# ABSTRACT OF THE THESIS

# Anatomical and Morphological Responses of Papaya _Carica papaya_ L. to Various Light Conditions

by

Daniel Joseph Buisson
Florida International University, 1991
Miami, Florida
Professor David W. Lee, Major Professor

Plants that develop under foliar shade encounter both low photosynthetically active radiation (PAR) and low red to far red ratios (R:FR). Both of these factors are important in determining developmental responses to shade. Papaya (_Carica papaya_ L.) seedlings grown under filtered shade (low PAR and low R:FR) were compared with seedlings grown under neutral shade (low PAR with R:FR similar to that of full sunlight), and high light (moderate PAR with R:FR similar to that of full sunlight). The results indicated that papaya exhibits a light seeking strategy as evidenced by morphological and anatomical differences between treatments. Based on past research the results also indicate shade developmental responses in papaya to be phytochrome mediated.

FLORIDA INTERNATIONAL UNIVERSITY
Miami, Florida

# Anatomical and Morphological Responses of Papaya *Carica papaya* L. to various light conditions

A thesis submitted in partial satisfaction of the
requirements for the degree of Master of Science
in Biology

by

Daniel Joseph Buisson

1991

To Professors: Jack B. Fisher
Jennifer H. Richards
Bruce Schaffer
David W. Lee

This thesis, having been approved in respect to form and mechanical execution, is referred to you for judgement upon its substantial merit.

Dean Arthur Herriot
College of Arts and Sciences

**The thesis of Daniel J. Buisson is approved.**

Professor Jack B. Fisher

Jennifer H. Richards

Bruce Schaffer

David W. Lee

Date of Examination: January 25, 1991

Dean Richard Campbell
Division of Graduate Studies

**Florida International University, 1991**

# DEDICATION PAGE

This thesis is dedicated to my father Paul Buisson and my daughter Caroline.

# ACKNOWLEDGEMENTS

I would like to thank all the members of my committee for their assistance and advice, and in particular my major professor Dr. David Lee for his patience and encouragement.

I would also like to thank all the people whom I had contact with in the Department of Biological Sciences at Florida International University, especially my fellow students for their help and support.

Finally I would like to thank my wife Dominique, and my mother Justine for their encouragement.

# TABLE OF CONTENTS

Page

# LIST OF TABLES

# LIST OF FIGURES

# INTRODUCTION

Plants that develop under canopy or foliar shade not only encounter a decrease in light intensity but also a shift in the spectral distribution of light. Leaves absorb heavily in the blue and red and transmit in the far-red wavelengths (Lee and Graham 1986). Therefore the light resulting from canopy shade is relatively poor in blue and red and rich in far-red wavelengths when compared to the spectral distribution of full sunlight.

The relative proportions of red and far red light influence plant developmental processes such as seed germination and flower initiation. The plant photoreceptor phytochrome is responsible for mediating these responses. Phytochrome exists in two forms: a red absorbing form (Pr), and a far red absorbing form (Pfr). When Pr and Pfr absorb respectively in their wavelength (approximately 660 and 730nm ), they are converted into the opposite form. Hence the ratio of these two forms reflects the relative quantities of red and far red light in the plant's environment (Borthwick 1972, Briggs 1976, Mohr 1969). This ratio was standardized by Smith (1982) as the ratio of quanta centered on 660 to that on 730nm, using a 10nm band width. This standard red to far red ratio (R:FR) is often used by researchers when characterizing light regimes. Full sunlight tends to have a R:FR of approximately 1.2, whereas under the deep canopy shade of the tropical forest this ratio may be as low as 0.10 with light intensity less than 1% of full sunlight when measured on the forest floor (Lee 1987). For broad leaf temperate forests R:FR values are variable and range from 0.15 to 0.5 depending on the species (Morgan and Smith 1981).

Most of the research designs involving plant developmental responses to shade have only taken into consideration light intensity or photosynthetically active radiation (PAR) ignoring low R:FR values. The results of these experiments have, however, provided valuable information regarding leaf anatomical and morphological responses to neutral shade conditions. Plants grown under neutral shade generally have thinner lamina or a greater specific leaf area (Jurik, et al. 1982, Blackman and Wilson 1951). Anatomical studies have shown this to be the result of reduced size and changes in the structure of the palisade mesophyll cells, a decrease in size and number of spongy mesophyll cells, and an increase in intercellular volume (Dengler 1980). Epidermal cells tend to be larger and stomatal densities smaller in plants grown in neutral shade compared to those growing in full sun (Anderson 1955, Knecht and O'Leary 1972). Chlorophyll content per unit area tends to be greater in leaves of plants grown in neutral shade compared to those growing in full sun. However there are conflicting reports with respect to chlorophyll content and plants developing in shade (Kapple and Flore 1983, Bjorkman 1981, Lee et al. 1990).

Grime (1981) observed that plant responses to natural shade are habitat dependant and he described plants as either shade-tolerant or shade-avoiding. Most of the information regarding the role of the R:FR in plant developmental responses to shade comes from the efforts of H. Smith and his students. These experiments have shown that shade-avoiding plants respond to low PAR and R:FR by allocating more resources to stem and petiole growth and less to lamina expansion (Vince-Prue 1976, Morgan and Smith 1978,1981). Branch initiation is also reduced as a result of apical dominance (Fitter and Ashmore 1974). Shade tolerant plants are comparatively unresponsive to low R:FR (Kwesiga and Grace 1986, Warrington et al. 1988, Morgan and Smith 1979). Anatomical and morphological studies of plants developing under low PAR and R:FR conditions showed that the characteristic changes in internal and external leaf structure and morphology as described above for neutral shade are enhanced (McClaren and Smith 1978, Richards and Lee 1986).

