Plant and Soil **255:** 179–187, 2003.

The effects of elevated atmospheric CO_2 and soil P placement on cotton root deployment

S.A. Prior[1,3], H.H. Rogers[1], G.L. Mullins[2] & G.B. Runion[1]
[1]*U.S. Department of Agriculture-Agricultural Research Service, National Soil Dynamics Laboratory, 411 South Donahue Drive, Auburn, AL 36832, USA.* [2]*Department of Crop and Soil Environmental Sciences, 422 Smyth Hall, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA.* [3]*Corresponding author**

Received 3 May 2002; accepted in revised form 15 November 2002

Key words: carbon dioxide, global change, *Gossypium hirsutum*, P uptake, root distribution, soil phosphorus

Abstract

Root proliferation into nutrient rich zones is an important mechanism in the exploitation of soil nutrients by plants. No studies have examined atmospheric CO_2 effects on cotton (*Gossypium hirsutum* L.) root distribution as affected by localized phosphorus (P). Cotton plants were grown in a Troup sand (loamy, thermic Grossarenic Kandiudults) using 17.2-l containers placed in open top field chambers (OTC) under ambient (360 μmol mol^{-1}) or enriched (720 μmol mol^{-1}) atmospheric CO_2 concentrations for 40 days. Equivalent amounts of P were added (150 mg P per kg of soil) to 100, 50, 25, 12.5, and 6.25% of the total soil volume; control containers with no added P were also included. Under extremely low P (controls), cotton was unresponsive to CO_2 enrichment. In treatments with both fertilized and unfertilized soil volumes, root proliferation was greater in the unfertilized soil under elevated CO_2 conditions. Stimulation of root growth occurred in the P-fertilized soil fraction; the pattern of stimulation was similar under both CO_2 levels. Under ambient CO_2, cotton plant response was positive (shoot mass, and total root mass and length) when soil P was confined to relatively small proportions of the total soil volume (6.25 and 12.5%). However, elevated CO_2 grown plants tended to respond to P regardless of its distribution.

Abbreviations: FACE – free fir CO_2 enrichment; OTC – open top chambers; P – phosphorus; TSV – total soil volume

Introduction

The unprecedented rise in atmospheric CO_2 concentration (Keeling and Whorf, 1994) attributed to accelerated activities such as fossil fuel consumption and land use change (Houghton et al., 1992) is expected to continue (Bolin et al., 1986). Since CO_2 is the essential substrate for photosynthesis, there is interest in how this CO_2 rise will affect fundamental crop processes in highly managed agricultural systems.

Most reports on the effects of elevated CO_2 on plants have placed emphasis on aboveground responses (Amthor, 1995; Kimball, 1983; Pritchard et al., 1999; Rogers and Dahlman, 1993). By comparison, effects of CO_2 on belowground processes have received far less attention. However, it has been suggested that the largest proportion of extra biomass under elevated CO_2 can occur belowground (Rogers et al., 1994, 1997). Some controlled environment experiments have demonstrated CO_2-induced root increases (i.e., mass and/or length) in the upper soil depths (Chaudhuri et al., 1990; Del Castillo et al., 1989), suggesting a more thorough exploration of a given soil volume; others report root increases at all soil depths (Chaudhuri et al., 1986; Rogers et al., 1992) or that roots of CO_2 enriched plants may reach deeper (Rogers et al., 1992), implying that the volume of soil explored may be greater.

Recent field studies, utilizing systems such as open top chambers (OTC) and free-air CO_2 enrichment

* FAX No: +1-334-887-8597
E-mail: sprior@acesag.auburn.edu

(FACE), have shown that elevated CO_2 can increase both above- and belowground biomass (Kimball et al., 1995; Mauney et al., 1994; Prior et al., 1994b), alter plant root morphology (Prior et al., 1995), and alter the root system's capacity to explore soil volume through shifts in fine root distribution patterns (Prior et al., 1994a, b; Weschsung et al., 1995, 1999). These changes in rooting patterns may influence nutrient dynamics, thus influencing crop performance when nutrient demand is high. Whole plant nutrient uptake is often higher, while tissue nutrient concentration is reduced for CO_2-enriched plants (Prior et al., 1998; Rogers et al., 1994, 1997).

Shifts in rooting patterns may alter their competitive effectiveness for edaphic resources. Root proliferation into nutrient rich zones can be an important mechanism in the exploitation of soil resources (Borkert and Barber, 1985; Jackson and Caldwell, 1989). Phosphorus (P) is an essential resource required to maintain optimum crop yields (Barber, 1984); precise management of P fertilizer is also an important consideration in environmentally sensitive areas with regard to reducing runoff into adjacent waterways. Understanding how crop root distribution patterns are altered by P placement and the relationship to P uptake is essential for the formulation of optimal fertilization practices. The ability of crops to acquire P from soil can be influenced by available soluble P in bulk soil, root morphological characteristics, root distribution patterns, and the solubilization of P within the rhizosphere by root exudates and/or microbial activity. Root growth stimulation in P-fertilized portions of the soil has been reported for several important crops (e.g., corn, Anghinoni and Barber, 1980; soybean, Borkert and Barber, 1985; wheat, Yao and Barber, 1986); however, no studies have evaluated elevated atmospheric CO_2 effects on crop root distribution in P-rich environments. Our objective was to examine these effects on cotton rooting patterns as affected by localized P in decreasing soil volumes.

