JOURNAL OF PLANT NUTRITION, 21(7), 1407–1426 (1998)

Effects of Carbon Dioxide Enrichment on Cotton Nutrient Dynamics

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ABSTRACT

The rise in atmospheric carbon dioxide (CO_2) concentration is predicted to have positive effects on agro-ecosystem productivity. However, an area which requires further study centers on nutrient dynamics of crops grown under elevated CO_2 in the field. In 1989 and 1990, cotton [*Gossypium hirsutum* (L.) 'Deltapine 77'] was grown under two CO_2 levels [370 μmol mol^{-1}=ambient and 550 μmol mol^{-1}=free-air CO_2 enrichment (FACE)]. At physiological maturity, nutrient concentration and content of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn) were determined for whole plant and individual plant organs. While the effects of added CO_2 on whole plant nutrient concentrations and contents were consistent, some differences among plant organs were observed

between years. FACE often decreased tissue nutrient concentration, but increased total nutrient accumulation. Results indicate that under elevated CO_2, field grown cotton was more nutrient efficient in terms of nutrient retrieval from the soil and nutrient utilization in the plant. This implies more efficient fertilizer utilization, better economic return for fertilizer expenditures, and reduced environmental impact from agricultural fertilization practices in the future.

INTRODUCTION

Since plants respond directly to CO_2, it is essential to determine how the rise in global atmospheric CO_2 concentration (Keeling et al., 1989) will affect productivity of vegetation in agro-ecosystems. Emission of CO_2 into the atmosphere is due to accelerated anthropogenic activities (fossil fuel consumption, deforestation, etc.); such continued patterns are expected to double the global CO_2 concentration by the end of the next century (Bolin et al., 1986).

Aboveground plant responses to elevated CO_2 are well documented; previous work has shown that high CO_2 often enhances plant water use efficiency, net photosynthesis, biomass production, and yield (Carlson and Bazzaz, 1980; Rogers and Dahlman, 1993; Amthor, 1995). In general, under elevated CO_2, whole plant nutrient uptake and nutrient utilization efficiency are increased while nutrient tissue concentration and nutrient uptake efficiency decline (Rogers et al., 1994).

Despite the importance of root systems in attaining soil resources, thereby dictating whole plant nutrition, effects of elevated CO_2 on crop root systems have received less attention relative to aboveground processes (Acock and Allen, 1985; Rogers et al., 1994). Several crop species have often shown increases in root dry weight under CO_2-enriched conditions (Chaudhuri et al., 1986, 1990; Del Castillo et al., 1989; Rogers et al., 1992b). Del Castillo et al. (1989) found that root systems of CO_2-enriched plants could more thoroughly explore a given soil volume (i.e., without increasing the volume of soil explored), whereas others have reported greater root proliferation throughout the soil profile (Chaudhuri et al., 1986). Furthermore, plants grown in high CO_2 attain maximum rooting depth faster relative to plants grown under ambient CO_2 (Chaudhuri et al., 1990). However, it is important to note that most CO_2 response studies have been conducted with containerized plants (i.e., confined rooting volume) in controlled growth chambers and greenhouses which may obscure responses (above- and belowground) that would occur in the field (Sionit et al., 1984; Arp, 1991; Thomas and Strain, 1991). Recently, efforts have focused on conducting CO_2 studies in the field utilizing open top chambers and FACE (free-air CO_2 enrichment) systems (Allen, 1994). For example, FACE increased aboveground cotton dry matter production (Mauney et al., 1994; Prior et al., 1994b), root density (both length and dry weight) in the uppermost soil layers (0-60-cm), and root density (and root biomass allocation) into interrow positions (Prior et al., 1994a). Such CO_2-induced changes in rooting patterns may influence

whole-plant nutrient dynamics, thus influencing crop performance when demand for nutrients is high.

Investigating crop responses to elevated CO_2 in the field is imperative to obtaining realistic data to determine if future management considerations will be altered. The objective of this study was to investigate whether FACE would alter nutrient dynamics of cotton grown in natural soil profiles in the field.

MATERIALS AND METHODS

Field experiments were conducted (1989 and 1990) 25 miles south of Phoenix, AZ, at the Maricopa Agricultural Center for Resources and Extension (MAC) of the University of Arizona at Maricopa, AZ (33°10′N, 112°0′W). Cotton [*Gossypium hirsutum* (L.) 'Deltapine 77'] was grown on a Trix clay loam [fine, loamy, mixed (calcareous), hyperthermic Typic Torrifluvents] under two atmospheric CO_2 levels (370 μmol mol^{-1}=ambient and 550 μmol mol^{-1}=FACE).

Recommended farming practices of the region were followed in managing both the soil and crop (Mauney et al., 1994). Briefly, after the experimental area had been chisel plowed, seeds were sown into dry raised beds using a one-meter row spacing on 17 April 1989 [day of year (DOY) 107] and 23 April 1990 (DOY 113) with plants being thinned to 10 per meter after 50% emergence. A subsurface drip tube system was used to irrigate the crop; drip tubing was located ~20 cm directly beneath the row. The crop received a total of 1270 and 1190 mm of water during the 1989 and 1990 growing season, respectively. The irrigation system was also used to apply fertilizer N (32% N solution) at a rate of 5.6 kg N ha^{-1} $week^{-1}$ for a total of 39.2 kg N ha^{-1} yr^{-1}. Foliar application of micronutrients also occurred as described by Mauney et al. (1994). In addition, two applications of Pix[1] (N, N-dimethylpiperidinium chloride) were made in 1989. No Pix was applied in 1990.