Most studies on the effect of shading on plant response focused on temperate herbaceous plants grown under artificial conditions using florescent and incandescent lighting. Lee (1985) developed a filtering film using a combination of pigments mixed in a varnish base which could be sprayed on any transparent surface. This film not only reduces the amount of light passing through the surface but also selectively reduces the amount of red light resulting in low PAR and R:FR resembling the conditions of the forest understory. Lee (1988), demonstrated that large shade houses could be covered with this filtering film. Thus, plants grown under reduced PAR and R:FR could be compared with plants grown under shade cloth at the same PAR but with the R:FR of full sunlight.

The papaya *Carica papaya* L. is cultivated throughout the tropics, and has become naturalized in many tropical areas. Although its exact origin is not known it is considered a new world species possibly having originated in the upper amazon or Central America (De Candolle 1884). In the wild state papaya often grows along roadsides and in forest clearings or gaps. However, papaya also grows and produces fruit in shaded areas. In shaded conditions the internodes are long and leaves appear smaller and less lobed or dissected. Papaya is cultivated in full sunlight and also often intercropped. Papaya was chosen for this study because this species develops relatively quickly and its morphological characteristics, such as lobing of the leaves and internode lengths, are very apparent in different light conditions and are therefore easy to measure.

## OBJECTIVES

The goal of this study was to compare the morphological and anatomical developmental responses of papaya seedlings grown under neutral shade to those grown under filtered (low R:FR) shade. The filtered shade conditions reflect tropical forest shade with extremely low R:FR and PAR.

## HYPOTHESIS

The morphological and anatomical developmental responses of papaya seedlings grown under filtered shade will be different than those found with plants grown under neutral shade of the same PAR suggesting shade responses in papaya are phytochrome mediated.

# MATERIAL AND METHODS

## EXPERIMENTAL DESIGN

This experiment was conducted at Fairchild Tropical Garden's Montgomery Foundation in Coral Gables, Florida. Plants were grown under three light environments: High Light (HL), R:FR similar to that of full sunlight; Filtered Shade (FS) with a low R:FR; and Neutral Shade (NS) with a R:FR similar to that of full sunlight. The two shade treatments were replicated once. Wooden frames eight feet wide by eight feet long and six feet high sloping to eight feet high were constructed. This sloped design allowed heat to escape through a vent on the eight foot wall. For the FS treatment two wooden frames were covered with clear reinforced nursery plastic. The plastic was painted using a mixture of pigments in a varnish base as described by Lee (1985) allowing light under the structure to be reduced and spectrally altered. For the NS treatment, two wooden frames were covered with 50% shade cloth and with 70% shade cloth. The two NS structures were then covered with clear nursery plastic so that the temperature conditions would be similar to the FS treatments. Plants in the HL treatment were grown in two separate areas within a greenhouse. Light intensity and spectral quality were measured using a Licor LI-1800 quantum radiometer. Light measurements were averaged from three locations in each treatment in morning, mid and late afternoon. This was done a total of five times through the course of the experiment. Temperature was monitored using maximum and minimum thermometers. The experimental conditions are summarized in table 1.

The 'Cariflora' variety of <u>Carica papaya</u> L. was used for this experiment since it is tolerant to the papaya ringspot virus and provides for a uniform seedling population (Conover et al.). Plants were germinated, and then transferred into seedling trays. After five weeks 84 of the most uniform seedlings were selected and transferred to pint sized pots and grown in a mixture containing canadian peat moss, pearlite, sand and black soil (2:2:1:1). Two weeks later, fourteen seedlings each in single pots were transferred into each of the treatments. Plants were spaced so as not to shade one another. Plants were grown in each treatment from January 10 until April 26, 1988. During the course of the experiment plants were fertilized with both soluble macro (NPK) and micro-nutrients (Peters'Professional 20-20-20 and Soluble Trace Elements Mix), and repotted once into 1 gallon pots using the same soil mixture.

Table 1. Ambient conditions for the growth of papaya seedlings grown in shade and glass houses with different light regimes.

| TREATMENT/REPLIC | TEMP °C | PAR $\mu mol\ m^{-2}s^{-1}$ | R:FR |
|---|---|---|---|
| HIGH LIGHT 1 | L-20 H-30 | 377.12 | 0.89 |
| Sx | 0.41 0.40 | 3.39 | 0.002 |
| HIGH LIGHT 2 | L-20 H-30 | 386.20 | 0.90 |
| Sx | 0.41 0.40 | 4.20 | 0.002 |
| FILTERED SHADE 1 | L-17 H-31 | 43.61 | 0.27 |
| Sx | 0.57 0.40 | 2.86 | 0.011 |
| FILTERED SHADE 2 | L-17 H-31 | 32.0 | 0.26 |
| Sx | 0.50 0.44 | 3.95 | 0.013 |
| NEUTRAL SHADE 1 | L-17 H-28 | 32.15 | 0.99 |
| Sx | 0.57 0.50 | .79 | 0.008 |
| NEUTRAL SHADE 2 | L-17 H-28 | 33.77 | 0.98 |
| Sx | 0.52 0.51 | 4.42 | 0.013 |

Column 1-treatment replication; 2-temperature in degrees celsius; 3-photosynthetically active radiation; 4-red:far red. The standard error is represented by Sx.

## MORPHOLOGICAL MEASUREMENTS:

Beginning April 26, 1988 plants were sampled during a ten day period. One plant per treatment replication was randomly chosen each day for a total of ten plants sampled for each treatment replication. Plant height, leaf area, internode length, and petiole length were measured on each plant. The leaf and internode measurements were taken from the eighth leaf from the shoot tip counting the first leaf over 20mm at the apex as leaf one. Leaf area was measured with the Delta T Devices area meter (128 Low Road, Burwell, Cambridge England). Leaf samples were collected for histological preparation and chlorophyll extraction. The degree of light interception on a per leaf basis was documented by determining the actual leaf area and comparing it to the area of a polygon defined by the lamina base and lobe tips (actual leaf area:calculated perimeter area-see fig 1). Except the light interception measurements in which five plants were sampled, a total of ten plants were sampled from each treatment replication for the morphological measurements.