Materials and methods

The soil series used in this study was a Troup sand (loamy, thermic Grossarenic Kandiudults). This soil was from the A horizon of an uncultivated field which had not been fertilized. The test soil had an average cation exchange capacity of 2.68 $cmol_c\ kg^{-1}$, organic matter content of 9.5 $g\ kg^{-1}$, and pH of 4.8. Regional soil test results (Mehlich I extractible) indicated that phosphorus (1.5 mg kg^{-1}) and potassium (10.5 mg kg^{-1}) were in the very low range, while magnesium (7.5 mg kg^{-1}) and calcium (32.5 mg kg^{-1}) were in the low range; soil test recommendations were followed to adjust nutrient status (Cope et al., 1980). The soil was sieved (6 mm) to remove plant debris and stones, and to assure uniform mixing. The soil was spread onto a large plastic sheet (20 mil) placed on the floor of a greenhouse (8 cm deep) and allowed to dry to about 10% water (w/w) before fertilizer addition. Potassium was applied as K_2SO_4 at a rate of 75 mg per kg of soil. Magnesium was applied as $Mg(OH)_2$ and calcium as $Ca(OH)_2$ to give respective rates of 52 mg Mg and 544 mg Ca per kg of soil. A complete complement of micronutrients was also added to the soil (Allen et al., 1976). A soil mixer was used to throughly distribute fertilizer within the soil. After fertilizer additions, the soil was placed back onto the greenhouse floor and lightly wetted, using a standard garden hose spray nozzle; this wetting process was repeated until the soil was near saturation. The soil was then allowed to dry to about 10% water (w/w) and was sieved; this entire process was repeated, giving two complete drying cycles. The base rate of 150 mg P per kg of soil, added as monocalcium phosphate, was mixed with 100, 50, 25, 12.5, and 6.25% of the total soil volume (TSV) of the container. Therefore, P rates (mg kg^{-1}) in the proportion of the soil volume receiving P fertilization (rates increased as volume decreased) were 150 in 100%, 300 in 50%, 600 in 25%, 1200 in 12.5%, and 2400 in 6.25%. Nitrogen was added at 50 mg kg^{-1} as a mixture of ammonium nitrate and potassium nitrate. The nitrogen solution supplied NH_4-N and NO_3-N at a ratio of 1:3.5. This solution was applied at planting and again 3 weeks later.

Containers (17.2-l) were filled with soil at a bulk density of 1.37 g cm^{-3}. The P-treated soil was separated vertically from the non-P soil by a mesh (1.67 mm) fiberglass screen which minimized mixing of the two soil zones while allowing roots to grow freely in the container. All zones extended from the top to the bottom of the container (Figure 1). Custom-made vertical plates (equipped with adjustable spacers) were set to the desired volume before mesh screen placement; after filling the non-P and P-treated zones, plates were carefully removed leaving the mesh screen in place. The vertical distribution pattern was similar to the layout reported by Borkert and Barber (1985). Control containers with no added P were also included. Cotton seeds (Sure-Grow 125) were screened for uniformity before planting at a rate of four per container. All pots

