Oecologia (1997) 110:1–9

David W. Lee · Steven F. Oberbauer
Baskaran Krishnapilay · Marzalina Mansor
Haris Mohamad · Son Kheong Yap

Effects of irradiance and spectral quality on seedling development of two Southeast Asian *Hopea* species

Received: 14 April 1996 / Accepted: 8 October 1996

Abstract Seedling developmental responses to understory shade combine the effects of reductions in irradiance and changes in spectral quality. We studied the seedling development of two Southeast Asian dipterocarp trees in response to differences in irradiance (photosynthetic photon flux density, PPFD) and spectral quality (red to far-red ratio, R:FR). The two species, *Hopea helferei* and *H. odorata*, are taxonomically closely related but differ in their ecological requirements; *H. helferei* is more drought-tolerant and typically grows in more open habitats. Seedlings were grown in six different replicated shadehouse treatments varying in percentage of solar PPFD and R:FR. The two species differed in the influence of light variables on most seedling characters, particularly for final height, internode distance, branch/trunk internodes, stem length/mass, leaf area/stem length, petiole length, and growth/mol of photons received. Most of the characters in both taxa were primarily influenced by PPFD, but spectral quality also influenced some characters – more so for *H. odorata*. The latter species grew more rapidly, particularly in the low PPFD treatments, and its leaves were capable of higher photosynthesis rates. However, growth in *H. helferei* was not reduced in direct sunlight. The growth of this taxon may be constrained by adaptations, particularly in leaves, for drought tolerance.

Key words Tropical rain forest · Seedling development · Physiology · Light climate · Red:far-red ratic

D. W. Lee (✉) · S. F. Oberbauer
Department of Biological Sciences,
Florida International University, Miami, FL 33199, USA
and Fairchild Tropical Garden, Miami, FL 33156, USA

B. Krishnapilay · M. Mansor · H. Mohamad · S. K. Yap
Forest Research Institute of Malaysia,
Kuala Lumpur 52109, Malaysia

Introduction

Although light is generally considered to be the most important factor controlling the establishment and growth of trees in tropical evergreen forests, its effects on individual taxa are not well understood. Light is especially crucial during the seedling phase of the life history of such trees (Whitmore 1996). Information on the light responses of seedlings comes from (1) distributional sampling of seedlings in the forest in relation to the size and age of gaps; (2) seedling survival studies in forest environments; and (3) common garden experiments under shade (Liew and Wong 1973; Fetcher et al. 1983; Oberbauer and Strain 1985; Popma and Bongers 1991; Brown and Whitmore 1992; Turner et al. 1992; Whitmore 1996; Ashton 1995). Lack of experimental research on the shade tolerance of tropical tree seedlings limits our ability to generalize (Kitajima 1994), but the few results available suggest that tree seedlings vary in shade tolerance, particularly between early successional and climax species.

Light climates and seedling growth

Seedlings growing in the gradient of shade microclimates within the forest experience dramatic changes in radiation contributing to photosynthesis (photosynthetic photon flux density at 400–700 nm, PPFD), as well as spectral quality (Chazdon et al. 1996). The selective filtering of foliage depresses the ratio of red to far-red quanta (R:FR of Smith 1994), which influences phytochrome equilibria and a variety of developmental responses. The majority of research on shade responses of seedlings has manipulated PPFD without altering R:FR. Under the deep shade conditions of these experiments, seedlings were exposed to very low PPFD, but the spectral quality of sunlight. Plant growth and developmental responses to such conditions are likely to underestimate shade responses in natural environments (Schmitt and Wulff 1993). Although Kitajima (1994) measured few

effects of reduced R:FR on plant growth and allocation patterns, Sasaki and Mori (1981) reported increases in height and internode distance of seedlings in *Shorea ovalis*. Lee (1988) observed significant developmental responses to reduced R:FR in three relatively shade-tolerant tropical vines, with specific morphological patterns varying between species. Most of the research on the influence of PPFD and R:FR on seedling physiology has examined photosynthetic characteristics, finding relatively little influence of R:FR (Kamaluddin and Grace 1992; Turnbull 1991; Kitajima 1994; Tinoco-Ojanguren and Pearcy 1995).

To assess the relative contributions of PPFD and R:FR to growth and development in seedlings, these two factors must be varied independently of each other. Lee et al. (1996) reported dramatically different influences of PPFD and R:FR on seedling development in six Asian tropical rainforest trees. Patterns of influence varied between taxa in a complex pattern.

Hypotheses of seedling shade responses

Tolerance of seedlings to shade can occur via one or more ecological or physiological mechanism. Whitmore (1996) hypothesized seedling shade tolerance as in (1) seedling survival; (2) the duration of survival; and (3) the amount of light necessary for seedling release. There may be physiological trade-offs between traits for shade tolerance and high-light requirements (Björkman 1981; Givnish 1988); growth responses are expected to maximize carbon gain and correlate with the functional ecology of individual species (Bazzaz 1979). Bazzaz hypothesized that understory species, more tolerant of shade at the seedling stage, should be adapted to efficiently use continuously low resource fluxes (light levels). Early successional species should have higher and more flexible metabolic rates capable of responding to resource pulses. Thus seedlings of early successional species should be more plastic in growth reponses to varying light conditions (Strauss-Debenedetti and Bazzaz 1996). Pearcy (1987) argued, to the contrary, that late-successional species require frequent gap events to attain the canopy, and are especially sensitive to variations in the light environment.

Both of these hypotheses are quite different from hypotheses 1 and 2 proposed by Whitmore (1996) (argued in more detail by Kitajima 1994, 1996). Survival in the understory, until rare gap events occur, may be more related to leaf life span and seedling resistance to herbivory. The more rapidly growing and less durable seedlings may thus be the least shade-tolerant. However, such durability has metabolic costs that may be associated with greater growth efficiency, even though the seedlings may not increase significantly in height.

