Simulating Forest Shade to Study the Developmental Ecology of Tropical Plants: Juvenile Growth in Three Vines in India

David W. Lee

Journal of Tropical Ecology, Vol. 4, No. 3 (Aug., 1988), 281-292.

Simulating forest shade to study the developmental ecology of tropical plants: juvenile growth in three vines in India

DAVID W. LEE

Department of Biological Sciences, Florida International University, Miami, FL 33199, USA

ABSTRACT. Both light quantity and quality affect the development and autoecology of plants under shade conditions, as in the understorey of tropical forests. However, little research has been directed towards the relative contributions of lowered photosynthetic photon flux density (PPFD) versus altered spectral distributions (as indicated by quantum ratios of 660 to 730 nm, or R:FR) of radiation underneath vegetation canopies. A method for constructing shade enclosures to study the contribution of these two variables is described. Three tropical leguminous vine species (*Abrus precatorius* L., *Caesalpinia bondicela* Fleming and *Mucuna pruriens* (L.) DC.) were grown in two shade enclosures with 3–4% of solar PPFD with either the R:FR of sunlight (1.10) or foliage shade (0.33), and compared to plants grown in sunlight. Most species treated with low R:FR differed from those treated with high R:FR in (1) percent allocation to dry leaf weight, (2) internode length, (3) dry stem weight/length, (4) specific leaf weight, (5) leaf size, and (6) chlorophyll a/b ratios. However, these plants did not differ in chlorophyll content per leaf dry weight or area. In most cases the effects of low R:FR and PPFD were additional to those of high R:FR and low PPFD. Growth patterns varied among the three species, but both low PPFD and diminished R:FR were important cues in their developmental responses to light environments. This shadehouse system should be useful in studying the effects of light on the developmental ecology of other tropical forest plants.

KEY WORDS: developmental ecology, forest shade, India, photosynthetic photon flux density (PPFD), red/far red, shadehouse, vine.

INTRODUCTION

All plants develop and function in response to the particular light environments in which they grow. Although numerous studies have been conducted on plant developmental responses to reduced irradiance, the experimental conditions have hardly ever been comparable to those that plants experience under the natural shade of vegetation. Light passing through vegetation is attenuated in the fluence rate affecting photosynthesis (quanta between 400–700 nm, or the photosynthetic photon flux density - PPFD). Foliage shade light is also altered in its spectral quality, and this shift can profoundly affect plant development. Leaves absorb radiation strongly in the range of 400–700 nm and very weakly at 750–1100 nm (Lee & Graham 1986). Thus, as radiation passes through foliage the ratio of quanta centering on 660 nm is reduced in relation

to quanta at 730 nm. This red to far-red ratio (the R:FR of Smith 1982) is approximately 1.10–1.25 under full sunlight and as little as 0.10 under forest canopies (Lee 1987, Tasker & Smith 1976). These two wavelengths affect the ratios of the Pfr and Pr forms of phytochrome, and can alter plant development in many ways (Smith 1981). Thus, the shortcoming in most previous studies of shade effects on plant development is that the PPFD reductions have not been accompanied by reductions in R:FR, conditions that plants would normally experience in natural environments.

The deficiency of research on the effects of natural shade on plant development, as well as on the effects of reduced PPFD compared to lowered R:FR, has been partly due to ignorance about the spectral quality of natural shade. The difficulty in devising experimental conditions that approximate natural shade has also contributed. Phytochrome equilibria have been altered by adding end-of-day doses of R or FR radiation (see Kasperbauer & Hamilton 1984), but such conditions do not occur in nature. The slight decreases in R:FR at sunset and sunrise are not sufficient to affect the phytochrome system (Salisbury 1981, Vince-Prue 1983). Some research has been conducted in growth chambers (Heathcote *et al.* 1979, Hébant & Lee 1984), but the difficulty of removing heat from incandescent lamps has limited the research to small plants and short experimental periods (Kwesiga & Grace 1986, Morgan & Smith 1981). Most previous research on the effects of reduced R:FR on plant development has been primarily due to the efforts of one scientist and his former students (Smith 1982). The latter research has also been limited in its ecological amplitude, primarily being studies of small European woodland herbs. Thus, there is a need to devise new experimental methods and to study other types of plants.

