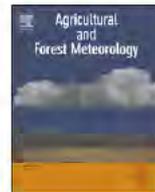




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journal homepage: www.elsevier.com/locate/agrformetSour orange fine root distribution after seventeen years of atmospheric CO₂ enrichmentS.A. Prior^{a,*}, G.B. Runion^a, H.A. Torbert^a, S.B. Idso^b, B.A. Kimball^c^a National Soil Dynamics Laboratory, Agricultural Research Service, U.S. Department of Agriculture, 411 S. Donahue Drive, Auburn, AL 36832, USA^b Center for the Study of Carbon Dioxide and Global Change, P.O. Box 25697, Tempe, AZ 85285, USA^c U.S. Arid-Land Agricultural Research Center, Agricultural Research Service, U.S. Department of Agriculture, 21881 North Cardon Lane, Maricopa, AZ 85238, USA

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ABSTRACT

Long-term (more than 15 years) effects of elevated CO₂ on belowground responses of trees have received limited attention in the literature. We report on a study in which sour orange trees (*Citrus aurantium* L.) grown in an Avondale loam in Phoenix, AZ, were exposed to ambient and elevated (ambient + 300 μmol mol⁻¹) levels of atmospheric CO₂ for 17 years. At study termination, soil cores were collected to determine how long-term CO₂ enrichment affected horizontal (0.5, 1.0, 1.5, and 2.0 m from each tree) and vertical (0–105 cm in 15 cm increments) standing crop fine root dry weight and length. Overall, elevated CO₂ increased both root length (35.6%) and root dry weight (39.1%) densities. There was no effect of CO₂ concentration on horizontal root distribution patterns. However, significant CO₂ by depth interactions were noted for both root length and root dry weight densities with differences occurring only in the top two depths. Elevated CO₂ increased fine root length density by 64.5 and 57.2% at the 0–15 and 15–30 cm depths. Respective increases for root dry weight were 80.3 and 82.8%. These large responses occurred under water and nutrient supplies typical of orchard conditions and suggest that long-term citrus productivity can be enhanced under future levels of atmospheric CO₂.

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1. Introduction

The concentration of CO₂ in the Earth's atmosphere is increasing primarily due to fossil fuel combustion and deforestation and is expected to double pre-industrial levels within this century (Keeling and Whorf, 1994). Most plants increase biomass production under enriched levels of atmospheric CO₂ (Kimball, 1983) due to enhancements in photosynthesis and water use efficiency (e.g. Rogers and Dahlman, 1993; Rogers et al., 1994). However, soil resources can limit CO₂ responses over time (Oren et al., 2001).

Vastly more aboveground investigations have been published than those that examine belowground responses. A review by Rogers et al. (1994) found that, for those that publish belowground data, the most frequently examined root response to elevated CO₂ was dry weight which increased in 87% of studies regardless of species or study conditions. Reported root increases have been concentrated in the upper portions of the soil profile (Del Castillo et al., 1989; Chaudhuri et al., 1990), suggesting a more thorough exploration of a given volume of soil under elevated CO₂. Others have reported enhancements at all soil depths (Chaudhuri et al., 1986; Rogers et al., 1992) implying that the volume of soil explored could

increase. These results suggest that elevated CO₂ will increase plant root growth and density. It should be noted that a majority of early studies were conducted in containerized systems which may not be reflective of conditions found in natural soil profiles (see review by Rogers et al., 1994). If roots become confined, whole plant response (including roots) to CO₂ can be lessened or negated (Arp, 1991; Thomas and Strain, 1991), indicating that work is needed on root system response in natural soil profiles in the field. Further, the majority of reports evaluating root response have dealt with agronomic crop species; however, tree species have been reported to exhibit similar root responses to increased levels of CO₂ (Rogers et al., 1994).

The present study utilized sour orange trees grown in the field under CO₂ enrichment in open top chambers. This exposure system ensured continuous CO₂ treatment within an unrestricted rooting environment. This sour orange study was the longest continuous CO₂ enrichment experiment conducted to date (17 years). Our objective was to determine how long-term CO₂ enrichment affected horizontal and vertical root distribution patterns.