Morgan and Smith (1979) demonstrated increased internode expansion among shade-intolerant taxa in a systematic survey of European herbs. They postulated that shade-intolerant taxa should generally exhibit a greater response to shifts in R:FR than shade-tolerant taxa, paralleling the hypothesis of Bazzaz. Kwesiga and Grace (1986) concluded that different growth responses in seedlings of *Khaya senegalensis* and *Terminalia ivorensis* under low R:FR were consistent with this hypothesis, but both of these species are relatively light-demanding. However, other growth trials varying R:FR produced growth patterns inconsistent with the hypothesis (Lee 1988; Lee et al. 1996).

Clearly, more research will differentiate among these conflicting hypotheses.

Species studied

The genus *Hopea*, with 102 species in the Dipterocarpaceae, is widely distributed in the evergreen forests and rainforests of the Asian tropics. Learning about the biology of species within this family is crucial to understanding the ecology of forests in tropical Asia (Ashton 1988). Both species are closely related in the subsection *Hopea* (Ashton 1982). Both are widely distributed in Indochina, ranging as far south as the northern Malayan peninsula. Hallé (1979) and Ng (1991) studied the patterns of seedling development in both species. As with all *Hopea* taxa studied, the architectural model of development (Hallé et al. 1979) conforms to the model of Roux, in which the plagiotropic lateral branches are produced at intervals on the orthotropic main axis. However, in *H. helferei* the first and subsequent lateral plagiotropic branches dominate, and the overall pattern of development looks superficially like the model of Troll, in which the plagiotropic branches replace each other to form a sympodial trunk. The resulting growth form produces little initial increase in height compared to *H. odorata*.

In Malaysia and Indochina, both taxa have similar geographical and altitudinal distributions, but different site preferences (Smitinand et al. 1980). *H. helferei* grows in deep soil on slopes, primarily in seasonally dry evergreen forests. The undersurfaces of its tough leaves are covered with scales, and it is relatively drought-tolerant. *H. odorata* is largely restricted to the damp soils of river and stream margins, but P. F. S. Ashton (personal communication) suggested that it is also somewhat drought-tolerant. It appears to be more shade-tolerant, but also grows more rapidly, than *H. helferei* in plantation trials (Appanah and Weinland 1993).

Research goals

Here we compare the seedling growth, development, and photosynthesis of these two closely related tropical Asian dipterocarps with contrasting ecologies under different light regimes. We employed an experimental approach combining variation in PPFD and R:FR in a factorial experimental design (Lee et al. 1996). We addressed the following questions. How do light intensity and spectral quality contribute to the shade responses of

these two species? Do they respond to shade conditions differently from each other? How do the seedling growth patterns of the two taxa correspond to their site preferences and natural distributions? We could thus evaluate the hypotheses of Bazzaz (1979), Pearcy (1987), Kitajima (1996), and Morgan and Smith (1979) in a model system where phylogenetic differences were minimized.

Materials and methods

Growth conditions

Culture methods followed the procedures described in detail by Lee et al. (1996). Seeds of *H. helferei* and *H. odorata* were obtained from tree populations established at the Forestry Research Institute of Malaysia (FRIM) Arboretum, collected earlier this century from sites in northern Malaya. Seeds were germinated in shallow trays in a shade enclosure, and then grown in polythene bags until 12–15 cm height, when they were introduced into shadehouses and transferred to 12-l pots. We used a fertile forest soil, supplemented with osmocote at the beginning of the trials. Pots were maintained near field capacity by regular hand watering.

Each shadehouse was 4×4 m with a roof line sloping from 2.5 to 2.0 m. External air was pulled through blind vents into the houses with an exhaust fan at the roof peak. We continually monitored PPFD and temperature in the open and in the center of the houses at 1 m height using Li-185s quantum sensors (LI-COR Inc., Lincoln, Neb., USA) and Campbell thermistor probes attached to Campbell CR-10 dataloggers (Campbell Scientific Inc., Logan, Utah, USA). The temperatures in the houses were similar, and within 3°C of ambient on the hottest afternoons. Light conditions in the shadehouses were determined by a combination of shade fabrics and energy films that reduced PPFD to an equivalent extent, but altered R:FR differently(3M Corp., St. Paul, Minn., USA). Metal sputter-coated films (REAL20) shaded approximately 85% of PPFD without changing R:FR, and dye-impregnated films (NEARL20) reduced R:FR to approximately 0.25 with a similar degree of shading. We measured spectral quality with a Li-1800 spectroradiometer (LI-COR Inc.) with R:FR defined as in Smith (1994), and spectral quality did not change during the experiments (Table 1). We constructed five shade treatments (Table 1): (1) 41% solar PPFD and 1.30 R:FR, HRR; (2) 12% PPFD and 1.30 R:FR, MRR; (3) 10% PPFD and 0.24 R:FR, MFR; (4) 3% PPFD and 1.31 R:FR, LRR; and (5) 3% PPFD and 0.23 R:FR, LFR. We also (6) grew seedlings in direct sunlight at an adjacent site (SRR). Measured PPFD values in the houses for different treatment durations were used to estimate the total amount of radiation available over the course of each of the treatments (Table 1). Replicates of the six light treatments were constructed on the roofs of two adjacent buildings to minimize shading from nearby tree crowns.

Before the beginning of the trials, five seedlings were harvested, dried, and weighed. Within each shadehouse ten seedlings were placed randomly on a 9×9 grid, 0.4 m apart, and their initial heights were measured. When the tallest treatment had reached approximately 1 m in height, we harvested all the seedlings. The trial duration for *H. helferei* was 744–807 days, and for *H. odorata* was 475–498 days.