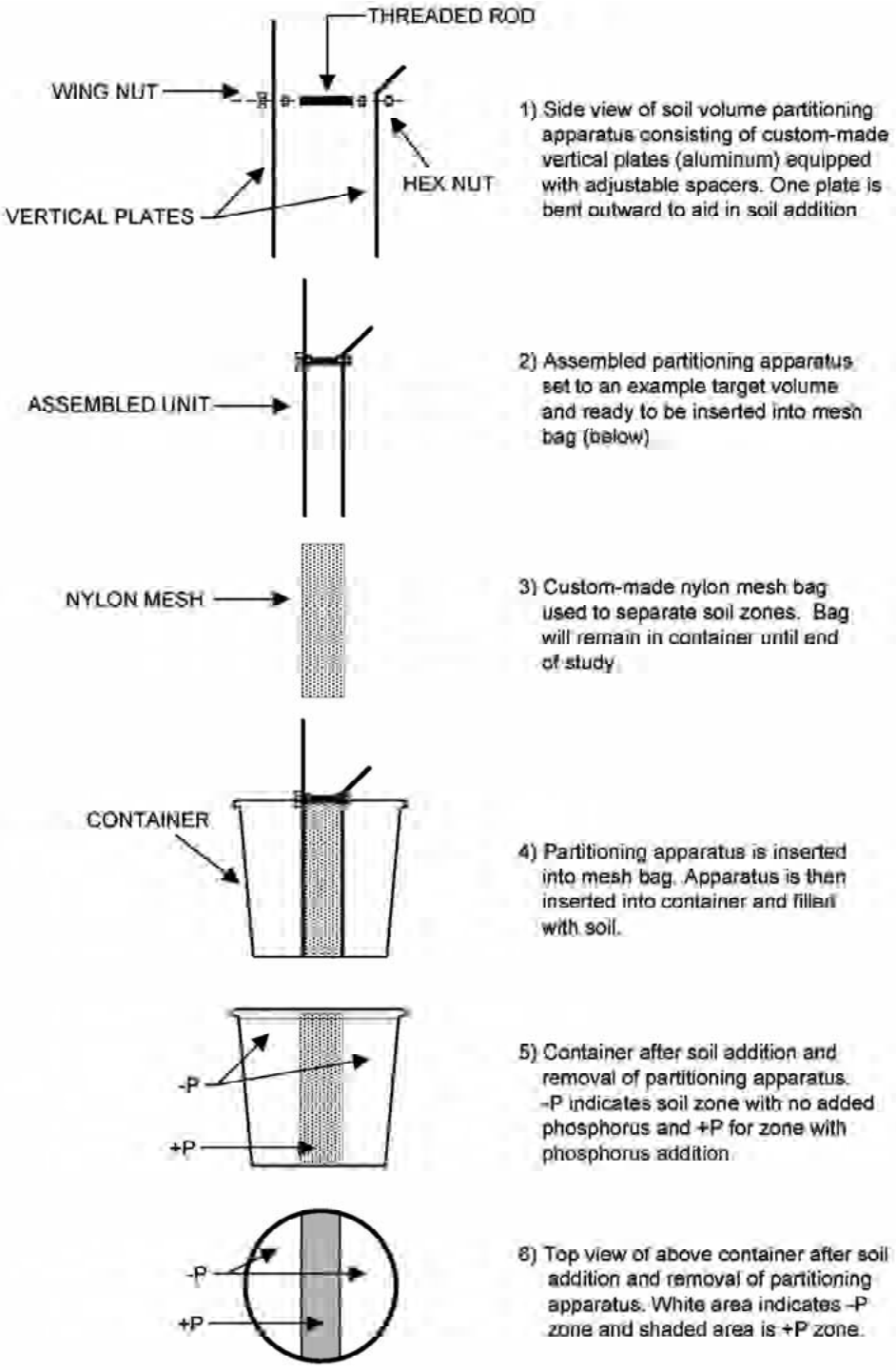

Figure 1. Conceptual drawing of methods used for filling a container with soil for a hypothetical P treatment.

were irrigated with deionized water every 2 days for the first 2 weeks; thereafter, plants were irrigated daily.

Plants were exposed to ambient (360 μmol mol^{-1}) or elevated (720 μmol mol^{-1}) CO_2 within an open top chamber system (OTC) described by Rogers et al. (1983) with slight modification (Mitchell et al., 1995). The open top field chambers were constructed of a structural aluminum frame (3 m in diameter by 2.4 m in height) covered with a PVC film panel (0.2 mm thickness). Carbon dioxide was supplied from a 12.7 Mg liquid CO_2 receiver through a high volume dispensing manifold and the atmospheric CO_2 concentration was elevated by continuous injection of CO_2 into plenum boxes. Air was introduced into each chamber through the bottom half of each chamber cover which was double-walled; the inside wall was perforated with 2.5-cm diameter holes to serve as ducts to distribute air uniformly into the chamber. Three chamber volumes were exchanged every minute. Carbon dioxide concentrations were continually monitored (24 h day^{-1}) using a time-shared manifold with samples drawn through solenoids to an infrared CO_2 analyzer (Model 6252, LI-COR, Inc., Lincoln, NE).* Values were continually recorded every 15 or 30 min for each chamber, depending upon whether or not an additional CO_2 study was on line; the monitoring system was computer controlled with continuous data acquisition of CO_2 concentrations. All chambers were fitted with Teflon (5 mil FEP) rain covers to exclude rainfall.

The chamber system was located at the soil bin facilities at the USDA-ARS National Soil Dynamics Laboratory, Auburn, AL (Batchelor, 1984). The bin used for the experimental set-up was 6 m wide and 76 m long and was modified for container studies; modifications consisted of installing a geomembrane liner (20 mil) and gravel drain system to ensure a good working surface and drainage for container studies.

Treatments were arranged in a split-plot design with five replications. Carbon dioxide treatments (main plots) were randomly assigned to chambers. Phosphorus treatments (subplots) were randomly assigned to containers within each chamber.