Large-scale test atmospheres of CO_2 were generated in the field using a technique called free-air CO_2 enrichment or FACE (Hendrey et al., 1993). Each exposure unit (i.e., circular array) was constructed of a 22 m diameter PVC torus (plenum chamber) with 32 vertical ventpipes (2 m height) spaced evenly around its perimeter. 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 windspeed and direction was utilized to release CO_2 upwind from sectors of vertical standpipes

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

in quantities proportional to windspeed, thus creating uniform atmospheres within each array. There were four replicates of two CO_2 treatments: four at concentrations of 550 μmol mol^{-1} CO_2 and four at 370 μmol mol^{-1} CO_2 arranged in a randomized complete block. Plots were positioned at least 100 m apart to reduce the possibility of CO_2 enriched air blowing into ambient CO_2 plots. Installation of arrays occurred immediately after planting, and CO_2 exposure was initiated after 50% seedling emergence and continued until physiological maturity.

Plant material was collected at physiological maturity in 1989 [September 27 (DOY 270)] and 1990 [September 17 (DOY 260)] as described elsewhere (Rogers et al., 1992a; Prior et al., 1994b). Plants were separated into leaves, stems, burs, seed, and lint. In 1989 and 1990, estimates of root system biomass and/or length were based on partial excavation of the taproot system (with associated laterals) and root soil cores (fine roots) as reported by Rogers et al. (1992a) and Prior et al. (1994a, 1995), respectively. All plant organs were oven dried at 55°C for 3 days before weight determination and were ground to pass a 2 mm screen (except for lint). Carbon (C) and N were determined in triplicate with a LECO CHN-600 analyzer (LECO Corp., Augusta, GA). Duplicate subsamples of plants parts (except lint) were heated in a muffle furnace for 4.5 hr at 450°C (Hue and Evans, 1986). The resulting ash was then dissolved in 1M HNO_3 and 1 M HCl, successively. Phosphorus, K, Ca, Mg, Cu, Fe, Mn, and Zn were then measured by inductively coupled plasma spectrophotometry (ICP 9000, Thermo Jarell-Ash Corp., Franklin, MA).

Nutrient concentration, nutrient uptake, nutrient utilization efficiency (unit of biomass produced per unit of nutrient), nutrient uptake efficiency (unit of nutrient per unit length of fine root), and nutrient removal from the field due to yield (unit of nutrient used per unit of lint produced) were determined for each plant organ and/or whole plant. The nutrient contents of the bur, leaves, and stems were also combined into a component designated as BLS; this biomass fraction represents non-yield biomass that would normally be returned to plots following standard tillage operations.

Statistical analysis of data were performed using the Mixed procedure of the Statistical Analysis System (SAS, 1996). The experimental design was a randomized complete block with four replications. A significance level of $P \leq 0.10$ was established *a priori*. Values which differed at the $0.10 < P \leq 0.20$ level were considered trends.

RESULTS

Biomass Production and Allocation

Elevated atmospheric CO_2 significantly increased total cotton biomass in both years of the study (Table 1). Although additional CO_2 increased the mean biomass of each plant organ, differences were noted in the significance levels between

TABLE 1. Biomass accumulation (individual organs and whole plant) and allocation of biomass to plant organs for cotton grown under ambient and CO_2-enriched conditions in 1989 and 1990.

	Biomass Accumulation (g / plant)					
	1989			1990		
	Atmospheric CO_2 Concentration (μmol mol^{-1})					
	370	550	% Change	370	550	% Change
Seed	41.21	52.92§	28.4	26.39	42.74*	62.0
Lint	25.40	34.64§	36.4	13.21	25.35*	91.9
Bur	29.17	39.05§	32.5	21.42	31.07§	45.1
Leaf	27.74	33.59	21.1	30.84	34.01	10.3
Stem	61.32	91.98*	50.0	74.81	91.62	22.5
Root	17.80	26.68*	49.9	18.12	24.24*	33.8
Total	202.63	278.86*	37.6	184.78	249.03*	34.8
	Biomass Allocation (%)					
Seed	20.21	18.91	-6.4	13.91	17.12§	23.1
Lint	12.43	12.44	0.1	6.97	10.17*	45.9
Bur	14.36	13.87	-3.4	11.39	12.44	9.2
Leaf	13.69	11.91*	-13.0	16.80	13.80*	-17.9
Stem	30.36	33.16§	9.2	40.97	36.58§	-10.7
Root	8.94	9.70	8.5	9.97	9.88	-0.9

*Indicates significance ($P \leq 0.10$).

