Gas Exchange of *Citrus* Seedlings at Different Temperatures, Vapor-pressure Deficits, and Soil Water Contents

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Abstract. Midday reductions of stomatal conductance and carbon dioxide assimilation rates (A_{CO_2}) in *Citrus* are typically attributed to large leaf-to-air vapor-pressure differences or high atmospheric vapor-pressure deficits (VPD). This study investigated air temperature (T_a) and available soil water (ASW) level as corollary factors of atmospheric VPD that influence midday reduction of net gas exchange in citrus leaves. The influence of elevated atmospheric CO₂ under conditions that inhibit net canopy A_{CO_2} was also investigated. Net canopy A_{CO_2} and evapotranspiration rates of Carrizo citrange [*Poncirus trifoliata* Raf x *Citrus sinensis* (L.) Osbeck] and Swingle citrumelo (*P. trifoliata* Raf x *C. paradisi* Macf.) seedlings grown in outdoor controlled-environment growth chambers were measured under two levels of T_a with concomitant changes in VPD and two levels of atmospheric CO₂ concentration, which were changed in steps over time. Cyclical depletion of ASW was allowed to occur at each set of T_a /VPD and CO₂ combinations. Highest net canopy A_{CO_2} rates at ambient CO₂ concentration (330 $\mu\text{mol}\cdot\text{mol}^{-1}$) were obtained at the low T_a /VPD level (29C/2.4 kPa) and ASW >50%. Diurnal canopy CO₂ uptake rates decreased at the high T_a /VPD level (37C/3.6 kPa), and midday depression of canopy A_{CO_2} was observed at ASW levels <50%. Net canopy A_{CO_2} decreased at higher levels of ASW under the high T_a /VPD treatment than at the low T_a /VPD treatment. At the elevated CO₂ concentration (840 $\mu\text{mol}\cdot\text{mol}^{-1}$) net canopy CO₂ uptake rates were double those that occurred at ambient CO₂ levels and they did not exhibit midday reduction. Our data indicate that, when soil water is not readily available, citrus seedlings are more sensitive to high levels of T_a and VPD which results in reduction of CO₂ uptake. The inhibitory effects of elevated VPD and reduced ASW on citrus net A_{CO_2} were lessened at the elevated atmospheric CO₂ level.

Commercial cultivation of citrus is extremely successful in subtropical areas where rainfall is seasonal, as well as in semi-arid and arid regions. While irrigation is required under these conditions, the conservative water use characteristics of citrus constitutes an important factor in its successful production in these regions.

Stomatal closure of citrus in response to increasing leaf-to-air humidity differences results in low, often nearly constant, transpiration rates (Kaufmann and Levy, 1976; Sinclair and Allen, 1982; Vu and Yelenosky, 1988). The response of net CO₂ assimilation rate (A_{CO_2}) in citrus under conditions of high temperature, high evaporative demand, and low soil water availability is poorly understood. Net A_{CO_2} rates of nonstressed citrus are low compared to other woody perennials (Downton et al., 1987; Kriedemann, 1971) and they frequently have a midday depression (Sinclair and Allen, 1982; Vu and Yelenosky, 1988). Although transpiration is

controlled primarily by stomatal activity, A_{CO_2} can also be affected by nonstomatal factors referred to collectively as mesophyll resistance. The potential contribution of nonstomatal factors to midday depression of citrus photosynthesis has been described (Bielorai and Mendel, 1969; Sinclair and Allen, 1982; Vu and Yelenosky, 1988), but little work has been conducted to determine the relative importance of stomatal and nonstomatal factors to low A_{CO_2} and midday reduction in citrus. This information is needed for development of irrigation practices that conserve water and are noninhibitory to citrus growth. The objective of this study was to identify atmospheric and soil water conditions that contribute to midday depression of A_{CO_2} in seedlings of two important citrus rootstock.

