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Free-Air Carbon Dioxide Enrichment of Cotton: Root Morphological Characteristics

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ABSTRACT

The response of plants to rising global CO_2 concentration is of critical research interest but one neglected aspect is its effect on roots. Root morphological changes in cotton [*Gossypium hirsutum* (L.) 'Delta Pine 77'] were examined in a 2-yr field study. The test crop was grown under two water regimes (wet, 100% of evapotranspiration [ET] replaced and dry, 75% [1990] and 67% [1991] of ET replaced) and two atmospheric CO_2 concentrations (ambient = 370 μmol mol^{-1} and free-air CO_2 enrichment [FACE] = 550 μmol mol^{-1}). A FACE technique that allows for CO_2 exposure under field conditions with minimal alteration of plant microclimate was used. Excavated root systems were partitioned into taproot and lateral roots at two growth phases (vegetative and reproductive). Vertical root-pulling resistance was determined at the second sampling; this measure was higher because of CO_2 enrichment but was unaffected by water stress. Water stress affected root variables only at the second sampling; water stress reduced taproot variables more than lateral variables. The larger diameter taproots seen at all sample dates under FACE exhibited large increases in dry weight and volume. FACE often increased lateral root number and lateral dry weights were higher at all sample dates. The development of more robust taproot systems in CO_2-enriched environments may allow for greater carbohydrate storage for utilization during periods such as boll filling and to ensure root growth for continued exploration of the soil profile to meet nutrient and water demands during peak demand periods.

THE RISE in global atmospheric CO_2 concentration has been well documented (Keeling et al., 1989). Increased levels of CO_2 will directly influence vegetation in natural and agricultural ecosystems. Carbon dioxide is not only a key component of the global carbon cycle, but it is also a critical input and regulator of plant growth. Our current knowledge must expand to allow accurate predictions of plant response to future conditions.

Aboveground responses of plants to elevated CO_2 concentration have been studied reasonably well. Increases in CO_2 have been experimentally observed to enhance resultant biomass production, plant growth, photosynthesis (Strain and Cure, 1985; Allen et al., 1987; Warrick, 1988) and water-use efficiency (Kimball and Idso, 1983; Dahlman et al., 1985). Plant responses to elevated CO_2 and their interaction with other environmental factors have been summarized in recent in-depth reviews (Allen, 1990; Kimball et al., 1990; Krupa and Kickert, 1989; Rogers and Dahlman, 1992). In comparison with canopy components, belowground processes within crop systems grown under elevated CO_2 have been neglected. Reports by Arp (1991) and Thomas and Strain (1991) highlight the importance of considering belowground aspects of plant growth under CO_2-enriched conditions. Their findings suggest, that in cases where confined rooting volumes are used (i.e., containerized studies), observed plant responses to elevated CO_2 may not be indicative of responses under real field conditions. Much of our current database has been derived from controlled environment studies using containerized plants. Therefore, investigating belowground responses to elevated CO_2 levels under field conditions is imperative.

The effects of CO_2 enrichment on root morphology have been directly addressed by only a few studies. Soybean [*Glycine max* (L.) Merr.] plants grown in soil bins of sunlit growth chambers exhibited higher numbers of actively growing roots, but no differences in root elongation rate, thus suggesting that more root branching occurred under CO_2-enriched conditions (Del Castillo et al., 1989). Other studies have observed that additional CO_2 increases root number in some cases (Chaudhuri et al., 1986), but not in others (Rogers et al., 1992b). To date, the most detailed account of root morphological changes under a CO_2- enriched environment was reported for soybean by Rogers et al. (1992b). Additional CO_2 led to substantial increases in total root length, volume, and dry weight. In addition, high CO_2 increased stele diameter, cortex width, and root diameter in the root hair zone. Since these studies were conducted in controlled environments, it is not certain whether similar responses will occur in the field.