§Values which differed at $0.10 < P \leq 0.20$ were considered trends.

years. In 1989, FACE increased stem, root, and total plant dry weight with similar trends being noted for reproductive organs (lint, seed, and bur). In 1990, FACE increased seed, lint, root, and total plant dry weight with a similar trend for the bur. It is important to note that the percent increase in dry matter production, due to added CO_2, was greater for the reproductive organs (i.e., seed, lint, and bur combined) in 1990, whereas the percent increase was greater for stem, roots, and total plant in 1989. Similarly, biomass allocation patterns differed between years. In 1990, more biomass was partitioned to the seed and lint while less was partitioned to stems under FACE (Table 1). In comparison, in 1989, CO_2 level had no effect on partitioning patterns for reproductive organs, but FACE resulted in more biomass being allocated to stems. There was no significant difference in leaf biomass accumulation between CO_2 treatments, but significantly less biomass was allocated to leaves under CO_2 enrichment.

Nutrient Concentration

Tissue concentrations of N, P, K, Ca, and Mg as affected by atmospheric CO_2 level are shown in Table 2. In general, tissue concentration of plant nutrients were lower with FACE compared to ambient CO_2, although some differences were observed between years. In 1989, N concentration was reduced under elevated CO_2 in the seed, bur, root, and total plant. In 1990, N concentrations in plant organs (except seeds) were lower under FACE. The P concentration was lower under FACE in bur and roots in 1989, but not in 1990. For K, the effect of CO_2 level was fairly consistent between years except for leaf tissue; in 1989, the concentration of K in the leaf tissue was higher under FACE, whereas in 1990 the opposite was observed. In comparison, the K concentration in seed, root, and total plant were lower under FACE. The seed Ca concentration in 1989 tended to be higher under FACE, whereas the opposite pattern was noted for leaf and stem tissue. In both years, the Ca concentration in root and total plant were lower under FACE. In 1989, leaf Mg concentration was higher under FACE, but the opposite pattern was seen in root tissue. In 1990, stem, root, and total plant Mg concentrations were reduced under CO_2-enriched conditions.

Micronutrient concentrations for plant organs are summarized in Table 3. In general, as with the macronutrients, the total concentrations of micronutrients were less in FACE compared to the ambient CO_2 treatment, but the individual plant organs showed no consistent pattern between years. In 1989, the Cu concentration for the seed and bur was lower under FACE, whereas the opposite pattern was noted for the leaf. In 1990, the Cu concentration for seed, leaf, root, and total plant was reduced under FACE. The Fe concentration for stem and root tissue in 1989 was lower under FACE; the reverse pattern was seen for leaf tissue. In 1990, Fe concentration in seed, leaf, and total plant was lower under FACE. In 1989, Mn concentration was lower under high CO_2 for root and total plant; no differences were observed in 1990. In 1989, the Zn concentration for seed, bur, and total plant

TABLE 2. Tissue nutrient concentration (N, P, K, Ca, and Mg in g kg^{-1}) in plant organs and whole plant for cotton grown under ambient and CO_2-enriched conditions in 1989 and 1990.

	N		P		K		Ca		Mg	
					1989					
	Atmospheric CO_2 Concentration (μmol mol^{-1})									
	370	550	370	550	370	550	370	550	370	550
Seed	49.9	46.1*	16.8	16.6	24.6	23.5*	4.2	4.4§	9.3	9.6
Bur	17.2	15.0§	5.1	4.4*	63.8	60.8	21.8	21.3	4.6	4.8
Leaf	31.9	32.3	5.3	6.1	37.4	44.0*	104.8	92.1§	12.9	14.3*
Stem	8.7	8.9	2.7	2.8	33.5	33.1	16.1	14.3§	4.3	4.1
Root	6.9	6.1*	2.8	2.1*	19.7	16.0*	6.9	6.0*	2.8	2.3*
Total	23.1	20.8*	6.8	6.4	35.7	35.0§	27.2	23.0*	6.7	6.6
					1990					
Seed	51.3	47.6	15.7	16.0	29.3	25.3*	3.2	3.2	9.4	9.1
Bur	22.2	14.7*	6.3	5.1	62.4	63.3	16.1	16.2	4.9	4.5
Leaf	34.4	29.1*	5.7	5.1	49.6	44.6*	109.8	116.0	13.4	13.2
Stem	8.7	6.8*	1.8	1.8	36.9	32.4	14.2	12.7	3.5	2.8*
Root	4.9	3.9*	1.3	1.0	7.8	6.6*	6.7	5.7*	1.7	1.5*
Total	19.4	16.9*	4.7	4.8	35.2	31.0*	27.1	23.8*	5.7	5.1*

*Indicates significance ($P \leq 0.10$).
§Values which differed at $0.10 < P \leq 0.20$ were considered trends.

TABLE 3. Tissue micronutrient concentration (Cu, Fe, Mn, and Zn in mg kg^{-1}) in plant organs and whole plant for cotton grown under ambient and CO_2-enriched conditions in 1989 and 1990.