Materials and Methods

Two-year-old Carrizo citrange (*Poncirus trifoliata* x *Citrus sinensis*) and Swingle citrumelo (*P. trifoliata* x *C. paradisi*) seedlings were grown in a greenhouse in 2-liter metal containers using a loam potting medium. On 9 Apr. 1985, 72 containers of each rootstock cultivar were placed separately in each of two sunlit, computer-controlled environment chambers. The design and verification of the dynamic computer control of these closed-circulation plant growth chambers has been described previously (Allen, 1990; Jones et al., 1984). The canopy in each chamber intercepted nearly all of the incoming radiation as determined with a line quantum sensor (model 191; LI-COR, Lincoln, Neb.) mounted inside each chamber to measure photosynthetic photon flux density (PPFD).

The containers, with holes near the bottom for drainage and

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flood irrigation, were placed in shallow ($1 \times 2 \times 0.15$ -m) galvanized metal trays in the chambers. Irrigation was provided by flooding the trays (when required) for ≈ 2 h near sunset and allowing them to drain naturally overnight. Two bathroom scales, fitted with linear variable displacement transducers with remote digital readout units, were placed under each metal tray that held the 72 containers and were used to measure daily weight changes of the containers attributable to evapotranspiration. The total available soil water content (ASW_{tot}) of containers in each chamber was determined as the weight of the plants plus containers the morning following an irrigation, when soil was assumed to be near field capacity, minus the weight they attained when temporary wilting of leaves occurred. The percentage ASW remaining each morning and early evening was determined by subtracting from ASW_{tot} the cumulative amount of cooling coil condensate collected in a closed container [$ASW = (ASW_{tot} - \text{total condensate}) / ASW_{tot} \times 100$]. Reported values represent ASW near sunset.

All plants were about the same size, 1.0 m high, when the study began. Plants in both chambers produced flushes of growth at the same time. Vertical growth was pruned after each flush so that shoots did not grow against the top of the chamber.

Dry-bulb temperature controls in the chambers were set for a diurnal pattern representative of outdoor conditions. Dry-bulb temperature control was reset each hour during the day and dewpoint temperature (DPT) was essentially constant during a 14-h daytime period beginning at 0600 and ending at 2000 HR. Maximum T_a and constant DPT control set points were 29/14 and 37/22C, for the low- and high-temperature levels, respectively; this resulted in maximum daytime vapor-pressure deficits of 2.4 and 3.6 kPa. Temperatures maintained in the chambers were typically within 1 to 2C of the control set points and temperature differences between the two chambers were typically <1C. Constant nighttime T_a /DPT controls were set at 16/8 and 22/8C, which resulted in overnight (2000 to 0600 HR) air vapor-pressure deficits of 0.8 and 1.6 kPa for the low- and high-temperature treatments, respectively. Dates and duration of environmental conditions within the chambers are given in Table 1. Environmental treatment conditions were imposed for 2 to 7 days.

The plant growth chambers and control systems provided control of air temperature, vapor pressure (via dewpoint temperature), CO_2 concentration, and soil water conditions, as well as continuous measurement of net canopy A_{CO_2} and transpiration rates. The length, width, and height dimensions of the chambers were 2.0, 1.0, and 1.5 m, respectively. The east, south, and west

walls were constructed of 0.18-mm Mylar polyester film, and the tops were made of 6.35 mm acrylic plate. About 89% of solar PPFD was transmitted by the transparent covers. The north wall was constructed of 9.52-mm acrylic plate with outflow and inflow plenums to and from the attached air circulation and conditioning ductwork. Four air-exchanges per minute were provided by impeller fans. A chilled-water heat exchanger in the ductwork condensed water from transpiration and was used to control dewpoint temperature. An electrical resistance heater restored air temperature to the treatment level. Air samples were pumped from each chamber to an adjacent laboratory and were analyzed for dewpoint temperatures (model 110 DP dewpoint hygrometer; General Eastern) and CO_2 concentrations (model 865 infrared gas analyzer; Beckman) sequentially over a 300-sec period. Based on these measurements, adjustments were made to the rate of chilled water flow through the heat exchanger, and to the rate of injection of CO_2 .