Destructive harvest occurred after 40 days of CO_2 exposure. Shoots were oven dried (55 °C) to a constant weight and dry weight recorded. Root length and fresh and dry root weight for each soil compartment were determined separately. For each compartment, roots were separated from soil using a hydropneumatic elutriation system (Smucker et al., 1982; Gillison's Variety Fabrication, Benzonia, MI) 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, Port Melbourne, Australia), roots dried as above, and dry weight recorded. Mean root diameter was calculated using root volume and length (Schenk and Barber, 1979). Shoots were ground to pass a 2-mm screen and analyzed for P using a dry ash procedure (Hue and Evans, 1986). Duplicate subsamples of ground tissue were heated in a muffle furnace for 4.5 h at 450 °C. The resulting ash was then dissolved in 1 *M* HNO_3 and 1 *M* HCl, successively. Phosphorus was then measured by inductively coupled plasma spectrophotometry (ICP 9000, Thermo Jarell-Ash Corp., Franklin, MA).

Data analysis was conducted using the Proc Mixed procedure of the Statistical Analysis System (Littell et al., 1996). Error terms appropriate to the split-plot design were used to test the significance of main effects variables and their interactions. In all cases, differences were considered significant at the $P \leq 0.05$ level.

Results and discussion

The nutrient status of plants is largely regulated by soil nutrient supply and root system development which determines the extent of nutrient extraction from the soil profile and subsequent growth response. In agroecosystems, P is an essential resource which needs to be applied in amounts sufficient to optimize yield (Barber, 1984). In the current study, quantity of P added per container remained constant for all treatments except the control, where no P was added. Relative to treatments with P addition, root variables for the control treatment (length and mass) were depressed, demonstrating that available soil P was low (Table 1); likewise, shoot variables reflected this condition (Table 2). Previous studies have also shown that low soil P severely limits growth of crops (e.g., Barber, 1984); therefore, our observations were not surprising and exemplify the chronic response expected of cotton grown in previously uncultivated soil with no history of P fertilizer addition.

In the control treatment (no added P), which exhibited severely limited growth, elevated CO_2 had no effect on either above- or belowground growth vari-

* Trade names and products are mentioned solely for information. No endorsement by USDA is implied.

Table 1. Effects of applying the same P rate per container, in decreasing soil volumes, on root variables for cotton grown under two levels of atmospheric CO_2; means of five replications shown.

		CO_2 concentration (μmol mol^{-1})					
		360	720		360	720	
P added (mg kg^{-1})	Soil volume (%)	Root dry mass[a] (g plant^{-1})		Pr > F [b]	Root length (m plant^{-1})		Pr > F [b]
0	100	0.06c	0.06e	ns	5.7f	4.9d	ns
150	100	0.36b	0.59b	**	44.4bc	72.4a	**
300	50	0.20c	0.49bc	**	29.7cd	51.3b	**
0	50	0.20c	0.37c	**	26.4de	33.7c	ns
600	25	0.12c	0.21d	ns	14.3ef	18.6d	ns
0	75	0.40ab	0.62b	**	41.9bc	53.0b	tr
1200	12.5	0.09c	0.17de	ns	10.9f	15.6d	ns
0	87.5	0.54a	0.88a	***	56.5ab	83.1a	**
2400	6.25	0.18c	0.08de	ns	7.8f	8.3d	ns
0	93.75	0.41ab	0.91a	***	63.1a	84.8a	**

[a] Means for a variable in a column followed by same letter are not different ($\propto$= 0.05).
[b] Difference between CO_2 treatment; * = $0.01 < p \leq 0.05$; ** = $0.0001 < p \leq 0.01$; *** = $p \leq 0.0001$; tr (trend) = $0.05 < p \leq 0.15$.

Table 2. Effects of applying the same P rate per container, in decreasing soil volumes, on shoot variables for cotton grown under two levels of atmospheric CO_2; means of five replications shown.

		CO_2 concentration (μmol mol^{-1})								
		360	720		360	720		360	720	
P added (mg kg^{-1})	Soil volume (%)	Shoot dry mass[a] (g plant^{-1})		Pr > F [b]	Shoot P concentration (g kg^{-1})		Pr > F[b]	Shoot P content (g P plant^{-1})		Pr > F[b]
0	100	0.22c	0.20d	ns	1.06d	0.85d	ns	0.23c	0.17d	ns
150	100	9.24b	13.75c	***	3.20b	2.57ab	**	28.57b	32.76c	tr
300	50	10.78ab	18.30ab	***	3.73a	2.70a	***	38.68a	47.65a	**
600	25	10.49ab	17.11b	***	3.08b	2.32ab	**	31.37b	38.83b	**
1200	12.5	12.06a	19.00a	***	2.51c	2.20bc	tr	29.32b	40.40b	***
2400	6.25	12.15a	18.05ab	***	2.67c	1.82c	**	31.54b	31.67c	ns

