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THE DEVELOPMENTAL RESPONSES OF PAPAYA LEAVES TO SIMULATED CANOPY SHADE[1]

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The developmental responses of plants to shade underneath foliage are influenced by reductions in irradiance and shifts in spectral quality (characterized by reductions in the quantum ratio of red to far-red wavelengths, R:FR). Previous research on the influence of shadelight on leaf development has neglected the reductions in R:FR characteristic of foliage shade, and these studies have almost certainly underestimated the extent and array of developmental responses to foliage shade. We have studied the effects of reduced irradiance and R:FR on the leaf development of papaya (*Carica papaya* L., Caricaceae). Using experimental shadehouses, replicates of plants grown in high light conditions (0.20 of sunlight and R:FR = 0.90) were compared to low light conditions (0.02 of sunlight) with either the spectral quality of sunlight (R:FR = 0.99) or of foliage shade (F:FR = 0.26). Although many characteristics, such as leaf thickness, specific leaf weight, stomatal density, palisade parenchyma cell shape, and the ratio of mesophyll air surface/leaf surface were affected by reductions in irradiance, reduced R:FR contributed to further changes. Some characters, such as reduced chlorophyll a/b ratios, reduced lobing, and greater internode length, were affected primarily by low R:FR. The reduced R:FR of foliage shade, presumably affecting phytochrome equilibrium, strongly influences the morphology and anatomy of papaya leaves.

Light is the most important environmental factor influencing the normal development of plants. Irradiance is normally reduced by the filtering effect of foliage by the same or neighboring plants. Leaves transmit and reflect little of the visible wavelengths and most of the wavelengths above 700 nm (Gates et al., 1965; Lee and Graham, 1987). Thus, solar radiation reflected by or transmitted through foliage is deficient in quanta in the visible wavelengths and relatively enriched in quanta above 700 nm. Smith (1982, 1986) was the first to stress the developmental significance of this spectrally altered shade light and the importance of phytochrome as a means of the "perception" of change in spectral quality. Spectral quality can thus be characterized by the ratio of quanta at 660 and 730 nm, using a 10-nm bandwidth and the symbol R:FR, as suggested by Smith (1982). Solar radiation typically has an R:FR of 1.05–1.25, and the R:FR of canopy shade may be reduced to 0.15 (Tasker and Smith, 1976; Lee, 1987).

The responses of plants to reduced irradiance, particularly in leaf structure, has been documented by numerous studies (Isonagle, 1944; Cormack, 1955; Jackson, 1967; Chabot and Chabot, 1977; Dengler, 1980; Jurik, Chabot, and Chabot, 1982). Little is known about the influence of reduced R:FR compared to that of decreased irradiance (or of light quantity vs. quality) on plant development, however. These studies incorporated shade fabrics that reduced solar irradiance without changing spectral quality or used varying numbers of fluorescent lamps in growth chambers. Previous research comparing effects of light quantity and quality has focused on shoot expansion in a small sample of European herbs (Morgan, 1981) and on leaf development in selected aquatic plants (Richards and Lee, 1986). This very small sample has shown a relationship between the degree of developmental effects of reduced R:FR and the light tolerance of taxa (Morgan and Smith, 1979; Kwesiga and Grace, 1986). In all cases treatments of reduced irradiance have underestimated the effects of foliage shade on plant development. To further understand the effects of natural shade on the development of leaf structure it is important to study additional taxa and examine changes in leaf structure in greater detail.

Papaya (*Carica papaya* L., Caricaceae) is grown throughout the tropics for edible fruit and a proteolytic enzyme purified from its latex. Although papaya is most often grown as a short-lived plant in field rows (Purseglove, 1968), it is also intercropped with other species in agroforestry systems (Nair, 1980). Papaya's tolerance of different growing conditions may result from its evolution as a pioneer species, growing in gaps of Central American forests (Purseglove, 1968). Its potential for use in different cropping systems makes information about its response to different light conditions all the more important.

The purpose of this research was to analyze the effects of reduced irradiance and reduced R:FR on the morphology, anatomy, and pigment composition of papaya leaves.