Carbon dioxide injection was executed every 20 sec based on an algorithm using measured solar radiation. This injection rate was adjusted each 300 sec based on measured CO_2 concentration within the chambers. Also, the electrical resistance heater was controlled every 20 sec based on measurements of a radiation-shielded thermocouple near the top center of the chamber.

Net canopy A_{CO_2} per unit ground area was computed every 300 sec for each chamber based on the amount of CO_2 injected, adjusted by the decrease or increase of CO_2 concentration inside each chamber. Evapotranspiration rates (ET) per unit ground area were also computed every 300 sec based on tipping bucket raingage measurements of condensate. The 300-sec A_{CO_2} and ET values were averaged over hourly intervals. Water-use efficiency (WUE), the ratio of A_{CO_2}/ET , was computed for the daytime hourly data. The environmental control system and data logging functions were managed by an ADAC PDP-1623 computer. Further details on operation and use of this system have been previously reported (Baker et al., 1990; Jones et al., 1985).

Treatments consisted of two levels of maximum daily dry-bulb air temperature/vapor-pressure deficit (T_a/VPD : 29C/2.4 kPa and 37C/3.6 kPa) and two levels of atmospheric CO_2 concentration (330 and 840 $\mu\text{mol}\cdot\text{mol}^{-1}$). Treatments were imposed at different times to plants in both chambers. At each treatment level, soil water depletion cycles were imposed by allowing water in the containers to be depleted until leaves began to wilt. The duration of a drying cycle varied according to the temperature and CO_2 level. At each combination of two levels of T_a/VPD and two levels of CO_2 concentration, changes in rates of net canopy A_{CO_2} and ET

Table 1. Dates and starting times of environmental conditions, daily maximum dry-bulb temperature, constant dewpoint temperature, and CO_2 concentrations in growth chambers during the study period, 10 Apr. to 14 May.

Date	Time (HR)	Temp ($^{\circ}\text{C}$)		CO_2 ($\mu\text{mol}\cdot\text{mol}^{-1}$)
		Dry bulb	Dewpoint	
10-18 Apr.	0730	29	14	330
18-21 Apr.	1530	37	22	330
21-25 Apr.	1915	29	14	330
25 Apr.	1255-1455	37	22	330
25 Apr.	1500-1820	29	14	330
25 Apr.	1825	37	22	330
29-30 Apr.	0725	37	22	840
30 Apr.-4 May	0800	29	14	840
4-10 May	0755	37	22	840
10-14 May	1430	37	22	330

The dry-bulb temperature setpoints for each hourly interval beginning at 0000 HR were 15, 15, 15, 14, 14, 14, 18, 22, 24, 26, 28, 28, 29, 29, 29, 27, 25, 21, 18, 17, 17, 16, 16, and 16C for the low-temperature treatment. Setpoints for each hourly interval were 8C higher for the high-temperature treatment.

were evaluated throughout a soil drying cycle. The dates available for representation of these conditions were limited by variable solar radiation. Data points plotted in the figures for response variables and environmental conditions are the means of the two rootstock cultivars (two chambers), with the range in differences between rootstock (chambers) indicated by vertical bars through each data point. Mean values reported in the remainder of the text refer to the average response of the two cultivars, or to the average of the growth chamber environmental conditions.

Results

Response to solar radiation. Net plant canopy CO_2 uptake rates showed a light compensation point at a PPFD of $\approx 100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Net canopy CO_2 uptake rates increased linearly with increasing photosynthetic photon flux density (PPFD) to $\approx 800 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and flattened out sharply over the 800 to 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ range (data not shown).

