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Developmental Light Level Affects Growth, Morphology, and Leaf Physiology of Young Carambola Trees

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Abstract. **Growth and leaf physiology responses of container-grown 'Arkin' carambola (*Averrhoa carambola* L.) trees to long-term exposure of ≈25%, ≈50%, or 100% sunlight were studied in four experiments in Guam and Florida. Shading increased rachis length and leaflet area, and decreased leaflet thickness. Shaded trees also had a more horizontal branch orientation. Shading reduced dark respiration (R_d) and light compensation and saturation points but increased chlorophyll concentration and N-use efficiency. Light-saturated net CO_2 assimilation (A) was not affected by developmental light level. Trees in full sun had smaller total leaf area, canopy diameter, and shoot : root ratio and exhibited leaflet movement to avoid direct solar radiation. Also, trees grown in 100% sunlight had a more vertical branch orientation and greater stomatal density than shaded trees. The ratio of variable to maximum fluorescence (F_v/F_m) declined during midday in 100% sunlight trees. This pattern was accompanied by a midday suppression of A in 100% sunlight-grown trees in Guam. 'Arkin' carambola trees exposed to ≈25%, ≈50%, or 100% sunlight for up to 39 weeks exhibited physiological and morphological adaptations that resulted in similar growth. These results indicate that carambola efficiently adapts to different developmental light intensities.**

Plants adapt to different irradiance levels by anatomical, morphological, and/or physiological changes that allow the maintenance of a positive carbon balance in a wide range of light environments (Bjorkman, 1981; Fitter and May, 1981; Kramer and Kozlowski, 1979). Low irradiance generally leads to larger leaves with reduced thickness, stomatal density, and conductive tissue per unit leaf area. Canopy responses to low light include increased internode length and reduced leaf area index. Plants also exhibit numerous physiological adaptations to low irradiance, including increased quantum yield and reduced R_d, light compensation and saturation points.

Campbell et al. (1985) suggested that shading of carambola trees results in reduced fruit production and recommended planting trees in sites exposed to full sun. However, in several areas, including Australia (Watson et al., 1988) and Florida (Crane, 1992), carambola trees are grown under shade coverings for insect or wind control. Furthermore, pruning of mature carambola trees is necessary for tree size control or to prevent overcrowding (Campbell et al., 1985; Crane, 1992), but little is known about optimum canopy size or the relationship of canopy size to natural shading and yield.

The rapidly increasing commercial production of carambola has resulted in the industry developing in advance of adequate research. Thus, a better understanding of the light-acclimation process of trees may lead to improved management practices under various conditions. The objectives of this study were to determine the influence of light level during plant development on growth, morphology, and leaf physiology of carambola trees and to classify carambola with respect to shade tolerance.

Materials and Methods

Three separate experiments were conducted on the island of Guam (lat. 13°N). Twelve quonset-style structures with a height of ≈1.5 m were constructed outdoors on top of raised benches to provide 24%, 47%, or 100% of ambient light conditions (four structures per transmittance level). Shading was achieved by covering the structures with neutral-woven polyethylene fabric, and sunlight transmittance was measured using a quantum sensor (model LI-190 SA; LI-COR, Lincoln, Neb.) oriented perpendicular to the solar beam. The full sun structures were left uncovered. The fabric on shaded structures extended to the bench top on the east and west sides of each structure, but the bottom halves of the north and south sides were left open to facilitate air flow. Numerous measurements indicated that no differences existed in ambient temperature among the structures. Thus, four replications of each light intensity were arranged in a completely randomized design.

Experiment 1. Carambola seedlings growing in 2.6-liter containers were grafted with 'Arkin' budwood in May 1991 and grown in an open-sided fiberglass structure (≈50% light transmittance) until the beginning of the experiment. The container medium consisted of 2 peat : 1 perlite : 1 sand (by volume). Trees were fertilized with a nutrient solution containing 7.5 mM N, made with HydroSol (W.R. Grace & Co., Fogelsville, Pa.) and calcium nitrate. Each tree received 125 ml solution per week, and was watered to container capacity every 2 days.

Twenty-four uniform trees with a mean height of 33 cm were moved to the experimental area on 27 Sept. 1991. Two trees were placed in each structure, and irrigation and fertilization were continued as previously described.

Canopy and leaf growth characteristics were determined after

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about 23 weeks for one tree in each structure. Length of the terminal leaflet was measured from Jan. (visible emergence) through Feb. 1992 for two leaves per tree. Canopy height, width, total shoot length, and leaf number were measured on 10 Mar. 1992. The terminal leaflets tagged for determining their expansion rate were then removed and the area was measured using an AgVision System Model DS (Decagon Devices, Pullman, Wash.). All leaf area determinations described hereafter were made using the same system. Two additional leaves were selected randomly from each tree canopy to determine leaflet number per leaf and rachis length and the number of major veins, length, and area of the terminal leaflets. The area of the entire leaf was measured before drying in a forced-draft oven at 60C to obtain dry weight.

All remaining leaves were removed from the trees and total leaf area per tree was determined. Two leaflets were randomly selected from each tree to determine lamina angle. The leaflet was cut with a razor blade perpendicular to the midrib at the widest point. The cut surface was placed on paper, the lamina outline was traced, and the tracing was measured with a protractor to determine lamina angle.

Four 20-cm terminal shoots were removed from the trees, the number of nodes were counted, and mean internode length was calculated. The shoots were dried at 60C to a constant dry weight, and specific stem length (SSL) was calculated as shoot length per unit dry weight.

Leaf area index (LAI) was calculated as total leaf area per two-dimensional canopy area. Leaf area density (LAD) and shoot length density (SD) were calculated as total leaf area or shoot length per unit canopy volume. Canopy volume was calculated as a prolate spheroid if height was greater than width, or as an oblate spheroid if height was less than width (Westwood, 1978).

