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IRRADIANCE AND SPECTRAL QUALITY AFFECT ASIAN TROPICAL RAIN FOREST TREE SEEDLING DEVELOPMENT[1]

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Abstract. Plant developmental responses to shade are the combination of reductions in photosynthetic photon flux density (PPFD) and changes in spectral quality (reductions in the quantum ratio of red to far-red band widths, R:FR). We studied the seedling development of six Asian tropical rain forest trees, *Dryobalanops aromatica, Endospermum malaccense, Hopea wightiana, Parkia javanica, Shorea singkawang,* and *Sindora echinocalyx* under varying PPFD and R:FR. Seedlings were grown in replicated shadehouse treatments: (1) 40% solar PPFD and 1.25 R:FR; (2) 11% PPFD and 1.25 R:FR; (3) 11% PPFD and 0.24 R:FR; (4) 3% PPFD and 1.25 R:FR; and (5) 3% PPFD and 0.23 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) percent 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. The characters in most taxa were primarily influenced by light intensity, but spectral quality also influenced characters in many cases. The taxa that responded most strongly to the light treatments were the most shade-intolerant: *E. malaccense* and *P. javanica*; the former species responded strongly to R:FR, particularly in stem mass allocation and leaf area/stem length. The four taxa with moderate-to-extreme shade tolerance varied considerably in responses of individual characters to R:FR and PPFD. The patterns of morphological responses to reduced PPFD and R:FR help explain how the shade tolerances of the seedlings of rain forest trees vary in a continuous manner. Recommendations concerning seedling shade tolerance for sylviculture or nursery practice may need revision if they were based on shade trials using spectrally neutral shade fabrics or slat houses. 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.

Key words: Asia; development; red : far-red ratio; shade tolerance; spectral quality; tree seedling; tropical rain forest.

INTRODUCTION

Light is the most important physical factor controlling the development of tree seedlings in tropical rain forests. Light environments in these forests are extremely heterogenous, and species are generally adapted to respond optimally to different light environments within forests (Whitmore 1995, Chazdon et al. 1996). The biological significance of seedling light responses is now being explored under the rubric of "gap phase dynamics" (Augspurger 1984, Brokaw 1985, Platt and Strong 1989), a concept originally developed to help explain the high tree species diversity of tropical forests.

Tree seedling shade responses have long been the subject of intensive research, the goal being to predict the light responses of plants under natural regeneration or in sylvicultural treatments. Tropical foresters have qualitatively assessed shade tolerances of seedlings to develop management systems (Whitmore 1984). Attempts to classify forest tree species into guilds, based on successional status and shade tolerance (cf. Whitmore 1989) have generated considerable discussion, with a growing consensus that there may be a continuum of shade responses among seedlings of different trees. Furthermore, some species may not partition light gaps (Welden et al. 1991).

Research on light responses in Asian tropical rain forest trees is largely limited to germination (Raich and Gong 1990) and seedling demography in natural or disturbed forest (Liew and Wong 1973, Brown and Whitmore 1992, Turner et al. 1992). Nicholson (1960) compared light requirements of five dipterocarp seedlings under partial shade, but light levels were too high to be of ecological significance. Sasaki and Mori (1981)

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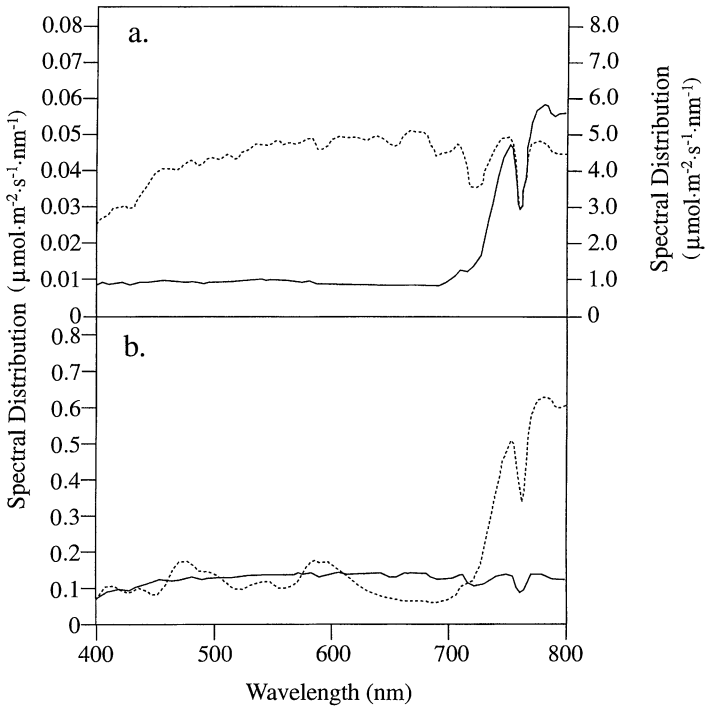

FIG. 1. Spectral distributions of natural and treatment radiation environments. (a) Full sunlight (----) in a clearing on a hazy but sunny day, PPFD = 1528 μmol·m^{-2}·s^{-1} and R:FR = 1.34 (right scale); and understory shade (———) in nearby secondary forest, 0.9% of sunlight, PPFD = 13 μmol·m^{-2}·s^{-1} and R:FR = 0.20 (left scale). (b) LFR treatment (----) of 2.4% sunlight, PPFD = 36 μmol·m^{-2}·s^{-1}, and R:FR = 0.22; LRR treatment (———) of 2.2% sunlight, PPFD = 33 μmol·m^{-2}·s^{-1}, and R:FR = 1.25.

employed a combination of field observations and experiments to assess the shade tolerances of *Shorea talura, S. ovalis, Hopea helferei,* and *Vatica odorata.* Seedling growth in all taxa was partially inhibited by light levels higher than 50% shade. Ashton and De Zoysa (1990) also documented the partial suppression of seedling growth under full sunlight in *Shorea trapezifolia* from Sri Lanka, and Ashton (1995) and Ashton and Berlyn (1992) demonstrated shading effects on seedling growth, leaf anatomy, and gas exchange characteristics in five Sri Lankan *Shorea* species with varying shade tolerances. On the other hand, seedlings of *Intsia palembanica* grew most rapidly in direct sunlight (Sasaki and Ng 1981). In general, little research has been published on seedling shade tolerances of Asian tropical rain forest trees, none on the taxa selected for this study (Whitmore 1995).

Natural light climates.—Light environments under vegetation canopies vary in quantity and quality. The intensity of radiation is altered by passage through foliage, surface reflectance, and penumbral effects due to small holes in the canopy. In tropical rain forests the mean intensity of radiation on the forest floor ranges from 5 to 25 μmol·m^{-2}·s^{-1} of photons 400–700 nm (photosynthetic photon flux density, PPFD), or 1–3% of sunlight above the canopy (Chazdon et al. 1996). Median values are much lower, since 10–85% of the photons are supplied during brief flecks of sunlight, above 50 μmol·m^{-2}·s^{-1}. Thus, daily totals of PPFD in forest understory are 0.3–1.0 mol·m^{-2}·d^{-1} (Chazdon 1986, Oberbauer et al. 1988, Raich 1989, Ashton 1992), compared to values above the canopy of ≈30 mol·m^{-2}·d^{-1}. Openings, or gaps, in the canopy allow more sunlight to penetrate, the total depending upon the size of the gap and the structure of the surrounding canopy. For instance, Raich (1989) measured PPFD of 2.6 mol·m^{-2}·d^{-1} in a small gap in a Malaysian dipterocarp forest.

