

Effects of free-air CO₂ enrichment on cotton root growth

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Abstract

The rise in atmospheric CO₂ concentration is predicted to have a positive effect on agroecosystem productivity. However, an area which requires further investigation centers on responses of crop root systems to elevated atmospheric CO₂ under field conditions. The advent of free-air CO₂ enrichment (FACE) technology provides a new method of CO₂ exposure with minimal alteration of plant microclimate. In 1990 and 1991, cotton (*Gossypium hirsutum* (L.) 'Deltapine 77') was grown under two atmospheric CO₂ levels (370 and 550 $\mu\text{mol mol}^{-1}$) and two water regimes (wet (100% of ET replaced) and dry (75% of ET replaced in 1990 and 67% in 1991)). Plant root samples were collected at early vegetative and mid-reproductive growth. Taproots of CO₂-enriched plants displayed greater volume, dry weight, length, and tissue density. Water treatment effects were noted for length, volume and dry weight of roots at the second sampling in 1991. In general, whole soil profile root densities (both length and dry weight densities) and root weight per unit length at the initial sampling were increased under CO₂ enrichment at each of three positions (0.00, 0.25, and 0.50 m) from row center to the middle of the inter-row space. At the second sampling, root length density and root dry weight density were generally unaffected by water stress, whereas root weight per unit length was somewhat higher. In addition, extra CO₂ increased whole profile root length density only at the 0.50 m inter-row position, whereas whole profile root dry weight density and root weight per unit length were generally higher under elevated CO₂ at all three positions. The results from this field experiment strongly indicated that increased atmospheric CO₂ level would enhance plant root growth.

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1. Introduction

Global rises in atmospheric CO₂ concentration may significantly affect plant productivity, as this trace gas is the sole source of carbon utilized in the photosynthetic process of green plants. The well-documented rise in atmospheric CO₂ concentration (Keeling et al., 1989) can be attributed to anthropogenic causes such as accelerated use of fossil fuels (Pearman, 1980), deforestation, burning of wood, and the subsequent decay of soil humic material (Woodwell, 1978). At the turn of the century, the CO₂ level was in the approximate range of 260–290 $\mu\text{mol mol}^{-1}$ (Bolin et al., 1986). By 1958 it had reached 315 $\mu\text{mol mol}^{-1}$, and today it exceeds 350 $\mu\text{mol mol}^{-1}$ (Bacastow et al., 1985). The global concentration is expected to double its present level within the next century (Gribbin, 1981). Regardless of the eventual outcome of the climate change debate (Smit et al., 1988; Idso, 1989; Rosenberg et al., 1990), vegetation in both natural and agro-ecosystems will be directly affected by CO₂ enrichment.

Numerous studies of plant response to increasing atmospheric CO₂ have shown enhancement of water use efficiency (Carlson and Bazzaz, 1980; Dahlman et al., 1985), photosynthesis, biomass production, and yield (Rogers et al., 1983; Sionit et al., 1984; Strain and Cure, 1985; Allen et al., 1987). In-depth reviews of CO₂ effects including their interactions with environmental factors have been published (Krupa and Kickert, 1989; Allen, 1990; Rogers and Dahlman, 1993). Much of the available data base has been collected in controlled environments. The confined rooting volumes often used in such experiments have recently been questioned, and work by Arp (1991), and Thomas and Strain (1991) has suggested that the restriction of roots may obscure the responses that could occur under field conditions. Another new question, that of altered root elongation rates against pot walls, has also arisen (Brown et al., 1991).

In their state-of-the art review, based on 184 research papers, Acock and Allen (1985) concluded that very little is known about crop root response to CO₂ enrichment. Since that review, our knowledge on root response to elevated CO₂ has been somewhat improved. A theoretical framework of the growth and carbon economy of wheat (*Triticum aestivum* L.) seedlings as affected by soil resistance to penetration and CO₂ level has been developed (Masle et al., 1990). A few crop species, including wheat (Chaudhuri et al., 1990), sorghum (*Sorghum bicolor* (L.) Moench., Chaudhuri et al., 1986), and soybean (*Glycine max* (L.) Merr., Del Castillo et al., 1989; Rogers et al., 1992b), have shown clear increases in root dry weight under CO₂-enriched conditions. Chaudhuri et al. (1986) found that root numbers and root dry weights were greater at all soil profile depths for plants grown in CO₂-enriched conditions. Del Castillo et al. (1989) reported that CO₂ enrichment increased the number of actively growing roots rather than elongation rate, suggesting that the affected root systems explored a given volume of soil more thoroughly rather than increasing the volume of soil explored. Plants exposed to elevated CO₂ were also found to attain their maximum rooting depth faster relative to plants grown in ambient conditions (Chaudhuri et al., 1990). In addition, extra CO₂ has not only led to increases in total root length and volume but has also been found to increase root diameter in the root hair zone and length of unbranched first-order laterals (Rogers et al., 1992b). In the studies mentioned above,

experiments were conducted in environmental growth chambers on plants grown in pots (Masle et al., 1990; Rogers et al., 1992b) or in large containers covered by sunlit chambers (Chaudhuri et al., 1986, 1990; Del Castillo et al., 1989).

These data indicate that increases in atmospheric CO₂ will stimulate root proliferation, but it was not known how elevated CO₂ would affect root systems growing in natural soil profiles under field conditions. Therefore, an experiment was initiated to study field-grown cotton under free-air CO₂ enrichment (FACE). In the work reported here, research efforts were focused on responses during two growth phases—early vegetative and mid-reproductive. In addition, the interacting effects of CO₂ and soil water availability on cotton root systems were investigated.

