ATMOSPHERIC CO_2 ENRICHMENT OF COTTON: ROOT DISTRIBUTION AND NUTRIENT UPTAKE AS AFFECTED BY PHOSPHORUS PLACEMENT

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Abstract

Root proliferation into soil zones rich in nutrients is an important mechanism ensuring effective exploitation of soil nutrients by plants. No studies have examined the effects of atmospheric CO_2 enrichment on cotton (*Gossypium hirsutum* L.) root distribution patterns as affected by localizing P in decreasing volumes of soil. Cotton plants were grown in a Troup Sand using 17.2 liter containers placed in open top field chambers under ambient (360 ppm) or enriched (720 ppm) atmospheric CO_2 conditions 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 soil volume; control containers with no added P were also included. Under extremely low P (controls), cotton was not responsive to atmospheric CO_2 enrichment. In treatments with both fertilized and unfertilized soil volumes, root proliferation was greater in the unfertilized soil due to elevated CO_2 conditions. Stimulation of root growth occurred in the P-fertilized soil fraction; the pattern of stimulation was similar under both levels of CO_2. Under ambient CO_2, cotton plants showed positive responses (shoot dry weight, and total root dry weight and length) to soil P when it was confined to relatively small proportions of the soil volume (12.5 and 6.25%). However, elevated CO_2 grown plants tended to respond to P regardless of its distribution in the soil.

Introduction

The unprecedented discharge of CO_2 into the atmosphere (mainly from fossil fuel burning and land use change associated with industrial and/or population expansion) has led to a significant rise in its global concentration (Houghton et al., 1990). The current rate of atmospheric CO_2 accumulation is 1.8 ppm per year. Continued increases are expected. Since CO_2 is a primary feedstock to crop growth, questions concerning its influence on fundamental crop growth processes have arisen.

Over the last decade, most reports on the effect of elevated CO_2 on crop plants have concentrated on aboveground responses; the majority of these studies showed enhanced growth and yield (Kimball 1983; Rogers and Dahlman 1991). In comparison, fewer studies have evaluated the potential effects of CO_2 on root responses and other belowground processes.

A recent review by Rogers et al. (1994) has noted that a large proportion of the increase in phytomass production (due to increased C uptake and assimilation) under CO_2 enriched conditions is allocated belowground. Recent field studies have shown that cotton plants exposed to elevated CO_2 have more robust taproot systems (Prior et al., 1995); root length and dry weight densities are often increased both vertically and horizontally within the soil profile (Prior et al., 1994). These observations could have important implications for agro-ecosystems where such change might alter competitive effectiveness for edaphic resources. A number of studies conducted under ambient levels of atmospheric CO_2 have shown that root proliferation occurs in soil zones rich in P (Borkert and Barber, 1985; Jackson and Caldwell, 1989). However, no studies have evaluated how elevated CO_2 will affect root distribution patterns in nutrient rich environments. The objective of this study was to help fill this knowledge gap.

Materials and Methods

The soil series used in this study was a Troup Sand (loamy, siliceous Grossarenic Paleudalts). This soil was from the A horizon of uncultivated soil which had not been fertilized. The soil was sieved (6 mm) to remove plant debris and stones, and to establish a uniform mixture of soil. The soil was spread on the floor of a greenhouse (8 cm deep) and allowed to dry to about 10 % water (wt./wt.) 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 into the greenhouse as described above and taken through two complete drying cycles; soil was sieved after each cycle. 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 of the container. Therefore, rates in mg kg^{-1} of fertilized soil (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 at 3 weeks after planting.

Containers (17.2 liter) 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 fiber glass screen which minimized mixing of the two soil zones while allowing roots to grow freely in the container. Control containers with no added P were also included in the study. Cotton

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seeds (Sure-Grow 125) were screened for uniformity before being planted at a rate of 4 per container on 16 June 1995. All pots were irrigated with deionized water every two days for the first two weeks; thereafter, plants were irrigated on a daily basis.

Plants were exposed to ambient (360 ppm CO_2) or elevated (720 ppm CO_2) CO_2 within an open top chamber system; chambers, CO_2 supply, and monitoring system have been previously described for this study site (Mitchell et al., 1995). All chambers were fitted with Teflon rain covers to exclude natural rainfall. Containers were placed in chambers and exposures initiated on June 20, 1995.

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. Fresh and dry root weight, and root length for each soil compartment were determined separately. Root length was measured using a Comair Root Length Scanner (Hawker de Havilland, Port Melbourne, Australia), roots were dried as above, and dry weight recorded. Mean root diameter was calculated using root volume and length as described by Schenk and Barber (1979). Shoots were analyzed for P using procedures described by Mullins and Burmester (1990).

Analysis was conducted using the GLM procedure of the Statistical Analysis System (SAS, 1985). 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

Although the amount of P applied per container remained constant, the P concentration in the fertilized compartment increased as this volume decreased. The only exception was the control where no P was added to the soil. Fine root distribution on a length and dry weight basis as affected by P placement and atmospheric CO_2 levels are shown in Table 1. Both root variables were extremely low for plants grown with no added P, demonstrating that the amount of available soil P was limiting plant growth. Carbon dioxide treatment had no affect under this condition. Mixing P with 100% of the soil volume resulted in much larger plants and CO_2 enrichment increased fine root dry weight and length by about 63%. In treatments with both fertilized and unfertilized soil volumes, root dry weights were higher in the unfertilized soil due to elevated CO_2 conditions; root dry weight in the fertilized volume was increased by CO_2 only at the 50% P-fertilized volume. Fine root length data showed similar patterns of response but exhibited more variability.