The little research completed to date suggests that shade-intolerant plants may be more affected by exposure to low R:FR radiation than shade-tolerant species (Corre 1983, Morgan & Smith 1979). In shade intolerant species lowered R:FR (1) promotes stem elongation, (2) reduces branch initiation, (3) promotes dry weight allocation to stems, and (4) affects leaf area and specific weight (Child *et al.* 1981, Corre 1983, Frankland & Letendre 1978, Kasperbauer 1971, LeCharney & Jacques 1982, McLaren & Smith 1978, Vince-Prue 1977, Whitlam & Johnson 1982, Young 1981). In these plants shade light promotes a 'searching' growth strategy whereas sunlight promotes an 'exploiting' growth response (Grime 1979).

Lee (1985) has developed a pigment combination which reduces R:FR as it reduces PPFD. It can be sprayed as a translucent varnish on any transparent medium, and the spectral distribution of sunlight passing through the film is very similar to shade-light underneath foliage. Plants grown under this film can be compared with those grown under light with the same PPFD but spectrally identical to sunlight (Richards & Lee 1986). The uniform climates of tropical latitudes provide ideal conditions for long-term experiments using shade-houses. The purpose of this paper is to describe an experimental shadehouse

system for studying the effects of reduced PPFD and lowered R:FR on plant development and to report the effects of these alterations on the juvenile growth of three tropical leguminous vines.

MATERIALS AND METHODS

The plants were grown from seed in three light environments constructed at the ASPEE Agricultural Research and Development Foundation Farm, Met, Thana District, Maharasthra State, India. Plants were grown in 61 cm^2 plots (randomized block design) in a 3.05 X 6.10 m raised bed of the local black cotton soil mixed with cow manure. One light environment was full sunlight. Two 3.05 X 6.10 m shadehouses were constructed adjacent to this bed, each with a south-facing roof on a 1.83 m to 1.22 m pitch. The houses were constructed of locally available pole timber and were covered with woven polyethylene fabric with a polyethylene film laminated to it. This fabric was subsequently spray-painted with either a black oil-based paint or a clear-base paint with experimental pigments (Lee 1985). The black film reduced light levels to 3.1 ± 1.0% (N = 20) of full sunlight PPFD at solar zenith. Since the fabric shaded out 50% of solar PPFD it was necessary to revise the pigment ratios in the experimental coating to 10 parts CI pigment violet 23:one part CI disperse yellow 64. The experimental film reduced light levels to 3.9 ± 0.6% (N = 20) of full sunlight. Fluence rates were measured with a Li-185 radiometer with a 190-S quantum sensor (Li-Cor Instruments, Lincoln, NB 68504, USA). Spectral quality of radiation within the houses and in full sunlight was measured with a Li-Cor 1800 spectroradiometer with a bandwidth of 6 nm. The R:FR ratio of the black shadehouse was 1.10 ± 0.01 (N = 5), that of the experimental house was 0.33 ± 0.01 (N = 5), a ratio chosen because of similar values measured in the shade of nearby moist deciduous forest (Lee, unpublished results, see Figure 1). These measurements were made under sunlight with a R:FR ratio of 1.18; sunlight ratios varied between 1.10–1.18 during the experimental period. The R:FR ratios in the house did not change substantially during the experimental period. Maximum PPFD at solar zenith ranged from 1560 μmol m^{-2} s^{-1} in January to 1760 μmol m^{-2} s^{-1} in March. Temperatures were measured at plant height with maximum–minimum thermometers. To minimize excess temperatures in the houses a ventilation system was installed and the plants were watered by fine spray with a simple sprinkler system. Both of these features insured that house temperatures did not exceed those outside (maximum of 42°C during the experiment). However, the average temperatures in the houses were higher than those outside, as were the soil temperatures. The relative humidity in the houses, although not measured, was very high, while that in the outside bed was much lower.