Growth characteristics

For each seedling we measured (1) final height; (2) diameter at collar; (3) dry mass of leaf blades, petioles, stems, and roots; (4) leaf area; (5) internode distance; (6) petiole length; (7) number of internodes in branches and main axis; (8) and total stem length. These measurements allowed the calculation of growth as mass increase per day or per mole of photons received, as well as allocation to plant organs. We also calculated quantitative indicators of plant structure and architecture: (1) stem robustness as stem mass/length; (2) total leaf area/stem length; (3) specific leaf mass; and (4) mean leaf area. The degree of branching was measured differently in the two taxa. In *H. odorata* the number of internodes in all lateral branches was compared to those in the main axis. In *H. helferei* the number of internodes in all other branches was compared to that in the dominant first lateral branch. We analyzed a maximum of ten plants for each treatment; in some treatments the numbers were slightly reduced because of the occasional death of seedlings.

Leaf gas exchange

We measured light-saturated photosynthesis (A_{max}), dark respiration (R_{dark}), and stomatal conductance using a LI-6200 photosynthesis system (LI-COR Inc.) and a 0.25-l cuvette mounted on a tripod. We chose the youngest fully mature leaf of each seedling for these measurements. Plants were removed from the shadehouses at least one hour in advance of measurements and allowed to equilibrate under open sky or under shade fabric at light levels near saturation (400–600 μmol m^{-2} s^{-1} PPFD). We constructed preliminary light response curves to determine the levels at which the plants were saturated. We completed all measurements no later than 2 h after solar noon, at 400–1000 μmol m^{-2} s^{-1} PPFD. LFR- and LRR-treated seedlings were exposed to the lower range of PPFD and all other treatments to the higher PPFD. Care was taken to avoid exposure of low PPFD-grown plants to high PPFD to minimize any

Table 1 Treatment regimes for light intensity and spectral quality. Means±SDs of photosynthetic photon flux density (*PPFD*, 400–700 nm, μmol m^{-2} day^{-1}) for the trials of each species are listed. Treatments are also summarized as percentages of full sunlight and for red to far red ratio (*R:FR*)(species abbreviations: *HH Hopea helferei*, *HO H. odorata)*

Species	Treatments					
	Low PPFD enriched in:		Medium PPFD		High PPFD	
	far-red LFR	red LRR	far-red MFR	red MRR	red HRR	red SRR
Replication 1						
HH	0.89±0.29	0.89±0.30	3.07±0.88	3.52±1.28	11.57±2.96	28.80±7.12
HO	0.84±0.25	0.81±0.28	2.84±0.84	2.90±1.00	11.92±2.93	28.91±7.27
%Shade	3.0	2.9	10.2	11.1	40.1	
R:FR	0.25	1.28	0.25	1.29	1.27	1.27
Replication 2						
HH	0.74±0.23	0.81±1.00	3.23±0.81	5.02±1.51	13.92±3.30	33.91±8.45
HO	0.81±0.21	0.94±0.24	2.97±0.72	3.92±1.03	14.17±2.72	33.51±6.49
%Shade	2.3	2.6	9.7	13.2	41.7	
R:FR	0.21	1.31	0.23	1.33	1.33	1.33

photoinhibition effects. We regulated PPFD by adding layers of shade fabric. We measured photosynthesis with 10-s depletion times, three periods per measurement; measurements were repeated until steady values were obtained. We mixed treatments and times to minimize any effect of time of day on the measurements. We estimated leaf areas by tracing exposed parts of the leaves on tracing paper, weighing the tracings, and then converting to area.

We measured R_{dark} in a darkened room. Plants were equilibrated to the dark conditions for at least 20 min, and were in complete darkness at least 5 min prior to measurement. We measured the same leaves used for A_{max}. For respiration we used 30-s depletion times repeated three times.

Leaf characteristics

We analyzed areas midway between the blade margin and midrib, of the same leaves measured for gas exchange. We measured stomatal density at 400× magnification, three times per leaf, in samples cleared by extraction in n,n-dimethyl formamide (Moran 1982).

Data analysis

For statistical analysis, replicates of each treatment were compared by the Students *t*-test, found similar, and lumped for one-way ANOVA, using Tukey's honest significant difference (HSD) test for post hoc pairwise comparisons (Norusis 1991). We assessed the data for normality with the Shapiro-Wilks test, applying a log-normal transformation when necessary. 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 PPFD 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 and Rohlf 1981). A three-way ANOVA assessed differences between species. We also constructed a Pearson product correlation matrix for selected characters.

Results

The seedlings grew well in the shadehouses, exhibiting no pathology, signs of nutrient deficiency, loss of branches, or root binding. Both the degree of shading and R:FR significantly affected many seedling growth characteristics. The two taxa also differed in their light responses. In overall architecture, the seedlings conformed to the descriptions and model of Hallé (1979), and the degree of lateral and vertical expansion was affected by the light treatments.

Growth

Three measurements are frequently used for assessing growth in tree seedlings. Height is easy to measure, and assesses the ability of seedlings to take advantage of increases in light availability. Collar diameter is conveniently measured, and indirectly assesses stem volume and carbohydrate storage. Dry mass increment is the most direct assessment of growth. All of these characteristics responded to the light treatments (Table 2). Despite the shorter growth period, height growth was greatest in *H. odorata*, and the influence of R:FR was also greatest in this taxon. Collar diameter increased with PPFD in both taxa, and was little influenced by R:FR.

Dry mass increment was assessed on a per day and per mol of photon basis (Table 2). Differing growth periods between species and within treatments made such an assessment imperative. Furthermore, daily totals of photons varied seasonally in the shadehouses, varied slightly between matched treatments of the same PPFD (as MFR and MRR; Table 1), and changed over the duration of the trials. This meant that more detailed assessment of growth per the average daily totals of photons received (mol photons m^{-2} day^{-1}) was even more important. Both species (1) grew more at higher irradiances; (2) grew slightly less at low R:FR; and (3) grew less in full sunlight than in partial shade. *H. odorata* grew much more rapidly than *H. helferei*, except at the highest PPFD.

