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EFFECTS OF IRRADIANCE AND SPECTRAL QUALITY ON THE SEEDLING DEVELOPMENT OF JELUTONG (*DYERA COSTULATA*)

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LEE, D. W., OBERBAUER, S. F., KRISHNAPILLAY, B., HARIS, M., MARZALINA, M. & YAP, S. K. 1999. Effects of irradiance and spectral quality on the seedling development of jelutong (*Dyera costulata*). Jelutong [*Dyera costulata* (Miq.) Hook. *f.*, Apocynaceae] is a long-lived pioneer tree that eventually becomes a giant emergent in the rain forests of Peninsular Malaysia and Sumatra. We conducted trials to determine responses of growth, morphology, leaf anatomy, architecture and physiology of jelutong seedlings to different irradiances (photon flux density, 400-700 nm, PFD) and spectral qualities (red/far-red quanta, or R:FR). Seedlings were grown in six replicated treatments: (1) direct sunlight and 1.25 R:FR; (2) 40 % solar PFD and 1.25 R:FR; (3) 13 % PFD and 1.25 R:FR; (4) 10 % PFD and 0.25 R:FR; (5) 3 % PFD and 1.25 R:FR; and (6) 3 % PFD and 0.25 R:FR. Based on dry mass increments, final height, collar diameter, architecture, and maximum photosynthesis, seedlings grew most rapidly in the 40 % sunlight treatment, and varied little in response to low- and medium-PFD environments. Spectral quality did not influence growth and development very much, but low R:FR reduced leaf allocation and area, and reduced growth as mass/day. Leaf anatomy and physiology were influenced exclusively by PFD. These results are consistent with observations of jelutong seedlings being shade-tolerant, slow growing, stunted in direct sunlight, and dramatically different to their behaviour in later developmental stages and that of short-lived pioneers.

Key words: Seedlings - photosynthesis - development - pioneer - rain forest - red/far-red ratio - allocation - shade - Malaysia

LEE, D. W., OVERBAUER, S. F., KRISHNAPILLAY, B., HARIS, M., MARZALINA, M. & YAP, S. K. 1999. Kesan sinaran dan kualiti spektrum terhadap perkembangan anak benih jelutung (*Dyera costulata*). Jelutung [*Dyera costulata* (Miq.) Hook. *f.*, Apocynaceae] adalah pokok perintis yang panjang hayatnya dan akan menjadi pokok gergasi di hutan hujan di Semenanjung Malaysia dan Sumatra. Kami membuat ujian untuk menentukan tindak balas pertumbuhan, morfologi, anatomi daun, binaan dan fisiologi anak benih jelutung terhadap sinaran yang berbeza (keamatan fluks-foton, 400-700 nm, PFD) dan kualiti spektrum (kuantum "red/far-red," atau R:FR). Anak benih ditanam di enam rawatan yang diulang: (1) cahaya matahari secara terus dan

1.25 R : FR; (2) 40% PFD cahaya dan 1.25 R:FR; (3) 13% PFD dan 1.25 R:FR; (4) 10% PFD dan 0.25 R:FR; (5) 3% PFD dan 1.25 R:FR; dan (6) 3% PFD dan 0.25 R:FR. Berdasarkan pertambahan biojisim kering, ketinggian akhir, garis pusat kolar, binaan, dan fotosintesis maksimum, anak benih didapati tumbuh paling cepat dalam 40 % rawatan cahaya matahari, dan sedikit berubah-ubah tindak balasnya terhadap persekitaran yang mendapat PFD rendah dan PFD pertengahan. Kualiti spektrum tidak begitu mempengaruhi pertumbuhan dan perkembangan pokok, tetapi R:FR rendah akan mengurangkan pengagihan daun dan luas daun, serta mengurangkan pertumbuhan sebagai jisim sehari. Anatomi dan fisiologi daun dipengaruhi oleh PFD. Keputusan ini adalah tetap dengan cerapan terhadap anak benih jelutong yang toleran-teduhan, lambat tumbuh, terbantut dalam cahaya matahari terus, dan tabiatnya berbeza secara mendadak pada peringkat perkembangan seterusnya dan juga dalam spesies perintis yang mempunyai hayat yang pendek.

Introduction

In tropical forest succession the first trees to establish after disturbance are pioneers. Such trees typically occur in large gaps, are light-demanding, are plastic in response to light conditions, photosynthesise rapidly, and are relatively short-lived (Bazzaz & Pickett 1979). Their growth and physiology have been contrasted with those of more shade-tolerant mature phase trees (Bazzaz & Pickett 1979, Fetcher *et al.* 1983, Turner *et al.* 1992, Whitmore 1996).

However, in tropical rain forests some pioneers are not short-lived trees, but are long-lived and eventually attain the canopy in mature forest (Whitmore 1984). Jelutong [*Dyera costulata* (Miq.) Hk. f.] is such a tree, occuring in tropical rain forests of Peninsular Malaysia and Sumatra. Jelutong grows to heights of 60 m and is among the more common non-dipterocarp emergents (Corner 1988). Its previous value as a latex tree and present exploitation as a non-durable but attractive timber has led to careful observation of its silvicultural characteristics (Watson 1934, Burkill 1966) and to growth trials for plantation forestry (Appanah & Weinland 1993).

