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Response of Cotton to Varying CO_2, Irrigation, and Nitrogen: Yield and Growth

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ABSTRACT

The CO_2 concentration of the atmosphere is increasing and is expected to double sometime near the middle of the next century. To determine the effects of such a CO_2 increase on cotton (*Gossypium hirsutum* L.) growth and productivity, a series of experiments from 1983 through 1987 were conducted with open-top CO_2-enriched field chambers at ample as well as limiting levels of water and N at Phoenix, AZ. Comparisons with open-field plots showed that there was a significant chamber effect, amounting to a 30% average increase in growth inside, but under dry conditions in 1985, the situation was reversed. No significant effects of CO_2 on harvest index, root–shoot ratio, or lint percentage were found, so the primary effect of elevated CO_2 was to produce plants that were larger. Comparing the results of 500 and 650 μmol mol^{-1} CO_2 treatments, the increments of growth from ambient (about 350 μmol mol^{-1}) to 500 μmol mol^{-1} were not significantly different from increments from 500 to 650 μmol mol^{-1}. No statistically significant interactions were detected between CO_2 level and either irrigation or nitrogen level, even when these variables were sufficiently low enough to limit growth. However, under well-maintained water stress conditions, the growth response to CO_2 tended to be somewhat larger than under normal irrigation levels. Averaging over all the data available from these experiments, seed cotton yield (lint plus seed) and above-ground biomass were increased by 60 and 63%, respectively, by CO_2 enrichment to 650 μmol mol^{-1}.

THE CO_2 CONCENTRATION of the atmosphere is increasing, and climate modelers have predicted a consequent global warming and changes in precipitation patterns. The report of the Intergovernmental Panel on Climate Change edited by Houghton et al. (1990) projects CO_2 increasing from present day concentrations of about 350 μmol mol^{-1} to over 800 μmol mol^{-1} by the end of the next century if no steps are taken to limit emissions. They predict this increase in CO_2 plus that of other radiatively active greenhouse gases—methane, nitrous oxide, chlorofluorocarbons (CFCs), ozone—would cause an increase in global mean temperature of about 4.2 °C. Some regions might receive increases in precipitation, while others might receive less. However, these changes are very uncertain.

As a feedstock for photosynthesis, increased CO_2 can accelerate plant growth and could potentially increase agricultural productivity. Doubled CO_2 concentrations have been shown to increase crop yields by an average of 30% or more in experiments conducted mostly under greenhouse and growth chamber conditions (Kimball 1983a,b, 1986b; Cure, 1985). Based on a small number of these growth chamber experiments, cotton appeared to respond more than most crops to elevated CO_2 levels (Mauney et al., 1978; Wong, 1979). Consequently, it was the objective of the experiments described herein to determine the growth and yield response of field-grown cotton to varying CO_2, irrigation, and N levels under more natural conditions. Experimental method details and raw growth data have been presented previously by Kimball et al. (1992). This paper presents a comprehensive statistical analysis of the mean cotton growth and yield responses, as well as of three measures of carbon partitioning: harvest index, root/shoot ratio, and lint percentage.

METHODS AND MATERIALS

A series of experiments from 1983 through 1987 were conducted using open-top CO_2–enriched field chambers at ample as well as limiting levels of water and nitrogen in Phoenix, AZ, where the soil is Avondale clay loam [fine-loamy, mixed (calcareous), hyperthermic, Anthropic Torrifluvent]. The particular treatment combinations varied from year to year, but the data was base amounted to 72 plot-years' worth of growth observations. Details of the methodology were presented in a previous report by Kimball et al. (1992), so this section will only present a brief overview.

Crop Culture

The cotton was planted in north–south rows at a 1.02-m spacing. The crops were thinned to a population density of 102 000 plants ha^{-1} (10 plants m^{-1}), and any gaps were filled with transplants. Generally, 'Deltapine-61' cotton was planted about mid-April, with the final harvest near the end of September. An exception was 1983, when the crop was planted on 8 June, so 'Deltapine-70', a relatively short-season variety, was selected for this experiment. The CO_2-enrichment chambers (3 m on a side, or 9 m^2) were erected in normally-planted fields of cotton, so that the chambers were surrounded by border rows. Open-field plots were marked using the same dimensions as the chambers in 1983–1985, and they were generally treated like the chamber plots with a few exceptions that will be discussed later. Each chamber or plot contained three, 3-m lengths of row. Destructive sampling was done through the course of the experiments on the outside rows using a selective protocol rotating among quadrants so as to prevent large holes from appearing in the canopies. The middle rows were reserved for nondestructive measurements and for the final harvests each year. The measurements reported herein are from the final harvests of the middle 3-m row in each plot.

