

Table 4. Effect of paclobutrazol and "Tre-Hold"<sup>z</sup> on amount of sprouts from 1-year-old rough lemon seedlings detopped to equal heights and maintained in pots in greenhouse for 42 days after treatment.

Growth retardant <sup>z</sup>	Concn (%)	Sprouts/seedlings	
		No.	O.D. wt (g)
Tre-Hold <sup>y</sup>	1.15 (a.i.)	2 a <sup>x</sup>	0.9 a <sup>x</sup>
Paclobutrazol	1.15 (a.i.)	6 b	2.3 b
Water	---	7 b	2.5 b

<sup>z</sup>5 ml brushed on 30 cm of stem length above soil level.

<sup>y</sup>Ethyl 1-naphthalene acetate.

<sup>x</sup>Mean separation within columns by Duncan's multiple range test, 5% level.

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HORTSCIENCE 21(1): 143-144. 1986.

## CO<sub>2</sub> Exchange Rate, Stomatal Conductance, and Transpiration in Attached Leaves of 'Valencia' Orange

J.C.V. Vu, G. Yelenosky, and M.G. Bausher

ARS/USDA, 2120 Camden Road, Orlando, FL 32803

*Additional index words.* Leaf gas exchanges, PPFD, VPD, *Citrus sinensis*

**Abstract.** CO<sub>2</sub> exchange rate (CER), stomatal conductance (C<sub>s</sub>), and transpiration in mature attached leaves of 'Valencia' orange [*Citrus sinensis* (L.) Osbeck] were determined outdoors from predawn to 1100 EDT. The maximum values of CER and C<sub>s</sub>, which were about 7 μmol CO<sub>2</sub>·s<sup>-1</sup>·m<sup>-2</sup> and 0.27 cm·s<sup>-1</sup>, respectively, at solar photosynthetic photon flux density (PPFD) of 500-700 μmol·s<sup>-1</sup>·m<sup>-2</sup>, remained at these levels as PPFD, temperature, and vapor pressure deficit (VPD) between leaf and air continued to increase. Transpiration rates, with maximum values ranging from 1 to 4 mmol H<sub>2</sub>O·s<sup>-1</sup>·m<sup>-2</sup>, increased throughout the measurement periods of the morning as leaf-air VPD increased. Thus, photosynthetic water use efficiency decreased with increasing VPD.

CO<sub>2</sub> exchange rates (CER) of the leaves have been used widely as an index of plant response to specific experimental treatments or environmental conditions. In citrus, basic knowledge on leaf gas exchanges is limited, compared to other agricultural crops. Alterations in CER apparently occur during cold-acclimation (15) and disease-infection and changes in vapor pressure deficit (13) in field-grown leaves. Acquisition of such information has been limited because technical and instrumental constraints have restricted photosynthetic studies under field conditions. Data obtained from controlled-environment measurements might not reflect the real conditions for the leaf in the field, since gas

exchange characteristics of the leaf at its growing site involve simultaneously complex effects of natural environmental parameters under which leaf is exposed.

In this report, we used a field-portable, closed gas-exchange photosynthesis system (LI-COR LI-6000, Lincoln, Nebraska) to measure the gas exchanges of attached citrus leaves under ambient O<sub>2</sub> and CO<sub>2</sub> concentrations and at naturally occurring solar irradiance. The results indicate that this system appears to have considerable potential for studying citrus leaf photosynthesis at the sites where trees are growing.

'Valencia' orange trees, which were developed from buds grafted on 14 June 1983, on 9-month-old rough lemon (*C. jambhiri* Lush.) rootstocks, were individually grown in 2.5-liter plastic pots containing Promix, a commercial mix of sphagnum peat moss, vermiculite, and perlite with additional major (N, P, K) and minor (Ca, Mg, Fe, Mn, Zn, B, Mo) nutrient elements. Trees were maintained under a glass greenhouse environment, watered daily, and fertilized monthly with a 1.6% solution of 15N-7P-7K liquid fertilizer. On 2 Apr. 1984, trees of uniform

appearance, about 50-cm tall, were selected and brought outside to natural field conditions. On 13 Apr. 1984, measurements of leaf gas exchanges were conducted under natural daylight in the morning, starting before sunrise (0530 EDT) and ending 1 hr before noon (1100 EDT). Measurements were restricted to individual mature leaves in the upper third of single-stem trees. CO<sub>2</sub> exchange rates (CER), stomatal conductance (C<sub>s</sub>), and transpiration (E) were monitored simultaneously with the LI-6000 System as solar PPFD increased from 0 at predawn to 2000 μmol·s<sup>-1</sup>·m<sup>-2</sup> by 1100 EDT. We used the 4-liter leaf chamber in which leaf temperature, chamber air temperature, relative humidity, CO<sub>2</sub> concentration, and PPFD were monitored (10). The return flow rate of air circulating within the closed system was 8 cm<sup>3</sup>·s<sup>-1</sup>, and five 60 sec observations were set for each measurement.