## ANATOMICAL MEASUREMENTS:

Samples were collected from areas between large veins on the eighth leaf and were fixed in formalin acetic acid alcohol ethanol (FAA) (Berlyn and Mikseh, 1976). Samples were infiltrated and embedded in Polyscience JB-4 plastic embedding resin. An American Optical microtome was used for sectioning the samples at 5 microns. Eight sections on each slide were stained in a .05% toluidine blue solution for 5 minutes. Slides were dried and mounted with Permount histological mounting media. Five slides were prepared for each sample treatment and ten measurements per slide were made for each variable. The following variables were measured: leaf thickness, upper epidermis height, upper epidermis width, palisade height, palisade width at the top of the cell, palisade width at the bottom of the cell, lower epidermis height, and lower epidermis width. The Bioquant System IV image analysis system (Nashville TE.) combined with a Leitz Dialux 20 microscope was used for these measurements. For the anatomical measurements a total of five plants were used per treatment (N=5).

CHLOROPHYLL CONTENT:

Samples of $4cm^2$ were collected from the same area on each leaf. A total of five plants were sampled per treatment replication (N=5). These samples were extracted by grinding the leaf material in a mortar and pestle with 80% acetone and ultimately bringing the volume up to 20ml. The suspension was centrifuged at approximately 1800 RPM in a bench top centrifuge to clarify the supernatent. Absorbance was measured using a Perkin-Elmer Lambda 4B UV/VIS spectrophotometer. Absorbance at 800 nm were used to detect any background scattering, and those at 645 and 663nm were used to detect total chlorophyll content and chlorophyll a:b ratio (Arnon 1949).

SPECIFIC LEAF WEIGHT:

This was calculated as mg of dry leaf mass per $cm^2$ of leaf. Leaves were dried at 60°C for 48 hours.

STOMATAL DENSITY:

Stomata were counted using the Bioquant System IV image analysis system combined with a Leitz Dialux 20 microscope. The density was calculated as number of stomates per 85,000 $\mu m^2$ and then converted to $mm^2$. A total of five samples were measured per treatment (N=5).

STATISTICS:

Statistical comparisons among treatments were performed using analysis of variance and Fisher's Least Square Difference at the 5% significance level. (Number Cruncher Statistical Systems version 4.1., 865 East 400 North Kaysville, UT.)

# RESULTS

## MORPHOLOGICAL DATA

The High Light (HL) treatment had a significantly greater leaf area and petiole length than the Filtered Shade (FS) and Neutral Shade (NS) treatments, and the leaf area and petiole length of the FS treatment were significantly greater than those of the NS treatment (Table 2). The leaf area:calculated perimeter area of the HL and NS treatments were significantly lower than that of the plants in the FS treatment. Plants in the FS treatment had significantly greater internode lengths than plants in both the HL and NS treatments. Internode length was not significantly different between the HL and NS treatments.

Plants grown in the FS treatments were significantly greater in height than plants in the other treatments. Plants in the HL treatment were significantly greater in height than the plants in the NS treatment. The plants grown in the HL treatment produced significantly greater stem diameters than plants grown in the other treatments. The plants in the FS treatment produced greater stem diameters than plants in the NS treatment. There were no significant differences between replications of a given treatment for any of the morphological parameters measured.

Table 2. Morphological differences among papaya seedlings grown under different light conditions.

| TREAT | LEAF AREA (cm$^2$) | LEAF AREA/ PERIM (%) | INTND LENGTH (mm) | PETIOLE LENGTH (mm) | PLANT HEIGHT (cm) | STEM DIAMETR (cm) |
|---|---|---|---|---|---|---|
| HL | 292.00 | 46.2 | 27.78 | 207.0 | 72.17 | 1.31 |
| Sx | 9.67 | .92 | .85 | 3.18 | 1.45 | .019 |
| sig | A | A | A | A | A | A |
| FS | 245.5 | 67.4 | 39.05 | 182.35 | 80.32 | 1.08 |
| Sx | 4.53 | 1.79 | 1.39 | 4.46 | 1.81 | .022 |
| sig | B | B | B | B | B | B |
| NS | 162.4 | 46.72 | 24.73 | 147.6 | 55.09 | 0.97 |
| Sx | 7.63 | 1.30 | 1.24 | 4.31 | 1.11 | .017 |
| sig | C | A | A | C | C | C |

Column 1= treatment; 2= leaf area; 3= leaf area divided by perimeter of lobes; 4= internode length; 5= petiole length; 6= plant height; 7= stem diameter. In the rows: HL= high light; FS= filtered shade; NS= neutral shade; Sx= standard error; sig= significance. In the columns means with the same letter are not significantly different at 5% level of significance.

## ANATOMICAL DATA

Plants grown in the HL treatment had significantly thicker leaves than plants grown in the other treatments. Plants grown in the NS treatment had significantly thicker leaves than plants grown in the FS treatments. There were no differences in upper epidermal and lower epidermal cell dimensions among treatments (Table 3). Leaves of plants grown in the HL treatment developed significantly longer palisade cells than leaves of plants in the other treatments. The palisade cells of the leaves of plants grown in the NS treatments were significantly greater in size than those of the plants grown in the FS treatment. The width of the top or adaxial end of the palisade cells of plants grown in the FS treatment was significantly greater than that of palisade cells of plants grown in the HL treatment (Table 3). When comparing the width of the adaxial ends of the palisade cells in leaves of plants growing in the FS treatment to those growing in the NS treatment, plants in the FS treatment had a significantly greater width of palisade cells than plants in the NS treatment. The width of the bottom or abaxial ends of the palisade cells in leaves of plants grown in the FS treatment was significantly less than those in the NS treatment, however the width was not significantly different between the FS and HL treatments or between the NS and HL treatments. The averages of each of the three measurements of the palisade cells (length, width adaxial surface, width abaxial surface) for each of the treatments and differences in the dimensions of the palisade cells of plants grown in the various light conditions are reviewed in Table 4. Cells were columnar in the HL treatment, columnar but shorter and thicker in the NS treatment, and conical in the FS treatment.