[a] Means within a column followed by same letter are not different ($\propto$ = 0.05).
[b] Difference between CO_2 treatment; * = $0.01 < p \leq 0.05$; ** = $0.0001 < p \leq 0.01$; *** = $p \leq 0.0001$; tr (trend) = $0.05 < p \leq 0.15$.

ables (Tables 1 and 2). Limitations in CO_2-induced growth response have been reported for cotton (Rogers et al., 1993) and other species when P supply was deficient (Conroy, 1992; Cure et al., 1988; Goudriaan and De Ruiter, 1983; Rogers et al., 1993). Conroy (1992) suggested that insufficient P supply inhibits the increase in photosynthetic activity often observed under elevated CO_2. At low P conditions, a CO_2-induced growth response may be precluded due to starch accumulation in cotton leaves resulting from source-sink imbalance (Rogers et al., 1993). Phosphorus deficiency can reduce cotton leaf expansion (Radin and Eidenbock, 1984) which may also limit response to high CO_2. In the current study, upon P addition, cotton was more responsive to CO_2 enrichment (Tables 1 and 2). For example, when P was mixed with 100% of the soil volume, elevated CO_2 increased total root mass and length by approximately 60% (Table 1).

Although the amount of P applied per container remained constant, the P concentration in the fertilized compartment increased as the volume of this compartment decreased (Table 1). In treatments with both fertilized and unfertilized soil volumes, root mass was higher in unfertilized soil due to elevated CO_2; increases ranged between 55 and 122%. Root length exhibited more variability and the relative degree of increase under elevated CO_2 was smaller. In the unfertilized portion of soil volumes, elevated CO_2 significantly increased root lengths by 47 and 34% for the 12.5 and 6.25%TSV treatments, respectively; a

similar trend was noted for the 25%TSV treatment. In treatments with both fertilized and unfertilized soil volumes, root mass and length were often higher for fertilized soil under elevated CO_2, but differences were usually not significant; these measurements were increased only in the 50%TSV treatment (Table 1).

Previous P-placement studies conducted with crops raised under ambient CO_2 conditions have reported root growth stimulation in fertilized compared to unfertilized portions of the soil (e.g., corn, Anghinoni and Barber, 1980; soybean, Borkert and Barber, 1985; wheat, Yao and Barber, 1986); when graphed, this root growth stimulation results in a relationship which lies above the line of equality. In the current study, we observed a similar relationship between the fraction of soil volume fertilized with P and the fraction of total root length in the P-fertilized soil zone (Figure 2), indicating a stimulation of root growth in the P-soil zones; further, this relationship was not altered by atmospheric CO_2 concentration.

Roots in the P-fertilized soil volumes had smaller mean root diameters relative to roots in the non-P soil (0.0493 and 0.0549 mm, respectively; $P = 0.0001$), a finding which has been observed with other crops (Barber, 1984). Under CO_2-enriched conditions, the mean root diameter (averaged over all soil treatments) was significantly larger than ambient grown plants (0.0553 and 0.0489 mm, respectively; $P = 0.0184$); no CO_2 by P interaction was observed. In a growth chamber study, roots of young CO_2-enriched soybean displayed increases in stele diameter, cortex width, and root diameter in the root hair zone (Rogers et al., 1992). Field studies with cotton showed that FACE increased root lineal density (Prior et al., 1994a), a measure that has been related to roots having larger diameters (Klepper, 1992). Shifts in root lineal density also coincided with increased taproot and lateral root tissue density (g cm^{-3}) observed under FACE (Prior et al., 1995). Collectively, such CO_2-induced changes may be associated with internal structural modifications such as more compact or denser tissue or alterations in carbohydrate storage, cell number, cell size, suberization or other structural changes.

Increases in root density under elevated CO_2 may facilitate exploitation of available soil nutrients. Total root mass and length (i.e., totals of both fertilized and unfertilized soil volumes within a container) were significantly increased by elevated CO_2 in most cases (Table 3). Under ambient CO_2 conditions, total root mass and length were higher in the 12.5 and 6.25%TSV treatments, relative to the 100%TSV treatment. Total root length under CO_2-enriched conditions showed this same pattern. However, total root mass under high CO_2 was higher (relative to the treatment with 100% P-soil mixture) when P was applied to any of the different soil fractions (i.e., 50–6.25%TSV). Carbon dioxide-induced shifts in rooting may affect crop production. Simulation models and sensitivity analysis have 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 like phosphorus (Nye and Tinker, 1977). Although the pattern of root growth stimulation in the P-fertilized soil fraction was similar under both levels of CO_2, absolute increases in total root density resulting from high CO_2 increases the likelihood of roots encountering and exploiting nutrient-rich patches which exist in variable soil environments found in the field.