The CO<sub>2</sub> exchange rates throughout the morning measurement periods are shown in Fig. 1A. Dark respiration averaged about 1 μmol CO<sub>2</sub>·s<sup>-1</sup>·m<sup>-2</sup>. The light compensation point (at CER = 0) occurred between 30 and 40 μmol·s<sup>-1</sup>·m<sup>-2</sup> of solar PPFD. CER approached the maximum level of about 7 μmol CO<sub>2</sub>·s<sup>-1</sup>·m<sup>-2</sup> at 500-600 μmol·s<sup>-1</sup>·m<sup>-2</sup> PPFD. Stomatal conductance C<sub>s</sub> increased rapidly from values of 0.03 cm·s<sup>-1</sup> in the dark to a maximum value of 0.27 cm·s<sup>-1</sup> at solar PPFD of about 500 μmol·s<sup>-1</sup>·m<sup>-2</sup> (Fig. 1B). Transpiration rates increased as PPFD increased from zero before sunrise to 2000 μmol·s<sup>-1</sup>·m<sup>-2</sup> at 1100 EDT (Fig. 1C).

As solar PPFD increased, air temperature inside the chamber in which the attached leaf was enclosed increased (Fig. 1, abscissa), and was 0.2° and 3°C higher than ambient air temperature at predawn and 1100 EDT, respectively. Responses of leaf temperatures throughout the morning measurements were similar to those of chamber air temperatures, except at 1500 to 2000 μmol·s<sup>-1</sup>·m<sup>-2</sup> of PPFD within which leaf temperatures were about 1° to 2° higher. The increases in leaf temperature throughout the measurement periods of the morning led to rapid increases in leaf saturation vapor pressure, resulting in large increases in vapor pressure deficit (VPD) between leaf and air (Fig. 1, abscissa). At a

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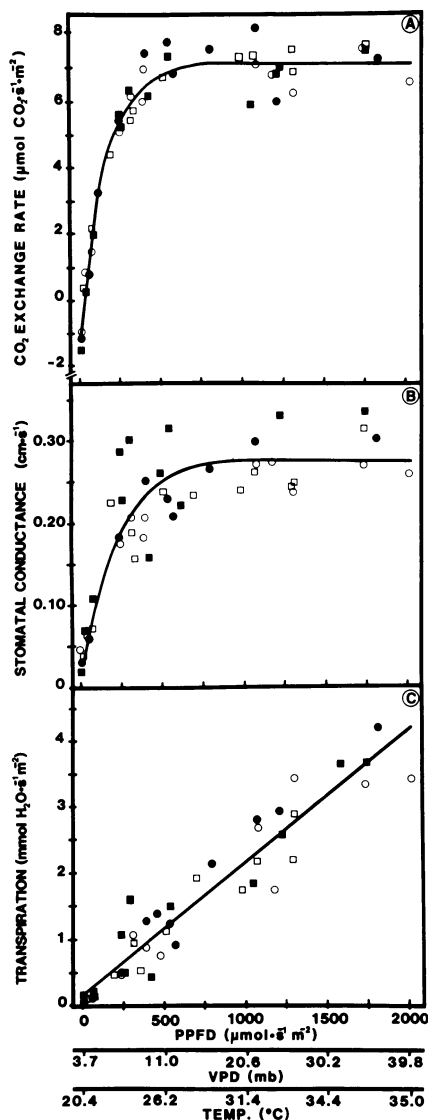


Fig. 1.  $\text{CO}_2$  exchange rate (A), stomatal conductance (B), and transpiration (C) of greenhouse-grown 'Valencia' orange leaves measured outdoors during the morning of 13 Apr. 1984 with the LI-6000, were plotted against solar irradiance PPFD, and corresponding values of leaf-air VPD and chamber air temperature calculated at 0, 500, 1000, 1500, and 2000  $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$  of PPFD. Symbols represent measurements of single fully-expanded attached leaves from 4 different trees.