Allocation

Differences in allocation to leaves, stems and roots reflect strategies for energy capture, spatial exploration,

Table 2 Growth and gas exchange measurements for both species in the different light treatments (as described in Table 1). Treatments sharing *uppercase letters* are not significantly different from each other

Species treatment	Height (cm)	Collar diameter (mm)	Growth rate (mg/day)	Growth/photon (mg/mol)	Photosynthesis mol CO_2 m^{-2} s^{-1}	Respiration mol CO_2 m^{-2} s^{-1}
Hopea helferei						
LFR	19.7±1.9 A	3.8±0.2 A	6.2±0.6 A	7.7±0.8 A	2.90±0.14 A	–0.14±0.01 A
LRR	20.2±2.1 A	5.1±0.3 A	14.8±1.7 A	17.7±2.1 B	2.96±0.15 A	–0.14±0.01 A
MFR	42.6±5.4 B	7.1±0.7 B	35.2±6.3 AB	11.2±2.0 A	2.69±0.21 A	–0.22±0.03 AB
MRR	33.4±2.9 B	9.8±0.5 C	53.4±3.7 B	13.0±1.1 B	2.97±0.20 A	–0.23±0.02 AB
HRR	36.3±3.1 B	12.6±0.6 DE	78.0±10.2 C	6.6±1.0 A	3.44±0.32 A	–0.32±0.02 B
SRR	42.4±5.8 B	10.4±1.1 CE	58.2±15.3 BC	2.1±0.6 A	4.81±0.69 B	–0.54±0.07 C
Hopea odorata						
LFR	54.3±2.5 AC	5.3±0.2 A	18.8±1.5 A	22.8±1.8 A	4.90±0.18 BC	–0.23±0.03 A
LRR	39.4±3.2 A	5.4±0.2 A	23.1±3.4 A	25.8±3.4 A	4.54±0.19 B	–0.26±0.02 AB
MFR	95.8±5.7 D	9.0±0.3 BC	80.7±6.2 B	27.7±2.1 A	4.34±0.28 B	–0.39±0.05 B
MRR	62.7±3.6 C	10.1±0.3 BC	100.8±5.9 B	30.1±1.8 A	2.70±0.20 A	–0.26±0.02 AB
HRR	58.8±2.3 BC	10.1±0.3 C	97.7±8.8 B	7.6±0.7 B	4.83±0.25 BC	–0.70±0.05 C
SRR	42.8±2.3 AB	18.8±0.3 B	79.9±16.4 B	2.7±0.6 B	6.01±0.62 C	–0.72±0.05 C

Table 3 Morphology and allocation to organs of plants grown under the light treatments (as described in Table 1). Treatments sharing *uppercase letters* are not significantly different from each other

Species treatment	Branch/trunk internodes	Stem mass (mg)/ length (cm)	Leaf area (cm^2)/ stem length (cm)	% leaves	% stems	% roots
Hopea helferei						
LFR	2.02±0.33 A	23.63±1.51 A	5.85±0.34 A	45.9±0.9 A	30.1±0.7 A	19.9±0.7 A
LRR	2.78±0.40 A	33.48±3.10 AB	9.57±0.58 B	49.1±0.7 AB	29.2±0.8 A	19.0±0.9 A
MFR	3.28±0.51 AB	52.12±5.13 B	6.46±0.46 AC	31.4±2.0 A	37.2±1.9 B	29.9±1.1 BD
MRR	5.44±1.00 AB	78.55±5.11 C	7.70±0.41 AB	27.1±1.4 B	40.6±1.7 B	31.1±1.3 BD
HRR	5.97±1.00 B	133.77±7.39 D	8.26±0.50 BC	21.2±1.4 B	40.2±1.4 B	37.7±2.3 C
SRR	–	112.28±24.27 D	6.69±1.75 AB	20.9±1.5 AB	39.6±2.6 B	38.3±1.8 CD
Hopea odorata						
LFR	3.12±0.14 AB	14.34±0.60 A	5.21±0.11 AC	46.8±0.7 C	33.0±0.7 A	20.2±0.9 A
LRR	4.01±0.34 AB	13.76±0.67 A	6.46±0.19 BC	52.6±0.6 D	28.3±0.5 A	18.5±0.6 A
MFR	4.18±0.17 B	37.85±1.79 B	5.08±0.19 AD	30.4±1.1 B	40.3±1.1 B	29.3±1.5 B
MRR	6.35±0.39 C	35.56±2.46 B	6.21±0.29 BCD	30.1±1.2 B	32.1±1.4 A	37.8±1.8 C
HRR	4.18±0.36 B	49.63±2.29 C	4.17±0.34 A	18.6±1.1 A	32.6±1.5 A	48.8±1.5 D
SRR	2.88±0.42 A	28.46±6.32 B	4.28±0.97 A	17.8±2.4 A	28.3±2.4 A	53.9±4.0 D

Table 4 Leaf characters and internode distances of seedlings grown under the light treatments (as described in Table 1). Treatments sharing *uppercase letters* are not significantly different from each other

