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Free-air CO_2 enrichment of cotton: vertical and lateral root distribution patterns

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Abstract

The objective of this investigation was to determine how free-air carbon dioxide enrichment (FACE) of cotton (*Gossypium hirsutum* L.) affects root distribution in a natural soil environment. For two years cotton was grown on a Trix clay loam under two atmospheric CO_2 concentrations (370 and 550 μmol mol^{-1}) and two water treatments [wet, 100% of evapotranspiration (ET) replaced and dry, 75% (1990) and 67% (1991) of ET replaced] at Maricopa, AZ. At early vegetative and mid-reproductive growth, 90 cm soil cores were taken at 0, 0.25, and 0.5 m perpendicular to row center; root variables were ascertained at three 30 cm depth increments. The effect of water stress alone or its interaction with CO_2 on measured variables during both samplings were rare and showed no consistent pattern. There was a significant CO_2 × position interaction for root length density at the vegetative stage (both years) and reproductive stage (1990 only); the positive effects of extra CO_2 were more evident at interrow positions (0.25 and 0.5 m). A CO_2 × depth × position interaction at the vegetative phase (1990) indicated that FACE increased root dry weight densities for the top soil depth increment at all positions and at the middle increment at the 0.5 m position. Similar trends were seen at the reproductive sampling for this measure as well as for root length density at both sample dates in 1990. In 1991, a CO_2 × depth interaction was noted at both periods; CO_2 enhancement of root densities (i.e., both length and dry weight) were observed within the upper and middle depths. Although variable in response, increases for root lineal density under high CO_2 were also seen. In general, results also revealed that the ambient CO_2 treatment had a higher proportion of its root system growing closer to the row center, both on a root length and dry wight basis. On the other hand, the FACE treatment had proportionately more of its roots allocated away from row center (root length basis only). Results from this field experiment clearly suggest that increased atmospheric CO_2 concentration will alter root distribution patterns in cotton.

Introduction

Increased atmospheric CO_2 concentration (Keeling et al., 1989) arising from anthropogenic sources (e.g., fossil fuel use, deforestation; Pearman, 1980; Woodwell, 1978) are predicted to double in the next century (Gribbon, 1981). Although CO_2-induced shifts in climate are debatable (Idso, 1989; Rosenberg et al., 1990; Smit et al., 1988), increased CO_2 levels will directly affect vegetation in natural and agro-ecosystems. There is solid evidence showing that increases in atmospheric CO_2 level will increase biomass production, growth, photosynthesis (Allen et al., 1987; Rogers et al., 1983; Sionit et al., 1984; Strain and Cure, 1985; Warrick, 1988) and water use efficiency (Carlson and Bazzaz, 1980; Dahlman et al., 1985; Kimball and Idso, 1983). There have been several recent reviews of plant responses to CO_2 (Allen, 1990; Kimball et al., 1990; Krupa and Kickert, 1989; Rogers and Dahlman, 1993). Most reported investigations have used plants grown in containers within controlled environments which may not entirely represent the variable and complex environments which exist under field conditions. Furthermore, it has recently been reported that the results

of studies using pot-grown plants where roots are confined may not always be indicative of field responses, i.e., source-sink relationships may be affected (Arp, 1991; Thomas and Strain, 1991). These findings not only emphasize the need for field studies, but also highlight the importance of investigating belowground responses, an area that has often been neglected.

There are far fewer belowground than aboveground investigations in the CO_2 response literature. The most commonly reported root descriptor, showing CO_2-induced enhancement, is root dry weight (Rogers et al., 1994). This has been observed in some important crop species such as sorghum [*Sorghum bicolor* (L.) Moech.], (Chaudhuri et al., 1986), soybean [*Glycine max* (L.) Merr.], (Del Castillo et al., 1989; Rogers et al., 1992b), and winter wheat [*Triticum aestivum* (L.)], (Chaudhuri et al., 1990). A few crop experiments have indicated that root increases (i.e., dry weight and/or length) were concentrated in the upper portions of the soil profile (Chaudhuri et al., 1990; Del Castillo et al., 1989) suggesting a more thorough exploration of a given volume of soil under elevated CO_2. Others have observed enhancements at all soil depths (Chaudhuri et al., 1986; Rogers et al., 1992b), thus implying that the volume of soil explored may be greater. Roots of CO_2 enriched plants also have been shown to reach deeper (Rogers et al., 1992b) or to attain maximum rooting depth ahead (in time) of plants grown under ambient CO_2 levels (Chaudhuri et al., 1990). Detailed morphological studies have also demonstrated that high CO_2 levels increase stele and cortex diameter, root diameter in the root hair zone, length of unbranched first order laterals, and total root length and volume (Rogers et al., 1992b). Collectively, results from the above studies suggest that more plant rooting may occur in a CO_2 enriched world; however, further work is warranted on root system response in natural soil profiles in the field.

The present study utilized cotton plants grown in the field under free-air carbon dioxide enrichment (FACE). This exposure system ensures continuous CO_2 treatment with minimal alteration of plant microclimate while allowing plants to grow in their natural environments. The objective was to investigate how CO_2 enrichment of a cotton canopy affects root distribution (vertical and horizontal) during two growth phases (vegetative and reproductive) under two water regimes.

Materials and methods

Experimental site

This study was conducted for two years (1990–1991) on a Trix clay loam [fine, loamy, mixed (calcareous), hyperthermic Typic Torrifluvents] at the Maricopa Agricultural Center for Resources and Extension (MAC) of the University of Arizona at Maricopa located 25 miles south of Phoenix, AZ. Cotton seeds [*Gossypium hirsutum* (L.) 'Delta Pine 77'] were sown into dry raised beds (1 meter row spacing) on 23 April 1990 and 16 April 1991 with plants being thinned to 10 per meter after 50% emergence. Recommended farming practices of the region as reported by Mauney et al. (1994) were used in managing both the soil and crop.

Experimental design

The experimental design was a split-plot arranged as a randomized complete block with four replications. The main plot factor was CO_2 concentration at two levels (ambient=370 μmol mol^{-1} and FACE=550 μmol mol^{-1}). The split plot treatments were soil water content (wet =100% of evapotranspiration (ET) replaced and dry = 75 and 67% of ET replaced in 1990 and 1991, respectively).

