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# FOREST SHADE AND SEEDLING DEVELOPMENT IN FIVE DIPTEROCARPS

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Seedling developmental responses to understory shade are the combination of reductions in irradiance and changes in spectral quality. We studied the seedling development of five dipterocarps, *Dryobalanops aromatica, Hopea helferei, H. odorata, H. wightiana*, and *Shorea singkawang* under varying intensity (photon flux density, PFD) and spectral quality (red to far-red, R:FR). Seedlings were grown in replicated shadehouse treatments: (1) 40 % solar PFD and 1.25 R:FR; (2) 12 % PFD and 1.25 R:FR; (3) 12 % PFD and 0.25 R:FR; (4) 3 % PFD and 1.25 R:FR; and (5) 3 % PFD and 0.25 R:FR. Species differed in the influence of light variables on seedling (1) total height; (2) internode distance; (3) branch to trunk internodes; (4) stem length/mass; (5) leaf area/stem length; (6) % allocation to leaf, stem and root mass; (7) specific leaf mass; (8) mean leaf area; (9) leaf thickness; (10) petiole length; and (11) stomatal density. The simple factorial design of treatments 2-5 allowed a two-way ANOVA and the calculation of coefficients of determination of the treatment effects. Most of the characters in most taxa were primarily influenced by light intensity, but spectral quality also influenced characters in many cases. Recommendations concerning seedling shade tolerance for silviculture or nursery practice may need revision if they are based on shade trials using spectrally neutral shade fabrics or slat houses. The patterns of morphological responses in reduced PFD and R:FR also help to explain how shade tolerances of the seedlings of rain forest trees vary in a continuous manner. Future research on the effects of shading on tree seedling development and ecology must consider the potential influence of changes in spectral quality under canopy shade.

## Introduction

Light is the most important physical factor in the survival and development of seedlings in tropical moist forests. The heterogeneity of light environments and their role in forest regeneration and dynamics are embodied in the concept of gap phase dynamics, an important model in tropical forest ecology (Brokaw & Scheiner 1989). This model predicts that differing gap sizes vary light climates and provide distinct opportunities for seedlings of varying shade tolerances. It also predicts that species will be adapted to these light conditions, and species with similar shade tolerances will form guilds. Controversy has arisen concerning the number of such guilds; Whitmore (1989) has suggested that there may only be early successional pioneers and mature forest taxa, the latter possessing a continuum of shade

tolerances. Shade response may be defined in several ways, and differences among species may be quite subtle (Whitmore 1994). Furthermore, chance and dispersal may actually be more important factors explaining seedling and tree distribution than shade tolerance for some species (Welden *et al.* 1991, Whitmore 1994).

Although our knowledge of the shade tolerances of dipterocarp seedlings primarily comes from the anecdotal observations of foresters, which is the basis of silvicultural treatment systems (Whitmore 1984), a small body of research does suggest that taxa are adapted to different light conditions in the forest. Most of the evidence comes from studies of distributional ecology in natural and disturbed forest. Differential seedling survival of several dipterocarp species has been shown in different shade environments (Fox 1973, Liew & Wong 1973, Turner 1990 a & b, Turner & Newton 1990, Brown & Whitmore 1992, Turner *et al.* 1992, Matsune *et al.* 1993).

Even more limited evidence has been derived on growth trial experiments under different shade conditions. Nicholson (1960) had earlier shown differences in growth rates of five dipterocarps, but the degrees of shading were too small to be of much ecological significance. Turner (1989) demonstrated differences in shade tolerances of dipterocarp seedlings, in coordination with his studies on the distributional ecology of the same taxa. Natural shade conditions underneath vegetation canopies vary in their intensity and spectral quality, dependent upon the intensity of sunlight, the thickness of foliage layers, and the contribution of penumbral light through small holes in the canopy. Foliage absorbs efficiently in the visible wavelengths (slightly less in the green bandwidths), and absorbs very little above 700 nm. Owing to the presence of the phytochrome pigment system, plants are extremely sensitive to the ratio of the red and far-red quanta, which determines the Pr and Pfr equilibrium and influences plant development at virtually every level of organization (Smith 1994). Smith has defined this indicator of spectral quality as the ratio of quanta at 660 and 730 nm, with a half-peak bandwidth of 10 nm. The R:FR of sunlight ranges 1.05-1.35, increased by greater atmospheric moisture content (Lee & Downum 1991), and is reduced to less than 0.20 under deep shade conditions in the tropical rain forest understory (Lee 1987, Turnbull & Yates 1992).

Despite this two-fold variation in shadelight, virtually all research has focused on the reduction of light intensity, or photosynthetic photon flux density (400-700 nm, or PFD) independent of reduction in R:FR, and its effect on seedling development. Such research will almost certainly underestimate the ability of seedlings to respond to natural shade conditions (Schmitt & Wulff 1993). Sasaki and Mori (1981) altered the spectral quality of radiation for dipterocarp seedlings using small boxes, but the results were compromised by the poor stability of the filters and the methods for radiation measurement. They did demonstrate an enhancement of height growth and lower root allocation under conditions of low R:FR in *Shorea ovalis*. Ashton and Berlyn (1992) and Ashton (1995) showed differing performance of taxa of *Shorea*, section Doona, to shade conditions where the R:FR was altered along with the reduction in PFD, in a manner similar to natural light climates. However, these

results do not allow the evaluation of the relative contributions of quantity and quality to seedling development.

The separation of effects of PFD and R:FR in experimental conditions is not a trivial matter. Such conditions can be simulated in growth chambers, but the costs of conducting replicated experiments with adequate sample sizes is prohibitive. Any filters must provide spectra similar to natural conditions and be sufficiently durable under direct sunlight. Lee (1985) described a spray varnish that altered spectral quality in a realistic fashion (also see Lee 1988. Ashton & Berlyn 1992), and discovered that the energy control films marketed by various manufacturers can be used in a similar fashion, providing product stability and ease of installation.