Passage of sunlight through the canopy also alters its quality, or spectral distribution. Leaves absorb 80–90% of the visible quanta, but few of the quanta above 700 nm (Gates et al. 1965, Lee and Graham 1986). Foliage thus functions as a selective filter, particularly altering the ratio of red to far-red wavelengths. Quantum ratios of these wavelengths determine phytochrome equilibria in tissues, and may profoundly influence plant development. Smith (1982, 1994) and colleagues have pioneered research on the ecological importance of foliage shade to plant development, defining the significant band widths as a ratio of quanta centering on 660 nm to that at 730 nm (with a half peak band width of 10 nm), or R:FR. R:FR is dramatically reduced under canopy shade, from a high of 1.05–1.35 in direct sunlight (Lee and Downum 1991) to 0.20 in dense shade (Stoutjestijk 1972, Tasker and Smith 1976, Lee 1987, Turnbull and Yates 1992; Fig. 1).

Seedling shade responses.—Shading affects plant development and functional ecology. Acclimation to shade occurs at all levels of organization, from general architecture to biochemistry (Grime 1979, Bjorkman 1981, Givnish 1988, Woodward 1990, Turnbull 1991, Chazdon et al. 1996). Shading alters: (1) internode distance, branch length and plant height; (2) axillary bud initiation and branching; (3) photosynthate allocation

to stems, leaves, and roots; (4) leaf area, specific mass and anatomy; (5) photosynthesis and transpiration; (6) chloroplast ultrastructure; and (7) the stoichiometry of components of both the light and dark reactions of photosynthesis. Ultimately, shade tolerance means the seedling's capability of growth and/or survival in these low light conditions.

The majority of research on shade effects has examined the effects of reduced light intensity without a corresponding reduction in R:FR. Such studies have documented developmental effects at different levels of plant organization, but the light conditions (as Chabot and Chabot 1977, Lichtenthaler et al. 1981, Jurik et al. 1982, Kappel and Flore 1983, Fetcher et al. 1983, Oberbauer and Strain 1985, Strauss-Debenedetti and Bazzaz 1991) have provided plants with mixed signals—the reduced intensity of shade and the spectral quality of sunlight. Such studies almost certainly underestimated the extent of developmental responses to canopy shading (Schmitt and Wulff 1993). Some research has also employed natural foliage or other experimental conditions that reduce R:FR along with intensity, not permitting the determination of the relative contributions of these two potential signals (Popma and Bongers 1988, Ashton and Berlyn 1992, Chazdon and Kaufmann 1993, Ashton 1995).

Significant contributions of reduced R:FR to development at different levels of structural complexity have been demonstrated for a small sample of crop plants, aquatic plants, trees, and European forest herbs (Morgan and Smith 1979, Corre 1983, Richards and Lee 1986, Taylor and Davies 1988, Ballare et al. 1993, Buisson and Lee 1993, Kasperbauer 1993, Smith 1994). In their studies on growth responses of dipterocarp seedlings Sasaki and Mori (1981) demonstrated increased internode length in seedlings of *Shorea ovalis* in reduced R:FR. However, the significance of these results was compromised by the method of light measurement and the durability of the shade film. Morgan and Smith (1979) showed a systematic relationship between shade tolerance and internode elongation in a small sample of European forest herbs. The stems of the shade-intolerant taxa elongated most rapidly in reduced R:FR, consistent with a search strategy for these plants (Grime 1979, Tilman 1988). Kwesiga and Grace (1986) studied the seedling growth and development of two light-demanding tropical African trees, *Khaya senegalensis* and *Terminalia ivorensis*. Both species increased internode length and shoot/root dry mass ratios under low R:FR, and *T. ivorensis* increased the leaf area and reduced the specific leaf mass, resulting in a greater relative growth rate under shade.

The most extensive research on the influence of R:FR and PPFD on tropical rain forest plant function has examined photosynthetic characteristics (Ramos and Grace 1990, Riddoch et al. 1991*a, b,* Turnbull 1991, Kamaluddin and Grace 1992). However, differences in photosynthetic characteristics do not seem to explain the overall growth responses of seedlings in the understory (Chazdon et al. 1996).

In general, the least shade-tolerant taxa should respond most strongly to reduced R:FR. The limited data suggest that shade-tolerant seedlings of canopy trees, capable of continuous growth in the understory, should respond less strongly to reduced R:FR than seedlings of pioneers. However, previous studies have provided limited morphological and anatomical detail of the developmental responses. Even among taxa that respond strongly to low R:FR, the patterns of effects, such as reduction in branching along with changes in leaf anatomy, have not been compared. In an analysis of development of three fairly shade-tolerant tropical vines, all taxa responded to reduced R:FR in addition to reduced PPFD, but the developmental pattern of response varied among them (Lee 1988).

The purpose of this investigation was to study the effects of reduced PPFD and reduced R:FR on the seedling developmental ecology of six tree species native to Asian tropical rain forests. We developed a system of shadehouses for this research that employs commercial energy films to vary PPFD independently of R:FR. We predicted that reduced R:FR would add to the effects of reduced intensity, influencing developmental patterns of the seedlings. Sensitivity to reduced R:FR should also vary among the tree seedlings of rain forest plants, even among those that appear to be shade-tolerant.

Materials and Methods

We conducted this research on the campus of the Forest Research Institute of Malaysia (FRIM), near Kuala Lumpur. Seeds of the selected species were collected from individual trees at FRIM or from other trees regularly observed for phenology (Table 1). Since these trees were open pollinated, considerable genetic variation should be expected among the seedlings. Seeds were germinated in shallow trays in a 90% shade enclosure, and seedlings were grown in poly bags. Forest soil, red-yellow ultisol of the Rengam series (a friable sandy-clay loam of good fertility) was employed in seedling establishment and all shade trials. Seedlings 10–15 cm high, uniform and healthy in appearance, were selected for the trials and grown in plastic pots with 8.3 L of soil volume. Pots were fertilized with 3 g Osmocote 9:14:19 and 0.2 g MgO at the beginning of the trials. Plants were watered daily during the trials, maintaining the soil continually moist.