	Cu		Fe		Mn		Zn	
				1989				
	Atmospheric CO_2 Concentration (μmol mol^{-1})							
	370	550	370	550	370	550	370	550
Seed	16.4	13.8§	144.8	130.5	32.7	33.0	112.3	105.6*
Bur	13.5	12.0*	226.2	257.7	70.5	66.7	40.0	35.1§
Leaf	21.0	27.8§	971.5	1383.9§	348.1	335.9	66.2	83.4*
Stem	11.6	11.1	213.1	149.3*	43.1	38.8	31.1	30.7
Root	14.6	12.7	375.3	283.3§	23.3	17.1*	26.8	24.4
Total	14.8	14.3	335.1	347.6	90.7	80.2*	56.4	54.0*
				1990				
Seed	25.2	22.2*	172.4	153.4*	28.4	27.8	108.8	105.5§
Bur	19.0	15.3	178.3	168.8	59.7	58.5	51.6	37.5§
Leaf	19.9	17.4*	816.2	669.4*	284.1	313.4	55.2	57.5
Stem	12.9	11.7	115.5	104.1	30.3	30.2	26.7	25.8
Root	16.6	12.7*	349.9	346.9	23.5	23.8	23.9	31.2
Total	16.0	13.6*	261.8	210.7*	73.0	68.9	43.9	42.8

*Indicates significance ($P \leq 0.10$).
§Values which differed at $0.10 < P \leq 0.20$ were considered trends.

was lower under FACE; similar trends were seen for the seed and bur in 1990. Leaf Zn concentration was significantly higher under FACE in 1989 only.

Nutrient Uptake

Content (i.e., weight per area basis) of N, P, K, Ca, and Mg for cotton as affected by atmospheric CO_2 level are shown in Table 4. Despite lower nutrient concentrations in both years, total content of N (1989 only), P, K, Ca (1990 only), and Mg tended to be higher under FACE. In 1989, the most consistent effect of CO_2 level was observed in the stem fraction; N, P, K, Ca, and Mg contents were increased under FACE. In this same year, the N, K, Ca, and Mg contents in roots were higher under FACE; a similar pattern was observed in 1990. In 1989, the accumulation of N, P, K, and Mg in leaf and BLS were higher under FACE. Similar patterns were also noted for Ca and Mg content in the seed and bur for that year. In 1990, accumulation of N, P, K, Ca, and Mg in seeds was significantly higher under FACE; this was also true for K and Ca accumulation in burs.

Micronutrient content data (i.e., weight per area basis) are summarized in Table 5. As with the macronutrients, micronutrients content was generally increased under FACE. In 1989, the Cu content was increased by FACE for leaf, stem, BLS, root, and total plant. Total Fe in bur, leaf, and total plant was increased by FACE and similar patterns were noted for total Mn in the seed, bur, and stem. In this same year, Zn content for leaf, stem, BLS, root, and total plant were significantly higher under FACE. In 1990, the most consistent CO_2 effect was observed in the seed; total Cu, Fe, Mn, and Zn contents increased under FACE. Total Fe and Mn content were also higher under FACE for the bur and root; similar trends were observed for Mn content in the leaf and BLS fraction. Total plant content of Cu, Mn, and Zn tended to be greater under CO_2-enriched conditions.

Nutrient Allocation

Distribution of N, P, K, Ca, and Mg among organs exhibited very little significant differences between CO_2 treatments and inconsistent patterns between years (Table 6). In 1989, stem tissue from the CO_2-enriched treatment tended to have higher percentages of N, P, K, and Ca relative to ambient CO_2 conditions; a similar trend was noted for Ca allocated to seeds. Less Ca was allocated to the leaf under FACE. In 1990, seeds tended to have higher percentages of N, P, Ca, and Mg under FACE; similar patterns were noted for K and Ca distribution to burs. The amounts of N, P, and K distributed to the leaf were lower under FACE; this was also true for allocation of N and Mg to stems.

Micronutrient allocation patterns among plant organs as affected by CO_2 level is illustrated in Table 7. In 1989, a lower amount of Cu was distributed to burs under FACE (vs. ambient CO_2 treatment). More Cu was distributed to leaves under FACE; similar trends were noted for Fe and Zn. Under FACE, less Fe and Mn was

TABLE 4. Tissue nutrient content (N, P, K, Ca, and Mg in kg ha^{-1}) in plant organs and whole plant for cotton grown under ambient and CO_2-enriched conditions in 1989 and 1990.