Leaflet growth rate was calculated as final leaflet length or area divided by the number of days for full expansion. Specific leaf density (SLD) was calculated as dry weight per unit area using measurements from entire leaves.

The remaining tree in each structure was used for all subsequent measurements. The influence of light intensity on chlorophyll fluorescence was determined throughout the photoperiod on 12 Mar. 1992 and repeated on 13 Mar. Chlorophyll fluorescence was measured using a fluorescence system (model CF-1000; P.K. Morgan Instruments, Andover, Mass.). Measurements were made at ambient temperature on the adaxial surface of recently matured leaves beginning pre-dawn and continuing at ≈2-h intervals until sunset. A 30-min period of dark adaptation was provided by the system cuvettes before each measurement. Photosynthetic photon flux (PPF) of excitation light was 500 $\mu mol\cdot m^{-2}\cdot s^{-1}$. The instantaneous PPF was determined with a quantum sensor at the time dark adaptation cuvettes were installed. In addition, PPF was integrated over the time periods between measurements with data from a weather station (model 012; Campbell Scientific, Logan, Utah) located about 50 m from the experimental site.

Net CO_2 assimilation was determined on single leaflets of trees within each structure at 2-h intervals throughout the day on 14 Mar. 1992 with a portable photosynthesis system, with 6 cm^2 exposed in a 1-liter leaf chamber (model 6250; LI-COR). Dark respiration was determined from CO_2 efflux before sunrise and after sunset. During gas-exchange determinations, temperature ranged from 26 to 31C, ambient CO_2 ranged from 360 to 375 $\mu l\cdot liter^{-1}$, and vapor pressure deficit (VPD) ranged from 0.7 to 1.8 kPa.

Pre-dawn and midday xylem potentials (ψ_x) were measured on two leaves per tree on 14 Mar. using a pressure chamber (model 650; PMS Instruments, Corvallis, Ore.). Fresh weights of two leaflets per tree were also determined at midday. Leaflet petioles were then immersed in water and the leaflets were maintained in dim light (≈40 $\mu mol\cdot m^{-2}\cdot s^{-1}$) for 24 h, before determining the turgid weight. Dry weight was obtained after drying at 60C. Relative leaf water content (RWC) was calculated as (fresh weight – dry weight)/(turgid weight – dry weight) × 100.

The influence of developmental light level on response of A to incident PPF was determined on 17 Mar. 1992. Whole plants were exposed to a range of PPF conditions by placing them under various transmittance levels of neutral shadecloth fabric. A 5-min adaptation period was allowed at each new PPF before recording A on 3 leaflets per replicate. Gas-exchange measurements were made as previously described. This process yielded 50 measurements of A throughout a PPF range of 175 to 1950 $\mu mol\cdot m^{-2}\cdot s^{-1}$ for plants in each developmental light treatment. Ambient conditions were 28 to 29 C, 365 to 370 $\mu l\cdot liter^{-1}$ CO_2, and 1.1 to 1.6 kPa VPD.

The trees were transferred to an open-air laboratory at 0700 HR on 18 Mar. 1992 to determine the response of A to PPF of 0 to 174 $\mu mol\cdot m^{-2}\cdot s^{-1}$. Light was supplied by a 1500-W quartz halogen lamp suspended above a thermal-filtering water bath, and the desired PPF was achieved by varying distance of the cuvette from the lamp and shading with layers of neutral fabric. Dark respiration was determined by inserting a leaflet into the chamber and enclosing the entire chamber in several layers of black plastic for 10 min. Gas exchange was measured as previously described. Laboratory conditions were 28C, 375 to 380 $\mu l\cdot liter^{-1}$ CO_2, and 1.2 to 1.3 kPa VPD.

The response of A to a range of CO_2 partial pressures (CA) was determined on three replicates per developmental light intensity on 19 to 20 Mar. 1992, as described by Marler et al. (1993). The response curves were determined under low light (24% sunlight) and high light (100% sunlight) conditions. The conditions during measurements were 150 to 720 $\mu l\cdot liter^{-1}$ CO_2, 28 to 31C and 1.3 to 1.7 kPa VPD.

Three plants per developmental light level were placed under 47% sunlight at 0700 HR on 21 Mar. 1992. Light-saturated A was measured as previously described on eight recently expanded leaflets per tree from 1000 to 1300 HR, when PPF ranged from 1000 to 1150 $\mu mol\cdot m^{-2}\cdot s^{-1}$. Ambient conditions were 29 to 31C, 370 to 375 $\mu l\cdot liter^{-1}$ CO_2, and 1.5 to 1.6 kPa VPD. Composite area and dry weight were determined and SLD was calculated. Leaf N content was determined on a dry-weight basis using the micro-Kjeldahl procedure (Jones et al., 1991). The SLD of each replicate was used to estimate N content per unit leaf area. Maximum A per unit leaf N was calculated as A/N per unit leaf area.

Leaf samples were removed from the plants on 23 Mar. 1992 and transported to a laboratory in a cooler. Leaflet thickness was measured on sections of the mid-region of three leaflets per tree using a compound microscope with an eyepiece micrometer. Stomatal densities were measured using epidermal strips taken from interveinal areas on the abaxial surface of leaflets. The stomata were counted in a 0.3-mm^2 field of view using a compound microscope. Five sectors were counted per tree for a total of 20 counts per treatment.