The harvests consisted of pulling the plants from the soil with as many roots attached as possible, except in 1987 when root data were not obtained. Because cotton has a tap root system, we believe most of the root biomass was obtained by this crude method, but some bias toward the wet treatment may exist because of the greater ease of pulling the plants from wet soil. The roots were washed, and plants were dissected into stems (with petioles), leaves, squares, green bolls, and mature bolls. The plants were dried, and the results tabulated.

A summary of the CO_2, irrigation, and N fertilizer treatments by year is presented in Table 1. In 1983 there were three levels of CO_2 concentration (ambient or about 350, 500, and 650 μmol mol^{-1}) in open-top chambers, as well as open field plots for comparison with the ambient CO_2 open-top chamber treatment. All plots were amply watered (wet irrigation treatment) and fertilized (N$^+$, nitrogen-added treatment). There were

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Abbreviations: HP, horsepower; LAI, leaf area index; N$^+$ and N$^-$, nitrogen added and no nitrogen added, respectively.

Table 1. Summary of CO$_2$, irrigation, and nitrogen treatments by year. The wet plots were well-watered comparable to normal grower practice using flood irrigation in 1983-1984 and using drip irrigation in 1985-87. The dry plots were water stressed and received about 2/3 as much water as the wet plots. The N$^+$ plots received added fertilizer nitrogen, whereas the N$^-$ plots received only a small amount (5 kg N ha^{-1}) in the irrigation water. There were two replicates each year, giving a total of eight plots in 1983 and 16 plots each year in 1984-1987.

YEAR	TREATMENT		
	CO$_2$/chamber	Irrigation	Nitrogen
1983	open field	wet	N+ (124 kg N ha^{-1})
	ambient chamber		
	500 μmol mol^{-1}		
	650 μmol mol^{-1}		
1984	open field	wet	N+ (150 kg N ha^{-1})
	ambient chamber	dry (poor control)	
	500 μmol mol^{-1}		
	650 μmol mol^{-1}		
1985	open field	wet	N+ (183 kg N ha^{-1})
	ambient chamber	dry	
	500 μmol mol^{-1}		
	650 μmol mol^{-1}		
1986	ambient chamber	wet	N+ (96 kg N ha^{-1})
	650 μmol mol^{-1}	dry	N− (none added)
1987	ambient chamber	wet	N+ (231 kg N ha^{-1})
	650 μmol mol^{-1}	dry	N− (none added)†

† Barley was grown over winter of 1986-1987 to remove N. Plot assignments were identical in 1987 to those in 1986.

two replicates to give a total of eight plots. In 1984 and 1985, the size of the experiment was doubled with the addition of a water-stress treatment (dry irrigation level) that received two-thirds as much water as the wet or well-watered treatment. In 1986 and 1987 the open field and 500 μmol mol^{-1} treatments were discontinued and instead a no-nitrogen-added (N$^-$) nitrogen treatment was started. With two replicates every year, there were a total of 16 plots each year from 1984–1987.

CO$_2$ Treatments

The CO$_2$ enrichment system was described in detail by Kimball et al. (1992) and to a lesser extent by Nakayama and Kimball (1988). Basically, the 3-m-on-a-side, 1.9-m-tall square chambers consisted of clear polyethylene film (0.15 mm thick, ultraviolet light resistant) hung from cables that were supported by steel fence posts at the corners, as well as in the middle row on the door (south) side. Blowers drew in outside air and discharged it into four 203-mm-diam. perforated lateral ducts which extended the length of the chambers between the plant rows. The air exited the lateral tubes through perforations (25 mm diam. in pairs spaced 10 mm apart). The blowers were equipped with 373 W (1/2 HP) motors and rated to deliver 1.2 m^3/s (four air changes per min.) at 125 Pa (1/2 inch water), which was the pressure in the ducts.