MATERIALS AND METHODS

Papaya seedlings, variety "Cariflora," were germinated on moist paper towels and transferred to seedling trays in vermiculite. Five-week-old seedlings were transferred to 10-cm pots with a soil mixture of peat moss, perlite, sand, and dark loam (2:2:1:1), grown under partial shade in a greenhouse. After 2 weeks, seedlings (uniform in size, morphology, and with five to six leaves) were transferred into 25-cm pots and placed in the treatment environments. Plants were fertilized at biweekly intervals with Peters' Professional 20:20:20 and Soluble Trace Elements Mix. The treatment period was 107 days (10 January to 26 April 1988).

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Experimental shade enclosures were constructed at the Montgomery Foundation of Fairchild Tropical Garden. The four enclosures were 2.5 × 2.5 m, with a roof sloping from 2.5 to 1.8 m, and blind vents to allow for air circulation. Reduced irradiance but no spectral alteration (neutral shade, or NS) was achieved by use of a double layer of 50% and 70% shade fabrics, with a clear layer of nursery plastic on the outside. Reduced irradiance and reduced R:FR (filtered shade, or FS) was created by spraying a clear greenhouse plastic cover with an experimental spray paint designed to reduce R:FR to ratios under forest canopies (Lee, 1985, 1988). Partial-shade treatments (high light, or HL) consisted of two separate areas of a greenhouse. Each light treatment was replicated once to diminish the probability of site-specific variation (Hurlbert, 1984), for a total of six separate treatments. Ten plants were grown in each treatment, spaced 0.6 m apart.

Irradiance and spectral quality within the treatments were compared to full sunlight with a Li-Cor 1800 spectroradiometer (Li-Cor Instruments, Lincoln, NE). Irradiance was measured as photosynthetically active radiation (μ mol m^{-2} sec^{-1} 400–700 nm, or PAR) scanned at three locations in each treatment, morning, midday, and afternoon, five times during the experiment. Neither the degree of full sunlight or R:FR (calculated at the appropriate wavelengths with the spectroradiometer) changed appreciably during the experimental period, and the means of the 45 measurements are presented in Table 1. Temperatures were measured with minimum-maximum thermometers at 1 m height, and daily readings of temperature extremes were taken during treatments (mean temperatures, defined as the average of daily maximum and daily minimum, are listed in Table 1).

At the end of the growing period plants were measured for height, petiole length (of the 8th leaf from shoot apex counting from the first leaf more than 20 mm long at the apex), and internode length (beneath the same leaf). By maturity the plants had produced 21–24 leaves greater than 20 mm in length. Stem diameter at the plant base was measured with a caliper. Total leaf area and perimeter was measured with a Delta T area meter (Delta T Devices, Burwell, Cambridge, U.K.). These leaves were also examined histologically and for chlorophyll content, as follows. Samples (4 cm^2) were ground in 0.80 acetone until no additional pigment was extracted. The mixture was centrifuged and absorbance measured at 645 and 663 nm (Arnon, 1949) in a Lambda 4B spectrophotometer (Perkin-Elmer Instruments, Norwalk, CT). The remainder of the leaf was dried at 60 C for 48 hours for the determination of specific leaf weight (mg dry leaf mass cm^{-2}).

Samples for leaf anatomical measurements were fixed in formaldehyde, acetic acid, and alcohol (Berlyn and Miksche, 1976), infiltrated, and embedded in JB-4 resin (PolySciences, Warrington, PA). Five-micron sections were stained in aqueous 0.005 toluidine blue solution for 5 minutes and mounted with Permount. Slides of leaves of five individuals from each treatment were sampled ten times for leaf thickness, palisade mesophyll height, palisade cell width at adaxial and abaxial ends, and adaxial and abaxial epidermis thickness. Measurements were recorded with a Bioquant System IV image analysis system (Bioquant, Inc., Nashville, TE) attached to a Leitz Dialux 20 microscope. Stomatal density was estimated from leaf samples cleared with ethanol and NaOH (Berlyn and Miksche, 1976) by counting with the image analysis system in a field of 8.5×10^4 μm^2, five samples per treatment. Two sections from leaves of five plants from each treatment were also analyzed with an AgVision image analysis system (Decagon Instruments, Pullman, WA). Mesophyll air space areas and perimeters were measured from leaf sections 200 μm in length. The proportion of intercellular air space in mesophyll tissue was directly related to their area ratios when leaves were viewed in transverse section (Parkhurst, 1982). The ratio of the area of contact between mesophyll cell surface in contact with air space (A_{mes}) to leaf surface area (A_{surf}) was estimated from the relationship