2. Materials and methods

Eight sour orange tree seedlings (*Citrus aurantium* L.) were planted directly into the ground in an Avondale loam [fine, loamy, mixed (calcareous), hyperthermic (alluvial) Typic Torrifluvents]

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in Phoenix, AZ in July, 1987. Sour orange was selected for this study because it is an ornamental tree often used for root stocks in commercial citrus orchards due to its disease and frost resistance. Seedlings were grown in four identically-vented, open-top, clear-plastic-wall chambers which were constructed around pairs of trees (Idso and Kimball, 1991). Initially, the chambers were 5.3 m long \times 2.6 m wide \times 2.0 m high. As the plants grew, the chambers were periodically enlarged until they were 6.3 m long \times 5.1 m wide \times 9.0 m high at termination of the experiment. One-half of the chambers were treated with ambient air and the other half were treated with air enriched to a target CO₂ concentration of 300 $\mu\text{mol mol}^{-1}$ above ambient; the automatic CO₂ sampling/control system associated with this experiment has been previously described (Kimball et al., 1992). Atmospheric CO₂ enrichment was continuous (24 h d⁻¹) from November, 1987 until January, 2005 with the exception of short down periods for chamber enlarging and very infrequent mechanical problems. The trees were fertilized and flood irrigated periodically to simulate commercial orchard practices used to maintain ample nutrients and soil moisture (Idso and Kimball, 2001).

In January, 2005, CO₂ enrichment was halted and a biomass harvest was initiated (Kimball et al., 2007). In February, 2005, soil cores (38 mm dia. \times 105 cm long) were collected for determination of fine root length and dry weight densities. Cores were extracted from each chamber using the methods described by Prior and Rogers (1992) at distances of 0.5, 1.0, 1.5, and 2.0 m from each tree in four radial lines corresponding to cardinal directions for a total of 128 cores. Soil cores were divided into 15 cm segments (0–15, 15–30, 30–45, 45–60, 60–75, 75–90, and 90–105 cm depth increments) and stored at 4 °C until processing. Roots from each segment were separated from soil using a hydropneumatic elutriation system (Gillison's Variety Fabrication, Inc., Benzonia, MI; Smucker et al., 1982) and stored in 20% ethanol (Bohm, 1979) at 4 °C. After organic debris was removed with tweezers and spring-loaded suction pipettes, root length was measured with a Comair Root Length Scanner (Hawker de Havilland, Port Melbourne, Australia). Root weight determinations were made after drying samples at 55 °C to a constant weight.

Data analyses were performed using the mixed models procedure (Proc Mixed) of the Statistical Analysis System (Littell et al., 1996). Data were analyzed using the procedures described in Kimball et al. (2007). Data were totaled for the four soil cores taken at the four cardinal directions around each tree prior to analysis; however, since cores were taken at more than one position (i.e. distance from the tree), position was an additional class that was a subsample within the main CO₂ treatment. Differences were considered significant at the $p \leq 0.05$ level. Values which differed at the $0.05 < p \leq 0.10$ level were considered trends.

3. Results and discussion

Overall (across depths and positions) elevated CO₂ tended to increase both fine root length density ($p=0.068$) and root dry weight density ($p=0.046$) by 35.6 and 39.1%, respectively. The effects of elevated CO₂ on belowground biomass have been understudied compared to those occurring aboveground. Nevertheless, large increases in both root dry weight and root length have been observed. A review by Rogers et al. (1994) showed that root dry weight (the most frequently reported variable) increased in 87% of studies regardless of species or study conditions; although less frequently examined, root length was also often stimulated by high CO₂. The majority of studies included in the above review involved plants growing in containers, generally with adequate resource and without competition. For example, Rogers et al. (1992) found that root dry weight (143%) and root length (110%) increased in young