Seeds of three vine species were obtained from woodlands and field margins adjacent to the ASPEE Experimental Farm. *Caesalpinia bondicela* Fleming and
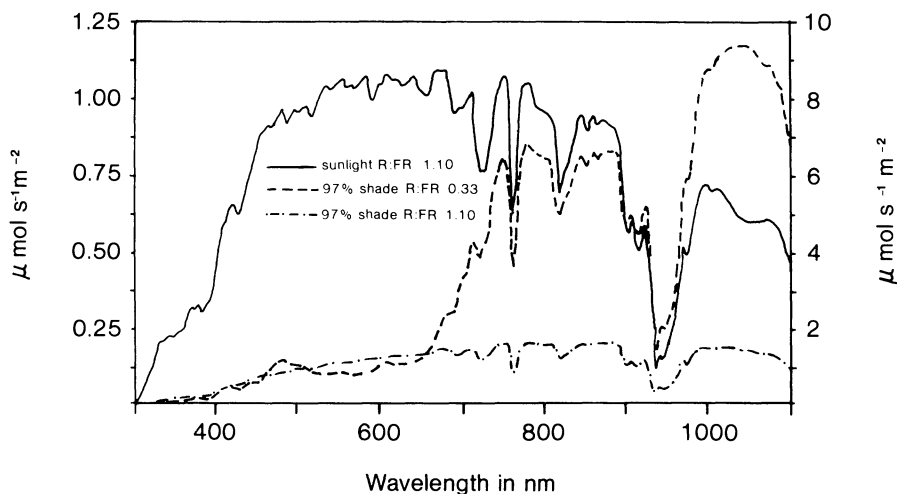
Figure 1. Spectral distribution of radiation for the three treatments. Legend for each treatment is given in the figure. Scale on the left side is for the shade treatments, that on the right is for full sunlight.

Mucuna pruriens (L.) DC. are native to the region, and *Abrus precatorius* L. is a well-established exotic. The plants were grown from seed for 74 days, from January through March in 1985, then five undamaged plants of each species and treatment were harvested and measured. The measurements quantified previously described growth strategies (Grime 1979). These measurements included (1) percentage dry weight allocation to leaves, stems and roots, (2) stem mass per length, or robustness, (3) leaf area per stem weight, (4) leaf area per stem length, and (5) length between second and third leaf. Additional measurements of two leaves (from the fourth to eighth to appear) per plant were chosen to document known responses in leaf anatomy and pigment composition to shade conditions (Björkman 1981): (1) specific leaf weight, (2) leaf area, (3) chlorophyll content per unit area and dry weight, (4) chlorophyll a/b ratio, (5) leaf thickness, (6) palisade parenchyma thickness, and (7) stomatal density. Mature fresh leaves were used for chlorophyll determinations by grinding pieces totalling 2 cm^2 in a small mortar and pestle and adding 80% acetone until no more pigment was extractable from the leaf pulp. Absorbance was measured with a cuvette holder attached via the fibre optic cable to the Li-1800, and chlorophyll concentrations and a/b ratios determined (Arnon 1949). Other measurements, including specific leaf weights and internode lengths, were from plants dried at 60°C for 48 hours. Leaf areas were measured with a planimeter. Small fresh leaf samples were fixed in 1% glutaraldehyde in 0.08 M phosphate buffer at pH 6.5 for later analysis of leaf anatomical characters. Leaf thickness and other features were measured from hand sections, with an ocular micrometer. Stomatal densities were counted from material cleared by immersion in 5% NaOH in 50% ethanol.

The three treatments of each species were compared by ANOVA, with differences considered significant at a level of P less than 0.05. The two low light

treatments were compared with the students t test, with a 0.05 level of significance.

<div align="center">RESULTS</div>

The three species grew well in both shadehouse environments as well as in open sunlight. Initial germination and growth was more rapid in the shadehouses, probably because the average soil temperature was higher than in the open. Once established, dry mass accumulated more rapidly in plants exposed to full sunlight (treatment C). For all species plant height or total stem length was greater in the shadehouses, and plant dry weight was greater in the full sunlight treatment. Treatments within species varied for most of these measurements, particularly full sunlight (C) versus shadehouse treatments (A and B). Plant architecture was changed by shadelight in the following ways (Table 1): stem mass per unit length was less; leaf area per unit stem weight was more; and internode length was greater. The percentage of dry mass allocation to leaves was greater in two species, but less in *A. precatorius* (AP), and the opposite was true for stem allocation. Unit leaf area per stem length was smaller, except for *M. pruriens* (MP). Similar differences were measured for leaf structure and pigment composition (Table 2). For the sunlight-exposed plants specific leaf weight was greatest, palisade and leaf thicknesses were greatest, stomatal densities were higher, chlorophyll a/b ratios were higher, and amount of chlorophyll per unit leaf dry weight was smaller. Leaf area was generally greater in the direct sunlight treatments (Figures 2 and 3), with the exception of *C. bondicela* CB, (Figure 4). Chlorophyll content per unit leaf area varied among the three taxa.