Experiment 2. Carambola seedlings growing in 2.6-liter containers were grafted with ‘Arkin’ budwood in Aug. 1991 and maintained as in Expt. 1 until Dec. 1991. Twelve 26-cm tall uniform trees were moved to the experimental area on 5 Dec., and one tree was placed in each of the structures. The trees were repotted in 5.1-liter containers on 15 Apr. 1992. The nutrient solution was applied at a rate of 250 ml per container per week thereafter.

The trees were grown for 39 weeks before harvesting to determine growth and morphological responses to developmental light level. Measurements were made on 2 and 3 Sept. 1992. Trunk diameter and canopy height, width, and total shoot length were measured. The distance from each shoot tip to the oldest leaf was measured, nodes were counted, and mean internode length was calculated. Branch orientation was determined by measuring the angle of major limbs in relation to the horizontal plane by placing a protractor on a bubble level held horizontally. After determining fresh leaf weight, leaves were counted and the total area was determined. Container medium was carefully removed from the roots by rinsing with tap water. The canopy and root systems were separated at the crown and fresh weights were obtained. Leaves, shoots, and roots were dried to constant weights at 60C and dry weights were determined. Shoot : root ratio was calculated based on dry weights. Leaf area index, LAD, and SD were calculated as previously described and SSL and SLD were calculated from entire canopy measurements. Leaf weight ratio (LWR) and leaf area ratio (LAR) were calculated as canopy leaf dry weight or area, respectively, per unit whole plant dry weight.

Experiment 3. Carambola seedlings growing in 2.6-liter containers were grafted with 'Arkin' budwood in Nov. 1991. The plants were maintained as described in Expt. 1, and were repotted into 5.1-liter containers on 9 July 1992. The nutrient solution was changed on 9 Oct. and thereafter to a commercial complete soluble fertilizer (Excel 15N–2.2P–12.5K, Grace-Sierra, Milpitas, Calif.). Nitrogen concentration of the solution and application rates remained unchanged.

Twelve uniform trees averaging 75 cm in height were moved to the experimental area on 27 Nov. 1992 and placed one per structure. The plants were maintained under these conditions for 15 weeks before repeating some of the measurements made during Expt. 1. Pre-dawn ψ_x, midday ψ_x, and midday RWC were measured on 11 Mar. 1993. The response of A to PPF in the range of 1400 to 75 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was obtained on 12 Mar. using the 1500 W lamp and neutral fabric as previously described. Dark respiration was measured as in Expt. 1. Laboratory conditions were 30 to 31C, 380 to 385 $\mu l \cdot liter^{-1}$ CO_2, and 1.2 to 1.3 kPa VPD. Diurnal measurements of chlorophyll fluorescence were repeated on 13 Apr. 1993 as previously described.

Experiment 4. Another experiment was conducted in Homestead, Fla. (lat. 25°) using 3-year-old grafted 'Arkin' carambola scions on 'Golden Star' seedling rootstocks growing in 11.4-liter containers. Container medium consisted of 4 peat : 4 pinebark : 2 sawdust : 1 sand (by volume). The trees were fertilized every 2 weeks with a granular 6N–2.6P–5K fertilizer. In addition, the container medium was drenched with Fer-A-Gro (AFEC Fertilizer & Chemical Co., Homestead, Fla.) and iron as Fe–EDDHA. The amount of fertilizer depended on the stage of development (i.e., as canopy size increased fertilizer rate was increased). Plants were irrigated as needed, generally three to four times per week.

The trees were placed outdoors in 25%, 50%, or 100% sunlight during the first week of Jan. 1993, when they were 120 to 130 cm in height. Shade treatments were achieved by enclosing plants in cubical wooden frames (3.0 × 3.0 × 1.5 m) covered with polyethylene fabric or placed in full sun. Numerous measurements indicated that temperature was no more than 2C higher in full sun than in the shade structures. Two trees were placed in each location. Thus, there were three replications per shade treatment with two single-tree samples per replication arranged in a randomized complete-block design.

Chlorophyll fluorescence, SLD, and leaf chlorophyll concentration were measured during the first 2 weeks of Mar. 1993 on leaves that developed under the different light environments. Chlorophyll fluorescence was measured with a chlorophyll measurement system (model CF-1000; Morgan) at 1300 HR on 1 Mar. Dark adaptation and excitation light were the same as described for Expt. 1. In addition, diurnal measurements of chlorophyll fluorescence were conducted at 2-h intervals from 0700 to 2000 HR on 4 Mar. Leaf chlorophyll concentration was determined on 9 Mar., as described by Marini and Marini (1983). Eight 0.32-cm^2 discs were obtained from each replication and placed in darkness for 48 h in 10 ml 80% MeOH. Total chlorophyll, chlorophyll a, and chlorophyll b were determined from absorbance at 642 and 660 nm using a spectrophotometer (model Spectronic 21; Milton Roy Co., Rochester, N.Y.) (Proctor, 1981). Specific leaf density was determined on 9 Mar. from the dry weight of eight 0.32-cm^2 discs per replication.

Statistical Analysis. Results of all growth and morphological variables were subjected to analysis of variance (ANOVA). The results from each experiment were analyzed separately. Significance of linear and quadratic models was determined with percent sunlight as the independent variable. Diurnal fluorescence and A data were analyzed as a percent sunlight × time of day factorial. The relationship between A and PPF was determined for each percent sunlight pretreatment separately using nonlinear regression. The response curves were defined by the equation $y = a(1–e^{-bx})$, where y = A and x = PPF. Light saturation points were estimated as 95% of maximum A. The linear portion of the response curve was determined by linear regression with the independent variable PPF in the range of 0 to 174 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The relationship between A and CA was defined by a linear model within the range of CO_2 used in this study.