Atmospheric and soil water effects on diurnal gas exchange at

Fig. 1. Hourly average net canopy CO_2 assimilation rate (A), photosynthetic photon flux density (PPFD), air dry bulb temperature (T_a), and atmospheric vapor-pressure deficit (VPD) at the low- (A-D) and high-temperature (E-H) levels. High and low available water levels (ASW) at the low-temperature/vapor-pressure deficit level were 56% and 37%, respectively, and 64% and 13%, respectively, at the high-temperature/vapor-pressure deficit level. Data points represent the mean of twelve 300-sec interval readings for Swingle citrumelo and Carrizo citrange during the indicated hour. Bars represent the range of differences between the two rootstock. Carbon dioxide concentration is $330 \mu\text{mol}\cdot\text{mol}^{-1}$.

ambient levels of CO_2 . A maximum mean net canopy A_{CO_2} per unit ground surface area of $14.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig. 1A) occurred before 1100 HR on 23 Apr. (a relatively clear day, Fig. 1 B) when exposed to the low ($29^\circ\text{C}/2.4 \text{ kPa}$) T_a/VPD treatment (Fig. 1 C and D) and ambient ($330 \mu\text{mol}\cdot\text{mol}^{-1}$) CO_2 concentration. Rates declined throughout the remainder of the day while solar radiation remained high. Similar trends were observed on other days at this temperature level when soil water was greater than 90% ASW (data not shown). These net canopy A_{CO_2} trends indicate that the citrus seedlings experienced some degree of stress at this T_a/VPD level when exposed to ambient levels of CO_2 . Typically, midday depression of net canopy A_{CO_2} was apparent at the low T_a/VPD level when soil water contents were below 50% ASW.

Maximum mean net canopy A_{CO_2} at the high ($37^\circ\text{C}/3.6 \text{ kPa}$) T_a/VPD level and soil water content $>50\%$ ASW was $10.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and was attained by 0900 HR on 11 May (Fig. 1 E). Mean canopy CO_2 uptake rates remained nearly constant, in the range 9.5 to $10.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, despite increasing PPFD during the day. Net canopy A_{CO_2} was reduced under the high T_a/VPD treatment, compared to rates obtained at the low T_a/VPD level, but midday depression typically was not observed while the soil water content remained $>50\%$ ASW. At the low soil water level (21% ASW) and high T_a/VPD level, the maximum mean net canopy A_{CO_2} rate of $7.4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ occurred before 0900 HR at a PPFD level of $886 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Midday reduction and late afternoon recovery of CO_2 uptake rates

Fig. 2. Water-use efficiency ($\mu\text{mol } CO_2$ uptake/ $\text{mmol } H_2O$ loss from plants and containers) of Swingle citrumelo citrus and Carrizo citrange at the low- (A) and high-temperature (B) levels. High and low available water levels (ASW) at the low-temperature/vapor-pressure deficit level were 56% and 37%, respectively, and 64% and 13%, respectively, at the high-temperature/vapor-pressure deficit level. Data points represent the mean of twelve 300-sec interval readings for both rootstock during the indicated hour. Carbon dioxide concentration is $330 \mu\text{mol}\cdot\text{mol}^{-1}$.

were typically observed under conditions of high T_a/VPD when available soil water fell below 60%.

Between T_a of 29 to 37°C and VPD of 2.4 to 3.6 kPa , the maximum mean net canopy A_{CO_2} changed about $-0.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ per $^\circ\text{C}$ or about $-3.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ per kPa under conditions when available soil water was $>50\%$. This decrease with increasing T_a or VPD shows the effect of the aerial environment on citrus CO_2 uptake rates at ambient CO_2 level.