These observations suggest a growth pattern quite different to that of typical early successional trees. Although jelutong grows rapidly as a sapling and tree (Appanah & Weinland 1993), it appears to grow slowly at the seedling stage, tolerant of shade. It is capable of persistence in a stunted condition and recovery from damage by falling branches (Aminuddin 1982). Yet, seedlings are present in the earliest stages of succession. Whitmore (1973) observed a deficiency in size classes between seedlings and adults in natural populations. Aminuddin (1982) grew seedlings in artificial shadehouses at 21, 33, 55, 88, and 100% of full sunlight. He observed maximum height and collar diameter in seedlings grown at 33% of sunlight. However, these shading trials only spanned the upper end of the range of conditions experienced by seedlings in a natural forest environment (Chazdon *et al.* 1996). Aminuddin concluded that jelutong is a relatively light-demanding species that grows best under partial shade.

Although soil nutrition and water relations may be important in determining the relative success of tree seedlings, light is the dominant ecological factor in the rain forest environment (Whitmore 1996). Seedlings growing in the gradient of shade microclimates within the forest experience dramatic changes in irradiance (normally defined as photosynthetic photon flux density, 400-700 nm, or PFD), as well as spectral quality [best described as the ratio of red to far-red quanta, or R:FR (Smith 1994)]. Foliage density and canopy gaps alter PFD and R:FR in a parallel manner (Lee 1987, Chazdon *et al.* 1996). Reduced R:FR influences phytochrome equilibria in plant tissues, and induces a variety of developmental responses (Smith 1994). Until recently virtually all research on plant shade responses has manipulated PFD without altering R:FR, thus exposing seedlings to the very low PFD of rain forest shade and the spectral quality of sunlight. Such research underestimates shade responses in the natural environment (Schmitt & Wulff 1993). Morgan and Smith (1979) demonstrated a significant increase in 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. 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. Thus, light-demanding, rapidly-photosynthesising, and fast-growing pioneer species are predicted to be strongly influenced by shifts in R:FR. The evidence concerning this hypothesis is mixed. Lee *et al.* (1996a) included two early successional species, *Endospermum malaccense* and *Parkia javanica*, in their study of seedling responses to PFD and R:FR by six Asian rain forest species. These two taxa varied in developmental responses to light conditions, but only the former species was strongly influenced by R:FR. Most of the research on the influence of PFD and R:FR on seedling function has examined photosynthetic characteristics, with relatively little influence of R:FR (Turnbull 1991, Kamaluddin & Grace 1992, Kitajima 1994, Tinoco-Ojanguren & Pearcy 1995). Kitajima (1994) detected no effects of reduced R:FR on plant growth and allocation patterns in thirteen taxa. Three of these were shade-intolerant pioneers, including *Ochroma pyramidale*. Sasaki and Mori (1981) reported increases in height and internode lengths of seedlings in *Shorea ovalis*, a shade-tolerant mature forest species. Lee (1988) observed significant developmental responses to reduced R:FR in three relatively shade-tolerant tropical vines, with specific morphological patterns varying between species.

Learning how rain forest tree seedlings respond to the two aspects of shadelight, photon flux density and spectral quality, will help us understand how individual species are adapted to conditions in the rain forest. We need to study more species, assessing the separate and interactive effects of PFD and R:FR on seedling development. The value of conducting research on the seedlings of jelutong is increased by its unique behaviour: the slow initial growth even in high light conditions, the persistence in understory, and the rapid growth as a sapling and tree.

In this research we employed the experimental system used by Lee *et al.* (1996a,b) to study seedling development in other tropical Asian forest species. This system manipulates PFD and R:FR in a simple factorial design that permits the assessment of contributions of these two factors to plant growth, development and physiology. What is the response of jelutong seedlings to shade conditions? How significant is R:FR in controlling development? How do anatomical and morphological characters help to explain the observed physiology and growth responses? How do these responses correspond to the actual performance of the species in the forest? We sought answers to these questions in our study.

Materials and methods

Seeds of *Dyera costulata* were obtained from a tree population established at the Forest Research Institute of Malaysia (FRIM) Arboretum, from seeds collected earlier this century from forest sites in Malaysia. Seeds were germinated and grown in shallow trays, transferred to poly bags, and grown until 12-15 cm height for approximately 12 months at 90% shade. Extra time was needed because of the delayed germination of jelutong seeds. Forest soil, red-yellow ultisol of the Rengam series (a friable sandy loam of good fertility) was used in the initial growth and all shade trials. Seedlings were transferred to plastic pots with 8.3 l of soil volume. These pots were fertilised with 3 g Osmocote 9:14:19 containing 0.2 g MgO at the beginning of the trials. Plants were watered regularly to maintain the soil near field capacity. We did not analyse roots of adult trees or our seedlings for the presence of mycorrhizae; we do not know if the species benefits from, or requires, these fungi. If required, the forest soils may have been adequately inoculated to infect the root systems of seedlings.