Shadehouses 4 × 4 m with a roof line sloping from 2.5 to 2 m were constructed for the experiments. They were cooled with blind vents at ground level and exhaust fans beneath the roof peak. Light conditions in the shadehouses were controlled by a combination of shade fabrics and energy films. Energy films reducing PPFD to an equivalent extent, but altering R:FR differently, were supplied by the 3M Corporation, St. Paul, Minnesota 55144. Metal sputter-coated films

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

Species	Family	Ecology*	Origin†	Treatment period (d)	Abbreviation
Endospermum malaccense M.A.	Euphorbiaceae	A	Beleyer F.R.	286–316	*Da*
Parkia javanica (Lamk.) Merr.	Fabaceae	B	Ulu Gombak F.R.	161–179	*Pj*
Hopea wightiana Wall.	Dipterocarpaceae	CE	FRIM (India)	491–503	*Hw*
Sindora echinocalyx (Benth.) Prain	Fabaceae	C	FRIM	437–440	*Se*
Dryobalanops aromatica Gaertn. f.	Dipterocarpaceae	C	Royal Selangor Golf Club, K.L.	326–343	*Em*
Shorea singkawang (Miq.) Burch	Dipterocarpaceae	D	Pasoh F.R.	270–276	*Ss*

* Symbols: A = pioneer; B = secondary forest margins; C = mature forest, relatively shade-tolerant; D = mature forest, very shade-tolerant; E = drought tolerant.
† FRIM = Forest Research Institute of Malaysia; K.L. = Kuala Lumpur; F.R. = Forest Reserve.

(REAL20) shaded ≈85% of PPFD without changing R:FR, and dye-impregnated films (NEARL20) reduced the R:FR to ≈0.25 with a similar degree of shading. We constructed five shade treatments: (1) 40% solar PPFD and 1.25 R:FR, HRR; (2) 11% PPFD and 1.25 R:FR, MRR; (3) 11% PPFD and 0.24 R:FR, MFR; (4) 3% PPFD and 1.25 R:FR, LRR; and (5) 3% PPFD and 0.23 R:FR, LFR (Table 2). Replications of the five light treatments were constructed on the roofs of two buildings, reducing interference from tree crowns. PPFD was monitored in the shadehouses by continuous measurements with LI-COR 185s quantum sensors (LI-COR Instruments, Lincoln, Nebraska 68504) connected to Campbell Cr-10 dataloggers (Campbell Scientific Instruments, Logan, Utah 84321). Temperature was monitored continuously with Campbell thermister probes connected to the dataloggers. PPFD and temperature sensors were also placed outside the houses at each site. Sensors were located in the center of each shadehouse 1 m above ground, and the dataloggers were programmed to sample data every 2 min and to store the daily average, maximum, and minimum values. We were thus able to determine the daily totals of photosynthetically active quanta for each treatment for the duration of the growth trials. The quantum sensors were calibrated at the factory prior to the growth trials, and were compared to a freshly calibrated sensor at the end of the trials. Temperature sensors documented the closeness of the treatments for mean and maximum values. Treatments were generally within 2°C of each other, and within 3°C of ambient air temperature; mean temperatures were within 1°C. On certain days maximum air temperatures may have depressed photosynthetic rates for 1–2 h in early afternoon, but should not have affected the treatments differently (Mori et al. 1992).

Spectral quality of the radiation in the shadehouses was measured with a LI-COR 1800 spectroradiometer,

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

	Treatments									
	Low PPFD				Medium PPFD				High PPFD	
	LFR (enriched in far-red)		LRR (enriched in red)		MFR (enriched in far-red)		MRR (enriched in red)		HRR (enriched in red)	
Species	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Replication 1										
Da	0.98	0.29	1.07	0.28	3.28	0.84	3.59	0.82	13.96	3.15
Em	0.87	0.20	1.03	0.22	2.98	0.71	3.74	0.78	14.72	2.50
Hw	0.87	0.23	1.00	0.26	3.07	0.75	3.81	0.78	14.89	3.15
Pj	0.83	0.20	0.90	0.22	2.71	0.67	3.53	0.76	13.76	2.60
Se	0.83	0.21	0.97	0.25	2.97	0.71	3.78	0.78	14.38	2.54
Ss	0.98	0.29	1.07	0.28	3.28	0.84	3.59	0.82	13.96	3.15
% shade	3.0	0.2	3.4	0.2	10.2	0.7	12.3	0.1	47.7	0.4
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
Em	0.91	0.29	0.96	0.30	2.89	0.89	2.95	0.96	13.50	2.73
Hw	0.97	0.31	0.95	0.43	3.12	0.92	3.16	1.02	14.89	3.14
Pj	0.81	0.28	0.74	0.28	2.66	0.88	2.76	1.07	11.14	2.48
Se	0.88	0.26	0.83	0.39	2.86	0.81	2.86	0.87	13.56	2.57
Ss	1.15	0.31	1.13	0.31	3.50	0.88	3.72	0.95	11.52	2.71
% shade	3.3	0.5	3.2	0.5	10.5	1.2	10.8	1.5	42.8	2.8
R:FR	0.21		1.31		0.23		1.33		1.33	

TABLE 3. Effects of light treatments on measurements (±1 SE) of plant growth. Treatments not sharing letters are significantly different (<0.05) from each other. For treatment abbreviations see *Materials and methods.*

	Height (cm)		Collar diameter (mm)		Growth/day (mg)		Growth/mol photons (mg)	
Treatment	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
Endospermum malaccense								
LFR	41.5AC	1.7	6.4A	0.2	19.8A	1.6	22.4AB	1.9
LRR	32.8A	2.8	6.7A	0.4	29.6A	4.9	30.0B	5.0
MFR	103.9B	8.3	10.9B	0.5	100.3B	9.6	34.3B	3.2
MRR	50.7C	2.4	11.5B	0.5	108.6B	9.4	34.0B	3.4
HRR	55.3C	3.0	12.3B	0.3	140.2C	6.0	9.8A	0.4
Parkia javanica								
LFR	52.4A	2.0	4.7A	0.1	26.9A	1.6	32.7A	1.9
LRR	51.7A	2.1	5.1A	0.6	34.1A	1.5	42.1A	2.1
MFR	108.0B	5.7	7.3B	0.3	100.3B	8.8	37.4A	3.3
MRR	108.3B	5.7	9.2C	0.6	179.1C	9.8	58.6B	4.6
HRR	50.2A	2.1	15.0D	0.5	378.3D	28.2	31.6A	2.7
Hopea wightiana								
LFR	34.9AB	1.8	4.2A	0.2	9.8A	0.9	10.6AC	1.0
LRR	32.9A	2.2	4.7A	0.2	13.2A	1.6	13.7BC	1.7
MFR	33.6A	3.0	6.3B	0.4	36.0B	5.2	11.6AB	1.7
MRR	45.0B	2.6	7.9C	0.3	58.7C	6.1	17.4B	2.1
HRR	44.1B	2.8	9.9D	0.4	106.7D	5.5	7.2A	0.5
Sindora echinocalyx								
LFR	31.2A	2.5	4.5A	0.1	9.8A	1.2	11.5A	1.4
LRR	30.4A	3.3	4.7A	0.2	11.5A	1.6	12.7A	1.6
MFR	59.7B	8.9	6.2B	0.4	32.2AB	6.0	11.0A	2.0
MRR	59.5B	8.3	6.4B	2.6	47.1B	7.8	13.3A	2.0
HRR	56.8B	6.5	8.2C	0.4	64.7B	9.0	4.6B	0.6
Dryobalanops aromatica								
LFR	66.0A	4.5	5.1A	0.3	18.4A	1.2	17.4A	1.2
LRR	51.4A	2.5	5.0A	0.1	22.3A	1.8	20.3A	1.6
MFR	124.8B	7.8	6.2B	0.3	58.9B	5.5	17.4A	1.6
MRR	93.4C	3.1	7.0B	0.2	80.4C	4.6	22.0A	1.3
HRR	103.4C	7.3	8.4C	0.3	100.7D	5.5	7.9B	0.4
Shorea singkawang								
LFR	34.2A	2.8	7.0A	1.1	27.0A	2.9	25.4A	3.0
LRR	26.3A	1.6	6.3A	0.4	28.9A	2.8	26.2A	2.6
MFR	85.9C	6.4	8.3AB	0.5	81.1B	7.5	24.0A	2.3
MRR	64.2B	4.1	10.3B	0.4	120.5C	10.2	33.0A	2.8
HRR	70.4BC	2.6	13.2C	0.4	180.0D	13.0	13.9B	0.9

