Drought, Leaf Gas Exchange, and Chlorophyll Fluorescence of Field-grown Papaya

Thomas E. Marler and Michael V. Mickelbart

College of Agriculture and Life Sciences, University of Guam, UOG Station, Mangilao, Guam 96923

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ABSTRACT. The influence of drought stress on leaf gas exchange and chlorophyll fluorescence characteristics of field-grown papaya (*Carica papaya* L.) plants was determined under a range of incident light fluxes and times of day. These data may aid in improving management systems for papaya production which minimize detrimental effects from suboptimal environmental conditions. Water was withheld from field-grown 'Red Lady' plants in one study and 'Tainung #2', 'Red Lady', and 'Sunrise' plants in a second study until soil matric potential was -60 to -70 kPa. Drought-stressed plants exhibited reduced net CO₂ assimilation (A_{CO_2}) above light saturation, photosynthetic photon flux (PPF) at which light saturation for A_{CO_2} occurred, and apparent quantum yield compared to well-watered plants. The light compensation point of drought-stressed plants was greater than that of well-watered plants. Leaf chlorophyll fluorescence characteristics were not influenced by drought stress. The daily pattern of leaf gas exchange was dependent on climatic conditions. For sunny days, A_{CO_2} , stomatal conductance of water (g_s), and water use efficiency of well-watered plants were maximal at mid-morning, declined during midday, and then partially recovered during late afternoon. In drought-stressed plants, leaf gas exchange was relatively constant after a brief early morning maximum. On overcast days, the responses of gas exchange variables in relation to time of day followed smooth bell-shaped patterns regardless of the level of drought stress. Combined with previously published data, these results indicate that the influence of drought stress on gas exchange is highly dependent on time of day, ambient sky conditions, plant size, and speed with which drought stress occurs.

Irrigation of papaya is recommended during dry periods to increase growth and fruit production (Malo and Campbell, 1986). However, the only reports on mechanisms by which drought stress influences papaya were limited to controlled container studies (Marler et al., 1994). In those studies, stomatal conductance (g_s) and net CO₂ assimilation (A_{CO_2}) were the first measured variables to decline as substrate water was depleted. Leaf relative water content and xylem pressure potential were unaffected by drought which manifested a 90% reduction in leaf gas exchange. Drought stress also reduced apparent quantum yield and the photosynthetic photon flux (PPF) at which light saturation occurred. These studies allowed the classification of papaya as a species which responds to drought primarily via dehydration postponement. However, the relatively small plant size required for and the rapid rate of water depletion when using container-grown plant material indicated a need for field research to corroborate the findings. Plant size (Blum and Sullivan, 1997) and the rate of stress development (Turner and Jones, 1980) exhibit a profound influence on plant response to water deficits.

The objectives of this study were to quantify the leaf gas exchange and chlorophyll fluorescence responses of papaya plants to development of drought stress under field conditions to determine if responses were consistent with those reported for small, containerized plants. The influence of time of day on gas exchange and chlorophyll fluorescence responses to drought stress were determined. Drought stress sensitizes the photosynthetic apparatus to damage by high light, and the chlorophyll fluorescence data may provide insight into the mechanism(s) by which drought stress influences the photosynthetic process. Results from this study may aid in improving irrigation management for papaya production or developing a model describing papaya plant responses to environmental variables.

Materials and Methods

Two field studies were conducted in Guam (lat. 13.5°N, long. 145.7°E) during the middle of the dry season in 1994 and 1996. Field soil was classified as clayey, gibbsitic, nonacid, isohyperthermic Lithic Ustorthents (Young, 1988), and the site was located 134 m above sea level. After transplanting as described for each experiment, plants were fertilized with granular fertilizer (16N–6.5P–12.5K) at 55 g/plant every 2 weeks for the first month, then 114 g/plant every 2 weeks thereafter. During establishment, the plants received at least 10 mm of water every other day by rainfall or microsprinkler irrigation.