2. Materials and methods

The experimental site was located 25 miles south of Phoenix, AZ, at the Maricopa Agricultural Center for Resources and Extension (MAC) of the University of Arizona at Maricopa. Cotton (*G. hirsutum* (L.), 'Deltapine 77') was grown on a Trix clay loam (fine, loamy, mixed (calcareous), hyperthermic Typic Torrfluvents) under two atmospheric CO₂ concentrations (control: 370 μmol mol⁻¹; FACE: 550 μmol mol⁻¹) and two water regimes (wet and dry).

2.1. Cultural practices

In both 1990 and 1991, the cotton crop and soil were managed according to recommended farming practices for the region. After the experimental area had been chisel plowed, seeds were planted into dry raised beds using a 1 m row spacing. Planting dates were 23 April 1990 (day of year (DOY) 113) and 16 April 1991 (DOY 106). Plants were thinned to 10 m⁻¹. Pre-planting applications of Karmex (Diuron (3-(3,4-dichlorophenyl)-1,1-dimethylurea))) (E.I. Dupont de NE MOURS & Co., Wilmington, DE) and hand weeding were used to control weeds within each study plot. Insect control was by ground and aerial applications of recommended insecticides (Mauney et al., 1994).

2.2. Exposure system

Large-scale test atmospheres of CO₂, with minimal alteration of normal meteorological conditions, were generated using an innovative technique called free-air CO₂ enrichment (FACE). Each exposure unit consisted of 32 individually valved vertical vent pipes (2 m height) evenly spaced around a PVC torus (22 m diameter ring), with the test gas leaving from port holes drilled at vertical intervals along the vent pipes. Collectively, this series of vertical vent pipes attached to the torus is referred to as an array. A computer program based on an algorithm keyed to wind speed and wind direction was utilized to release CO₂ upwind from sectors of vertical standpipes in quantities proportional to wind speed, thus creating uniform atmospheres within each array (Hendrey et al., 1988). There were four replicates of two CO₂ treatments:

four at nominal concentrations of $550 \mu\text{mol mol}^{-1} \text{CO}_2$ (FACE) and four ambient plots at $370 \mu\text{mol mol}^{-1} \text{CO}_2$ (control). Each ambient plot was located within a control array to insure similar surrounding conditions for all study plots. Plots were positioned at least 100 m apart to prevent CO_2 -enriched air blowing into the control plots. Arrays were installed immediately after planting, and daytime CO_2 exposure was initiated after 50% seedling emergence and continued until physiological maturity. One-quarter of each study plot (22 m circular array) was allocated for studying below-ground processes.

2.3. Irrigation

A subsurface drip tube irrigation system, with tubes located about 25 cm beneath each crop row, was used to water the plants during the cropping season. An initial application of irrigation water (i.e. 293 mm in 1990 and 272 mm in 1991) was made immediately after sowing, and differential water treatments were initiated on 3 July in 1990 (DOY 184) and 20 May in 1991 (DOY 140). Main plots were split and each half was irrigated at different specified rates. Water was applied at 2–10 day intervals, depending on plant size and estimated evapotranspiration (ET) rates. The two water regimes were: (1) wet (a target rate of 100% of ET being replaced); (2) dry (75% and 67% of ET replaced in 1990 and 1991, respectively). A description of the methods used to calculate ET as well as a chronological history of soil water content (as monitored by neutron probe) and seasonal precipitation (i.e. between planting and harvest) have been discussed in detail by others (Hunsaker et al., 1994; Mauney et al., 1994). The irrigation system was also used to apply fertilizer N (32% N solution) at a rate of $5.6 \text{ kg N ha}^{-1} \text{ week}^{-1}$, to give a total of $39.2 \text{ kg N ha}^{-1} \text{ year}^{-1}$. In addition, foliar application of micronutrients was carried out during the season as described by Mauney et al. (1994).

2.4. Experimental design

The experimental design was a split-plot with a randomized complete block arrangement of the main-plot factor (two atmospheric concentrations of CO_2 ; control and FACE) for which there were four blocks. The treatment of the second factor (water treatment: wet and dry) was assigned to subplots (each half of the study plot) within each main plot.

2.5. Plant measurements

Cotton response to CO_2 enrichment was assessed at early vegetative growth and at mid-reproductive growth. Sampling dates were 18 June (DOY 168) and 17 September (DOY 260) in 1990, and 12 June (DOY 163) and 2 August (DOY 214) in 1991. Corresponding leaf area index values were approximately 1.0 and 4.0 in 1990, and 0.7 and 3.0 in 1991. Although this research emphasized below-ground responses, related above-ground data were also collected. The following above-ground variables were determined: leaf, stem, reproductive (squares, bolls) and total top dry

weights (oven dried at 55°C); stem height; stem diameter. A total of eight plants per study subplot were collected at the first harvest in 1990 and at both harvests in 1991. Four plants per subplot were collected at the second harvest in 1990.

At each sampling date, below-ground data were collected from excavated taproots and soil cores (90 cm length, 38 mm diameter). Taproots and attached lateral roots were retrieved after loosening with a drain spade. The roots collected were those of the above-ground plants that were harvested for dry matter production. The total length, volume, dry weight (55°C), and density (dry weight per unit length) for the taproot–lateral root system were measured. Soil cores for whole profile root length density, root dry weight density, and root weight per unit length were taken at three positions—crop row center (0.00 m) and the inter-row zone (at 0.25 and 0.5 m from the row center). In 1990, four soil cores were taken at each position within each subplot, to give a total of 192 cores per sampling period. The number of cores per position was increased to eight in 1991, to give a total of 384 cores per sampling period. In 1990, an experimental version of a pneumatic core driver was used to drive cores and a modified automotive car jack was used for core extraction. In 1991, soil cores were collected using the prototype of a pneumatic post driver for driving core tubes and an electric winch-operated tube extractor as described by Prior and Rogers (1992). In both cases, Model 51-505 soil core tubes (Giddings Machine Company, 1985) fitted with reinforced steel collars (at the top) and Model 134 heavy duty quick relief bits were used. The actual soil cores were collected in Model BL 1750 butyrate liners which could be removed from the core tube, and Styrofoam spacers were inserted to keep the cores intact and capped. All samples were immediately transported by truck in a large custom-built refrigerator to Auburn, Alabama, and placed in cold storage until they were processed. Roots were washed from each core using a Gillison's hydropneumatic elutriation system (Smucker et al., 1982; Gillison's Variety Fabrication, Inc., 1990) and held in 20% ethanol (Bohm, 1979) at 4°C until separation of roots from organic debris with tweezers and suction pipets. After measuring root length with a Comair root length scanner (Hawker de Havilland, 1985), dry weight determinations (55°C) were made.