where R:FR was defined as the quantum ratio of the band widths 658–662/728–732, ≈10 nm band widths centering on 660 and 730 nm given the 6 nm band width of the instrument (Fig. 1). Shadehouses did not differ in R:FR at the beginning and the end of the growth trials.

Potted seedlings were placed randomly on a 9 × 9 grid within the shadehouses, 0.4 m apart, and their initial height measured; five seedlings were dried and weighed. Most seedlings grew for at least 7 mo, or to a maximum height of 1.5 m for one of the treatments, before destructive measurements were completed (Table 1).

At the end of each growth trial we measured: (1) plant height; (2) length of three internodes beneath the most recent fully expanded leaf; (3) area, fresh mass, dry mass, and petiole length of three top-most fully expanded leaves; (4) total number of leaves; (5) total number of internodes; (6) number, internode number, mass, and length of branches; (7) total leaf area and dry mass; (8) petiole dry mass and length; and (9) root dry mass. We then calculated the (1) relative dry mass allocation to leaves, roots and stems; (2) degree of branching as number of internodes in branches compared to internodes on the main axis; (3) stem robustness as total mass/length; (4) leaf area/stem length; and (5) specific leaf mass as dry leaf mass/area. Tissue midway between the midrib and margin of a recently developed leaf was fixed in FAA (formalin, acetic acid, ethanol, 10:10:80) for microscopic measurements of leaf thickness and stomatal density, three measurements per leaf.

After checking for normality, replications were compared by t test. Finding no significant differences, the replications (n = 7–10) were lumped and ratios and percentages were again tested for normality (Shapiro–Wilks test), and transformed log normally if necessary. The five light treatments were compared by one-way

ANOVA. Posthoc comparisons were performed from ANOVA using Tukey's Honest Difference test, and a significance level of 0.05. Contributions of R:FR and PAR to treatment differences were estimated by two-way ANOVA of the low and medium irradiance treatments (LRR, LFR, MRR, and MFR). The relative influences of PPFD and R:FR on the development of selected traits were estimated by calculating their coefficients of determination (Sokal and Rohlf 1981), dividing the sums of squares from two-way ANOVA, using the simultaneous processing of variables, by the total sums of squares from the one-way ANOVA. Statistical analysis was performed with SPSS-PC (Norusis 1990).

Results

Plants grew well in the shadehouses, with little insect or fungal damage. Some taxa grew much more rapidly than others, indicated by the durations of growth trials (Table 1). Growth rates varied more than morphological characters within treatments, possibly influenced by genetic differences among the seedlings.

Growth of forest seedlings is normally assessed in three ways. Seedling height is an indication of an individual's competitiveness when light becomes available (King 1994). Collar diameter is correlated with stem volume and carbohydrate storage capacity for future growth, and dry mass increments are directly correlated with carbon fixation.

Taxa differed in the response of these growth parameters in the shade treatments. Plant height was strongly influenced by PPFD and R:FR (Table 3), with the influence of R:FR most pronounced at the medium (11%) levels. Collar diameter was primarily influenced by PPFD among all taxa. Although the spectrally neutral high irradiance treatment (43% full sunlight, or HRR, Table 2) increased dry mass the most among all taxa, plants frequently appeared unhealthy, with chlorotic leaves. Dry mass increments varied among species because of different lengths of the growth trials and small changes in shade conditions. Therefore, mean daily growth rates and growth per mole of photons were calculated (Table 3) using summaries for daily photons received (Table 2). Species differed in rates of growth; *Parkia javanica* grew most rapidly in all treatments, and *S. echinocalyx* and *Hopea wightiana* grew most slowly.

Species also varied in the influence of light on allocation to plant organs (Table 4). HRR treatments substantially increased allocation to roots in all taxa. Low R:FR conditions generally reduced allocation to leaves, but this effect varied among species (Table 4, Fig. 2). Varying PPFD generally affected allocations more than R:FR.

Morphological characters differed among the treatments, and the character patterns varied among the taxa (Tables 5 and 6). The HRR treatment strongly affected most characters and taxa. This treatment increased stem mass/length, branch/trunk internodes, allocation to root mass, leaf specific mass and thickness, and stomatal density. Treatments at lower intensities, both for low and high R:FR, also influenced plant morphology. Low R:FR reduced leaf area/stem length in all taxa, and reduced R:FR was most effective at medium intensity (MFR).

TABLE 4. Effects of light treatments on photosynthate allocation to leaves, roots, and stems. Abbreviations as in Table 3.

Treatment	Percent to leaves		Percent to roots		Percent to stems	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
Endospermum malaccense						
LFR	40.1A	0.8	25.0A	0.9	35.0A	0.9
LRR	41.5A	1.2	31.2BC	1.4	27.3B	0.8
MFR	22.8B	1.6	34.4C	1.4	43.3C	1.5
MRR	29.2C	1.1	42.2D	1.4	28.6B	0.9
HRR	19.8B	0.8	52.3E	1.2	27.2B	1.5
Parkia javanica						
LFR	39.7A	2.4	24.7AB	2.8	33.0A	1.3
LRR	45.3B	0.8	20.9A	0.7	33.8A	0.7
MFR	31.9C	0.6	23.4AB	1.0	44.7B	1.0
MRR	32.4C	1.0	27.2B	0.8	40.4B	1.0
HRR	10.6D	0.6	58.7C	1.4	30.7A	1.3
Hopea wightiana						
LFR	46.7A	0.8	26.5A	0.8	26.8AB	0.6
LRR	49.3A	0.9	25.8A	1.0	24.9A	0.5
MFR	30.6B	0.8	39.7B	1.3	29.7B	1.1
MRR	30.8B	1.4	41.0B	1.6	28.2AB	1.0
HRR	23.4C	0.9	49.0C	1.2	27.6AB	1.2
Sindora echinocalyx						
LFR	43.0AB	2.0	31.2A	2.2	25.9AB	1.3
LRR	46.0B	2.0	31.5A	1.9	22.5A	0.6
MFR	34.5A	2.0	36.3A	2.8	29.2B	1.7
MRR	41.0AB	2.8	31.2A	2.6	27.8AB	1.6
HRR	35.9A	1.9	36.5A	1.7	27.6AB	1.9
Dryobalanops aromatica						
LFR	51.5AB	0.8	14.7AB	0.6	33.8AB	0.7
LRR	59.2A	2.4	11.9A	0.9	28.8A	1.7
MFR	37.8C	1.8	18.0B	1.1	43.8C	1.7
MRR	50.7B	1.0	13.4A	0.7	35.8B	0.6
HRR	36.8C	1.6	18.4B	1.1	44.7C	1.6
Shorea singkawang						
LFR	54.8A	1.0	20.5A	0.8	24.6A	1.0
LRR	56.3A	1.7	20.8A	1.2	22.8A	1.0
MFR	46.6B	1.4	20.3A	0.7	33.1BC	1.6
MRR	47.6B	1.5	22.7A	0.8	29.7B	1.8
HRR	29.6C	0.8	32.0B	1.2	38.4C	1.2