EXPERIMENT 1. 'Red Lady' papaya seeds were planted on 3 Dec. 1993 in flats with 5-cm-diameter cells and maintained under lucite screening (BioQuip Products, Santa Monica, Calif.) to prevent the possible introduction of aphid-transmitted viruses. Midday maximum PPF under this screening was $\approx 1250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ on sunny days. Substrate was Sunshine Mix 4 (Sun Gro Horticulture, Bellevue, Wash.), and the flats were fertilized weekly by drenching with a solution of complete soluble fertilizer (Excel; Grace-sierra, Milpitas, Calif.) at a concentration based on 7.5 mm N.

The seedlings were transplanted to the field with 3 m between each plant on 18 Feb. 1994 and managed as previously described. Twelve plants with a mean height of 105 cm were selected on 1 May, and supplemental water was withheld from six plants. The remaining six plants were maintained under the described irrigation regime. The treatments were arranged in a completely randomized design.

There were two tensiometers positioned 50-cm from the base of each plant, and their average was considered the mean for the plant. We allowed soil matric potential (ψ_m) to decline to -60 to -70 kPa, as in previous studies where gas exchange was minimal at this ψ_m (Marler et al., 1994).

The mean ψ_m for the plants from which water was withheld was about -60 kPa on 2 June, when the irrigated plants were 141 cm tall and the unirrigated plants were 115 cm tall on average. The daily pattern of gas exchange was determined throughout several days from 2 through 8 June. Measurements commenced before sunrise and continued until after sunset on ≈ 2 -h intervals. For each

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measurement, one fully expanded leaf on each plant was inserted into a cuvette with 2.5 cm² of leaf surface exposed, and gas exchange was measured using an open system (CIRAS-1, PP Systems, Stotfield, Hitchin, Herts, U.K.). Leaf transpiration (*E*), *g_s*, and *A_{CO₂}* were determined, and ambient PPF, temperature, CO₂, and vapor pressure deficit (VPD) were recorded. Leaf temperature was measured with a thermistor, and instantaneous water use efficiency (WUE) was calculated as *A_{CO₂}*/*E*.

Chlorophyll fluorescence was measured (model CF-1000; P.K. Morgan Instruments, Andover, Mass.) on the same days and intervals as gas exchange measurements. To begin each measurement, a period of 30 min of dark was administered using the manufacturer's field cuvettes. Fluorescence from excitation light with PPF of 900 μmol·m⁻²·s⁻¹ was determined on the adaxial surface of two fully exposed leaves per plant.

Matric potential was measured at sunrise and sunset on each day of gas exchange measurements. The mean of the two measurements was considered the ψ_m corresponding to gas exchange measurements for each day.

These same plants were used on 9 June to determine *A_{CO₂}* as a function of incident PPF within the range of 150 to 2033 μmol·m⁻²·s⁻¹ under field conditions. Measurements were confined to mid-morning. Mean ψ_m was -68 kPa for the drought-stressed plants and -20 kPa for the control plants. The range of PPF was obtained under ambient sunlight by placing black nylon screen of varied densities between the plant and the sun. Conditions during measurement were 30 to 34 °C, 356 to 365 μL·L⁻¹ ambient CO₂, and 1.8 to 2.3 kPa VPD.

EXPERIMENT 2. 'Tainung #2', 'Red Lady', and 'Sunrise' papaya seeds were planted in flats on 22 Oct. 1995 and maintained as described in Expt. 1. Eighteen plants of each cultivar were transplanted to the field on 13 Dec. 1995. Water was withheld from one-half of the plants of each variety beginning 23 Feb. 1996 when height ranged from 0.9 to 1.1 m. Within each variety, treatments were arranged in a completely randomized design.

Gas exchange data were obtained from 21 Mar. to 3 Apr. 1996, when ψ_m of drought-stressed plants was -60 to -70 kPa. At this time, irrigated plants averaged 1.1 to 1.5 m in height, and unirrigated plants averaged 1.0 to 1.2 m in height.