We constructed replicates of five shadehouse environments, plus one full sunlight treatment, for a total of 12 treatments. 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 PFD and temperature in the open and in the centre of the houses at 1 m height using Li-185s quantum sensors (LI-COR Inc, Lincoln, NE 68504) and Campbell thermistor probes attached to Campbell CR-10 dataloggers (Campbell Scientific Inc, Logan, UT 84321). The temperatures in the houses were comparable, and within 3 °C of ambient on the hottest afternoons (36 °C). Light conditions in the shadehouses were controlled by a combination of shade fabrics and energy films. Energy films reducing PFD to an equivalent extent and absorbing UV-B wavelengths, and altering R:FR differently, were supplied by the 3M Corporation, St. Paul, MN 55144. Metal sputter-coated films (RE20) shaded approximately 85% of PFD without changing R:FR, and dye-impregnated films (NR20) reduced the R:FR to approximately 0.25 with a similar degree of shading. Additional shading was achieved by covering those enclosures with shade fabric. We measured spectral quality with a Li-1800 spectroradiometer (LI-COR Inc, Lincoln, NE 68504), with R:FR defined as in Smith (1994), and spectral quality did not change at the beginning, middle and end of the experiments (Table 1). Mean daily totals of PFD were used to determine the light conditions for the duration of each growth trial. We constructed five shade treatments (Table 1): (1) 40% solar PFD and 1.30 R:FR, HRR; (2) 14% PFD and 1.30 R:FR, MRR; (3) 10% PFD and 0.24 R:FR, MFR; (4) 3% PFD and 1.31 R:FR, LRR; and (5) 3% PFD and 0.23 R:FR, LFR. We also grew seedlings in direct sunlight at an adjacent site, SRR. Replicates of these six treatments were randomly located on the roofs of two adjacent buildings, for a total of twelve treatments.

Ten potted seedlings of 12-15 cm height were placed randomly on a 9 by 9 grid within each shadehouse, 0.4 m apart, and their initial heights were measured. Five seedlings were dried and weighed just before the growth trials, for comparison to treatments.

Seedlings grew in the shadehouses for 429-441 days (12 days were required to complete the harvest). We harvested seedlings when the tallest had reached approximately 50 cm in height. 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 mol of photons received. 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; (4) mean leaf area; and (5) allocation to seedling organs. The degree of branching was estimated by counting the internodes in all lateral branches compared to those in the main axis. We analysed a maximum of ten plants for each treatment; the numbers were reduced in some treatments because of the occasional loss of seedlings (Table 1). A few seedlings failed to grow and a few died. We grew five seedlings in the direct sunlight treatments (SRR) and lost six seedlings in one MRR treatment, for unknown reasons.

We measured light-saturated photosynthesis (A_{max}), stomatal conductance, and dark respiration (R_{dark}), using a LI-COR LI-6200 photosynthesis system and a 0.25 L cuvette mounted on a tripod. We chose the youngest fully mature leaf of each seedling for these measurements. We removed plants from the shadehouses at least one hour in advance of measurements and allowed them to equilibrate under shade fabric or open sky at light levels near saturation (400-600 μmol $m^{-2} s^{-1}$ PFD). We constructed preliminary light response curves to determine the levels at which the plants were saturated. We completed the final measurements no later than 2 h after solar noon, at 400-1000 μmol m^{-2} s^{-1} PFD. LFR- and LRR-treated seedlings were exposed to the lesser intensity and all other treatments at the higher intensity. We regulated PFD by adding layers of shade fabric. Care was taken to avoid exposing low light grown plants to high PFD to minimise the possibility of photoinhibition. We measured photosynthesis with 10 s depletion times, three periods per measurement. We repeated measurements until steady values were obtained. We mixed treatments and times to minimise any effect of time of day on the measurements. We estimated leaf areas by tracing enclosed parts of the leaves on tracing paper, weighing, and then converting to area.

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

On the same leaves measured for A_{max} and R_{dark}, we measured chlorophyll a and b concentrations from 1 cm diameter samples obtained with a cork borer, with the n,n-dimethyl formamide technique of Moran (1982).

For the anatomical analysis, 4 mm^2 samples of the same leaves used for photosynthesis were fixed in FAA, sampled midway between the midrib and margin. We cut hand-sections with a razor blade to determine leaf and mesophyll thickness (mean of three measurements per section), and maximum palisade length and width (three measurements per section), at 400 X magnification. We also measured stomatal density at 400 X magnification, three times per leaf, in the samples cleared from the chlorophyll extraction.

