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Leaf Photosynthetic and Growth Responses on Four Tropical Tree Species to Different Light Conditions in Degraded Tropical Secondary Forest, Peninsular Malaysia

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Abstract

Leaf ecophysiological responses and height growth were studied in four indigenous tree seedlings planted under different size gaps in degraded tropical secondary forest. *Dyera costulata*, *Dipterocarpus baudii*, *Neobalanocarpus heimii*, and *Pouteria* sp. were selected for study species. The leaf photosynthetic rate at light saturation (A_{max}), light compensation point (I_c), leaf nitrogen content, and SPAD value were measured at two months after planting. The ratio of variable to the maximum fluorescence (F_v/F_m), which represents the maximal photochemical efficiency of photosystem II was also determined at two months after planting. All measurement leaves were old leaves, which had acclimated before the planting light condition. Canopy openness above the seedlings was estimated from a hemispherical photograph, ranged from 6 to 53%. The relationships between canopy openness and A_{max} among species were categorized into two groups. The first group (*N. heimii* and *Pouteria*), which had relatively high wood density and late successional status, showed that the maximum A_{max} appeared under relatively low canopy openness such as approximately 10%. A_{max} of the second group (*D. costulata* and *Dip. baudii*), which had relatively low wood density and high light demand, maximized from 20 to 40% of canopy openness. Seedling height growth of the first group was lower than the second group. The first group also showed lower F_v/F_m at high canopy openness than the second group. These responses indicated that the first group may be categorized to less tolerant species for strong light conditions during the early transplanted stage. I_c of *D. costulata*, *N. heimii* and *Pouteria* decreased with decreasing canopy openness. These species have high acclimation ability to shade conditions from the early transplanted stage, since these responses contribute to raise the photosynthetic efficiency under shade conditions.

Discipline: Forestry and forest products
Additional key words: dipterocarp, enrichment planting, photosynthesis, stomatal conductance, wood density

Introduction

Degraded secondary forests after burning or other disturbances are widely distributed throughout Southeast Asia[62]. These secondary forests usually show significantly lower above ground biomass, species richness and various forest products such as timber and medicine compared with late successional tropical rainforests[9,10,13,39,42]. Enrichment planting in the secondary forest may be a highly effective method for rehabilitating the forest, using endemic tree species, which provides benefits including timber and medicinal products[1,29,34,35,48]. A better understanding of ecological traits such as strong light tolerance for the target species could improve techniques for enrichment planting in the secondary forest[4,26,32]. Leaf ecophysiological traits should provide valuable ecological information, since leaf photosynthesis is essential to

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carbon assimilation[37].

Although various environmental factors affect the leaf traits, leaf ecophysiological traits are closely related to the light environment[25,36–38]. For instance, under strong light conditions such as degraded grassland, leaves generally have greater leaf mass per area (LMA), corresponding to a higher maximum photosynthetic rate (A_{max})[24]. On the other hand, leaves under shade conditions have higher leaf chlorophyll content and lower LMA, so as to maintain the low light compensation point[36]. Even the old leaves, which had adapted to a previous light condition, usually change their photosynthetic traits such as A_{max} and chlorophyll content to acclimate to a new light environment[31,45,54]. However, it is also known that shade adapted old leaves of several species significantly suffer damage to photosystem II (PSII) by strong sunlight[28]. These physiological changes of old leaves to sudden light change may relate to initial seedling performance such as growth under the new light condition during the early transplanted stage before maturation of newly flushed leaves[56]. In addition, seedling performance to sudden light change relates to not only leaf physiological changes but also their successional status and wood traits such as wood density[46,52,55,64]. For example, the growth response of late successional trees to a sudden increment in light intensity was slower than mid successional trees[64].

Light environment in the degraded secondary forest may be diverse, because light condition changes by forest structure such as gap formation and time span after the disturbance[60]. It is therefore necessary to consider species-specific favorable planted light conditions when we conduct effective enrichment planting to degraded secondary forests. However, we have little information about the leaf ecophysiological responses of various tropical tree species to different light conditions of the degraded secondary forest. In addition, these leaf responses to the light environment differ between species even in the same taxonomic group[21,47,49]. In this study, we measured seedling growth and leaf ecophysiological traits related with photosynthesis of the old leaves after planting under different sizes of artificial gaps in degraded secondary forest to determine favorable planted light conditions in four endemic Malaysian tree species. We also focused on leaf properties and seedling growth in relation to their successional status and wood density.