## STOMATAL DENSITY

The greatest stomatal density was found in leaves of plants grown in the HL treatment and these values were significantly greater than those of the two shade treatments. There were no significant differences between the two shade treatments (Table 5).

## SPECIFIC LEAF WEIGHT

The specific leaf weight of plants grown in the HL treatment was significantly greater than those of the shade treatments. The plants grown in the NS treatment had a significantly greater specific leaf weight than those of the plants grown in the FS treatment (Table 5).

## CHLOROPHYLL CONTENT

Plants grown in the HL treatment had a significantly lower leaf chlorophyll content than plants grown in the shade treatments. There was no significant difference in leaf chlorophyll content between the two shade treatments.

Plants grown in the FS treatment had a significantly lower leaf chlorophyll a:b ratio than plants grown in the HL and NS treatments. There were no significant differences in leaf chlorophyll a:b ratio between plants grown in the HL treatment and those grown in the NS treatment.

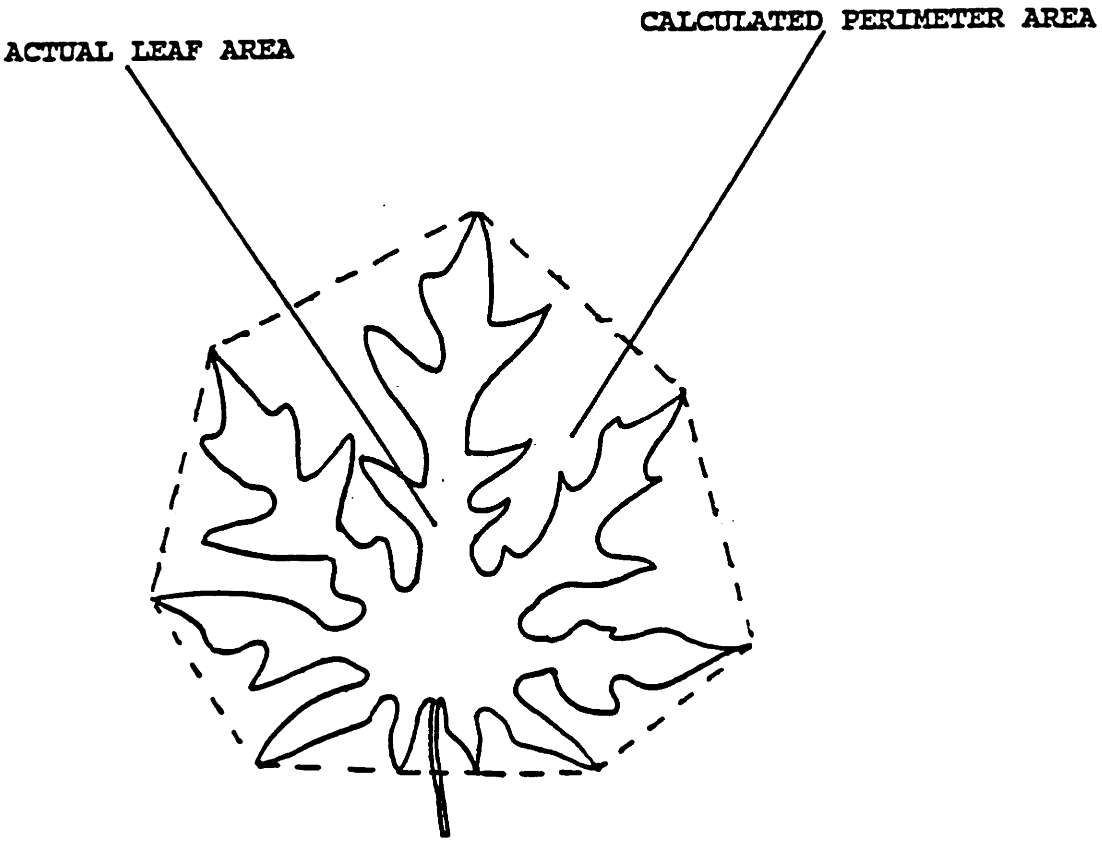
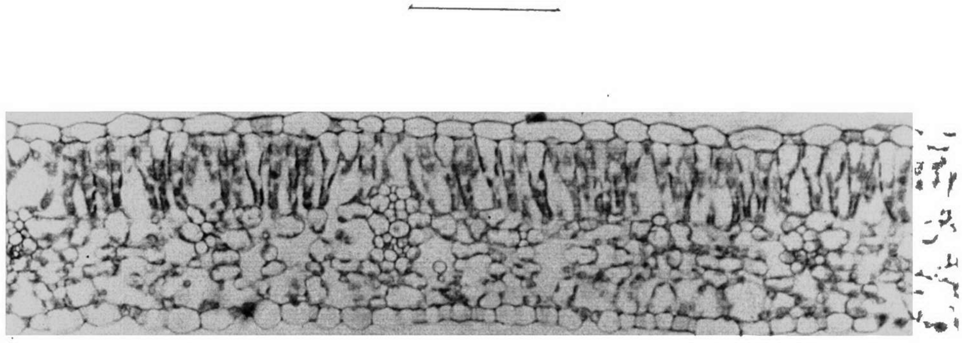
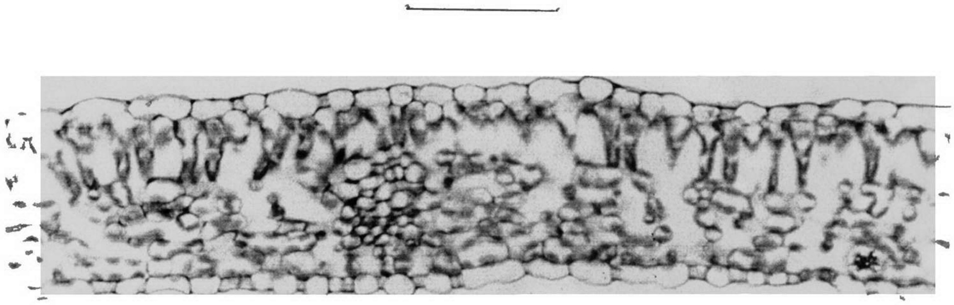