CO_2 exposure system

A technique called free-air carbon dioxide enrichment (FACE) was utilized to create large-scale test atmospheres of CO_2 in the field with minimal alteration of microclimate (Fig. 1). Each circular array (i.e., exposure unit) was constructed of a 22 m diameter PVC torus (plenum chamber) with 32 vertical ventpipes (2 m height) spaced evenly around its diameter. Each ventpipe was individually valved and had gas exit ports drilled at vertical intervals along its length. A computer program (based on an algorithm keyed to wind velocity and CO_2 measured at the center of the experimental plot; see Fig. 1) controlled the release of CO_2 into the array. Carbon dioxide was dumped upwind from open sectors of the vertical pipes in amounts equivalent to windspeed such that a circular plot was uniformly fumigated (Hendrey et al., 1993). There were eight experimental plots, four at nominal CO_2 concentrations of 550 μmol mol^{-1} (surrounded by the 22 m FACE array) and four controls at ambient, 370 μmol mol^{-1} (surrounded by a dummy array). Plots were spaced so as to maximize distance between them

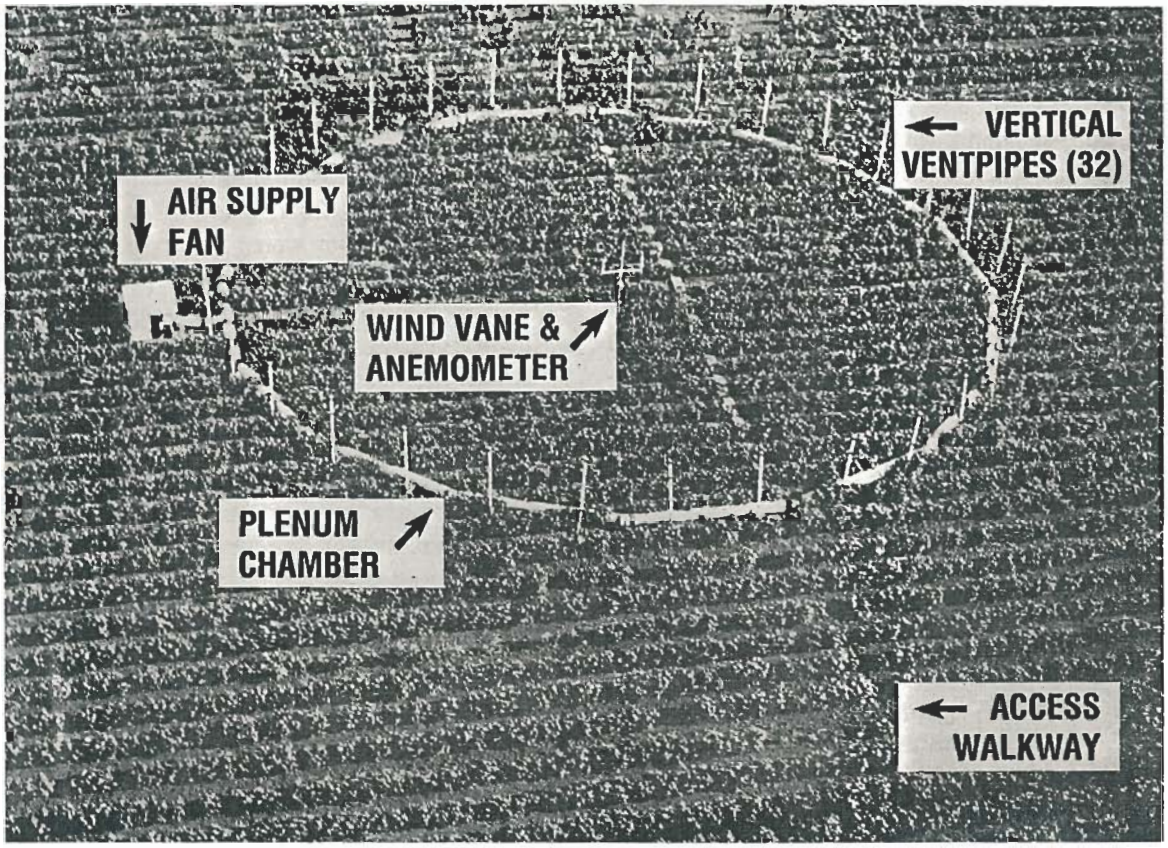

Fig. 1. Photograph of a FACE array in the cotton experiment at Maricopa, AZ, in 1990. Shown are the air supply fan housing, 22 m diameter plenum chamber, the 32 vertical ventpipes, wind measurement mast, and access walkway. (Hendrey et al., 1993).

(at least 100 m), thus reducing the possibility of CO_2 enriched air blowing into controls. Arrays were put in place immediately after planting. Exposure was initiated at 50% seedling emergence and continued until plants reached physiological maturity. One quarter of each experimental plot was used for plant root sampling.

Irrigation

The cotton crop was irrigated with a subsurface drip tube system. A single drip tube was installed 25 cm below each crop row. Initial irrigations of 254 and 272 mm of water were applied immediately after planting in 1990 and 1991, respectively. Main plots were split and each half differentially irrigated on a biweekly basis starting on 3 July in 1990 and 20 May in 1991. The irrigation system was also used for fertilizer N and micronutrient applications during the season as described by Mauney et al. (1994).

Root samples

Soil cores (38 mm diameter) measuring 90 cm in length were collected to determine root length density, root dry weight density, and root lineal density on 18 June and 17 September in 1990, and 12 June and 2 August in 1991. These dates corresponded to aboveground harvests occurring at early vegetative growth and at middle or late reproductive growth as reported elsewhere (Prior et al., 1994). At each sampling date respective measures of leaf area index were about 1.0 and 4.0 in 1990 and 0.7 and 3.0 in 1991. During each sampling, soil cores were taken in-row (0 m) and at distances of 0.25 and 0.50 m perpendicular to the row. In 1990, 192 soil cores were taken at each sampling, representing four cores per position within each subplot. In 1991, the number of cores per position was increased to eight, increasing the total number of cores per sampling to 384. Pneumatic hammers for driving core tubes and electric core tube extraction devices were used to collect root-soil cores (Prior and Rogers, 1992; Prior et al., 1994). A large custom-built cool-

er was used to transport samples by truck to Auburn, AL, where they were placed in cold storage until processing. A hand-held electric band saw was used to cut each 90 cm core into 15 cm segments. After processing, core segments were combined to form three 30 cm depth increments (i.e., 0–30, 30–60, and 60–90 cm) for statistical analyses. Roots were washed from each core segment with a hydropneumatic elutriation system (Gillison's 1990; Smucker et al., 1982) and stored in 20% ethanol (Bohm, 1979) at 4°C. After organic debris had been removed with tweezers and spring-loaded suction pipettes, root length was measured with a Comair Root Length Scanner (Hawker de Havilland, 1985). Root weight determinations were made after drying samples at 55°C.

Data analyses

All analyses were performed using the general linear models procedure of the Statistical Analysis System (SAS, 1985). Core position and depth increments were treated as additional split-plot treatments within the overall study design and an average of the replicate core samples (four in 1990 and eight in 1991) was used for statistical analyses. Proper error terms were specified for each split-plot treatment. Contrast statements were used to determine the significance between interacting main effect variables. Differences were considered significant at the $p < 0.10$ level. Values which differed at the $0.10 < p < 0.20$ level were considered trends.

Results and discussion

At both growth stages, the effects of water stress alone or its interaction with CO_2 were rare and, when detected, showed no consistent pattern. Previous findings (Prior et al., 1993) suggest that such variable results may be related to an interaction occurring in certain root diameter size classes and not in others. In that study, first order lateral roots were partitioned into different size classes based on root diameter. During vegetative growth, significant $CO_2 \times$ water interactions were detected for root variables (length, dry weight, and volume) in the smallest class size (< 1.00 mm); as growth progressed, interactions were detected (length, dry weight, volume, number, and tissue density) for the third largest class size (1.5–2.0 mm). This indicated that some smaller roots continue to exhibit $CO_2 \times$ water interactions later in the cotton crop life cycle. If patterns such as these do occur in the field, then trying to detect interactions becomes very arduous. This topic, without a doubt, requires further investigation.