$$A_{mes}/V_{surf} = \frac{PTF}{A}$$

where P = air space perimeter (or length of mesophyll cells in contact with air spaces), T = mean mesophyll thickness in the section, A = area of mesophyll tissue in section, and F = a shape factor (Parkhurst, 1982 and personal communication). The shape factor of 1.20 for the air spaces in these leaves was estimated by their deviation from a uniform distribution (1.272; Parkhurst, 1982 and personal communication; Thain, 1983). Surface to volume ratios of the air spaces were estimated from the relationship of

$$A_{mes}/V_{surf} = \frac{PF}{A_{air}}$$

where A_{mes} = mesophyll air space surface, A_{air} = area of air space in leaf mesophyll, and V_{air} = air volume in mesophyll. Measurements were in μm.

Treatments were statistically compared from average values of individuals using analysis of variance and Fisher's Least Square Difference at a significance level of 0.05 (Number Cruncher Statistical Systems version 4.1, Kaysville, UT). Each value is reported in the text and tables as mean ± standard error (SE).

TABLE 1. *Environmental conditions of replications of different light treatments of the papaya plants*

Treatment	Mean temperature in ° Celsius	Portion of solar PAR	R:FR
High light (HL)			
Replication 1	25.0 ± 0.4	0.204 ± 0.002	0.89 ± 0.00
Replication 2	25.0 ± 0.4	0.209 ± 0.002	0.90 ± 0.00
Neutral shade (NS)			
Replication 1	22.5 ± 0.5	0.017 ± 0.002	0.99 ± 0.01
Replication 2	22.5 ± 0.5	0.018 ± 0.002	0.98 ± 0.01
Filtered shade (FS)			
Replication 1	24.0 ± 0.5	0.024 ± 0.002	0.27 ± 0.01
Replication 2	24.0 ± 0.5	0.017 ± 0.002	0.26 ± 0.01

RESULTS

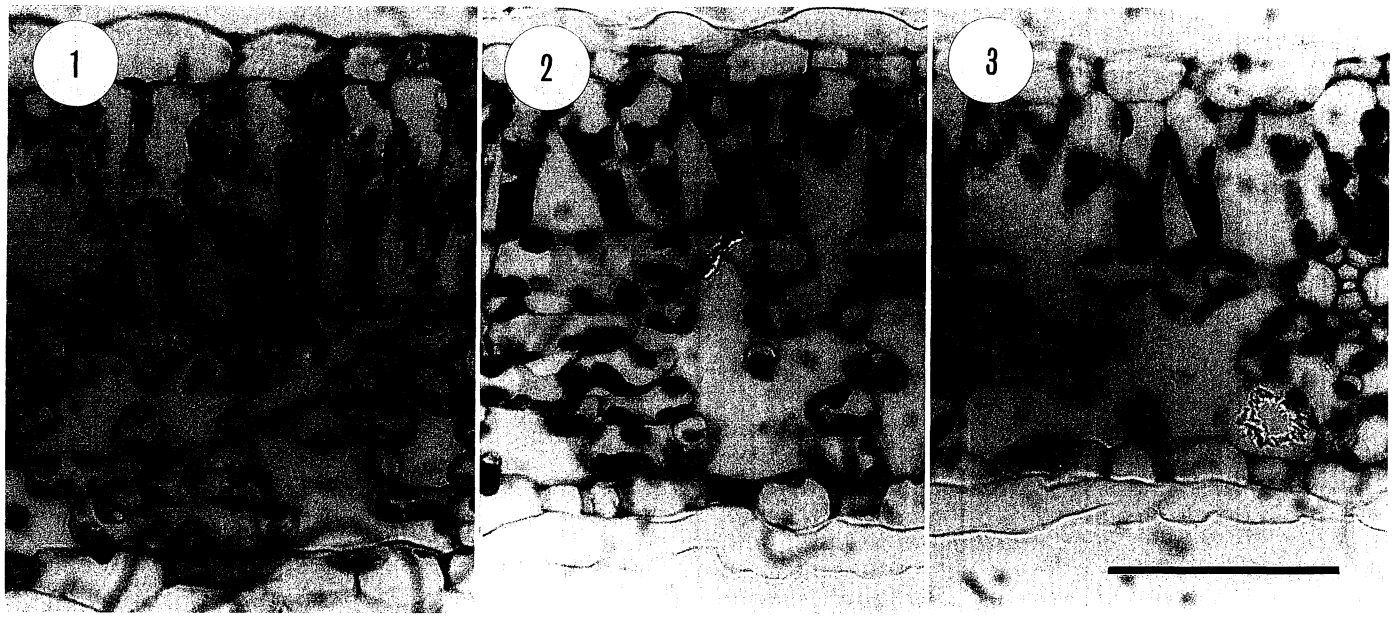
The plants grew vigorously in the experimental treatments. None of the replicates were significantly different for any of the measured characters, so the samples of the replicates were pooled for final statistical comparisons.

