SEEDLING DEVELOPMENT OF *GONOSTYLUS BANCANUS* (RAMIN MELAWIS) IN RESPONSE TO LIGHT INTENSITY AND SPECTRAL QUALITY

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LEE, D.W., KRISHNAPILLAY, B., HARIS, M., MARZALINA, M. & YAP, S.K. 1996. Seedling development of *Gonostylus bancanus* (ramin melawis) in response to light intensity and spectral quality. We studied seedling development of *Gonostylus bancanus* (ramin melawis, Thymeliaceae) in response to shade conditions, to learn about the tree's functional ecology. Shadelight comprises reductions in solar irradiance (photosynthetic photon flux density, 400-700 nm, or PFD) and changes in spectral quality, as reductions in the red:far-red ratio (or R:FR). We studied the separate and interactive effects of PFD and R: FR on seedling development by growing them under six different replicated shadehouse treatment conditions. Seedlings grew least at low light levels and full sunlight. Seedling branching was not strongly affected by the light treatments, but stem robustness was promoted by PFD, and leaf area/stem length was decreased by low R:FR. Photosynthate allocation to leaves was low, and was primarily reduced by increasing PFD. Most of the effects on development were influenced by PFD; only internode length and leaf area/stem length were more influenced by R:FR. Seedlings of ramin malawis are intolerant of extreme shade and direct sunlight, growing most rapidly in partial shade, with daily percentages of 40 % and more of full sunlight. Such seedlings are probably only at a competitive advantage in the inundated soils of their natural distribution.

Key words: Seedlings - *Gonostylus bancanus* - development - shade response - spectral quality - Malaysia - Borneo

LEE, D.W., KRISHNAPILLAY, B., HARIS, M., MARZALINA, M. & YAP, S.K. 1996. Pertumbuhan anak benih *Gonystylus bancanus* (ramin melawis) di dalam tindakbalas kepada keamatan cahaya dan kualiti spektrum. Kami mengkaji pertumbuhan anak benih *Gonystylus bancanus* (ramin melawis, Thymeliaceae) dari segi tindakbalas terhadap teduhan untuk mengetahui mengenai fungsi ekologi pokok ini. Sinaran di bawah teduhan mengandungi kurang sinaran solar (ketumpatan fluks foton fotosintesis, 400-700 nm, atau PFD) dan perubahan dalam kualiti spektrum, iaitu pengurangan di dalam nisbah "red: far-red" (atau R:FR). Kami mengkaji kesan secara interaktif dan berasingan PFD dan R:FR ke atas perkembangan anak benih dengan menanam anak benih di dalam enam rumah teduhan dengan keadaan rawatan yang berbeza. Anak benih didapati tumbuh pada kadar terendah di bawah paras cahaya yang rendah dan di dalam keadaan cahaya sepenuhnya. Penghasilan cabang pada anak benih tidak begitu dipengaruhi oleh rawatan cahaya yang berbeza, tetapi kekuatan batang meningkat dengan PFD, dan luas permukaan daun/panjang batang menurun dengan R:FR yang rendah. Pengagihan fotosintesis dalam daun adalah rendah, dan menurun dengan peningkatan PFD. Kebanyakan kesan ke atas pertumbuhan anak benih adalah dipengaruhi oleh PFD; hanya panjang ruas dan luas permukaan daun/panjang batang lebih dipengaruhi oleh R:FR. Anak benih ramin melawis tidak toleran kepada keadaan teduhan yang ekstrim dan pancaran terus cahaya matahari, tumbuh paling baik di dalam separa teduhan, dengan peratus cahaya matahari harian sebanyak 40% atau lebih. Anak benih-anak benih seumpama ini mungkin dapat bersaing dengan baik di kawasan taburan semulajadinya.

Introduction

Gonostylus bancanus (Miq.) Kurz. (Thymeliaceae) is a large tree native to swamp forests in Southeast Asia (Airy Shaw 1953, Whitmore 1973). It produces a light hardwood known in the trade as ramin, or ramin melawis, which has become an important timber commodity, used for furniture manufacture. It is the single most important timber extracted from peat and freshwater swamp forests in West Malaysia and Borneo (Laurent 1986). In selective felling ramin melawis is depleted from fresh water swamp forests (Sutisna *et al.* 1988). Research on the silviculture of these forests has been summarised by Whitmore (1984). Ramin is shade intolerant and slow-growing; it does not regenerate well in secondary forests. Research on factors controlling the regeneration of this species in natural forests is important for devising techniques of silvicultural treatment. This article describes research on the shade responses of ramin melawis seedlings.