The objective of this study was to determine whether elevated CO_2 would alter root morphological characteristics of cotton grown under field conditions. Partial excavation of the root system (i.e., taproot and attached lateral roots) was carried out during two growth phases (vegetative and reproductive). The interactive effects of CO_2 and soil water content on the root system were evaluated.

MATERIALS AND METHODS

Field experiments were conducted in 1990 and 1991 at the Maricopa Agricultural Center (MAC) of the Univ. of Arizona at Maricopa, 25 miles south of Phoenix. Cotton ('Delta Pine 77') was grown on a Trix clay loam (fine-loamy, mixed [calcareous], hyperthermic Typic Torrifluvents). The experimental site was managed according to local cultural practices as a conventionally tilled, irrigated production system. Seeds were planted into raised beds at a row spacing of 1 m on 23 Apr. 1990 and 16 Apr. 1991. Immediately after sowing an initial amount of irrigation water (i.e., 293 mm in 1990 and 272 mm in 1991) was applied. After establishing the cotton stand all study plots were thinned to 10 plants m^{-1}. A preplant

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Abbreviations: ET, evapotranspiration; FACE, free-air CO_2 enrichment; MAC, Maricopa Agricultural Center; PVC, polyvinyl chloride; AZMET, Arizona Meteorological Network.

application of Karmex[1] [Diron (3-[3,4-dichlorophenyl-1, 1-dimethyurea]); E.I. Dupont de NE MOURS & Co., Wilmington, DE] was made to control weeds; subsequent weed control was done by hand as needed. A detailed description of other significant culture events and the experimental protocol for both years has been reported elsewhere (Mauney et al., 1994).

The experimental design was a split plot with a randomized complete block arrangement of the main plot factor (two concentrations of CO_2: ambient = 370 μmol mol^{-1} and FACE = 550 μmol mol^{-1}) with four replications. The second factor was water regime (wet [a target rate of 100% of ET being replaced] and dry [75 and 67% of ET replaced in 1990 and 1991, respectively]) which was assigned to subplots (half of the main plots).

A new technique called FACE was used to create large-scale test atmospheres of CO_2 in the field with minimal alteration of meteorological conditions (Fig. 1). Each exposure unit consisted of 32 individually valved vertical vent pipes (2 m height) evenly spaced around a polyvinyl chloride (PVC) torus (22 m diam. array). Test gas exited from port holes drilled at vertical intervals along the vent pipes. A computer program based on an algorithm keyed to windspeed and direction was used to release CO_2 upwind from open sectors of vertical standpipes in quantities proportional to windspeed, thus creating relatively uniform atmospheres, with respect to CO_2 level, inside each array (Hendrey et al., 1993). A total of eight study plots were used each year, four at nominal concentrations of 550 μmol mol^{-1} (surrounded by a 22-m FACE array) and four control plots at 370 μmol mol^{-1} (surrounded by a dummy array). Each ambient plot was located within a dummy control array to ensure similar conditions for all study plots. Plots were positioned far enough apart to prevent CO_2-enriched air within FACE plots from being blown over control plots. Installation of arrays occurred immediately after planting, and CO_2 exposure was initiated after 50% seedling emergence. Exposure was discontinued when plants attained physiological maturity.

A subsurface drip tube irrigation system whose tubes were installed approximately 25 cm beneath each crop row was used to water the crop during the season. Irrigation tubing was replaced each year. Each half (i.e., subplot) of the main plots was differentially irrigated (wet or dry) on a biweekly basis starting on 3 July in 1990 and 20 May in 1991. The timing of irrigation and the amount of irrigation water applied was based upon estimates of crop consumptive water use. The change in water regime noted within the dry treatment (i.e., 75 vs. 67%) for the different years was caused by using different methods of estimating ET (Mauney et al., 1994). In 1990, potential ET measured from a field evaporation pan was used to calculate replacement irrigation volume (i.e., wet treatment). In 1991, timing and volume or irrigation was based on calculated potential ET provided by the Arizona Meteorological Network (AZMET; Univ. of Arizona). In 1990, the total amount of irrigation water applied to wet and dry plots were 1190 and 1060 mm, respectively. In 1991, irrigation totals were 1048 and 792 mm for wet and dry plots, respectively.