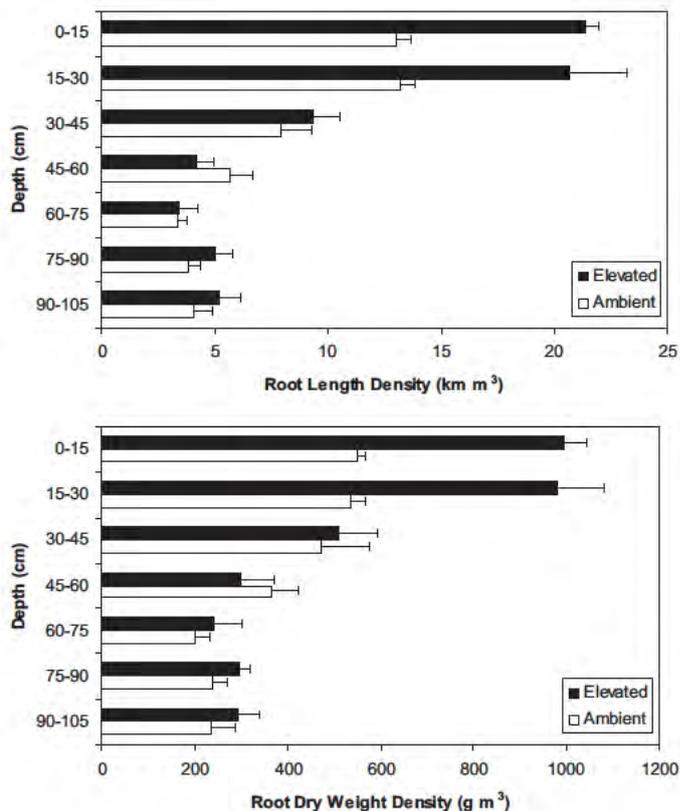


Fig. 1. The effect of CO₂ concentration (ambient and elevated) on sour orange root length density (A) and root dry weight density (B) at seven 15 cm depth increments following 17 years of exposure. Means and standard errors are shown.

soybean (*Glycine max* (L.) Merr.) growing in containers. Prior et al. (1997) found that container-grown longleaf pine (*Pinus palustris* Mill.) exposed to elevated CO₂ for 20 months showed a 58% increase in total root dry weight with adequate soil nitrogen (N), but showed no response when N was limiting. Further, Runion et al. (2006) found a large increase (71.9%) in root dry weight of longleaf pine following three years of CO₂ enrichment after planting in the field. In this same study, sand post oak (*Quercus margaretta* Ashe) showed a non-significant increase of only 11.9%, demonstrating that not all plants will be stimulated by rising CO₂ levels in more natural environments. In general, young plants exhibit greater response to CO₂ than do older plants (Idso and Kimball, 1997). In fact, Idso and Kimball (1991) reported a 175% increase in root biomass for three-year-old sour orange trees; this was a larger stimulatory response to elevated CO₂ than we observed at 17 years. Our results with fine roots were in better agreement with the belowground response of Kimball et al. (2007) who reported a 51.4% increase in belowground biomass and a 26.6% in root length for the large lateral roots which were excavated with the stumps of these 17-year-old sour orange trees. Further, root increases are in general agreement with the overall increase in biomass production (fruit + wood) of 70%, with much of the enhancement coming from greater numbers of fruits rather than changes in fruit size (Kimball et al., 2007).

In this study, a significant CO₂ by depth interaction for fine root length density ($p=0.001$) was observed. Elevated CO₂ increased root length density by 64.5% at the 0–15 cm depth ($p<0.001$) and by 57.2% at the 15–30 cm depth ($p=0.001$; Fig. 1A). There was no effect of CO₂ at any other depth increment. A similar interaction was noted for root dry weight density ($p=0.001$), with weights being greater under elevated CO₂ in the top two depth increments ($p<0.001$) only (Fig. 1B). These respective CO₂-induced increases were 80.3 and 82.8%. At three years, these sour orange