2.6. Data analyses

All analyses were performed using the SAS general linear models procedure (Statistical Analysis Systems Institute Inc., 1985). Significance in plant variables between the two CO₂ treatments was tested using the mean square for the block by CO₂ interaction as the error mean square. If the CO₂ by soil water interaction was significant, contrast statements were used to determine the significance between the CO₂ treatments within each soil water treatment. If the block by CO₂ by soil water interaction was significant ($P < 0.20$), its mean square was used as the error mean square to test the significance of the soil water treatment, the CO₂ by soil water interaction and the contrast statements. If the block by CO₂ by soil water interaction was not significant, it was removed from the analysis and the standard error was used to test significance. Differences were considered significant at the $P < 0.10$ level. Tables include probability values to facilitate discussion.

Table 1

Above-ground growth variables of cotton (per plant basis) during vegetative growth in 1990 (DOY 168) and 1991 (DOY 163) — height, diameter, leaf dry weight, stem dry weight, square dry weight and top dry weight under ambient conditions and CO₂ enrichment (means, standard errors and probabilities are shown)

Variable	CO ₂ Concentration ($\mu\text{mol mol}^{-1}$)		<i>P</i> > <i>F</i> ^a
	370	550	
<i>1990</i>			
Height (cm)	57.6 ± 1.1	68.1 ± 1.3	0.0315
Diameter (mm)	10.0 ± 0.2	11.6 ± 0.2	0.0001
Leaf dry wt. (g)	9.7 ± 0.5	14.3 ± 0.6	0.0276
Stem dry wt. (g)	8.3 ± 0.5	13.8 ± 0.6	0.0001
Square dry wt. (g)	0.3 ± 0.05	0.4 ± 0.05	0.0368
Top dry wt. (g)	18.3 ± 1.0	28.6 ± 1.2	0.0001
<i>1991</i>			
Height (cm)	24.3 ± 0.8	28.9 ± 0.8	0.1460
Diameter (mm)	6.4 ± 0.1	7.4 ± 0.1	0.0078
Leaf dry wt. (g)	3.3 ± 0.1	4.4 ± 1.4	0.0362
Stem dry wt. (g)	2.0 ± 0.1	3.3 ± 0.2	0.0101
Square dry wt. (10 ⁻² g)	1.2 ± 0.3	1.2 ± 0.3	0.8626
Top dry wt. (g)	5.3 ± 0.3	7.6 ± 0.4	0.0177

^aProbability of greater *F* value by chance.

3. Results and discussion

3.1. Vegetative stage

At the early vegetative growth sampling date in 1990, the water stress treatment had been implemented for only about a week and showed no effect on measured variables. Likewise, in 1991, low soil moisture availability had no effect on measured parameters and therefore analyses were performed on data combined over irrigation treatments (Tables 1 and 2, and Fig. 1). It is not clear why the 1991 crop showed no response to water stress, as at time of harvest differential irrigation had been continued for over a month. The lack of difference may have been due to small plant size and soil water deficits being too low to cause a large difference in plant water deficit at this stage of growth (Sionit and Kramer, 1976; Prior et al., 1991).

3.2. Above-ground variables

The increases observed here in many above-ground growth parameters as a result of CO₂ enrichment (Table 1) are in general agreement with results reported elsewhere (Acock and Allen, 1985; Krupa and Kickert, 1989; Rogers and Dahlman, 1993; Mauney et al., 1994). In both years, stem diameter, leaf dry weight, stem dry weight, and top dry weight were greater under CO₂-enriched conditions (*P* < 0.10). Plant height was significantly higher in 1990, and showed a strong tendency to increase in the elevated CO₂ treatment in 1991 (*P* = 0.15). Increases in square dry

Table 2

Taproot variables of cotton during vegetative growth in 1990 (DOY 168) and 1991 (DOY 163) — total length, dry weight, volume and density under ambient conditions and CO₂ enrichment (means, standard errors and probabilities are shown)

Variable	CO ₂ Concentration ($\mu\text{mol mol}^{-1}$)		<i>P</i> > <i>F</i> ^a
	370	550	
<i>1990</i>			
Length (cm)	251.6 ± 14.8	299.6 ± 12.1	0.0011
Volume (cm ³)	10.9 ± 0.6	16.0 ± 0.6	0.0001
Dry wt. (g)	1.7 ± 0.1	2.9 ± 0.1	0.0223
Density (10 ⁻³ g cm ⁻¹)	7.4 ± 0.6	9.7 ± 0.3	0.2086
<i>1991</i>			
Length (cm)	93.9 ± 4.3	124.2 ± 5.3	0.0041
Volume (cm ³)	3.1 ± 0.2	4.4 ± 0.2	0.0038
Dry wt. (g)	0.4 ± 0.02	0.7 ± 0.04	0.0079
Density (10 ⁻³ g cm ⁻¹)	4.9 ± 0.2	6.0 ± 0.3	0.0667

^aProbability of greater *F* value by chance.

weight were observed in 1990, but not in 1991. This lack of response may be attributable to less irrigation water being applied between planting and sampling than in 1990 and some year-to-year weather differences, which delayed plant development. Changes in irrigation amounts were related to the use of different methods of estimating evapotranspiration in the two years (for details, see Mauney et al., 1994). In addition, there was some indication of lower night-time temperatures in 1991, which may have contributed to slower crop establishment and subsequent growth which could have resulted in smaller plants. Not only were square weight values smaller, but lower values were also observed for many of the variables measured in 1991.