Species treatment	Internode length (mm)	Leaf area (cm^2)	Petiole (mm)	Specific leaf mass (mg/cm^2)	Stomatal density ($10^4/cm^2$)	Conductance ($mol\ m^{-2}\ s^{-1}$)
Hopea helferei						
LFR	13.4±0.9 A	13.8±1.0 A	3.8±0.1 A	5.32±0.07 A	1.39±0.05 A	0.041±0.003 A
LRR	13.3±1.1 A	21.4±1.6 AB	3.8±0.1 A	5.17±0.10 A	1.32±0.05 A	0.047±0.006 A
MFR	15.6±1.3 A	28.0±2.7 B	5.4±0.3 B	6.79±0.06 B	1.48±0.10 A	0.048±0.014 A
MRR	15.8±0.3 A	26.2±1.9 B	4.8±0.2 B	7.10±0.14 B	1.60±0.08 A	0.046±0.005 A
HRR	13.7±1.2 A	29.4±2.4 B	4.7±0.3 B	8.31±0.10 C	2.09±0.09 B	0.044±0.006 A
SRR	11.7±1.0 A	24.1±4.3 AB	5.1±0.7 B	8.72±0.29 C	2.40±0.08 B	0.050±0.009 A
Hopea odorata						
LFR	40.2±2.0 B	16.8±0.5 A	8.8±0.3 A	3.88±0.08 A	1.21±0.03 A	0.080±0.005 AC
LRR	28.0±1.8 A	17.6±1.0 A	8.1±0.2 A	3.91±0.11 A	1.16±0.03 A	0.066±0.007 A
MFR	64.8±3.0 C	22.4±0.7 B	10.8±0.3 B	5.64±0.09 B	1.73±0.06 B	0.068±0.008 A
MRR	46.6±2.7 B	20.3±0.6 AB	9.1±0.3 A	5.23±0.18 B	1.67±0.05 B	0.042±0.005 A
HRR	38.9±1.6 B	18.7±0.8 A	9.0±0.3 A	6.99±0.10 C	2.69±0.06 C	0.104±0.010 AC
SRR	22.2±2.0 A	14.2±1.1 A	8.4±0.5 A	7.96±0.32 D	2.49±0.13 C	0.135±0.018 C

and water and nutrient absorption (Grime 1979; Tilman 1988). The two species were similar in their responses to the light treatments (Table 3). Low R:FR reduced allocation to leaves only at the lowest PPFD treatment, and increased allocation to stems at medium intensities (MFR) only in seedlings of *H. odorata*. Allocation to roots was not influenced by R:FR and was increased at the highest PPFD treatments, particularly in *H. odorata*.

Architecture

The light treatments affected seedlings of both taxa, but in different ways. In *H. helferei* neither PPFD or R:FR influenced internode length, but both factors affected this character in *H. odorata* (Table 4). Full sunlight reduced internode elongation, especially in *H. odorata*. Low R:FR reduced branching in both taxa (Table 3). Since branching patterns in the two species were documented differently, the degree of branching could not be directly compared between the species. Stem mass/length documents the robustness of the stem, which was increased by higher PPFD in both species and was much greater in *H. helferei*. Stem robustness was reduced in full sunlight (Table 3).

Leaf area per unit stem length documents the functional consequences of plant architecture, since leaf area limits carbon assimilation and stem length spatially displays the leaves. This ratio was comparable between the two species, and was slightly reduced by low R:FR in both species.

Leaf characteristics

Mean leaf areas of both species were slightly influenced by light treatments, but the influence of R:FR depended on the light level (Table 4). Petiole lengths were greater in *H. odorata*, and were only promoted in that species by the lower R:FR and medium PPFD treatment (MFR).

Table 5 Pearson product correlation matrix of selected measurements of growth, architecture, leaf characters and physiology in seedlings of *H. helferei* and *H. odorata*. Values in *boldface* are significant at $P<0.05$. *Asterisks* indicate levels of significance: $*P<0.05$, $**P<0.005$, $***P<0.0005$

Hopea helferei Variable (symbol)	MDA	%LF	LSM	LAS	STO	CON	PHO	RES
Mass/day (MDA)	–	–0.717 ***	**0.792** ***	**0.395** ***	**0.483** ***	0.029 ns	0.116 ns	**0.419** ***
% Leaf (%LF)	**–0.674** ***	–	**–-0.871** ***	0.146 ns	**–0.636** ***	0.117 ns	–0.070 ns	**–0.509** ***
Leaf Specific mass (LSM)	**0.695** ***	**–0.854** ***	–	0.025 ns	**0.654** ***	–0.034 ns	**0.201** *	**0.608** ***
Leaf Area/Stem length (LAS)	–0.046 ns	**0.629** ***	**–0.561** ***	–	0.052 ns	0.110 ns	0.185 ns	–0.093 ns
Stomatal density (STO)	**0.630** ***	**0.841** ***	**0.868** ***	**0.509** ***	–	0.077 ns	**0.289** **	**0.450** ***
Stomatal conductamce (CON)	–0.070 ns	**0.220** *	**0.201** *	**–0.316** **	**0.265** ***		**–0.424** ***	0.177 ns
Photosynthesis (PHO)	**–0.340** ***	–0.044 ns	0.025 ns	–0.139 ns	0.074 ns	**0.423** ***	–	**0.450** ***
Respiration (RES)	**0.427** ***	**–0.593** ***	**0.674** ***	**–0.354** ***	**0.698** ***	**0.398** ***	**0.274** **	–