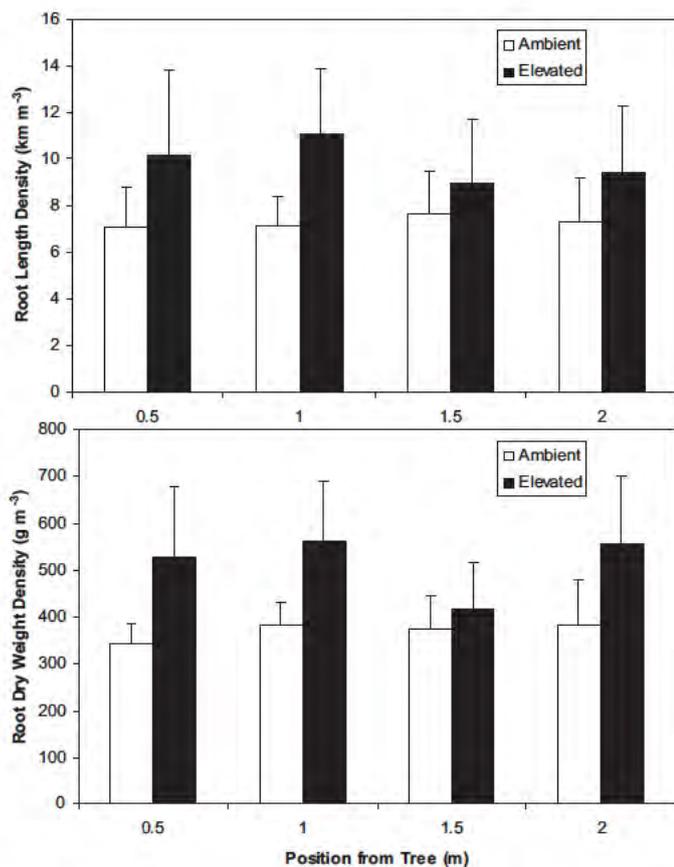


Fig. 2. The effect of CO₂ concentration (ambient and elevated) on sour orange root length density (A) and root dry weight density (B) at four positions (0.5, 1.0, 1.5, and 2.0 m away from the tree) following 17 years of exposure. Means and standard errors are shown.

trees showed a similar response to CO₂ enrichment in that root biomass was increased at 0–40 cm depth, but not at lower depths (Idso and Kimball, 1991). Carbon dioxide enrichment increased root growth in the upper soil profile for both longleaf (Pritchard et al., 2001a) and loblolly pine (*P. taeda* L.; Pritchard et al., 2001b). Prior et al. (1994) reported that increases in cotton (*Gossypium hirsutum* L.) root growth under free-air CO₂ enrichment (FACE) occurred from 0–60 cm. In other FACE systems, researchers have reported increased root growth extending to greater depth (> 15 cm), particularly when CO₂ enrichment continues for several years (Norby et al., 2004; Pritchard et al., 2008). Differences in root pattern dynamics under elevated CO₂ are influenced by plant species, soil type, and growing conditions (Iversen, 2009). For example, while others have found CO₂ responses as deep as 60–80 cm (Norby et al., 2004; Prior et al., 1994; Wechsung et al., 1999), the fact that we observed increased rooting to only 30 cm is likely due to these sour orange trees receiving supplies of nutrients and irrigation reflective of orchard practices, as well as differences in species and soil type.

Distance from the tree (position) did not significantly impact either fine root length ($p=0.916$) or dry weight density ($p=0.495$). Further, the respective CO₂ by position interactions for these measures were also not significant ($p=0.762$ and $p=0.517$). In general, trees under elevated CO₂ had higher root lengths and dry weights than under ambient CO₂ at all positions (Fig. 2). Both measures were essentially equal across distances under ambient CO₂ with high CO₂ values being slightly more variable (Fig. 2). Similar results were noted for these trees at three years of age in that elevated CO₂ increased root biomass density at all horizontal sampling positions (Idso and Kimball, 1991). In contrast, greater root densities were