3.3. Taproot variables

Taproot measurements at early vegetative growth are shown in Table 2. Elevated CO₂ significantly increased total taproot length, volume, and dry weight (by 19%, 47%, and 71%, respectively, in 1990; by 32%, 42%, and 75%, respectively, in 1991). Rogers et al. (1992b) reported that soybean exposed to elevated CO₂ under controlled environmental conditions for 18 days exhibited increases of 110%, 80%, and 143% for total root length, volume, and dry weight, respectively. Additional CO₂ tended to increase taproot density in 1990 (*P* = 0.209) and increased this measurement by 22% in 1991.

3.4. Fine root variables

Core samples collected at right angles to rows allowed for characterization of horizontal distribution patterns of roots across rows in terms of whole profile root

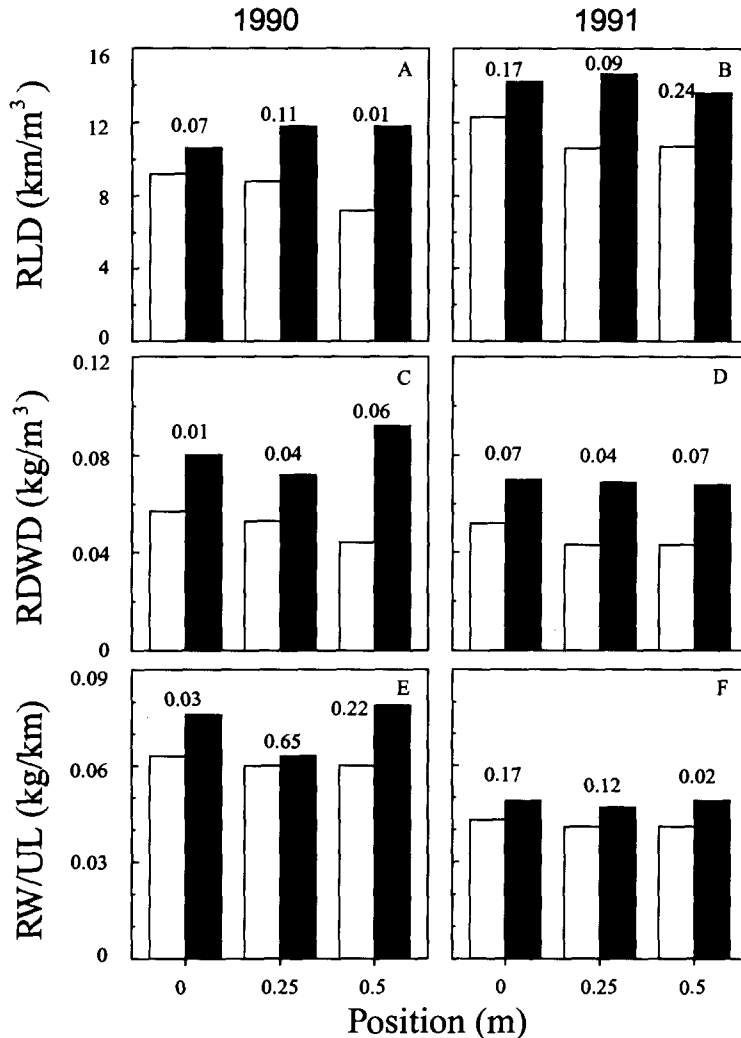


Fig. 1. The effect of CO₂ concentration (\square , 370 $\mu\text{mol mol}^{-1}$; \blacksquare , 550 $\mu\text{mol mol}^{-1}$) on root length density (RLD; A and B), root dry weight density (RDWD; C and D), and root weight per unit length (RW/UL; E and F) at various positions (0 m, 0.25 m, and 0.50 m) away from the crop row during vegetative growth in 1990 (A, C, and E) and 1991 (B, D, and F). Bar height indicates mean parameter estimate; numbers refer to the probability of obtaining a larger *F* value by chance.

length density, root dry weight density, and root weight per unit length at three positions (0.00, 0.25, and 0.50 m) from the row center to the middle of the inter-row space (Fig. 1). In 1990, the high CO₂ increased root length density by 15% and 64% at the 0.00 m and 0.50 m positions, respectively (Fig. 1A). In comparison, the 0.25 m position in 1991 was the only position showing a significant difference (38%; Fig. 1B). However, strong trends were observed at the 0.25 m position in 1990 ($P = 0.11$) and at two positions (0.00 m and 0.50 m) in 1991 ($P = 0.17$ and

$P = 0.24$, respectively). Root dry weight density values during vegetative growth were significantly greater under CO₂ enrichment in both years (Figs. 1C and 1D). In 1990, elevated CO₂ enhanced root dry weight density at the 0.00, 0.25, and 0.50 m positions by 40%, 36%, and 109%, respectively, and similar measurements taken in 1991 were increased by 35%, 60%, and 58%, respectively. Rogers et al. (1992b) reported that CO₂ enrichment increased young soybean root dry weight (percentage basis) more than root length. In our experiment, as in theirs, CO₂ enrichment consistently increased root dry weight density more than root length density at each horizontal position. More importantly, increases in whole profile root density (i.e. length or dry weight per unit volume of soil) observed under high-CO₂ conditions during vegetative growth, caused by either actual increases in rooting density of individual plants or overlap of roots from adjacent rows or neighboring plants in the same row, may insure a more thorough exploration of soil volume and, therefore, enhanced sorption of available nutrients and water during plant establishment. Del Castillo et al. (1989) reported that elevated CO₂ increased root branching rather than root elongation rate, thus implying a more thorough exploration of a given volume of soil without an increase in the volume explored. In contrast, Rogers et al. (1992b) suggested that the volume of soil explored would be increased, as CO₂ enrichment resulted in a 110% increase in root length with no change in branching. Nevertheless, both studies suggest increased rooting, as does ours.