Replicates of each treatment were randomly located on the roofs of two adjacent buildings. We used a treatment design appropriate for a physiological experiment, with sample sizes as the total number of individuals, and not the number of replications. Results were analysed as a stratified random block design using the General Linear Models Procedure of ANOVA (SAS Institute 1985). Initial data were checked for normality, and were rank-transformed when necessary. *Post-hoc* comparisons were performed from ANOVA using the Fisher's Least Significant Difference test, with a significance threshold of $p<0.05$. Comparative contributions of R:FR and PFD to treatment differences were estimated by 2-way ANOVA of the low and medium irradiance treatments (LRR, LFR, MRR, and MFR). The relative influences of PFD and R:FR on the development of different traits were visualised by calculating their coefficients of determination (Sokal & Rohlf 1981), dividing the sums of squares from 2-way ANOVA, using the simultaneous processing of variables, by the total sums of squares. We also constructed a Pearson Product Correlation matrix for selected characters, using rank-transformed data.

Results and discussion

Seedlings generally grew well in the treatment enclosures, free from disease or insect damage, although those growing in direct sunlight appeared stunted by the exposure. Shadehouses approximated light environments encountered within the rain forest environment (Table 1, Chazdon *et al.* 1996). The LFR and LRR treatments were of similar PFD to that of rain forest understory. Small gaps were approximated by the MFR and MRR treatments, and a large gap by the HRR treatment. The spectral quality of LFR and MFR treatments was similar to that of the understory (Lee 1987). The factorial design also meant that certain light environments combined PFD and R:FR in unnatural combinations, as LRR – with the intensity of deep forest shade and the spectral quality of direct sunlight.

These treatments affected jelutong seedling growth, architecture and physiology, but the effects were small compared to previous studies (Lee *et al.* 1996a,b, 1997).

Table 1. Photosynthetic photons received per day for each of the shade treatments, and for each replication. We report data as means ± standard deviations. Reported R:FR values were measured mid-way during growth trials, and the % of PFD is the mean of the two replications. The number of seedlings harvested per treatment (N) is also given.

Treatments					
LFR	LRR	MFR	MRR	HRR	SRR
Replication 1					
0.83 ± 0.21	0.84 ± 0.24	2.93 ± 0.76	3.75 ± 1.32	10.81 ± 2.73	27.94 ± 6.76
N = 9	7	6	10	10	4
Replication 2					
0.74 ± 0.19	0.82 ± 0.23	3.18 ± 0.82	5.09 ± 1.64	13.94 ± 3.60	33.40 ± 9.25
N = 6	6	6	4	8	4
% PAR					
2.6	2.8	10.0	13.4	40.2	-
R:FR					
0.25	1.25	0.25	1.25	1.25	1.25

Growth

Rates of growth, as assessed by final height, collar diameter (diameter at transition between root and stem), and dry mass increase (Table 2) were small at low and medium PFD. Height increases were less than for other species grown in the same treatments (Lee *et al.* 1996a). Dry mass increase was assessed on a per day basis, because some seedlings grew for slightly different periods (429–441 days). More importantly, the light levels at low (LRR and LFR) and, especially, medium (MRR and MFR) treatments were not perfectly matched (Table 1), making an assessment per mol of photons received the best comparison. Growth rates as mass/day were not significantly different between LRR and MRR, or LFR and MFR, but the low R:FR treatments depressed growth rates at both PFD. Dry mass increment/mol of photons was significantly decreased at the medium light treatments, and lower (but not significantly) for reduced R:FR. Growth was highest in the HRR treatment, and significantly decreased in full sunlight.

Architecture

Plant architecture was not strongly affected by the low and medium light treatments (Table 3). Seedlings produced virtually no branches during the growth period. Internode length was promoted by greater PFD and reduced R:FR, but the effects were not large. Stem robustness, as mass/length, was increased by higher PFD, and slightly decreased by low R:FR. Leaf area/stem length ratio, an indicator of allocation of leaf surface per unit of axis extension, was not strongly affected by PFD, and was slightly reduced by low R:FR, especially at medium PFD (MFR).

Table 2. Effects of light treatments on plant height and growth. Treatment abbreviations are described in the methods section and Table 1. Values are means ± standard errors. Values sharing lower case letters are not significantly different from each other.

Treatment	Height (cm)	Collar diameter (mm)	Dry mass (mg)/ day	Dry mass (mg)/ mol photons
LFR	32.1 ± 3.1ac	7.14 ± 0.56a	14.50 ± 4.06a	18.33 ± 1.82d
LRR	36.0 ± 2.7ace	8.43 ± 0.51ac	23.63 ± 3.62bd	28.45 ± 1.63e
MFR	42.7 ± 3.4bde	8.20 ± 0.60ac	17.30 ± 4.34ad	5.67 ± 1.95b
MRR	39.8 ± 3.4bc	8.83 ± 0.66ac	33.79 ± 4.76be	8.19 ± 2.14c
HRR	51.7 ± 2.9d	11.79 ± 0.53b	44.18 ± 3.82ce	3.68 ± 1.72a
SRR	32.5 ± 3.9ac	9.55 ± 0.71c	28.05 ± 5.12b	3.29 ± 2.30a

Table 3. Effects of light treatments on plant architecture. Treatment abbreviations are described in the methods section and Table 1. Values are means ± standard errors. Values sharing lower case letters are not significantly different from each other.

