



# The effect of long-term atmospheric CO<sub>2</sub> enrichment on the intrinsic water-use efficiency of sour orange trees

S.W. Leavitt <sup>a,\*</sup>, S.B. Idso <sup>b</sup>, B.A. Kimball <sup>b</sup>, J.M. Burns <sup>a</sup>, A. Sinha <sup>c</sup>, L. Stott <sup>c</sup>

<sup>a</sup> Laboratory of Tree-Ring Research, 105 W. Stadium, Bldg. #58, University of Arizona, Tucson AZ 85721, USA

<sup>b</sup> US Water Conservation Laboratory, 4331 E. Broadway Road, Phoenix AZ 85040, USA

<sup>c</sup> Department of Geological Sciences, University of Southern California, Los Angeles CA 90089, USA

## Abstract

Every two months of 1992, as well as on three occasions in 1994–1995, we obtained leaf samples together with samples of surrounding air from eight well-watered and fertilized sour orange (*Citrus aurantium* L.) trees that were growing out-of-doors at Phoenix, Arizona, USA. These trees had been planted in the ground as small seedlings in July of 1987 and enclosed in pairs by four clear-plastic-wall open-top chambers of which two have been continuously maintained since November of that year at a CO<sub>2</sub> concentration of 400  $\mu\text{mol mol}^{-1}$  and two have been maintained at 700  $\mu\text{mol mol}^{-1}$ . In September 2000, we also extracted north–south and east–west oriented wood cores that passed through the center of each tree's trunk at a height of 45 cm above the ground. Stable-carbon isotope ratios (<sup>13</sup>C/<sup>12</sup>C) derived from these leaf, wood and air samples were used to evaluate each tree's intrinsic water-use efficiency (iWUE). The grand-average result was an 80% increase in this important plant parameter in response to the 300  $\mu\text{mol mol}^{-1}$  increase in atmospheric CO<sub>2</sub> concentration employed in the study. This increase in sour orange tree iWUE is identical to the long-term CO<sub>2</sub>-induced increase in the trees' production of wood and fruit biomass, which suggests there could be little to no change in total water-use per unit land area for this species as the air's CO<sub>2</sub> content continues to rise. It is also identical to the increase in the mean iWUE reported for 23 groups of naturally occurring trees scattered across western North America that was caused by the historical rise in the air's CO<sub>2</sub> content that occurred between 1800 and 1985. Published by Elsevier Science Ltd.

**Keywords:** CO<sub>2</sub> fertilization effect; Carbon dioxide; Carbon isotopes; Stomatal conductance; Transpiration; Water-use efficiency

## 1. Introduction

There is abundant experimental evidence that C<sub>3</sub> woody plants respond to elevated atmospheric CO<sub>2</sub> concentrations with significant increases in biomass (Poorter, 1993; Ceulemans and Mousseau, 1994; Wullschlegel et al., 1995, 1997), especially in the early stages of their life cycles (Idso, 1999). In a comprehensive review of the pertinent literature, for example, Saxe et al. (1998) determined that “close to a doubling” of the

ambient atmospheric CO<sub>2</sub> concentration leads to an approximate 50% increase in the biomass production of angiosperm trees and a 130% increase in the biomass production of coniferous species. As has recently been demonstrated by Idso and Kimball (2001), however, this substantial initial growth stimulation—which rose as high as 200% at the two-year point of their study of well-watered and fertilized sour orange trees—may decline significantly over the following few years before reaching a long-term equilibrium level several years later. After nearly a decade had elapsed in the Idso and Kimball study, for example, a near-constant and still-substantial 80% increase in biomass production was ultimately established, which has continued undiminished to the time of this writing some five years later.

\* Corresponding author. Tel.: +1-520-621-6468; fax: +1-520-621-8229.

E-mail address: sleavitt@lrr.arizona.edu (S.W. Leavitt).