$C_s$  value of  $0.27 \text{ cm}\cdot\text{s}^{-1}$ , E ranged from 1.3 to  $4 \text{ mmol H}_2\text{O}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ . As long as stomata are open, the increases in VPD are responsible for continued increases in transpiration rates.

Plotting E against CER shows that E continued to increase even after CER had reached the maximum level (Fig. 2). This constancy of CER and the increase in E, as VPD between leaf and air increased, show a decrease in photosynthetic water-use efficiency (9). Similar patterns of curvilinear relationship between CER and E have been reported in leaves of other plant species (1, 3).

Data from previously reported studies on different citrus species growing in pots and measured with conventional infrared gas

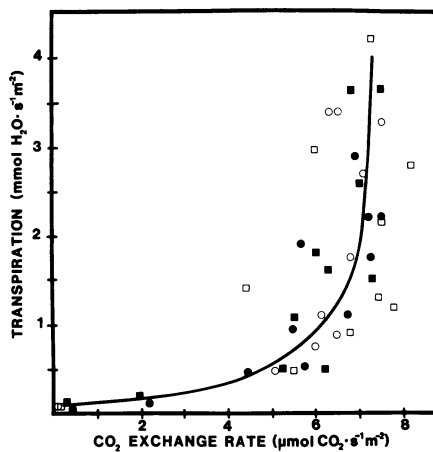


Fig. 2. Transpiration vs.  $\text{CO}_2$  exchange rate of greenhouse-grown 'Valencia' orange leaves measured outdoors during the morning of 13 Apr. 1984, with the LI-6000. Symbols represent measurements of single fully-expanded attached leaves from 4 different trees.

analysis system indicated that, under optimum conditions, citrus leaves exhibited CER in the range of  $6\text{--}12 \mu\text{mol CO}_2\cdot\text{s}^{-1}\cdot\text{m}^{-2}$  and reached saturation at artificial lamp irradiances of  $500\text{--}600 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ , which is equal to about one-fourth full solar PPFD (5, 6, 7, 14). Similar levels of solar PPFD saturated CER have been demonstrated by Sinclair and Allen (12) using a mobile laboratory to monitor  $\text{CO}_2$  and  $\text{H}_2\text{O}$  vapor exchange in field-grown citrus trees. These data are in general consistent with our results on 'Valencia' orange. From the quantum flux absorbed by the leaves in the light-limiting range (0 to  $110 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$  PPFD, early morning periods), computed value of the quantum yield (slope of the curve, Fig. 1A) averaged  $0.043 \text{ mol CO}_2$  per absorbed quantum mol. This is comparable to reported value of  $0.052$  for a variety of  $\text{C}_3$  plant species (2). The minimum values of stomatal and cuticular conductance in fully expanded leaves of orange were  $0.03\text{--}0.04 \text{ cm}\cdot\text{s}^{-1}$  at low irradiance, and maximum values were  $0.25\text{--}0.29 \text{ cm}\cdot\text{s}^{-1}$  at saturating PPFD (7). This range compares favorably to our results on stomatal conductance. Maximum transpiration rates in citrus leaves were between  $1.1\text{--}2.8 \text{ mmol H}_2\text{O}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$  (4, 7, 8, 11, 12), which are also in the range of our values.

The overall response shapes of CER,  $C_s$ , and E (Fig. 1) reflected combining responses to the progressively changing environmental parameters throughout the morning, which included solar irradiance, temperature, and VPD between leaf and air. Continued increases in solar irradiance, temperature, and leaf-air VPD with the progress of the morning seemed not to affect CER and  $C_s$ , once their maximum levels had been reached. Leaf transpiration, however, was responding more to the continued increases in VPD between leaf and air. Since measurements were made in the field under close-to-natural conditions, these leaf gas exchange data, when compared to those of artificially controlled-environment measurements in the laboratory

using conventional infrared gas analysis systems, would represent more truly the photosynthetic characteristics of the leaves at their growing sites. Despite the fact that the environmental conditions within the leaf chamber of the closed system are progressively changing during measurements, the direct and rapid measurements on many leaves at the tree-growing sites make the portable LI-6000 a useful alternative for heavy and high-cost conventional systems to document leaf gas exchange in field experiments.

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