Most CO_2 investigations have used plants grown in containers within controlled environments which may not represent the variable and complex environments found in the field (Rogers et al., 1994). Results from studies using containers that confine the root system may or may not be indicative of field responses, i.e., source-sink relationships may be affected (Arp, 1991; Thomas and Strain, 1991). Likewise, investigations of crop response to localized soil P (i.e., conducted under ambient CO_2 conditions) have used similar experimental setups; however, results from these container studies have shown similar results to field investigations (Barber, 1984). Further, CO_2-induced increases in belowground responses seen under controlled environments (Rogers et al., 1994) have also been supported by field findings (e.g., Prior et al., 1994b, 1995, 1997); therefore, it is plausible that results from the current study (which represents a bridge between growth chamber and in-ground studies) may reflect responses that would occur in the field. However, CO_2-induced responses of crop roots in P-rich zones requires validation under field conditions (i.e., observational data from field soil profiles).

Aboveground variables are shown in Table 2. As expected, cotton grown with no added P exhibited the lowest values for all shoot variables, and as observed with root variables, there was no effect of CO_2 treatment. Shoot mass was increased by CO_2 enrichment (49–70%) at all treatments with P addition. Tissue P concentration was often lowered by additional CO_2 at all treatments with added P (trend at 12.5%TSV), while shoot P content was increased at the 50, 25, and 12.5%TSV treatments; a similar trend for increase

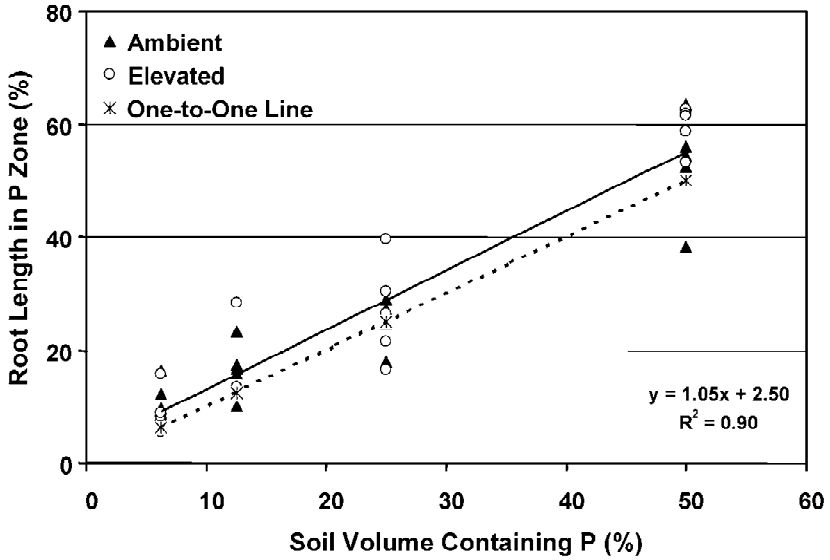

Figure 2. Percentage of the total root length found in the P soil zone (root length in P zone/total root length in container) for the various P soil volume treatments (6.25, 12.5, 25, and 50% of the total soil volume containing P). Means ($n = 5$) from each open top chamber are shown for the elevated (720 μmol mol^{-1}) and ambient (360 μmol mol^{-1}) CO_2 treatments. The linear equation describing this relationship, and associated R^2 statistic, are included.

Table 3. Effects of applying the same P rate per container, in decreasing soil volumes, on total root variables for cotton grown under two levels of atmospheric CO_2; means of five replications shown.

		CO_2 concentration (μmol mol^{-1})					
		360	720		360	720	
P added (mg kg^{-1})	Soil volume (%)	Total root dry mass[a] (g plant^{-1})		Pr > F [b]	Total root length (m plant^{-1})		Pr > F[b]
0	100	0.06d	0.06e	ns	5.7c	4.9c	ns
150	100	0.36c	0.59d	**	44.4b	72.4b	**
300	50	0.41bc	0.86bc	***	56.1ab	84.9ab	**
600	25	0.52ab	0.83c	**	56.2ab	71.6b	tr
1200	12.5	0.63a	1.04a	***	67.9a	98.7a	**
2400	6.25	0.58a	0.99ab	***	70.9a	92.2a	*

[a] Means within a column followed by same letter are not different ($\propto = 0.05$).
[b] Difference between CO_2 treatment; * = $0.01 < p \leq 0.05$; ** = $0.0001 < p \leq 0.01$; *** = $p \leq 0.0001$; tr (trend) = $0.05 < p \leq 0.15$.

P content was noted at the 100% TSV treatment. According to the literature, plant nutrient uptake is often higher and tissue nutrient concentration is lower in CO_2-enriched plants (Rogers et al., 1994, 1997). Shoot mass under ambient CO_2 conditions was higher (relative to the treatment with 100% P-soil mixture) in the 12.5 and 6.25% TSV treatments. Corresponding measures of P content were similar to the 100%TSV treatment due to lower tissue concentration. However, CO_2 enrichment increased shoot mass (relative to the 100% P-soil mixture) when P was applied to any of the different soil fractions (i.e., 50–6.25%TSV). Corresponding measures of P tissue concentration were similar (50, 25, and 12.5%TSV) or lower (6.25%TSV treatment) while P uptake was similar (6.25%TSV treatment) or higher (50, 25, and 12.5% TSV) when compared to the 100%TSV treatment.