Another well-established consequence of exposing  $C_3$  woody plants to elevated levels of atmospheric  $CO_2$  is an increase in their water-use efficiency, or the amount of biomass produced per unit of water transpired (Morrison, 1993; Saxe et al., 1998). Like the  $CO_2$ -induced increase in biomass, however, there is little information on how this phenomenon behaves in the long-term. Furthermore, the relative contribution to increased water-use efficiency from increase in biomass (by the aerial fertilization effect of atmospheric  $CO_2$  enrichment) versus  $CO_2$ -induced decrease in leaf stomatal conductance (reducing the amount of water transpired from each unit area of a tree's foliage) is not known. The purpose of the work described in this paper, therefore, was to answer these questions with isotopic measurements of air and plant matter.

## 2. Methodology

### 2.1. Materials

The trees with which we worked were the sour orange (*Citrus aurantium* L.) trees of the still-ongoing study (Fig. 1) of Idso and Kimball (2001). This long-term experiment was begun in July of 1987 with the planting of eight 30-cm-tall seedlings in a fine-loamy, mixed (calcareous), hyperthermic, Anthropic Torrifluent soil at Phoenix, Arizona, USA. Shortly after planting, the trees were enclosed in pairs within four open-top chambers constructed of walls made of clear polyethylene, where they have been continuously maintained under well-watered and fertilized conditions. Records of exact quantities of added water and fertilizer are not available, but the trees have always been fertilized and irrigated as per recommendations of local experts with the intent of keeping them free of water and nutrient stresses. By means of the  $CO_2$  measurement and supply systems described by Kimball et al. (1983) and Idso et al. (1984), ambient air of approximately  $400 \mu\text{mol mol}^{-1}$   $CO_2$  is continuously pumped through two of the chambers, while air enriched to  $700 \mu\text{mol mol}^{-1}$   $CO_2$  is pumped through the other two chambers. Air movement within the chambers is provided by blowers that introduce outside air, with or without added  $CO_2$ , into all chambers at identical rates of mass flow. Systematic measurements of most meteorological parameters within the chambers have not been made for several years. However, recent air temperature and periodic vapor pressure measurements suggest that conditions within all chambers are essentially identical.

### 2.2. Theory

Our approach to answering the questions posed in Section 1 is based on the conceptual framework devel-



Fig. 1. Photographs of sour orange tree experiment at Phoenix, Arizona, in October 1991 (top) and September 1999 (bottom left and right).

oped by Farquhar et al. (1982), who defined intrinsic water-use efficiency (iWUE) as the ratio of the photosynthetic uptake of  $CO_2$  through leaf stomata to the simultaneous transpirational loss of water vapor through the same openings, expressed in units of  $\text{mmol } CO_2 \text{ mol}^{-1} H_2O$ :

$$iWUE = A/g = c_a[1 - (c_i/c_a)](0.625) \quad (1)$$

where  $A$  is the rate of  $CO_2$  assimilation by the trees' leaves,  $g$  is leaf stomatal conductance, and  $c_i$  and  $c_a$  are leaf intercellular and atmospheric  $CO_2$  concentration, respectively. The  $c_i/c_a$  ratio of this equation may be further expressed as

$$c_i/c_a = (\delta^{13}C_{\text{plant}} - \delta^{13}C_{\text{air}} + a)(a - b)^{-1} \quad (2)$$

where  $a$  represents isotopic fractionation during  $CO_2$  diffusion through the stomata ( $\sim 4.4\%$ ) and  $b$  represents isotopic fractionation by ribulose biphosphate carboxylase ( $\sim 27\%$ ). Last of all,  $\delta^{13}C$  is defined in terms of stable-carbon isotope measurements ( $^{13}C$ ,  $^{12}C$ ) of the air and plant materials, and the international PDB isotopic standard (Craig, 1957; Coplen, 1996):

$$\delta^{13}\text{C} = \left[ \left( \frac{{}^{13}\text{C}/{}^{12}\text{C}_{\text{sample}}}{{}^{13}\text{C}/{}^{12}\text{C}_{\text{PDB standard}}} \right) - 1 \right] (1000) \quad (3)$$