In this paper we describe results of experiments underway at the Forest Research Institute of Malaysia (FRIM) since 1991 on the effects of PFD and R:FR on the developmental ecology of rain forest tree seedlings. This research has encompassed growth, morphological and physiological responses of ten taxa. Here we limit our discussion to results on the growth and morphology of the dipterocarp species in this project. Our aim is to understand how intensity and spectral quality separately and interactively affect growth, photosynthate allocation, and morphology of seedlings grown under extended periods in the shadehouses. Our more general goal is to understand the mechanisms of seedling response to natural forest light conditions for a better understanding of the functional ecology of the taxa and, ultimately, better silvicultural practice.

## Materials and methods

The taxa in this study were selected on the basis of their availability, economic value and ecological importance (Table 1). Seeds were collected and grown in the nursery until 12-15 cm in height and were then introduced into the shadehouses (Lee *et al.*, submitted for publication, a). Each shadehouse was 4 x 4 m with a roofline sloping from 2 to 1.5 m. External air was pulled through blind vents into the houses and out with an exhaust fan at the roof peak. We monitored the houses continually for temperature and PFD. The temperatures in the houses were roughly comparable, and within 3 °C of ambient on the hottest afternoons. Light conditions in the shadehouses were controlled by a combination of shade fabrics and energy films. Energy films reducing PFD to an equivalent extent, but altering R:FR differently, were supplied by the 3M Corporation, St. Paul, MN 55144. Metal sputter-coated films (REAL20) shade approximately 85 % of PFD without changing R:FR, and dye-impregnated films (NEARL20) reduced the R:FR to approximately 0.25 with a similar degree of shading. We constructed five shade treatments: (1) 40 % solar PFD and 1.25 R:FR, HRR; (2) 12 % PFD and 1.25 R:FR, MRR; (3) 12 % PFD and 0.25 R:FR, MFR; (4) 3 % PFD and 1.25 R:FR, LRR; and (5) 3 % PFD and 0.25 R:FR, LFR (Table 2). Replications of the five light treatments were constructed on the roofs of two buildings at FRIM, reducing interference from tree crowns. PFD values in the houses for different treatment durations could be used to estimate the total amount of radiation available (Table 2).

**Table 1.** Tree species included in this research, including origins, period of treatment, and ecological requirements

| Species | Ecology | Origin | Treatment period (days) | Abbreviation |
|---|---|---|---|---|
| *Dryobalanops aromatica* | A | Royal Selangor Golf Club, K.L. | 286-316 | DA |
| *Hopea helferei* | C | FRIM | 744-807 | HH |
| *Hopea odorata* | CA | FRIM | 475-498 | HO |
| *Hopea wightiana* | C | FRIM (India) | 491-503 | HW |
| *Shorea singkawang* | B | Pasoh F.R. | 270-276 | SS |

Symbols: A = relatively shade-tolerant; B = very shade-tolerant; C = drought tolerant;
FRIM = Forest Research Institute of Malaysia; K.L. = Kuala Lumpur; F.R. = Forest Reserve.

**Table 2.** Mean daily photosynthetic photons received for each of the species treatments, values in mol photons (400-700 nm) $m^{-2}$ $d^{-1}$. For species abbreviations see Table 1 and treatment abbreviations see text. Mean percentages of full sunlight and R:FR for all treatments also given.

| | Treatments | | | | |
|---|---|---|---|---|---|
| | Low PFD | | Medium PFD | | High PFD |
| Enriched in: species | Far-red LFR | Red LRR | Far-red MFR | Red MRR | Red HRR |
| Replication 1 | | | | | |
| DA | 0.98 ±0.29 | 1.07 ±0.28 | 3.28 ±0.84 | 3.59 ±0.82 | 13.96 ±3.15 |
| HH | 0.89 ±0.29 | 0.89 ±0.30 | 3.07 ±0.88 | 3.52 ±1.28 | 11.57 ±2.96 |
| HO | 0.84 ±0.25 | 0.81 ±0.28 | 2.84 ±0.84 | 2.90 ±1.00 | 11.92 ±2.93 |
| HW | 0.87 ±0.23 | 1.00 ±0.26 | 3.07 ±0.75 | 3.81 ±0.78 | 14.89 ±3.15 |
| SS | 0.98 ±0.29 | 1.07 ±0.28 | 3.28 ±0.84 | 3.59 ±0.82 | 13.96 ±3.15 |
| % shade | 3.4 ±0.5 | 3.3 ±0.5 | 10.8 ±1.1 | 11.5 ±1.5 | 41.0 ±2.4 |
| R:FR | 0.25 | 1.28 | 0.25 | 1.29 | 1.27 |
| Replication 2 | | | | | |
| DA | 1.15 ±0.31 | 1.13 ±0.31 | 3.50 ±0.88 | 3.72 ±0.95 | 11.52 ±2.71 |
| HH | 0.74 ±0.23 | 0.81 ±1.00 | 3.23 ±0.81 | 5.02 ±1.51 | 13.92 ±3.30 |
| HO | 0.81 ±0.21 | 0.94 ±0.24 | 2.97 ±0.72 | 3.92 ±1.03 | 14.17 ±2.72 |
| HW | 0.97 ±0.31 | 0.95 ±0.43 | 3.12 ±0.92 | 3.16 ±1.02 | 14.89 ±3.14 |
| SS | 1.15 ±0.31 | 1.13 ±0.31 | 3.50 ±0.88 | 3.72 ±0.95 | 11.52 ±2.71 |
| % shade | 2.8 ±0.5 | 3.1 ±0.5 | 10.3 ±0.8 | 12.6 ±1.2 | 45.1 ±3.4 |
| R:FR | 0.21 | 1.31 | 0.23 | 1.33 | 1.33 |