Hopea odorata

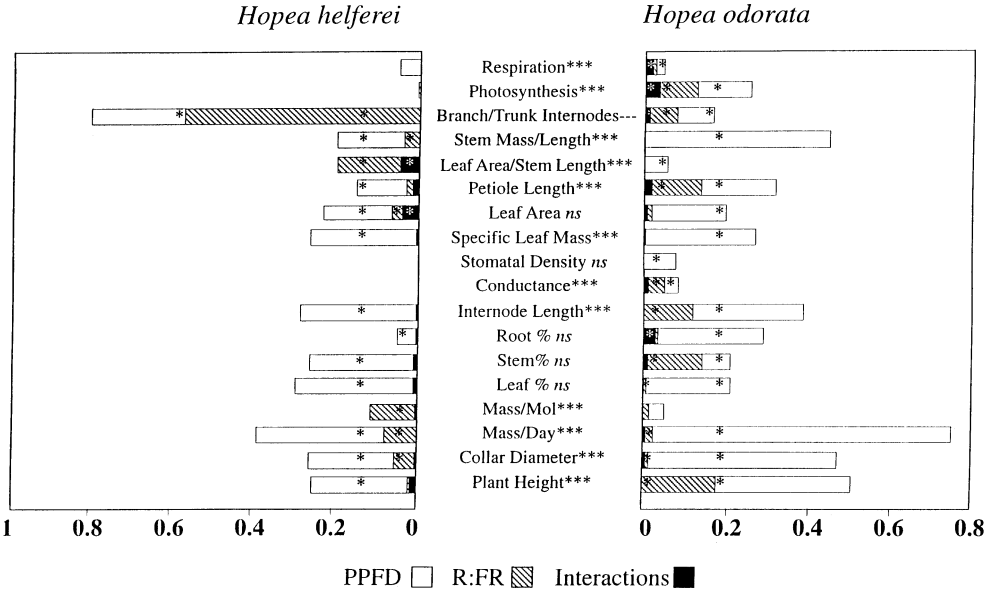

Fig. 1 Coefficients of determination of characters of growth, morphology and physiology, of *Hopea helferei* and *H. odorata* seedlings. Total plasticity is seen in the addition of effects of photosynthetic photon flux density (*PPFD*), red to far red ratio (*R:FR*) and interactions. *Asterisks* indicate the significance of treatment differences between the two species by three-way ANOVA, and for treatment effects by two-way ANOVA: $*P<0.05$, $**P<0.005$, $***P<0.0005$, *ns* not significant, – not comparable

Leaf specific mass was greater in *H. helferei*, probably partly because of the dense layer of scales on the abaxial surface. Spectral quality did not influence this character, which increased with exposure to higher PPFD. Stomatal density did not significantly vary among any light treatments in *H. helferei*, and did increase in the high light treatments for *H. odorata*. Stomatal densities were significantly higher for most treatments in the latter species (Fig. 1). Stomatal aperture lengths were also greater in *H. odorata* (15.5±0.5 μm, n=10) for all treatments, compared to *H. helferei* (12.4±0.4 μm).

Gas exchange

Maximum photosynthesis and dark respiration were little affected at the low and medium PPFD treatments, and generally increased in plants exposed to the higher levels (HRR and SRR; Table 5). However, photosynthesis and respiration were significantly reduced in *H. odorata* for the MFR treatment. Stomatal conductance did not differ significantly for any treatments in *H. helferei*, and only increased in the SRR treatments for *H. odorata*.

Discussion

The response of the *Hopea* seedlings to shade conditions is the sum of the effects of PPFD, spectral quality (R:FR), and their interactions, if any. The factorial design of the low and medium PPFD experiments made it possible to assess these effects by comparing their coefficients of determination, as well as to contrast the responses of the two species (Fig. 1).

Shade responses

The overall shade responses of the two species and the characters that determine them differed considerably (Fig. 1). *H. odorata* grew most rapidly in the shade and was also the most plastic in response to a range of shade conditions; the mean of all coefficients of determination was 0.295. *H. helferei* was less responsive, with a mean of all coefficients of determination of 0.226. In both species much variation was probably due to genetic differences among the seedlings, and the light conditions (LRR, LFR, MRR, MFR) represented only a portion of the range of responses. Both species were within the range of variation seen among six rain forest tree seedlings, using the same experimental design (Lee et al. 1996).

Some characters were much more responsive to different shade conditions than others: internode length, plant height, collar diameter, stem mass/length and specific leaf mass. Some characters were particularly responsive for one species, and not for the other (Fig. 1). For instance, internode length varied more in *H. odorata*.

Total growth rates were strongly influenced by shade conditions in both taxa (Fig. 1). Growth per day was primarily affected by PPFD, and much more responsive in *H. odorata*. Growth per day at the lowest PPFD was also 2–3 times greater in *H. odorata*, consistent with observations of its ability to grow under natural shade conditions. Although mean growth rates of *H. odorata* exceeded those of *H. helferei* in all treatments, the highest growth rates of *H. odorata* were attained at lower PPFD, possibly as a result of the large allocation to root biomass in the higher light treatments. Conversely, the highest growth rates in *H. helferei* were in the HRR treatment, indicating a preference for sites more open to sunlight. However, both taxa were less efficient in growth per mole of photons received in direct sunlight (Table 2). Seedlings of *H. helferei* grew the slowest, and seedlings of *H. odorata* grew at about the average rate of the six taxa reported by Lee et al. (1996).

Photosynthesis was also greater in *H. odorata* than in *H. helferei* in all treatments except MRR. Photosynthesis generally increased with treatments at higher PPFD, even in direct sunlight, although not in proportion to the actual increase in PPFD. Respiration increased in a similar pattern.

The total growth rate of seedlings of both taxa was strongly correlated with leaf specific mass and negatively correlated with percent allocation to leaf dry mass (Table 5). These two characters were strongly influenced by increasing PPFD (Tables 2 and 5). Growth of seedlings of *H. helferei* was also significantly correlated with the ratio of leaf area to stem length, but not so in *H. odorata* (Table 5). This character is more responsive to light treatments in the former species. Maximimum photosynthesis (A_{max}) was not correlated with growth rates in seedlings of *H. helferei*, and was negatively correlated in *H. odorata*. Maximum photosynthesis has not been found to be a good predictor of rainforest tree seedling growth in other studies (Turnbull 1991; Chazdon et al. 1996), except for differences between early successional and mature forest species. Dark respiration rates were correlated with growth rates in both species, most likely a consequence of the greater leaf specific mass (Table 5).