Large shifts in root dry weight density owing to CO₂ enrichment also suggest possible changes in root quality. Tissue density can be inferred from calculations of root weight per unit root length (Figs. 1E and 1F) and likewise point to quality changes. In 1990, the 0.00 m position (row center) exhibited an increase of 21%, whereas the next position (0.25 m) showed no difference and the 0.50 m location (mid-inter-row) tended to be higher under CO₂ enrichment ($P = 0.22$). Results from the second year showed strong trends toward increasing tissue density at the first two positions ($P = 0.17$ and $P = 0.12$, respectively), and the increase was greater (20%) at the last position. One possible explanation of these changes could have been the presence of large lateral root segments in the samples. However, inspections of individual samples indicated that this possibility was unlikely. Therefore, it appears plausible that changes in root quality may be brought about by additional atmospheric CO₂. Tissue density alterations as reported here for fine roots, as well as for taproots (see Table 4 below), could be the result of shifts in carbohydrate storage, cell number, cell size, and percentage of intercellular space or other structural modifications. Growth chamber studies conducted by Rogers et al. (1992b) showed that soybean plants grown under CO₂ enrichment exhibited a 27% increase in root diameter in the root hair zone. Detailed examination showed increases in stele diameter (23%) and cortex width (28%). Very few studies have addressed CO₂-induced changes in root structure, and further research is needed, especially for field environments.

3.5. Reproductive stage

Above-ground variables

Table 3 shows the effects of CO₂ enrichment and water stress on above-ground

Table 3

Above-ground growth variables of cotton during reproductive growth in 1990 (DOY 260) and 1991 (DOY 214) — height, diameter, leaf dry weight, stem dry weight, boll dry weight and top dry weight under ambient and CO₂-enriched conditions and two water regimes (means, standard errors and probabilities are shown)

Variable	CO ₂ Concentration ($\mu\text{mol mol}^{-1}$)		<i>P</i> > <i>F</i> ^a	Soil water content		<i>P</i> > <i>F</i> ^a
	370	550		Wet	Dry	
<i>1990</i>						
Height (cm)	158.9 ± 7.9	160.9 ± 8.7	0.8169	174.4 ± 7.0	145.1 ± 5.3	0.0056
Diameter (mm)	13.6 ± 0.4	15.1 ± 0.4	0.0749	15.0 ± 0.3	13.7 ± 0.5	0.0386
Leaf dry wt. (g)	28.0 ± 2.4	31.4 ± 1.9	0.4270	32.4 ± 1.5	27.0 ± 2.4	0.1097
Stem dry wt. (g)	68.2 ± 5.6	85.3 ± 7.9	0.1444	83.2 ± 6.6	66.9 ± 7.8	0.0424
Boll dry wt. (g)	66.6 ± 6.5	110.1 ± 7.7	0.0226	80.1 ± 10.6	96.6 ± 10.3	0.0475
Top dry wt. (g)	159.4 ± 10.0	226.8 ± 12.5	0.0509	195.7 ± 16.3	190.5 ± 17.7	0.7068
<i>1991</i>						
Height (cm)	97.7 ± 2.1	101.4 ± 2.4	0.4051	113.0 ± 1.8	86.1 ± 1.3	0.0001
Diameter (mm)	11.8 ± 0.2	13.2 ± 0.3	0.0320	13.1 ± 0.2	11.8 ± 0.3	0.0001
Leaf dry wt. (g)	24.5 ± 1.2	26.9 ± 1.2	0.2886	28.7 ± 1.3	22.7 ± 1.0	0.0002
Stem dry wt. (g)	32.6 ± 2.0	45.8 ± 2.4	0.0472	46.6 ± 2.5	31.8 ± 1.7	0.0001
Boll dry wt. (g)	29.8 ± 1.6	42.8 ± 2.2	0.0015	37.0 ± 2.2	35.6 ± 2.0	0.7681
Top dry wt. (g)	86.9 ± 4.4	115.5 ± 5.1	0.0225	112.3 ± 5.3	90.2 ± 4.4	0.0005

^aProbability of greater *F* by chance.

measurements during reproductive growth. As reported elsewhere for cotton (Rogers et al., 1992a; Mauney et al., 1994), elevated aerial CO₂ concentration stimulated many above-ground variables at this stage. Statistically significant enhancement owing to CO₂ enrichment was observed for stem diameter, boll dry weight, and top dry weight in both years. Elevated CO₂ tended to increase stem dry weight in 1990, and significantly increased this measure by 40% in 1991. Plant height and leaf dry weight were not influenced by the level of CO₂ in either year.