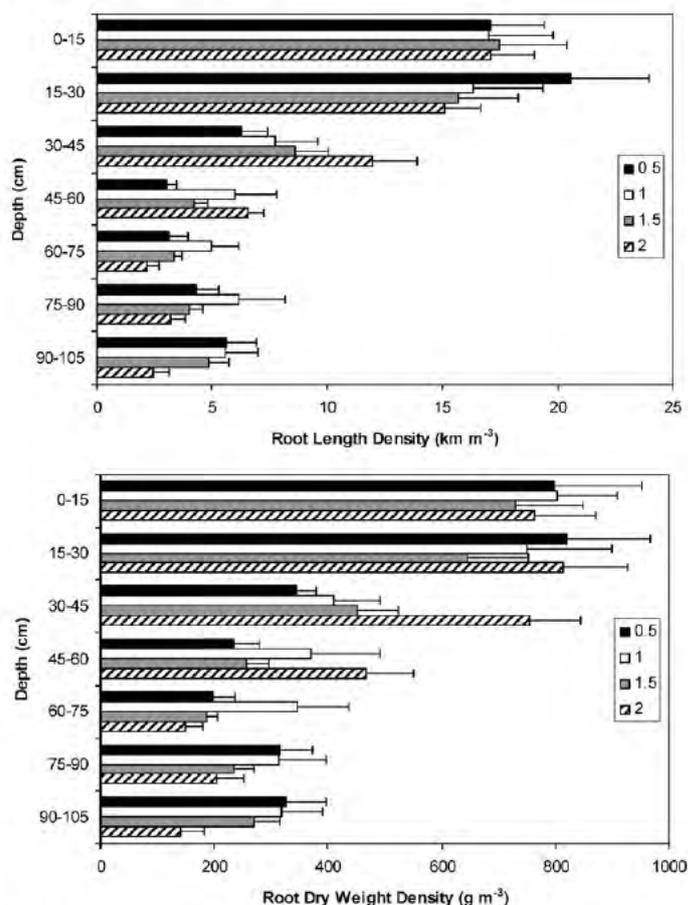


Fig. 3. Sour orange root length density (A) and root dry weight density (B) at the seven 15 cm depth increments and four positions (0.5, 1.0, 1.5, and 2.0 m away from the tree) averaged across both CO₂ treatments. Means and standard errors are shown.

observed away from the plant than at row center in both cotton (Prior et al., 1994) and wheat (*Triticum aestivum* L.; Wechsung et al., 1999) under FACE. Still, it is not surprising that positional effects were not observed in the current study given the age difference between these species.

However, the position by depth interaction was significant for fine root length ($p=0.002$). At the 15–30 cm depth, root length was greater at 0.5 m from the tree than at other distances (Fig. 3A). Conversely, at the 30–45 cm depth, root length was greater at the 2.0 m position. At all other depths there were no positional differences in root length. Root dry weight also showed a significant depth by position interaction ($p=0.001$). At the 2.0 m position, root dry weights at 30–60 cm depth tended to be greater than at other depths. In general, this pattern was reversed at lower depths (60–105 cm) in that root dry weights at the 2.0 m position were lowest (Fig. 3B). Fibrous roots of citrus tend to arise in bunches from the woody laterals (Noling, 2003). The rooting pattern observed here could be related to lateral roots being closer to the surface near the main stem and extending deeper as they grew away from the tree.

The three-way interactions (CO₂ by position by depth) were not significant for either fine root length density ($p=0.235$) or root dry weight density ($p=0.258$). Despite this lack of significance, the complete data sets are shown to illustrate that elevated CO₂ generally increased both root length (Fig. 4) and root dry weight (Fig. 5) only at the top 2 depth increments, regardless of position from tree (as was seen for the CO₂ by depth interactions discussed above).

The issue of CO₂ effects on root growth as related to soil resource (water and nutrients) acquisition is extremely complex (Berntson