There were also differences between the two shade treatments, but these varied among the three taxa. In measurements of plant architecture (Table 1) plants grown under conditions of low R:FR were different from those grown at high R:FR. Percentages of dry mass allocation to leaves were less in MP, more
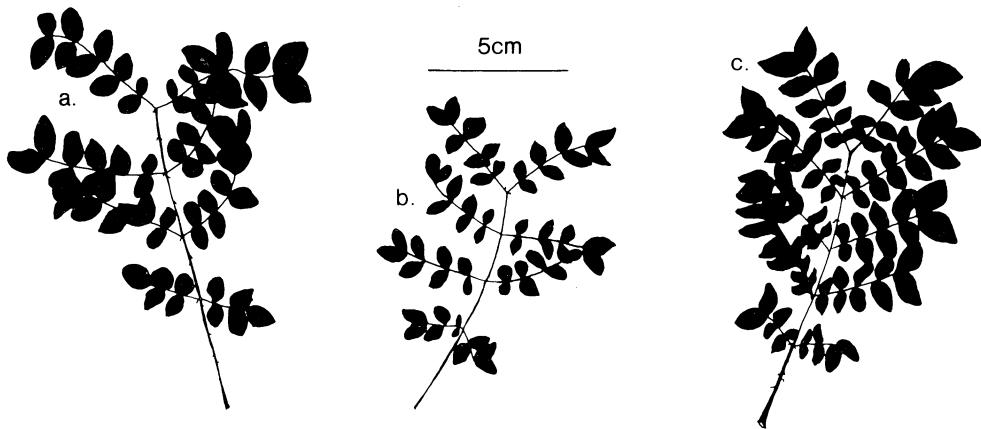

Figure 2. Silhouettes of leaves of *Caesalpinia bondicella*. a. is for 97% shade and R:FR of 0.33; b. is for 97% shade and R:FR of 1.10; c. is for full sunlight. Scale is given in the figure.

Table 1. Data and statistical analyses for measurements of plant architecture of the three species and three treatments. F values and significance for ANOVA are given, as are t values and levels of significance for the pair-wise students t test between treatments A and B.

Species and treatment	Plant architecture						
	% dry wt leaves	% dry wt stems	% dry wt roots	Stem wt (mg)/length (cm)	Leaf area (cm²)/stem wt (mg)	Leaf area (cm²)/stem length (cm)	Internode distance (cm)
Abrus precatorius (AP)							
A 3% PPFD; R:FR = 0.33	0.576 ± 0.019	0.327 ± 0.033	0.097 ± 0.017	4.22 ± 0.65	0.958 ± 0.050	4.05 ± 0.79	1.0 ± 0.3
B 3% PPFD; R:FR = 1.10	0.510 ± 0.019	0.396 ± 0.016	0.095 ± 0.024	2.65 ± 0.50	0.979 ± 0.148	2.52 ± 0.70	1.5 ± 0.2
C 100% PPFD; R:FR = 1.10	0.540 ± 0.027	0.336 ± 0.025	0.124 ± 0.046	15.79 ± 5.97	0.310 ± 0.083	5.04 ± 2.73	0.3 ± 0.1
F	11.19, < 0.01	10.94, < 0.01	3.40, < 0.05	21.26, < 0.01	69.66, < 0.01	2.80, < 0.05	13.05, < 0.1
tA + B	5.39, < 0.01	4.24, < 0.01	0.20, NS	4.28, < 0.01	0.307, NS	3.24, < 0.02	3.07, < 0.2
Caesalpinia bondicella (CB)							
A	0.344 ± 0.040	0.504 ± 0.057	0.144 ± 0.076	54.8 ± 21.5	0.234 ± 0.33	5.10 ± 1.24	5.4 ± 1.6
B	0.357 ± 0.019	0.466 ± 0.019	0.177 ± 0.022	41.8 ± 5.6	0.293 ± 0.68	3.77 ± 0.82	6.2 ± 1.7
C	0.481 ± 0.025	0.359 ± 0.022	0.159 ± 0.025	123.9 ± 45.0	0.211 ± 0.013	26.10 ± 9.90	2.1 ± 3.0
F	33.75, < 0.01	20.73, < 0.01	0.61, NS	11.71 < 0.01	4.59, < 0.01	23.47, < 0.01	4.94, < 0.01
tA + B	1.67, NS	1.41, NS	0.95, NS	1.38, NS	1.76, NS	2.00, NS	0.83, NS
Mucuna pruriens (MP)							
A	0.414 ± 0.017	0.543 ± 0.021	0.044 ± 0.007	2.78 ± 0.60	0.511 ± 0.057	1.39 ± 0.18	19.1 ± 4.6
B	0.486 ± 0.027	0.467 ± 0.029	0.048 ± 0.005	2.86 ± 0.77	0.772 ± 0.109	2.20 ± 0.65	15.2 ± 4.5
C	0.544 ± 0.036	0.382 ± 0.058	0.073 ± 0.043	8.18 ± 2.50	0.272 ± 0.072	1.92 ± 0.44	7.8 ± 4.3
F	27.90, < 0.01	21.10, < 0.05	2.02, NS	19.96, <0.05	46.07, < 0.01	3.89, < 0.05	35.89, < 0.01
tA + B	5.03, < 0.01	4.76, < 0.01	1.00, NS	0.20, NS	4.73, < 0.01	2.67, < 0.05	2.14, < 0.05