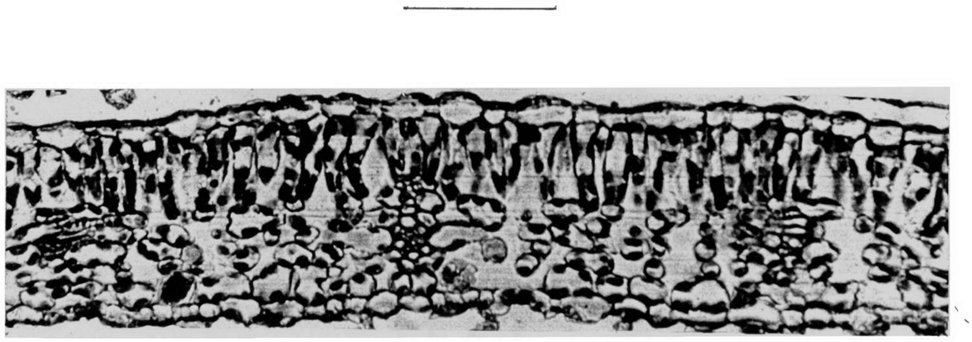
Figure 1. Diagram of measurement of the ratio of actual leaf area to perimeter calculated area.



A- HIGH LIGHT



B-FILTERED SHADE



C-NEUTRAL SHADE

Figure 2. Light micrographs of cross sections of leaves from the different treatments. The bar is equal to 100$\mu$m

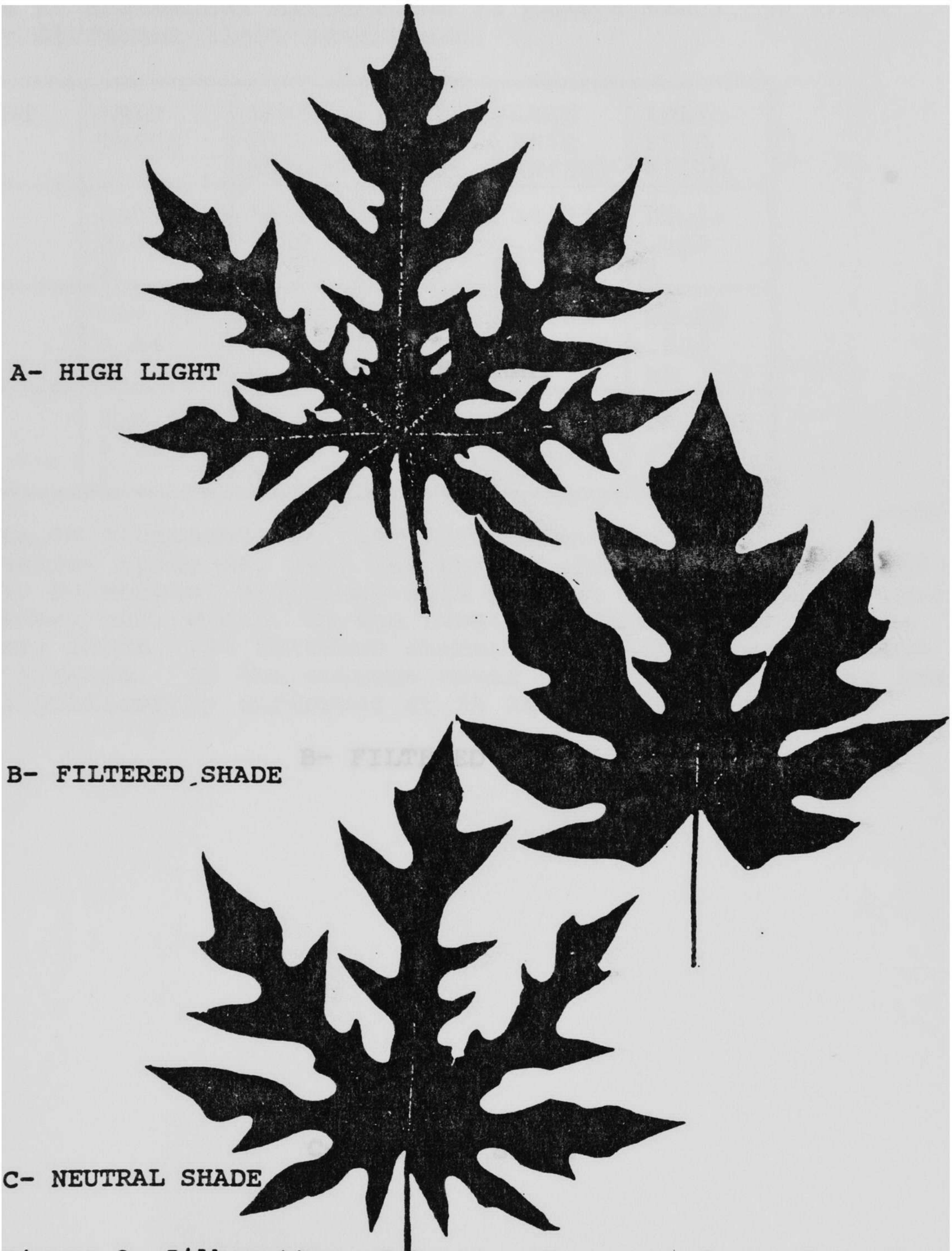


Figure 3. Silhouettes of leaves of papaya plants from the different treatments.