Despite differing atmospheric CO₂ regimes, above-ground plant response to water stress was similar in both years, as the CO₂ by water treatment interaction was nonsignificant. This was also noted for below-ground responses (Table 4; Figs. 2 and 3). In contrast, numerous investigators have reported that water stress is ameliorated by elevated concentrations of CO₂ (Gifford, 1979; Sionit et al., 1980, 1981; Rogers et al., 1984; Prior et al., 1991). For example, several studies have shown that although water stress greatly reduces plant growth, the relative increases in total dry weight and yield of water-stressed plants in response to CO₂ enrichment were as great as those for well-watered plants (Gifford, 1979; Sionit et al., 1980, 1981). Furthermore, these workers reported that plants grown under high-CO₂ and water-stressed conditions had a yield and total dry matter production greater than those grown under low-CO₂ and well-watered conditions. In the present study, water stress reduced plant height, stem diameter, stem dry weight, and top dry weight; these effects were more notable in 1991. Unlike 1991, the applied water stress had no effect on top

Table 4

Taproot variables of cotton during reproductive growth in 1990 (DOY 260) and 1991 (DOY 214) — total length, dry weight, volume and density under ambient and CO₂-enriched conditions and two water regimes (means, standard errors and probabilities are shown)

Variable	CO ₂ Concentration ($\mu\text{mol mol}^{-1}$)		$P > F^a$	Soil water content		$P > F^a$
	370	550		Wet	Dry	
<i>1990</i>						
Length (cm)	507.8 ± 28.0	615.1 ± 30.1	0.1830	583.9 ± 31.0	539.5 ± 28.3	0.3869
Volume (cm ³)	29.0 ± 1.0	36.4 ± 1.3	0.0123	34.5 ± 1.3	30.9 ± 1.2	0.1525
Dry weight (g)	9.0 ± 0.3	12.4 ± 0.5	0.0398	10.9 ± 0.4	10.5 ± 0.5	0.5875
Density (10^{-2} g cm ⁻¹)	2.0 ± 0.1	2.2 ± 0.1	0.0862	2.1 ± 0.1	2.1 ± 0.1	0.8039
<i>1991</i>						
Length (cm)	274.9 ± 10.7	323.4 ± 11.2	0.0278	331.7 ± 11.2	266.5 ± 10.0	0.0207
Volume (cm ³)	19.6 ± 0.9	26.7 ± 1.4	0.0254	26.2 ± 1.3	20.1 ± 1.0	0.0001
Dry weight (g)	5.3 ± 0.3	8.5 ± 0.4	0.0026	7.5 ± 0.4	6.3 ± 0.4	0.0103
Density (10^{-2} g cm ⁻¹)	2.0 ± 0.1	2.7 ± 0.1	0.0038	2.3 ± 0.1	2.4 ± 0.1	0.5637

^aProbability of greater F by chance.

dry weight during 1990. These differences were probably related to the different water regimes used in each year. In 1990, the crop was probably under less stress (i.e. 75% of ET replaced) compared with the following year, when less irrigation water was applied (i.e. 67% of ET replaced).

Taproot variables

Total taproot length, dry weight, volume, and tissue density, as affected by water regime and CO₂ concentration during the reproductive phase, are shown in Table 4. No significant water stress by CO₂ interaction was noted, indicating that plants in both water regimes responded similarly to extra CO₂. In contrast to the data for 1991, the water stress treatment did not reduce taproot length or dry weight during 1990. However, water stress tended to decrease taproot volume in 1990 and significantly reduced it in 1991. In both years, taproot tissue density was unaffected by the water stress treatment. Data from the first year showed that total taproot volume and dry weight were increased by 26% and 38%, respectively, at the high CO₂ level. Taproot length showed a strong tendency toward increase ($P = 0.18$). Taproot length, volume, and dry weight were increased under CO₂ enrichment by 18%, 36%, and 60%, respectively, in 1991. Rogers et al. (1992a) observed similar changes for taproot parameters of cotton grown under CO₂ enrichment and well-watered conditions. Taproot tissue density was increased by 14% in 1990 and by 35% in 1991 at the 550 $\mu\text{mol mol}^{-1}$ treatment level vs. 370 $\mu\text{mol mol}^{-1}$ in the present study.

Fine root variables

Root measurements across the row, as affected by CO₂ enrichment and water regime during reproductive phase, are shown in Figs. 2 and 3. The response of fine