Materials and methods

1. Study site

The study was carried out in the Ayer Hitam Forest Reserve (1,248 ha, 3°00’N 101°38’E), Puchong, Selangor, Malaysia. The forest is surrounded by housing infrastructures and communities[28]. The area has a humid tropical climate, with weak seasonal changes in rainfall and temperature. Annual rainfall and average temperature are about 2,700 mm and 25.3°C[6].

The planting area (about 1 ha) was typical degraded secondary forest that mainly consisted of pioneer trees such as genus *Endospermum*, *Macaranga*, *Artocarpus*, and *Ficus*. Tree height varied from 15 to 25 m. The forest floor is less dark, and sunflecks commonly penetrate. The relative light intensity was approximately 10% in the forest. Artificial canopy gaps were created in different sizes by cutting canopy trees of secondary forest in September, 2005.

2. Plant materials and canopy openness

The planted species were *Dyera costulata* (Miq.) Hook. *f.* (Apocynaceae), *Dipterocarpus baudii* Korth (Dipterocarpaceae), *Neobalanocarpus heimii* (King) Ashton (Dipterocarpaceae), and *Pouteria* sp. (Sapotaceae). All species were native to the lowland dipterocarp forests of Malaysia. Two dipterocarp tree species chosen in this study are canopy tree species that produce useful timber[5,53]. Two of the other studied species were also useful for timber and *D. costulata* produces latex, which is an ingredient for chewing gum[65]. *D. costulata* is preferably used for growth in a canopy gap and is a fast growing species[3] (Table 1). Wood density is also the lowest among the study species (Table 1). *Dip. baudii* is also a relatively fast growing mid successional species and has middle wood density among the species (Table 1). In contrast, *N. heimii* is a slow growing late successional species and has high wood density. The species traits of *Pouteria* sp. were unknown but this genus included many medium to high wood density (up to 1,220 kg m^{-3}) and mid to late successional species[12,50,61].

The seeds were collected from natural rain forest of west Malaysia and planted to plastic pots (diameter: 15 cm, height: 20 cm). These seedlings were fostered in a nursery approximately 12 months at light intensity of 35% to full sun. Initial seedling height varied from 61 to 126 cm among species (Table 1). These seedlings were transplanted in the degraded secondary forest, which included various size gaps. From the planted seedlings, 12 to 13 individuals per species were randomly selected from various light conditions for the study (Table 1). Seedling height just after planting and 6 months after planting were measured, and the height difference during the period was used to calculate the relative growth rate of seedling height (RGRh). All studied seedlings survived one year after being transplanted. Canopy openness above the seedlings was estimated from a hemispherical photograph (Coolpix 5400, Nikon; Fisheye Converter FC-E9,

Table 1. Some characteristics of studied species and relative height growth rate during first 6 months

Family	Species	Wood density ($kg\ m^{-3}$)	Successional status	Seedling number	Height (cm)	RGRh ($cm\ cm^{-1}\ y^{-1}$)
Apocynaceae	*Dyera costulata*	415–495	gap	12	64.7	1.19
Dipterocarpaceae	*Dipterocarpus baudii*	610–800	mid	12	126.1	0.47
	Neobalanocarpus heimii	915–981	late	12	62.0	0.27
Sapotaceae	*Pouteria* sp.	medium to high (up to 1,220)	mid to late	13	104.1	0.06

Wood density and successional status based on Gan & Lim (2004), Soerianegara & Lemmens (1994), Symington (2004) and Wong (2002). Wood density and successional status of *Pouteria* sp. is genus discription. Relative height growth (RGRh) is average value for all seedlings.

Nikon, Tokyo, Japan)[63], ranged from 6 to 53%.