### 2.3. Measurements

On 1 September 2000, north–south and east–west oriented 4-mm-diameter wood cores were bored from each of the eight trees at a height of 45 cm above the ground. The majority of cores passed within 1 cm of the tree center. These cores—which provided four bark-to-pith radial wood samples emanating from the four cardinal points of the compass and thus helped reduce circumferential isotopic variability (Leavitt and Long, 1984)—were sanded with a number of progressively finer abrasives in an attempt to make their yearly growth rings more visible. Unfortunately, the evergreen character of the trees and the prolonged growing season at Phoenix that results from year-round favorable (warm to hot) temperatures did not lead to the production of clearly identifiable ring boundaries. Hence, we were unable to develop annual chronologies of changes in water-use efficiency during the course of the experiment and were limited to performing bulk analyses on the entire cores.

The four radial cores of each tree were ground together to 40-mesh consistency for bulk stable-carbon isotope analysis. Splits of all samples were extracted sequentially with toluene/ethanol, ethanol, and boiling water, after which they were delignified to holocellulose in an acidified sodium chlorite solution and rinsed (Leavitt and Danzer, 1993). The cellulose was then combusted to  $\text{CO}_2$  in the presence of excess oxygen in a recirculating microcombustion system and the  $\text{CO}_2$  analyzed mass-spectrometrically with the results expressed as  $\delta^{13}\text{C}$  in ‰.

Leaf and air samples had also been collected throughout 1992 (January, March, May, July, September, December), as well as on three occasions in 1994–1995 (August, December, September). Several ( $\geq 5$ ) leaves were sampled from each of the eight trees and air was collected from all four open-top chambers on these occasions. Leaves sampled from March to December in 1992 were primarily newly formed (current season) leaves, whereas the January 1992 leaves were from the previous growing season. Therefore, new leaf isotope composition dominated our 1992 annual isotopic average. Flask air samples were not taken at the same time of day on all occasions, but they were sampled in either late morning or early afternoon.

The 1992 set of leaves was similarly treated to determine the  $\delta^{13}\text{C}$  of the cellulose, while the latter set was analyzed for whole-tissue  $\delta^{13}\text{C}$ . The precision of all measurements was estimated to be about 0.2‰, which is the standard deviation of long-term, repeated combustion and analysis of cellulose laboratory standards. The

average isotopic difference of (1992) leaves between the paired trees in replicates was about 1.2‰ (standard deviation,  $s = 1.0\text{‰}$ ) and 0.6‰ ( $s = 0.7\text{‰}$ ) for enriched and ambient treatments, respectively, whereas cores from paired trees differed by an average of 0.9‰ ( $s = 0.5\text{‰}$ ) and 0.2‰ ( $s = 0.2\text{‰}$ ) in enriched and ambient air, respectively.

The  $\delta^{13}\text{C}$  of the commercial  $\text{CO}_2$  used to raise the  $\text{CO}_2$  concentration of the air in the  $\text{CO}_2$ -enriched chambers to  $700 \mu\text{mol mol}^{-1}$  was measured only once (1994) and found to have a value of  $-35.5\text{‰}$ ; but this value is believed to have been fairly uniform throughout the experiment. This assumption is based on the 1991–1996 average  $\delta^{13}\text{C}$  of the commercial  $\text{CO}_2$  used in the free-air  $\text{CO}_2$  enrichment (FACE) experiments conducted at the Maricopa Agricultural Center south of Phoenix (Leavitt et al., 1994, 1996, 2001). The FACE studies used the same commercial source of  $\text{CO}_2$  as was used in the sour orange tree experiment; and its long-term  $\delta^{13}\text{C}$  value was determined over the course of those studies to be  $-38.1\text{‰}$  ( $s = 2.2\text{‰}$ ), based on frequent measurements over the six-year period.