Results

Experiments 1 and 3. Twenty-three weeks of growth under 100%, 47%, or 24% sunlight had no effect on canopy height, width, SD, leaf number, or shoot length of carambola trees (data not shown). Total leaf area, LAI, LAD, mean internode length, and SSL of the terminal 20 cm of shoot growth increased as developmental light level decreased (Table 1). Developmental light level had no effect on the duration of leaflet expansion (data not shown); however, the average leaflet growth rate was greater for trees growing in reduced sunlight (Table 2). The increased total leaf area in reduced sunlight was due to an increase in average leaflet area, since leaflet number did not differ among the light treatments. Mean rachis length was greater on trees in reduced sunlight compared to those in full sun. Interveinal area was greatly increased in trees growing in 24% sunlight compared to trees

Table 1. Growth and morphological characteristics of 'Arkin' carambola trees grown under three light levels. Measurements were made on 10 Mar. 1992 and treatments were initiated 27 Sept. 1991.

Variable	% Sunlight 100	47	24	Significance	r^2
Total leaf area (cm^2)	3487	4825	5204	L^{**}	0.54
Leaf area index ($m^2 \cdot m^{-2}$)	1.49	1.95	2.14	L^{*}	0.41
Leaf area density ($m^2 \cdot m^{-3}$)	3.95	5.30	6.42	L^{*}	0.36
Specific stem length ($cm \cdot g^{-1}$)	23.9	30.2	54.5	L^{*}	0.42
Internode length (cm)	1.64	2.01	2.04	L^{**}	0.27

*,**Linear models were significant at $P \leq 0.05$ or 0.01, respectively.

Table 2. Leaf characteristics of 'Arkin' carambola trees grown under three light levels. Measurements were made in Mar. 1992 and treatments were initiated 27 Sept. 1991.

		% Sunlight				
Variable	n	100	47	24	Significance	r^2
Leaflet growth (cm/day)	8	0.31	0.34	0.37	L^{**}	0.59
Leaflet growth (cm^2/day)	8	0.75	0.85	1.01	L^{**}	0.51
Area/leaf (cm^2)	8	85.3	98.5	130.1	L^{**}	0.53
					Q^{**}	0.76
Rachis length (cm)	8	8.9	11.9	13.4	L^{**}	0.65
Specific leaf density ($mg \cdot cm^{-2}$)	8	8.02	7.92	6.23	L^{**}	0.41
					Q^{**}	0.70
Veins/leaflet	8	18	21	17	Q^{**}	0.32
Interveinal distance (cm)	8	0.68	0.67	0.84	L^{**}	0.32
					Q^{**}	0.62
Interveinal area (cm^2)	8	1.64	1.67	2.29	L^{**}	0.42
					Q^{**}	0.71
Leaflet thickness (m)	12	287	248	213	L^{**}	0.62
Lamina angle (degrees)	8	106	134	145	L^{**}	0.92
Stomata/mm^2 leaf area	20	521	448	381	L^{**}	0.38

**Linear (L) or quadratic (Q) models are significant at $P \leq 0.01$.

growing in 100% or 47% sunlight (Table 2). The number of major lateral veins did not increase with the mean increase in leaflet area, leading to a greater distance between veins on leaflets developed in 24% sunlight compared to those in the other treatments.

Leaflet thickness and SLD were positively correlated to light level (Table 2). The lamina angle was smallest in trees under 100% sunlight, averaging 73% of the angle for trees in 24% sunlight. The area between stomata also increased in response to reduced sunlight; there were 27% fewer stomata per unit area on trees in 24% sunlight compared with those in 100% sunlight (Table 2).

The diurnal pattern of F_v/F_m was dependent on developmental light level and time of day (interaction $P \leq 0.01$). For trees in 47% or 24% sunlight, F_v/F_m was stable throughout the day (Fig. 1). There was a quadratic ($P \leq 0.01$) diurnal trend for trees in 100% sunlight, with the minimum F_v/F_m corresponding to midday, when the integrated PPF was at a maximum.

The diurnal pattern of A was also dependent on developmental light level and time of day (interaction $P \leq 0.01$). Trees grown in 47% and 24% sunlight exhibited a smooth diurnal curve, with A increasing from pre-dawn to midday, then decreasing until after sunset (Fig. 2). The A rate of trees in 100% sunlight, however, increased rapidly to a daytime high by 0700 HR and immediately decreased to a midday suppression.

The light response curves over the PPF range of 175 to 1950 $\mu mol \cdot m^{-2} \cdot s^{-1}$ were similar for trees grown in 47% or 100% sunlight (Fig. 3). Above light saturation, A of trees grown in 24% sunlight was also similar to that of trees grown in the other developmental light levels (Fig. 3). Net CO_2 assimilation between PPF of 175 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and light saturation was higher for the trees grown in 24% sunlight than for trees grown in 47% or 100% sunlight. Light-saturated A (95% of maximum A) was thus achieved at a PPF of 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 24% sunlight-grown trees and 950 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 47% and 100% sunlight-grown trees.