**Table 3.** Effects of light treatments on measurements of plant growth

| Species treatment | Height (cm) | Collar diameter (mm) | Growth/day (mg) | Growth/mol photons (mg) |
|---|---|---|---|---|
| *Dryobalanops aromatica* | | | | |
| LFR | 66.0 a | 5.1 a | 18.4 a | 17.4 a |
| | ± 4.5 | ± 0.3 | ± 1.2 | ± 1.2 |
| LRR | 51.4 a | 5.0 a | 22.3 a | 20.3 a |
| | ± 2.5 | ± 0.1 | ± 1.8 | ± 1.6 |
| MFR | 124.8 b | 6.2 b | 58.9 b | 17.4 a |
| | ± 7.8 | ± 0.3 | ± 5.5 | ± 1.6 |
| MRR | 93.4 c | 7.0 b | 80.4 c | 22.0 a |
| | ± 3.1 | ± 0.2 | ± 4.6 | ± 1.3 |
| HRR | 103.4 c | 8.4 c | 100.7 d | 7.9 b |
| | ± 7.3 | ± 0.3 | ± 5.5 | ± 0.4 |
| *Hopea helferei* | | | | |
| LFR | 19.6 a | 3.8 a | 6.2 a | 7.7 ac |
| | ± 1.9 | ± 0.2 | ± 0.6 | ± 0.8 |
| LRR | 19.5 a | 5.1 a | 14.8 a | 17.7 b |
| | ± 2.1 | ± 0.3 | ± 1.7 | ± 2.1 |
| MFR | 35.7 b | 7.1 b | 29.4 ab | 9.3 ac |
| | ± 5.4 | ± 0.7 | ± 6.0 | ± 1.9 |
| MRR | 32.7 b | 9.5 c | 50.9 b | 12.4 bc |
| | ± 3.1 | ± 0.6 | ± 4.3 | ± 1.2 |
| HRR | 35.8 b | 12.5 d | 78.0 c | 6.6 a |
| | ± 2.8 | ± 0.5 | ± 9.7 | ± 0.9 |
| *Hopea odorata* | | | | |
| LFR | 54.3 ab | 5.2 a | 18.2 a | 22.1 a |
| | ± 2.5 | ± 0.2 | ± 1.4 | ± 1.7 |
| LRR | 39.9 a | 5.4 a | 22.6 a | 25.6 a |
| | ± 3.1 | ± 0.2 | ± 3.0 | ± 3.0 |
| MFR | 95.8 c | 8.9 b | 78.4 b | 26.9 a |
| | ± 5.7 | ± 0.3 | ± 6.4 | ± 2.2 |
| MRR | 62.7 b | 9.9 b | 97.2 b | 29.0 a |
| | ± 3.6 | ± 0.4 | ± 6.7 | ± 2.1 |
| HRR | 58.8 b | 10.1 b | 97.7 b | 7.6 b |
| | ± 2.3 | ± 0.3 | ± 8.8 | ± 0.7 |
| *Hopea wightiana* | | | | |
| LFR | 34.9 ab | 4.2 a | 9.8 a | 10.6 ac |
| | ± 1.8 | ± 0.2 | ± 0.9 | ± 1.0 |
| LRR | 32.9 a | 4.7 a | 13.2 a | 13.7 bc |
| | ± 2.2 | ± 0.2 | ± 1.6 | ± 1.7 |
| MFR | 33.6 a | 6.3 b | 36.0 b | 11.6 ab |
| | ± 3.0 | ± 0.4 | ± 5.2 | ± 1.7 |
| MRR | 45.0 b | 7.9 c | 58.7 c | 17.4 b |
| | ± 2.6 | ± 0.3 | ± 6.1 | ± 2.1 |
| HRR | 44.1 b | 9.9 d | 106.7 d | 7.2 a |
| | ± 2.8 | ± 0.4 | ± 5.5 | ± 0.5 |
| *Shorea singkawang* | | | | |
| LFR | 34.2 a | 7.0 a | 27.0 a | 25.4 a |
| | ± 2.8 | ± 1.1 | ± 2.9 | ± 3.0 |
| LRR | 26.3 a | 6.3 a | 28.9 a | 26.2 a |
| | ± 1.6 | ± 0.4 | ± 2.8 | ± 2.6 |
| MFR | 85.9 c | 8.3 ab | 81.1 b | 24.0 a |
| | ± 6.4 | ± 0.5 | ± 7.5 | ± 2.3 |
| MRR | 64.2 bd | 10.3 b | 120.5 c | 33.0 a |
| | ± 4.1 | ± 0.4 | ±10.2 | ± 2.8 |
| HRR | 70.4 cd | 13.2 c | 180.0 d | 13.9 b |
| | ± 2.6 | ± 0.4 | ±13.0 | ± 0.9 |

Treatments not sharing letters are significantly different from each other. Treatment abbreviations are defined in the text.

Seedlings were harvested when the tallest treatment had reached approximately 1 m in height. For each seedling, mass of leaf blades, petioles, stems, and roots was measured. Leaf area, internode distance, number of internodes in branches and main axis, and total stem length were also measured. A maximum of ten plants for each treatment were analyzed. These measurements allowed the calculation of growth as mass increase per day or per mol of photons, allocation to plant organs, as well as a variety of morphological indicators (Table 3).