Light is generally the most important environmental factor influencing the survival and growth of tree seedlings in tropical rain forests. Knowledge of the light requirements of tree seedlings helps in predicting their responses in natural and silvicultural systems (Whitmore 1996). Light requirements of different taxa can be inferred from disciplined field observations (Liew & Wong 1973, Raich & Gong 1990, Brown & Whitmore 1992, Turner *et al.* 1992), or from experimental trials (Turner 1989, Ashton & De Zoysa 1990, Whitmore 1996). Little such experimental research has been published on species native to Malesian tropical rain forests. Nicholson (1960) studied shade requirements of five diperocarp seedlings, but the light values were too high to have any ecological meaning. Aminuddin (1982) showed that the seedlings of *Dyera costulata* performed best at 33 % full sunlight, but Sasaki and Ng (1981) demonstrated the high light requirements of *Intsia palembanica.* Detailed research on ecologically and commercially important taxa is needed.

Light environments in rain forests are exceedingly heterogenous, ranging from the bright sunlight of large gaps to the somber shade of dense understory (Raich 1989, Chazdon *et al.* 1996). These light environments also vary in spectral quality (Lee 1987, Turnbull & Yates 1992). Such changes, along with intensity, may profoundly influence seedling growth and development. Plants are most sensitive to changes in spectral quality through the phytochrome pigment system, which affects development at virtually every level of organisation (Smith 1994). A convenient measure of shifts in spectral quality affecting phytochrome is the red:far-red ratio (R:FR), defined by Smith (1994) as the ratio of quanta centering on 660 and 730 nm with a band width of 10 nm. There are even fewer studies of the separate and interactive effects of the varied intensity and quality of light on tree seedling development, particularly of tropical taxa. Ashton (1995) reduced PFD (photosynthetic photon flux density, 4-700 nm) and R:FR together in his research on seedling development in Sri Lankan *Shorea.* Sasaki and Mori (1981) studied the effects of shading on the development of five dipterocarp taxa, and included shifts in spectral quality on the growth of *Shorea ovalis* seedlings. Lee *et al.* (1996) studied the effects of shifts in PFD and R:FR on the development of six Asian tropical rain forest tree seedlings. Reduction in spectral quality affected the development of some characters for all taxa, but some more than others. The patterns of effects of R:FR and PFD varied among the taxa and did not necessarily correlate with the alleged shade tolerances of the taxa. In this research we report on the developmental responses of seedlings of *Gonostylus bancanus* to reductions in PFD and R:FR.

Materials and methods

Seeds of *G. bancanus* were collected from fresh water peat swamp forest in the Pekan Forest Reserve, Pahang, on 24 March 1992. Seeds were germinated in shallow trays on 26 March in a shade enclosure, and seedlings were transferred to polybags on 13 April. We used forest soil, red-yellow ultisol of the Rengam series (a friable sandy-clay loam of good fertility) in seedling establishment and all shade trials. Seedlings 25 - 40 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 fertilised with 3 g Osmocote 9:14:19 and 3 parts MgO at the beginning of the trials, starting on 16 February 1993. Plants were watered daily during the trials, maintaining the soil continually moist. Treatments and measurements are described in greater detail by Lee *et al.* (1996).

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 PFD to an equivalent extent, but altering R:FR differently, were supplied by the 3M Corporation, St. Paul, MN 55144. Metal sputter-coated films (REAL20) shaded approximately 85 % of PFD without changing R:FR, and dye-impregnated films (NEARL20) reduced the R:FR to approximately 0.25 with a similar degree of shading. Adding spectrally neutral shade fabrics of 50 % and 73 % permitted the construction of six treatments (Table 1). Replications of the light treatments were constructed on the roofs of two adjacent buildings, minimising interference from tree crowns. PFD was monitored in the shade houses by continuous measurements with Li-Cor 185s quantum sensors (Li-Cor Instruments, Lincoln, NE 68504) connected to Campbell Cr-10 dataloggers (Campbell Scientific Instruments, Logan, UT 84321). Temperature was monitored continuously with Campbell thermister probes connected to the dataloggers. PFD 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 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 photosynthesis rates for 1- 2 h in early afternoon, but should not affect the treatments differently (Mori *et al.* 1992).