A few factors which may have contributed to these variable root responses (i.e., between years) under CO_2 enrichment bear mentioning. Some differences could be related to changing irrigation patterns. More specifically, less irrigation water was applied between planting and sampling in 1991 than in 1990 due to the use of different methods of estimating evapotranspiration for the two years. A detailed description of these methods and the rationale for their use, including a chronological record of soil water content and seasonal rainfall, have been reported elsewhere (Hunsaker et al., 1994; Mauney et al., 1994). In addition, some of the variability may be ascribed in part to the fact that in 1991, early season night-time temperatures were lower than the previous season which may have slowed crop development resulting in smaller plants. Furthermore, spatial variability of the soil profile often encountered in the field can cause roots to be non-uniformly distributed and in itself may have hindered statistical separation of treatment effects. Nevertheless, some important differences in root response due to CO_2 enrichment were detected and are discussed below.

Effect of increased CO_2 on root length density

Positive shifts in rooting patterns due to extra atmospheric CO_2 during vegetative growth may have important implications in terms of seedling vigor. In the present study, there were significant $CO_2 \times$ position interactions for root length density ($p = 0.04$–0.08) at the vegetative sampling in both years (Fig. 2). At the in-row position (0 m) FACE tended to increase root length density in 1990 ($p = 0.13$; Fig. 2A) and significantly increased this measure (15%) in 1991 (Fig. 2B). FACE enhanced root length density more at the 0.5 m position in 1990, whereas in 1991, increases in this measure were most apparent at the 0.25 m position. For example, at the 0.25 and 0.5 m positions this measure was increased by 33 and 64% in 1990 and by 38 and 27% in 1991, respectively. Results show that elevated CO_2 resulted in more prolific rooting, especially at the interrow positions. This may well confer an advantage to CO_2-enriched plants for more readily acquiring soil water and nutrients needed for development, especially when these factors limit seedling growth. Consequently, establishment of crop stands would be enhanced. In the present study, FACE significantly increased corresponding measures of aboveground dry matter by 56

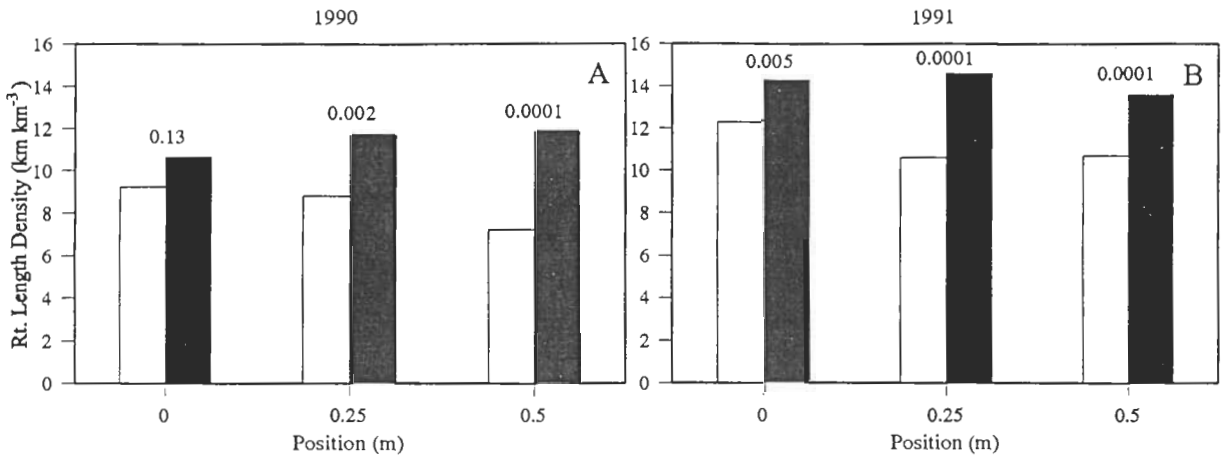

Fig. 2. The effect of CO_2 concentration (□ = 370 μmol mol^{-1}; ■ = 550 μmol mol^{-1}) on cotton root length density at three positions (0, 0.25, and 0.5 m away from the crop row center) during vegetative growth in 1990 (**A**) and 1991 (**B**). Means and probabilities are shown.

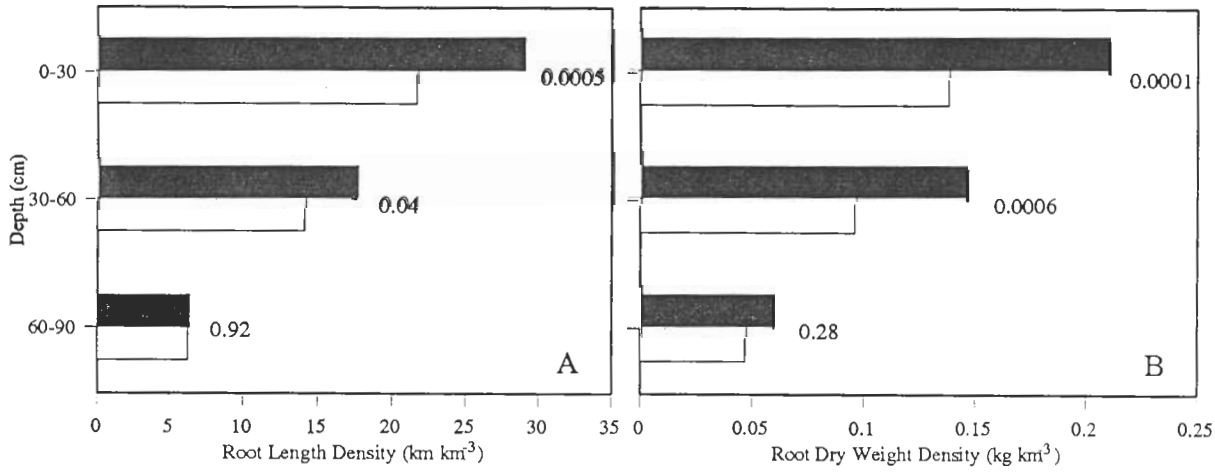

Fig. 3. The effect of CO_2 concentration (□ = 370 μmol mol^{-1}; ■ = 550 μmol mol^{-1}) on cotton root length density and root dry weight density at three depth increments during reproductive growth in 1990 (**A**) and 1991 (**B**). Means and probabilities are shown.

and 43% relative to ambient CO_2 levels in 1990 and 1991, respectively (Prior et al., 1994).

Changes in rooting patterns under high CO_2 environments may also have important implications for crop performance during critical periods of reproductive growth, such as boll filling, when plants have high demands for water and nutrients. Positive shifts in root length density due to FACE were seen at the reproductive samplings while corresponding measures of aboveground responses also showed that FACE increased boll biomass values by 65 and 44% in 1990 and 1991, respectively (Prior et al., 1994). Observations for the root samples collected during reproductive growth (data not shown) were similar to those reported for the vegetative growth samples in 1990 (Fig. 2A); for example, significant increases in root length densities due to elevated CO_2 were observed at both interrow positions (p = 0.002–0.02). A trend toward a CO_2 × depth × position interaction observed at the initial sampling (p = 0.14) was also seen during the reproductive stage (p = 0.19; data not shown); root length densities under FACE were higher at the two upper most depths (i.e., 0–30 cm and 30–60 cm) at the interrow positions. In the following year, a significant CO_2 × depth interaction was detected at the vegetative sampling (p = 0.02; data not shown) and was also observed during the reproductive sampling (Fig. 3A; p = 0.05). At both times, increased root length densities due to elevated CO_2 were found at the upper and middle depth increments; the 0–30 cm depth showed increases of 30 and 34% while the 30–60 cm depth had increases of 21 and 25%. Chaudhuri et al. (1986) observed that

sorghum grown in glass-sided boxes filled with topsoil under CO_2 enrichment also exhibited root length increases in the upper parts of the soil profile. Likewise, enhancements in root length density due to CO_2 enrichment in our study are similar to those reported by others (Rogers et al., 1992a).