3. Measurement of leaf ecophysiological traits and leaf characteristics

Leaf ecophysiological traits related with photosynthesis were measured at two months after planting (November, 2005). We used a portable photosynthesis meter (LI-6400, Li-Cor, Lincoln, NE) to measure the leaf gas exchange rate. All measurements took place from 0800 to 1100 in the morning to avoid the midday photosynthesis depression[14,20]. The relation between photon flux density and carbon assimilation rate was determined for fully expanded leaves and apparently non-senescing leaves, which flushed before planting stage. The measured light intensity was 0, 10, 25, 50, 100, 300, 700, and 1,500 (μmol photon $m^{-2}\ s^{-1}$) and the temperature was approximately 30°C[21,24]. CO_2 concentration and air humidity in the leaf chamber were kept at 360 ppm and approximately 60%, respectively. The photosynthetic rate at light saturation (A_{max}) and light compensation point (I_c) was calculated from the measurements[21]. A_{max} and RGRh against canopy openness curve (Fig. 1 and Fig. 2) were drawn using the distance weight least squares smoothing technique[59] provided in a statistical package (Origin ver. 7.0, OriginLab, MA, USA). Stomatal conductance at A_{max} (gs_{max}) also recorded and water use efficiency (WUE, A_{max}/gs_{max}), which is the ratio of A_{max} and gs_{max}, was calculated.

After the gas exchange measurements, the leaves were collected and their leaf nitrogen content and SPAD value were measured to evaluate nitrogen and chlorophyll partitioning to light capture component in the leaf among different light conditions[36]. Leaf nitrogen and carbon content were determined by a NC analyzer (Sumigraph NC-900, Shimadzu, Kyoto, Japan) after all leaves had been dried at 60ºC for 3 days and the dry mass measured. The SPAD value, which is an index for the chlorophyll content in the leaf[15], was determined using a SPAD-502 (Konica Minolta Holdings Co. Ltd., Tokyo, Japan).

The initial (F_o) and maximum fluorescence (F_m) of the same leaves of the photosynthesis measurement were also determined using a portable fluorometer (Mini-PAM, Walz, Effeltrich, Germany) with the saturating light for F_m[17,28]. The ratio of variable to maximum fluorescence (F_v/F_m where $F_v = F_m - F_o$) an after overnight dark-adaptation, which represents the maximal photochemical efficiency of photosystem II (PSII) was also determined[28]. The overnight dark-adaptation was achieved by covering leaves with aluminum foil in the previous evening and F_v/F_m was measured early the next morning after an additional 15-min-dark adaptation with dark leaf clips (DLC-8, Walz)[28].

Results and discussion

1. Leaf ecophysiological responses and height growth to high canopy openness

The canopy openness in relation to seedling growth and leaf photosynthetic properties such as A_{max} and F_v/F_m among species was divided into two groups (Figs. 1A and 1B) and these differences in the properties indicated interspecific light acclimation ability. The first group (*N. heimii* and *Pouteria* sp.) showed that the maximum A_{max} appeared at relatively dark conditions such as approximately 10% of canopy openness (Fig. 1A). The relative height growth (RGRh) of the group was also low and not significantly related with canopy openness, though high RGRh was observed at 15% of canopy openness in *Pouteria* sp. (Table 1, Fig. 2A). In contrast, the A_{max} of the second group (*D. costulata* and *Dip. baudii*) maximized from 20 to 40% of canopy openness (Fig. 1A). RGRh of the second tree group also showed a favorable rate at relatively high light conditions such as 20 to 40% of canopy openness (Fig. 2A). This high growth rate in the group may correspond to their high photosynthetic rate and low wood density, because RGRh of the group was significantly related to A_{max} (Table 1, Fig. 2B) and a negative re-

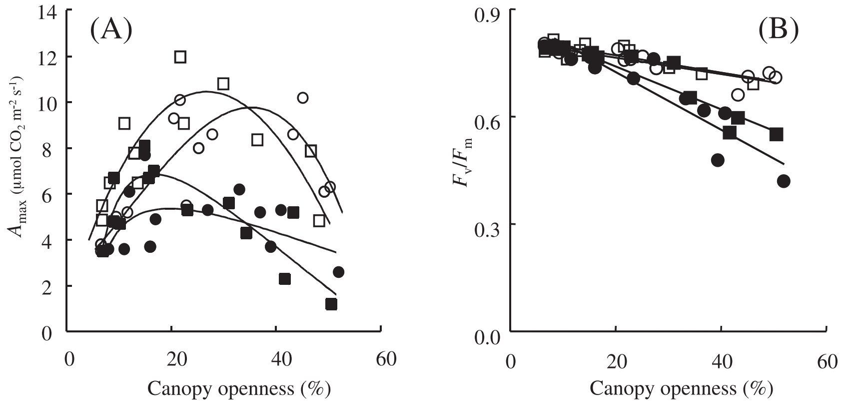

Fig. 1. Canopy openness related with (A) photosynthetic rate at light saturation (A_{max}) and (B) the ratio of variable to maximum fluorescence (F_v/F_m where $F_v = F_m - F_o$)

Correlation coefficients of regression lines for (A) are *D. costulata*: $r^2 = 0.73$; *Dip. baudii*: $r^2 = 0.69$; *N. heimii*: $r^2 = 0.34$; and *Pouteria* sp.: $r^2 = 0.71$.