Discussion

All species in this investigation are large (≈30 m) trees growing in primary forest. *Endospermum malaccense* is frequently encountered as seedlings in large gaps, and *Parkia javanica* is also considered to be a light-demanding species because of its frequent occurrence at forest margins. The other four taxa are somewhat shade-tolerant, with *Shorea singkawang* and *Dryobalanops aromatica* known to be very tolerant of understory shade (Appanah and Weinland 1993). Thus,

TABLE 5. Effects of light treatments on measurements of plant architecture. Abbreviations as in Table 3.

Treatment	Internode length (cm)		Branch/trunk internodes		Stem mass/length (mg/cm)		(Leaf area)/(stem length) (cm^2/cm)	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
Endospermum malaccense								
LFR	2.5A	0.2	0.00A		1.46A	0.06	0.76A	0.03
LRR	1.6A	0.7	0.00A		1.66A	0.12	1.04B	0.06
MFR	4.3B	1.9	0.00A		4.81BC	0.31	0.67A	0.05
MRR	2.4A	0.3	0.00A		4.83C	0.30	1.18B	0.06
HRR	2.2A	0.2	0.00A		9.14D	0.61	1.01B	0.04
Parkia javanica								
LFR	4.8A	0.5	0.00A		2.42A	0.54	0.87A	0.05
LRR	4.8A	0.3	0.00A		2.27A	0.12	1.09BA	0.05
MFR	12.2B	0.6	0.00A		3.34A	0.22	0.91AB	0.05
MRR	11.2B	0.8	0.00A		6.94A	0.46	1.49C	0.08
HRR	7.1C	0.5	0.00A		69.78B	5.91	1.66C	0.08
Hopea wightiana								
LFR	1.2A	0.1	0.87A	0.12	14.74A	1.51	4.54A	0.48
LRR	1.2A	0.0	1.14A	0.11	17.50A	1.06	6.51B	0.27
MFR	1.3A	0.1	2.35B	0.33	30.24B	2.80	4.99AC	0.32
MRR	1.2A	0.0	2.87B	0.35	37.95B	2.56	5.94BC	0.18
HRR	1.1A	0.1	2.86B	0.32	60.95C	5.15	6.19BC	0.40
Sindora echinocalyx								
LFR	3.4ABC	0.2	0.00A		15.11A	1.18	7.05A	0.53
LRR	3.4AB	0.1	0.00A		15.21A	0.87	8.78AB	0.93
MFR	4.1AC	0.2	0.00A		29.74B	2.03	8.35AB	0.51
MRR	3.7ABC	0.2	0.00A		34.27B	2.57	9.99BC	0.56
HRR	3.4ABC	0.1	0.00A		54.94C	7.20	11.57C	0.44
Dryobalanops aromatica								
LFR	5.1AC	0.8	3.74AC	0.29	1.27A	0.10	3.38A	0.22
LRR	2.2B	0.2	4.51C	0.22	1.14A	0.06	3.61A	0.15
MFR	6.9C	0.4	3.61A	0.25	2.82BC	0.42	2.97A	0.19
MRR	5.6AC	0.3	6.14B	0.34	2.08B	0.12	3.98A	0.17
HRR	5.0A	0.5	7.24B	0.50	3.47C	0.21	3.12A	0.26
Shorea singkawang								
LFR	2.2A	0.3	0.00A	0.00	5.13A	0.44	1.68AB	0.14
LRR	1.0A	0.1	0.02A	0.01	5.95A	0.41	2.11B	0.18
MFR	7.6AC	0.6	0.13AB	0.04	7.52A	0.56	1.29A	0.06
MRR	5.7BD	0.6	0.23B	0.07	11.54B	1.21	2.28B	0.16
HRR	7.0CD	0.4	0.49C	0.07	19.05C	1.84	1.75A	0.12

considerable variation in growth responses to the shade treatments was expected.

Within the treatments, the factorial design of low and medium intensities and low and high R:FR permitted calculations of coefficients of determination to ascertain the relative contributions of light quality and intensity to the overall variation observed in each of the characters (Table 7). For this analysis 13 characters were selected that quantified different aspects of plant organization. For instance, specific leaf mass was used instead of leaf thickness, and internode distance rather than plant height. There were significant differences among the characters and between the taxa.

Growth responses.—No evidence of extreme shade acclimation (or greater growth rates at the lowest irradiances) was seen in any of the taxa. The two light-demanding taxa also grew most rapidly at the lowest flux (Table 3). The other taxa were generally less plastic in growth responses, *S. echinocalyx* and *H. wightiana* growing the most slowly. R:FR strongly influenced height growth in most taxa, along with PPFD. However, the seedling heights of the pioneer species responded to light in dramatically different ways. *Parkia javanica* was exclusively affected by PPFD, and *E. malaccense* primarily influenced by R:FR (Table 7). Collar diameter was primarily influenced by R:FR in all species. Dry mass increment was influenced moderately by the range of treatments of 3–11% of full sunlight, and low R:FR generally decreased growth. This reduction was due to less leaf allocation (Table 4) and smaller leaf area per stem length (Table 5). There was no strong correlation between the growth rates and the putative shade tolerances of the taxa, except for the strong plasticity in the two more light-demanding taxa. Even lower irradiances (10–15 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD, or <1% of direct sunlight), more typical of understory shade minus light flecks, may be more useful for assessing the success of seedlings than those produced in the LFR and LRR treatments (Table 2).

Comparisons among characters.—Few of the mor-

TABLE 6. Effects of light treatments on leaf development. Abbreviations as in Table 3.