	N		P		K		Ca		Mg	
					1989					
	Atmospheric CO_2 Concentration (μmol mol^{-1})									
	370	550	370	550	370	550	370	550	370	550
Seed	205.6	244.1	69.5	87.5	101.6	124.4	17.4	23.2*	38.7	50.8§
Bur	49.7	58.8	14.9	17.3	186.7	235.9	62.6	81.6*	13.3	18.7*
Leaf	87.6	105.7§	14.6	19.7*	103.9	145.1*	292.8	318.8	35.6	48.5§
Stem	53.2	81.7*	16.3	25.2*	206.5	303.1*	99.8	131.7*	26.2	37.9*
BLS	190.6	246.0*	45.8	62.2*	497.2	684.1*	455.2	532.1	75.0	105.1*
Root	12.4	16.3*	5.0	5.6	35.1	42.5§	12.4	15.8*	5.0	6.2*
Total	408.7	506.6§	120.3	155.4*	633.9	851.0*	485.0	571.2	118.8	162.1*
					1990					
Seed	132.0	203.9§	40.7	66.5*	78.0	107.2*	8.5	13.3*	24.6	38.5*
Bur	47.7	45.8	13.2	16.0	129.9	195.7*	34.1	49.6*	10.5	14.0
Leaf	106.2	99.2	17.4	17.4	153.1	151.8	341.3	392.7	41.8	44.8
Stem	65.0	62.7	13.1	16.4	277.1	299.6	106.2	115.5	26.3	25.0
BLS	218.9	207.8	43.7	49.9	560.2	647.0	481.6	557.9	78.6	83.9
Root	8.9	9.6*	2.3	2.4	14.0	16.0§	12.1	13.8§	3.1	3.7*
Total	359.9	421.4	86.7	118.8*	652.2	770.2§	502.2	585.0§	106.3	126.0§

*Indicates significance ($P \leq 0.10$).

§Values which differed at $0.10 < P \leq 0.20$ were considered trends.

TABLE 5. Tissue micronutrient content (Cu, Fe, Mn, and Zn in g ha^{-1}) in plant organs and whole plant for cotton grown under ambient and CO_2-enriched conditions in 1989 and 1990.

	Cu		Fe		Mn		Zn	
				1989				
	Atmospheric CO_2 Concentration (μmol mol^{-1})							
	370	550	370	550	370	550	370	550
Seed	68.0	75.6	590.1	698.3	134.9	176.4§	464.8	560.6
Bur	38.4	46.7	653.3	998.1*	203.2	256.3*	115.1	137.3
Leaf	57.6	91.4*	2713.0	4758.2§	969.4	1149.1	181.5	272.3*
Stem	70.9	102.4*	1307.5	1389.8	263.7	357.0*	189.5	281.8*
BLS	166.9	240.6*	4673.8	7136.1	1436.4	1762.3	486.1	691.4*
Root	26.3	33.7§	665.9	754.9	41.9	45.6	47.6	64.8*
Total	261.2	349.9*	5929.8	8589.3§	1613.2	1984.3	998.6	1316.8*
				1990				
Seed	66.9	96.3§	451.5	652.9*	76.1	117.6*	286.1	445.6*
Bur	41.4	46.6	358.5	526.8*	126.0	179.7*	113.1	116.5
Leaf	61.6	59.5	2510.6	2287.8	876.7	1067.8§	169.2	197.1
Stem	96.4	105.0	873.6	914.4	227.5	272.4	198.9	227.5
BLS	199.4	211.2	3742.7	3729.0	1230.3	1519.9§	481.3	541.1
Root	29.9	30.7	644.2	833.7§	43.2	57.3§	43.4	75.4
Total	296.2	338.3§	4838.3	5215.6	1349.6	1694.9§	810.7	1062.2*

*Indicates significance ($P \leq 0.10$).

§Values which differed at $0.10 < P \leq 0.20$ were considered trends.

TABLE 6. Allocation (%) of nutrients (N, P, K, Ca, and Mg) for cotton grown under ambient and CO_2-enriched conditions in 1989 and 1990.

	N		P		K		Ca		Mg	
	1989									
	Atmospheric CO_2 Concentration (μmol mol^{-1})									
	370	550	370	550	370	550	370	550	370	550
Seed	49.9	48.0	57.2	56.0	15.9	14.6	3.6	4.2§	32.2	31.4
Bur	12.2	11.5	12.5	11.1	29.4	27.5	13.1	14.8	11.3	11.6
Leaf	21.6	20.9	12.2	12.8	16.4	17.0	60.1	54.2§	30.0	29.4
Stem	13.2	16.3§	13.8	16.4§	32.6	35.9§	20.5	23.9§	22.1	23.7
Root	3.1	3.3	4.4	3.7	5.7	5.1	2.6	3.0	4.4	3.9
	1990									
Seed	36.0	47.7§	45.9	56.5§	11.6	14.2	1.6	2.3§	22.7	30.2*
Bur	13.0	11.0	15.1	13.0	19.7	25.7*	6.7	8.4§	9.6	11.2
Leaf	29.8	24.0*	20.5	14.7*	23.6	19.9*	67.6	67.4	39.4	35.6
Stem	18.5	15.0§	15.7	13.6	42.9	38.0	21.5	19.5	25.4	20.1§
Root	2.6	2.3	2.8	2.1	2.2	2.2	2.5	2.4	3.0	3.0

*Indicates significance ($P \leq 0.10$).
§Values which differed at $0.10 < P \leq 0.20$ were considered trends.

allocated to stems. In 1990, a higher percentage of Fe was distributed to seeds and burs under FACE; a similar trend was noted for Mn (seed). Less Cu and Fe tended to be allocated to leaf tissue in 1990 under FACE.