The regression lines for (B) are *D. costulata*: y = 0.81 – 0.002x, $r^2 = 0.82$, $P < 0.001$; *Dip. baudii*: y = 0.81 – 0.002x, $r^2 = 0.78$, $P < 0.001$; *N. heimii*: y = 0.86 – 0.006x, $r^2 = 0.88$, $P < 0.001$; and *Pouteria* sp.: y = 0.88 – 0.008x, $r^2 = 0.85$, $P < 0.001$.

□: *D. costulata*, ○: *Dip. baudii*, ●: *N. heimii*, ■: *Pouteria* sp.

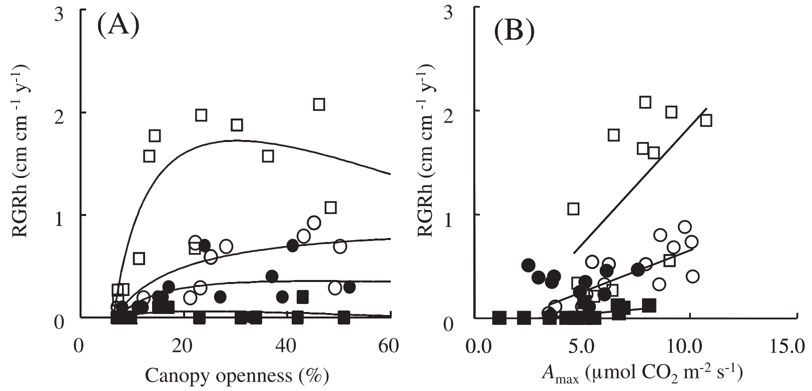

Fig. 2. Relative height growth rate (RGRh) in relation to canopy openness (A) and maximum photosynthetic rate (B)

Correlation coefficients of regression lines for (A) are *D. costulata*: $r^2 = 0.63$; *Dip. baudii*: $r^2 = 0.52$; *N. heimii*: $r^2 = 0.21$; and *Pouteria* sp.: $r^2 = 0.11$.

The regression lines for (B) are *D. costulata*: y = –0.42 + 0.23x, $r^2 = 0.33$, $P < 0.05$; *Dip. baudii*: y = –0.15 + 0.08x, $r^2 = 0.57$, $P < 0.05$; *N. heimii*: y = 0.23 + 0.008x, $r^2 = 0.004$, ns; and *Pouteria* sp.: y = –0.05 + 0.02x, $r^2 = 0.38$, $P < 0.05$.

□: *D. costulata*, ○: *Dip. baudii*, ●: *N. heimii*, ■: *Pouteria* sp.

lation between wood density and their growth rate was common among tropical trees[43,51]. Especially *D. costulata*, which had the lowest wood density, and the highest A_{max} and light demand, showed the highest growth rate among the studied species (Table 1). F_v/F_m of the first group also showed a significant decrease with increasing canopy openness (Fig. 1B, $P < 0.05$). Especially F_v/F_m of *N. heimii* under a large canopy gap had a value less than 0.5 (Fig. 1B). This low F_v/F_m of the old leaves of *N. heimii* indicated that this species may suffer chronic photoinhibition by strong sunlight under high canopy openness[8,11,18,49]. In addition, midday depression of photosynthesis may be clear in *N. heimii* under a large gap, because the depression was marked in *N. heimii* compared with other dipterocarp species under open dry conditions[16]. Therefore, daily carbon gain of *N. heimii* may be limited under strong light conditions such as a large canopy gap. In fact, several researchers reported that height and diameter growth rates of this species under strong light conditions were smaller than other late successional tree species, including dipterocarp trees[19,58]. These responses indicated that the first tree group (*N. heimii* and *Pouteria* sp.) may be categorized to low productivity of photosynthesis and less tolerant for photoinhibition under strong light conditions during the early transplanted stage. Therefore these species may need some treatments such as a long hardening period before the planting stage and shading by a canopy of nurse plants to avoid environmental stress to the leaves when these seedlings are planted to strong light conditions[2,4,22,44,66].