Treatment	Area (cm^2) $\bar{X}$	SE	Specific mass (mg/cm^2) $\bar{X}$	SE	Petiole length (mm) $\bar{X}$	SE	Thickness (μm) $\bar{X}$	SE	10^4 stomata/cm^2 $\bar{X}$	SE
Endospermum malaccense										
LFR	10.4AB	0.5	2.14A	0.04	13.2A	0.7	121A	3	1.59A	0.05
LRR	10.6AB	0.7	2.29A	0.06	13.5A	1.0	139A	6	1.81AB	0.07
MFR	12.8A	0.7	3.86B	0.20	20.9B	0.7	129A	6	1.93BC	0.10
MRR	12.6A	0.8	4.07B	0.19	17.3C	0.9	165B	4	2.17C	0.07
HRR	9.0B	0.3	6.39C	0.21	10.6A	0.6	201C	4	2.67D	0.11
Parkia javanica										
LFR	58.6A	3.5	2.93A	0.13	27.4A	0.8	78A	2	1.16A	0.05
LRR	80.9AB	4.7	2.87AB	0.15	30.2A	0.7	87AB	4	1.12A	0.04
MFR	109.3B	5.8	3.47B	0.07	41.4BC	1.0	94B	2	2.36B	0.10
MRR	175.8C	8.0	4.12C	0.09	40.8B	0.9	94B	3	2.34B	0.10
HRR	237.6D	16.9	4.88D	0.24	46.1C	2.3	123C	2	1.12A	0.04
Hopea wightiana										
LFR	9.4A	0.5	5.27A	0.11	4.3A	0.2	121A	1	2.92AB	0.11
LRR	11.1A	0.4	5.24A	0.08	4.8A	0.1	122A	2	2.91A	0.09
MFR	14.9B	0.9	6.20B	0.11	6.4B	0.4	133B	2	3.06AB	0.15
MRR	14.8B	0.6	6.80C	0.20	6.2B	0.2	138B	2	3.35B	0.09
HRR	17.5B	1.0	8.34D	0.11	7.1B	0.3	155C	2	3.35B	0.09
Sindora echinocalyx										
LFR	67.9A	8.0	4.13A	0.10	53.8A	4.8	94A	2	2.15A	0.09
LRR	78.1AB	8.0	4.21A	0.12	57.8A	4.4	96A	2	2.26A	0.08
MFR	122.2BC	16.5	4.87AC	0.14	84.4B	8.3	105B	1	2.48AB	0.12
MRR	124.4BC	14.9	5.75BC	0.38	76.2A	8.0	103B	1	2.47AB	0.07
HRR	143.3C	12.6	6.67B	0.16	86.0B	4.9	126C	2	2.73B	0.09
Dryobalanops aromatica										
LFR	13.8A	0.4	5.69A	0.07	27.4A	0.8	154A	4	1.67A	0.07
LRR	14.3AB	0.8	6.45AB	0.58	30.2A	0.7	168B	3	1.80AB	0.09
MFR	12.6A	0.5	7.34B	0.15	41.4B	1.0	180BC	2	2.22B	0.06
MRR	15.3B	0.6	7.67B	0.30	40.8B	0.9	187C	2	2.04B	0.04
HRR	11.5A	11.5	9.4C	0.55	46.1B	2.3	214D	3	3.16C	0.11
Shorea singkawang										
LFR	57.8AB	6.1	6.95A	0.16	2.11A	0.19	122A	4	1.65A	0.09
LRR	56.0B	5.5	7.00A	0.14	1.93A	0.11	140AB	3	1.78A	0.09
MFR	79.2A	4.3	8.04B	0.15	2.00A	0.16	146B	2	1.92A	0.08
MRR	102.7C	6.0	8.09B	0.15	1.71AB	0.18	163C	4	1.78A	0.08
HRR	80.3A	5.7	10.51C	0.27	1.21B	0.14	190D	7	2.56B	0.15

phological characters were solely influenced by PPFD or R:FR (Tables 7 and 8, Fig. 2). Nearly all the characters in most taxa were primarily influenced by light intensity, but spectral quality also influenced characters in many cases. For instance, intensity affected 80% of the changes in internode length, with considerable variation among taxa. Percent allocation to stem mass was strongly influenced by both R:FR and PPFD, with 58% of the treatment effect due to intensity. Again, there was considerable variation among taxa in this effect, with influence of R:FR particularly strong in *E. malaccense* (Fig. 3). The variable most strongly influenced by spectral quality was the ratio of leaf area to stem length, a combination of factors controlling leaf and stem development, with a mean of 0.82 of all coefficients of determination (Table 8). Reduced PPFD, along with Low R:FR, generally suppressed branching (Tables 5 and 8) and increased internode length and total height (Tables 3, 5, and 8) in the seedlings of all taxa. Both signals promoted the development of a "searching" morphology modelled for tropical rain forest trees by Kohyama (1991).

We observed little interaction between spectral quality and intensity in controlling seedling morphology. Even effects that were statistically significant (0.05 in ANOVA) were probably not biologically important, although the strongest evidence for interactions occurred in treatments of *P. javanica*—accounting for 10% of the variation. Some interactions might be expected because reflections from neighboring plants could slightly alter spectral quality in all of the treatments. Ballare et al. (1993) and Kasperbauer (1993) have demonstrated the potential influence of light reflected by neighboring plants in promoting internode elongation. Thus, even in the high LRR and MRR treatments reduced R:FR reflected from neighboring plants could influence development. However, small interactions, even for internode length, indicate that neighborhood effects were not important in this study.

Light treatments affected characters differently. In-

TABLE 7. Coefficients of determination for effects of spectral quality (R:FR) and quantum flux (PPFD) on seedling growth and morphology.