Spectral quality

Seedlings of both species were more affected by PPFD than R:FR. Only 16% of the coefficients in *H. helferei* and 17% in *H. odorata* were contributed by R:FR (Fig. 1). Contributions of R:FR to the growth and morphology of these two species were generally less than for the six species compared by Lee et al. (1996). Interactions between R:FR and PPFD were of little importance. Such interactions might be expected in high R:FR treatments where reflected light from adjacent plants might serve as a developmental signal (Ballare et al. 1993). Absence of interactions suggests that reflected light was not important for these plants, in these experiments.

However, R:FR contributed significantly to the control of certain characters. It was most important for leaf area/stem length in both species, most important for plant height and stem allocation in *H. odorata*, and most strongly associated with growth/mol photons in *H. helferei.*

Species differences and ecology

The responses of the seedlings to the differing light conditions are not entirely consistent with what can be inferred from their ecological distribution. Found in densely forested riverine habitats, *H. odorata* may grow in deeper shade than *H. helferei*. In these experiments it grew most rapidly and with highest A_{max} in the least light (LFR and LRR). However, it also responded the most in height and internode length when exposed to higher light conditions, similar to being released from extreme shade suppression in natural forest (Pearcy 1987). Its growing stems were less robust (smaller mass/length) and more erect in architecture than *H. helferei* in all treatments. Seedlings of *H. odorata* were more plastic in response to varying shade conditions (including R:FR), than those of *H. helferei*, and inconsistent with the hypothesis of Morgan and Smith (1979). For instance, seedlings allocated much higher percentages of root mass in high light conditions (HRR and SRR). Their growth was dramatically higher in moderate shade and the most suppressed by direct sunlight.

H. helferei typically establishes in open habitats of evergreen forest slopes, and was less responsive in growth and morphology to changing light conditions than *H. odorata*. Its stems were more robust and its architecture less erect in all conditions than *H. odorata*. Root allocation and seedling growth were also less affected by exposure to direct sunlight.

The basis for variation in growth rates among plants is a complex physiological and ecological problem

(Lambers and Poorter 1992). Faster-growing species tend to exhibit a greater degree of plasticity in growth, physiology and morphology to environmental factors, including R:FR, as was found for *H. odorata*. The differences in seedling growth between *H. helferei* and *H. odorata*, however, may be more a function of their drought tolerances and less a function of their shade responses. On upland slopes of evergreen forest habitats, *H. helferei* should experience more frequent soil water deficits. A rapid growth rate may not be advantageous under these conditions of water limitation (Chapin 1991). Instead, a slower growing, more drought-tolerant behavior (Spurr and Barnes 1980) may be advantageous in these sites. Leaves of *H. helferei* were (1) more robust; (2) had fewer stomata per unit area, of smaller size; and (3) produced a dense layer of scales on the abaxial surface. All of these characters help account for the reduced stomatal conductance in *H. helferei*. Given the gas exchange compromise between H_2O and CO_2 (Givnish 1988), reduced stomatal conductance should also limit the rate of CO_2 diffusion into the leaves. Intense sunlight, with an associated increase in water use, may also be a cue for the development of structures increasing drought tolerance. Thus, the expected plasticity of light responses of the more shade-intolerant species (*H. helferei*) may be reduced by its greater drought tolerance.

Conclusion

In seedlings of *H. helferei* and *H. odorata*, both light intensity and spectral quality influenced growth and architecture. Although PPFD was the most important factor, R:FR predominantly influenced the development of some characters, such as stem allocation in *H. odorata*. Seedlings of the two taxa responded to PPFD and R:FR differently from each other; *H. odorata* responded more to the both differences in shading and R:FR. Seedlings of *H. odorata* grew more rapidly at the medium PPFD, while those of *H. helferei* grew optimally at higher PPFD. Maximum photosynthesis, although lower in the slower-growing seedlings of *H. helferei*, was poorly correlated with growth rates in both species.

H. odorata, considered the more shade-tolerant of the two taxa, grew more rapidly in shade and was more plastic in response to varied light conditions. Such growth responses are most consistent with those predicted by Pearcy (1987), but we lack the rigorous data on seedling persistance used by Kitajima (1994, 1996) to distinguish between these taxa.

It is possible that the light responses of *H. helferei* may be modified by seedling tolerance of drought. Keys to understanding the interaction between drought and shade tolerance in the two species may be discovered from a more detailed analysis of leaf structure and its relation to function. Such research is now underway.

Acknowledgements We thank Dato Salleh Mohamed Noor, former Director-General of FRIM for encouragement and support. We received technical support from Siti Asha Abu Bakar, Zaiton Salleh, K. C. Ang, Zaini Bahari, Noraida Idaris, Hamsinah Hashim, Juntak So, Rosli Alias, and Akoh Jin. We benefited from advice by Peter Ashton, S. Appanah, Joel Trexler, Tom Turner, and an anomymous reviewer. The German GTZ mission at FRIM provided lodging for the U.S. authors. Research was supported by NSF grant DEB-9020137 and a donation of materials from the 3M Corporation.