Nutrient Efficiencies

Under FACE, nutrient utilization efficiencies (nuse=unit of biomass produced per unit of nutrient) for all elements were significantly increased, or displayed a tendency toward increase in both years of the study (Tables 8 and 9), but CO_2 level had no effect on nutrient uptake efficiency (unit of nutrient per unit weight of root) in either year (data not shown). However, nutrient uptake efficiency, expressed on

TABLE 7. Allocation (%) of micronutrients (Cu, Fe, Mn, and Zn) for cotton grown under ambient and CO_2-enriched conditions in 1989 and 1990.

	Cu		Fe		Mn		Zn	
				1989				
	Atmospheric CO_2 Concentration (μmol mol^{-1})							
	370	550	370	550	370	550	370	550
Seed	25.7	21.5	9.9	8.9	8.3	9.0	46.0	42.3
Bur	14.8	13.2*	11.1	12.0	12.8	13.2	11.6	10.3
Leaf	22.1	26.0*	45.3	52.5§	59.9	56.8	18.3	20.8§
Stem	27.2	29.3	22.2	16.7*	16.3	18.6§	19.1	21.6
Root	10.2	10.0	11.6	9.8	2.7	2.4	4.9	5.0
				1990				
Seed	21.8	28.4	9.1	12.5*	5.5	7.1§	34.5	41.8
Bur	13.7	13.9	7.5	10.0*	9.3	10.6	13.6	10.9
Leaf	21.0	17.7§	52.3	43.6*	65.0	62.9	21.3	18.7
Stem	33.4	31.0	17.7	17.8	17.0	15.9	25.3	21.7
Root	10.0	9.0	13.4	16.1	3.3	3.4	5.4	6.8

*Indicates significance ($P \leq 0.10$).
§Values which differed at $0.10 < P \leq 0.20$ were considered trends.

a root length basis (nupl), for P, K, Mg, and Zn tended to be higher under FACE in 1989. In 1989, nutrient uptake per unit of lint produced (nl) was not affected by CO_2 level. However, in 1990, nutrient uptake per unit of lint produced was significantly lower, or exhibited decreasing trends under FACE (vs. ambient CO_2 treatment) for all elements.

DISCUSSION

Previous work has shown that increases in atmospheric CO_2 concentration often increases biomass production and yield (Rogers and Dahlman, 1993; Rogers et al., 1994; Goudriaan and Zadoks, 1995). In the current study, additional CO_2 increased

total cotton biomass and biomass of various plant organs. Close examination of experimental procedures for each study year (Mauney et al., 1994) indicate that differences between years were probably not related to irrigation and rainfall patterns since amounts were similar each year. Differences observed between years may have been the result of two applications of Pix in 1989 and none in 1990. Pix is a plant growth regulator that is applied during reproductive growth which may impact canopy structure and yield (Guinn, 1986). The applications of Pix in 1989 may have altered the allocation patterns of biomass compared to 1990, with a biomass shift toward the reproductive organs (Table 1). While the impact of elevated CO_2 on total biomass production was similar between years, there appeared to be a dampening of the positive effect of CO_2 on reproductive organs in 1989 vs. 1990. In 1990 when no Pix was added, the yield components exhibited a larger increase due to elevated CO_2, and the percentage of total biomass allocated to seed and lint was also increased (Table 1). Differences observed between years for plant nutrient status may also be related to the differences in Pix application.

Current reviews of the literature (Rogers et al., 1994, 1997) suggest that whole plant nutrient uptake is often higher, while tissue nutrient concentration is reduced for CO_2-enriched plants. However, results vary perhaps reflecting the great diversity of experimental procedures used in these studies (e.g., different nutritional levels were employed). For instance, plants grown in high CO_2 with nutrient levels ranging from adequate to deficient often exhibit lower tissue nutrient concentrations (Norby et al., 1986a, 1986b; Yelle et al., 1989), whereas under high soil nutrient conditions the tissue nutrient concentration and/or nutrient uptake efficiency are usually not affected by added CO_2 (Israel et al., 1990). Furthermore, most CO_2 response work has been conducted with plants grown in containers which may not reflect the dynamics of plant mineral nutrition that would occur under actual field conditions. Implications of results may be further confounded by the fact that many previous experiments were short-term and conducted with young plants.

The nutrient status of plants is largely governed by root system development which influences the extent of nutrient extraction from the soil profile. Thus, positive effects of CO_2 on root system proliferation as reported for these plants (Rogers et al., 1992a; Prior et al., 1994a) may have influenced whole-plant nutrition. In the current study, plants were grown to maturity in the field, thus realistic root to soil nutrient interactions could be expected. Under such conditions, whole-plant concentration of both the macro and micronutrients was often decreased (Tables 2 and 3), while total uptake of plant nutrients was often increased (Tables 4 and 5). These field data indicate that elevated CO_2 resulted in a cotton root system that was effective in gathering plant nutrients, resulting in increased total nutrient uptake. Rogers et al. (1994) reported that nutrient utilization efficiency generally increases under elevated CO_2, while nutrient uptake efficiency declines in most instances. In the current study, FACE resulted in cotton plants that were more efficient in nutrient utilization, resulting in increased plant growth per unit of nutrient

TABLE 8. Nutrient (N, P, K, Ca, and Mg) utilization efficiency (nuse=unit of biomass produced per unit of nutrient), nutrient uptake efficiency (nupl=unit of nutrient per unit length of fine root), and nutrient removal from the field due to lint yield (nl=unit of nutrient used per unit of lint produced) for cotton grown under ambient and CO_2-enriched conditions in 1989 and 1990.