Table 1. Treatments used for the study of seedling responses

Treatment	Symbol	% Solar PFD	R:FR
Direct sunlight	SRR	100	1.05
Lightly filtered sunlight	HRR	40	1.05
Medium neutral filtered shade	MRR	14	1.05
Medium far-red enriched shade	MFR	10	0.25
Deep neutral filtered shade	LRR	3	1.05
Deep far-red enriched shade	LFR	3	0.25

Spectral quality of the radiation in the shadehouses was measured with a Li-Cor 1800 spectroradiometer, where R:FR was defined as the quantum ratio of the band widths 658-662/728-732, roughly 10 nm band widths centering on 660 and 730 nm given the 6 nm band width of the instrument. 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 by 9 grid within the shadehouses, 0.4 m apart, and their initial height measured. Initial sample sizes of each replication were 10 seedlings, but some final samples were 1-2 individuals smaller because of random mortality. Five other seedlings were dried and weighed at the beginning of the experimental trial. Seedlings grew for 429-441 days, and to a maximum height of 70 cm for one of the treatments, before destructive measurements were completed.

At the end the growth trials we measured (1) plant height (above collar); (2) collar diameter, measured with calipers; (3) length of three internodes beneath the most recent fully expanded leaf; (4) area, fresh weight, dry weight, blade width and length, and petiole length of three top-most fully expanded leaves; (5) total number of leaves; (6) total number of internodes; (7) number, internode number, mass, and length of branches; (8) total leaf area and dry mass; (9) petiole dry mass and length; and (10) 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.

Replicates of each treatment were located on roofs of adjacent buildings to minimize the probability of error by pseudo replication. Results were analysed as a stratified random block design using the General Linear Models Procedure of ANOVA (Ray 1982). Initial data were checked for normality with the Shapiro-Wilks test and were log-normally 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 PAR 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 selected traits were estimated 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 from the one-way ANOVA.

Results and discussion

The seedlings grew satisfactorily (no effects of temperature, disease or insect damage) in all light treatments, but very slowly under the LRR and LFR treatments (Figure 1). Since PFD within low and medium light treatments differed from each other (Table 2), growth as dry weight increment per day was not directly comparable (Table 3). The growth data were easily compared when considered for the irradiance totals for each treatment. Dry mass increment could thus be calculated as mg dry mass increase per mol of photons at 400-700 nm (Table 3). Compared to other taxa studied in the same shade conditions, growth rates were very low (Lee *et al.* 1996). Seedling growth was reduced at the medium and low flux densities, and reduced again in full sunlight. These results suggest that maximum growth rates in seedlings of *G. bancanus* occur in partial sunlight or very lightly shaded understory. Growth as dry mass increment was roughly comparable to data from final seedling height (Table 3). The HRR treatment promoted maximum height growth, although low R:FR slightly increased seedling heights. Collar diameter increased with light level, but was slightly reduced in full sunlight.