Effect of increased CO_2 on root dry weight density

Although root dry weight often exhibit substantial increases due to elevated atmospheric CO_2 (Rogers et al., 1994), little data exist on how extra CO_2 alters horizontal and vertical distribution patterns within actual soil profiles. In our study, the effect of increased CO_2 on root dry weight density varied between samplings and years. In 1990, there were significant $CO_2 \times$ depth $\times$ position interactions for root dry weight density at the vegetative sampling ($p = 0.02$; Fig. 4), but only a trend could be seen at the reproductive sampling ($p = 0.19$; data not shown). In comparison, $CO_2 \times$ depth interactions were detected at both sampling dates in 1991 ($p = 0.04$–0.10; Fig. 3B, only reproductive data shown). In general, the root dry weight distribution patterns were similar to those observed for root length density.

Representative results for root dry weight density are shown in Figures 3B and 4. At the initial sampling in 1990, FACE increased root dry weight densities at the upper depth increment, 0–30 cm, at all sample positions (0, 0.25, and 0.5 m) by 40, 33, and 111%, respectively (Fig. 4). Although values were numerically higher for some depth increments at the 0 m position (i.e., 30–60 cm; Fig. 4A) and at the 0.25 m position (i.e., 60–90 cm; Fig. 4B), these differences were only marginally non-significant ($p = 0.11$). However, the middle depth increment (30–60 cm) at the 0.5 m position exhibited a large increase in root dry weight density (200%) due to FACE conditions (Fig. 4C). Rogers et al. (1992b) reported that in soybean (18 day old) grown under CO_2 enriched conditions in growth chambers, rooting increased over a depth of 45 cm which also resulted in a substantial rise in root dry weight (143%). In the current study, by the reproductive sampling there was only a tendency for a $CO_2 \times$ depth $\times$ position interaction ($p = 0.19$; data not shown); rooting patterns were somewhat like those observed at the vegetative sampling (Fig. 4). However, the extra aerial CO_2 did significantly increase root dry weight density by 38% when averaged over all horizontal positions and depth increments at this sampling ($p = 0.04$; data not shown). In 1991, the significant $CO_2 \times$ depth interaction was related to a CO_2 induced increase in rooting at the two upper most depth increments (50% each) at both sample periods (Fig. 3B). By comparison, Chaudhuri et al. (1986) reported that sorghum grown in glass-sided boxes filled with topsoil under CO_2 enrichment exhibited increases in root length in the upper parts of the soil profile while increases in root dry weight were observed at all depths. Other containerized studies utilizing outdoor sunlit chambers for CO_2 exposure of soybean (Del Castillo et al., 1989) and winter wheat (Chaudhuri et al., 1990) have shown that CO_2 enrichment had little affect on root dry weight at depth increments below about 45 cm. Utilization of different CO_2 exposure systems, measurement methods, growth media, and cultivar studied may account for these varying responses.

Our root dry weight density data (as well as root length density data) resemble the distribution pattern for cotton roots described by Klepper et al. (1973) where rooting density generally declines exponentially with depth under optimum soil water conditions. A common pattern noted in our data was that CO_2 enrichment exerted most of its affect at the upper and middle portions of the profile while having no apparent affect on the distribution of root dry matter (or length) to the lowest profile depth (Figs. 3 and 4). Rogers et al. (1992b) reported that roots of high CO_2 grown soybean penetrated deeper into the profile and Chaudhuri et al. (1990) that maximum rooting depth of wheat was reached quicker. We are unable to conclusively determine whether elevated CO_2 had no effect on deep rooting since core samples were not collected beyond 90 cm. However, it is possible that other factors (e.g., oxygen diffusion rate, high soil strength, etc.) at lower depths were limiting root development even for the CO_2-enriched cotton plants. Furthermore, it is important to note that the influence of irrigation line placement within the profile as a reason for more root proliferation at the upper to middle depths was unlikely since results by Kamara et al. (1991) demonstrated that the depth of trickle irrigation lines had no significant affect on the depth or horizontal distribution of cotton roots during the course of a growing season.

Effect of increased CO_2 on spatial distribution of roots

In addition to examining changes in absolute root length density, data were expressed as a percent of total root length to ascertain whether proportionately more rooting occurred at a given position under one treatment than another. There were significant $CO_2 \times$

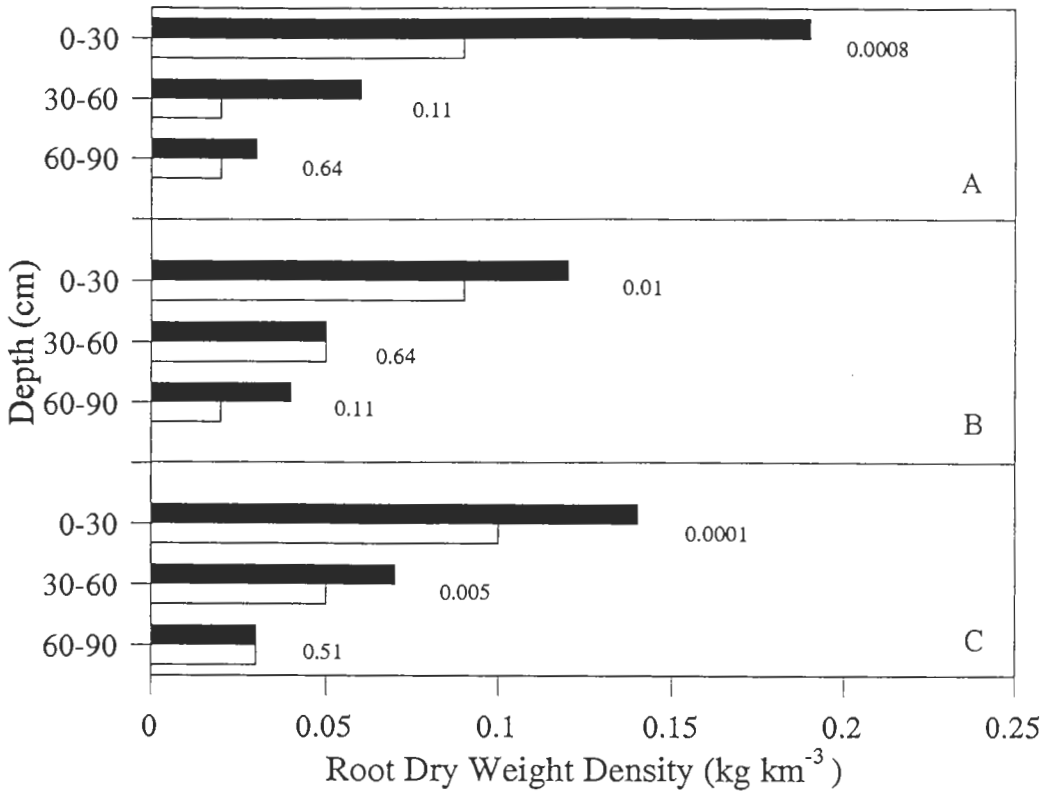

Fig. 4. The effect of CO_2 concentration (□ = 370 μmol mol^{-1}; ■ = 550 μmol mol^{-1}) on cotton root dry weight density at the three depth increments and positions (**A** = 0 m, **B** = 0.25 m, and **C** = 0.5 m) away from crop row center during vegetative growth in 1990. Means and probabilities are shown.