Treatment	Internode length (cm)	Stem mass (mg) /length (cm)	Leaf area (cm^2)/ stem length (cm)
LFR	2.7 ± 0.6a	47.3 ± 10.9a	11.40 ± 1.51be
LRR	3.7 ± 0.5ac	55.8 ± 9.7ab	15.98 ± 1.39d
MFR	4.7 ± 0.7bce	67.7 ± 11.7bc	6.16 ± 1.67a
MRR	6.0 ± 0.6b	101.9 ± 12.2cd	14.48 ± 1.81cde
HRR	7.7 ± 0.6d	103.8 ± 10.9d	11.41 ± 1.56bc
SRR	3.5 ± 0.7ae	133.2 ± 15.4d	10.81 ± 4.39abd

Allocation

Relative allocations to plant organs represent strategies for the exploration for or exploitation of resources (Grime 1979, Tilman 1988). Percentage of dry mass allocation to leaves, stems and roots varied among the treatments (Figure 1). Allocation to leaves was reduced with increasing PFD, and was also reduced at low R:FR. Leaf allocation was extremely small in the stunted seedlings grown in direct sunlight (SRR). Stem mass allocation varied little with treatment. However, root mass allocation increased with light intensity, was not significantly affected by R:FR, and was 42 % of total dry mass in plants grown in direct sunlight.

Leaf morphology

Mean leaf area was not strongly affected by the treatments, but was reduced by low R:FR and full sunlight (Table 4). Petiole length and leaf shape (as width/ length) changed very little. Leaf specific mass increased only in the HRR and SRR treatments. Leaf morphology was not strongly affected by these treatments, except for the stunting in full sunlight (SRR).

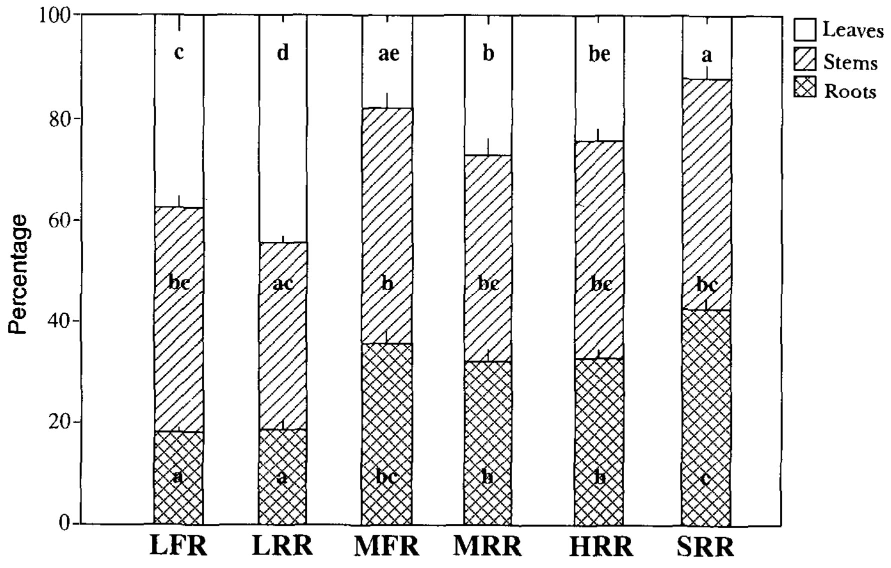

Figure 1. Allocation of dry mass to leaves, stems and roots in seedlings of jelutong. Treatment symbols are described in the methods section and Table 1. Vertical bars indicate standard errors, and identical letters between treatments indicate that they are not significantly different from each other.

Table 4. Effects of light treatments on leaf morphology and anatomy. Treatment abbreviations are described in the methods section and Table 1. Values are means ± standard errors. Values sharing lower case letters are not significantly different from each other.

Treatment	Area (cm^2)	Specific mass ($mg\ cm^{-2}$)	Petiole (mm)	Width/length	Palisade width (µm)
LFR	46.1 ± 5.3b	3.58 ± 0.33a	23.7 ± 1.5bc	0.23 ± 0.01a	19.8 ± 0.5b
LRR	62.6 ± 4.0cd	3.94 ± 0.16a	25.4 ± 1.3c	0.26 ± 0.01b	20.3 ± 0.5b
MFR	41.0 ± 4.9ab	4.14 ± 0.22a	20.6 ± 2.1ab	0.26 ± 0.01b	17.9 ± 0.6ac
MRR	61.6 ± 9.3bd	4.09 ± 0.22a	22.2 ± 1.7abc	0.27 ± 0.01c	19.3 ± 0.5bc
HRR	48.9 ± 6.1b	6.33 ± 0.24a	24.7 ± 1.3bc	0.27 ± 0.01b	17.6 ± 0.5a
SRR	28.1 ± 3.9a	6.54 ± 1.13b	17.9 ± 1.4a	0.26 ± 0.01b	16.7 ± 0.7a

Leaf anatomy

Leaf thickness did not vary among the low- and medium-intensity treatments, but did increase in the SRR and HRR treatments (Figure 2). These effects were paralleled in measurements of mesophyll thickness and palisade length. Palisade width increased at low light levels, and stomatal density increased from the lowest PFD to direct sunlight (Tables 4 & 5). R:FR contributed little to leaf anatomy characteristics.