Table 2. Data and statistical analyses for measurements of leaf parameters of the three species and three treatments. Legends for F and tA + B are as for Table 2.

| Species and treatment	Leaf characters							
	Specific leaf mg/cm²	Leaf area cm²	Chlorophyll a/b	mg chlorophyll/ g dry wt	mg chl/ cm² leaf	Palisade thickness (μm)	Leaf thickness (μm)	Stomatal density (10^3/cm²)
Abrus precatorius (AP)								
A 3% PPFD; R:FR = 0.33	1.86 ± 0.24	7.97 ± 1.63	2.11 ± 0.09	14.90 ± 2.72	0.028 ± 0.005	14 ± 3	76 ± 6	4.88 ± 1.07
B 3% PPFD; R:FR = 1.10	1.34 ± 0.21	5.20 ± 0.49	2.10 ± 0.01	17.59 ± 3.96	0.024 ± 0.005	19 ± 3	100 ± 13	8.39 ± 0.54
C 100% PPFD; R:FR = 1.10	5.49 ± 1.33	5.46 ± 0.80	2.35 ± 0.13	4.56 ± 0.72	0.025 ± 0.004	55 ± 10	129 ± 15	12.11 ± 1.47
F	40.76, <0.01	9.92, <0.01	6.62, <0.01	18.02, <0.01	0.52, NS	98.59, <0.01	43.89, <0.01	44.17, <0.01
tA + B	3.66, <0.1	3.64, <0.01	0.062, NS	0.967, NS	0.955, NS	3.02, <0.02	4.63, <0.01	4.67, <0.01
Caesalpinia bondicella (CB)								
A	2.89 ± 0.19	41.3 ± 3.4	2.04 ± 0.06	14.12 ± 1.79	0.041 ± 0.003	50 ± 4	152 ± 17	9.34 ± 0.76
B	2.69 ± 0.38	33.2 ± 3.1	2.19 ± 0.01	15.97 ± 1.94	0.042 ± 0.003	58 ± 5	166 ± 21	10.06 ± 1.25
C	6.38 ± 0.73	63.9 ± 21.3	2.53 ± 0.26	6.0 ± 1.88	0.026 ± 0.004	95 ± 14	239 ± 36	13.30 ± 1.98
F	178.9, <0.01	8.10, <0.01	12.27, <0.01	40.08, <0.01	31.46, <0.01	64.64, <0.01	28.2, <0.01	11.02, <0.01
tA + B	1.49, NS	4.02, <0.01	3.15, <0.02	1.565, NS	0.738, NS	3.70, <0.01	1.47, NS	0.85, NS
Mucuna pruriens (MP)								
A	1.50 ± 0.11	37.8 ± 9.8	2.06 ± 0.12	20.53 ± 2.86	0.031 ± 0.004	22 ± 6	81 ± 10	10.16 ± 1.09
B	1.36 ± 0.11	39.1 ± 5.5	2.27 ± 0.09	23.07 ± 1.11	0.031 ± 0.002	29 ± 3	98 ± 17	9.42 ± 1.68
C	5.43 ± 0.75	30.3 ± 14.7	2.93 ± 0.89	7.32 ± 1.76	0.042 ± 0.009	71 ± 34	202 ± 41	25.58 ± 6.1
F	271.1, <0.01	0.16, NS	3.73, <0.01	107.95, <0.01	3.56, <0.05	50.08, <0.01	62.80, <0.01	33.75, <0.01
tA + B	2.82, <0.05	0.44, NS	3.24, <0.02	2.169, NS	0.325, NS	3.48, <0.02	2.66, <0.05	0.85, NS
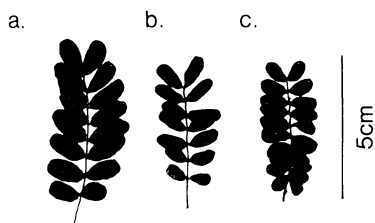
Figure 3. Silhouettes of leaves of *Abrus precato-rius*. a., b. and c. are as for Figure 2.
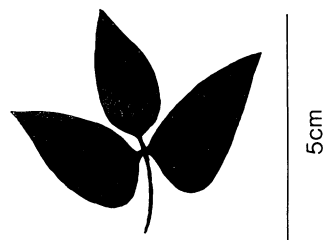
Figure 4. Silhouettes of leaf of *Mucuna pruriens*. Leaf size and shape of all treatments were the same.