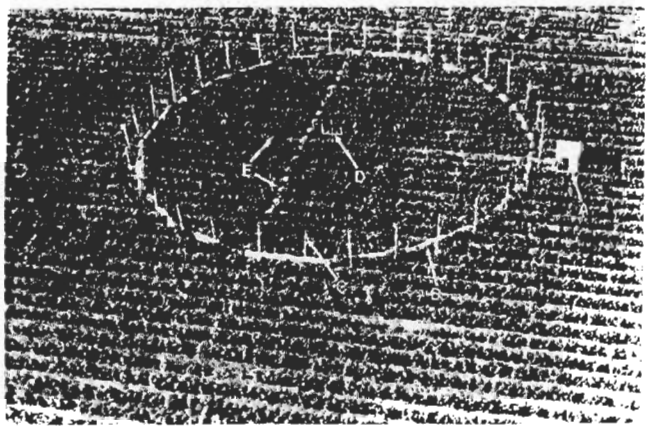

Fig. 1. Photograph of a FACE array located in a cotton field at Maricopa, AZ, in 1990: (*A*) Fan housing, (*B*) 22 m diameter PVC torus, (*C*) vertical vent pipes, (*D*) anemometer and wind direction mast, and (*E*) walkways (Hendrey et al., 1993).

Root samples (taproots and attached lateral roots) were taken at early vegetative (i.e., late square to first bloom) growth and reproductive growth (i.e., middle to late boll loading). Sampling dates were 18 June and 17 September in 1990 and 12 June and 2 August in 1991. Corresponding leaf area index values for the respective sampling dates were approximately 1.0 and 4.0 in 1990, and 0.7 and 3.0 in 1991. In 1990, the cumulative irrigation amount at the initial harvest was similar in wet and dry plots (i.e., 635 mm). At the second harvest in the same year the irrigation amounts were similar to the seasonal totals previously stated. At the first harvest in 1991, irrigation amounts were 385 and 335 mm for wet and dry plots, respectively. At the last harvest in 1991, the respective amounts of applied irrigation water were 740 and 560 mm for wet and dry plots.

A total of eight root samples per study plot were collected at the first harvest in 1990 and at both harvests in 1991. Four root samples per plot were collected at the second harvest in 1990. The simple spade method (Bohm, 1979) was used to gather data on the root system in the upper soil horizon. To loosen the soil, drain spades were inserted into the profile about 25 cm away from the row (one spade on each side of row) to a depth of about 30 cm; drain spades or hand trowels were inserted only to a depth of about 15 cm perpendicular to row center to avoid damaging irrigation lines located directly below the crop row. After loosening, the soil clump containing the taproot and attached lateral roots was carefully removed by hand, labeled, and placed in plastic bags for storage in coolers. The roots collected were those associated with aboveground plants that were harvested for dry matter production (Prior et al., 1994b). All samples were immediately transported in a large custom-built cooler (i.e., with bags of ice) by truck to Auburn, AL, and placed in cold storage (4°C) until processing. Roots (taproot and attached laterals) were washed free of soil by first soaking samples in water and using gentle agitation. Any remaining soil was removed by using a soft bristle brush. After the samples were cleaned they were stored in 20% ethanol (Bohm, 1979) at 4°C until measurements were made. First order lateral roots were removed from the taproot and measurements made on each separately. Successive branching orders (secondary, tertiary, etc.) were not measured. Measurements made on the taproot included diameter, length, volume (based on water displacement), and dry weight and density (dry weight per unit volume). Diameter measurements were made with a digital caliper at three locations: below the root collar (top), midway along the taproot's length (middle) and just above the broken end of the taproot (bottom). Measurements made on the first order lateral roots were similar to those made on the taproot except that detailed measures of root diameter were not taken.