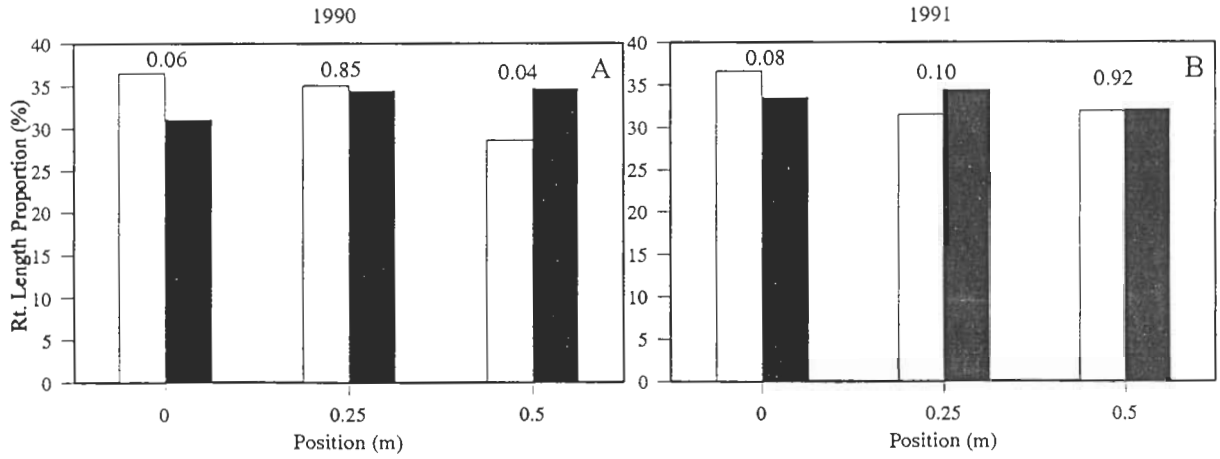

Fig. 5. The effect of CO_2 concentration (□ = 370 μmol mol^{-1}; ■ 550 μmol mol^{-1}) on root length proportion at three positions (0, 0.25, and 0.5 m away from crop row center) during vegetative growth in 1990 (**A**) and 1991 (**B**). Means and probabilities are shown.

position interactions for root length proportion (p = 0.02) at both samplings in 1990, but only for the vegetative sampling in 1991. At the vegetative samplings, the ambient treatment had a higher percentage of its total root length distributed at the in-row (0 m) position compared to the elevated CO_2 treatment (Fig. 5). However, at the interrow positions, the opposite was observed; in 1990 significantly more root length was found at the 0.5 m position under FACE (Fig. 5A) while in 1991 a similar pattern was observed at the

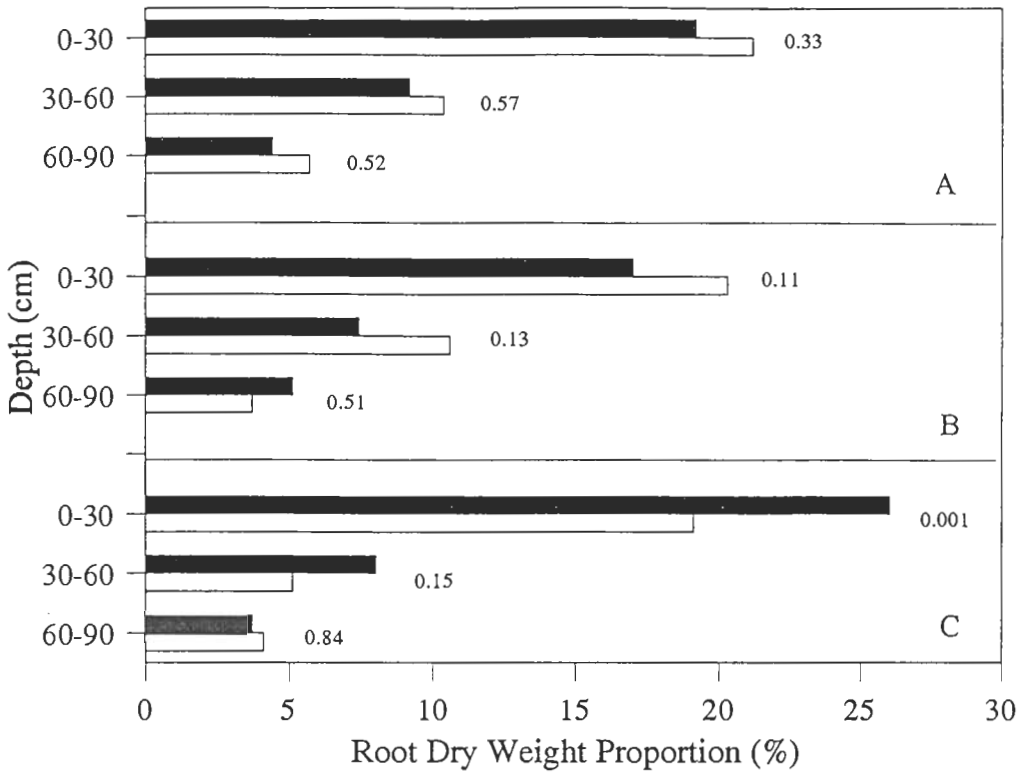

Fig. 6. The effect of CO_2 concentration (□ = 370 μmol mol^{-1}; ■ 550 μmol mol^{-1}) on root dry weight proportion at three depth increments and positions (**A** = 0 m, **B** = 0.25 m, and **C** = 0.5 m away from crop row center) during vegetative growth in 1990. Means and probabilities are shown.