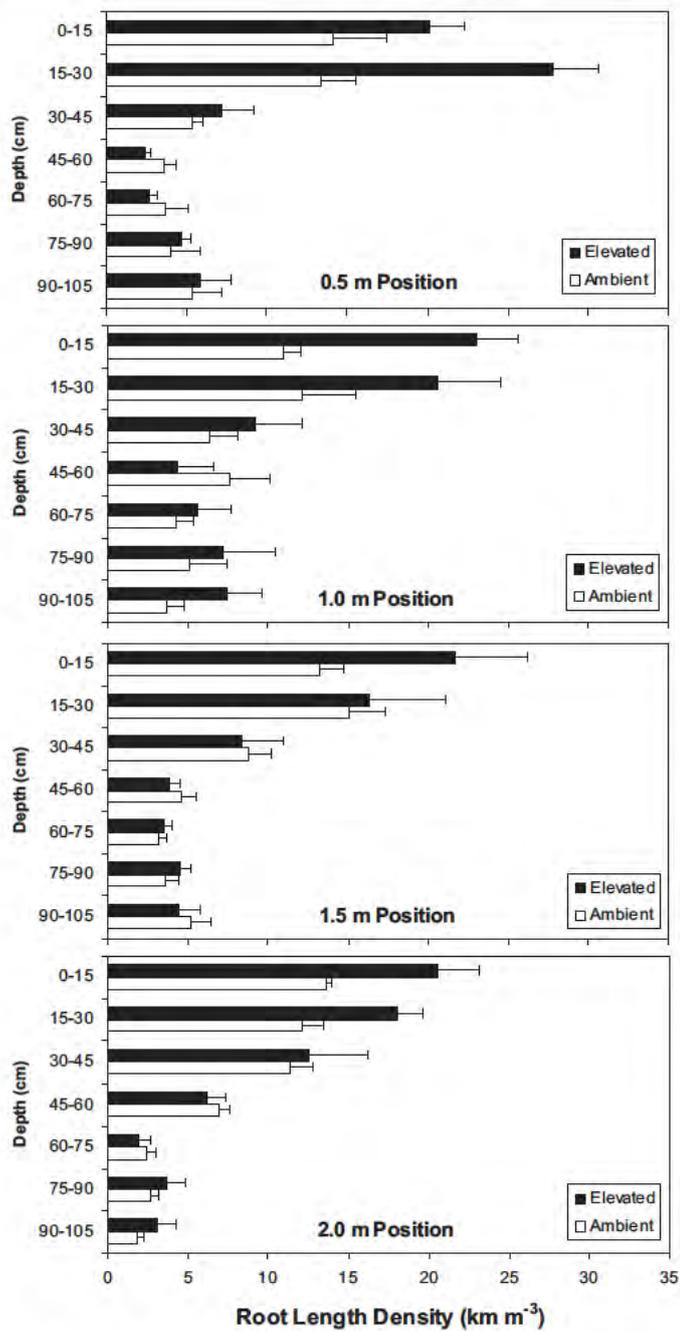


Fig. 4. The effect of CO₂ concentration (ambient and elevated) on sour orange root length density at the seven 15 cm depth increments and four positions (0.5, 1.0, 1.5, and 2.0 m away from the tree) following 17 years of exposure. Means and standard errors are shown.

and Bazzaz, 1996; Prior et al., 1997). In the case of nutrients, there are issues related to both uptake (unit of nutrient per unit of root) and utilization (unit of biomass produced per unit of nutrient) efficiencies. Whole plant nutrient status will be largely governed by root system development through its effects on nutrient extraction from the soil profile. In cotton field studies (Prior et al., 1998), FACE plants had larger root systems that effectively gathered plant nutrients and increased total nutrient uptake. Further, FACE resulted in increased plant growth due to more efficient nutrient utilization. Given that fertilizer application was similar under both ambient and FACE conditions (and all plots received frequent irrigation), elevated CO₂ increased fertilizer use efficiency. In addition, there was no indication of a reduction in nutrient uptake efficiency as