At the reproductive sampling in both years, an additional

[1] Trade names and products are mentioned solely for information. No endorsement by the USDA is implied.

eight plants were selected for vertical root-pulling resistance measurements (Bohn, 1979). A manual winch (Model No. 527, Fulton, Milwaukee, WI) mounted onto a portable metal tripod and a cable gripping tool (Model No. 72285K8, Klein Tools, Chicago, IL) attached to the cotton stalk were used to break the roots from the soil; a scale (Model No. 8920, Hanson, Northbrook, IL) set up to measure the peak force (load kg plant^{-1}) required to uproot the plant was used. Plants adjacent to pulled plants were not sampled in subsequent measurements.

All statistical analyses were performed using the general linear models procedure of the Statistical Analysis System (SAS Inst., 1985). Differences were considered significant at the $P < 0.10$ level.

RESULTS AND DISCUSSION

Vegetative Phase

Root morphological data collected during the vegetative phase are shown in Table 1. Differential irrigation had no effect in either year. In 1990, the water stress treatment had only been implemented 7 d prior to sampling. Although the differential water treatment had been ongoing for more than 4 wk in 1991, the difference in cumulative irrigation amounts between wet and dry treatments were small (i.e., 385 vs. 335 mm). In the FACE experiment, early season leaf water potential were similar regardless of the irrigation level and CO_2 treatment (Bhattacharya et al., 1994). Others have reported that small plant size in conjunction with soil water deficits being too low may cause small differences in whole plant water deficit during early season growth stages (Sionit and Kramer, 1976; Prior et al., 1991).

Table 1. Cotton taproot and lateral root variables: length, diameters, dry weight, volume, and density under ambient and CO_2-enriched conditions, June 1990 and 1991. Means and probabilities are shown.

	CO_2 concentration, μmol mol^{-1}		
	370	550	Pr > F†
	June 1990		
Taproot			
Length, cm	33.3	36.7	0.44
Top diam., mm	11.1	12.8	0.0001
Mid diam., mm	3.0	3.3	0.13
Bottom diam., mm	1.2	1.4	0.05
Volume, cm^3	8.5	12.4	0.03
Dry wt., g	1.45	2.35	0.03
Density, g cm^{-3}	0.17	0.19	0.003
	Laterals		
Length, cm	218.3	262.9	0.15
Number	36.3	45.3	0.06
Volume, cm^3	2.3	3.6	0.001
Dry wt., g	0.27	0.52	0.04
Density, g cm^{-3}	0.12	0.15	0.001
	June 1991		
Taproot			
Length, cm	19.4	22.7	0.27
Top diam., mm	5.8	7.1	0.02
Mid diam., mm	2.5	3.1	0.002
Bottom diam., mm	1.0	1.0	0.57
Volume, cm^3	2.53	3.61	0.01
Dry wt., g	0.39	0.63	0.01
Density, g cm^{-3}	0.15	0.22	0.24
Laterals			
Length, cm	74.5	101.6	0.01
Number	21.4	24.2	0.08
Volume, cm^3	0.55	0.74	0.27
Dry wt., g	0.05	0.09	0.03
Density, g cm^{-3}	0.11	0.12	0.65

† Probability of greater F value by chance.

Relative differences in root variables observed between years may be attributable to less water being applied between planting and sampling in 1991. The cumulative irrigation amount at this sampling was about ~635 and ~360 mm in 1990 and 1991, respectively. Changes in irrigation amounts were related to the different methods of estimating evapotranspiration in the 2 yr (for details see Mauney et al., 1994). In addition, year-to-year weather differences could also help explain the variable root responses observed between years; cooler nighttime temperatures in 1991 probably contributed to slower crop establishment and growth resulting in plants with a less developed root system.