The  $\delta^{13}\text{C}_{\text{air}}$  values employed in our calculations were those measured in 1992 and 1994–1995, while the  $\delta^{13}\text{C}_{\text{plant}}$  values were those obtained from the 1992 leaf cellulose, the 1994–1995 leaf whole-tissue, and the cellulose of the wood cores obtained on 1 September 2000. In addition, whole-wood tissue from the cores was analyzed on 4 trees (2 trees from each treatment) and was found to average  $1.18\text{‰}$  ( $s = 0.17\text{‰}$ ) more negative than the corresponding cellulose. Applying this correction factor to the mean cellulose values of the treatments,  $c_i/c_a$  was also calculated from the estimated whole-wood isotopic composition. Furthermore, the isotopic composition of the leaf whole-tissue associated with the 1992 leaf cellulose and the wood-core cellulose was estimated with average correction factors taken from the literature (Leavitt and Long, 1982, 1985, 1986, 1991; Leavitt et al., 1994), which yielded a value of  $-2\text{‰}$  when going from whole wood to leaf whole-tissue and a value of  $-1.5\text{‰}$  when going from leaf cellulose to leaf whole-tissue. Thus, with the calculated  $c_i/c_a$  ratios in hand, along with the measured ambient  $\text{CO}_2$  concentration ( $C_a$ ), Eq. (1) was finally solved for iWUE for the various situations investigated.

### 3. Results

Over the course of 1992, the  $\delta^{13}\text{C}$  of the cellulose of the leaves from the  $\text{CO}_2$ -enriched chambers averaged  $-36.69\text{‰}$  ( $s = 0.10\text{‰}$ ), whereas that from the ambient-treatment chambers averaged  $-24.58\text{‰}$  ( $s = 0.34\text{‰}$ ). During the same period, the  $\delta^{13}\text{C}$  of the air averaged  $-22.91\text{‰}$  ( $s = 2.70\text{‰}$ ) in the  $\text{CO}_2$ -enriched chambers and  $-9.51\text{‰}$  ( $s = 1.05\text{‰}$ ) in the ambient-treatment

chambers. In 1994–1995, the whole-tissue  $\delta^{13}\text{C}$  of the leaves was  $-40.0\text{‰}$  ( $s = 0.4\text{‰}$ ) in the  $\text{CO}_2$ -enriched chambers and  $-28.3\text{‰}$  ( $s = 0.3\text{‰}$ ) in the ambient-treatment chambers, while the air  $\delta^{13}\text{C}$  was  $-19.5\text{‰}$  and  $-8.6\text{‰}$  in the  $\text{CO}_2$ -enriched and ambient treatments, respectively.

Using these results as described in the Materials and methods section, iWUE was found to always be significantly greater in the  $\text{CO}_2$ -enriched trees than in the ambient-treatment trees (Fig. 2). Leaf cellulose, wood cellulose and whole-wood isotopic compositions yielded iWUEs ranging from 203 to 226  $\text{mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$  in air of  $700 \mu\text{mol mol}^{-1} \text{ CO}_2$  and from 114 to 128  $\text{mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$  in air of  $400 \mu\text{mol mol}^{-1} \text{ CO}_2$ , indicative of a mean  $\text{CO}_2$ -induced iWUE enhancement of 77.3%. Likewise, using the actual 1994–1995 isotopic composition of leaf whole-tissue and an estimate of leaf whole-tissue corresponding to the wood and 1992 leaf values, calculated iWUEs ranged from 159 to 168  $\text{mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$  in air of  $700 \mu\text{mol mol}^{-1} \text{ CO}_2$  and from 86 to 92  $\text{mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$  in air of  $400 \mu\text{mol mol}^{-1} \text{ CO}_2$ , indicative of a mean  $\text{CO}_2$ -induced iWUE enhancement of 83.7%. Thus, the  $300 \mu\text{mol mol}^{-1}$  atmospheric  $\text{CO}_2$  concentration differential employed in this experiment resulted in an approximate 80% increase in the iWUE of the sour orange trees in two specific years as well as over the course of the whole experiment. The iWUE estimates, however, are sensitive to the  $\delta^{13}\text{C}_a$  values used in the calculations (represented in the “error” bars in Fig. 2).