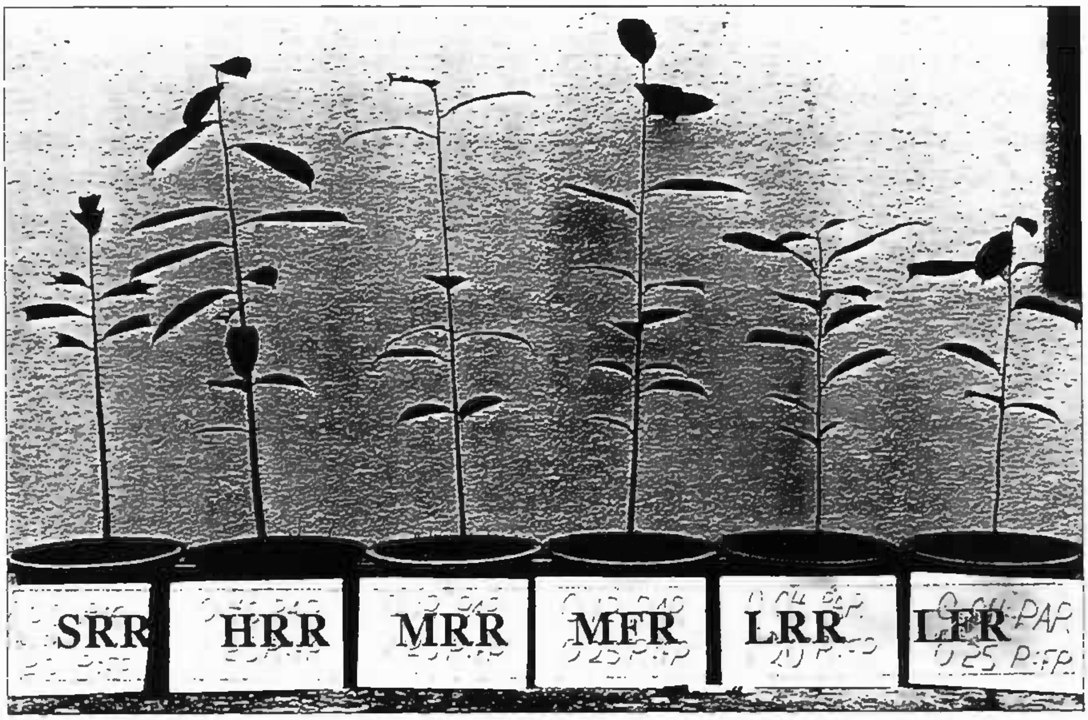

Figure 1. Representative seedlings of *Gonostylus bancanus* taken from each of the six treatments at the end of the growth trials. Abbreviations for shade treatments are described in Table 1. For scale the height of the photograph is 112 cm.

Table 2. Daily photosynthetic photon flux totals ± sd (mol photons/day, 400 - 700 nm) for the different treatment conditions and the replications. Mean percentages of full sunlight are also provided for the treatments. Treatment abbreviations are described in Table 1.

	Treatment					
	LFR	LRR	MFR	MRR	HRR	SRR
Replication 1						
	0.83	0.84	2.93	3.75	10.81	27.94
	± 0.21	± 0.24	± 0.76	± 1.32	± 2.73	± 6.96
Replication 2						
	0.74	0.82	3.18	5.09	13.94	33.40
	± 0.19	± 0.23	± 0.82	± 1.64	± 3.60	± 9.25
Percentage of full sunlight						
	2.6	2.7	10.0	14.3	40.2	100.0

Table 3. Effects of light treatments on plant height and growth. Treatments are described in Table 1. Values are means ± se. Treatments not sharing letters are significantly different from each other (p<.05).

Treat-ment	Height (cm)	Collar diameter (mm)	Dry mass (mg)/day	Dry mass (mg)/ mol photons
LFR	41.9 a ± 2.8	8.01 a ± 0.50	6.41 a ± 4.53	8.44 b ± 1.34
LRR	39.7 a ± 2.9	8.43 ae ± 0.51	8.37 a ± 4.67	10.50 b ± 1.38
MFR	57.4 bc ± 3.2	9.99 bd ± 0.58	20.64 b ± 5.04	6.85 b ± 1.50
MRR	52.7 b ± 3.1	9.52 be ± 0.55	29.60 b ± 4.16	6.85 b ± 1.47
HRR	65.7 c ± 2.7	12.65 c ± 0.47	88.52 d ± 4.12	7.25 b ± 1.22
SRR	49.3 ab ± 3.9	11.65 cd ± 0.68	47.88 c ± 6.17	1.60 a ± 1.83

The shade treatments influenced plant architecture in several ways. Internode length was slightly promoted by low R:FR, and reduced in full sunlight (Table 4). These results correlate with those for height increase (Table 3). Seedlings branched sparingly in all treatments. Seedlings of ramin malawis developed extremely robust stems, with stem mass per length (Table 4) several times greater than other rain forest tree seedlings (Lee *et al.* 1996). Stem robustness was significantly increased by higher PFD, but not significantly affected by R:FR. Despite the low percentage of dry leaf mass, leaf area/stem length in these seedlings was comparable to seedlings of other taxa (Lee *et al.* 1996), and slightly influenced by PFD and R:FR (Table 6).

Table 4. Effects of light treatments on plant architecture. Treatment abbreviations are described in Table 1. Values are means ± se. Treatments not sharing letters are significantly different from each other (p<.05).