Character	R:FR	PPFD	Interactions	Character	R:FR	PPFD	Interactions
Endospermum malaccense				*Sindora echinocalyx*			
Plant height	0.361*	0.214*	0.179*	Plant height	0.000	0.212*	0.000
Collar diameter	0.005	0.500*	0.000	Collar diameter	0.006	0.186*	0.001
Mass/day	0.006	0.436*	0.000	Mass/day	0.011	0.151*	0.007
Mass/mole	0.010	0.050*	0.012	Mass/mole	0.010	0.000	0.001
% leaf	0.029*	0.439*	0.012*	% leaf	0.041	0.109*	0.007
% stem	0.458*	0.086*	0.045*	% stem	0.032	0.096*	0.008
% root	0.109*	0.231*	0.001	% root	0.014	0.012	0.020
Internode length	0.188*	0.167*	0.025	Internode length	0.015	0.103*	0.010
Specific leaf mass	0.002	0.231*	0.000	Specific leaf mass	0.023*	0.131*	0.016
Leaf area/stem length	0.408*	0.000	0.031*	Leaf area/stem length	0.076*	0.061*	0.000
Stem mass/length	0.000	0.166*	0.000	Stem mass/length	0.001	0.270*	0.004
Branch/trunk internodes	...	...	...	Branch/trunk internodes	...	...	...
Stomatal density	0.043*	0.100*	0.000	Stomatal density	0.003	0.092*	0.004
Parkia javanica				*Dryobalanops aromatica*			
Plant height	0.000	0.590*	0.000	Plant height	0.095*	0.456*	0.013
Collar diameter	0.011*	0.127*	0.010*	Collar diameter	0.010	0.190*	0.019*
Mass/day	0.019*	0.122*	0.013*	Mass/day	0.026*	0.397*	0.013*
Mass/mole	0.165*	0.080*	0.030	Mass/mole	0.058*	0.003	0.003
% leaf	0.004	0.149*	0.002	% leaf	0.192*	0.224*	0.033
% stem	0.005	0.300*	0.025	% stem	0.0141*	0.247*	0.008
% root	0.001	0.020*	0.023*	% root	0.165*	0.069*	0.001
Internode length	0.003	0.627*	0.003	Internode length	0.094*	0.355*	0.001
Specific leaf mass	0.018*	0.165*	0.026*	Specific leaf mass	0.016	0.114*	0.003
Leaf area/stem length	0.188*	0.054*	0.039*	Leaf area/stem length	0.022	0.015	0.002
Stem mass/length	0.069*	0.180*	0.081*	Stem mass/length	0.015	0.332*	0.003
Branch/trunk internodes	...	...	...	Branch/trunk internodes	0.225*	0.020	0.031*
Stomatal density	0.001	0.659*	0.000	Stomatal density	0.000	0.092*	0.014*
Hopea wightiana				*Shorea singkawang*			
Plant height	0.214*	0.361*	0.111*	Plant height	0.053*	0.491	0.012
Collar diameter	0.040*	0.186*	0.014*	Collar diameter	0.008	0.127*	0.033*
Mass/day	0.024*	0.127*	0.015*	Mass/day	0.019	0.237*	0.016
Mass/mole	0.017*	0.095*	0.019	Mass/mole	0.149*	0.046	0.027
% leaf	0.004	0.467*	0.003	% leaf	0.003	0.118*	0.000
% stem	0.034*	0.107*	0.001	% stem	0.017	0.191*	0.001
% root	0.000	0.357*	0.002	% root	0.012	0.004	0.008
Internode length	0.032	0.008	0.005	Internode length	0.045*	0.463*	0.002
Specific leaf mass	0.010*	0.189*	0.012*	Specific leaf mass	0.000	0.110*	0.000
Leaf area/stem length	0.163*	0.000	0.020	Leaf area/stem length	0.241*	0.008	0.030
Stem mass/length	0.012*	0.142*	0.003	Stem mass/length	0.050*	0.156*	0.010
Branch/trunk internodes	0.021	0.310*	0.000	Branch/trunk internodes	0.010	0.083*	0.006
Stomatal density	0.021	0.088*	0.021	Stomatal density	0.001	0.022*	0.008

* Denotes contributions are significantly different (<0.05) from two-way ANOVA.

ternode length was most strongly affected by light, and stem mass/length was least affected (Fig. 2). This variation was influenced by at least two factors. First, the range of light conditions, 3–11% of full sunlight, was only a portion of the range of tolerance of these species. Secondly, although healthy seedlings were selected for uniform height at the beginning of the trials, they probably differed genetically. Such variation would be present along with the treatment effects.

Comparisons among taxa.—The taxa in this study span a spectrum of shade tolerances to rain forest environments, from a putative shade-intolerant pioneer (*E. malaccense*) to extremely shade-tolerant climax species (*S. singkawang* and *D. aromatica,* Table 1). The taxa that responded most strongly in growth and morphology to the light treatments were supposedly the most shade-intolerant: *E. malaccense* and *P. javanica.* Only the former species responded strongly to R:FR, particularly in stem mass allocation and leaf area/stem length. *Parkia javanica* only responded strongly to R:FR in leaf area/stem length, and was influenced in internode length—and final height—only by PPFD (Table 4). The other taxa responded less to the light treatments, and differently from each other (Figs. 2 and 3). The smallest light responses were for *S. echinocalyx,* a canopy tree whose shade tolerance is not well known, and *Hopea wightiana,* a moderately shade-tolerant dipterocarp from evergreen forests in South India, the most drought tolerant of the species studied. *Shorea singkawang,* probably the most shade-tolerant taxon, responded moderately to the light treatments and primarily to changes in intensity. Thus, the four taxa that

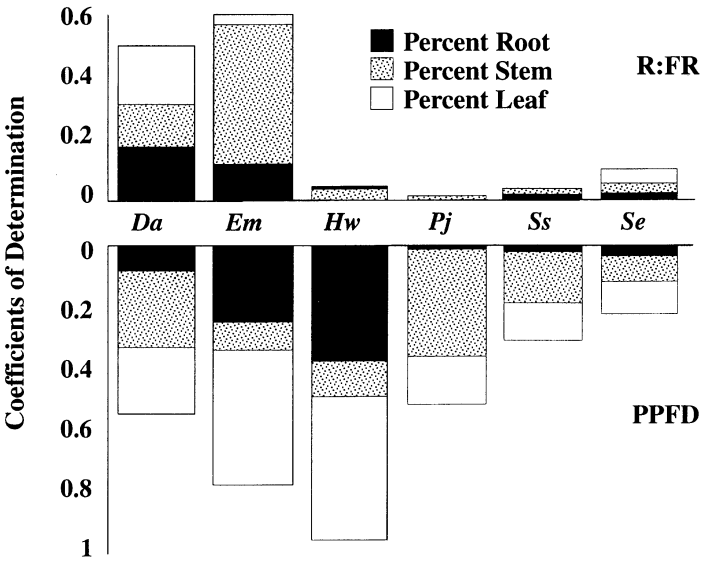

FIG. 2. Relative influence of R:FR (top graph) and PPFD (bottom graph) on photosynthate allocation to seedlings of the six species analyzed, shown by adding coefficients of determination for each. Species abbreviations are provided in Table 1.

establish in understory conditions varied considerably in responses of individual characters to R:FR and PPFD.

Significance of the light environments.—The five treatments included natural and artificial light conditions (Table 2). Two shadehouses combined signals of shade and full sun. The LRR treatment combined the PPFD of forest shade with the R:FR of full sunlight. Conversely, the MFR treatment combined moderate light, similar to a sun fleck, but with R:FR of forest shade. The more natural treatments included LFR, i.e., PPFD and R:FR of full shade, and MRR and HRR, i.e., PPFD and R:FR of a sun fleck or a gap. In the LFR treatment, the median PPFD was higher than typical rain forest understory, since there were no light flecks contributing to the total daily flux. Plants should grow more rapidly than the daily photon totals would suggest for a natural environment. Although actual values of 3% sunlight would produce a higher R:FR (Lee 1987), the daily average in an understory environment would have similar PPFD and R:FR.

Poor growth of the mature forest species in the HRR treatment indicates they would not grow well in highly exposed sites, but the two pioneer species *P. javanica* and *E. malaccense* were not adversely affected by the 40% full sunlight conditions. *S. echinocalyx* grew the least of all taxa at the lowest light levels, and therefore may be the least shade-tolerant of the mature forest species.