The relationship of *A_{CO₂}* and incident PPF from 0 to 200 μmol·m⁻²·s⁻¹ was determined during the morning of 21 Mar., when mean ψ_m was -62 kPa for the drought-stressed plants and -20 kPa for the control plants. The relationship of *A_{CO₂}* and incident PPF from 200 to 2145 μmol·m⁻²·s⁻¹ was determined during the morning of 29 Mar., when mean ψ_m was -68 kPa for the drought-stressed plants and -23 kPa for the control plants. Methods were as described for Expt. 1.

Several days were selected to determine the diurnal pattern of gas exchange for papaya leaves. Data were obtained from six of the plants per treatment for each variety using the methods described for Expt. 1. We used an interval of ≈3 h between measurement periods due to the large number of measurements required for three varieties.

STATISTICAL ANALYSIS. Results of all measured variables within Expt. 1 were subjected to ANOVA within each day of measurement. Diurnal fluorescence and gas exchange data were analyzed as drought × time of day factorial. The relationship between *A_{CO₂}* and incident PPF was determined using nonlinear regression. The response curves were defined by the equation $A_{CO_2} = a(1 - e^{-bxPPF})$.

For Expt. 2, data from each variety were analyzed separately. The diurnal gas exchange measurements were analyzed as described for Expt. 1. The relationship between *A_{CO₂}* and incident PPF >200 μmol·m⁻²·s⁻¹ was determined for each replication using the procedure described for Expt. 1, then the light saturation point

for *A_{CO₂}* (*Q_A*) was calculated as the PPF at 95% of maximum *A_{CO₂}*. The relationship between *A_{CO₂}* and incident PPF from 0 to 200 μmol·m⁻²·s⁻¹ was determined for each replication by linear regression, with the independent variable defined as PPF. The slope of this line was considered the apparent quantum yield (ϕ_i). Light compensation point (*Q₀*) was calculated from the equation for each replication. Data for *Q_A*, ϕ_i , and *Q₀* were subjected to ANOVA with drought treatment as the source of variation.

Results

DEPENDENCE OF *A_{CO₂}* ON IRRADIANCE. Withholding water until soil ψ_m was -68 kPa caused *A_{CO₂}* of 'Red Lady' plants to decline to ≈50% of well-watered plants throughout the entire response curve above a PPF of 150 μmol·m⁻²·s⁻¹ (Expt. 1, Fig. 1). Drought stress also slightly reduced the PPF at which light saturation of *A_{CO₂}* occurred. For Expt. 2, the curve depicting *A_{CO₂}* of 'Tainung #2', 'Red Lady', or 'Sunrise' leaves as influenced by PPF followed the same pattern as that in Fig. 1 (data not shown). Maximum *A_{CO₂}* was 23 to 26 μmol·m⁻²·s⁻¹ for well-watered plants and 11 to 14 μmol·m⁻²·s⁻¹ for drought-stressed plants. The *Q_A* for drought-stressed plants was ≈75% of that for the well-watered plants (Table 1). Drought stress reduced ϕ_i of 'Tainung #2', 'Red Lady', and 'Sunrise' leaves to 58% to 64% of that for well-watered plants (Table 1). Dark respiration was not influenced by drought stress, and ranged from 1.1 to 1.2 μmol·m⁻²·s⁻¹ for the three varieties. The consistent decrease in ϕ_i resulting from drought stress led to an increase in *Q₀*. Light compensation point for drought-stressed plants was 163% to 172% of that for well-watered plants (Table 1).

DAILY TIME COURSE OF GAS EXCHANGE. The sky conditions during which measurements were made in June 1994 were either clear or slightly overcast with diffuse clouds. Water use efficiency, *A_{CO₂}*, *g_s*, or *E* under both types of sky conditions were dependent on drought stress and time of day (interaction *P* ≤ 0.01). Under clear conditions, with midday PPF of up to 2000 μmol·m⁻²·s⁻¹ and maximum VPD of 2.4 kPa (Fig 2A), leaf gas exchange variables for well-watered plants

Fig. 1. Net CO₂ assimilation (*A_{CO₂}*) of leaves from well-watered or drought-stressed 'Red Lady' papaya plants at ambient CO₂ as influenced by photosynthetic photon flux (PPF). Data were obtained on 9 June 1994 when soil matric potential was -68 kPa for drought-stressed plants and -20 kPa for well-watered plants. Response equations were $A_{CO_2} = 27.8(1 - e^{-0.0013 \times PPF})$ (*r*² = 0.93, well-watered) and $A_{CO_2} = 12.4(1 - e^{-0.0017 \times PPF})$ (*r*² = 0.84, drought-stressed).