The hour-by-hour CO_2 uptake rates of the two cultivars were very similar for the 4 days shown in Fig. 1. The vertical bars on each data point show the range of values between the two, paired, hourly measurements. For many cases, the range is hidden by the size of the plotted data points. Taken across these 23 paired, hourly data sets, the summation of the CO_2 uptake in the Carrizo citrange chamber was nearly identical to that of Swingle citrumelo, although the maximum deviation was as high as $2.57 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Net canopy A_{CO_2} remained very similar for the two cultivars for each hour of measurement throughout the entire study period, 10 Apr. to 14 June 1985.

Maximum mean ET (expressed as $\mu\text{moles of } H_2O/\text{m}^2$ of ground

Fig. 3. Hourly average net canopy CO_2 assimilation rate (A) and evapotranspiration rate (ET) of Swingle citrumelo citrus seedlings at the low-temperature level with short-term exposure to the high temperature. Arrows indicate the period of elevated dry-bulb temperature. Hourly average photosynthetic photon flux density (PPFD), dry bulb air temperature (T_a) and atmospheric vapor-pressure deficit (VPD) throughout the day (B-D, respectively) are also shown. Data points represent the mean of twelve 300-sec interval readings during the indicated hour. Carbon dioxide concentration is $330 \mu\text{mol}\cdot\text{mol}^{-1}$.

surface area/sec) at soil water contents >50% ASW (associated with the data of Fig. 1) increased from 4980 to 8280 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at the low and high T_d /VPD treatments, respectively. At low soil water contents ET attained a maximum during the early morning hours and remained nearly constant throughout most of the day as the T_d /VPD level increased. At low soil water levels (<50% ASW), maximum mean ET values were 4650 and 4770 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at the low and high T_d /VPD levels, respectively.

High values of WUE occurred at the low T_d /VPD during the

morning hours, typically before 1000 HR (Fig. 2). Values declined during the middle of the day as a result of decreasing net canopy A_{CO_2} accompanied by increasing or steady ET. Water-use efficiency was greatly reduced throughout the day under the high T_d /VPD conditions at both high and low levels of available soil water compared to values obtained at the low level of T_d /VPD. Higher WUE values during the late afternoon reflect declining ET resulting from reduced VPDs.

The immediate effects of high T_a and high VPD on A_{CO_2} and ET

Fig. 4. Hourly average net canopy CO_2 assimilation rate (A), photosynthetic photon flux density (PPFD), dry bulb air temperature (T_a), and atmospheric vapor-pressure deficit (VPD) at the low- (A–D) and high-temperature (E–H) levels and elevated ($840 \mu\text{mol}\cdot\text{mol}^{-1}$) CO_2 level. High and low available water levels (ASW) at the low-temperature/vapor-pressure deficit level were 69% and 18%, respectively, and 70% and 31%, respectively, at the high-temperature/vapor-pressure deficit level. Data points represent the mean of twelve 300-sec interval readings for Swingle citrumelo and Carrizo citrange during the indicated hour. Bars represent the range of differences between the two rootstock.

(Fig. 3A) are apparent when T_a /DPT controls were switched abruptly from 29/ 14C to 37/22C (Fig. 3C) between 1200 and 1400 HR on 25 Apr. Within 10 min of the temperature change, net canopy A_{CO_2} of the Swingle citrumelo plants dropped and remained nearly constant at rates less than $1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ until temperatures were switched at 1400 HR to their previous levels (Fig. 3A). Carbon dioxide exchange rates of Carrizo citrange fell from 7.6 to $0.8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ within 25 min of the T_a /DPT change and were slightly higher than rates for Swingle citrumelo during the period of elevated temperatures (data not shown). In comparison, evapotranspiration rates were less affected by the increased temperature and VPD (Fig. 3C). Carbon dioxide uptake rates attained values nearly equal to those existing before the change within 25 min of reestablishment of previous temperatures.