All of the taxa in this study grew in shade conditions

TABLE 8. Summary of comparisons of coefficients of determination for the six species and seven characters in Table 7.

Species or character	R:FR		PPFD		Interactions		Total	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
Species								
Endospermum malaccense	0.158	0.075	0.114	0.029	0.016	0.007	0.289	0.070
Parkia javanica	0.069	0.034	0.294	0.095	0.028	0.010	0.391	0.068
Hopea wightiana	0.041	0.021	0.090	0.026	0.012	0.003	0.143	0.020
Sindora echinocalyx	0.023	0.010	0.108	0.031	0.006	0.002	0.137	0.030
Dryobalanops aromatica	0.049	0.019	0.165	0.055	0.005	0.002	0.220	0.065
Shorea singkawang	0.072	0.034	0.142	0.054	0.011	0.005	0.225	0.057
Mean ± 1 SE	0.069	0.019	0.152	0.030	0.013	0.003	0.234	0.039
Characters								
Mass/mole	0.068	0.029	0.046	0.016	0.015	0.005	0.129	0.041
Internode length	0.063	0.028	0.287	0.096	0.008	0.004	0.358	0.093
% stem allocation	0.114	0.071	0.171	0.036	0.015	0.007	0.299	0.072
Specific leaf mass	0.013	0.005	0.157	0.019	0.010	0.004	0.178	0.020
Leaf area/stem length	0.189	0.056	0.034	0.012	0.018	0.006	0.229	0.057
Stem mass/length	0.024	0.012	0.208	0.031	0.017	0.013	0.249	0.034
Branch/trunk internodes ($N = 3$)	0.085	0.070	0.138	0.088	0.012	0.009	0.235	0.070
Stomatal density	0.012	0.007	0.176	0.097	0.008	0.003	0.195	0.094
Mean ± 1 SE	0.071	0.021	0.152	0.029	0.013	0.001	0.234	0.025

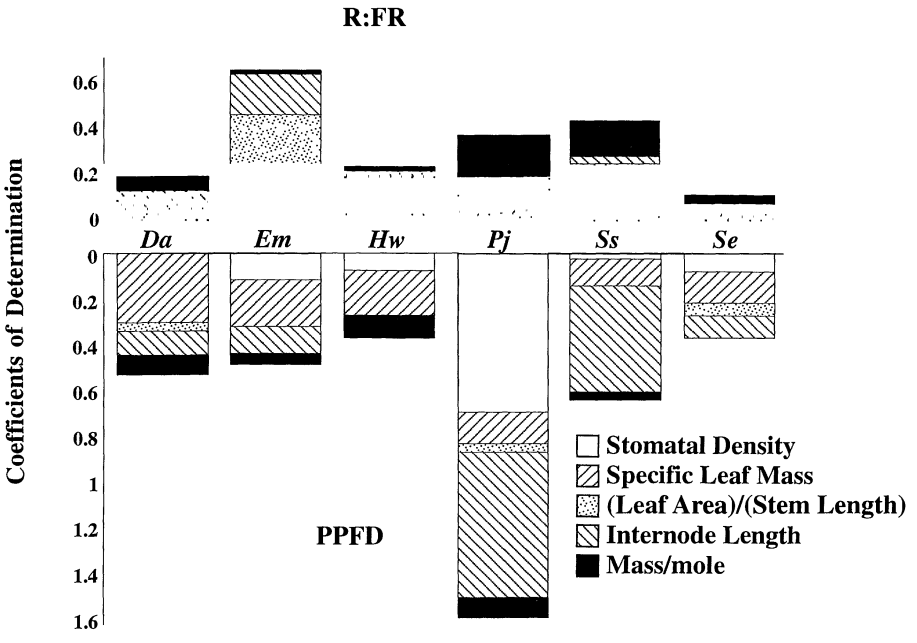

FIG. 3. Relative influence of R:FR (top graph) and PPFD (bottom graph) on seedling characters of the six species analyzed, shown by adding coefficients of determination for each. Species abbreviations are provided in Table 1.

approaching those of a rain forest understory. Our results suggest that studies using neutral shading materials to duplicate different percentages of sunlight will almost certainly underestimate the ability of a species to acclimate to shade conditions.

These shade treatments tested variables of light quantity and quality under uniform conditions, but actual light environments in the forest understory are extremely heterogenous. Thus, we did not assess the effects of rapid shifts in PPFD and R:FR on plant development. Phytochrome equilibria respond rapidly to spectral shifts, but the long-term developmental responses, as those documented in this study, are more likely to be affected by the median values of R:FR (Smith 1994). Wayne and Bazzaz (1993) documented the developmental consequences of brief exposures to direct sunlight. Ashton (1995) interspersed light flecks in a uniform environment of spectrally altered shade. Simple modifications to the shadehouses developed for research reported here would allow the testing of sunfleck effects in both spectrally neutral and altered shade light.

CONCLUSIONS

Although we are largely ignorant of the effects of reduced R:FR and PPFD on plant development in natural ecosystems, limited experimental results from a small sample of plants has led to the tentative conclusion that shade-intolerant taxa should respond most strongly to reduced R:FR (Morgan and Smith 1979). Our research demonstrates the developmental responses of rain forest taxa with a range of tolerances to shade, under similar experimental conditions. Although the least shade-tolerant species (*E. malaccense*) did respond most strongly to reduced R:FR, all species in the study responded to R:FR for some characters, in addition to reduced PPFD. The specific pattern of response varied among the taxa.

Such interspecific differences may be explained in at least three ways. Differences in these developmental patterns may be understood from more careful examination of the functional ecology of each taxon. Ecological differences, even among closely related taxa, suggest that the light-activated genes controlling development may be relatively variable and, under selection, may influence character development differently in different taxa (Thompson and White 1991, Quail 1994). Secondly, the markedly different light responses among these taxa may be partly tied to their evolutionary histories. Comparative analysis of development, considering phylogenetic history (Felsenstein 1985, Miles and Dunham 1993), would benefit from a larger sample than the present study. However, additional research, now in progress, may permit such an analysis in the near future.

Thirdly, these results clearly show the complexity of shade responses by rain forest seedlings (Fig. 2). Whitmore (1995) described shade tolerance as (1) seedling survival; (2) the duration of time for survival; and (3) the amount of light necessary for seedling release. The responses of these six species reveal differing plasticity of separate characters (as percent leaf allotment vs. branching) that could contribute to fitness in different ways. Some of these separate developmental responses

could, in effect, cancel each other, actually reducing different species' total responses to shadelight. Welden et al. (1991) showed that most taxa in the 50-ha plot at Barro Colorado Island were generalists, performing equally well in a variety of conditions. Gap specialists may occur more frequently among uncommon species. The complexity of developmental patterns reported here adds to our appreciation of the subtlety of shade responses by seedlings of rain forest trees.

The most significant result of this study is the unambiguous demonstration of the influence of spectral quality on tree seedlings in natural shade environments. These patterns of morphological responses in reduced PPFD 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 plant development and ecology must consider the potential influence of changes in spectral quality under canopy shade.

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