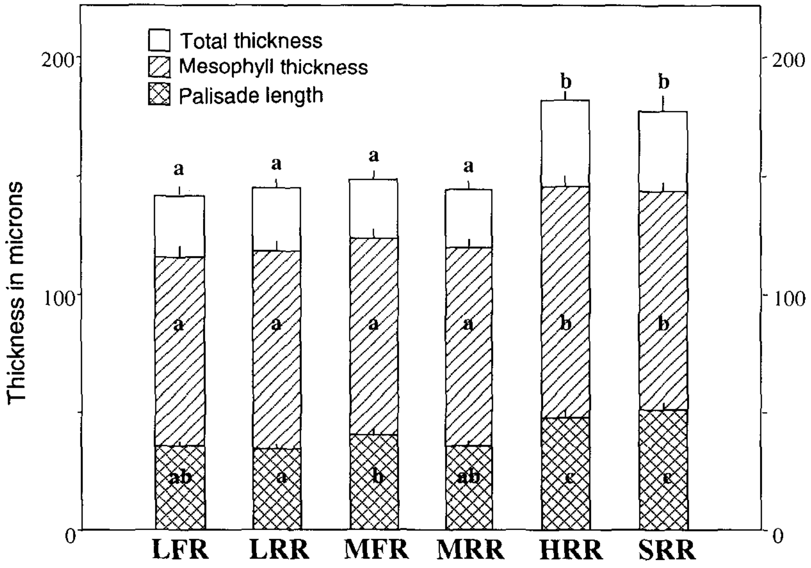

Figure 2. Leaf and mesophyll thickness, and palisade cell length, among the different shade treatments. Tallest bars are total leaf thickness. Treatment symbols are described in the methods section and Table 1. Vertical bars indicate standard errors, and identical letters between treatments indicate that they are not significantly different from each other.

Physiology

Pigment composition, both per area and a/b, varied little among all of the treatments (Table 5). Maximum photosynthesis (A_{max}), dark respiration (R_{dark}) and stomatal conductance were little affected by the low and middle intensity treatments (Figure 3). These processes all increased significantly in plants grown at 40% and direct sunlight, and A_{max} was highest in plants grown in the former condition. In these treatments and experimental conditions, A_{max} was comparable to that of *Hopea odorata*, a relatively shade-tolerant Malesian dipterocarp species (Lee *et al.* 1997). These maximum rates were similar to those of late successional tropical forest Moraceae (Strauss-Debenetti & Bazzaz 1991) and shade-tolerant neotropical forest species (Kitajima 1994).

The effects of PFD and R:FR on seedling growth, architecture and physiology can be assessed by comparing the coefficients of determination for each trait resulting from the factorial analysis of variance of the low and medium treatments (Table 6). The coefficients are not absolute values, their range limited by the treatment conditions for the factorial design (LFR, LRR, MFR, MRR) and the genetic variation within the seedlings – independent of treatment effects. These coefficients do indicate the relative contributions of PFD and spectral quality to each of the traits, and the total variation of each trait to the range of shade conditions (plasticity).

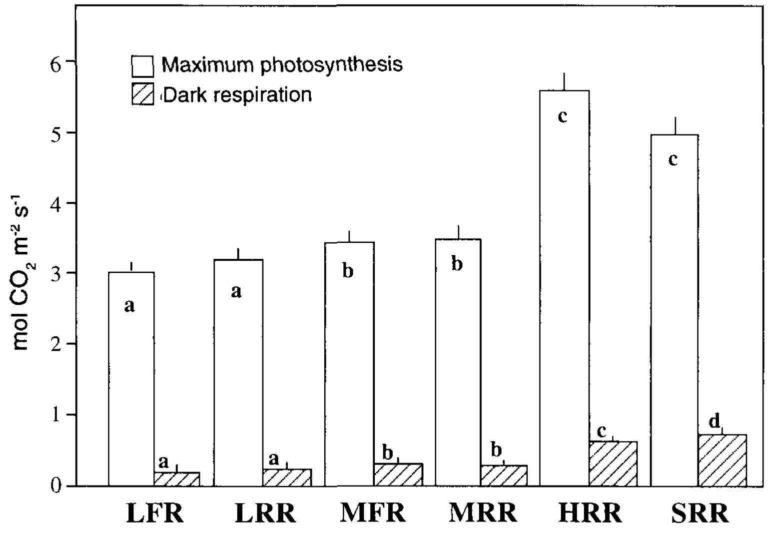

Figure 3. Maximum photosynthesis (A_{max}) and dark respiration (R_{dark}) in leaves from seedlings of the different shade treatments. Treatment symbols are described in the methods section and Table 1. Vertical bars indicate standard errors, and identical letters between treatments indicate that they are not significantly different from each other.