The effects of CO_2 enrichment on taproot and associated first order lateral roots are shown in Table 1. The larger taproot diameters observed in 1990 (top and bottom diameters) and 1991 (top and middle diameters) under FACE account for substantial increases in taproot dry weight (62%) and volume (40%). Measurements of lateral root volume were significant only in 1991. Additional CO_2 substantially increased lateral root dry weight in 1990 (48%) and 1991 (80%). The larger diameter taproots of FACE plants did support significantly greater numbers of lateral roots. Although fine root length and dry weight densities taken from soil core increments approximating taproot excavation depth at this sampling, showed enhancements because of FACE (Prior et al., 1994a), extra CO_2 increased lateral length only in 1990, but had no effect on taproot length in either year. The breakage and loss of roots during the excavation procedure probably contributed to inaccurate assessment of taproot and lateral root length. This may have been more of a problem in 1991 since the overall smaller root system seen at this time was probably composed of fleshier roots. This may be a reason that increases in taproot and lateral root tissue density because of additional CO_2 were observed in 1990 but not in 1991. Nevertheless, in those cases where differences were noted (1990), such CO_2-induced changes may be related to internal structural modifications (e.g., alterations in cell size and number, carbohydrate storage, and possibly more suberization). A recent investigation using roots from CO_2-enriched soybean plants grown in chambers has shown increases in stele diameter, cortex width, and root diameter in the root hair zone (Rogers et al., 1992b). Field studies of this nature have not been done, but will be needed if elevated CO_2 effects on root tissue makeup and function are to be determined.

Reproductive Phase

Taproot and associated laterals as affected by water regime and CO_2 concentration during reproductive growth are shown in Table 2. In both years, plants in both water regimes responded similarly to added CO_2 while the CO_2 by water interaction was nonsignificant; aboveground response of plants associated with this root

Table 2. Taproot and lateral root variables of cotton during reproductive growth: length, diameters, dry weight, volume, and density under ambient conditions and CO_2 enrichment, and two water regimes. Means and probabilities are shown.

	CO_2 level, μmol mol^{-1}			Soil water content		
	370	550	Pr > F†	Wet	Dry	Pr > F†
			September 1990			
Taproot						
Length, cm	37.0	40.4	0.05	38.4	39.0	0.71
Top diam., mm	15.5	17.2	0.02	16.9	15.8	0.06
Mid diam., mm	5.4	5.5	0.41	5.7	5.3	0.16
Bottom diam., mm	1.9	2.1	0.28	2.0	2.1	0.40
Volume, cm^3	23.1	29.1	0.08	27.7	24.5	0.03
Dry wt., g	7.8	10.6	0.07	9.4	9.0	0.58
Density, g cm^{-3}	0.34	0.37	0.33	0.34	0.37	0.05
Laterals						
Length, cm	470.8	574.7	0.19	545.0	500.5	0.38
Number	31.8	39.0	0.21	37.0	33.8	0.10
Volume, cm^3	5.9	7.4	0.25	6.8	6.4	0.75
Dry wt., g	1.2	1.8	0.01	1.5	1.5	0.71
Density, g cm^{-3}	0.32	0.30	0.73	0.30	0.32	0.80
			August 1991			
Taproot						
Length, cm	36.4	40.3	0.16	40.1	36.6	0.02
Top diam., mm	12.1	14.0	0.01	13.7	12.4	0.0001
Mid diam., mm	5.5	6.2	0.06	6.1	5.6	0.31
Bottom diam., mm	1.6	2.1	0.02	1.9	1.9	0.97
Volume, cm^3	15.65	21.04	0.01	20.9	15.8	0.0001
Dry wt., g	4.57	7.28	0.001	6.4	5.4	0.01
Density, g cm^{-3}	0.29	0.43	0.20	0.31	0.42	0.28
Laterals						
Length, cm	238.5	283.1	0.05	291.6	230.0	0.03
Number	30.7	34.5	0.02	35.0	30.1	0.12
Volume, cm^3	3.94	5.70	0.13	5.3	4.3	0.04
Dry wt., g	0.69	1.23	0.05	1.03	0.88	0.15
Density, g cm^{-3}	0.17	0.20	0.03	0.20	0.19	0.88