For statistical analysis, replicates of each treatment were compared by the Student *t* - test, found similar, and lumped for one way ANOVA, using Tukey's Honest Difference test for post-hoc pairwise comparisons (Norusis 1991). The factorial design of the low and middle shade environments allowed the use of a two-way ANOVA. Comparison of the sums of squares for the treatment effects of R:FR and PFD permitted the calculation of coefficients of determination (using the total sums of squares from the one way ANOVA as denominator) for assessing the influence of light quantity and quality on seedling growth and development (Sokal & Rohlf 1981).

## Results and discussion

The data in this article were taken from the more detailed studies of Lee *et al.* (submitted for publication, a & b).

### *Seedling growth rates*

Seedling growth among the five taxa was assessed in three ways (Table 3). Diameter at collar is correlated with stem volume and energy storage; it was enhanced by higher light treatments and little affected by R:FR among all of the taxa (Table 6). Height growth is related to the competitive ability of seedlings in mixed populations; greater height allows for more efficient capture of energy when the light climate promotes rapid seedling growth (King 1994). Plant height was reduced by the high light treatments among all taxa; height growth was promoted by reduced R:FR for some light levels among all taxa (Table 3). R:FR added to the predominant effect of PFD among all taxa, and was least important in *H. helferei*.

The most direct measure of seedling growth is the measurement of dry weight. Dry weight increments were assessed in terms of the treatment period and the amount of PFD received by the seedlings (Table 3, Figure 1). Growth per day increased with PFD among all species except *H. odorata*, indicating that the latter was the most reduced by high light intensity. *Shorea singkawang* seedlings grew most rapidly among the five taxa, and were the least adversely affected by high PFD. Growth per mol of photons received indicates the relative efficiency of light use of the different shade treatments; all taxa were reduced in growth per mole of photons at 40% shade. *Hopea helferei* and *H. wightiana*, the two species native to drier evergreen forest habitats, grew the least efficiently at the 3% treatments.

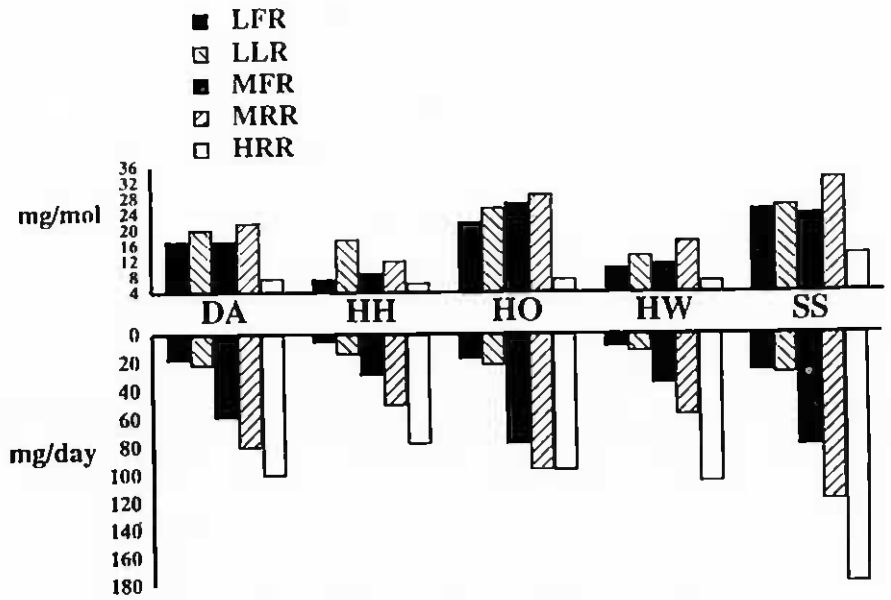


**Figure 1.** Influence of the treatments on dry mass increments, as mg day$^{-1}$ on the bottom graph, and mg mol$^{-1}$ photons received on the top graph. Species abbreviations are described in the text.

Although height growth tended to be enhanced by reduced R:FR, the same treatment suppressed dry weight increases among most taxa (Table 3). Other factors may be involved, but the most obvious explanation is the reduced leaf mass allocation at low R:FR and the reduction in leaf area/stem length among all taxa (Table 4). Thus, natural shade affects two variables that could contribute to seedling fitness, height and relative leaf area—but in opposite ways.

### *Photosynthate allocation*

Allocations of biomass to plant organs can be interpreted as strategies to improve the fitness of seedlings under a variety of environmental conditions (Grime 1979, Tilman 1988). An increase in leaves suggests a greater capacity for energy capture and carbon fixation. An increase in stems suggests a strategy of exploration to situate a plant better for future energy capture. An increase in roots suggests an increased ability to absorb water and nutrients, even under conditions of moisture stress. Shade treatments affected allocation to all of these organs. Allocation to roots was generally increased at the highest PFD (HRR), and not strongly affected by PFD or R:FR at the lower fluxes. Allocation to leaves was generally reduced by low R:FR and the highest fluxes. Allocation to stems was not as strongly affected by spectral quality (Table 6). The general shade response of these plants, enhanced by low R:FR, was increased height growth and stem allocation, along with reduced allocation for leaf energy capture, a general strategy for exploration.