Table 5. Effects of light treatments on stomatal density and conductance, and pigment composition. Treatment abbreviations are described in the methods section and Table 1. Values are means ± standard errors. Values sharing lower case letters are not significantly different from each other.

Treatment	Stomatal density	Stomatal conductance	Chlorophyll	
	(10^4 cm^{-2})	(mol m^{-2} s^{-1})	(µg cm^{-2})	(a/b)
LFR	1.47 ± 0.07b	0.055 ± 0.006a	28.45 ± 1.43ac	2.38 ± 0.04a
LRR	1.32 ± 0.07a	0.047 ± 0.006a	31.65 ± 1.32bc	2.33 ± 0.04a
MFR	1.89 ± 0.07d	0.059 ± 0.006a	29.18 ± 1.57bcd	2.37 ± 0.04a
MRR	1.70 ± 0.07c	0.050 ± 0.006a	30.04 ± 1.39bce	2.38 ± 0.04a
HRR	2.39 ± 0.07e	0.089 ± 0.006b	27.15 ± 1.39ade	2.38 ± 0.04a
SRR	3.32 ± 0.09f	0.094 ± 0.008b	24.08 ± 1.86a	2.40 ± 0.05a

Limited variation in light treatments

In general, the range of flexibility of these traits, compared to those for other species under the same experimental conditions (Lee *et al.* 1996a,b, 1997) was rather small. Since the treatment variation was most likely contributed by different genotypes, plasticity may only explain part of these responses (Nicotra *et al.* 1997). These results suggest that jelutong seedlings were somewhat indifferent to the shade conditions. The greatest responses for the characters were among plants grown at 40% full sunlight. Limited response to varying shade may be characteristic of plants that are tolerant of shade, and intolerant of direct sunlight (Bazzaz & Pickett 1979). Seedlings of jelutong thus do not seem adapted to the full sun conditions of early succession, but grow more slowly under partial shade conditions. These results are consistent with the growth trials of Aminuddin (1982), and also demonstrate a limited acclimation, or perhaps persistence, to deep shade.

Table 6. Coefficients of determination for the treatment effects of irradiance (PFD) and spectral quality (R:FR), as well as interactions, on the characters reported in Tables 2-5

Character	R:FR	PFD	Interactions
Height	0.001	0.112 *	0.023
Collar diameter	0.048	0.029	0.008
Growth mass/day	0.202 ***	0.023	0.002
Growth mass/mol	0.056 *	0.418 ***	0.024
Internode length	0.057 *	0.209 ***	0.000
Stem mass/length	0.039	0.126 **	0.001
Leaf area/stem length	0.242 ***	0.069 *	0.024
% Leaf allocation	0.092 **	0.386 ***	0.003
% Stem allocation	0.070 *	0.028	0.000
% Root allocation	0.021	0.414 ***	0.007
Leaf area	0.138 **	0.005	0.001
Specific leaf mass	0.013	0.055	0.016
Petiole length	0.008	0.059	0.001
Leaf width/length	0.157 **	0.052	0.000
Stomatal density	0.062 *	0.371 ***	0.001
Leaf thickness	0.003	0.030	0.014
Mesophyll thickness	0.001	0.040	0.019
Palisade cell length	0.089 *	0.076 *	0.005
Palisade cell width	0.036	0.092 *	0.009
Maximum photosynthesis	0.002	0.068 *	0.001
Maximum respiration	0.006	0.297 ***	0.036
Stomatal conductance	0.079 *	0.008	0.000
Chlorophyll/cm^2	0.029	0.001	0.011
Chlorophyll a/b	0.008	0.020	0.000

*Denotes treatment effect in two-way ANOVA as < 0.05, ** as < 0.005, and *** as < 0.0005.

Small contribution of spectral quality to treatment effects

Reduction in R:FR is generally not very important in controlling the development of jelutong seedlings, about half the contribution of intensity (Table 6). Effects of R:FR were only important in controlling (1) growth as mass/day; (2) leaf area/stem length; (3) and leaf shape and area. Reduced leaf allocation (Figure 1) may be related to the slightly smaller area per leaf, and the reduced leaf area/stem length. A correlation matrix for these characters (Table 7) shows strong positive relationships between growth as mass/day and leaf area/stem length. Reduced leaf area may limit total capacity for carbon assimilation, thereby reducing growth rates. Such effects were probably more important in the low R:FR treatments. These patterns are consistent with the growth data of Kitajima (1994), and photosynthesis was also not shown to be significantly influenced by R:FR in her research, or that of others (Kwesiga & Grace 1986, Turnbull 1991, Tinoco-Ojanguren & Pearcy 1995).

Table 7. Pearson product correlations of growth and photosynthesis with plant architecture and leaf structure.