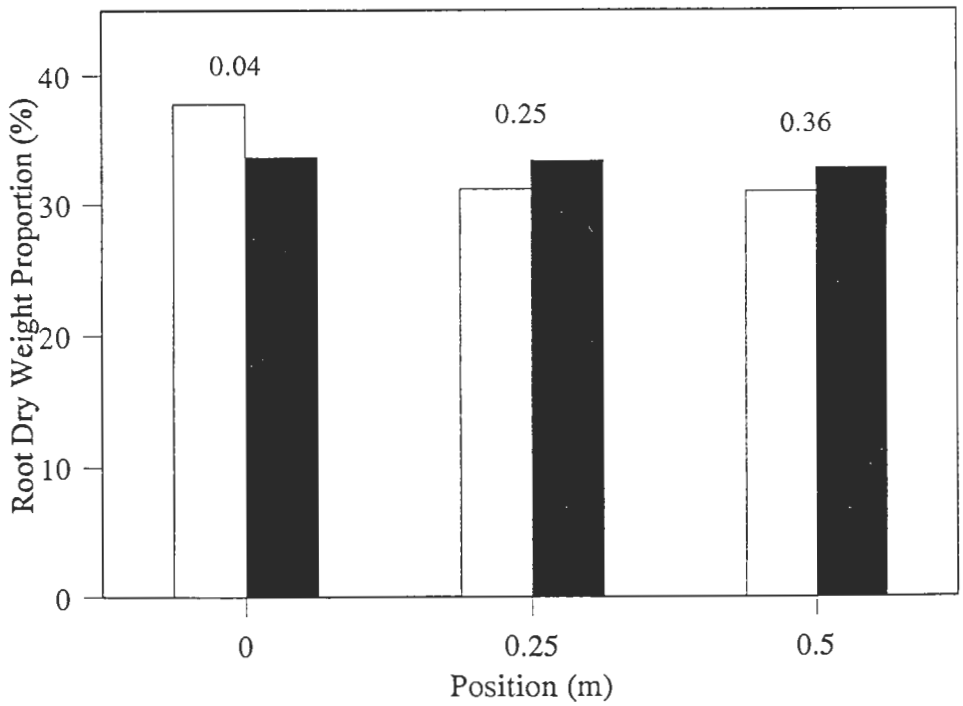

Fig. 7. The effect of CO_2 concentration (□ = 370 μmol mol^{-1}; ■ = 550 μmol mol^{-1}) on root dry weight proportion at three positions (0, 0.25, and 0.5 m away from crop row center) during vegetative growth in 1991. Means and probabilities are shown.

0.25 m position (Fig. 5B). Observations at the reproductive sampling in 1990 (data not shown) were like those observed at the vegetative sampling (Fig. 5A). A trend toward a CO_2 × depth × position interaction for this variable was also seen at both samplings in 1990 (p = 0.14–0.17; data not shown) where patterns were similar to data described above, but limited to the upper depth (0–30 cm) increment.

Root proportion was also calculated on a dry weight basis (Figs. 6 and 7). There were CO_2 × depth × position interactions at both samplings in 1990 (p = 0.06–0.09). At the vegetative sampling, there was a trend for a higher root dry weight proportion at the two upper depths (0–30 cm and 30–60 cm) at the 0.25 m position under ambient CO_2 conditions (p = 0.11 and 0.13; Fig. 6B). Conversely, at the 0.5 m position, values from FACE were significantly higher at 0–30 cm depth while this same measure at the next depth level (30–60 cm) tended to be higher (p = 0.15; Fig 6C). At the reproductive sampling, (this measure at the 0 and 0.25 m positions) was significantly higher or tended to be higher under ambient CO_2 levels at the 0–30 cm depth (data not shown; p = 0.0002 and p = 0.14, respectively). However, under FACE more of the root system's dry weight, relative to the ambient CO_2 treatment, tended to be allocated to the lowest depth level at the 0 m position (p = 0.10) and 0.5 m position (p = 0.15). By comparison, in 1991 there were CO_2 × position interactions with the same pattern being observed at both dates (p = 0.04–0.10); the ambient CO_2 treatment had a higher proportion of its root dry weight allocated to the in-row position (0 m) compared to FACE (Fig. 7). No differences were seen at the remaining two positions.

The changes in root proportion reported here may be related to different rates of extension of first-order lateral roots and further root branching. The higher proportion of root length and weight observed at the in-row (0 m) position under ambient CO_2 may be due to first-order lateral roots having slower elongation rates (relative to high CO_2 plants) which may have resulted in more higher-order branching occurring close to the taproot or center row position. On the other hand, increases in lateral root growth (and further root branching) possibly explain the greater root length proportion at the interrow positions under FACE. It is, however, unclear why root length proportion differed away from row center while corresponding measures of root dry weight did not, unless it was somehow related to root fineness.

We did not make detailed measurements of root branching patterns or root elongation rates. However, results from a few other studies conducted in growth chambers should be mentioned. Rogers et al. (1992b) reported that elevating CO_2 had no significant effect on soybean root branching but did increase the length of first-ordered laterals (110%). The use of perlite (a media with large pore size distribution) may have allowed for unimpeded root elongation, leading to large increases in root length without the added expense of extensive branching. Conversely, Del Castillo et al. (1989) observed that CO_2 enrichment enhanced root branching rather than elongation rate in soybean. In this case, it appears that elongation rates were measured on higher-order lateral roots rather than on first-order laterals. In addition, a soil mixture (i.e., equal volume mix of sand and vermiculite) was used which probably represented a media having an overall smaller pore size distribution which may have impeded root extension enough to induce more branching (Russell, 1977). We suspect that the findings of both investigations may occur in natural soil profiles, depending upon edaphic conditions. Our data for the larger taproot systems (total volume, dry weight, and length) under FACE (Prior et al., 1994) revealed larger diameter taproots which supported greater number of first-order lateral roots, collectively representing more root length (Prior et al., 1993). These changes may well have been accompanied by more branching which could explain the higher proportion of root length found within interrow positions under FACE. These observations could have important implications for both agricultural and natural ecosystems where such change might alter competitive effectiveness for belowground resources, especially if some plant species are affected more or less, relative to neighboring species.

Effect of increased CO_2 on root lineal density

Calculations of root lineal density (i.e., root weight per unit root length) were made to make inferences about possible changes in root structure and composition due to CO_2 enrichment. The CO_2-induced shifts in root lineal density were highly variable between both samplings and year. In the first year a significant CO_2 × depth × position interaction (p = 0.008) was seen at the vegetative sampling (Fig. 8). FACE increased lineal root density at the 0 m position (i.e., 0–30 cm depth; Fig. 8A) and 0.5 m position (i.e., 0–30 cm and 30–60 cm depths; Fig. 8C). An increase in root lineal density under ambient CO_2 conditions was only seen