in AP, and not different in CB, and the opposite was seen in biomass allocation to stems. There were no differences in allocation to roots. The ratio of stem mass per length was greater only for AP, but leaf area per unit stem weight was less for all three taxa grown at low R:FR. Leaf area per stem length was less for MP, more for AP and not different for CB. Internode lengths were smaller in AP, more in MP, and not different in CB. Differences between species were also observed for leaf structure and pigment composition (Table 2). Specific leaf weight was greater for low R:FR treatments of AP and MP, but not different for CB. Leaf areas were greater in AP and CB, but not different for MP (Figures 2–4). There were no differences in chlorophyll content of leaves on a weight or area basis for any of the species, but chlorophyll a/b ratios were lower in CB and MP. For the low R:FR treatment (A) the leaves were thinner in all species but CB, and the palisade layer was thinner in all species. Stomatal densities were lower only in AP.

DISCUSSION

Shadehouse performance

The shadehouses worked well in these field conditions. The woven poly-ethylene fabric, without UV-protectant chemicals, had begun to deteriorate by the end of the experimental period, but the spectral properties of the spray-painted fabric did not change during this time. In most parts of the world UV-stable shade films are available for construction of shadehouses; all should be suitable providing they transmit a minimum of 50% of visible radiation. It will be necessary to change the ratios of the experimental pigments depending upon the combinations of the required shading and spectral alteration. Where the film is highly transparent the formulation of Lee (1985) may be used. In this study the woven film absorbed 50% of PPFD, and the pigment ratio was altered to give the required R:FR. The film and paint may be measured with a spectro-radiometer, or with a spectrophotometer and calculated for spectral scans of sunlight.

Since the spray paints, black or experimental, strongly absorb radiation, it is important to control temperature in the houses. For these experiments the

maximum daily temperatures could be maintained at ambient levels through the construction of ventilation ports that were covered to prevent the penetration of direct skylight. Since the roof was pitched hot air rose to the highest point within the houses and passed out of the ventilation ports. The evaporative cooling of the water sprayed during midday also assisted. The principal problem in building shadehouse structures of varying dimensions will be that of temperature control, but temperature can be kept at or below ambient through a combination of venting and evaporative cooling by a fog system or cooling pads. It was not possible to compare the growth rates of plants in the two shadehouses because of slight differences in quantum flux densities between the two. The differences of $3.1 \pm 1.0\%$ of solar PPFD for the black treatment and $3.9 \pm 0.6\%$ seem small, but the latter is 26% greater than the former. In future studies it will be possible to more carefully adjust light intensity to compare growth rates. The growing conditions in the shadehouses were very similar in temperature and high relative humidity and differed in these variables from the sunlight treatment. It will be possible to develop a high light treatment with similar microclimatic conditions by construction of a shadehouse using a low percentage shade fabric.

An additional advantage of this shadehouse system is its low cost. The construction of the two shadehouses described in this report cost less than US$200. Much physiological research suffers from the problem of 'pseudoreplication' (Hurlbert 1984). These shadehouses can be duplicated inexpensively to create more rigorous experimental designs to study the effects of light quantity and quality on plant growth.

Plant development

Two of the species grown under shade (*Mucuna pruriens* and *Caesalpinia bondicela*) adopted a developmental pattern of reduced allocation to photosynthetic assimilation (smaller proportion of leaf weight and less investment per unit leaf weight). These are typical plant responses to shade conditions (Björkman 1981, Grime 1979), and both reduced PPFD and lowered R:FR contributed to the plant response. In *Abrus precatorius* the shade treatment of low R:FR (A) produced larger leaves and higher percentage of dry weight as leaves than the other treatments (Tables 1 and 2, Figure 3). *A. precatorius* had a heteroblastic sequence as a seedling. The first 14–15 leaves had very short internodes. Then the internode distance abruptly increased and the plant adopted a viny habit. Thus, in *A. precatorius* the early response to natural shade is greater investment in photosynthetic assimilation. *M. pruriens* developed as a prostrate vine in all treatments, and *C. bondicela* developed in an erect fashion, with more rapid vertical growth in the shade treatments.