Treatment	Internode length (cm)	Branch/trunk internodes	Stem mass (mg)/ length (cm)	Leaf area (cm^2)/ stem length (cm)
LFR	2.7 bc ± 0.2	0.00 a ± 0.00	68.7 a ± 7.7	5.86 a ± 0.46
LRR	2.0 ab ± 0.3	0.01 a ± 0.01	72.5 ab ± 7.9	7.64 b ± 0.46
MFR	3.2 c ± 0.3	0.02 a ± 0.01	94.8 b ± 8.5	5.35 a ± 0.49
MRR	2.3 ab ± 0.3	0.04 a ± 0.01	122.1 c ± 8.4	6.10 a ± 0.49
HRR	3.3 c ± 0.2	0.05 a ± 0.01	202.8 d ± 7.4	8.57 b ± 0.42
SRR	1.8 a ± 0.3	0.03 a ± 0.02	201.4 d ± 10.9	5.06 a ± 0.65

Changes in leaf morphology may strongly influence plant function. Leaves generally increased in area from the LFR to SRR treatments - most affected by PFD (Table 5). Specific leaf mass (leaf mass per unit area) was also reduced by low and high R:FR, and little affected by R:FR. Petiole length was not significantly affected by the light treatments, and leaf shape was only broadened under full sunlight treatments. Leaf life span is directly correlated with the percentage of leaf loss during the treatment period. Percentage of leaf loss was increased by the MFR, MRR and SRR treatments. Changes in leaf morphology in *G. bancanus* were smaller than others observed (Ashton & Berlyn 1992, Buisson & Lee 1993, Lee *et al.* 1996).

Table 5. Effects of light treatments on leaf morphology of ramin melawis. Values are means ± se. Treatment abbreviations are described in Table 1. Treatments not sharing letters are are significantly different from each other (p<.05).

Treatment	Area (cm^2)	Specific mass ($mg\ cm^{-2}$)	Petiole (mm)	Width/length	% Leaf loss
LFR	36.9 a	9.94 a	9.8 a	0.421 a	22.7 ad
	± 3.6	± 0.46	± 0.5	± 0.016	± 5.2
LRR	42.3 ad	8.65 a	10.4 ab	0.431 a	19.8 a
	± 3.6	± 0.46	± 0.5	± 0.011	± 5.4
MFR	51.3 bd	10.42 b	11.5 b	0.423 a	49.6bc
	± 4.1	± 0.50	± 0.5	± 0.011	± 5.8
MRR	54.5 b	12.19 c	10.6 ab	0.422 a	37.6 bcd
	± 3.8	± 0.57	± 0.6	± 0.012	± 5.7
HRR	64.6 c	13.67 d	11.3 bc	0.418 a	25.3 ad
	± 3.2	± 0.42	± 0.4	± 0.009	± 4.8
SRR	54.4 bcd	14.29 d	9.7 ac	0.495 b	54.8 bc
	± 5.1	± 0.77	± 0.7	± 0.015	± 7.2

Both R:FR and PFD influenced photosynthate allocations to leaves, stems and roots, PFD being the most important factor (Figure 2). Compared to results from six taxa previously reported (Lee *et al.* 1996), seedling leaves were a small portion of total plant biomass and were further reduced at very low and high intensities. Stem biomass increased slightly with greater solar exposure, and root biomass was increased mostly in partial shade (HRR) and full sun conditions (SRR). However, the overall plasticity of allocation in these light conditions was quite small compared to the other taxa, with very little influence of R:FR.

The development of ramin melawis seedings is mostly influenced by light intensity (PFD). Coefficients of determination for the treatment variables of intensity and spectral quality (R:FR) allowed an assessment of their contribution within the range of 2.5 to 13 % of full sunlight. The only morphological characteristics that were more strongly affected by R:FR were internode length and leaf area/stem length (Table 6). From a small sample of European herbs, Morgan and Smith (1979) proposed that shade intolerant species should respond most strongly to reduced R:FR. Kwesiga and Grace (1986) extended this generalisation in their study of two African trees. The results reported here suggest that such generalisations do not hold. These results are consistent with those of Lee (1988) and Lee *et al.* (1996). Most of the measured characteristics in these seedlings were significantly affected by PFD. The most strongly affected characters were % leaf allocation, % stem allocation, % of leaf loss and specific leaf mass. Effects of shading on seedling development are markedly reduced compared to six other taxa studied by the same methods (Lee *et al.* 1996).