A positive relation between leaf nitrogen content and A_{max} in the old leaves of *Dip. baudii* (Fig. 3, $P < 0.05$) suggested that high nitrogen content in the leaf may contribute to increasing the leaf photosynthetic rate in this species[24]. In contrast, other species (*D. costulata*, *N. heimii* and *Pouteria* sp.) showed no significant relation between A_{max} and nitrogen content in the old leaf (Fig. 3), though nitrogen content of newly flushed leaves after being transplanted may positively relate with A_{max}[36].

Maximum stomatal conductance (*gs*) and water use efficiency (*WUE*, A_{max}/gs) under different canopy openness also divided into two groups (Figs. 4A and 4B). The first group (*N. heimii* and *Pouteria* sp) showed lower *gs* value and higher *WUE* than second group (*D. costulata* and *Dip. baudii*) especially under large canopy gap (Figs. 4A and 4B). High *gs* species generally have high water consumption by their transpiration activity[37,41]. Thus *D. costulata* and *Dip. baudii* may require large amounts of water uptake to maintain their photosynthesis and growth[40].

2. Leaf ecophysiological responses to low canopy openness

The changes in light compensation point (I_c) with canopy openness indicated photosynthetic efficiency under shaded conditions among species. The light compensation point (I_c) on *D. costulata*, *N. heimii* and *Pouteria* sp. significantly decreased with decreasing canopy openness (Fig. 5A, $P < 0.05$). Old leaves of these species may have high acclimation ability to low light conditions such as the forest floor under a closed canopy from the early transplanted stage, since low I_c contributes to increasing the photosynthetic efficiency under shade conditions[23,24,36]. In contrast, a stable value of I_c with canopy openness on *Dip. baudii* indicated that shade acclimation of the old leaves by changes in I_c of this species was weaker than that of other species (Fig. 5A).

Larger chlorophyll content and chlorophyll to nitrogen ratio in the leaves related to a lower I_c value and permitted better acclimation under low light conditions. Both SPAD value, which is an index for leaf chlorophyll content[15], and the ratio of SPAD value to leaf nitrogen content (SPAD/N) increased with decreasing canopy openness in all species, except for the relation of SPAD/N ratio on *D. costulata* (Figs. 5B and 5C). In general, large chlorophyll content and chlorophyll/nitrogen ratio in the leaves contribute to reduce the leaf I_c value[36], though SPAD value is not always linearly related to chlorophyll content[57]. In our study, there was also a negative correlation between SPAD and I_c values in *D. costulata* and *Pouteria* sp. (Fig. 6A), indicating that high chlorophyll content in the old leaves of these species contributes to the light harvesting efficiency at low light availability. The

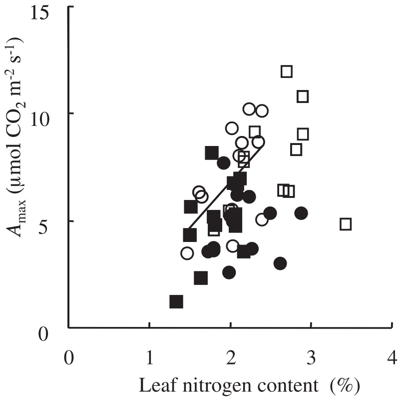

Fig. 3. The relation of leaf nitrogen content to photosynthetic rate at light saturation (A_{max})

The regression lines are *D. costulata*: y = 5.06 + 1.05x, $r^2 = 0.05$, ns; *Dip. baudii*: y = 1.70 + 4.24x, $r^2 = 0.29$, $P < 0.05$; *N. heimii*: y = 3.84 + 0.39x, $r^2 = 0.01$, ns; and *Pouteria* sp.: y = 1.29 + 3.42x, $r^2 = 0.24$, ns.

□: *D. costulata*, ○: *Dip. baudii*, ●: *N. heimii*, ■: *Pouteria* sp.

