EFFECTS OF LIGHT INTENSITY ON THE GROWTH AND ALLOMETRY OF TWO BORNEAN *DRYOBALANOPS* (DIPTEROCARPACEAE) SEEDLINGS

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ITOH, A., YAMAKURA, T. & LEE, H. S. 1999. Effects of light intensity on the growth and allometry of two Bornean *Dryobalanops* (Dipterocarpaceae) seedlings. Biomass growth and allometry of *Dryobalanops aromatica* and *D. lanceolata* seedlings were compared among five neutral shade conditions [7, 12, 27, 48 and 100% relative light intensity (RLI)]. The estimated optimum RLIs for seedling growth were not much different between the species; 26.9% and 31.8% for *D. aromatica* and *D. lanceolata* respectively. But seedling allometry showed significant interspecific differences. *Dryobalanops aromatica* allocated more above-ground biomass to stem and made taller seedlings than *D. lanceolata*. This allometric difference seems to be related to the differences in gap regimes of the sites where they are distributed in the study forest.

Key words: Allometry - Borneo - dipterocarp - *Dryobalanops aromatica* - *Dryobalanops lanceolata* - seedling growth - shading experiment

ITOH, A., YAMAKURA, T. & LEE, H. S. 1999. Pengaruh keamatan cahaya terhadap pertumbuhan dan alometri dua anak benih *Dryobalanops* (Dipterocarpacae) Borneo. Pertumbuhan biojisim dan alometri anak benih *Dryobalanops aromatica* dan *D. lanceolata* dibandingkan di bawah lima keadaan teduhan neutral [7, 12, 27, 48 dan 100% keamatan cahaya relatif (RLI)]. Anggaran optimum RLI bagi pertumbuhan anak benih tidak banyak berbeza antara spesies; masing-masing 26.9 dan 31.8% bagi *D.aromatica* dan *D.lanceolata.* Bagaimanapun, alometri anak benih menunjukkan perbezaan bererti antara spesies. *Dryobalanops aromatica* memperuntuk lebih banyak biojisim atas-tanah kepada batang dan menjadikan anak benihnya lebih tinggi berbanding dengan anak benih *D. lanceolata.* Perbezaan alometri didapati berkaitan dengan perbezaan dalam regim ruang tapak yang diagihkan di hutan kajian.

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Introduction

Dryobalanops aromatica Gaertn *f.* and *Dryobalanops lanceolata* Burck (Dipterocarpaceae) are common canopy species in a mixed dipterocarp forest of Lambir Hills National Park, Sarawak, East Malaysia. Spatial distributions of the two species are segregated in accordance with the soil difference; *D. aromatica* is found mainly on sandy soils, while *D. lanceolata* is on clay soils (Itoh 1995). Both species are unusual for tropical rain forest trees in making dominant stands within their suitable habitats (Itoh *et al.* 1997).

Forest floor light conditions and gap regimes are different between the sand and clay sites in Lambir (Ashton & Hall 1992, Itoh *et al.* 1997). The differences in gap regimes may affect their regeneration processes and their spatial distributions. Light difference affects both the growth and morphology of tree seedlings (King 1994). The optimum light conditions for seedling growth are varied among dipterocarp species (e.g. Nicholson 1960, Sasaki & Mori 1981, Ashton & de Zoysa 1989, Turner 1989). This suggests that they require different size gaps for regeneration. Seedling morphology has been analysed using allometric relationship among plant parts, and the differences in juvenile allometry are important for waiting strategies for gap formation (e.g. Kohyama 1987, King 1990, Kohyama & Hotta 1990).

In this study we compare the biomass growth and allometry of the two *Dryobalanops* seedlings grown under different light intensities. We discuss the effects of the different gap regimes on their regeneration in the study forest.

Methods

Shading experiment

The shading experiment was conducted at the Long Term Ecological Research (LTER) Project field house in Miri (4° 23'N, 114° 00'E), *c.* 20 km north of Lambir Hills National Park. The climate is aseasonal; the average annual rainfall is 2764 mm (1967-1993; Momose *et al.* 1994), and the annual mean temperature is 27.2°C (Brunig 1974) at Miri Airport, adjacent to the field house.