Table 1. Apparent quantum yield (ϕ_i), light compensation point (Q_0), and light saturation point for A_{CO_2} (Q_A) of field-grown 'Tainung #2', 'Red Lady', and 'Sunrise' papaya plants as influenced by drought stress. Data for ϕ_i and Q_0 were obtained on 21 Mar. 1996, when ψ_m was -62 kPa for the drought-stressed plants and -20 kPa for the well-watered plants. Data for Q_A were obtained on 29 Mar., when ψ_m was -68 kPa for the drought-stressed plants and -23 kPa for the well-watered plants; $n = 9$.

Treatment	ϕ_i (mol CO_2 /mol incident quanta)	Q_0 ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Q_A ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)
Tainung #2			
Control	0.039 ± 0.001	27 ± 1	1293 ± 14
Drought	$0.025 \pm 0.001^{**}$	$46 \pm 1^{**}$	$986 \pm 9^{**}$
Red Lady			
Control	0.041 ± 0.001	29 ± 1	1325 ± 15
Drought	$0.024 \pm 0.001^{**}$	$50 \pm 2^{**}$	$1007 \pm 10^{**}$
Sunrise			
Control	0.040 ± 0.001	30 ± 1	1279 ± 16
Drought	$0.024 \pm 0.001^{**}$	$49 \pm 1^{**}$	$991 \pm 14^{**}$

^{**}Significant at $P = 0.01$.

rapidly increased to an early or midmorning peak that lasted several hours (Fig. 2 B–D). By late morning, however, gas exchange declined to a midday minimum. The midday minimum of g_s , for instance, was $\approx 50\%$ of the morning maximum. Partial recovery of leaf gas exchange occurred in late afternoon, creating a two-peaked pattern throughout the day. In contrast, leaf gas exchange of drought-stressed plants was rather constant throughout the day after a brief early morning peak. The diurnal pattern for E mirrored that of g_s for well-watered and drought-stressed plants. Maximum E was $5.4 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for well-watered plants and $2.9 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for drought-stressed plants.

Under diffuse overcast conditions, with a PPF of $\approx 1200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and maximum VPD of 1.8 kPa (Fig. 3A), the shape of the curves depicting gas exchange variables throughout the photoperiod was bell-shaped for well-watered and drought-stressed plants (Fig. 3 B–D). The major difference in gas exchange between the drought-stressed and well-watered plants was the amplitude, which was reduced consistently throughout the day by drought stress. Maximum E was $4.7 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for well-watered plants and $3.3 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for drought-stressed plants, and the diurnal pattern for E mirrored that of g_s .

Water use efficiency of drought-stressed plants was similar to that of well-watered plants on clear days (Fig. 2D). Only during the morning and late afternoon peaks of A_{CO_2} did well-watered plants exhibit a greater WUE than drought-stressed plants. In contrast, WUE of well-watered plants was greater than that of drought-stressed plants throughout the day on the slightly overcast days (Fig. 3D). After the brief early morning peak, g_s of drought-stressed plants was $\approx 100 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for the remainder of the sunny photoperiod (Fig. 2C). However, g_s of drought-stressed plants remained at 150 to $175 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ throughout the day under slightly overcast sky conditions (Fig. 3C).

Conditions were mostly sunny during Expt. 2, hence, we did not experience slightly overcast sky conditions as in Expt. 1. The pattern of gas exchange during the sunny days was similar to that in Fig. 2. In every case, well-watered 'Tainung #2', 'Red Lady', and 'Sunrise' plants exhibited a two-peaked pattern with amplitude of the morning peak in excess of that for the afternoon peak; and drought-stressed plants exhibited fairly constant gas exchange throughout the day following a moderate peak of short duration in the early morning (data not shown).