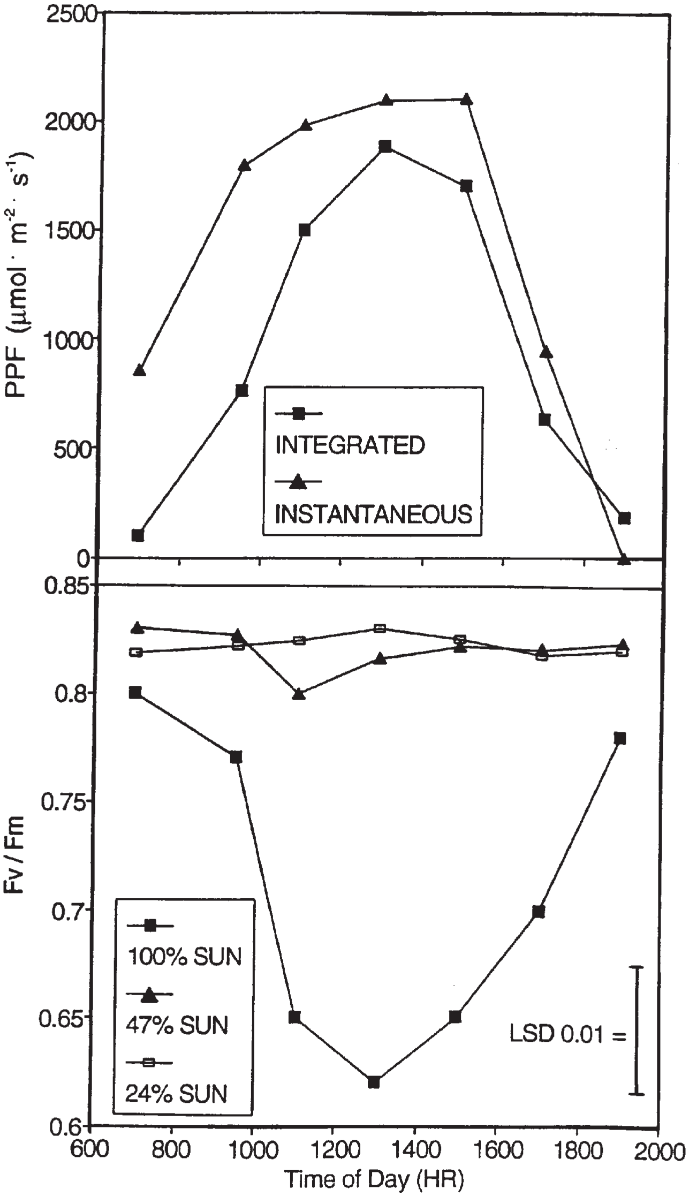

Fig. 1. Photosynthetic photon flux (PPF) and the ratio of variable to maximum fluorescence (F_v/F_m) of 'Arkin' carambola leaves as influenced by time of day and preconditioning to 100%, 47%, or 24% sunlight from 27 Sept. 1991 to 13 Mar. 1992. Instantaneous PPF was determined in full sunlight at the time the dark adaptation cuvettes were placed on leaflets, and integrated PPF is for the period preceding each measurement. Measurements were made with quantum sensors positioned perpendicular to the horizontal plane.

Apparent quantum yield (i.e., 0 to 174 $\mu mol \cdot m^{-2} \cdot s^{-1}$) did not differ among plants grown in the three levels of sunlight (Fig. 3). However, R_d was lower in trees grown in reduced sunlight (Fig. 3, Table 3). The light compensation point of 31 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for trees grown in 24% sunlight was about half of that for 100% sunlight-grown trees.

A positive linear correlation between A and CA was observed up to about 700 $\mu l \cdot liter^{-1}$ CO_2 for all of the trees in this study (Table 4). Moreover, this response was linear regardless of light intensity during the measurements. No differences in CO_2-use efficiency occurred among the trees in the various developmental light levels. Net CO_2 assimilation increased more with increased CA when measured in high light compared to determinations in low light, regardless of developmental light level (Table 4).

No differences in pre-dawn Ψ_x or midday RWC and Ψ_x oc-

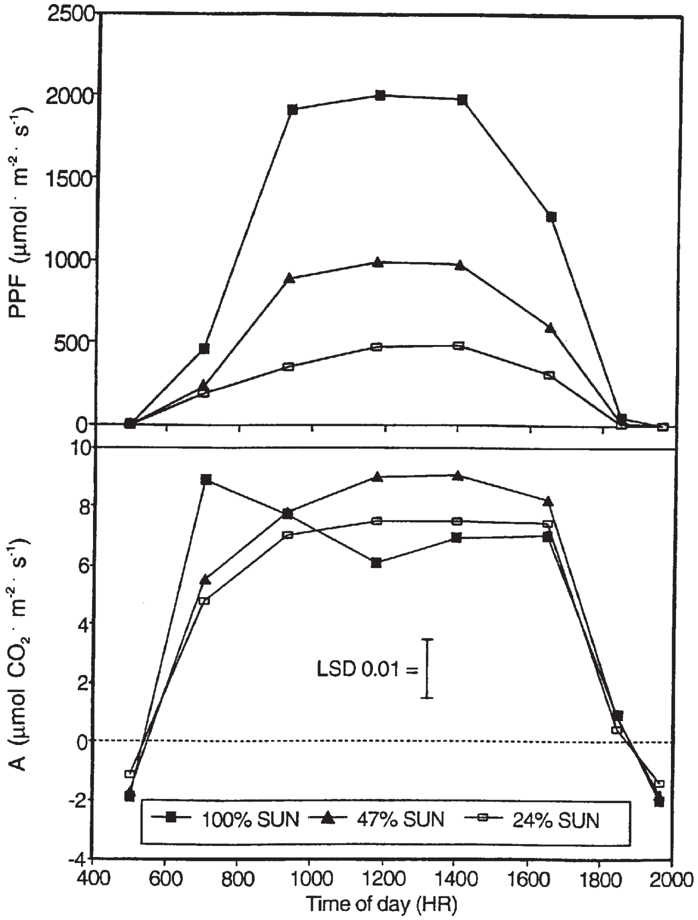

Fig. 2. Photosynthetic photon flux (PPF) and net CO$_2$ assimilation (A) of 'Arkin' carambola leaves as influenced by time of day and preconditioning to 100%, 47%, or 24% sunlight from 27 Sept. 1991 to 14 Mar. 1992.