TABLE 2. *Measurements of morphology, anatomy, and pigment composition of plants grown in the three different light environments*

Character	Treatments		
	HL	NS	FS
Leaf thickness (μm)	137 ± 3 A	119 ± 3 B	107 ± 2 C
Specific leaf weight (mg cm^{-2})	4.70 ± 0.12 A	2.86 ± 0.07 B	2.09 ± 0.06 C
Stomatal density per mm^2	465 ± 12 A	330 ± 7 B	312 ± 11 B
Chlorophyll content (μg cm^{-2})	3.57 ± 0.28 A	5.16 ± 0.24 B	4.80 ± 0.10 B
Degree of air spaces	0.29 ± 0.01 A	0.33 ± 0.01 B	0.34 ± 0.01 B
Leaf area (cm^2)	292 ± 10 A	162 ± 8 B	246 ± 4 C
Palisade cell adaxial width (μm)	10.9 ± 0.2 A	12.6 ± 0.4 B	14.2 ± 0.4 C
Palisade cell length (μm)	54.9 ± 1.6 A	45.9 ± 0.4 B	37.4 ± 0.6 C
Palisade cells (cm^{-2} × 10^4)	4.8 ± 0.1 A	4.4 ± 0.1 B	4.1 ± 0.1 C
Mesophyll thickness (μm)	113 ± 2 A	97 ± 2 B	85 ± 1 C
Cell-air contacts A_{mes}/A_{is}	15.0 ± 0.4 A	11.8 ± 0.2 B	10.5 ± 0.2 C
Internode length (mm)	28 ± 1 A	25 ± 1 A	39 ± 1 B
Chlorophyll a/b	2.64 ± 0.10 A	2.62 ± 0.05 A	2.45 ± 0.09 B
Leaf area/Perimeter	0.46 ± 0.01 A	0.47 ± 0.01 A	0.67 ± 0.02 B
Mesophyll air space, A_{mes}/V_{air}	0.46 ± 0.01 A	0.37 ± 0.01 B	0.36 ± 0.01 B
Petiole length (mm)	207 ± 3 A	148 ± 4 B	182 ± 4 C

The light treatments affected plant morphology. HL-grown plants produced the thickest stems (diameters of 1.31 ± 0.02 cm) compared to 1.08 ± 0.02 cm for the FS, and 0.97 ± 0.02 cm for the NS treatments. FS-grown plants were the tallest (80.3 ± 1.8 cm), followed by the HL (72.2 ± 1.4 cm) and NS (55.1 ± 1.1 cm) treatments.

Reduced flux and reduced R:FR affected leaf development in papaya. Leaves of both shade treatments were



Figs. 1–3. Leaf transverse sections of papaya from the different light treatments. **1.** High light (HL). **2.** Neutral shade (NS). **3.** Filtered shade (FS). Bar = 100 μm.

significantly thinner with lower specific weights than the high light treatments (Table 2; Figs. 1–3). They also had fewer stomata, produced more chlorophyll per unit area, and developed a larger proportion of air spaces within mesophyll tissue.

The two shade treatments influenced certain leaf characters differently. The NS treatment reduced leaf area more than the FS treatment (Table 2). Leaf thickness was reduced in the NS treatment, and further reduced in the FS treatment. Both shade treatments broadened the palisade cell adaxial width and decreased the cell length (Table 2). These changes resulted in lower densities of palisade cells per unit leaf area (Table 2). Shade treatments also decreased the mesophyll air surface/leaf surface ratio (A_{mes}/A_{ls}, Table 2), the FS treatment adding to the effects of the NS treatment.