References

Appanah S, Weinland G (1993) Planting quality timber trees in Peninsular Malaysia (Malaysian Forest Record 38). Forest Research Institute of Malaysia, Kuala Lumpur

Ashton PFS (1982) Dipterocarpaceae. In: Steenis CGGJ van (ed). Flora Malesiana series I, 9:237–582

Ashton PFS (1988) Dipterocarp biology as a window to the understanding of tropical forest structure. Annu Rev Ecol Syst 19:347–370

Ashton PMS (1995) Seedling growth of co-occurring *Shorea* species in the simulated light environments of a rain forest. For Ecol Manage 72:1–12

Ballare CL, Scopel AL, Sanchez RA, Radosevich SR (1993) Photomorphogenic processes in the agricultural environment. Photochem Photobiol 56:777–788

Bazzaz FA (1979) Physiological ecology of plant succession. Annu Rev Ecol Syst 10:351–371

Björkman O (1981) Responses to different quantum flux densities. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Encyclopedia of plant physiology, NS vol 12A. Springer, Berlin Heidelberg New York, pp 57–107

Brown ND, Whitmore TC (1992) Do dipterocarp seedlings really partition tropical rain forest gaps? Philos Trans Roy Soc B 335:369–78

Chapin FS III (1991) Integrated responses of plants to stress. BioScience 41:29–36

Chazdon RL, Pearcy RW, Lee DW, Fetcher N (1996) Photosynthetic responses to contrasting light environments. In: Mulkey S, Chazdon RL, Smith AP (eds) Tropical plant ecophysiology. Chapman and Hall, New York, pp 5–55

Fetcher N, Strain BR, Oberbauer SF (1983) Effects of light regime on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees. Oecologia 58:314–319

Givnish TJ (1988) Adaptation to sun and shade: a whole-plant perspective. Aust J Plant Physiol 15:63–92

Grime JP (1979) Plant strategies and vegetation processes. Wiley, New York

Hallé F (1979) Premieres données architecturales sur les Dipterocarpaceae. Mem Mus Ser B Bot 26:20–36

Hallé F, Oldeman RAA, Tomlinson PB (1979) Tropical trees and forests: an architectural analysis. Springer, Berlin Heidelberg New York

Kamaluddin M, Grace J (1992) Photoinhibition and light acclimation in seedlings of *Bischofia javanica*, a tropical forest tree from Asia. Ann Bot 69:47–52

Kitajima K (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. Oecologia 98:419–428

Kitajima K (1996) Ecophysiology of tropical tree seedlings In: Mulkey S, Chazdon RL, Smith AP (eds) Tropical plant ecophysiology. Chapman and Hall, New York, pp 559–596

Kwesiga FR, Grace J (1986) The role of the red/far-red ratio in the response of tropical tree seedlings to shade. Ann Bot 57: 283–90

Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Adv Ecol Res 23:187–261

Lee DW (1988) Simulating forest shade to study the developmental ecology of tropical plants: juvenile growth in three vines in India. J Trop Ecol 4:281–292

Lee DW, Krishnapilay B, Mansor M, Mohamad H, Yap SK (1996) Effects of light intensity and spectral quality on the growth

and development of seedlings of six Asian rainforest trees. Ecology 77:568–580
Liew TC, Wong FO (1973) Density, recruitment, mortality and growth of dipterocarp seedlings in virgin and logged-over forests in Sabah. Malay For 36:3–15
Moran G (1982) Formulae for determination of chlorophyllous pigments extracted with n,n-dimethyl formamide. Plant Physiol:1376–81
Morgan CCR, Smith H (1979) A systematic relationship between phytochrome-controlled development and species habitat, for plants grown in simulated natural radiation. Planta 145:255–258
Ng F (1991) Manual of forest fruits, seeds and seedlings, vol 1 (Malaysian Forest Record 34). Forest Research Institute of Malaysia, Kuala Lumpur
Norusis MJ (1990) SPSS base system user's guide. SPSS, Chicago
Oberbauer SF, Strain BR (1985) Effects of light regime on the growth and physiology of *Pentaclethra macroloba* (Mimosaceae) in Costa Rica. J Trop Ecol 1:303–320
Pearcy RW (1987) Photosynthetic gas exchange responses of Australian forest trees in canopy, gap and understory micro-environments. Funct Ecol 1:169–178
Popma J, Bongers F (1991) Acclimation of seedlings of three Mexican tropical rain forest tree species to a change in light availability. J Trop Ecol 7:85–97
Sasaki S, Mori T (1981) Growth responses of dipterocarp seedlings to light. Malay For 44:319–345
Schmitt J, Wulff RD (1993) Light spectral quality, phytochrome and plant competition. Trends Ecol Evol 8:47–51
Smith H (1994) Sensing the light environment: the functions of the phytochrome family. In: Kendrick RE, Kronenberg GHM (eds) Photomorphogenesis in plants, 2nd edn. Kluwer, Dordrecht, pp 377–416
Smitinand T, Santisuk T, Plengklai C (1980) The manual of the Dipterocarpaceae of mainland southeast Asia. Cabinet Printing Office, Bangkok, Thailand
Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. Freeman, New York
Spurr SH, Barnes BV (1980) Forest ecology. Wiley, New York
Strauss-Debenedetti S, Bazzaz FA (1996) Photosynthetic characteristics of tropical trees along successional gradients. In: Mulkey S, Chazdon RL, Smith AP (eds) Tropical plant ecophysiology. Chapman and Hall, New York, pp 162–186
Tilman D (1988) Dynamics and structure of plant communities. Princeton University Press, Princeton
Tinoco-Ojanguren C, Pearcy RW (1995) A comparison of light quality and quantity effects on the growth and steady-state and dynamic photosynthetic characteristics of three tropical tree species. Funct Ecol 9:222–230
Turnbull MH (1991) The effect of light quantity and quality during development on the photosynthetic characteristics of six Australian rainforest tree species. Oecologia 87:110–117
Turner IM, Raich JW, Gong WK, Ong JE, Whitmore TC (1992) The dynamics of Pantai Acheh Forest Reserve: a synthesis of recent research. Malay Nat J 45:166–174
Whitmore TC (1996) A review of some aspects of tropical rain forest seedling ecology with suggestions for further enquiry. In: Swaine MD, Alexander I (eds) Ecology of tropical tree seedlings. Man and Biosphere Series, UNESCO, Paris, pp 3–39