	FHT	MDA	MMO	SML	LAS	LF%	PHO	CON	LTH	STM
Height (FHT)	-	0.577 ***	- 0.038 ***	0.384 **	0.045	- 0.074	0.358 **	0.137	0.096	0.160
Mass/day (MDA)		-	0.060	0.667 ***	0.464 ***	0.117	0.497 ***	0.238 *	0.258 *	0.299 **
Mass/mol (MMO)			-	- 0.266 *	0.551 ***	0.740 ***	- 0.440 ***	- 0.372 ***	- 0.491 ***	- 0.756 ***
Stem mass/ length (SML)				-	0.109	- 0.340 **	0.430 ***	0.280 *	0.287 *	0.477 ***
Leaf area/ stem L. (LAS)					-	0.729 ***	- 0.064	- 0.211	- 0.147	- 0.253 *
% Leaf (LF%)						-	- 0.245 *	- 0.237 *	- 0.298 *	- 0.587 ***
Photosynthesis (PHO)							-	0.598 ***	0.412 ***	0.540 ***
Conductance (CON)								-	0.293 **	0.478 ***
Leaf thickness (LTH)									-	0.546 ***
Stomatal density (STM)										-

Levels of significance of correlations are depicted as * = ≤ 0.05, ** = ≤ 0.005, *** = ≤ 0.0005.

Predictors of seedling growth

Measures of seedling growth (mass/day – MDA, final height and collar diameter) were strongly correlated with each other and further comparisons of growth with other characters used only the mass/day data (Table 7). Dry mass increment per mole of photons received (MMO in Table 7) is really an indicator of the efficiency of growth with the amount of radiation received. Since such efficiency is reduced at higher fluxes, MMO is not positively correlated with measurements of growth (Table 7). However, such characters that document capacity for assimilation—as percentage leaf allocation and leaf area per stem length—were significantly correlated with growth efficiency. Growth efficiency of jelutong seedlings at low flux was average for the six taxa reported by Lee *et al.* (1996a) and the lowest—the most suppressed—at 40 % full sunlight (HRR) compared to these taxa. Growth, as MDA, was correlated with two architectural characters, stem mass per length (SML) and leaf area per stem length (LAS). Greater leaf area would allow for more total carbon fixation and more growth. Growth was also strongly correlated with A_{max} and other characters associated with gas exchange: conductivity, leaf thickness and stomatal density.

Photosynthesis (A_{max}) was strongly correlated with leaf anatomy, with increases in leaf thickness, stomatal conductance and stomatal density. Conductivity and A_{max} were measured at the same time, and both are strongly dependent on stomatal density.

Photosynthesis was not correlated with chlorophyll/area or chlorophyll a/b; neither of these varied much among the treatments and they were not included in Table 7. The increase in air-cell contacts associated with the thicker leaf and mesophyll may contribute to gas exchange (Sharkey 1985, Nobel 1991, Parkhurst 1994), but the main effect is likely to be stomatal conductance (Wong *et al.* 1979). Clearly the seedling leaves of jelutong are relatively thick and durable, markedly different from the thin and expendable leaves of short-lived pioneers which are also capable of much higher rates of photosynthesis (Strauss-Debenedetti & Berlyn 1994).

Seedling functional ecology

The seedlings of jelutong are limited in the variation of their responses to light climates during their establishment. Even though they may be present in the seed bank and establish as early pioneers, they are stunted by direct sunlight and grow most rapidly under partial shade. Their plasticity of root allocation to light conditions suggests that they may possess adaptations to water stress to which early successional environments may be exposed. They are capable of continued but slow growth under conditions approaching forest understory, and thus may persist for long periods under deep shade. They may encounter such shade when overtopped by faster-growing short-lived pioneers. They persist, continue to grow, and eventually become established as fast growing saplings. This change in growth rates suggests that there are likely to be age- and size-related physiological and anatomical correlates. Such ontogenetic shifts in the flexibility of light responses have been documented in other tropical trees (Clark & Clark 1992, Farnsworth & Ellison 1996). These changes were not observed during the limited duration of these trials, but Appanah and Weinland (1993) noted that leaves of the tree are thicker and tougher than those of seedlings.

Conclusion

Jelutong (*Dyera costulata*) is a long-lived pioneer which eventually becomes a gigantic rain forest emergent. In early succession its seedlings grow slowly, are shade tolerant, and stunted by direct sunlight. These seedlings vary little in a range of light conditions, and are little affected by shifts in spectral quality. Yet, as saplings and adult trees they are capable of very rapid growth. The results of seedling trials on jelutong contrast strongly with those of *Endospermum malaccense* (Lee *et al.* 1996a), which may be present in the seed bank in the same forests, establishes early, and attains a height of 40 m in mature forest. Its seedlings grow rapidly at low PFD, vary in overall responses to light, and are strongly affected by reduced R:FR. No clear factors emerge which constrain growth rates in these plants (Lambers &

Poorter 1992). These results demonstrate the complexity of seedling growth and establishment in tropical rain forests, emphasising the danger of generalising about species responses as members of guilds, whether they are associated with gaps of different sizes or not. Additional research on a variety of species will certainly help us understand the complexity of seedling ecology and establishment in tropical rain forests.

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