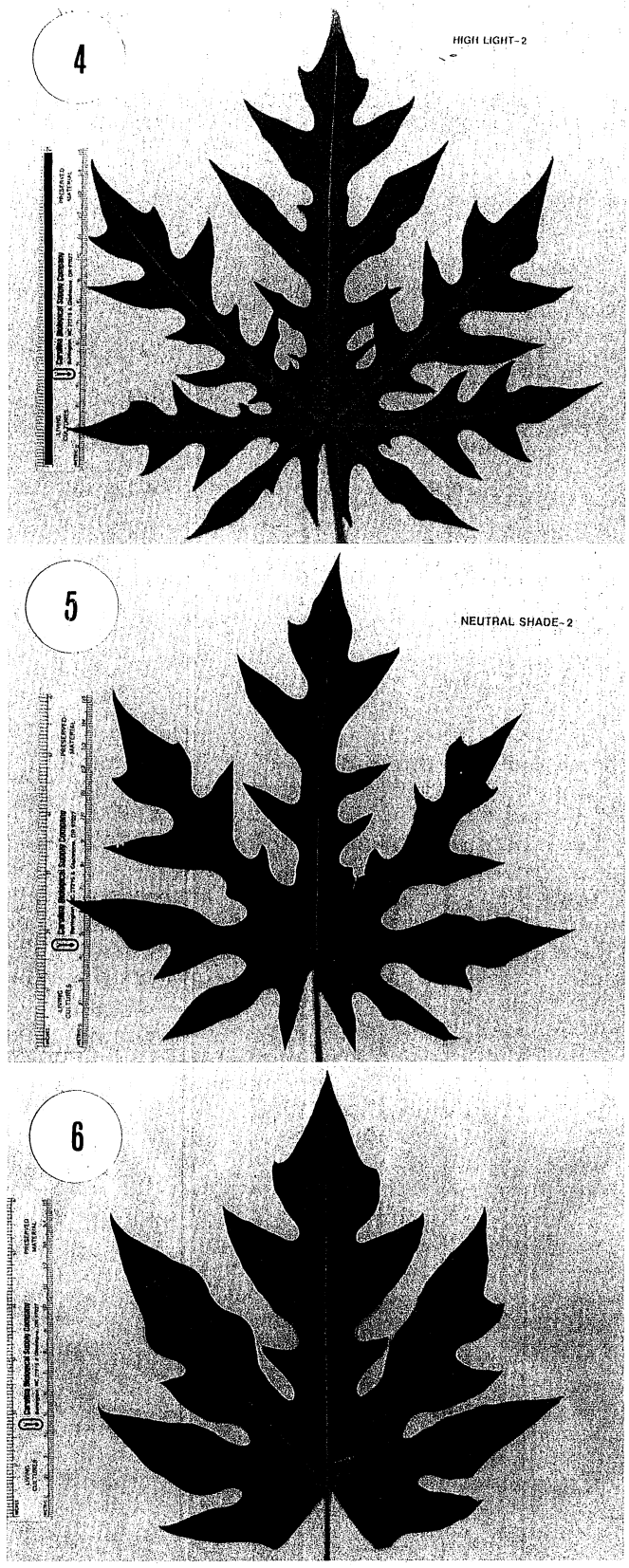
Internode length, chlorophyll a/b ratio, and leaf area/perimeter were only significantly influenced by the low R:FR FS treatment. In the HL and NS treatments the leaves were highly dissected (Figs. 4, 5), but the lobing was dramatically reduced in the low R:FR FS treatment (Fig. 6).

DISCUSSION

Leaf structures produced in both shade treatments may be functionally advantageous in low light environments. Leaves of the FS and NS treatments were thinner with reduced specific leaf weights than in the HL treatments (Fig. 2; Table 2). Such differences have been observed in numerous studies on the effects of shading on leaf morphology (cited in the Introduction). This reduction is correlated with palisade mesophyll cell shape. In the HL treatment these cells were long and columnar (Fig. 1) in contrast to their cone-shape in the shade treatments (Figs. 2, 3). Increase in width of the adaxial end was associated with a reduction in cell length (Table 2; Figs. 2, 3). Reduction in leaf thickness was also associated with thinner spongy mesophyll tissue in the shade treatments.