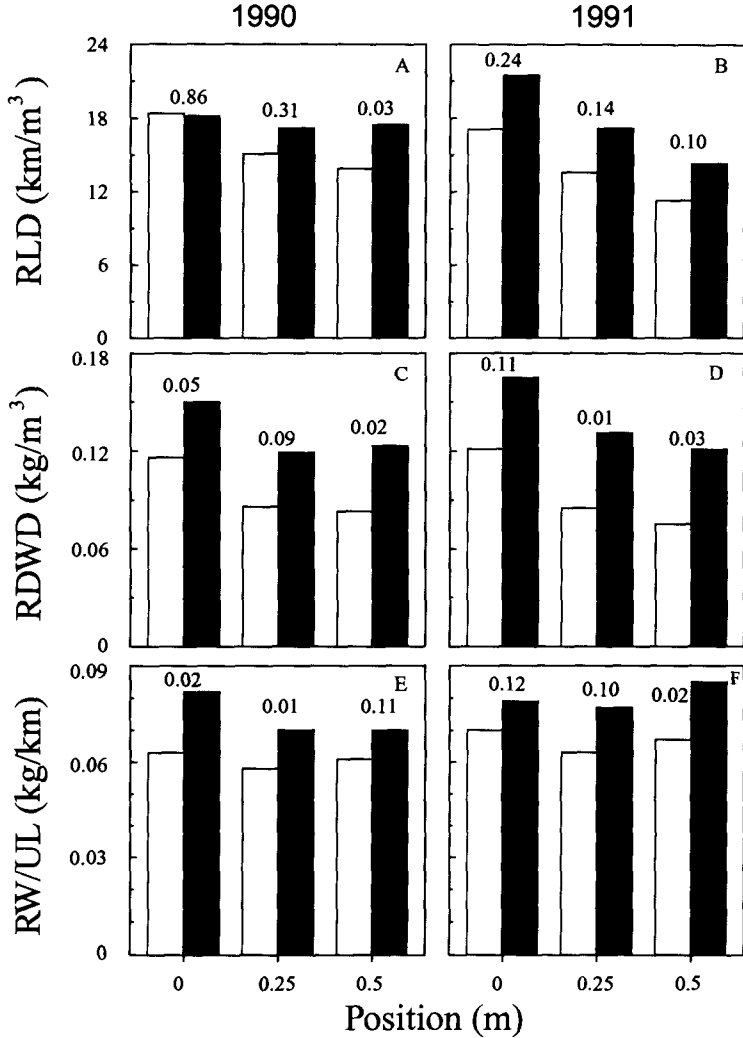


Fig. 2. The effect of CO_2 concentration (\square , $370 \mu\text{mol mol}^{-1}$; \blacksquare , $550 \mu\text{mol mol}^{-1}$) on root length density (RLD; A and B), root dry weight density (RDWD; C and D), and root weight per unit length (RW/UL; E and F) at various positions (0 m, 0.25 m, and 0.5 m) away from the crop row during reproductive growth in 1990 (A, C, and E) and 1991 (B, D, and F). Bar height indicates mean parameter estimate; numbers refer to the probability of obtaining a larger F value by chance.

roots in both water regimes to extra CO_2 was similar to those of the above-ground variables and taproots. Water stress tended to decrease whole profile root length density only at the 0.00 m position in both years ($P = 0.10$ and $P = 0.12$; Figs. 3A and 3B). Root dry weight density was unaffected by water stress except at the 0.50 m position in 1991, where it tended to be lower ($P = 0.11$; Fig. 3D). However, at most positions, root weight per unit length showed either significant increase, or trends of increase under water stress conditions ($P = 0.002$ – 0.20 ; Figs. 3E and 3F). Chaudhuri

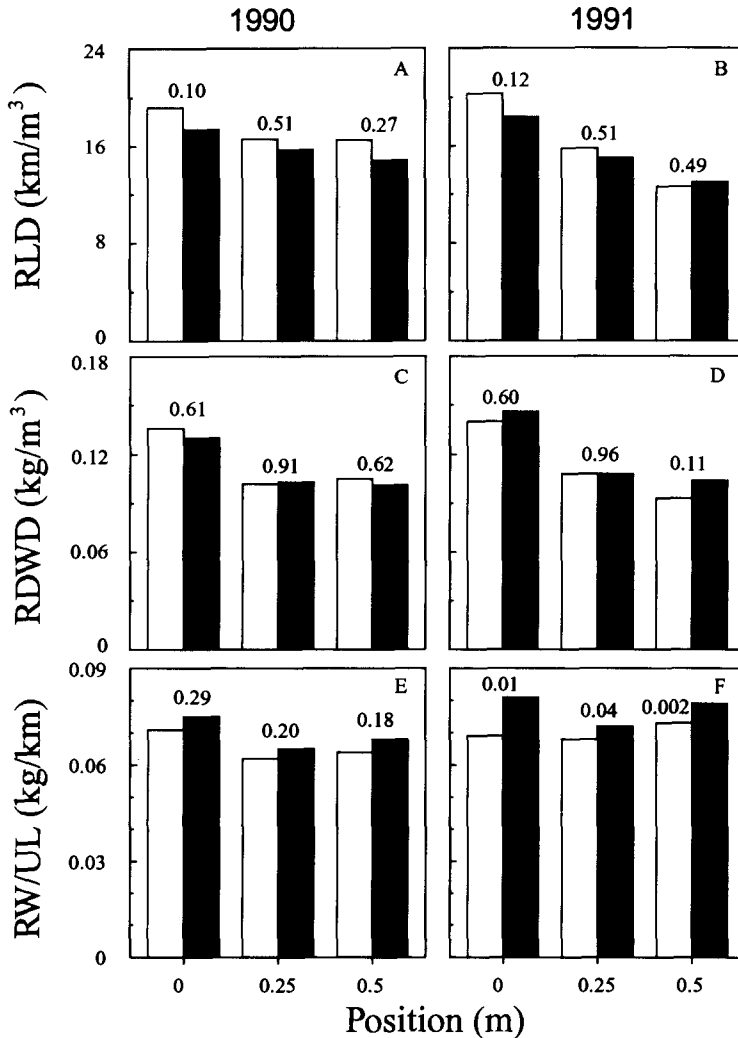


Fig. 3. The effect of soil water regime (\square , wet; \blacksquare , dry) on root density (RLD; A and B), root dry weight density (RDWD; C and D) and root weight per unit length (RW/UL; E and F) at various positions (0 m, 0.25 m, and 0.50 m) away from the crop row during reproductive growth in 1990 (A, C, and E) and 1991 (B, D, and F). Bar height indicates mean parameter estimate; numbers refer to the probability of obtaining a larger F value by chance.

et al. (1990) reported a significant CO_2 by water stress interaction for wheat root response, indicating that high CO_2 could compensate for the reduction in root growth caused by water stress. These investigators found that roots of water-stressed plants grown under high CO_2 had a greater dry weight relative to roots from well-watered plants grown under ambient conditions. The absence of a water stress compensation effect by CO_2 in our study may be due to the spatial soil variability that roots normally encounter in various horizons of natural soil profiles. In contrast, the

study of Chaudhuri et al. (1990) used plants grown in a rhizotron which contained sieved topsoil and no subsoil. Another explanation could be that wheat and cotton respond very differently to the interacting effects of CO₂ and water treatment. Research to examine how wheat responds to the interacting effects of FACE and water treatment is currently under way.