CHLOROPHYLL FLUORESCENCE. The ratio variable fluorescence to maximal fluorescence (F_v/F_m) differed with time of day ($P \leq 0.01$) on clear days (Fig. 4). In contrast, on slightly overcast days

the diurnal pattern of F_v/F_m was not influenced by time of day. Drought stress did not influence F_v/F_m during any of the days of measurement during this study (Fig. 4).

Fig. 2. The influence of time of day and drought stress on (B) net CO_2 assimilation (A_{CO_2}), (C) stomatal conductance (g_s), and (D) water use efficiency of 'Red Lady' papaya plants under clear, sunny conditions on 3 June 1994. Also included are (A) vapor pressure deficit (VPD) and photosynthetic photon flux (PPF). Bars within B, C, and D represent pooled LSD at $P = 0.01$. Sunrise was ≈ 0550 HR and sunset was ≈ 1825 HR. Soil matric potential was -60 kPa for drought-stressed and -19 kPa for well-watered plants; $n = 6$.

Fig. 3. The influence of time of day and drought stress on (B) net CO_2 assimilation (A_{CO_2}), (C) stomatal conductance (g_s), and (D) water use efficiency of 'Red Lady' papaya plants under diffuse, overcast conditions on 5 June 1994. Also included are (A) vapor pressure deficit (VPD) and photosynthetic photon flux (PPF). Bars within B, C, and D represent pooled LSD at $P = 0.01$. Sunrise was ≈ 0550 HR and sunset was ≈ 1825 HR. Soil matric potential was -65 kPa for drought-stressed and -21 kPa for well-watered plants; $n = 6$.

Discussion

The values for papaya leaf A_{CO_2} of 23 to 26 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ reported herein are relatively high compared with maximum values for other fruit crops (see for example Schaffer and Andersen, 1994a, 1994b). A relatively high rate of carbon gain is consistent with the vigorous growth habit of papaya (Malo and Campbell, 1986). Using once-over harvesting methods in several studies, we have measured more than 50 kg of fruit being supported by single 9-month-old plants (Marler, unpublished). Whiley and Searle (1996) report that papaya, with yields in excess of 20 $\text{t}\cdot\text{ha}^{-1}$, is one of the highest yielding tropical fruit species. The absolute values for gas exchange variables were also greater for the field-grown plants in this study than for the container-grown papaya plants from previous studies (Marler et al., 1994). For example, light-saturated A_{CO_2} for well-watered container-grown plants was $\approx 60\%$ of that for well-watered field plants. Similarly, ϕ_i was 0.039 to 0.041 $\text{mol}\cdot\text{mol}^{-1}$ for the field plants, but ≈ 0.30 $\text{mol}\cdot\text{mol}^{-1}$ for the container-grown plants. Root restriction has been implied as a limitation of photosynthesis for container-grown plants (Arp, 1991).

Although absolute values were dissimilar between the container plants and the field plants, the shape of the curve depicting the dependence of A_{CO_2} on PPF for field-grown papaya plants in this study was similar to that for container-grown plants (Marler et al., 1994). The light saturation point for A_{CO_2} was >1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in each case. Although this is a relatively high value for single leaf response curves, this characteristic was confirmed for papaya leaves by a previous report (Allan and de Jager, 1978).

Withholding water from small, containerized papaya plants led to ψ_m of -60 to -70 kPa in ≈ 1 week (Marler et al., 1994). In contrast, 4 to 5 weeks of withholding water was required under field conditions of this study to reach this same range of ψ_m . For the container-grown plants, A_{CO_2} of plants at ψ_m of -60 to -70 kPa was reduced 85% below that of control plants (Marler et al., 1994). However, for field-grown plants in this study, A_{CO_2} of plants at this ψ_m was reduced $\approx 50\%$ below that of control plants. Similarly, drought stress reduced ϕ_i to a greater degree in the container-grown plants (Marler et al., 1994) than in the field-grown plants. We attribute these dissimilarities in the influence of drought stress between the two studies to the more rapid water depletion in media of potted plants (Turner and Jones, 1980). Although there were dissimilarities between these two studies, A_{CO_2} , Q_A , and ϕ_i were always depressed by drought stress and Q_O was always increased by drought stress. The depression of Q_A is evidence that drought stress reduced the potential of papaya leaves to use light for maximum carbon gain.