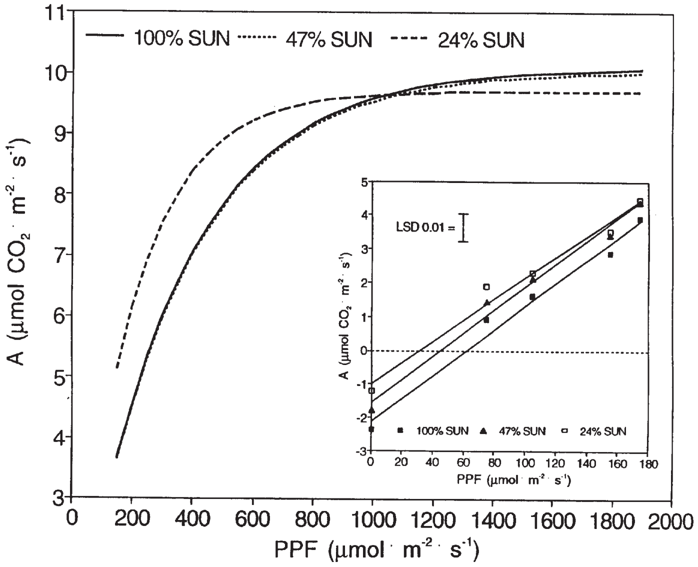

Fig. 3. Net CO$_2$ assimilation (A) of 'Arkin' carambola leaves preconditioned to 100%, 47%, or 24% sunlight as a function of photosynthetic photon flux (PPF). Treatments were begun on 27 Sept. 1991. Response curves obtained on 17 Mar. 1992 are based on 50 measurements per developmental light level, and are described by the following equations: 100%: $A = 10.09(1–e^{-0.003x})$, $r^2 = 0.56$; 47%: $A = 10.04(1–e^{-0.003x})$, $r^2 = 0.75$; 24%: $A = 9.70(1–e^{-0.005x})$, $r^2 = 0.53$. Insert: Obtained on 18 Mar., regression equations are as follows: 100%: $A = –2.10 + 0.034$ PPF, $r^2 = 0.96$; 47%: $A = -1.53 + 0.034$ PPF, $r^2 = 0.97$; 24%: $A = –0.97 + 0.031$ PPF, $r^2 = 0.97$.

Table 3. Leaf physiology characteristics of 'Arkin' carambola trees grown under three light levels.

		% Sunlight				
Variable	n	100	47	24	Significance	r^2
Dark respiration^{z} (μmol CO$_2$/m per sec)	8	2.38	1.78	1.23	L*	0.38
Leaf nitrogen conc.^{y} (%)	3	2.35	2.40	2.30	NS	
Leaf nitrogen conc.^{y} (mg·cm^{-2})	3	0.18	0.19	0.15	Q*	0.73
A/N^{y} (nmol CO$_2$/mg N per sec)	3	5.90	5.76	6.82	Q*	0.58

^{z}Represents 4 replications each from Expts. 1 and 3. Data from Expts. 1 and 3 were pooled due to lack of significant differences between experiments.

^{y}Each replication represents measurements on eight leaflets, performed on 21 Mar. 1992.

^{NS,*}Linear (L) or quadratic (Q) models are nonsignificant or significant at $P \leq 0.05$, respectively.

Table 4. Influence of external CO$_2$ (μl·liter^{-1}) and light level on net CO$_2$ assimilation (A, μmol CO$_2$/m^{-1} per sec) of 'Arkin' carambola leaves that developed under 100%, 47%, or 24% sunlight. No differences in slope occurred among sunlight treatments. Significance indicated is between measurement light levels within each percent sunlight treatment level. Measurements were made on 19 and 20 Mar. 1992; treatments were initiated on 27 Sept. 1991. External CO$_2$ range: 150 to 720 μl·liter^{-1}.

Percent sunlight	Measurement light level	Regression equation	r^2
100	100	$A = –5.30 + 0.037\ (CO_2)$	0.97
	24	$A = –4.44 + 0.027\ (CO_2)^{**}$	0.94
47	100	$A = –6.38 + 0.042\ (CO_2)$	0.96
	24	$A = –4.14 + 0.026\ (CO_2)^{**}$	0.98
24	100	$A = –3.82 + 0.034\ (CO_2)$	0.96
	24	$A = –3.54 + 0.029\ (CO_2)^{*}$	0.94

*,**Significant difference between measurement light level at $P \leq 0.05$ or 0.01, respectively.

curred among the trees in different developmental light levels during Expt. 1 or 3 (data not shown).

Leaf N per unit dry weight was not influenced by developmental light level; however, leaflets on trees in 24% sunlight had lower N per unit area than leaflets on trees in the 47% or 100% light treatments (Table 3). The trees in 24% sunlight also exhibited higher A/N than trees growing in 47% or 100% sunlight.

Experiment 2. There was an inverse linear relationship of canopy diameter to developmental light level following 39 weeks of growth (Table 5). Canopies of trees in 100% sunlight were less than 70% of the width of canopies of trees growing in 24% sunlight, while canopy height was unaffected by developmental light level. Trees in 47% sunlight had the greatest total shoot length, trunk diameter, shoot dry weight, and canopy dry weight (Table 5). The trees developed in 24% sunlight developed the largest leaves on average and had the greatest total leaf area. Mean internode length was also greatest for trees grown in 24% sunlight. Root dry weight, leaf number, leaf dry weight, and SSL were not influenced by developmental light level (data not shown). The shoot : root ratio was inversely related to developmental light level. The shoot : root ratio of trees in 100% sunlight was about 80% of that of trees in 24% sunlight (Table 5).