Gas exchange under elevated CO_2 conditions. Midday depression of net A_{CO_2} was not observed in plants subjected to the elevated CO_2 concentration ($840 \mu\text{mol}\cdot\text{mol}^{-1}$) regardless of T_a /VPD level or soil water status (Fig. 4). At the elevated CO_2 concentration, maximum mean net canopy A_{CO_2} values at soil water levels >50% ASW were 2-fold greater than the maximum rates that occurred at respective T_a /VPD levels under the ambient CO_2 concentration. At the low T_a /VPD level (29C/2.4 kPa) and high soil water content (69% ASW), the range of mean net canopy A_{CO_2} was 30.0 to $34.8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ between 0800 and 1500 HR and it was reduced to 21.2 to $26.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ when the ASW was 18% (Fig. 4A). At the high CO_2 concentration and T_a /VPD level (37C/3.6 kPa), maximum mean net canopy A_{CO_2} at all soil water levels were reduced relative to rates obtained at the low T_a /VPD level (Fig. 4E). Maximum mean canopy A_{CO_2} occurred before 1000 HR under all conditions with nearly constant rates between 1000 and 1500 HR.

Evapotranspiration rates at the elevated CO_2 concentration and both T_a /VPD levels were comparable in terms of range and diurnal pattern to rates obtained under ambient CO_2 conditions (Table 2). Maximum mean WUE was greater at the elevated CO_2 concentration than under the ambient concentration. Maximum mean WUE appeared to be affected more by the T_a /VPD level than by the soil water level. Water-use efficiency declined during the early morning hours and remained low during the middle of the day before increasing slightly during the late afternoon.

Carbon dioxide uptake during drought cycles. The effect of soil water depletion at each temperature and CO_2 concentration combination is summarized by plotting maximum and minimum mean canopy CO_2 uptake rates between 1000 and 1500 HR at the daily average AS-W level $[(ASW_{\text{morning}} + ASW_{\text{evening}})/2]$ throughout a soil drying cycle (Figs. 5 and 6). Minimum net canopy A_{CO_2} rates indicate changes in midday depression that would not be reflected in the maximum values. Daily total PPFD between 0700 and 1900

HR remained high throughout the duration of the drying cycles and thus solar radiation was unlikely to be a limiting factor (Figs. 5 and 6). At the Gainesville latitude of $\approx 29.6^\circ\text{N}$, daylight hours over the period 21 Apr. to 14 May increased from 13 h, 3 min to 13 h, 37 min, or ≈ 34 min (derived from List, 1949). This 4% increase in daylight hours should not have had much influence on maximum or minimum CO_2 assimilation rates or the occurrence of midday depression of CO_2 uptake rates throughout the study.

Net canopy A_{CO_2} rates at the low T_a /VPD treatment and ambient CO_2 concentration (Fig. 5A) were limited in the early part of the soil drying cycle, probably by previous exposure to the high T_a /VPD treatment (19,20, and 21 Apr.). Consequently, the maximum mean CO_2 uptake rate of $14.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ occurred on the third day of drying (23 April) at $\approx 50\%$ ASW. Net canopy A_{CO_2} declined slightly on 24 Apr. at 30% ASW and declined significantly on 25 Apr. at 13.5% ASW.

At the high T_a /VPD treatment and ambient CO_2 concentration, mean net canopy A_{CO_2} began to decline when ASW reached 40% and dropped steadily thereafter to $5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at 11% ASW on the last day of the drying cycle (Fig. 5B). Maximum daily A_{CO_2} remained nearly constant to a lower ASW level under the low T_a /VPD treatment compared to the high T_a /VPD treatment, i.e., the reduction in maximum A_{CO_2} occurred between 48% and 30% ASW at the low T_a /VPD level, and between 64% and 39% ASW at the high T_a /VPD level.

