EFFECTS OF ATMOSPHERIC CO₂ ENRICHMENT ON REGROWTH OF SOUR ORANGE TREES
(CITRUS AURANTIUM; RUTACEAE) AFTER COPPINGIC

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Sixteen sour orange tree (Citrus aurantium L.) seedlings were grown out-of-doors at Phoenix, Arizona, in eight clear-plastic-wall open-top enclosures maintained at four different atmospheric CO₂ concentrations for a period of 2 years. Over the last year of this period, the trees were coppiced five times. The amount of dry matter harvested at each of these cuttings was a linear function of the atmospheric CO₂ concentration to which the trees were exposed. For a 75% increase in atmospheric CO₂ from 400 to 700 microliter per liter (μL liter⁻¹), total aboveground biomass rose, in the mean, by a factor of 3.19; while for a 400 to 800 μL liter⁻¹ doubling of the air’s CO₂ content, its rose by a factor of 3.92. The relative summer (mean air temperature of 32.8 C) response to CO₂ was about 20% greater than the relative winter (mean air temperature of 16.4 C) response.

Atmospheric CO₂ enrichment significantly enhances the growth of most plants. In a comprehensive review of the literature, Kimball (1983) reported that herbaceous species typically experience a growth stimulation on the order of 30% to 40% for a 300 microliter per liter (μL liter⁻¹) increase in the CO₂ content of the air; and a number of subsequent reviews of this expanding field of study have reached the same conclusion (Cure and Acock, 1986; Mortensen, 1987; Allen, 1990; Lawlor and Mitchell, 1991; Poorter, 1993). In experiments we have conducted on woody species, however, much greater responses have been observed. In sour orange trees, for example, biomass production rose by 175%, both above and below ground, in response to a 300 μL liter⁻¹ increase in the air’s CO₂ content (Idso and Kimball, 1991, 1992), and in Eldarica pine trees we have studied it rose by 275% (Idso and Kimball, unpublished data). In addition, similar growth responses have been suggested by net photosynthesis and dark respiration measurements we have made on three Australian tree species (Idso and Kimball, 1993a).

As the magnitudes of these woody plant responses to atmospheric CO₂ enrichment are so large, we felt it important to provide further support for their reality. Hence, we conducted a second study of sour orange trees in which we destructively harvested the aboveground portions of the trees five different times over the course of a year.

MATERIALS AND METHODS

On 11 March 1991, 16 Citrus aurantium L. seedlings were planted in a field of Avondale loam at Phoenix, Arizona. Shortly thereafter, they were surrounded in pairs by eight clear-plastic-wall open-top enclosures, through which air was introduced and exhausted at a rate of four enclosure-volume exchanges per minute. Two of these enclosures were continuously supplied with ambient air, while two received air targeted for a CO₂ concentration 150 μL liter⁻¹ above ambient, two received air targeted for 300 μL liter⁻¹ above ambient, and two received air targeted for 450 μL liter⁻¹ above current concentrations.

From the start of the experiment, the trees were flood-irrigated every 3 to 6 days to ensure that they were never short of water. After the first summer of growth, however, this frequency was cut back to every 2 to 3 weeks. A common commercial fertilizer was also applied according to specifications of the Maricopa County Agricultural Extension Service. Under these protocols, there were never any visual indications of either water or nutrient stresses throughout the entire period of study.

The differential CO₂ treatments were begun on 18 April 1991. Over the next 11 months, the trees were pruned periodically to keep them from growing out the tops of the CO₂ enrichment chambers; and on 11 March 1992, they were coppiced at approximately 10 cm above the soil surface. Five periods of regrowth and repeated coppicing followed: 11 Mar–27 May (78 days), 27 May–Aug 6 (69 days), Aug 8–Oct 6 (66 days), 8 Oct–Jan 89 (89 days), and 4 Jan–23 Mar 79 (79 days). For each of these regrowth periods we obtained the total dry weight of coppiced plant tissue and plotted the results against the mean CO₂ concentrations of the air to which the trees were exposed.

RESULTS AND DISCUSSION

Figure 1 depicts our results in graphical format, while Table 1 presents the results of linear regression analyses of the data. As can be seen from these presentations, the dry weight of regrowth responded linearly to atmospheric CO₂ enrichment over the entire range of CO₂ concentrations investigated in all five regrowth periods; and the response was large. For a 75% enrichment of the air’s CO₂ concentration from 400 to 700 μL liter⁻¹, the dry weight of regrowth rose by a mean multiplicative factor of 3.19; while for a 400 to 800 μL liter⁻¹ doubling of the air’s CO₂ content, it rose by a factor of 3.92.

These growth enhancement factors are similar to those observed previously in sour orange trees (Idso and

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sponses to atmospheric CO₂ enrichment may be significantly reduced (Masle, Farquhar, and Gilford, 1990; Arp, 1991; Thomas and Strain, 1991).