	N		P		K		Ca		Mg	
	1989									
	Atmospheric CO_2 Concentration (μmol mol^{-1})									
	370	550	370	550	370	550	370	550	370	550
nuse (g^2/mg)	7.70	11.78*	26.18	38.55*	4.96	7.02*	6.50	10.59*	26.51	36.85*
nupl (mg/m)	2.34	2.83	0.68	0.87§	3.62	4.76§	2.77	3.23	0.68	0.91§
nl (kg/100kg)	16.30	14.97	4.78	4.58	25.20	25.23	19.22	16.61	4.74	4.77
	1990									
nuse (g^2/mg)	9.50	14.75*	39.40	53.12§	5.24	8.18*	6.84	10.71*	32.32	49.37*
nupl (mg/m)	2.47	2.60	0.59	0.73	4.46	4.73	3.48	3.61	0.74	0.78
nl (kg/100kg)	29.25	16.95*	7.12	4.98§	53.26	32.45*	41.14	24.84*	8.73	5.20*

*Indicates significance ($P \leq 0.10$).

§Values which differed at $0.10 < P \leq 0.20$ were considered trends.

TABLE 9. Micronutrient (Cu, Fe, Mn, and Zn) utilization efficiency (nuse=unit of biomass produced per unit of nutrient), nutrient uptake efficiency (nupl=unit of nutrient per unit length of fine root), and nutrient removal from the field due to lint yield (nl=unit of nutrient used per unit of lint produced) for cotton grown under ambient and CO_2-enriched conditions in 1989 and 1990.

	Cu		Fe		Mn		Zn	
	1989							
	Atmospheric CO_2 Concentration (μmol mol^{-1})							
	370	550	370	550	370	550	370	550
nuse (g^2/mg)	12.12	17.30*	0.53	0.75§	1.95	3.03*	3.15	4.54*
nupl (μg/m)	1.50	1.97	33.86	48.73	9.21	11.23	5.71	7.37§
nl (g/100kg)	10.51	10.43	236.91	261.26	64.03	58.22	39.92	38.91
	1990							
nuse (g^2/mg)	11.57	18.46*	0.71	1.20*	2.53	3.72*	4.22	5.86*
nupl (μg/m)	2.03	2.08	32.88	32.17	9.21	10.44	5.59	6.55
nl (g/100kg)	24.05	14.05*	396.10	217.34*	109.97	72.76§	66.85	44.02*

*Indicates significance ($P \leq 0.10$).

§Values which differed at $0.10 < P \leq 0.20$ were considered trends.

(Tables 8 and 9). Since the same amount of fertilizer was applied to the cotton in both the ambient and FACE plots, these data imply that elevated CO_2 would also increase fertilizer use efficiency. In addition, there was no indication for a reduction in nutrient uptake efficiency (i.e., when expressed on fine root length basis); instead, this variable remained constant under FACE (relative to ambient CO_2) or tended to increase in some instances (Tables 8 and 9).

The observed shift in plant nutrient allocation was similar to that seen for plant biomass allocation, with a damping of the CO_2 effect on the reproductive plant organs in 1989. This can be seen best in the effect of CO_2 level on the BLS fraction (non-harvested aboveground material = sum of stem, leaves, and burs) compared to the seed component between years. In 1989, elevated CO_2 significantly increased most of the plant nutrient contents for the BLS, but had little significant effect on seed nutrient content. In 1990, the opposite consequence was noted. A possible explanation, as with the biomass, was that the growth regulator Pix shifted the allocation of nutrients in the plant between years.

Nutrient accumulation or content of cotton biomass can be viewed in the context of nutrients that are removed from the field (i.e., due to cotton seed harvest) or left in the field (i.e., BLS and roots). In 1989 (Pix applied), no differences due to elevated CO_2 in N, P, and K removal due to harvesting seed cotton was observed; similar results were found for most micronutrients (Tables 4 and 5). The only cases where nutrient removal due to harvesting seed cotton was increased by elevated CO_2 occurred with Ca, Mg, and Mn. However, accumulation of nutrients (except Ca, Fe, and Mn) in BLS indicate that more nutrients (from this combined biomass fraction) would be returned to the field after tillage operations under FACE. This was also generally true for the root fraction, a finding which was observed in both years. However, in 1990 (no Pix applied), the opposite conclusion could be reached. That is, nutrient accumulation (all elements) in seeds were higher under FACE, indicating that more nutrient removal from the field due to harvesting seed cotton could occur. Also, in this year, accumulation of nutrients in the BLS fraction was usually not affected by FACE.

Regardless of the possible influence of Pix, elevated CO_2 may result in cotton production with more efficient fertilizer utilization. The implications of this would be a better economic return for fertilizer expenditures in the future and a reduction in the potential environmental impacts from agricultural fertilization practices.