**Table 4.** Effects of light treatments on measurements of plant architecture

| Species treatment | Internode length (cm) | Branch/trunk internodes | Stem mass (mg) /length (cm) | Leaf area ($cm^2$)/ stem length (cm) |
|---|---|---|---|---|
| *Dryobalanops aromatica* | | | | |
| LFR | 5.1 ac | 3.74 a | 12.72 ad | 3.38 a |
| | ± 0.8 | ± 0.29 | ± 1.00 | ± 0.22 |
| LRR | 2.2 b | 5.22 b | 11.41 a | 3.61 a |
| | ± 0.2 | ± 0.58 | ± 0.59 | ± 0.15 |
| MFR | 6.9 c | 3.61 a | 28.21 bc | 2.97 a |
| | ± 0.4 | ± 0.25 | ± 4.22 | ± 0.19 |
| MRR | 5.6 ac | 6.14 bc | 20.83 bd | 3.98 a |
| | ± 0.3 | ± 0.34 | ± 1.19 | ± 0.17 |
| HRR | 5.0 a | 7.24 c | 34.75 c | 3.12 a |
| | ± 0.5 | ± 0.50 | ± 2.12 | ± 0.26 |
| *Hopea helferei* | | | | |
| LFR | 13.4 a | 2.02 a | 23.63 a | 5.85 a |
| | ± 0.9 | ± 0.33 | ± 1.51 | ± 0.34 |
| LRR | 13.3 a | 2.78 ac | 33.48 ab | 9.57 b |
| | ± 1.1 | ± 0.40 | ± 3.10 | ± 0.58 |
| MFR | 15.6 a | 3.18 abc | 52.12 b | 6.46 a |
| | ± 1.3 | ± 0.49 | ± 5.13 | ± 0.46 |
| MRR | 15.8 a | 5.28 bc | 78.55 c | 7.70 ab |
| | ± 0.3 | ± 0.96 | ± 5.11 | ± 0.41 |
| HRR | 13.7 a | 6.06 b | 133.77 d | 8.20 b |
| | ± 1.2 | ± 1.20 | ± 7.39 | ± 0.48 |
| *Hopea odorata* | | | | |
| LFR | 41.6 b | 2.99 a | 14.34 a | 5.22 ab |
| | ± 2.9 | ± 0.19 | ± 0.60 | ± 0.11 |
| LRR | 28.0 a | 4.01 a | 13.76 a | 6.46 b |
| | ± 1.7 | ± 0.34 | ± 0.67 | ± 0.19 |
| MFR | 64.6 c | 4.14 a | 36.83 b | 5.08 ac |
| | ± 2.9 | ± 0.17 | ± 1.88 | ± 0.19 |
| MRR | 46.6 b | 6.35 b | 35.56 b | 6.21 bc |
| | ± 2.7 | ± 0.39 | ± 2.46 | ± 0.29 |
| HRR | 39.0 b | 3.91 a | 49.33 c | 4.17 a |
| | ± 1.4 | ± 0.39 | ± 2.17 | ± 0.34 |
| *Hopea wightiana* | | | | |
| LFR | 12.3 a | 0.87 a | 14.74 a | 4.54 a |
| | ± 0.6 | ± 0.12 | ± 1.51 | ± 0.48 |
| LRR | 11.5 a | 1.14 a | 17.50 a | 6.51 b |
| | ± 0.5 | ± 0.11 | ± 1.06 | ± 0.27 |
| MFR | 13.4 a | 2.35 b | 30.24 b | 4.99 ac |
| | ± 1.0 | ± 0.33 | ± 2.80 | ± 0.32 |
| MRR | 11.7 a | 2.87 b | 37.95 b | 5.94 bc |
| | ± 0.5 | ± 0.35 | ± 2.56 | ± 0.18 |
| HRR | 10.9 a | 2.86 b | 60.95 c | 6.19 bc |
| | ± 0.8 | ± 0.32 | ± 5.15 | ± 0.40 |
| *Shorea singkawang* | | | | |
| LFR | 2.2 a | 0.00 a | 5.13 a | 1.68 ab |
| | ± 0.3 | ± 0.00 | ± 0.44 | ± 0.14 |
| LRR | 1.0 a | 0.02 a | 5.95 a | 2.11 b |
| | ± 0.1 | ± 0.01 | ± 0.41 | ± 0.18 |
| MFR | 7.6 bc | 0.13 ab | 7.52 a | 1.29 a |
| | ± 0.6 | ± 0.04 | ± 0.56 | ± 0.06 |
| MRR | 5.7 c | 0.23 b | 11.54 b | 2.28 b |
| | ± 0.6 | ± 0.07 | ± 1.21 | ± 0.16 |
| HRR | 7.0 de | 0.49 c | 19.05 c | 1.75 a |
| | ± 0.4 | ± 0.07 | ± 1.84 | ± 0.12 |

Treatment abbreviations are defined in the text.