Table 5. Growth and morphological characteristics of ‘Arkin’ carambola trees grown under three light levels. Measurements were made in Sept. 1992 and treatments were initiated 5 Dec. 1991.

	% Sunlight				
Variable	100	47	24	Significance	r^2
Canopy width (cm)	79.0	107.4	116.5	L^{**}	0.66
Total shoot length (cm)	770	1051	840	Q^{**}	0.95
Total leaf area (1000 cm^2)	11.4	13.6	15.2	L^{*}	0.41
Area/leaf (cm^2)	81.0	90.1	124.9	L^{**}	0.72
Trunk diameter (cm)	22	24	20	Q^{*}	0.38
Shoot dry wt (g)	54	76	54	Q^{*}	0.52
Canopy dry wt (g)	111	135	103	Q^{*}	0.44
Shoot : root ratio	0.75	0.89	0.92	L^{*}	0.41
Leaf area index (m^2·m^{-2})	2.48	1.50	1.49	L^{*}	0.39
Leaf area density (m^2·m^{-3})	4.95	2.17	2.71	L^{*}	0.44
Shoot length density (m·m^{-3})	33.2	17.1	14.8	L^{**}	0.63
Specific leaf density (mg·cm^{-2})	5.02	4.36	3.31	L^{**}	0.60
Leaf area ratio (cm^2·g^{-1})	44.4	47.5	73.1	L^{*}	0.34
Internode length	1.38	1.93	2.61	L^{**}	0.52
(cm)	Q^{*}	0.55			
Shoot angle^z	53.3	31.1	17.3	L^{**}	0.45

^{z}Degrees from horizontal plane.

*,**Linear (L) or quadratic (Q) models are significant at $P \leq 0.05$ or 0.01, respectively.

Table 6. Chlorophyll concentration and midday chlorophyll fluorescence ratio (F_v/F_m) of ‘Arkin’ carambola trees grown under three light levels. Treatments were initiated Jan. 1993 and measurements were made in Mar. 1993. Each replication consists of the mean of eight samples (chlorophyll) or 2 samples (F_v/F_m).

	% Sunlight				
Variable	100	50	25	Significance	r^2
Chlorophyll conc. (g·cm^{-2})	17.57	33.25	33.01	L^{**} Q^{**}	0.81 0.91
F_v/Fm	0.55	0.71	0.75	L^{*}	0.86

*,**Linear (L) or quadratic (Q) models are significant at $P \leq 0.05$ or 0.01, respectively.

The variation in fresh weight was similar to that of dry weight and whole plant fresh and dry weight did not differ among plants in the different developmental light levels. Mean fresh weight of these trees was 732 g, and dry weight was 255 g. Percent sunlight had a strong influence on the orientation of major limbs. The angle from a horizontal orientation of these limbs on trees in 100% sunlight was more than three times as great as that of trees in 24% sunlight (Table 5). A linear decrease in SLD calculated from the entire canopy, however, occurred with a decrease in developmental light level.

Canopy volume of trees grown in 100% sunlight was less than 40% that of trees grown in 47% or 24% sunlight (data not shown.). As a result, LAI, LAD, and SD were directly related to developmental light level (Table 5). Similarly, there was a strong inverse relationship of LAR and developmental light level. In contrast, LWR was not influenced by the light treatments (data not shown).

Experiment 4. The SLD did not differ among leaflets that developed under 25%, 50%, or 100% sunlight (data not shown). However, chlorophyll content per unit leaflet area was almost twice as great in carambola leaflets grown in 25% or 50% sunlight than in leaflets grown in full sunlight (Table 6). Developmental light level had no effect on the chlorophyll a : chlorophyll b ratio (data not shown). The diurnal pattern of F_v/F_m on 4 Mar. 1993 from these trees was similar to that measured in Expts. 1 and 3 (Fig. 1). The F_v/F_m of trees in 25% or 50% sunlight was stable throughout the day, but that of trees grown in 100% sunlight exhibited a quadratic ($P \leq 0.01$) diurnal trend. The midday F_v/F_m minimum of 0.57 in the 100% sunlight-grown trees was slightly below that of the 100% sunlight trees in Expts. 1 and 3 (Fig. 1). These measurements were confirmed on 1 Mar., where an inverse linear relationship occurred between percent sunlight and F_v/F_m at 1300 HR (Table 6).

Discussion

Morphological responses to shade were apparent in the carambola trees grown in 24% light, and leaf responses were more rapid than canopy responses. Shaded leaflets were larger, thinner, and had reduced SLD compared with leaflets of trees in 100% sunlight. There was no effect of light environment on leaflet number, but rachis length of 24% sunlight leaves was 1.5 times that of 100% sunlight leaves. Shoot internodes and leaf rachis were longer, branch and leaflet lamina angle were more horizontal, and canopies were wider in trees receiving 24% sunlight than those in 100% sunlight. These modifications of the shaded trees maximized light interception while reducing mutual shading, as indicated by reduced LAI and LAD (Table 5). Reduced stomatal density and conductive tissue as indicated by larger interveinal areas are common adaptations to low light (Kramer and Kozlowski, 1979), and were evident in carambola leaves that developed in 24% sunlight. Leaf weight ratio was also unaffected by the various light treatments. A constant LWR over various light regimes indicates a plant’s ability to maintain normal development, and probably indicates that the treatment light levels are well within the range of light intensities to which a species is adapted (Fitter and May, 1981).

Carambola trees grown in 100% sunlight exhibited morphological adaptations to high light. A reduced lamina angle minimized light interception for each leaflet, and a more vertical orientation of limbs increased mutual leaf shading. Reductions in average leaf area, total leaf area, and SLD, which are adaptations to high light that help plants maintain favorable water status (Bjorkman, 1981), occurred in carambola trees grown in full sun. These sun-grown carambola trees did not appear to be experiencing water stress according to the RWC and y_x measurements.