The CO$_2$ concentrations were monitored and controlled using an automatic computer-controlled sampling/control system, as described by Kimball et al. (1992). The air from each open-top chamber and from each open-field plot was continuously sampled with a pump in each chamber, which drew in the air sample from a sampling manifold. The system sequentially routed the air samples through an Anarad[1] Model 600 AR (Santa Barbara, CA) nondispersive infrared CO$_2$ analyzer, and then adjusted the flow rate of CO$_2$ going to each enriched chamber. Pure CO$_2$ from a 12 Mg storage tank was injected into the blower for each enriched chamber at the rate required to achieve the desired set point concentration. About 15 to 20 min were required to sample and analyze the air samples from all the plots; consequently, the flow rate to each enriched chamber was adjusted three or four times per hour. The chambers were enriched 24 h a day all season long, starting soon after chamber erection in the spring. As summarized in Table 1, a set point concentration of 650 μmol mol^{-1} was used all 5 yr, and 500 μmol mol^{-1} was included in 1983–1985.

At the end of each hour, average CO$_2$ concentrations and standard deviations and average flow rates were transmitted to the main laboratory computer for storage and later analysis. The standard deviations of the individual observations were typically about 40 and 65 μmol mol^{-1} for the ambient and 650 μmol mol^{-1} treatments, respectively. The season-long average CO$_2$ concentrations were within 10 μmol mol^{-1} of the set points. The season-long daytime-only and whole-24-h-day average ambient CO$_2$ concentrations were 336 and 356 μmol mol^{-1}, respectively in 1983, and in 1987 they were 344 and 363 μmol mol^{-1}, which is about a 1.5 μmol mol^{-1} yr^{-1} increase in ambient CO$_2$ concentration at this location, just slightly less than the global 1.8 μmol mol^{-1} yr^{-1} reported by Houghton et al. (1990).

Irrigation Treatments

As listed in Table 1, there was a wet or well-watered irrigation treatment all 5 yrs of the experiment, which was intended to have minimal water stress and which utilized amounts of water comparable to or slightly larger than normal grower practice for the area. Starting in 1984, a dry or water-stress treatment was included, which received about two-thirds as much water as the wet treatment.

In 1983 and 1984 the fields were flood irrigated, which is the usual grower practice in the area. The wet plots were irrigated on a 2-wk schedule with about 15 cm applied each time, as also is the common practice for the area. The dry plots, on the other hand, were similarly irrigated with 15-cm applications but on a 3-wk schedule. Unfortunately, unusually heavy rains upset the irrigation schedules, so the dry treatment was not stressed as often or as severely as planned, which may have affected the results, as will be discussed later.

In 1985 an aboveground drip irrigation system was installed to obtain greater control of the dry treatment. The system also enabled a more precise definition of the amount of water to apply to the wet treatment. Following the work of several researchers, as reviewed by Rosenberg et al. (1983, p. 225), the ratio of actual to potential evaporation appears to vary with the square root of the leaf area index (LAI), reaching a value of 1.0 at a LAI of about 3.0, and then remaining at about 1.0 for higher LAI. However, it also appears that a straight line relationship would not introduce much error, and since this study was intended to be just a guide, the well-watered wet plots were irrigated weekly with an amount of water determined by the following formula:

$$\text{irrigation amount} = \text{pan evaporation} \times (\text{LAI}/3),$$

where LAI is the leaf area index projected for the week from prior destructive plant harvests, up to a LAI of 3.0. Above 3.0, the irrigation amount was the same as the pan evaporation amount of the previous week. To be sure the application amount was adequate, the largest LAI was used, which generally was that of one of the 650 μmol mol^{-1} CO$_2$ plots. Pan evaporation was measured with a Class A pan located beside the field. Corrections were made for rainfall. This same irrigation system and application strategy were also used in 1986 and 1987.

Nitrogen Treatments

Nitrogen fertilizer was applied to all the plots from 1983–1985 (N$^+$ treatment, Table 1). In 1983, 124 kg ha^{-1} of N as

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[1] Trade names and company names are included for the benefit of the reader and do not imply any endorsement or preferential treatment of the product listed by the authors, the U.S. Department of Agriculture, or the U.S. Department of Energy.

urea were broadcast in a single preplant application. In 1984, 75 kg N ha^{-1} were broadcast as preplant and another 75 kg N ha^{-1} were applied on 11 June. With installation of the drip irrigation system in 1985, about 17 kg N ha^{-1} was applied as urea with most irrigations, and the total amount applied was 183 kg N ha^{-1}.