**Table 5.** Effects of light treatments on photosynthate allocation to leaves, roots and stems

| Species treatment | % Leaves | % Stems | % Roots | Specific leaf mass (mg $cm^{-2}$) |
|---|---|---|---|---|
| *Dryobalanops aromatica* | | | | |
| LFR | 51.5 a | 33.8 ab | 14.7 ab | 5.69 a |
| | ± 0.8 | ± 0.7 | ± 0.6 | ± 0.07 |
| LRR | 59.2 b | 28.8 a | 11.9 a | 6.45 ab |
| | ± 2.4 | ± 1.7 | ± 0.9 | ± 0.58 |
| MFR | 37.8 c | 43.8 c | 18.0 b | 7.34 b |
| | ± 1.8 | ± 1.7 | ± 1.1 | ± 0.15 |
| MRR | 50.7 a | 35.8 b | 13.4 a | 7.67 b |
| | ± 1.0 | ± 0.6 | ± 0.7 | ± 0.30 |
| HRR | 36.8 c | 44.7 c | 18.4 b | 9.40 c |
| | ± 1.6 | ± 1.6 | ± 1.1 | ± 0.55 |
| *Hopea helferei* | | | | |
| LFR | 45.9 a | 30.1 a | 19.9 a | 5.32 a |
| | ± 0.9 | ± 0.7 | ± 0.8 | ± 0.07 |
| LRR | 49.1 a | 29.2 a | 19.0 a | 5.14 a |
| | ± 0.7 | ± 0.8 | ± 0.9 | ± 0.10 |
| MFR | 31.4 b | 37.2 b | 29.9 b | 6.43 b |
| | ± 2.0 | ± 1.9 | ± 1.1 | ± 0.33 |
| MRR | 27.7 bd | 40.1 b | 31.0 b | 6.88 b |
| | ± 1.6 | ± 1.7 | ± 1.3 | ± 0.22 |
| HRR | 21.1 c | 39.9 b | 38.1 c | 8.31 c |
| | ± 1.3 | ± 1.4 | ± 2.2 | ± 0.10 |
| *Hopea odorata* | | | | |
| LFR | 46.8 c | 33.0 a | 20.2 a | 3.89 a |
| | ± 0.7 | ± 0.7 | ± 0.9 | ± 0.07 |
| LRR | 52.0 c | 29.5 a | 18.5 a | 3.91 a |
| | ± 0.8 | ± 1.3 | ± 0.9 | ± 0.10 |
| MFR | 30.4 b | 40.3 b | 29.3 b | 5.44 b |
| | ± 1.1 | ± 1.1 | ± 1.5 | ± 0.17 |
| MRR | 30.1 b | 32.1 a | 37.8 c | 5.23 b |
| | ± 1.2 | ± 1.4 | ± 1.8 | ± 0.19 |
| HRR | 18.4 a | 32.7 a | 48.9 d | 7.02 c |
| | ± 1.1 | ± 1.4 | ± 1.4 | ± 0.21 |
| *Hopea wightiana* | | | | |
| LFR | 46.7 a | 26.8 ab | 26.5 a | 5.27 a |
| | ± 0.8 | ± 0.6 | ± 0.8 | ± 0.11 |
| LRR | 49.3 a | 24.9 a | 25.8 a | 5.24 a |
| | ± 0.9 | ± 0.5 | ± 1.0 | ± 0.08 |
| MFR | 30.6 b | 29.7 a | 39.7 b | 6.20 b |
| | ± 0.8 | ± 1.1 | ± 1.3 | ± 0.11 |
| MRR | 30.8 b | 28.2 ab | 41.0 b | 6.80 c |
| | ± 1.4 | ± 1.0 | ± 1.6 | ± 0.20 |
| HRR | 23.4 c | 27.6 ab | 49.0 c | 8.34 d |
| | ± 0.9 | ± 1.2 | ± 1.2 | ± 0.11 |
| *Shorea singkawang* | | | | |
| LFR | 54.8 a | 24.6 a | 20.5 a | 6.95 a |
| | ± 1.0 | ± 1.0 | ± 0.8 | ± 0.16 |
| LRR | 56.3 a | 22.8 a | 20.8 a | 7.00 a |
| | ± 1.7 | ± 1.0 | ± 1.2 | ± 0.14 |
| MFR | 46.6 b | 33.1 bc | 20.3 a | 8.04 b |
| | ± 1.4 | ± 1.6 | ± 0.7 | ± 0.15 |
| MRR | 47.6 b | 29.7 b | 22.7 a | 8.09 b |
| | ± 1.5 | ± 1.8 | ± 0.8 | ± 0.15 |
| HRR | 29.6 c | 38.4 c | 32.0 b | 10.51 c |
| | ± 0.8 | ± 1.2 | ± 1.2 | ± 0.27 |

Treatment abbreviations are defined in the text.

**Table 6.** Coefficients of determination for effects of light intensity and spectral quality on seedling growth and development