Leaflets on trees grown in 100% sunlight exhibited a daily change in orientation, beginning each photoperiod with a near horizontal orientation. However, by mid-morning on sunny days, leaflets exhibited a vertical orientation and remained vertical for the rest of the day. In previous studies, carambola leaflets exhibited this active movement in response to mechanical stimulus (Marler and Zozor, 1992). A vertical leaf orientation under high-light conditions reduces single-leaf radiation load and temperature and is considered an important morphological adaptation for protecting leaves from damage caused by excessive light or heat (Ludlow and Bjorkman, 1984; McMillen and McClendon, 1979).

Carambola trees exhibited physiological adaptations to the various light intensities. Trees had higher chlorophyll content (on a leaf area basis) in the shade than in full sun (Table 6). An increase in chlorophyll in leaves of shaded plants has been reported for shade-tolerant species, whereas shade-intolerant species exhibited a decrease or no consistent change in chlorophyll with shade (Bjorkman and Holmgren, 1963; Thompson et al., 1992). Shading carambola led to lower R_d, light compensation, and saturation points, but did not influence apparent quantum yield. Reduced respiration is one of the key adaptations of shade-tolerant plants and is lacking in shade-intolerant species (Leopold and Kriedemann, 1975). Increased apparent quantum yield is also a common shade adaptation in plants that are considered tolerant (Fitter and May, 1981). However, other reports have indicated adaptation to low light by a reduced light compensation point solely via reduced R_d (Osmond et al., 1980). The high photosynthetic capacity of shade-adapted carambola leaflets under short-term exposure to high light may indicate that inner canopy leaves have a high capacity to utilize sun flecks that provide high PPF for a short duration (Leopold and Kriedemann, 1975).

Carambola trees grown in 24% sunlight were under light limiting conditions throughout the day, reaching a daily maximum of A of ≈7 μmol CO_2/m^{-2} per sec, whereas trees in 47% sunlight were under light-limiting conditions during early morning and late afternoon hours (Fig. 2). Midday suppression in A for sun-grown trees was probably not due to substantial increases in VPD, as midday VPD during this study on Guam was moderate (e.g., 1.8 kPa on 14 Mar. 1992). However, midday suppression of A has been linked with a direct inhibitory effect of high PPF (Valenzuela et al., 1991), and the low F_v/F_m, which has been correlated with photoinhibition and reduced quantum yield (Demmig and Bjorkman, 1987), could support this explanation.

The midday decline in F_v/F_m of 100% sunlight-grown trees in Guam and Florida indicated that a decline in photochemical efficiency of carambola leaves may be common during a typical sunny day in the tropics and subtropics. The diurnal measurements in Guam revealed a strong linear relationship between F_v/F_m and the integrated PPF of the period preceding each measurement ($r^2 = 0.88$). Other reports have indicated that healthy trees experiencing no apparent stress (except high light) exhibit a decline and recovery of chlorophyll fluorescence throughout the day (Bjorkman and Powles, 1984; Marler, 1994; Ogren, 1988). Ogren (1988) reported that a systematic decline and recovery of fluorescence throughout a sunny day was also accompanied by a reduction of quantum yield during periods of high PPF. The rapid recovery of F_v/F_m in leaflets of full-sun carambola trees each afternoon may indicate an increase in thermal energy dissipation during periods of high PPF, rather than photoinhibitory inactivation of the PS II reaction centers (Demmig-Adams and Adams, 1992).

The midday decline in F_v/F_m of leaves from sun-grown carambola trees ranged from 0.55 to 0.57 in Florida and from 0.62 to 0.64 in Guam. A possible explanation of these differences may be that the trees in Florida were experiencing relatively low temperatures that were inhibitory to A. Temperature minima on the days of measurement were ≈13 to 19C in Florida, whereas in Guam they were 26 to 27C.

Nitrogen-use efficiency (A/N) was enhanced in carambola leaves grown in 24% sunlight. An enhancement of N-use efficiency due to low light conditions was also reported for other species (Jurik et al., 1982; Thompson et al., 1992), and it indicates a reduced nutrient cost in achieving photosynthetic capacity.

Photosynthetic CO_2-use efficiency was similar for carambola leaves grown in the various light regimes. The slope of the A : CA response curve measured under low light was depressed only 15% below that of the response curve measured under high light in the trees grown in 24% sunlight (Table 4). Alternatively, there was more than a 25% decrease in the A : CA slope from high to low light measurements for the plants grown in 47% and 100% sunlight. Teskey and Shrestha (1985) concluded that high CO_2-use efficiency may aid in maintaining a positive carbon balance in low light conditions, and that a minimal difference in CO_2-use efficiency between light-limited and light-saturated conditions indicates greater shade tolerance.

The carambola trees in 24% sunlight were very leggy, so maintaining a desirable canopy width could be a problem when growing carambola trees in deep shade. Furthermore, these trees rarely flowered throughout Expts. 1 and 2. In contrast, trees in 47% and 100% sunlight flowered numerous times. Certainly, adequate adaptation and growth of carambola trees in deep shade is of little value without fruit production.

The results of this study indicate that carambola trees adapt to and survive a wide range of light intensities. Many tropical and subtropical regions have seasons with periods of extended overcast weather, and carambola may maintain productivity under these conditions. Furthermore, the moderate shading provided by overhead baffles in constructed windbreaks (Crane, 1992) or by insect-protective screen (Watson et al., 1988) commonly used in carambola production probably does little to diminish productivity, and may be beneficial according to our measurements of A, chlorophyll fluorescence, and growth of trees under shaded conditions.

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