Although elevated CO₂ did not significantly affect whole profile root length density at the 0.00 m and 0.25 m positions in 1990 (Fig. 2A), extra CO₂ did tend to increase these parameters in 1991 ($P = 0.24$ and $P = 0.14$; Fig. 2B). At the 0.50 m position, root length densities at the 550 $\mu\text{mol mol}^{-1}$ treatment level were 26% and 27% higher than at the 370 $\mu\text{mol mol}^{-1}$ level in 1990 and 1991, respectively. Rogers et al. (1992a) found that 6 weeks of FACE tended to enhance whole profile root length density at the center row position. They also reported that this same measure for the following season was increased by 18% after 14 weeks of FACE. Nearly all corresponding root dry weight density values were significantly increased under CO₂-enriched conditions (Figs. 2C and 2D). In 1990, root dry weight density was increased by 29%, 38%, and 48% at the 0.00 m, 0.25 m, and 0.50 m positions, respectively. In 1991, this same measure at the first position showed a strong tendency toward increase ($P = 0.11$). Enhancements of 54% and 50% were noted at the 0.25 m and 0.50 m positions, respectively. These observations resemble previously reported values (at the center row position) for well-watered FACE cotton (Rogers et al., 1992a).

Increases in whole profile root density (i.e. length or dry weight per unit volume of soil) as reported here suggest that extra CO₂ may facilitate exploitation of available soil nutrients, especially in the variable soil environments so often encountered in the field. CO₂-induced shifts in rooting may affect crop production, as the use of simulation models and sensitivity analysis has shown that total root density influences nutrient uptake in numerous soils more than any other root property (Barber, 1984). This has been found to be especially true for uptake of immobile nutrients such as phosphorus (Nye and Tinker, 1977). It also has been demonstrated that root proliferation occurs in nutrient-rich zones or patches (Anghinoni and Barber, 1980; Barber, 1984; Jackson and Caldwell, 1989), which are often found under field conditions. More specifically, extra root proliferation means that water and/or nutrient requirements may be more effectively met during periods of critical demand, such as reproductive development. In the present study, increases in boll dry weight and top dry weight were significant under CO₂-enriched conditions regardless of water treatment (Table 3). Similarly, others have reported increases in boll and biomass production rates throughout reproductive growth under FACE (Mauney et al., 1994).

The influence of CO₂ enrichment on root quality (root weight per unit length) is also shown in Figs. 2E and 2F. In 1990, increases of 30% and 21% were observed at the 0.00 m and 0.25 m positions, respectively. At the 0.50 m position, a strong trend of increase was observed ($P = 0.11$). In 1991, root weight per unit length at all three positions tended to be higher at the 550 $\mu\text{mol mol}^{-1}$ treatment level ($P = 0.02$ – 0.12). Shifts in tissue density under CO₂-enriched conditions may be related to internal structural modifications, such as those demonstrated by Rogers et al. (1992a) in soybean. Tissue density changes relate not only to possible changes in root function in high-CO₂ environments, but may also lead to changes in other below-ground

activities (e.g. rhizosphere and soil processes). Altered microbial activity observed in FACE soils (Rogers et al., 1992a; Runion et al., 1994) may be related to CO₂-induced changes in the composition and amount of root-derived carbon products used by soil microbes, as suggested by Van Veen et al. (1991). Results from the present study suggest that added CO₂ not only affects carbon inputs to the soil (i.e. increased root mass), but also the quality or composition of root tissue, as changes in root tissue density were detected. Such changes have implications for carbon cycling and storage in terrestrial ecosystems. Both short-term CO₂ enrichment studies (Lekkerkerk et al., 1990) and evaluations of soils after 3 years of FACE (Leavitt et al., 1994) suggest possible increases in carbon storage under well-watered conditions. However, responses are less clear under water-deficit conditions, which are commonly found in real field conditions (Wood et al., 1994). The collective action of more rooting in conjunction with possible alterations in microbial activity and carbon cycling in a high-CO₂ world may induce physicochemical changes which could change soil physical properties (such as aggregation and porosity). As biological and physical processes are both complex and dynamic, future studies need to consider short-term (i.e. periodic sampling over the season) and long-term sampling (i.e. sampling over many years) to determine the effect of elevated CO₂ on below-ground processes.

4. Summary

A study was made of root response to elevated atmospheric CO₂ in plants growing in natural soil profiles under field conditions. Development of fine roots and taproots was altered. For example, increases in root tissue density caused by CO₂ enrichment, as seen in both taproot and fine root data at vegetative and reproductive phases, indicate shifts in root tissue structure and/or quality.

Increased CO₂ affected whole profile root density (i.e. length or dry weight per unit volume of soil) at various horizontal positions relative to control conditions. This suggests increased root proliferation as a result of CO₂ enrichment. From an environmental point of view, increased rooting caused by elevated CO₂ might enhance nitrogen recovery, thus minimizing contamination of ground water by nitrogen leached from the vadose zone. Changes in rooting also raise the possibility of shifts in weed–crop competition in agro-ecosystems. Furthermore, this may have important implications for natural ecosystems where limitations in nutrients and water can be extreme.

The interactive effects of CO₂ and soil water availability on cotton root systems under realistic field conditions were examined. The amount of water stress imposed on the crop during vegetative growth was not great enough to affect measured root variables. During reproductive growth, root response to water stress was similar under ambient and CO₂-enriched conditions, as no significant water treatment by CO₂ interaction was noted (Table 4 and Fig. 3). Although the spatial soil variability of natural soil profiles may render it difficult to detect interactions, another contributing factor could be that the stress level used (i.e. 75% or 67% of ET) in this

study did not produce a sufficient degree of water stress. Clearly, more fieldwork is required before reliable predictions can be made on the interactive effects of CO₂ and soil water deficits on crop root response.

This study has shown that elevated atmospheric CO₂ concentrations may significantly increase the growth of the cotton root system in the field. Because roots are the plant's interface to the soil, factors which affect them are important to agricultural production and to the function of natural communities. This observed increase in rooting may allow more edaphic resources to be taken up, thus leading to a more efficient utilization of rising global CO₂.

Additional research with various economically important species is needed. Response of root systems to CO₂ enrichment and its implications for agro-ecosystem productivity merit further study. Functional aspects of root growth need to be explored in this context.

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