| Species | Character | R:FR | PFD | Interactions |
|---|---|---|---|---|
| *Dryobiranops aromatica* | | | | |
| | Plant height 0.095* | 0.456* | 0.013 | |
| | Collar diameter | 0.010 | 0.190* | 0.019* |
| | Mass/day | 0.026* | 0.397* | 0.013* |
| | Mass/mol | 0.058* | 0.003 | 0.003 |
| | % leaf | 0.189* | 0.220* | 0.011 |
| | % stem | 0.141* | 0.247* | 0.008 |
| | % root | 0.165* | 0.069* | 0.001 |
| | Internode length | 0.094* | 0.355* | 0.001 |
| | Specific leaf mass | 0.016 | 0.114* | 0.003 |
| | Leaf area/stem length | 0.022 | 0.015 | 0.002 |
| | Stem mass/length | 0.026* | 0.210* | 0.012 |
| | Branch/trunk internodes | 0.176* | 0.007 | 0.012 |
| *Hopea helferi* | | | | |
| | Plant height 0.002 | 0.162* | 0.002 | |
| | Collar diameter | 0.046* | 0.127* | 0.004 |
| | Mass/day | 0.033* | 0.128* | 0.006 |
| | Mass/mol | 0.143* | 0.011 | 0.040* |
| | % leaf | 0.000 | 0.381* | 0.014* |
| | % stem | 0.004 | 0.270* | 0.012 |
| | % root | 0.000 | 0.247* | 0.002 |
| | Internode length | 0.002 | 0.162* | 0.002 |
| | Specific leaf mass | 0.000 | 0.006* | 0.000 |
| | Leaf area/stem length | 0.186* | 0.012 | 0.046* |
| | Stem mass/length | 0.027* | 0.111* | 0.006* |
| | Branch/trunk internodes | 0.031* | 0.051* | 0.007 |
| *Hopea odorata* | | | | |
| | Plant height 0.173* | 0.315* | 0.025* | |
| | Collar diameter | 0.001 | 0.047* | 0.001 |
| | Mass/day | 0.013* | 0.419* | 0.005 |
| | Mass/mol | 0.008 | 0.024* | 0.000 |
| | % leaf | 0.379* | 0.017* | 0.005* |
| | % stem | 0.141* | 0.099* | 0.024* |
| | % root | 0.008* | 0.186* | 0.019* |
| | Internode length | 0.156* | 0.272* | 0.004* |
| | Specific leaf mass | 0.000 | 0.158* | 0.001 |
| | Leaf area/stem length | 0.101* | 0.003 | 0.002 |
| | Stem mass/length | 0.002 | 0.374* | 0.001 |
| | Branch/trunk internodes | 0.150* | 0.174* | 0.020* |
| *Hopea wightiana* | | | | |
| | Plant height 0.214* | 0.361* | 0.111* | |
| | Collar diameter | 0.040* | 0.186* | 0.014* |
| | Mass/day | 0.024* | 0.127* | 0.015* |
| | Mass/mol | 0.017* | 0.095* | 0.019 |
| | % leaf | 0.004 | 0.467* | 0.003 |
| | % stem | 0.035* | 0.119* | 0.000 |
| | % root | 0.000 | 0.357* | 0.002 |
| | Internode length | 0.032 | 0.008 | 0.005 |
| | Specific leaf mass | 0.010* | 0.189* | 0.012* |
| | Leaf area/stem length | 0.163* | 0.000 | 0.020 |
| | Stem mass/length | 0.012* | 0.142* | 0.003 |
| | Branch/trunk internodes | 0.015 | 0.246* | 0.001 |
| *Shorea singkawang* | | | | |
| | Plant height 0.053* | 0.491* | 0.012 | |
| | Collar diameter | 0.008 | 0.127* | 0.033* |
| | Mass/day | 0.019 | 0.237* | 0.016 |
| | Mass/mol | 0.149* | 0.046 | 0.027 |
| | % leaf | 0.003 | 0.118* | 0.000 |
| | % stem | 0.023 | 0.183* | 0.002 |
| | % root | 0.012 | 0.004 | 0.008 |
| | Internode length | 0.045* | 0.463* | 0.002 |
| | Specific leaf mass | 0.000 | 0.110* | 0.000 |
| | Leaf area/stem length | 0.241* | 0.008 | 0.030 |
| | Stem mass/length | 0.027* | 0.074* | 0.012* |
| | Branch/trunk internodes | 0.010 | 0.083* | 0.006 |

*indicates a significant effect for the treatment variable in the two-way ANOVA, at 0.05.

### *Morphological responses*

The light treatments affected seedling development among the five taxa in a variety of ways. Internode length, in coordination with plant height, was influenced by both R:FR and PFD. Leaf specific mass and stem mass/length were predominantly reduced by lower fluxes (Tables 4, 5 and 6). The degree of branching and the leaf area/stem length were influenced by both R:FR and PFD, and the relative influence of the two light factors varied among the species. In *D. aromatica* and *H. wightiana* R:FR almost exclusively controlled the degree of branching, less so in *H. helferei* and *H. odorata*, and there was little branching in *S. singkawang* (Table 4). Leaf area/stem length was primarily reduced by R:FR among all taxa (Tables 4 and 6).

In general, reduced R:FR decreased capacity for light capture and carbon fixation by lowering the investment in leaves. Leaves were reduced as a percentage of total mass and as a proportion to stem length. The result was a taller and more narrow seedling with fewer leaves.

### *Differences among taxa*

The five species in this study grow in a variety of environmental conditions. *Drobalanops aromatica* and *S. singkawang* both grow in rain forest, and the former is reputed to be extremely shade-tolerant (Appanah & Weinland 1992, Kachi *et al.* 1993). All three *Hopea* species are indigenous to drier evergreen forests; *Hopea wightiana* is native to Southwest India and the other two taxa to northern Malaya and Indochina. *Hopea helferei* grows in a variety of habitats, including upper dipterocarp forests ranging to 500 m in Indo-China (Smitinand *et al.* 1980). *Hopea odorata* has a similar range, but it is limited to stream margins in the southern end of its distribution and is more shade-tolerant.

Seedlings of these species vary in their responses to shade conditions, but in patterns that defy any simple explanation. The relative responses of the five species, including effects of R:FR and PFD as well as total plasticity, can be seen by comparing the coefficients of determination for selected variables (Table 7 and Figure 2). The species were roughly comparable in their total responses to the treatment conditions—in their plasticity. However, the contributions of R:FR and PFD to plant characters varied among the taxa. For instance, the degree of branching was influenced by PFD in *H. wightiana* and partly by R:FR in *H. helferei*. Percentage of leaf allocation was primarily influenced by R:FR in *H. odorata* and primarily by PFD in *H. helferei*, and these two taxa are closely related to each other (Ashton 1982). Species also varied in their ranking for various growth and developmental characteristics (Table 8). For instance, *S. singkawang* grew the most rapidly of the five taxa, yet was the least plastic in allocation response to light conditions.