The daily pattern of carbon acquisition as influenced by drought was highly dependent on the climatic conditions of each day (Figs. 2 and 3). For example, maximum values of A_{CO_2} were greater on cloudless days, but the mean of all A_{CO_2} measurements throughout the photoperiod was greater for the slightly overcast days. The major climatic differences among these days were greater PPF and VPD on the clear days as compared with the mild overcast days (Figs. 2 and 3). In addition, air temperature during midday on clear days was $\approx 34^\circ\text{C}$ compared with $\approx 32^\circ\text{C}$ on overcast days. This is a small difference, but well-watered plants were able to maintain leaf temperature to within 0.2°C of air temperature on overcast days. In contrast, leaf temperature of well-watered plants was 1.1

Fig. 4. The influence of time of day and drought stress on the ratio variable to maximal fluorescence (F_v/F_m) of 'Red Lady' papaya plants under clear, sunny conditions on 3 June 1994 (closed symbols) and under diffuse, overcast conditions on 5 June 1994 (open symbols). Bar represents LSD at $P = 0.01$ for time of day comparisons on 3 June. There were no differences among measurement periods or drought treatments on 5 June; $n = 6$.

°C greater than air temperature on clear days. Leaf temperature was >35 °C for much of the day on clear days. Allan and de Jager (1978) reported that A_{CO_2} declined at temperatures >31 °C for 'Honey Gold' papaya leaves. Although PPF of clear days was ≈50% higher than that of the slightly overcast days, it is unlikely that high light stress was responsible for the decline in gas exchange of well-watered plants at midday on clear days. Although midday F_v/F_m of well-watered plants was significantly lower than early morning F_v/F_m (Fig. 4), the values of ≈0.75 are within the range of typical values (Bolhar-Nordenkamp et al., 1989) and thus do not indicate the substantial decline in photochemical efficiency that would accompany high light stress. Midday VPD peaked at ≈2.4 kPa on clear days, and papaya is reportedly highly responsive to VPD. El-Sharkawy et al. (1985) reported that A_{CO_2} of papaya at VPD of 3.5 to 4.5 kPa was <50% of A_{CO_2} at VPD of 1.0 to 1.5 kPa. Thus, mild heat stress or high VPD may be causal factors in the substantial decline of leaf gas exchange of well-watered papaya plants during midday on clear days.

Chlorophyll fluorescence provides a rapid and sensitive examination of the effects of various stresses on the photosynthetic apparatus. For papaya plants in this study, drought which reduced A_{CO_2} to <50% of well-watered plants did not influence chlorophyll fluorescence variables determined. Furthermore, rapidly developing water deficits of container grown papaya plants (Marler et al., 1994), which reduced A_{CO_2} to <20% of well-watered plants did not influence chlorophyll fluorescence variables determined. Drought stress sensitizes the photosynthetic apparatus to damage by high light, and a severe inhibition of photosynthesis by water stress may precede any appreciable change in fluorescence (Björkman and Powles, 1984; Ludlow and Björkman, 1984).

Taken as a whole, the data from previous studies (Marler et al., 1994) and from this study indicate that modeling the influence of soil water deficits on carbon gain of papaya plants may require elaborate procedures. Predicting the influence of drought stress on responses of A_{CO_2} to single variables, such as PPF in this study, may be straightforward. However, homogeneous PPF rarely occurs under natural conditions, and the rapid responses of papaya leaves to fluctuations in PPF are altered by drought (Clemente and Marler, 1996). Moreover, the contrasting results from previous container studies and this field study indicate that the speed with which soil water deficits occur or the size of the plant may profoundly modify the influence of drought on gas exchange.

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