† Probability of greater F value by chance.

sampling also showed no significant CO_2 by water interaction (Prior et al., 1994b). Other studies have shown that water-stressed plants exhibited a greater stimulatory effect over well-watered plants because of CO_2 enrichment; such responses have been noted for aboveground growth as well as for roots (Rogers et al., 1994). In this study, although water stress did have a negative impact on measured root variables (see below), the level of water stress may not have been great enough to elicit root responses as noted in other studies. In the FACE experiment, leaf water potential differences were generally small throughout most of the growing season across both water regimes and CO_2 treatments (Bhattacharya et al., 1991, 1994). Open-top field chambers studies conducted with cotton to investigate water stress-CO_2 interactions noted that the relative stimulation of additional CO_2 was unaffected by water stress (Kimball and Mauney, 1993). The discrepancy in observed responses between these studies may be related to different responses of plant species to CO_2 enrichment or to the different methodologies used in these experiments (Rogers et al., 1994). In the first year of the present study (1990), low soil water availability reduced taproot top diameter, volume, tissue density, and the total number of first order lateral roots. In 1991, taproot length, top diameter, volume, and dry weight were significantly reduced by water stress. The dry treatment reduced total lateral length and volume.

Changes in the taproot/lateral root system of cotton during reproductive growth because of elevated CO_2 were similar to those observed by Rogers et al. (1992a) under well-watered conditions. The larger diameter taproots found under FACE in 1990 (top diameter) and 1991 (top, middle, and bottom diameters) probably led to the greater increases in taproot volumes of 26 and 34% observed in each respective year. These changes were accompanied by substantial increases in taproot dry weight. Elevated CO_2 increased this measure by 36 and 59% in 1990 and 1991. Substantial increases in total lateral dry weights of 50 and 78% were seen in each respective year. Such large increases are important since these may influence soil carbon storage in addition to microbial activity. In addition, the larger root system observed here may represent greater carbohydrate storage. Hendrix et al. (1994) reported that regardless of water level, the FACE treatment resulted in greater taproot nonstructural carbohydrate storage that fluctuated strongly during the season; changes in carbohydrate content were thought to be due to the metabolic requirements of the developing crop. Significant increases in carbohydrate pools are needed during boll filling and to ensure root growth for continued exploration of the soil profile to meet nutrient and water demands during peak demand periods. The high metabolic requirement of developing cotton bolls (i.e., carbohydrate sinks) may be a reason why changes in root tissue density (i.e., assuming that changes in carbohydrate storage affects tissue density) under CO_2-enriched conditions were variable (Table 2). For taproot and total lateral root density, no significant CO_2 by water treatment interaction was detected in either

year, indicating that response to water stress was similar regardless of CO_2 level. In fact, the only notable response to water stress occurred with total lateral tissue density in 1990. The only increase in root tissue density because of CO_2-enriched conditions occurred with the lateral roots in 1991.

The overall larger taproot found under CO_2-enriched conditions generally supported greater numbers of lateral roots, but the total lateral volumes were similar across CO_2 treatments in both years. Taproot and lateral length was higher only in 1990 because of CO_2 enrichment. It is important to note, however, that increases in fine root density (i.e., data collected from soil cores) on both a length and dry weight basis because of FACE were observed at this sampling (Prior et al., 1994b). A limitation of the excavation sampling method used in our study is that the whole taproot with its laterals cannot be collected; this may have been more of a problem in 1991 since the smaller root system seen here was probably composed of fleshier roots that were susceptible to breakage and loss during the excavation and washing procedures. Chaudhuri et al. (1986) reported that well-watered sorghum [*Sorghum bicolor* (L.) Moench.], a fibrous rooted plant, exhibited increased root number, weight, and length in response to elevated CO_2 during reproductive growth. In their root box study, however, root measures were reflective of the whole soil profile.