**Table 7.** Summary of comparisons of coefficients of determination for the species and characters

| Species | R:FR | PFD | Interactions | Total |
|---|---|---|---|---|
| *Dryobalanops aromatica* | 0.099 ±0.009 | 0.138 ±0.016 | 0.006 ±0.001 | 0.242 ±0.020 |
| *Hopea helferei* | 0.044 ±0.023 | 0.139 ±0.045 | 0.014 ±0.006 | 0.209 ±0.043 |
| *Hopea odorata* | 0.105 ±0.041 | 0.145 ±0.042 | 0.008 ±0.003 | 0.259 ±0.047 |
| *Hopea wightiana* | 0.032 ±0.017 | 0.180 ±0.052 | 0.007 ±0.003 | 0.220 ±0.043 |
| *Shorea singkawang* | 0.057 ±0.028 | 0.121 ±0.047 | 0.010 ±0.004 | 0.187 ±0.048 |
| Mean | 0.067 ±0.005 | 0.145 ±0.010 | 0.009 ±0.001 | 0.223 ±0.013 |
| Characters | R:FR | PFD | Interactions | Total |
| Mass/mol | 0.075 ±0.030 | 0.036 ±0.017 | 0.018 ±0.008 | 0.129 ±0.036 |
| Internode length | 0.066 ±0.027 | 0.252 ±0.078 | 0.003 ±0.004 | 0.321 ±0.090 |
| % Leaf allocation | 0.115 ±0.075 | 0.241 ±0.083 | 0.007 ±0.003 | 0.362 ±0.062 |
| % Stem allocation | 0.076 ±0.027 | 0.184 ±0.034 | 0.009 ±0.004 | 0.262 ±0.041 |
| % Root allocation | 0.037 ±0.032 | 0.173 ±0.063 | 0.006 ±0.004 | 0.216 ±0.054 |
| Specific leaf mass | 0.005 ±0.003 | 0.115 ±0.031 | 0.003 ±0.002 | 0.124 ±0.034 |
| Leaf area/stem length | 0.143 ±0.038 | 0.008 ±0.003 | 0.020 ±0.008 | 0.170 ±0.044 |
| Stem mass/length | 0.019 ±0.005 | 0.182 ±0.053 | 0.007 ±0.002 | 0.208 ±0.048 |
| Branch/trunk internodes | 0.076 ±0.036 | 0.112 ±0.043 | 0.009 ±0.003 | 0.198 ±0.049 |
| Mean | 0.068 ±0.020 | 0.145 ±0.038 | 0.009 ±0.003 | 0.215 ±0.041 |

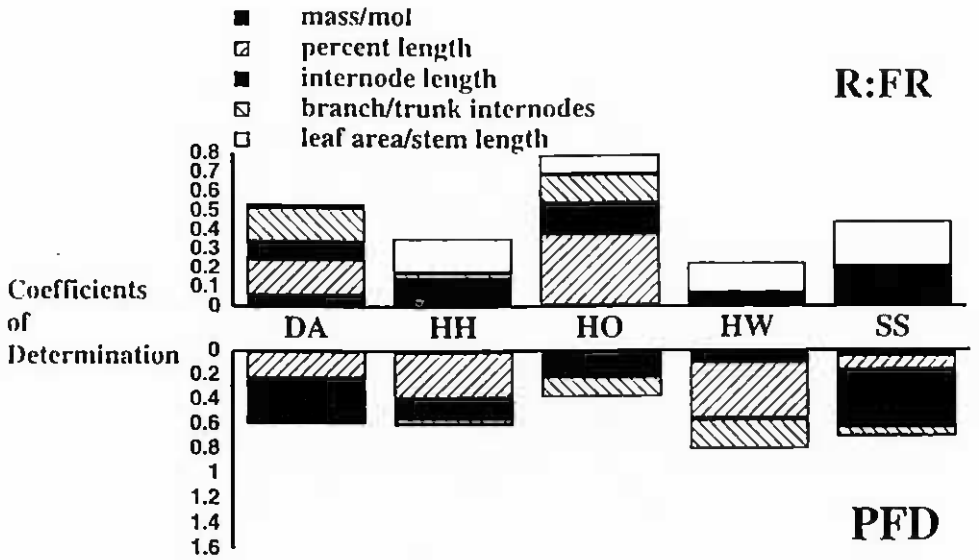


**Figure 2.** Relative influence of R:FR (top graph) and PFD (bottom graph) on seedling morphology of the five species analyzed, shown by adding coefficients of determination for each. Species abbreviations are described in the text.

**Table 8.** Rank of species responses

| Species | Growth rate | Allocation | | Morphology | | High light inhibition |
|---|---|---|---|---|---|---|
| | | Plasticity | R:FR | Plasticity | R:FR | |
| *Dryobalanops aromatica* | *** | ***** | **** | **** | **** | * |
| *Hopea helferei* | * | **** | * | * | ***** | ** |
| *Hopea odorata* | **** | ** | ***** | *** | ** | ***** |
| *Hopea wightiana* | ** | *** | ** | *** | * | *** |
| *Shorea singkawang* | ***** | ** | *** | ***** | *** | **** |

Five asteriks, first response; growth rate in mg $mol^{-1}$ photosynthetic photons; allocation refers to the % mass in plant organs; plasticity is the total light response; R:FR refers to the relative contribution of R:FR to allocation; morphology refers to the characters that describe stem robustness, branching and relative leaf area, with plasticity and R:FR just described. High light inhibition refers to the degree of reduction in growth (mg $mol^{-1}$) compared to growth and low and medium intensities.

## Conclusion

Since shade responses are manifested by a variety of characters, at different levels of structural organization, the overall response may be subtle and continuous from the additive effects of the different characters. When the concept of gap phase dynamics was developed, considerable optimism arose about the possibility of explaining seedling responses to the heterogenous light conditions in the tropical rain forest understory. Although there is evidence for varying shade tolerances of

seedlings among dipterocarp taxa, which may help to explain some of the extraordinary diversity in this family, these results help to show how complex shade responses are (Figure 2, Table 9). Not only do the morphological bases for these shade responses vary among the five taxa, but the morphogenic signals (light quality and quantity) may affect each taxon in a unique way, confounding our attempts to correlate responses with functional ecology. For dipterocarp seedlings other factors such as soil type and drought tolerance may be as important as shade tolerance (Ashton 1988). At the very least, these results show clearly the roles that R:FR plays in seedling light responses, and suggest strongly that future research on shade responses should include the influence of spectral quality.

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