Lowered resource allocation to leaves is considered an important developmental response to shade conditions in shade intolerant plants (Corre 1983, Grime 1979, Morgan & Smith 1979). This allocation is normally measured as a percentage of total plant dry weight, but such measurements may be misleading.

What is really important is allocation of resources to leaf surface area, or the unit of light absorptance. Leaf surface area is partially dependent upon allocation of dry weight, but equally dependent upon leaf specific weight. Although *C. bondicella* and *M. pruriens* had lowered percentages of leaf dry weight in plants grown under low R:FR, leaf area per unit stem length was greater in the former and less in the latter. In *A. precatorius* leaf area/stem lengths in full sunlight and low R:FR treatments were not different.

None of the species studied responded to lowered PPFD and R:FR in the same way, although both variables were important in controlling developmental responses to shade. These results contrast with the small sample, primarily of temperate herbs, reported in the literature. Previous research has shown that lowered PPFD is very important in determining leaf thickness and anatomical features (Chabot & Chabot 1977, Dengler 1980, Jurik *et al*. 1982). My results indicate that lowered R:FR has an additional effect. Palisade mesophyll was significantly thinner in the low R:FR treatments among the three species, and leaves were thinner in *M. pruriens* and *A. precatorius*. Thus, the syndrome of leaf adaptations to extreme shade (Björkman 1981) was controlled by both reduced PPFD and lowered R:FR in these species. Branching has been shown to be promoted by full sunlight, and suppressed by low R:FR. In these results only the sunlight-grown plants of *M. pruriens* branched significantly, and this branching was only partly suppressed by both low R:FR and low PPFD treatments.

Some of the developmental changes described here, induced by both low R:FR and reduced PPFD, have important physiological consequences for the plants. Leaf thickness and palisade thickness affect the carbon dioxide diffusion characteristics within leaves. Decreases in stomatal density, affected by lowered PPFD in the three vines and additionally affected by low R:FR in *A. precatorius*, control CO_2 uptake as well as water relations. Decreases in chlorophyll a/b ratios, affected by lowered PPFD in the three species and lowered R:FR in *C. bondicela* and *M. pruriens*, reflect differences in chloroplast ultastructure, and greater allocations to Photosystem II compared to Photosystem I reaction centres (Glick *et al*. 1985, Kasperbauer & Hamilton 1984). Thus, lowered PPFD and R:FR affect growth strategies and also physiological processes.

Previous research has demonstrated that shade-intolerant herbs are strongly affected by both lowered PPFD and R:FR (Corre 1983, Morgan & Smith 1979). The most important conclusion from this research is that lowered PPFD and R:FR not only affect another ecological group differently, but also taxa within one group differently. The three species studied here are all leguminous vines native to tropical forests, yet each responded differently to light quantity and quality. Thus, although both light quantity and quality are important environmental determinants affecting plant development, the pattern of developmental response may be unique for each species, depending upon its specific ecological requirements. Lowered R:FR is an environmental cue that plants can use in a

variety of ways to mediate an appropriate developmental response to the light climate.

The experimental shadehouses used in this research should prove useful in analysing the shade responses of other tropical plants.

LITERATURE CITED

ARNON, D. I. 1949. Copper enzymes in isolated chloroplasts. Polyphenoloxidase in *Beta vulgaris. Plant Physiology* 24:1-5.

BJÖRKMAN, O. 1981. Responses to different quantum flux densities. Pp. 57-107 in Lange, O. L., Nobel, P. S., Osmond, C. B. & Ziegler, H. (eds). *Physiological plant ecology* I. Encyclopaedia of Plant Physiology, N.S., 12A. Springer-Verlag, Heidelberg.

CHABOT, B. F. & CHABOT, J. F. 1977. Effects of light and temperature on leaf anatomy and photosynthesis in *Fragaria vesca. Oecologia*, Berlin 26:363-377.

CHILD, R., MORGAN, D. C. & SMITH, H. 1981. Morphogenesis in simulated shadelight quality. Pp. 409-420 in Smith, H. (ed.). *Plants and the daylight spectrum.* Academic Press, New York. 508 pp.

CORRE, W. J. 1983. Growth and morphogenesis of sun and shade plants II. The influence of light quality. *Acta Botanica Nederlandica* 32:185-202.