Interactions between PFD and R:FR were only significant for specific leaf mass. Interaction effects might be expected if spectrally altered reflected radiation from adjacent plants could influence development in the spectrally neutral (LRR or MRR) environments (Ballare *et al.* 1992). These results indicate that such neighborhood effects are not important for these seedlings.

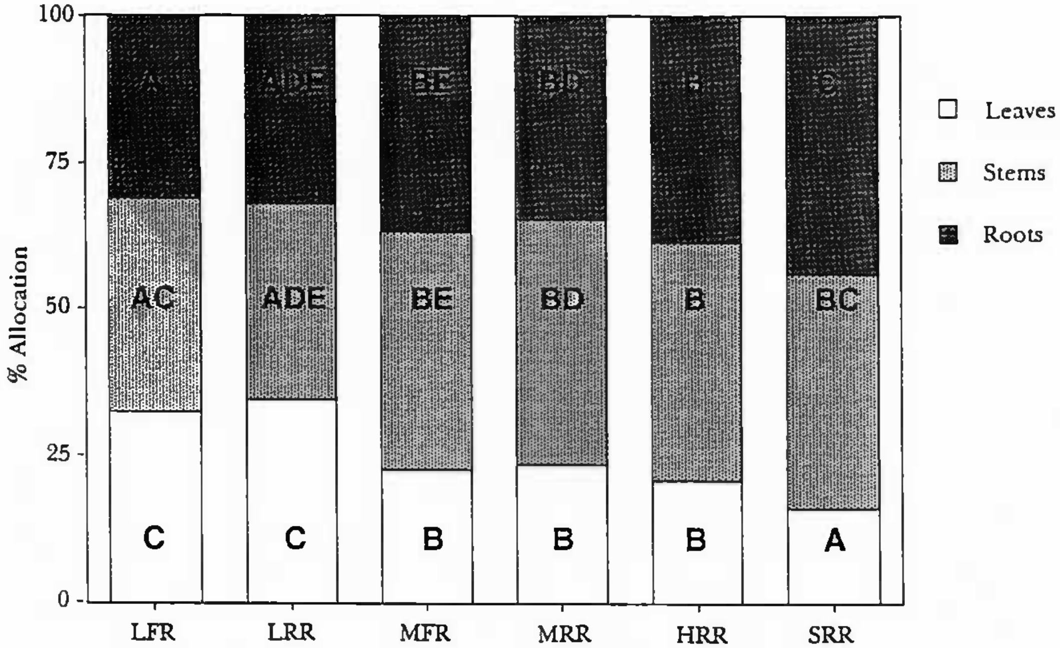

Figure 2. Percentage allocations of biomass to leaves, stems and roots. Treatment abbreviations are described in Table 1. Treatments not sharing letters are significantly different from each other.

Table 6. Coefficients of determination for treatment effects at low and medium light intensities

Character	R:FR	PFD	Interactions	Total
Mass/day	0.016	0.162*	0.000	0.177
Mass/mol	0.013	0.014	0.007	0.034
Collar diameter	0.001	0.047*	0.001	0.049
Internode length	0.098*	0.023	0.002	0.123
% Stem allocation	0.008	0.204*	0.015	0.227
% Leaf allocation	0.005	0.287*	0.001	0.293
% Root allocation	0.000	0.068*	0.004	0.072
Mean leaf area	0.010	0.107*	0.001	0.118
Specific leaf mass	0.001	0.098*	0.052*	0.151
% Leaf loss	0.016	0.159*	0.005	0.180
Leaf area/stem length	0.059*	0.039*	0.010	0.108
Stem mass/length	0.009*	0.062*	0.005	0.076
Branch/trunk internodes	0.000	0.000	0.000	0.000

* Indicates significance below 0.05 for 2-way ANOVA.

Conclusion

Seedlings of ramin melawis (*Gonostylus bancanus*) are relatively shade intolerant, growing most rapidly in partial sunlight. Seedlings develop a very robust main axis, branch sparingly in early development, and allocate a small portion of their photosynthate to leaf production. Leaf area is further reduced by the high specific mass of the leaves. Such a morphology helps explain the low growth rates of these seedlings. Robust stems and leaves may protect against damage from falling branches and herbivores.

These low growth rates and small height increases suggest to us that the seedlings of ramin melawis are not competitive in most forest conditions, but more successful under the inundated conditions in swamp forest where more rapidly growing generalists cannot establish. In swamp forests successful establishment of ramin melawis seedlings will require a fairly open canopy.

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