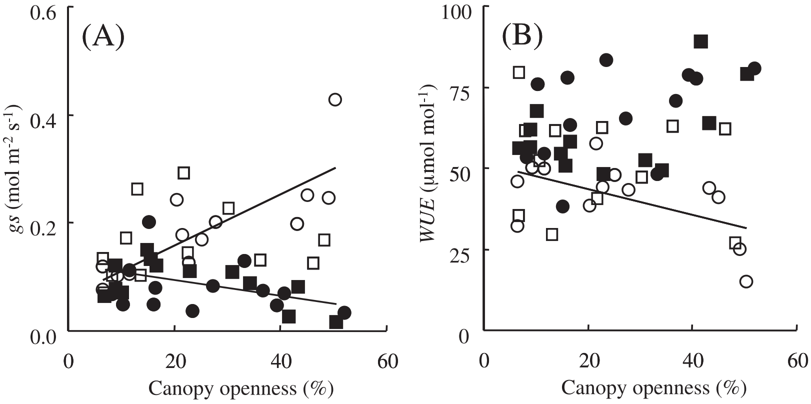

Fig. 4. Canopy openness in relation to (A) leaf stomatal conductance (*gs*) and (B) leaf water use efficiency (*WUE*)

The regression lines for (A) are *D. costulata*: y = 0.15 + 0.001x, $r^2 = 0.02$, ns; *Dip. baudii*; y = 0.06 + 0.005x, $r^2 = 0.67$, $P < 0.05$; *N. heimii*: y = 0.10 + 0.001x, $r^2 = 0.01$, ns; and *Pouteria* sp.: y = 0.12 – 0.001x, $r^2 = 0.29$, $P < 0.05$.

The regression lines for (B) are *D. costulata*: y = 56.4 – 0.19x, $r^2 = 0.03$, ns; *Dip. baudii*: y = 51.3 – 0.40x, $r^2 = 0.32$, $P < 0.05$; *N. heimii*: y = 55.1 + 0.45x, $r^2 = 0.19$, ns; *Pouteria* sp.: y = 51.0 + 0.40x, $r^2 = 0.25$, ns.

□: *D. costulata*, ○: *Dip. baudii*, ●: *N. heimii*, ■: *Pouteria* sp.

ratio of chlorophyll/N acts as an indicator of the allocation of leaf nitrogen to chlorophyll-protein complexes[27,30,33]. Therefore, a negative relation between SPAD/N ratio and I_c value in *N. heimii* and *Pouteria* sp. (Fig. 6B) suggested the amount of leaf nitrogen in these species was allocated preferentially to chlorophyll-protein complexes under shade conditions[7]. The shade acclimation ability of the old leaves may be larger in *N. heimii* and *Pouteria* sp. than other species, because these species showed high slopes between I_c and canopy openness (Fig. 5A) and also efficiently allocated leaf nitrogen to chlorophyll-protein complexes (Fig. 6B).

3. Conclusion

We conclude that ecophysiological traits of the old leaves such as A_{max}, I_c and SPAD value corresponded well to canopy openness, successional status, wood density, and seedling growth in the degraded tropical secondary forest. These changes significantly differed among species and species specific patterns could be used as indicators of seedling ecological traits such as tolerance to strong sunlight and to shade conditions. From our results, *D. costulata* and *Dip. baudii*, which have relatively low wood density and high light demand, may be suitable for planting to canopy openness conditions of 20 to 40% in secondary forests by their high A_{max} and height growth

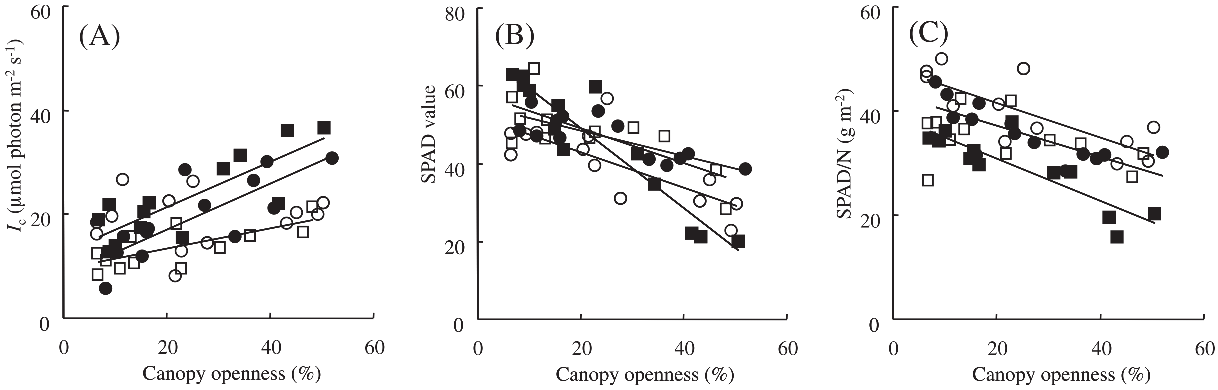

Fig. 5. Canopy openness in relation to (A) light compensation point (I_c), (B) SPAD value and (C) SPAD/N ratio