Starting in 1986, the three-way interaction between increased CO_2 concentration, water stress, and N deficiency was investigated (Table 1). There were two levels of CO_2, ambient and 650 μmol mol^{-1}; two levels of irrigation, wet and dry; two levels of N fertilizer application, N^+ and N^-. Nitrogen fertilizer was applied to the N^+ plots as urea (96 kg N ha^{-1}) through the drip irrigation system. The amount of N applied was half that planned because of a communication error. No fertilizer N was added to the N^- plots, but a very small amount of nitrate (2 mg N kg^{-1}) was already in the irrigation water. Therefore, a total of about 5 kg N ha^{-1} was passively applied in the irrigation water. Leaf NO_3^-–N analyses revealed levels that generally were close to the threshold considered adequate, except the plants receiving the wet–650–N treatment were deficient (Soil Improvement Committee, California Fertilizer Association, 1985).

Mean soil NO_3^-–N concentrations (0- to 15-cm depth) were about 22.7 mg N kg^{-1} at the beginning of the 1986 season and about 5.0 at the end, with no significant treatment differences detected. For a bulk density of 1400 kg m^{-3} and a soil depth of 15 cm, the change in NO_3^- concentration suggests at least about 37 kg N ha^{-1} were removed from the soil over the growing season.

To remove more N from the soil, after the 1986 cotton harvest, the field was planted to a winter crop of barley, which was removed before maturity. Plot assignments in 1987 were exactly the same as in 1986. Because the N^- plots had received no N during both 1986 and 1987, and because the N stress effect was expected to be cumulative over the 2 yrs, year was a repeated measure factor in the statistical analyses of the 1986–1987 data. Year was a main treatment factor in all the other experiments with only the N^+ treatment.

Early in 1987, urea was injected into the irrigation water applied to the N^+ plots, but on 14 July, a switch was made to Uran-32, which has 7.8% readily available NO_3^-–N, as well as 7.8% NH_4^+-N and 16.4% urea-N. The total amount of N applied to the N^+ plots was 231 kg ha^{-1}. Again, about 5 kg N ha^{-1} was applied to all plots from the naturally-occurring NO_3^-. As expected, the N^+ treatment significantly increased NO_3^--N concentrations of the petioles, and the concentrations in the N-treatment would generally be regarded as deficient (Soil Improvement Committee, California Fertilizer Association, 1985).

Soil NO_3^-–N concentrations were determined at the beginning and end of the 1987 season in all plots at 0- to 30-, 15- to 30-, and 30- to 60-cm depths. The concentrations were low, about 3 mg N kg^{-1} of soil, both at the beginning and end with no consistent changes. The amounts of N uptake represented by the concentration changes were small compared to the 231 kg ha^{-1} of N applied to the N^+ plots.

Data Analyses

The raw seed cotton (seed plus lint) yields and biomass data were subjected to statistical analyses of variance, as were three measures of carbon partitioning: harvest index, root–shoot ratio, and lint percentage. The biomass data were those only of the above-ground organs (stems with petioles, leaf blades, squares, green bolls, and mature bolls) because this is more common in the literature, and because root data were not obtained in 1987. Root-shoot ratios were analyzed for 1983 to 1986, where the roots were those that remained attached to the stems as the plants were pulled out of the ground. The harvest indices were obtained by dividing the seed cotton yield by the aboveground biomass. The lint percentages were the portions of the seed cotton yields that were lint.

Only some of treatments were administered in any given year's experiment (Table 1). Therefore, the statistical analyses were run on various subsets of the data to test the effect of particular treatments using the maximum amount of data available for that particular test (i.e., include all the years for that particular treatment comparison).

RESULTS AND DISCUSSION

Chamber Effect

A comprehensive comparison of the differences in the environment of an open-top chamber compared to an open field plot is beyond the scope of this paper. Generally, however, the air inside the chambers was slightly warmer (2–3 °C) and more humid than outside. The walls shaded portions of the crop, and they drastically altered wind flow. Soil CO_2 concentrations were decreased inside (Nakayama and Kimball, 1988),and so were populations of some insects (Butler, 1985; Butler et al., 1986).