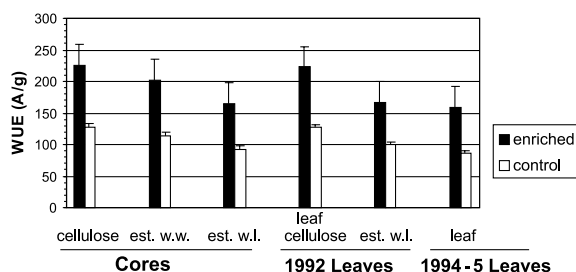


Fig. 2. Intrinsic water-use efficiency ( $A/g$  in units of  $\text{mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ ) calculated from the measured carbon isotopic composition of the 2000 wood cellulose from the trunk, the 1992 leaf cellulose, and the 1994–1995 leaf whole-tissue, as well as from the estimated carbon isotopic composition of whole wood and the leaf whole-tissue corresponding to the wood and the 1992 leaves. The top of each bar is iWUE calculated from the average of the  $\delta^{13}\text{C}_{\text{air}}$  measured in the experimental chambers in 1992 and 1994–1995. The “error” bars actually represent the spread of the calculations when the 1992 and 1994–1995  $\delta^{13}\text{C}_{\text{air}}$  values are used separately in all calculations, with the upper limit iWUE calculated from the 1992  $\delta^{13}\text{C}_{\text{air}}$  values). Values used for ambient and  $\text{CO}_2$ -enriched  $\text{C}_a$  were 400 and  $700 \mu\text{mol mol}^{-1}$ , respectively. “est.w.w.” = estimated whole wood; “est.w.l.” = estimated whole leaf tissue.

#### 4. Discussion

Although we measured isotopic composition of foliage, the leaves were sampled from around the canopy (same height), and thus the isotope measurements yield canopy-level estimates of iWUE rather than leaf-level iWUE. Likewise, the tree rings provide distinctly canopy-level iWUE estimates as they integrate gas exchange from foliage over all heights, directions, and light levels in the canopy.

The consistency among iWUE results from leaves in different years of the experiment and in wood growing over the length of the experiment is encouraging. Although we could not analyze individual annual growth rings to develop a time series of iWUE changes, the consistency among measurements representing different time scales suggests the iWUE advantage under elevated  $\text{CO}_2$  may have been fairly constant throughout the experiment. When the experiment ends, perhaps wood samples can again be taken and the growth in each year could be approximated from the record of frequent stem diameter measurements to test for subtle changes in iWUE.

In reference to the first of the two questions posed in Section 1, we note that the 80% increase in the mean iWUE we derived for the sour orange trees is identical to the long-term  $\text{CO}_2$ -induced increase in the trees’ wood and fruit biomass production (Idso and Kimball, 2001). This observation suggests that the increase in the sour orange trees’ water-use efficiency was driven primarily by the aerial fertilization effect of the extra  $300 \mu\text{mol mol}^{-1} \text{ CO}_2$  employed in the study, in answer to the second of the two questions we initially raised. Independent support for this inference is provided by the study of Idso et al. (1993), who found the stomatal conductance of the sour orange trees (leaf level) was reduced by less than 10% under the  $300 \mu\text{mol mol}^{-1}$  increase in atmospheric  $\text{CO}_2$  concentration. This finding is also in harmony with the conclusion of Saxe et al. (1998), who in a massive review of the pertinent literature observed that “increasing numbers of experiments show a lack of stomatal sensitivity to  $\text{CO}_2$ ,” especially when the data come “from long-term experiments on larger trees rooted directly in the ground,” as may also be deduced from the work of Eamus (1996). Hence, although citrus orchards in a future high- $\text{CO}_2$  world—and possibly future forests—may produce much more biomass than they do currently, there is no guarantee they will use less water than at present.