A- HIGH LIGHT

B- FILTERED SHADE

C- NEUTRAL SHADE

Figure 3. Silhouettes of leaves plants from the different treatments.

Table 3. Anatomical differences in papaya seedlings grown under different light conditions.

| TREAT | LEAF THICK | ADAX EPID HEIGHT | ADAX EPID WIDTH | ABAX EPID HEIGHT | ABAX EPID WIDTH |
|---|---|---|---|---|---|
| HL | 136.70 | 15.47 | 25.74 | 14.21 | 22.11 |
| Sx | 2.54 | .819 | .705 | .253 | .422 |
| sig | A | A | A | A | A |
| FS | 107.42 | 15.45 | 25.38 | 13.69 | 22.40 |
| Sx | 1.84 | .396 | .858 | .544 | .514 |
| sig | B | A | A | A | AB |
| NS | 118.52 | 15.88 | 27.34 | 13.32 | 23.63 |
| Sx | 2.72 | .390 | .843 | .261 | .552 |
| sig | C | A | A | A | B |

Column 1= treatment; 2= leaf thickness; 3= adaxial epidermal cell height; 4= adaxial epidermal cell width; 5= abaxial epidermal cell height; 6= abaxial epidermal cell width. In the rows: HL= high light; NS= neutral shade; FS= filtered shade; Sx= standard error; sig= significance. In the columns means with the same letter are not significantly different at 5% level of significance.

Table 4. Anatomical differences of palisade mesophyll cells in papaya seedlings grown under different light conditions.

| TREATMENT | PALISADE LENGTH | ADAXIAL PAL WIDTH | ABAXIAL PAL WIDTH |
|---|---|---|---|
| HIGH LIGHT | 54.95 | 10.91 | 7.43 |
| Sx | 1.59 | .220 | .12 |
| sig | A | A | A |
| FILTERED SHADE | 37.43 | 14.23 | 7.06 |
| Sx | .614 | .412 | .218 |
| sig | B | B | A |
| NEUTRAL SHADE | 45.90 | 12.61 | 7.91 |
| Sx | .417 | .444 | .151 |
| sig | C | C | B |

Column 1= treatment; 2= palisade length; 3= adaxial palisade cell width (top of cell); 4= abaxial palisade cell width (bottom of cell). In the rows: Sx= standard error; sig= significance. In the columns means with the same letter are not significantly different at 5% level of significance.

Table 5. Differences in specific leaf weight, chlorophyll content, chlorophyll a:b ratio, and stomatal density among papaya seedlings grown under different light conditions.

| TREATMENT | S.L.W. (mg/cm$^2$) | CHL. CONTENT | CHL. A:B RATIO | STOM.DEN. (per mm$^2$) |
|---|---|---|---|---|
| HIGH LIGHT | 4.70 | 3.57 | 2.64 | 465.0 |
| Sx | .117 | .280 | .102 | 12.35 |
| sig | A | A | A | A |
| FILTERED SHADE | 2.09 | 4.80 | 2.45 | 311.9 |
| Sx | .057 | .100 | .094 | 10.58 |
| sig | B | B | B | B |
| NEUTRAL SHADE | 2.86 | 5.16 | 2.62 | 329.8 |
| Sx | .066 | .243 | .046 | 7.41 |
| sig | C | B | A | B |

Column 2= specific leaf weight; 3= chlorophyll content; 4= chlorophyll a:b ratio; 5= stomatal density (per mm$^2$). In the rows: Sx= standard error, sig= significance. In the columns means with the same letter are not significantly different at 5% level of significance.

# DISCUSSION

Grime (1981) categorized plant responses to shade as shade-avoiding or shade-tolerant. Shade-avoiding plants exhibit morphogenetic plasticity and responses, such as increased internode length, petiole length and leaf morphology, are very obvious. Shade tolerant plants on the contrary respond far less to shade and exhibit less morphogenetic plasticity. Smith and others have shown shade-avoiding responses to be phytochrome mediated for many temperate herbaceous and woody species (Vince-Prue 1976, Morgan and Smith 1978,1981). My work with papaya indicated that this species is shade-avoiding as characterized by the most evident responses in the low R:FR shade conditions. For papaya, light interception per unit area was greater in the FS treatment. The ratio of actual leaf area to perimeter calculated area (see Fig 1) is related to light interception for that leaf. Both the HL and NS-grown plants had actual leaf area:perimeter calculated area ratios of around 45% and were not significantly different from each other whereas the FS-grown plants had ratios of around 65% or 20% more light interception per leaf. Although papaya generally exhibited a light-seeking response, light interception was greater with plants grown in the FS treatments on a per leaf basis. Plants in the shade treatments (both FS and NS) had leaves that were comparable in length and width but not in actual leaf area per perimeter calculated area. This difference appeared to result from increased leaf width around the major veins within the leaf lobes in the FS treatment thus giving leaves in the NS treatment a more dissected appearance. Talbert and Holch (1956) used a similar analysis to describe lobing of sun and shade leaves of various deciduous tree species. Their results showed that shade leaves in the center of the canopy, where R:FR ratio and light intensity is low, were less lobed than the sun leaves. In my study, the HL leaves were greater in length and width than the shade treatments and were greater in area. The FS grown plants had a greater leaf area than the NS grown plants. My results are consistent with previous experiments dealing with shade avoiding plants, such as Dengler's (1980) work with <u>Helianthus</u> <u>annus</u> where leaf area was greater in high PAR treatments.

Petiole length was greatest for plants grown in the HL-treatment because of the large size of the leaves. However, petioles of the FS-grown leaves were significantly longer than those of the NS grown leaves despite the similarity of size of the leaves. Vince-Prue (1976) also found that a low R:FR stimulated petiole elongation in strawberry plants. Richards and Lee (1986) also showed that light quality (R:FR) had a profound effect on petiole morphology in water hyacinth.