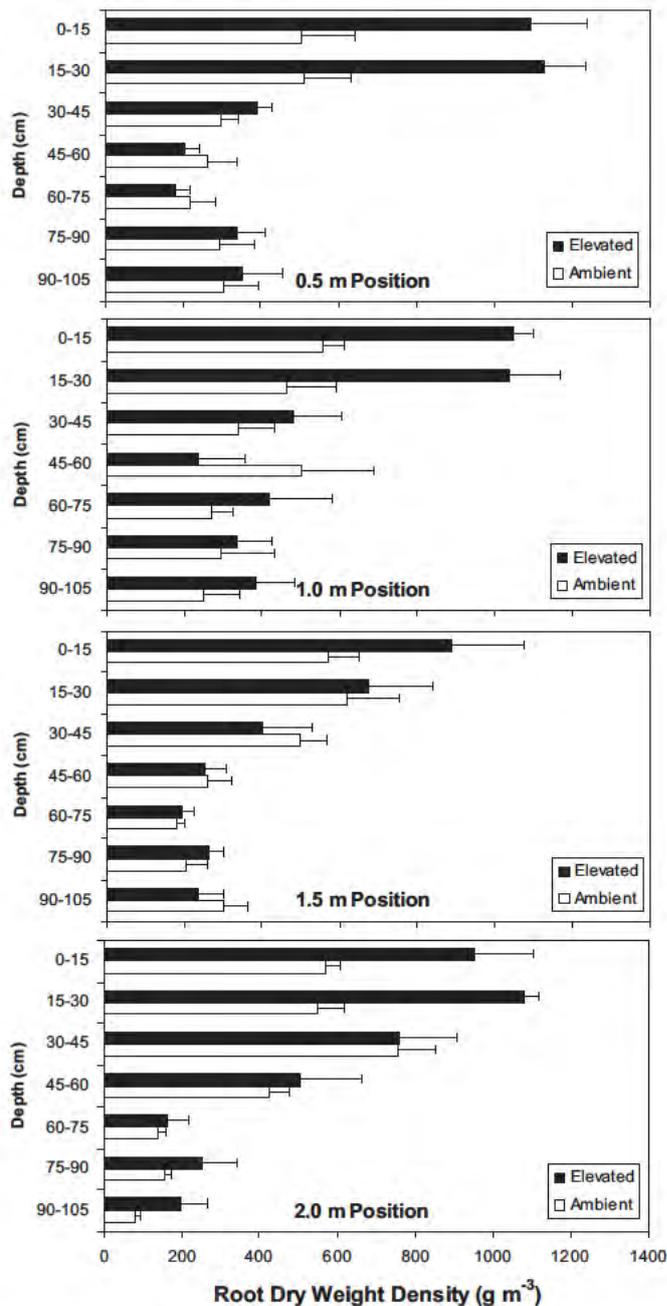


Fig. 5. The effect of CO₂ concentration (ambient and elevated) on sour orange root dry weight density at the seven 15 cm depth increments and four positions (0.5, 1.0, 1.5, and 2.0 m away from the tree) following 17 years of exposure. Means and standard errors are shown.

suggested by the review of Rogers et al. (1994) which largely covered containerized plants. Since these sour orange trees also received fertilization and irrigation, the positive effects of CO₂ on root system proliferation may have influence plant nutrient dynamics in a similar fashion.

Water uptake and utilization can also be effected by elevated CO₂ and its influence on root growth; however, issues of water are further complicated by the effects of CO₂ on transpiration. Elevated CO₂ slows transpiration rate by inducing the partial closure of guard cells that form stomates on leaf surfaces contributing to an increase in water use efficiency (WUE=the ratio of carbon fixed to water transpired; Rogers and Dahlman, 1993). Whole plant water use

can increased under elevated CO₂, despite increased WUE, due to increases in plant size (Runion et al., 1999). However, whole-plant transpiration decreased for both sorghum (*Sorghum bicolor* (L.) Moench) and soybean when grown under high CO₂ (Dugas et al., 1997) despite increased above- and belowground growth for both crops (Prior et al., 2003).

Mycorrhizae, the symbiotic association of plant roots with fungi, benefit their hosts via increased nutrient and water uptake (Bowen, 1973). Soil water and nutrient status, as well as elevated CO₂, can also influence root colonization by mycorrhizal fungi. Runion et al. (1997) suggested that sink/source relationships regulate mycorrhizal development under high CO₂. That is, when photosynthate supply is not source-limited (elevated CO₂) or when tissue N concentrations are low (low soil N), plants alter allocation to soil resource acquisition by investing in roots and mycorrhizas. Conversely, when N supply is not limiting, plants shift allocation above-ground resulting in lower levels of mycorrhizal colonization. Kimball et al. (2007) reported minimal responsiveness of arbuscular mycorrhizal fungi to elevated CO₂ for sour orange trees in this study. Lower rates of mycorrhizal colonization have frequently been observed at high fertility (Marx et al., 1977; Reid et al., 1983); thus, the lack of response of sour orange may be due to being grown with more than adequate nutrition. It is also possible that vesicular-arbuscular mycorrhizae are less responsive to CO₂ enrichment (O'Neill, 1994; Runion et al., 1997). Nonetheless, the observed increase in sour orange root length may have increased total mycorrhizae per tree.

4. Conclusion

Seventeen years of CO₂ enrichment resulted in significant stimulation of both fine root length and dry weight densities (35–40%). This stimulation occurred in the upper 30 cm of the soil profile (root length ~60%; root dry weight ~80%), but was not affected by distance from the tree (up to 2 m). These large root responses, along with the large increases in fruit and wood production noted by Kimball et al. (2007), indicate that long-term citrus productivity can be enhanced as atmospheric CO₂ continues to rise, particularly when trees are grown under conditions of water and nutrient supply typical of orchard conditions. Whether or not sour orange trees can be grown with less water and/or nutrients as atmospheric CO₂ concentration continues to rise will depend upon the complex belowground interactions involving roots and resource acquisition.

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