Newly fallen mature seeds of each species were collected from Lambir in September 1991. Seed fresh weight was not significantly different between the species (*t*-test, $p > 0.1$, $N = 20$ per species); 5.47 ± 1.16 g (mean ± s.d.) and 5.25 ± 0.81 g for *D. aromatica* and *D. lanceolata* respectively. The sepal wings were detached, and six conspecific seeds were sown in each of 20 cylindrical ceramic pots (34 cm diameter and 20 cm deep) filled with mixture of peat soil and forest top soil. Four pots (two for each species) were placed at the centre of the four shading chambers and outside of the chambers (open treatment). The chambers (1 m × 1 m × 80 cm height) were covered with black nylon mesh, and the inside light intensities were controlled by changing the number of layers of the mesh and/or the mesh size. Light intensity was measured by photometers (Minolta T-1H) inside and outside of the chambers simultaneously at 30-min intervals from 0700h to 1800h on 14 January 1992. The relative light intensities (RLI) of each treatment was estimated by linear regression between inside and outside light intensities (r^2 = 0.806–0.960, $p < 0.0001$) as 7, 12, 27, 48 and 100% respectively. The RLIs in the chambers may have been slightly underestimated relative to the actual relative diffuse light intensities because the measurement was done on a fine day. The daily maximum and minimum temperatures were measured in the chambers for two weeks from 4 January. There were no significant differences in the minimum temperatures among the chambers (range: 20–24 °C), but the maximum temperatures of the open (36–50 °C) were significantly higher than those in the chambers (29–37 °C).

The pots were watered twice every day at 0800h and 1600h, throughout the experiment, except on rainy days. The positions of pots were randomised several times at irregular intervals (1–3 weeks) within each treatment. The height, diameter at the base of cotyledons, number of branches and number of leaves produced and lost were measured monthly for all living seedlings. Fallen leaves were collected individually; only two *D. lanceolata* seedlings under 100% RLI and one *D. aromatica* seedling under 50% RLI lost leaves (1–2 per seedling). The seedlings were harvested at the end of the experiment, four months later. All the living leaves were photocopied to transparent plastic sheets individually, and the leaf area was measured by an automatic area meter (AAM-8, Hayashi Denko Co.Lt.) from the sheets. The seedlings were divided into leaf (including fallen leaves), stem (including branches) and root fractions, dried at 80 °C for 48 h and then weighed.

Data analysis

Effects of shading and pot differences on seedling growth were analysed by a nested analysis of variance (ANOVA) within species (Sokal & Rohlf 1981). Seedlings which had died during the experiment (0–2 per pot) were excluded from the analysis. Mortality happened only within one month from the sowing suggesting that the cause was not the competition within the pots but most likely the poor root development (personal observation).

To estimate 'optimum RLIs', we applied the optimum growth model proposed by Hozumi *et al.* (1960). In this study, an optimum RLI means the RLI that gives the largest total or part weight. Thus optimum RLIs for plant part weights are not necessarily the optimal RLI for total plant growth.

Hozumi *et al.* (1960) formulated the effect of 'optimum factor' on plant growth as

$$\frac{1}{w} = \frac{A_1}{f} + A_2 f + B, \qquad (1)$$

where w is mean weight, f is the amount of the factor [RLI(%) in this study] and A_1, A_2, and B are coefficients specific to the period of growth. Equation (1) gives an optimum curve with maximum values of w at an optimum level of f (f_{opt}) which is given by

$$f_{opt} = \sqrt{\frac{A_1}{A_2}} \tag{2}$$

Coefficients of equation (1) were determined by a linear least squares method using a computer program written in BASIC.

Allometric relationships between total seedling weight and other growth measures, i.e. height, diameter, root, stem and leaf weights, were analysed by the methods of Kohyama (1987). There were allometric relationships between individual seedling weights and other growth measures expressed by

$$\log_{10} y = a \log_{10} x + b, \tag{3}$$

where y is seedling weight, x is one of the other growth measures, a and b are the slope and intercept of the regression line respectively. The slope and intercept were compared statistically (Sokal & Rohlf 1981) between species to evaluate the interspecific morphological differences in seedlings.

Results

No effects of the pots were significant ($p > 0.1$) for all the growth measures, i.e. root, leaf, stem and total dry weights, height, diameter and leaf area. Shading had significant effects ($p < 0.001$) on all of them. Means of the growth parameters showed a peak under intermediate shade (Table 1). An optimum curve defined by equation (1) fitted well and independently to leaf, stem, root and total mean weight of each species (Figure 1). The estimated optimum RLIs for total weight were 26.9 and 31.8% for *D. aromatica* and *D. lanceolata* respectively. The optimum RLI increased for leaf (21.9 and 25.6% for *D. aromatica* and *D. lanceolata* respectively), stem (26.1 and 33.5%) and root weight (49.8 and 61.6%), in that order within species.