Internode length was greatest for the FS-grown plants and was not significantly different between the HL and NS grown plants. The effect of low R:FR ratios on internode length is well documented for temperate herbaceous plants (Kasperbauer 1971, Vince-Prue 1977, Corre 1983). Smith et al. used stem extension rate as a means of describing light seeking responses due to low R:FR. They found that the stem extension rate was greater for open habitat plants such as _Chenopodium album_ and _Sinapsis alba_ developed under low PAR and low R:FR than for plants developed under low PAR and high R:FR (Morgan et. al 1980).

Plant height was greatest for the FS-grown plants as a result of greater stem elongation. The HL-grown plants were taller than the NS-grown plants. Thus plant height and stem elongation were presumably phytochrome mediated since the FS-grown plants were almost twice the size of the NS-grown plants.

Leaf thickness was greatest for plants grown in the HL-treatment. Leaves in the NS treatment were significantly thicker than those in the FS-treatment. Past studies with neutral shade showed that the lamina of strawberry and _Vicea_ were thinner for shade-grown than sun-grown plants (Jurik et al. 1982, Cormack 1955). Mclaren and Smith (1978) showed that both light quality and quantity contribute to shade developmental responses in Rumex obtusifolius, and leaves of seedlings were thinner in the low R:FR and PAR treatment compared to just low PAR. Papaya plants in the HL treatment had leaves with the greatest specific leaf weight, and the leaves of plants grown in the NS treatment had a greater SLW than those of plants grown in the FS treatment. This reflects the results of leaf thickness and the internal organization of the leaves. Anderson (1955) showed in Cornus and Acer that cell elongation, especially that of the palisade mesophyll, to contribute to leaf thickness. In a more detailed study with Helianthus annus Dengler (1980) also found cell elongation to be an important factor in leaf thickness and in area. Others have also observed cell expansion to be a major factor in leaf thickness (Bjorkman and Holmgren 1963, Cameron 1970, Chabot and Chabot 1970, Jurik, Chabot and Chabot 1982). Palisade mesophyll thickness of Carica papaya was significantly reduced in the shade treatments. The FS-grown plants had the thinnest palisade cell layer of all the treatments. Mclaren and Smith (1978) showed that there was further reduction in palisade thickness of Rumex obtusifolius when low PAR was accompanied by a low R:FR. Thus, reduced PAR affects the development of the leaf palisade parenchyma, and R:FR affects the shape of the cells. The FS-grown plants had palisade cells that were small and conical shaped. The NS-grown plants had palisade cells that were more columnar in shape with a greater height (see fig. 2). Although intercellular space was not measured in my study, plants from the FS treatment had visibly more intercellular space than those from the NS treatment and the HL-grown plants (see fig. 3). Increased leaf intercellular space developmental response to shade has been observed in many studies (Wylie 1951, Ballantine and Forde 1970, Cameron 1970). Stomatal density in the current study was significantly reduced in the shade treatments, but differences between the NS and FS-grown plants were not significant. The reduction of stomatal density of plants grown in low light levels has been shown for many plant species (Dengler 1980, Cooper and Qualls 1967, Knect and Oleary 1972). Chlorophyll content in leaves of plants has been shown to increase in plants grown under low PAR when compared to plants grown under high PAR (Kapple and Flore 1983). Other studies have shown conflicting results (Bjorkman 1981). My results showed that papaya plants grown in both the FS and NS shade treatments had a significantly higher chlorophyll content than that of plants grown in the HL treatment. There was no significant difference between the two shade treatments.

When low PAR is accompanied by low R:FR there is often a decrease in the chlorophyll a/b and this decrease is considered to be a consequence of an increased development of the photosystem II reaction center (Bjorkman 1981, Glick et al. 1985, Kasperbauer and Hamilton 1984). In my study, the FS shade treatment had a significantly lower chlorophyll a/b ratio than the HL and NS treatments. There was no significant difference in chlorophyll a:b ratios between the HL and NS-grown plants.

The results of this study show that papaya exhibits significant morphogenetic plasticity, with regard to developmental light condition, in stem extension, petiole extension and leaf morphology. As mentioned in the introduction papaya grows under a variety of conditions from a full sun monoculture to growing wild in shaded and semi-shaded habitats.

This adaptability is very typical of some pioneer species. Perhaps the most striking example of morphogenetic plasticity in papaya is the difference in light interception (on a per leaf basis) due to differences in leaf morphology resulting from the different light conditions. Although exhibiting a shade-avoidance strategy, this species, by increasing light interception (on a per leaf basis), can contend with rather low light conditions.

# SUMMARY

The purpose of this study was to compare developmental responses of papaya seedlings in neutral shade to those in filtered shade in order to show that shade developmental responses of papaya are mediated by phytochrome. These results show that there is a difference in shade developmental response between papaya plants developing under filtered (low R:FR) shade and those developing under neutral (high R:FR) shade. The responses of papaya plants developing under filtered shade were characteristic of a shade-avoidance response found in nature whereas those plants grown under neutral shade showed less of a shade-avoidance response. These results indicate that shade developmental responses in *Carica papaya* are partly mediated by phytochrome.

# LITERATURE CITED

Anderson, Y.O., 1955. Seasonal development in sun and shade leaves. Ecology 36:430-439.

Ballantine, J.E.M., and Forde, B.J., 1970. The effect of light intensity and temperature on plant growth and chloroplast ultrastructure in soybean. American Journal of Botany 57(10):1150-1159.

Bjorkman, O., 1981. Responses to different quantum flux densities. In Encyclopedia of Plant Physiology New Series Volume 12A, Physiological Plant Ecology (Eds O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler), pp. 57-107. Springer-Verlag. Berlin.