There were significant chamber effects in these experiments, with plants tending to do better inside the chambers, especially under well-watered conditions (Table 2). For all 3 yrs under the wet treatment, yield increased about 20% and biomass increased more than 30% inside compared to the open-field plots. Under the dry treatment (Table 2b) the results were inconsistent between the 2 yr., possibly due to the poor water control in 1984. In 1985, when the dry treatment was well maintained, the distribution of dry matter by the plants in the chambers was much different than under the wet treatment with yield, harvest index, root/shoot ratio, and lint percentage trends all changed. However, compared to the CO_2 effects discussed in the next section, the magnitude of these chamber effects was relatively minor. Therefore, open-top chambers can provide an environment sufficiently representative of open fields that analyses of the relative growth of plants among chambers with different CO_2 treatments can provide valid comparisons. Nevertheless, to obtain the best information about the environment in the chambers for use in predicting the absolute plant growth with a simulation model, the actual temperatures, humidities, radiation levels, etc., should be measured and utilized as inputs to the model, rather than those from a weather station outside.

Effect of Elevated Carbon Dioxide under Well-Watered, Added-Nitrogen Conditions

Under well-watered, added-nitrogen conditions for 1983, 1984, and 1985, concentrations of 500 and 650 μmol mol^{-1} increased seed cotton yields significantly by 40 and 74%, respectively (Table 3a). Biomass was similarly increased by 39 and 70%, although there was a significant year × CO_2 interaction, with the biomass response to CO_2 being larger in 1984 than the other years. At the same time, harvest index was significantly lower in 1984. There was no significant effect of CO_2 enrichment on harvest index, root/shoot ratio, or lint percentage. The effects of the first increment of enrichment (500 μmol mol^{-1}) tended to be somewhat larger than those of the second (650 μmol mol^{-1}), but the difference was not statistically significant.

Averaged over 5 yr, the 650 μmol mol^{-1} treatment increased yield 60% and biomass 62% (Table 4a). Again,

Table 2. Responses of cotton to open-top chamber conditions at ambient CO_2 compared to open field plots at well-watered (wet) and water-stressed (dry) irrigation levels.

Treatment		Seed cotton yield	Aboveground biomass	Harvest index	Root/shoot ratio	Lint percentage
Irrigation	Condition					
		g m^{-2}	g m^{-2}			%
		a. Under well-watered irrigation level for 1983, 1984, and 1985				
wet	open field	328a†	874a	0.366a	0.075a	35.5a
wet	ambient chamber	407b	1136b	0.352a	0.083a	37.3b
	% increase‡	(24)	(30)			(5)
	comments§	A,D	A,D	A,E		A,D,E

Treatment		Seed cotton yield		Aboveground biomass		Harvest index		Root/shoot ratio		Lint percentage	
Irrigation	Condition										
		b. Under well-watered (wet) and water-stressed (dry) irrigation levels for 1984 and 1985									
		1984	1985	1984	1985	1984	1985	1984	1985	1984	1985
wet	open field	438d	376c	1065c	834b	0.410cd	0.451e	0.081ab	0.067a	38.5b	36.0a
wet	ambient chamber	515e	449d	1391d	1116c	0.369b	0.403bc	0.089bc	0.081ab	37.0a	36.0a
	% increase	(+18)	(+19)	(+31)	(+34)	(−10)	(−11)			(−4)	
dry	open field	488e	300b	1143c	741ab	0.426cde	0.404bc	0.104c	0.081ab	38.5b	38.0b
dry	ambient chamber	527f	185a	1190c	646a	0.444de	0.286a	0.090bc	0.143d	37.0a	36.5a
	% increase	(+8)	(−38)				(−29)		(+77)	(−4)	(−4)
	comments	A,D,E,F,G		A,D,F		C,D,E,G		B,C,D,E,G		A,B,C,D	

† Means not followed by the same letter are significantly different by at least the 0.05 probabilty level within the chamber group (a) or within the chamber–irrigation–year group (b).

‡ % increase of the ambient chamber value over that of the open field.