Change in palisade cell shape altered other anatomical characters in ways that could affect photosynthetic activity. The more cone-shaped palisade cells were associated with larger and more equidiametric air spaces in section, whereas the narrower palisade cells were adjacent to numerous very narrow air spaces between the cells and connected with larger spaces beneath (Fig. 1). The differences in the shape of these air spaces is reflected in the mesophyll air space surface to volume ratios (Table 2), largest in the HL treatments. This greater surface to volume ratio also helps explain the much greater A_{mes}/A_{ls} for the HL-treatment. The greater mesophyll thickness also contributes to this ratio despite the lower proportion of air spaces in these leaves (0.29, Table 2).

The proportion of air space was positively correlated with gas exchange and photosynthesis in *Plectranthus* (Nobel, Zaragoza, and Smith, 1975) and in other plants, particularly evergreen perennials (Nobel, 1977; Parkhurst and Mott, 1990; Lloyd et al., 1992). However, the extent of intercellular air space may not significantly influence gas exchange in some plants (Araus et al., 1986). Another significant control on gas exchange is stomatal resistance (von Cammerer and Farquhar, 1981). Both shade treatments produced leaves with reduced stomatal densities.



Figs. 4–6. Leaf shapes of papaya seedlings grown in different light treatments. **4.** High light (HL). **5.** Neutral shade (NS). **6.** Filtered shade (FS). Bar = 10 cm.

Palisade cell shape may also influence the efficiency of light absorption. The narrow cells display chloroplasts stacked on top of each other and allow some passage of light through the cell via the central vacuole (Lee et al., 1990). The cone-shaped cells permit chloroplasts along side walls to be more directly exposed to sunlight, forming a more uniform layer of chloroplasts. The effect of cell shape on the mutual shading of chloroplasts may be physiologically important to the plants, or the attendant reduction in palisade cell density per unit area (Table 2) may simply be a mechanism that reduces leaf thickness and specific weight.

Both shade treatments also produced higher chlorophyll contents per unit leaf area, presumably contributing to greater total light absorption. Increased and decreased chlorophyll density due to shading has been reported elsewhere (Björkman, 1981; Lichtenthaler et al., 1981; Lee et al., 1990).

Exposure to low R:FR produced two alterations with other functional advantages in extreme shade. 1) Leaves from the FS treatment were more shallowly lobed than the other treatments (Table 2; Fig. 2). Along with reduced specific weights, the leaves presented a more efficient surface in terms of structural cost (more efficient mechanical support) for the absorption of irradiance. The longer internodes reduced the degree of shading by upper leaves, partly offset by shorter petioles in the shade plants. 2) Leaves in the FS treatment produced significantly lower chlorophyll a/b ratios. Since chlorophyll b is particularly associated with the light harvesting complex II (LHCII; Glazer and Melis, 1987), a lower ratio is indicative of an increase in chlorophyll b concentration and a shift in the stoichiometry of the photosystem I and II reaction centers (Anderson, 1986). Some authors have reported a specific reduction of chlorophyll a/b under FR-enriched light conditions (Lee, 1988); others have reported no effect (Björkman, 1981; Anderson, 1986). Effects may be due to shifts in phytochrome equilibria or the sensitivity of the two photosystems (Chow et al., 1990), and the increase in the photosystem II reaction center may constitute a chromatic acclimation to the spectral enrichment of FR under natural shade conditions (Chow, Melis, and Anderson, 1990).

The results of this study help explain the dramatic acclimation potential of papaya to a wide range of light environments. Although many characteristics, such as leaf thickness, specific leaf weight, stomatal density, and palisade parenchyma cell shape, were changed by reductions in PAR, reduced R:FR contributed to further changes. Some characters, such as reduced chlorophyll a/b ratios, internode length, and the degree of lobiness were affected primarily by low R:FR. Reduced R:FR, presumably affecting phytochrome equilibrium, strongly influenced the developmental responses of papaya leaves to natural shade. This research shows clearly how the two environmental factors of light quantity and quality interact to control leaf morphology, anatomy, and pigment composition in papaya.

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