DENGLER, N. G. 1980. Comparative histological basis of sun and shade leaf dimorphism in *Helianthus annus. Canadian Journal of Botany* 58:717-730.

FRANKLAND, B. & LETENDRE, R. J. 1978. Phytochrome and effects of shading on growth of woodland plants. *Photochemistry and Photobiology* 27:223-230.

GLICK, R. E., McCAULEY, S. W. & MELIS, A. 1985. Effect of light quality on chloroplast-membrane organization and funtion in pea. *Planta* 164:487-494.

GRIME, J. P. 1979. *Plant strategies and vegetation processes.* John Wiley, New York. 222 pp.

HEATHCOTE, L., BAMBRIDGE, K. R. & MCLAREN, J. S. 1979. Specially constructed growth cabinets for simulation of the spectral photon distributions found under natural vegetation canopies. *Journal of Experimental Botany* 30:347-353.

HÉBANT, C. & LEE, D. W. 1984. Ultrastructural basis and developmental control of blue iridescence in *Selaginella* leaves. *American Journal of Botany* 71:216-219.

HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187-211.

JURIK, T. W., CHABOT, J. W. & CHABOT, B. F. 1982. Effects of light and nutrients on leaf size, CO_2 exchange, and anatomy in wild strawberry (*Fragaria virginiana*). *Plant Physiology* 70:1044-1048.

KASPERBAUER, M. J. 1971. Spectral distribution of light in a tobacco canopy and effects of end-of-day light quality on growth and development. *Plant Physiology* 47:775-778.

KASPERBAUER, M. J. & HAMILTON, J. L. 1984. Chloroplast structure and starch grain accumulation in leaves that received different red and far-red levels during development. *Plant Physiology* 74:967-970.

KWESIGA, F. & GRACE, J. 1986. The role of the red/far-red ratio in the response of tropical tree seedlings to shade. *Annals of Botany* 57:283-290.

LECHARNEY, A. &. JACQUES, R. 1982. Photo-inhibition of internode elongation rate in light-grown *Vigna sinensis* L. Control by light quality. *Plant, Cell and Environment* 5:31-36.

LEE, D. W. 1985. Duplicating foliage shade for research on plant development. *HortScience* 20:116-118.

LEE, D. W. 1987. The spectral distribution of radiation in two neotropical forests. *Biotropica* 19:161-166.

LEE, D. W. & GRAHAM, R. 1986. Leaf optical properties of rain-forest sun and extreme shade plants. *American Journal of Botany* 73:1100–1108.

McCLAREN, J. S. SMITH, H. 1978. Phytochrome control of the growth and development of *Rumex obtusifolius* under simulated canopy light environments. *Plant, Cell and Environment* 1:61–67.

MORGAN, D. C. R. & SMITH, H. 1979. A systematic relationship between phytochrome-controlled development and species habitat, for plants grown in simulated natural radiation. *Planta* 145:253–258.

MORGAN, D. C. R. & SMITH, H. 1981. Control of development in *Chenopodium album* L. by shade-light: the effect of light quantity (total fluence rate) and light quality (red/far-red ratio). *New Phytologist* 88:239–248.

RICHARDS, J. H. & LEE, D. W. 1986. Light effects on leaf morphology in water hyacinth (*Eichhornia crassipes*). *American Journal of Botany* 73:1741–1747.

SALISBURY, F. B. 1981. Twilight effect: initiating dark measurement in photoperiodism of *Xanthium*. *Plant Physiology* 67:1230–1238.

SMITH, H. (ed.). 1981. *Plants and the daylight spectrum.* Academic Press, New York. 508 pp.

SMITH, H. 1982. Light quality, photoreception and plant strategy. *Annual Review of Plant Physiology* 33:481–518.

TASKER, R. & SMITH, H. 1976. The function of phytochrome in the natural environment. V. Seasonal changes in radiant energy quality. *Photochemistry and Photobiology* 16:487–481.

VINCE-PRUE, D. 1977. Photocontrol of stem elongation in light-grown plants of *Fuchsia hybrida*. *Planta* 133:149–156.

VINCE-PRUE, D. 1983. The perception of light-dark transitions. *Philosopical Transactions of the Royal Society of London* B303:523–536.

WHITLAM, G. C. & C. B. JOHNSON. 1982. Photomorphogenesis in *Impatiens parviflora* and other species under simulated natural canopy radiations. *New Phytologist* 90:611–618.

YOUNG, J. E. 1981. Light quality and stem growth in *Impatiens parviflora* DC. *New Phytologist* 89:47–59.