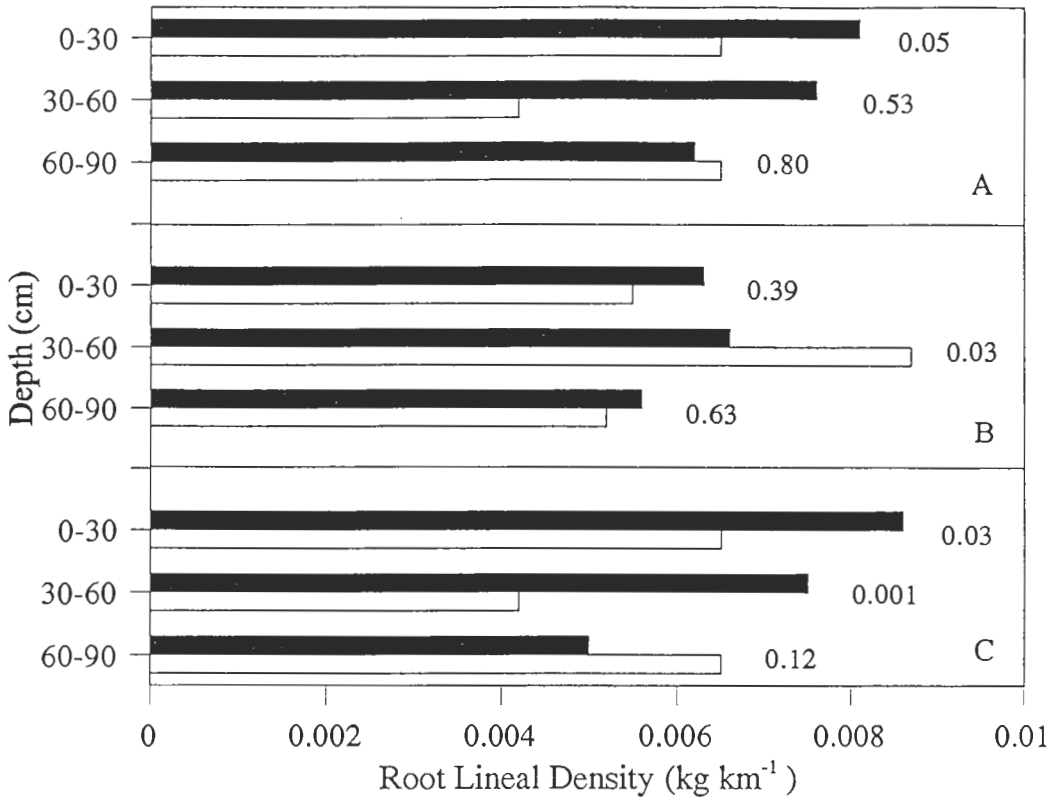

Fig. 8. The effect of CO_2 concentration (□ = 370 μmol mol^{-1}; ■ = 550 μmol mol^{-1}) on root lineal density at three depth increments and positions (**A** = 0 m, **B** = 0.25 m, and C = 0.5 m away from crop row center) during vegetative growth in 1990. Means and probabilities are shown.

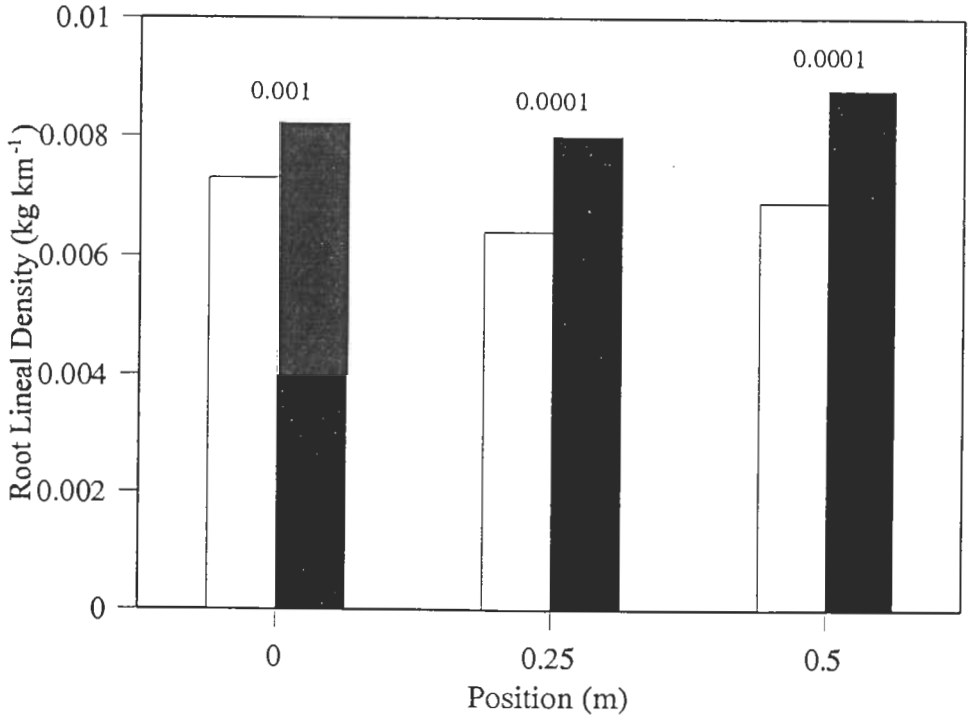

Fig. 9. The effect of CO_2 concentration (□ = 370 μmol mol^{-1}; ■ = 550 μmol mol^{-1}) on root lineal density at three positions (0, 0.25, and 0.5 m away from crop row center) during reproductive growth in 1991. Means and probabilities are shown.

at the 0.25 m position (30–60 cm depth; Fig. 8B). A similar trend was observed at the 0.5 m position (p = 0.12; 60–90 cm depth). We have no clear explanation for this reversal which only occurred once. By comparison, data from 1991 indicated a trend for an overall effect of CO_2 on root lineal density ($p = 0.11$; data not shown). At the reproductive sampling, the $CO_2 \times$ position interaction significance level was $p = 0.11$ in 1990 and $p = 0.03$ in 1991. However, in 1990 additional CO_2 resulted in a 27% increase in root lineal density when data were averaged across all depths and positions (p = 0.05; data not shown). In 1991, root lineal density was higher under elevated CO_2 at all three positions (i.e., 0, 0.25, and 0.5 m; Fig. 9).

Changes in root lineal density most likely occurred in smaller lateral roots and/or successive branching orders of first-order lateral roots since large root segments (i.e., woody first-order lateral roots) were rarely found in individual samples. Increased lineal root density has been related to roots having larger diameters (Klepper, 1992). It is also possible that changes in root lineal density may be related to more compact or denser tissue or to alteration in carbohydrate storage, cell number, cell size, and other structural modifications, or combinations thereof. A growth chamber study showed that roots of young soybean plants grown at high CO_2 concentrations exhibited larger diameters (in the root hair zone) (Rogers et al., 1992b). A significant enhancement of both stele diameter and cortex width was also seen. In the present study, taproots and their associated first-ordered lateral roots often showed increases in root tissue density (g/cm^3) under FACE (Prior et al., 1993). Although such measurements were not made on smaller higher-order branch roots, the increases in root lineal density reported here possibly coincide with changes in root tissue density. If such is the case, root function may be altered along with the quality of carbon inputs into the soil. This, in turn, could affect both microbial activity and soil physical properties as well as soil carbon storage.

Conclusions

Despite variation between years, results from this field study suggest that rising atmospheric CO_2 concentration could be beneficial to a cotton crop with respect to enhanced root proliferation. Stimulation of crop rooting may help ensure exploitation of soil resources. In general, vertical changes in absolute root density (both length and dry weight) due to CO_2 enrichment are most likely to occur in the uppermost soil layers (0–30 cm and 30–60 cm depths in this study). Results gathered here also indicate that additional CO_2 can alter horizontal rooting patterns by increasing root proliferation into interrow positions (0.25 m and/or 0.50 m). It was also noted that under ambient CO_2 conditions a higher proportion of the root system (length and/or dry weight basis) was often distributed closer to center row whereas the FACE treatment usually had proportionately more of its root system allocated away from row center. If some plant species are affected in this manner while others are not, this finding could have implications for both agricultural and natural ecosystems associated with the strategy by which plants compete for belowground resources. However, before final conclusions are made, further work with other important plant species is needed. Functional aspects of root growth as affected by elevated atmospheric CO_2 clearly need detailed study. Future work must consider not only how CO_2 enrichment affects crop rooting, but also how it impacts other belowground processes, both physical and biological.

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References

Allen L H Jr 1990 Plant responses to rising carbon dioxide and potential interactions with air pollutants. J. Environ. Qual. 19, 15–34.

Allen L H Jr, Boote K J, Jones J W, Jones P H, Valle R R, Acock B, Rogers H H and Dahlman R C 1987 Response of vegetation to rising carbon dioxide: photosynthesis, biomass, and seed yield of soybean. Global Biogeochem. Cycles 1, 1–14.