These several observations all lend credence to the findings of our prior studies and raise the tantalizing possibility that the long-term growth responses of most of earth's trees to atmospheric CO₂ enrichment may be several times greater than those of its herbaceous plants. The recent discovery of a 60% growth enhancement in high-elevation subalpine conifers over the past two centuries (Graybill and Idso, 1993), when the CO₂ content of the air rose from 280 to 360 μL liter⁻¹ (Nefel et al., 1985; Friedli et al., 1986; Keeling and Whorf, 1990), also supports this hypothesis, as this growth enhancement is of the same magnitude as what our sour orange tree response to CO₂ suggests. Hence, it is possible that the CO₂-induced stimulation of earth's "global forest" may be responsible for the bulk of the yearly increase in the amplitude of the air’s annual CO₂ cycle as measured at Mauna Loa, Hawaii over the past three and a half decades—a suggestion that has been made by nearly everyone who has studied this phenomenon (Pearman and Hyson, 1981; Cleveland, Frenny, and Gaedel, 1983; Bacaetow, Keeling, and Whorf, 1985; Keeling et al., 1983; Enting, 1987; Kohlmaier et al., 1989)—for this amplitude increase is also of the same magnitude as what our sour orange tree response to CO₂ suggests (Idso, 1991a, b).

Another aspect of our results that merits mention is the effect of temperature upon the CO₂-induced growth enhancement factor. In Table 1 it can be seen that two of our regrowth periods were very warm, two were rather cool, and one was intermediate. Hence, we combined the two warm results and the two cool results and plotted the three resultant data points against the similarly averaged mean air temperatures for the three periods, obtaining the solid-line linear relationship of Fig. 2. Also shown there is the dashed-line linear relationship derived by Idso and Idso (in press) from dry weight production data for 16 other species as reported in ten previously published CO₂ enrichment studies.

Although the slopes of the two relationships are not significantly different from each other, they clearly have vastly different zero-intercepts, suggestive of more than quantitative differences in plant responses to atmospheric CO₂ enrichment in the winter. For the 16 plants represented by the dashed line, for example, at mean air temperatures of 13 °C or less there would be no growth stimulation provided by atmospheric CO₂ enrichment; while for the sour orange trees there would still be more than

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**Table 1.** Results of linear regression analyses run on the dry weight of regrowth (Y) vs. mean atmospheric CO₂ concentration (X) data obtained for sour orange trees growing in the field within clear-plastic-wall, open-top, CO₂-enrichment enclosures at Phoenix, Arizona.

<table>
<thead>
<tr>
<th>Regrowth period</th>
<th>Mean air temp. (°C)</th>
<th>Equation</th>
<th>r²</th>
<th>Y(700) ( Y(400) )</th>
<th>Y(800) ( Y(400) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>11 Mar-27 May</td>
<td>24.6</td>
<td>Y = 0.442X - 120</td>
<td>0.972</td>
<td>3.33</td>
<td>4.12</td>
</tr>
<tr>
<td>27 May-04 Aug</td>
<td>33.0</td>
<td>Y = 0.356X - 123</td>
<td>0.997</td>
<td>2.86</td>
<td>3.49</td>
</tr>
<tr>
<td>04 Aug-08 Oct</td>
<td>32.6</td>
<td>Y = 0.488X - 146</td>
<td>0.979</td>
<td>3.98</td>
<td>4.96</td>
</tr>
<tr>
<td>08 Oct-04 Jan</td>
<td>17.2</td>
<td>Y = 0.0734X - 14.1</td>
<td>0.989</td>
<td>2.45</td>
<td>2.94</td>
</tr>
<tr>
<td>04 Jan-23 Mar</td>
<td>15.6</td>
<td>Y = 0.0731X - 19.8</td>
<td>0.952</td>
<td>3.31</td>
<td>4.09</td>
</tr>
</tbody>
</table>

Mean growth enhancement ratios: 3.19 3.92
± Standard errors of means: ±0.26 ±0.34
a doubling of growth, if the linear trend established by our three data points were extrapolated to cooler temperatures. Such extrapolation may not be valid, however, for one could easily draw a curve through the three points that would decline to unity at a small positive value of air temperature. It is also possible that the large relative growth enhancement of our sour orange trees in winter might be merely a reflection of the greater root reserves that may be called upon to support regrowth in the CO₂-enriched trees. Consequently, one must remain agnostic on the question of wintertime CO₂ effects on sour orange tree growth based on the regrowth data of this experiment. A scan can be determined from trunk cross-sectional area data obtained from our long-term sour orange tree study (Idso and Kimball, 1993b), however, this is essentially a mpot point; for we typically observe either no net growth or even a slight loss of biomass over winter.

In view of the many potential ramifications of this research, including the possibility that earth's trees may sequester carbon at rates that could slow or possibly even halt the anthropogenic-induced rise in atmospheric CO₂ content (Follett, 1993), it is imperative that additional studies of more and different trees be conducted under a variety of environmental conditions to gain further insight into this intriguing phenomenon. Although much has been learned, it is clear that more experiments will be needed to provide independent confirmation of the large CO₂-induced growth responses of trees that we have encountered in the course of our several CO₂ enrichment studies of sour orange trees grown under the environmental conditions of Phoenix, Arizona in well-fertilized, irrigated field soil.

LITERATURE CITED


Masle, J., G. D. Farquhar, and R. M. Gifford. 1990. Growth and


