. Oxford University Press, Oxford, UK, pp 282.
- Wright, S.J. 2005. Tropical forests in a changing environment. *Trends in Ecology and Evolution*, **20**: 553–560.
- Yoneda, R., Matsumoto, Y., Kenzo, T., Alias, M.A. & Mjid, N.M. 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 Environments*, **47**: 113–118. (in Japanese with English summary)

Received 27th Mar. 2007

Accepted 22nd May 2007