Observed responses could influence nutrient management decisions in a future CO_2-enriched environment. Our findings suggest that cotton grown under ambient CO_2 was more dependent on P placement compared to that under elevated CO_2. Common practices used to apply P fertilizer are broadcasting followed by incorporation into a uniform soil volume

(i.e., plow layer) or banding which localizes fertilizer near the row. Localizing P fertilizer rather than broadcasting represent a means of increasing fertilizer efficiency when soil fixation is a factor (Anghinoni and Barber, 1980). Our results clearly indicate that P addition was required to optimize growth. Under ambient CO_2, the two most concentrated P fractions (12.5 and 6.25% TSV) were required for above- and below-ground biomass enhancement, whereas CO_2-enriched cotton exhibited increases across all P fractions. This observation is supported by field data wherein ambient CO_2 resulted in a cotton root system which was distributed close to row center, while CO_2 enrichment resulted in proportionately more of the root system allocated into interrow areas (Prior et al., 1994a). Thus, management strategies that use band application of P could be adjusted to match anticipated rooting patterns and may be more flexible under elevated CO_2 conditions. These findings also suggest that the entire soil management system should be studied in the context of anticipated changes in future environmental conditions.

Acknowledgements

The authors are indebted to Barry G. Dorman, Tammy K. Dorman, and William H. Bryce for technical assistance. Support from Terrestrial Carbon Processes Program of the Environmental Sciences Division, U.S. Department of Energy (Interagency Agreement No. DE-AI05-95ER62088) and the Alabama Agricultural Experiment Station, Auburn University, is gratefully acknowledged.

References

Allen S E, Terman G L and Clements L B 1976 Greenhouse techniques for soil-plant-fertilizer research. Bull. Y-104. Natl. Fertil. Dev. Center, Muscle Shoals, AL.

Amthor J S 1995 Terrestrial higher-plant response to increasing atmospheric [CO_2] in relation to the global carbon cycle. Global Change Biol. 1, 243–274.

Anghinoni I and Barber S A 1980 Phosphorus application rate and distribution in the soil and phosphorus uptake by corn. Agron. J. 44, 1041–1044.

Arp W J 1991 Effects of source-sink relations on photosynthetic acclimation to elevated CO_2. Plant Cell Environ. 14, 869–875.

Barber S A 1984 Soil Nutrient Bioavailability. A Mechanistic Approach. John Wiley and Sons, NY. 398 pp.

Batchelor J A Jr 1984 Properties of Bin Soils at the National Tillage Machinery Laboratory, Publ. 218. USDA-ARS National Soil Dynamics Laboratory, Auburn, AL. 16 pp.

Borkert C M and Barber S A 1985 Soybean shoot and root growth and phosphorus concentration as affected by phosphorus placement. Soil Sci. Soc. Am. J. 49, 152–155.

Bohm W 1979 Methods for Studying Root System, Ecological Series, Volume 33. Springer, New York. 188 pp.

Bolin B, Doos, B R, Jager J and Warrick R A 1986 Scope 29 – The Greenhouse Effect, Climatic Change, and Ecosystems. John Wiley & Sons, Chichester. 188 pp.

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.

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.

Conroy, J P 1992 Influence of elevated atmospheric CO_2 concentration on plant nutrition. Aust. J. Bot. 40, 445–456.

Cope J T Jr, Evans C E and Williams H C 1980 Soil test fertilizer recommendations for Alabama crops, Auburn, AL: Auburn University, Agricultural Experiment Station, Circular 251.

Cure J D, Rufty T W and Israel D W 1988 Phosphorus stress effects on growth and seed yield responses of non-nodulated soybean to elevated carbon dioxide. Agron. J. 80, 897–902.

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.

Goudriaan J and de Ruiter H E 1983 Plant growth in response to CO_2 enrichment, at two levels of nitrogen and phosphorus supply. 1. Dry matter, leaf area, and development. Neth. J. Agric. Sci. 31, 157–169.

Houghton J T, Callander B A and Varney S K 1992 Climate Change 1992: The Supplementary Report to the IPCC Scientific Assessment. Cambridge University Press, Cambridge. 200 pp.

Hue N V and Evans C E 1986 Procedures used for soil and plant analysis by the Auburn University soil testing laboratory. Departmental Series No. 106, pp. 1–31.

Jackson R B and Caldwell M M 1989 The timing and degree of root proliferation in fertile-soil microsites for three cold-desert perennials. Oecologia 81, 149–153.