There were no significant interspecific differences in the slopes of the regression lines between seedling weight and any of the other growth measures ($F = 0.209–2.597$, $df = 1, 89$, $p = 0.110–0.679$) (Figures 2 and 3). This means that the morphological differences of the two species show the same tendency in any seedling size and under any shade conditions. Differences in the intercepts were not significant between the species in the seedling weight and diameter or root weight relations ($F = 0.490–0.919$, $df = 1, 90$, $p = 0.340–0.486$). *Dryobalanops aromatica* had significantly larger intercepts ($F = 30.1–36.7$, $df = 1, 90$, $p < 0.0001$) in the relations between plant weight and height or stem weight, and had a significantly smaller intercept ($F = 17.6$, $df = 1, 90$, $p < 0.001$) in the plant weight and leaf weight relation (Figures 2 and 3). These results indicate that seedlings of *D. aromatica* were taller and allocated more biomass to stem and less to leaf compared to *D. lanceolata* seedlings of the same total weight.

Table 1. Results of the shade experiment of *Dryobalanops aroamatica* and *D. lanceolata.* Means and standard errors (in parentheses) are presented. n: sample size

	D. aromatica Relative light intensity (% lux/lux)					*D. lanceolata* Relative light intensity (% lux/lux)				
	7	12	27	48	100	7	12	27	48	100
n	8	10	9	8	9	9	10	10	11	9
Height (cm)	37.3 (3.44)	47.3 (3.71)	48.8 (4.52)	41.7 (3.71)	26.4 (1.97)	37.9 (3.15)	38.3 (1.32)	47.7 (2.80)	43.3 (1.63)	30.3 (2.40)
Diameter (mm)	2.58 (0.13)	3.26 (0.20)	3.34 (0.12)	3.48 (0.26)	2.89 (0.13)	3.12 (0.15)	3.20 (0.08)	3.83 (0.16)	3.87 (0.10)	3.69 (0.17)
Leaf weight (g)	0.62 (0.11)	0.82 (0.16)	1.00 (0.09)	0.84 (0.16)	0.40 (0.03)	1.27 (0.15)	1.05 (0.07)	2.30 (0.26)	1.69 (0.14)	1.06 (0.17)
Stem weight (g)	0.45 (0.06)	0.78 (0.10)	0.91 (0.05)	0.77 (0.12)	0.48 (0.03)	0.68 (0.09)	0.67 (0.03)	1.25 (0.14)	1.09 (0.07)	0.83 (0.12)
Root weight (g)	0.25 (0.03)	0.43 (0.06)	0.50 (0.04)	0.54 (0.09)	0.52 (0.05)	0.36 (0.03)	0.51 (0.05)	0.70 (0.07)	0.81 (0.07)	0.77 (0.12)
Total weight (g)	1.32 (0.18)	2.03 (0.29)	2.41 (0.17)	2.15 (0.34)	1.41 (0.09)	2.31 (0.24)	2.23 (0.13)	4.26 (0.46)	3.58 (0.26)	2.66 (0.40)
Leaf area (cm^2)	107 (18.7)	131 (25.8)	159 (15.4)	124 (25.6)	53.4 (3.99)	308 (37.5)	223 (16.0)	472 (51.7)	307 (23.5)	144 (36.9)

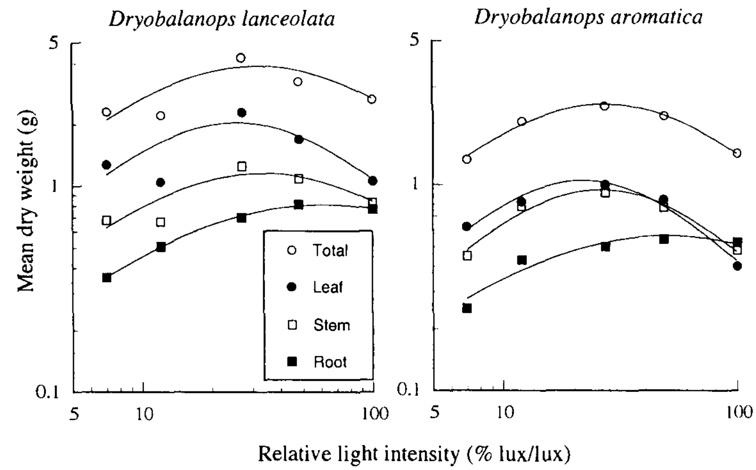

Figure 1. Relationships between relative light intensity and mean dry weights of leaf, stem, root or total *Dryobalanops aromatica* and *D. lanceolata* seedlings grown under various light intensities. Solid lines are estimated optimum curves formulated by equation (1) in the text.