These data illustrate the potential impact that elevated CO_2 may have on management decisions in agricultural production. For example, the application of Pix may limit the potential benefit of elevated CO_2 on cotton yields in the future as atmospheric CO_2 increases. Also, if removal of plant nutrients is increased under elevated CO_2, as was observed in 1990, then soils may become depleted in nutrients over the long-term and require increased fertilizer applications (especially micronutrients that are not normally applied). Assuming that Pix played a role in the diverging results (between years) obtained in the current study, these data highlight the importance of conducting CO_2 field experiments under conditions

that are reflective of management decisions made by farmers. Currently, farmers often apply Pix to their cotton crop, thus the 1989 data, may be more reflective of how a cotton crop may respond to atmospheric CO_2 increases.

ACKNOWLEDGMENTS

The authors recognize J.H. McFarlin, B.E. McLean, J.H. Walden, B.J. Vice, and T.K. Counts (National Soil Dynamics Lab., ARS-USDA) for technical assistance and the contributions of G.R. Hendrey, K.F. Lewin, and J. Nagy (Brookhaven National Lab.); B.A. Kimball (U.S. Water Conservation Lab., ARS-USDA); and R.S. Rauschkolb (Maricopa Agricultural Center, University of Arizona). Support from the Office of Biological and Environmental Research/Environmental Sciences Division, U.S. Dept. of Energy (Interagency Agreement No. DE-AI05-95ER62088), and the Alabama Agricultural Experiment Station, Auburn University, is gratefully acknowledged.

REFERENCES

Acock, B. and L.H. Allen, Jr. 1985. Crop responses to elevated carbon dioxide concentrations. pp. 53-98. In: B.R. Strain and J.D. Cure (eds.), Direct Effects of Increasing Carbon Dioxide on Vegetation. Dept. of Energy, Washington, DC.

Allen, Jr., L.H. 1994. Carbon dioxide increase: Direct impacts on crops and indirect effects mediated through environmental changes. pp. 425-459. In: K.J. Boote, T.R. Sinclair, and J.M. Bennett (eds.), Physiology and Determination of Crop Yield. American Society of Agronomy, Madison, WI.

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.

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

Bolin, B., B.R. Doos, J. Jager, and R.A. Warrick. 1986. Scope 29—The greenhouse effect, climatic change, and ecosystems. John Wiley and Sons, Chichester, England.

Carlson, R.W. and F.A. Bazzaz. 1980. The effects of elevated CO_2 concentration on growth, photosynthesis, transpiration, and water use efficiency of plants. pp. 609-612. In: J. Singh and A. Deepak (eds.), Environmental and Climatic Impact of Coal Utilization. Academic Press, New York, NY.

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

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

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

Goudriaan, J. and J.C. Zadoks. 1995. Global climate change: Modeling the potential responses of agro-ecosystems with special reference to crop protection. Environ. Pollut. 87:215-224.

Guinn, G. 1986. Hormonal relations during reproduction. pp. 113-136. In: J.R. Mauney and J. McD. Stewart (eds.), Cotton Physiology. The Cotton Foundation, Memphis, TN.

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

Hue, N.V. and C.E. Evans. 1986. Procedures used for soil and plant analysis by the Auburn University Soil Testing Laboratory. Alabama Agric. Exp. Stn. Dep. Series 106.

Israel, D.W., T.W. Rufty, Jr., and J.D. Cure. 1990. Nitrogen and phosphorus nutritional interactions in a CO_2 enriched environment. J. Plant Nutr. 13:1419-1433.

Keeling, C.D., R.B. Bacastow, A.F. Carter, S.C. Piper, T.P. Whorf, M. Heimann, W.G. Mook, and H. Roeloffzen. 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.

Mauney, J.R., B.A. Kimball, P.J. Pinter Jr., R.L. LaMorte, K.F. Lewin, J. Nagy, and G.R. Hendrey. 1994. Growth and yield of cotton in response to a free-air carbon dioxide enrichment (FACE) environment. Agric. For. Meteorol. 70:49-67.

Norby, R.J., E.G. O'Neill, and R.J. Luxmoore. 1986a. Effects of atmospheric CO_2 enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in a nutrient-poor soil. Plant Physiol. 82: 83-89.

Norby, R.J., J. Pastor, and J.M. Melillo . 1986b. Carbon-nitrogen interactions in CO_2-enriched white oak: Physiological and long-term perspectives. Tree Physiol. 2:233-241.

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

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

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

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

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

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

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

Rogers, H.H., G.B. Runion, S.A. Prior, and H.A. Torbert. 1997. Response of plants to elevated atmospheric CO_2: Root growth, mineral nutrition, and soil carbon. In: J.R. Seemann, Y. Luo, and H.A Mooney (eds.), Carbon Dioxide and Environmental Stress. Academic Press, San Diego, CA.

SAS Institute. 1996. SAS System for Mixed Models. Statistical Analysis System Institute, Inc., Cary, NC.

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

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

Yelle, S., R.C. Beeson, Jr., M.J. Trudel, and A. Gosselin. 1989. Acclimation of two tomato species to high atmospheric CO_2. I. Starch and sugar concentrations. Plant Physiol. 90:1465-1472.