Maize (*Zea mays* L.) breeders have used the method of vertical root-pulling resistance to evaluate plant standability (see Bohm, 1979 for review; Beck et al., 1987). Maize hybrids exhibiting high vertical root-pulling resistance had the greatest root volume, dry weight, number of lateral roots, and tensile strength of thick diameter root sections (Beck et al., 1988). At the reproductive sampling in our study, water stress had no effect on this measure, however, CO_2 enrichment had a substantial effect on the peak force required to remove the taproot system from the soil (Fig. 2). Vertical root-pulling resistance was increased by 34 and 37% in each respective year because of CO_2 enrichment. As previously noted, plants grown under CO_2 enrichment had larger diameter taproots that exhibited large increases in both dry weight and volume; increases in lateral dry weight were also seen whereas changes in lateral volume and root number were more variable (Table 2). The difference in vertical root-pulling resistance observed between years was attributed to the overall larger taproot system seen in 1990 relative to 1991. Increases in vertical root-pulling resistance because of CO_2 enrichment may not only be important for plant standability, but may also be important in conservation till systems where stabilization of the soil matrix (i.e., due to a larger taproot system) is critical on highly erodible land in terms of minimizing wind and water erosion.

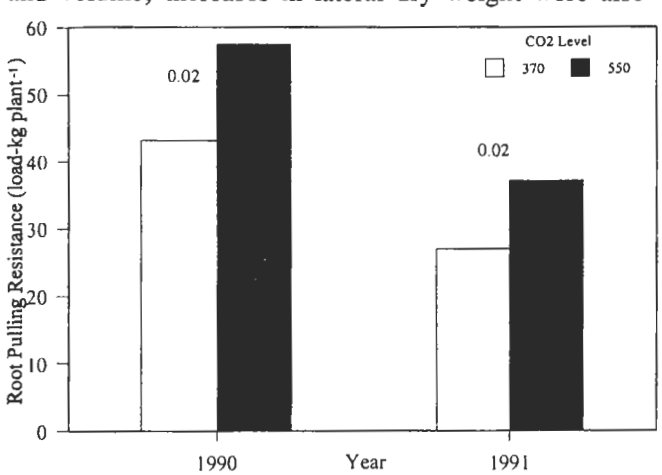

Fig. 2. Vertical root pulling resistance for cotton at the reproductive sampling in 1990 and 1991. Means and probabilities are shown.

SUMMARY AND CONCLUSIONS

Collectively, CO_2-induced increases in the growth of the taproot and associated lateral roots resulted in a larger root system that may ensure better crop stand production. The larger taproot diameter seen under FACE conditions may allow for more photosynthate storage and translocation to greater numbers of lateral roots. The development of more robust taproot systems in CO_2-enriched environments may lead to a more thorough exploration of the soil profile, thus allowing a greater exploitation of available nutrients and water, especially during periods of peak demand such as boll filling.

Our results show that elevated CO_2 leads to increases in the dry weight of taproots and their associated laterals. Implications of such changes including their impact on microbial activity as well as carbon cycling and storage require further study. Plant rooting in a high CO_2 environment may not only affect microbial processes, but could result in physicochemical changes that would alter soil physical properties. Stabilization of the soil matrix because of the larger taproot system found under CO_2-enriched conditions can be inferred from the observed increases in vertical root-pulling resistance; this may have important implications towards reducing wind and water erosion in conservation till systems used on highly erodible lands.

Results from this investigation indicate that increases in atmospheric CO_2 can alter the morphological makeup of cotton root systems. Further research is warranted if plant root responses to CO_2 concentration are to be fully understood. In fact, much more work will be needed if we are to explain the detailed aspects of root structure, function, and interaction with edaphic factors within CO_2-enriched agricultural ecosystems.

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