The regression lines for (A) are *D. costulata*: y = 9.43 + 0.20x, $r^2 = 0.54$, $P < 0.05$; *Dip. baudii*: y = 18.04 + 0.03x, $r^2 = 0.01$, ns; *N. heimii*: y = 8.14 + 0.44x, $r^2 = 0.63$, $P < 0.05$; and *Pouteria* sp.: y = 12.51 + 0.44, $r^2 = 0.68$, $P < 0.001$.

The regression lines for (B) are *D. costulata*: y = 57.88 – 0.44x, $r^2 = 0.56$, $P < 0.05$; *Dip. baudii*: y = 52.05 – 0.46x, $r^2 = 0.57$, $P < 0.05$; *N. heimii*: y = 54.98 – 0.33x, $r^2 = 0.64$, $P < 0.05$; and *Pouteria* sp.: y = 69.65 – 1.03x, $r^2 = 0.89$, $P < 0.001$.

The regression lines for (C) are *D. costulata*: y = 37.66 – 0.13x, $r^2 = 0.15$, ns; *Dip. baudii*: y = 48.15 – 0.33x, $r^2 = 0.61$, $P < 0.05$; *N. heimii*: y = 43.20 – 0.33x, $r^2 = 0.61$, $P < 0.05$; and *Pouteria* sp.: y = 38.81 – 0.40x, $r^2 = 0.76$, $P < 0.001$.

□: *D. costulata*, ○: *Dip. baudii*, ●: *N. heimii*, ■: *Pouteria* sp.

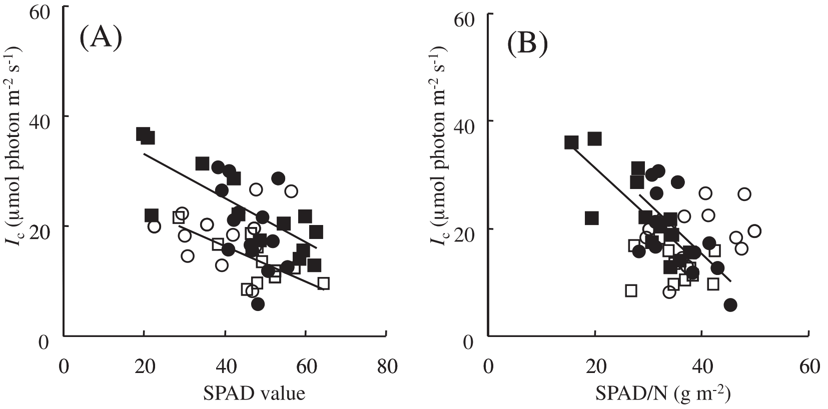

Fig. 6. Light compensation point (I_c) in relation to SPAD value and SPAD/N ratio

The regression lines for (A) are *D. costulata*: y = 29.1 – 0.32x, $r^2 = 0.51$, $P < 0.05$; *Dip. baudii*: y = 15.4 + 0.08x, $r^2 = 0.03$, ns; *N. heimii*: y = 49.9 – 0.65x, $r^2 = 0.23$, ns; and *Pouteria* sp.; y = 41.0 – 0.40x, $r^2 = 0.68$, $P < 0.001$.

The regression lines for (B) are *D. costulata*: y = 19.8 – 0.17x, $r^2 = 0.05$, ns; *Dip. baudii*: y = 9.9 + 0.22x $r^2 = 0.09$, ns; *N. heimii*: y = 52.9 – 0.94x;, $r^2 = 0.42$, $P < 0.05$; and *Pouteria* sp.: y = 49.7 – 0.92x, $r^2 = 0.64$, $P < 0.001$.

□: *D. costulata*, ○: *Dip. baudii*, ●: *N. heimii*, ■: *Pouteria* sp.

in these conditions. In contrast, *N. heimii* and *Pouteria* sp., which are relatively high wood density and middle or late successional status, may be preferably planted to canopy openness conditions of less than 20%, because these species had relatively high shade acclimation ability but were sensitive to photoinhibition of the leaf photosystem by the strong light irradiance. These results will improve the techniques for enrichment planting in degraded secondary forests in tropical Southeast Asia.

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