At the low T_a /VPD level and elevated CO_2 concentration, the maximum mean net canopy A_{CO_2} dropped on the third day of the soil drying cycle (Fig. 6A). The large decrease in A_{CO_2} , when available soil was still >50%, was not associated with an important change in environmental factors. At 20% available soil water there was no further reduction of A_{CO_2} . At the high T_a /VPD level and elevated CO_2 concentration, daily maximum mean net canopy A_{CO_2} was $\approx 25.0 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ during the first 4 days until available soil water was depleted to $\approx 30\%$ (Fig. 6B). Maximum mean A_{CO_2} dropped to $\approx 23 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ on the sixth day when $\approx 5\%$ of the available soil water remained. Irrigation was applied before midday depression of A_{CO_2} was observed.

Discussion

The results of this study indicate that highest citrus canopy CO_2 uptake rates at ambient CO_2 concentration were obtained at the low T_a /VPD (29C/2.6 kPa) level and lowest rates were obtained at the high (37C/3.6 kPa) T_a /VPD level. Low temperature optima for citrus have been reported (Khairi and Hall, 1976a, 1976b; Kriedemann, 1968). Our findings also concur with those of Bielorai and Mendel (1969) and Thompson et al. (1965); as T_a /VPD

Table 2. Maximum average canopy CO_2 assimilation rate, evapotranspiration rate, and water-use efficiency of citrus seedlings in response to dry-bulb temperature/vapor-pressure deficit level and available soil water at high CO_2 concentration ($840 \mu\text{mol}\cdot\text{mol}^{-1}$) and daily maximum photosynthetic photon flux density. Values are from 300-sec measurements. Maximum values of water-use efficiency did not necessarily occur at the same time as maximum values of assimilation or evapotranspiration.

Date	Dry-bulb temp/vapor-pressure deficit			
	Low (29C/2.4 kPa)		High (37C/3.6 kPa)	
	30 Apr.	3 May	5 May	8 May
Photon flux density ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	1650	1520	1910	1850
Available soil water (%)	69	18	70	13
CO_2 assimilation rate ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	34.8	26.1	25.6	21.2
Evapotranspiration $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	5500	4800	7600	4400
Water-use efficiency ($\mu\text{mol } CO_2/\text{mmol } H_2O$)	7.5	7.4	4.8	4.8

^aCarrizo citrange [*Poncirus trifoliata* Raf $\times$ *Citrus sinensis* (L.) Osbeck] and Swingle citrumelo (*P. trifoliata* Raf $\times$ *C. paradisi* Macf.).

increased, there was a limited increase in transpiration rate and a reduction in A_{CO_2} that was attributed to stomatal closure. This feedback response of citrus transpiration to increases in atmospheric humidity deficit has been attributed to stomatal closure in other studies as well (Hall et al., 1975; Kaufmann and Levy, 1976; Sinclair and Allen, 1982).

Under ambient CO_2 levels, midday depression of net CO_2 uptake rates was not apparent at either T_a/VPD treatment at high soil water levels. However, at low soil water contents, midday depression of net CO_2 uptake rates occurred at both temperature levels. Daily maximum and minimum net canopy CO_2 assimilation plotted over the percentage remaining available soil water throughout various soil water depletion cycles indicated that maximum net CO_2 assimilation was reduced at higher soil water levels at the high T_a/VPD level compared to the low T_a/VPD level. This indicates that there was an increasing sensitivity of citrus net CO_2 assimilation rate to soil water depletion as the T_a/VPD level increased. Thus, midday depression of net CO_2 assimilation in citrus could likely be avoided with timely irrigation practices and that irrigation will become more critical as the atmospheric vapor-pressure deficit increases.

At the elevated CO_2 level, maximum net canopy CO_2 assimilation was reduced slightly by the increase in vapor-pressure deficit, but maximum CO_2 assimilation rates remained nearly constant to a much lower soil water content than occurred at the ambient CO_2 level. Our study showed that at the elevated CO_2 level, midday depression of CO_2 uptake at low soil water contents was alleviated under low and high vapor-pressure deficit conditions. An implication of this is reduced sensitivity of stomatal conductance to the

leaf-to-air vapor-pressure deficit, as has been reported in other studies (Bunce 1993), and to soil water stress. These results suggest that citrus, at higher than ambient levels of CO_2 , could tolerate some of the adverse effects of high temperature and drought.