Keeling C D and Whorf T P 1994 Atmospheric CO_2 records from the sites in the SIO air sampling network. *In* Trends '93: A Compendium of Data on Global Change, ORNL/CDIAC-65. Eds. T A Boden, D P Kaiser, R J Sepanski and F W Stoss. pp. 16–26. The Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN.

Kimball B A 1983 Carbon dioxide and agricultural yield: An assemblage and analysis of 430 prior observations. Agron. J. 75, 779–788.

Kimball B A, Pinter P J Jr, Garcia R L, LaMorte R L, Wall G W, Hunsaker D J, Wechsung G, Wechsung F and Kartschall Th 1995 Productivity and water use of wheat under free-air CO_2 enrichment. Global Change Biol. 1, 429–442.

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

Littell R C, Milliken G A, Stroup W W and Wolfinger R D 1996 SAS System for Mixed Models. Cary, SAS Institute, Inc., NC. 633 pp.

Mauney J R, Kimball B A, Pinter P J Jr, LaMorte R L, Lewin K F, 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. 70, 49–67.

Mitchell R J, Runion G B, Prior S A, Rogers H H, Amthor J S and Henning F P 1995 Effects of nitrogen on *Pinus palus-*

tris foliar respiratory responses to elevated atmospheric CO_2 concentration. J. Exp. Bot. 46, 1561–1567.

Nye P H and Tinker P B 1977 Solute Movement in the Soil-Root System. University of California Press, Berkeley, CA. pp 243–289.

Prior S A, Rogers H H, Runion G B and Hendrey G R 1994a Free-air CO_2 enrichment of cotton: Vertical and lateral root distribution patterns. Plant Soil 165, 33–44.

Prior S A, Rogers H H, Runion G B and Mauney J R 1994b Effects of free-air CO_2 enrichment on cotton root growth. Agric. For. Meteor. 70, 69–86.

Prior S A, Rogers H H, Runion G B, Kimball B A, Mauney J R, Lewin K F, Nagy J and Hendrey G R 1995 Free-air CO_2 enrichment of cotton: Root morphological characteristics. J. Environ. Qual. 24, 678–683.

Prior S A, Rogers H H, Runion G B, Torbert H A and Reicosky D C 1997 Carbon dioxide-enriched agro-ecosystems: Influence of tillage on short-term soil carbon dioxide efflux. J. Environ. Qual. 26, 244–252.

Prior S A, Torbert H A, Runion G B, Mullins G L, Rogers H H and Mauney J R 1998 Effects of CO_2 enrichment on cotton nutrient dynamics. J. Plant Nutr. 21, 1407–1426.

Pritchard S G, Rogers H H, Prior S A and Peterson C M 1999 Elevated CO_2 and plant structure: A review. Global Change Biol. 5, 807–837.

Radin J W and Eidenbok M P 1984 Hydraulic conductance as a factor limiting leaf expansion of phosphorus-decicient cotton plants. Plant Physiol. 75, 372–377.

Rogers G S, Payne L, Milham P and Conroy J 1993 Nitrogen and phosphorus requirements of cotton and wheat under changing atmospheric CO_2 concentrations. *In* Plant Nutrition – From Genetic Engineering to Field Practice. Ed. N J Barrow. pp 257-260. Kluwer Academic Publishers, Dordrecht, The Netherlands.

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

Rogers H H, Heck W W and Heagle A S 1983 A field technique for the study of plant responses to elevated carbon dioxide concentrations. Air Pollut. Cont. Assoc. J. 33, 42–44.

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

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

Rogers H H, Runion G B, Prior S A and Torbert H A 1997 Response of plants to elevated atmospheric CO_2: Root growth, mineral nutrition, and soil carbon. *In* Carbon Dioxide and Environmental Stress. Eds. Y Luo and H A Mooney. pp. 215–244. Academic Press, San Diego, CA.

Schenk M K and Barber S A 1979 Root characteristics of corn genotypes as related to P uptake. Agron. J. 71, 921–924.

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.

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.

Weschsung G, Weschsung F, Wall G W, Adamsen F J, Kimball B A, Garcia R L, Pinter P J Jr and Kartschall Th 1995 Biomass and growth rate of a spring wheat root system grown in free-air CO_2 enrichment (FACE) and ample moisture. J. Biogeogr. 22, 623–634.

Weschsung G, Weschsung F, Wall G W, Adamsen F J, Kimball B A, Pinter P J Jr, Kartschall Th, Garcia R L and LaMorte R L 1999 The effects of free-air CO_2 enrichment and soil water availability on spacial and seasonal patterns of wheat root growth. Global Change Biol. 5, 519–529.

Yao J and Barber S A 1986 Effect of one phosphorus rate placed in different soil volumes on P uptake and growth of wheat. Commun. Soil Sci. Plant Anal. 17, 819–827.