Bjorkman, O. and Holmgren, P., 1963. Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. Physiologia Plantarum. 16:889-914.

Berlyn, G.P., and Miksche, J.P., 1976. Botanical microtechnique and cytochemistry. The Iowa State University Press, Ames.

Blackman, G.E. and Wilson, G.L., 1951. Physiological and ecological studies in the analysis of plant environment. VII. An analysis of the differential effects of light intensity on the net assimilation rate, leaf-area ratio, and relative growth rate of different species. Annals of Botany 15:373-408.

Borthwick, H., 1972. History of phytochrome. In Phytochrome (Eds Mitrakos and W. Shropshire, Jr.), Academic Press,Inc. New York

Briggs, W.R., 1976. H.A. Borthwick and S.B. Hendricks-pioneers of photomorphogenisis. In Light and plant development (Ed H. Smith) pp. 1-6. Butterworth & Co., Ltd., London.

Cameron, R.J., 1970. Light intensity and the growth of Eucalyptus seedlings. I. Ontogenetec variation in E. fastigata. Australian Journal of Botany 18:29-43.

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

Conover, R.A., Litz, R.E. and Malo, S.E., 1986. 'Cariflora', a papaya for south Florida with tolerance to papaya ringspot virus. Institute of Food and Agricultural Sciences, University of Florida, Circular S-329.

Cooper, C.S., and Qualls, M., 1967. Morphology and chlorophyll content of shade and sun leaves of two legumes. Crop Science 7:672-673.

Cormack, R.G.H., 1955. Effect of extreme shade upon leaf form and structure in Vicea americana. Canadian Journal of Botany 33:293-297.

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

De Candolle, A., 1886. Origin of Cultivated Plants. 2nd. ed. Reprinted New York: Haffner, 1959.

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

Fisher, J.B., 1980. The vegetative and reproductive structure of papaya (Carica papaya). Lyonia 1(4):191-208.

Fitter, A.H., and Ashmore, C.J., 1974. Response of two Veronica species to a simulated woodland light climate. New Phytologist 73:997-1001.

Glick, R.E., McCauley, S.W and Melis, A., 1985. Effect of light quality on chloroplast-membrane organization and function in pea. Planta 164:487-494.

Grime, J.P., 1981. Plant strategies in shade. In Plants and the daylight spectrum (Ed H. Smith), pp. 147-158. Academic Press, London.

Jurik, T.W., Chabot, J.F. and Chabot, B.F., 1982. Effects of light and nutrients on leaf size, CO2 exchange, and anatomy in wild strawberry (Fragaria virginiana). Plant Physiology 70:1044-1048.

Kapple, F. and Flore, J.A., 1983. Effect of shade on photosynthesis, specific leaf weight, leaf chlorophyll content, and morphology of young peach trees. Journal of the American Society for Horticultural Science 108(4):541-544.

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., and 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.

Knecht, G.N. and O'Leary, J.W., 1972. The effect of light intensity on stomate number and density of Phaseolus vulgaris L. leaves. Botanical Gazette 133:132-134.

Kwesiga, F. and 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.

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., 1988. Simulating forest shade to study the developmental ecology of tropical plants: juvenile growth in three vines in India. Journal of Tropical Ecology 4:281-292.

Lee, D.W. and Graham, R., 1986. Leaf optical properties of rain-forest sun and extreme shade plants. American Journal of Botany 73:1100-1108.

McClaren, J.S. and Smith, H., 1978. Phyochrome control of the growth and development of Rumex obtusifolius under simulated canopy light environments. Plant, Cell and Environment 1:61-67.

Mohr,H. 1969., Photomorphogenesis. In Physiology of plant growth and development (Ed Wilkins, M.B.), McGraw-Hill Book Company, New York.

Morgan,D.C., O'Brien,T. and Smith,H., 1980. Rapid photomodulation of stem extension in light grown Sinapsis alba L.: studies on kinetics, site of perception and photoreceptor. Planta 150:95-101.

Morgan, D.C. and Smith, H., 1979. A systematic relationship between phytochrome-controled development and species habitat, for plants grown in simulated natural radiation. Planta, Berlin 145:253-258.

Morgan, D.C. and Smith,H., 1978. The relationship between phytochrome photoequilibrium and development in light grown Chenopodium album L. Planta 142:187-193.

Morgan, D.C. and Smith, H., 1981. Non photosynthetic responses to light quality. In Encyclopedia of Plant Physiology New Series Volume 12A, Physiological Plant Ecology (Eds O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler), pp. 109-134. Springer-Verlag, Berlin.

Morgan, D.C. and Smith, H., 1981. Control of development in Chenopodium album L. by shadelight: the effect of light quantity (total fluence rate) and light quality (red:far-red ratio). New Phytologist 88: 239-248.

Richards, J.H. and Lee, D.W., 1986. Light effects on leaf morphology in water hyacinth (Eichhornia crassipes). American Journal of Botany 73(12):1741-1747.

Smith, H., 1982. Light quality, photoreception and plant strategy. Annual Review of Plant Physiology 33:481-518.

Talbert, C.M. and Holch, A.E. 1957. A study of the lobing of sum and shade leaves. Ecology 38(4):655-658.

Vince-Prue, D., Guttridge, C.G. and Buck, M.W., 1976. Photocontrol of petiole elongation in light-grown strawberry plants. Planta, Berlin 131:109-114.

Warrington, I.J., Rook, D.A. Morgan, D.C. and Turnbull, H.L., 1988. The influence of simulated shadelight and daylight on growth, development and photosynthesis of Pinus radiata, Agathis australis, and Dacrydium cupressinum. Plant, Cell and Environment 11:343-356.

Wylie, R.B., 1951. Principles of foliar organization shown by sun-shade leaves from ten species of deciduous dicotyledonous trees. American Journal of Botany 38:355-361.