Downton et al. (1987) noted that photosynthetic rates of well-watered citrus plants at 25C were from 18 to 77% greater at CO_2 concentrations of $800 \mu\text{mol}\cdot\text{mol}^{-1}$ than at $400 \mu\text{mol}\cdot\text{mol}^{-1}$ depending on the developmental stage. A doubling of citrus CO_2 assimilation at a CO_2 concentration of $840 \mu\text{mol}\cdot\text{mol}^{-1}$ is supported by the results of this study. Subsequently, data collected over a 3-year period (1988–90) by Idso and Kimball (1991) on sour orange trees at Phoenix, Ariz., continuously enriched with $300 \mu\text{mol}\cdot\text{mol}^{-1}$ of CO_2 above ambient (i.e., $650 \mu\text{mol}\cdot\text{mol}^{-1}$), showed 2.2-fold increases in mean CO_2 uptake of individual leaves and 2.8-fold increases in mean trunk plus branch volume. The large increase in citrus biomass under CO_2 enrichment found by Idso and Kimball (1991) was possible because of continuous incremental crown growth and light capture without mutual shading or competition for water and nutrients by the spaced trees, as well as increased leaf CO_2 uptake rates. Allen and Amthor (1994) pointed out that, under the climatic conditions of Arizona, leaves of both ambient-air and CO_2 -enriched grown trees showed midday depression of photosynthesis that persisted throughout the afternoon. Furthermore, the afternoon depression of photosynthesis was much more severe in the ambient-air exposed trees, with leaf A_{CO_2} being only $\approx 1.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, whereas the leaf A_{CO_2} was $\approx 4.8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for the enriched trees. These responses of field-grown trees to a hot, high VPD environment are consistent with our data, although we did not see midday depression in our CO_2 -enriched plants, probably

Fig. 5. Hourly maximum and minimum net canopy CO_2 assimilation rates (A) of Swingle citrumelo and Carrizo citrange citrus seedlings at the daily average level of available soil water during drying cycles under ambient ($330 \mu\text{mol}\cdot\text{mol}^{-1}$) CO_2 concentrations at the low- (A) and high-temperature (B) levels. Data points represent the mean of twelve 300-sec interval readings during the indicated hour. In panel A, the chambers were operated at the high-temperature level on the first day (21 Apr.) of the drying cycle. Daily total photosynthetic photon flux density (PPFD) is indicated for each day of the drying cycle by filled diamonds.

Fig. 6. Hourly maximum and minimum net canopy CO_2 assimilation rates (A) of Swingle citrumelo and Carrizo citrange citrus seedlings at the daily average level of available soil water during drying cycles under elevated ($840 \mu\text{mol}\cdot\text{mol}^{-1}$) CO_2 concentrations at the low- (A) and high-temperature (B) levels. Data points represent the mean of twelve 300-sec interval readings during the indicated hour. Daily total photosynthetic photon flux density (PPFD) is indicated for each day of the drying cycle by filled diamonds.

because our enrichment level was higher and T_A/VPD was lower than the field conditions at Phoenix.

The decrease of maximum canopy CO_2 uptake rates at the onset of the elevated CO_2 treatment could be an example of partial downward regulation (end-product feedback inhibition) of citrus photosynthetic rates in response to a greater photoassimilate supply as has been found in some natural system and crop vegetation (Allen, 1990). Nevertheless, the CO_2 uptake rates were still at least 2-fold greater when exposed to these elevated CO_2 concentrations, whereas other examples of downward regulation acclimation to elevated CO_2 exposure have actually shown a decrease of CO_2 uptake rates back to those of the previous lower CO_2 exposure levels, or even negative responses to CO_2 after a few days.

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