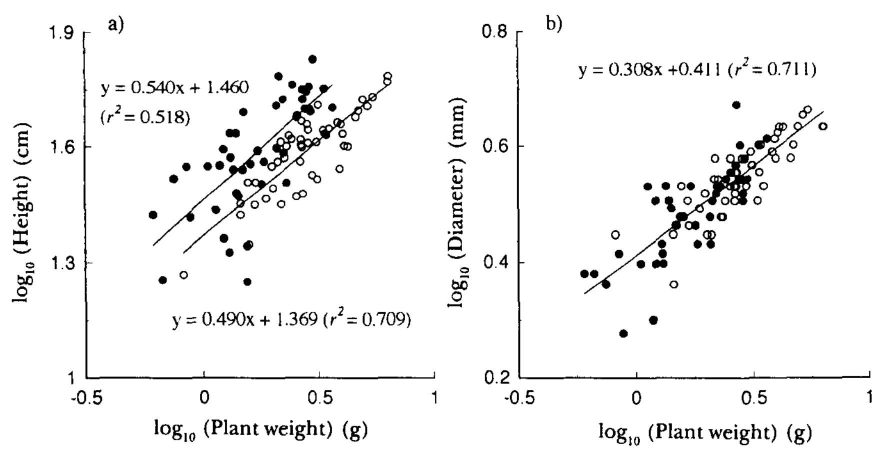

Figure 2. Allometric relations between total seedling weight and a) height or b) diameter of *Dryobalanops aromatica* (open circle) and *D. lanceolata* (closed circle) grown under various light intensities. Solid lines are linear regression lines on a double logarithmic scale. Data of the two species were pooled in b) because of insignificant interspecific difference in the regression lines.

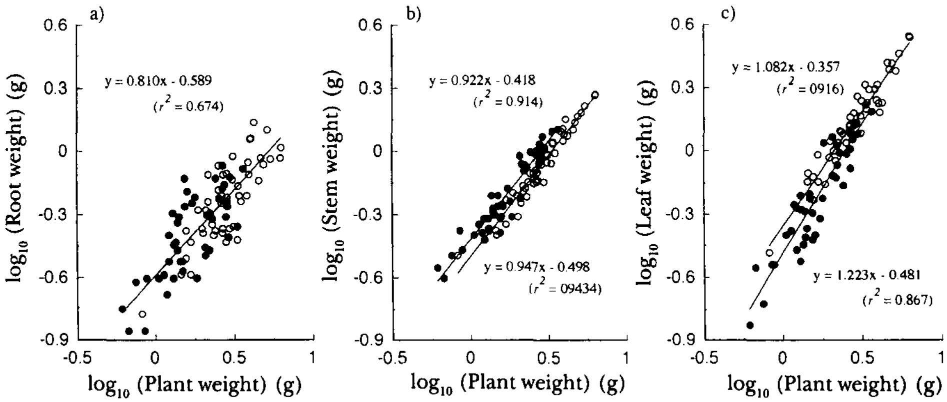

Figure 3. Allometric relations between total seedling weight and a) root, b) stem or c) leaf weight of *Dryobalanops aromatica* (open circle) and *D. lanceolata* (closed circle) grown under various light intensities. Solid lines are linear regression lines on a double logarithmic scale. Data of the two species were pooled in a) because of insignificant interspecific difference in the regression lines.

Discussion

Response of biomass growth to light intensity was quite similar between the two *Dryobalanops* species. They showed the largest seedling growth under intermediate shade conditions (27–32% RLI). However, the allometry of the two seedling species was significantly different. Height growth seemed to be a higher priority in *Dryobalanops aromatica* than in *D. lanceolata*. *Dryobalanops aromatica* allocated more above-ground biomass to stem than *D. lanceolata*, and made taller seedlings.

Seedlings which maximise height growth have a competitive advantage in less shaded conditions. On the other hand, seedlings which expand their leaves in a wider area with well-developed lateral branches are more effective in sunfleck interception and likely to survive under deep shade (Kohyama 1987, Zipperlen & Press 1996). From the view point of seedling morphology, *D. aromatica* is therefore more suitable for the sites which have frequent gap formation. In contrast, *D. lanceolata* takes advantage in the sites with less frequent gap formation.

The results are consistent with the observed differences in gap regimes between the *D. aromatica* and *D. lanceolata* stands in the Lambir forest. Ashton and Hall (1992) suggested that the gap formation is more frequent and predictable on the sandy parts, where *D. aromatica* is distributed, than on the clay parts, where *D. lanceolata* occurs. Itoh *et al.* (1997) found that the forest floor was significantly more shaded in a *D. lanceolata* stand [1.6% of average diffuse site factor (DSF; Anderson 1964)] than in a *D. aromatica* stand (2.1% DSF).

The results of the current study indicated that the allometric features of *D. aromatica* and *D. lanceolata* seedlings are likely to be suitable for the local gap regimes of the sites where they are presently distributed. It is, howeve, yet to be clarified how the reported allometric differences work in their regeneration processes. Field experiments such as a transplanting of the two species into different sites should be interesting to understand the importance of the reported seedling allometry in their regeneration.

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