Our data indicated a stimulation of root growth in the P-fertilized soil fraction. This pattern was similar under both levels of CO_2. The distribution of fine root length between P-soil and non-P soil zones as affected by the fraction of soil fertilized can be characterized by the equation $Y = 0.025 + 1.051 (x)$; x is the fraction of soil volume fertilized with P and y is the fraction of total root length in the P-fertilized soil zone (R^2=0.89). Somewhat similar relationships have been reported by others (Borkert and Barber, 1985). In addition, fine roots in the P-fertilized soil volumes tended to have smaller mean root diameters relative to roots in the non-P soil. The mean root diameter for fine roots under CO_2-enriched conditions, averaged over all soil treatments, was slightly larger than ambient grown plants (data not shown).

Total fine root variables for all treatments are shown in Table 2. Total fine root dry weight and length (i.e., totals of fertilized and unfertilized soil volumes within a container) were significantly higher under CO_2-enriched conditions in most cases. Total root dry weights and lengths under ambient CO_2 conditions were higher, relative to the treatment with 100% P-soil mixture (150 mg kg^{-1}), in the 12.5% and 6.25 % P treatments. Total fine root length under enriched CO_2 conditions showed this same pattern. However, total root dry weights were higher, relative to the treatment with 100% P-soil mixture, when P was applied to any of the different soil fractions (i.e., 50% to 6.25%).

Cotton aboveground variables for all treatments are shown in Table 3. Plants grown with no added P had the lowest shoot dry weights, tissue P concentration, and total P uptake. No affect of CO_2 treatment was observed under these conditions. Shoot dry weight was increased by CO_2 enrichment at all other P treatments, while tissue concentration was lowered by additional CO_2 in most cases. Total P uptake was increased under CO_2 enrichment when P was added to 50, 25, and 12.5 % of the soil volume. Shoot dry weights under ambient CO_2 conditions were higher, relative to the treatment with 100% P-soil mixture (150 mg kg^{-1}), in the 12.5% and 6.25 % P treatments. Corresponding measures of P uptake were similar due to lower tissue concentration. However, under enriched CO_2 conditions shoot dry weights were higher, relative to the treatment with 100% P-soil mixture, when P was applied to any of the different soil fractions (i.e., 50% to 6.25%). Corresponding measures of P tissue concentration were variable and total P uptake were significantly higher when P was applied to 50, 25, and 12.5% of the soil volume.

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

		CO_2 concentration (ppm)			
		360	720	360	720
P added	Soil volume	Fine Root Dry Weight		Fine Root Length	
mg/kg	%	g plant^{-1}		m plant^{-1}	
0	100	0.06a	0.06a	5.7a	4.9a
150	100	0.36a	0.59b	44.4a	72.4b
300	50	0.20a	0.49b	29.7a	51.3b
0	50	0.20a	0.37b	26.4a	33.7a
600	25	0.12a	0.21a	14.3a	18.6a
0	75	0.40a	0.62b	41.9a	53.0a
1200	12.5	0.09a	0.17a	10.9a	15.6a
0	87.5	0.54a	0.88b	56.5a	83.1b
2400	6.25	0.18a	0.08a	7.8a	8.3a
0	93.75	0.41a	0.91b	63.1a	84.8b

[1]Means for a variable in a row followed by same letter are not different, LSD ($\propto$ = 0.05).

Table 2. Effects of applying the same P rate per container, in decreasing soil volumes, on total fine root variables for cotton grown under two levels of atmospheric CO_2. Means of five replications shown.[1,2]

	CO_2 concentration (ppm)			
	360	720	360	720
P added	Total Fine Root Dry Weight		Total Fine Root Length	
mg/kg	g plant^{-1}		m plant^{-1}	
0	0.06d	0.06d	5.7c	4.9c
150	0.36c	0.59c	44.4b	72.4b
300	0.41bc	0.86b	56.1ab	84.9ab
600	0.52ab	0.83b	56.2ab	71.6b
1200	0.63a	1.04a	67.9a	98.7a
2400	0.58a	0.99b	70.9a	92.2a

[1]Means within a column followed by same letter are not different, LSD ($\propto$ = 0.05).

[2]LSD ($\propto$ = 0.05) for CO_2 effects = 0.16 and 19.1 for root dry weight and length, respectively.

Table 3. 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.[1,2]

	CO_2 concentration (ppm)					
	360	720	360	720	360	720
P added	Shoot Dry Weight		Shoot P Concentration		Total P in Shoot	
mg/kg	g plant^{-1}		g kg^{-1}		g P plant^{-1}	
0	0.22c	0.20d	1.06d	0.85d	0.23c	0.17d
150	9.24b	13.75c	3.20d	2.57ab	28.57b	32.76c
300	10.78ab	18.30ab	3.73a	2.70a	38.68a	47.65a
600	10.49ab	17.11b	3.08b	2.32ab	31.37b	38.83b
1200	12.06a	19.00a	2.51c	2.20bc	29.32b	40.40b
2400	12.15a	18.05ab	2.67c	1.82c	31.54b	31.67c

[1]Means within a column followed by same letter are not different, LSD ($\propto$ = 0.05).

[2]LSD ($\propto$ = 0.05) for CO_2 effects = 1.78, 0.39, and 4.65 for shoot dry weight, P concentration, and total P, respectively.