Another instructive question we could ask at this point is how our results compare with similar measurements that have been made on various trees in the natural environment that have been exposed to the historical rise in the air’s  $\text{CO}_2$  concentration over the past two centuries. Perhaps the best source of information on this topic is Feng (1999), who assembled and

analyzed stable-carbon isotope data from 23 different sets of trees scattered throughout western North America. For the period 1800–1985, over which time the air's CO<sub>2</sub> concentration rose by 62  $\mu\text{mol mol}^{-1}$  (from 284 to 346  $\mu\text{mol mol}^{-1}$ ), the iWUEs of the 23 groups of trees rose from 10% to 25%, or by a mean of 17.5%, which is equivalent to an increase of approximately 28% per 100  $\mu\text{mol mol}^{-1}$  increase in CO<sub>2</sub>, which compares very favorably with the increase of 27% per 100  $\mu\text{mol mol}^{-1}$  increase in CO<sub>2</sub> implied by our work (80% increase in iWUE per 300  $\mu\text{mol mol}^{-1}$  increase in CO<sub>2</sub> = 27% increase in iWUE per 100  $\mu\text{mol mol}^{-1}$  increase in CO<sub>2</sub>).

Even greater water-use efficiency responses have been observed in European tree-ring studies. Bert et al. (1997), for example, found an iWUE increase of about 50% per 100  $\mu\text{mol mol}^{-1}$  increase in CO<sub>2</sub> between 1860 and 1980 in white fir (*Abies alba*) in France, while Hemming (1998) found a similar rate of iWUE increase between 1895 and 1994 in beech, oak and pine trees.

All of these observations, including ours, provide substantial support for the conclusions of Feng (1999), specifically, that the long-term trends in iWUE in naturally occurring trees “are largely caused by the anthropogenic increase of the atmospheric CO<sub>2</sub> concentration,” and that this phenomenon “would have caused natural trees in arid environments to grow more rapidly, acting as a carbon sink for anthropogenic CO<sub>2</sub>.” They also suggest that the ongoing rise in the air's CO<sub>2</sub> content could continue to do the same for Earth's trees in the future, subject to limitations of other nutrients (e.g., nitrogen) and ultimate saturation of the carbon-fixing enzyme (Rubisco) when CO<sub>2</sub> concentrations reach 800–1000  $\mu\text{mol mol}^{-1}$  (Körner and Bazzaz, 1996).

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- S.W. Leavitt** has been a Professor at the Laboratory of Tree-Ring Research since 1990, educated at the Universities of Illinois (B.S.), Virginia (M.S.) and Arizona (Ph.D.). His research uses isotopes to extract environmental information from plant matter, and to understand and exploit CO<sub>2</sub> effects on plants and soil organic carbon.
- S.B. Idso**, a Research Physicist with the USDA's Agricultural Research Service since 1967, holds B. Phys., M.S. and Ph.D. degrees from the University of Minnesota. His research interests include the biological and climatic effects of the ongoing rise in the air's CO<sub>2</sub> content and their implications for natural and agro-ecosystems.
- B.A. Kimball** (Ph.D.) is Research Leader for Environmental and Plant Dynamics. He researches effects of increasing atmospheric CO<sub>2</sub> and changing climate variables on crop growth and water-use; free-air CO<sub>2</sub> enrichment (FACE), and CO<sub>2</sub> open-top chambers and greenhouses; micrometeorology and energy balance; plant growth modeling.
- J.M. Burns** is on the Scientific Staff of the Laboratory of Tree-Ring Research, where he has helped date tree rings from around the world. He is responsible for X-ray densitometric analysis of tree rings, and contributes to image analysis and isotope analysis.
- A. Sinha** (Ph.D.) is currently a Lecturer in Earth Science at California State University Dominguez Hills, California. His research and teaching interests include application of stable isotopes to environmental and ecological problems arising from human interaction with the environment and vice versa.
- L. Stott** is a professor in the Dept. of Earth Sciences at University of Southern California. His research interests include stable isotope geochemistry and Cenozoic paleoceanography, paleoclimatology and paleoecology.