Arp W J 1991 Effects of source-sink relations on photosynthetic acclimation to elevated CO_2. Plant, Cell Environ. 14, 869–975.

Bohm W 1979 Methods of studying root systems. Spring-Verlag, NY. 188 p.

Carlson R W and Bazzaz F A 1980 The effects of elevated CO_2 concentration on growth, photosynthesis, transpiration, and water use efficiency of plants. *In* Environmental and Climatic Impact of Coal Utilization. Eds. J Singh and A Deepak. pp 609–612. Academic Press, NY.

Chaudhuri U N, Kirkham M B and Kanemasu E T 1990 Root growth of winter wheat under elevated carbon dioxide and drought. Crop Sci. 30, 853–857.

Chaudhuri U N, Burnett R B, Kirkham M B and Kanemasu E T 1986 Effect of carbon dioxide on sorghum yield, root growth, and water use. Agric. For. Meteorol. 37, 109–122.

Dahlman R C, Strain B R and Rogers H H 1985 Research on the response of vegetation to elevated atmospheric carbon dioxide. J. Environ. Qual. 14, 1–8.

Del Castillo D, Acock B, Reddy V R and Acock M C 1989 Elongation and branching of roots on soybean plants in a carbon dioxide-enriched aerial environment. Agron. J. 81, 692–695.

Gillison's Variety Fabrication, Inc 1990 Basic operation of the hydropneumatic root washer. 3033 Benzie Hwy., Benzonia, MI 49616.

Gribbon J 1981 The politics of carbon dioxide. New Sci. 90, 82–84.

Hawker de Havilland 1985 User's Manual. 304 Lorimer Street, Port Melbourne, Victoria, 3207, Australia.

Hendrey G R, Lewin K F and Nagy J 1993 Free-air carbon dioxide enrichment: development, progress, results. Vegetatio 104/105, 17–31.

Hunsaker D J, Hendrey G R Kimball B A, Lewin K F, Mauney J R and Nagy J 1994 Cotton evapotranspiration under field conditions with CO_2 enrichment and variable soil moisture regimes. Agric. For. Meteorol. (*In press*).

Idso S B 1989 Carbon Dioxide and Global Change: Earth in Transition. IBR Press, Tempe, AZ. 292 p.

Kamara L, Zartman R and Ramsey R H 1991 Cotton-root distribution as a function of trickle irrigation emitter depth. Irrig. Sci. 12, 141–144.

Keeling C D, Bacastow R B, Carter A F, Piper S C, Whorf T P, Heimann M, Mook W G and Roeloffzen H 1989 A three dimensional model of atmospheric CO_2 transport based on observed winds: Observational data and preliminary analysis. *In* Aspects of Climate Variability in the Pacific and the Western Americas. Vol. 55. American Geophysical Union.

Kimball B A, Rosenberg N J and Allen L H Jr 1990 Impact of CO_2, trace gases, and climate change on global agriculture. ASA Special Publication No. 53, Am. Soc. Agron., Madison, WI. 133 p.

Kimball B A and Idso S B 1983 Increasing CO_2: Effects on crop yield, water use and climate. Agric. Water Manage. 7, 55–72.

Klepper B, Taylor H M, Huck M G and Fiscus E L 1973 Water relations and growth of cotton in drying soil. Agron. J. 65, 307–310.

Klepper B 1992 Development and growth of crop root systems. *In* Limitations to plant root growth. Eds. J L Hatfield and B A Stewart. Advances in Soil Science Volume 19. pp 1–25. Springer-Verlag, New York.

Krupa S V and Kickert R N 1989 The greenhouse effect: Impacts of ultraviolet-B (UV-B) radiation, carbon dioxide (CO_2), and ozone (O3) on vegetation. Environ. Pollut. 61, 263–396.

Mauney J R, Kimball B A, Pinter Jr P J, LaMorte R L, Lewin K, Nagy J and Hendrey, G R 1994 Growth and yield of cotton in response to a free-air carbon dioxide enrichment (FACE) environment. Agric. For. Meteorol. (*In press*).

Pearman G I 1980 The global carbon cycle and increasing levels of atmospheric carbon dioxide. *In* Carbon Dioxide and Climate: Australian research. Ed. G I Pearman. pp 11–20. Australian Academy of Science, Canaberra.

Prior S A and Rogers H H 1992 A portable soil coring system that minimizes plot disturbance. Agron. J. 84, 1073–1077.

Prior S A, Rogers H H and Runion G B 1993 Effects of free-air CO_2 enrichment on cotton root morphology. Supplement to Plant Physiol. 102 (1), 173 (Abstract).

Prior S A, Rogers H H, Runion G B and Mauney J R 1994 Effects of free-air CO_2 enrichment on cotton root growth. Agric. For. Meteorol. (*In press*).

Rogers H H and Dahlman R C 1993 Crop responses to CO_2 enrichment. Vegetatio 104/105, 117–131.

Rogers H H, Runion G B and Krupa S V 1994 Plant responses to atmospheric CO_2 with emphasis on roots and the rhizosphere. Environ. Pollut. 83, 155–189.

Rogers H H, Thomas J F and Bingham G E 1983 Response of agronomic and forest species to elevated atmospheric carbon dioxide. Science 220, 428–429.

Rogers H H, Prior S A and O'Neil E G 1992a Cotton root and rhizosphere responses to free-air CO_2 enrichment. Crit. Rev. Plant Sci. 11, 251–263.

Rogers H H, Peterson C M, McCrimmon J M and Cure J D 1992b Response of soybean roots to elevated atmospheric carbon dioxide. Plant, Cell Environ. 15, 749–752.

Rosenberg N J, Kimball B A, Martin P and Cooper C F 1990 From climate and CO_2 enrichment to evapotranspiration. *In* Climate Change and U.S. Water Resources. Ed. P E Waggoner. pp 151–175. John Wiley and Sons, NY.

Russell R S 1977 Plant Root Systems: Their Function and Interaction with the Soil. McGraw-Hill, UK. 298 p.

Sionit N, Rogers H H, Bingham G E and Strain B R 1984 Photosynthesis and stomatal conductance with CO_2-enrichment of container and field-grown soybeans. Agron. J. 65, 207–211.

SAS Institute, Inc 1985 SAS User's guide: statistics. Statistical Analysis System (SAS) Institute, Inc., Cary, NC. 956 p.

Smit, B, Ludlow L and Brklacich M 1988 Implications of a global climatic warming for agriculture: A review and appraisal. J. Environ. Qual. 17, 519–527.

Smucker A J M, McBurney S L and Srivastava A K 1982 Quantitative separation of roots from compacted soil profiles by the hydropneumatic elutriation system. Agron. J. 74, 500–503.

Strain B R and Cure J D 1985 Direct effects of increasing carbon dioxide on vegetation. DOE/ER-0238. The Office of Energy Research. U. S. Dept. of Energy, Washington, DC. 286 p.

Thomas R R and Strain B R 1991 Root restriction as a factor in photosynthetic acclimation of cotton seedlings grown in elevated carbon dioxide. Plant Physiol. 96, 627–634.

Warrick R A 1988 Carbon dioxide, climatic change and agriculture. Geographical J. 154, 221–233.

Woodwell G M 1978 The carbon dioxide question. Sci. Am. 238, 34–43.