§ Guide to comments: A–significant effect of year; B–significant effect of irrigation; C–significant effect of year × irrigation interaction; D–significant main effect of chamber; E–significant effect of year × chamber interaction; F–significant effect of irrigation × chamber interaction; G–significant effect of year × irrigation × chamber interaction.

no significant effects of CO_2 enrichment on harvest index, root/shoot ratio, or lint percentage were found.

As mentioned in the introduction, doubled CO_2 concentrations have tended to increase crop growth and yields by 30% or more on the average (Kimball, 1983a,b, 1986b; Cure, 1985). Previous CO_2–enrichment studies on cotton have reported a wide range of results: Mauney et al. (1978), 153% for yield and 46% for growth; Wong (1979), 118% for growth; Morison and Gifford (1984), 19% for growth; DeLucia et al. (1985), 72% for growth. Thus, a 60% increase in the growth of cotton for a 5-yr study under conditions approaching those of an open field (see previous section) appears both definitive and remarkable.

What are the reasons for this large response of cotton? One possible reason is because cotton is a woody perennial with an indeterminant growth habit. Thus, there is always a sink for assimilate present (i.e. synthesis of

Table 3. Comparison of responses of cotton grown in open-top chambers at CO_2 concentrations of 650, 500, and ambient (about 350) μmol mol^{-1} and at well-watered (wet) and water-stressed (dry) irrigation levels.

Treatment		Seed cotton yield	Aboveground biomass	Harvest index	Root/shoot ratio	Lint percentage
Irrigation	CO_2					
	μmol mol^{-1}	g m^{-2}	g m^{-2}			%
	a. Under well-watered irrigation levels and added N fertilizer for 1983, 1984, and 1985					
	ambient	407a†	1136a	0.352a	0.083a	37.3a
	500	570b	1576b	0.356a	0.082a	38.0a
	% increase‡	(+40)	(39)			
	650	709c	1926c	0.365a	0.083a	36.5a
	% increase	(74)	(70)			
	comments§	A,D	A,D,E	A		
	b. Under well-watered and water-stressed irrigation levels with added N for 1984 and 1985					
wet	ambient	482b	1253b	0.386a	0.085a	36.5a
wet	500	697c	1828d	0.386a	0.084a	37.3a
	% increase	(45)	(46)			
wet	650	842d	2199e	0.388a	0.082a	37.0a
	% increase	(75)	(75)			
dry	ambient	356a	918a	0.365a	0.116bc	36.8a
dry	500	493b	1219b	0.390a	0.122c	36.8a
	% increase	(38)	(33)			
dry	650	654c	1515c	0.413a	0.110b	36.8a
	% increase	(84)	(65)			
	comments	A,B,C,D,E	A,B,D,E,F	A,C	A,B,C	A

† Means not followed by the same letter are signficantly different by at least the 0.05 probability level within the CO_2 group (a) or within the CO_2–irrigation group (b).

‡ % increase over the ambient value.

§ Guide to comments: A–significant effect of year; B–significant effect of irrigation; C–significant effect of year × irrigation interaction; D–significant main effect of CO_2; E–significant effect of year × CO_2 interaction; F–significant effect of irrigation × CO_2 interaction; G–significant effect of year × irrigation × CO_2 interaction.

Table 4. Comparison of responses to cotton grown in open-top chambers at CO_2 concentrations of 650 μmol mol^{-1} and ambient (about 350 μmol mol^{-1}), irrigation levels of well-watered (wet) and water-stressed (dry), and added (N^+) and none-added (N^-) levels of fertilizer nitrogen.

Treatment			Seed cotton yield	Aboveground biomass	Harvest index	Root†/shoot ratio	Lint percentage
Nitrogen	Irrigation	CO_2					
		μmol mol^{-1}	g m^{-2}	g m^{-2}			%
a. Under well-watered irrigation levels and added N fertilizer (1983, 1984, 1985, 1986, and 1987)							
N^+	wet	ambient	400a‡	1036a	0.395a	0.079a	38.0a
N^+	wet	650	638b	1674b	0.387a	0.078a	37.7a
	% increase§		(60)	(62)			
	comments¶		A,D,E	A,D,E	A		A
b. Under well-watered and water-stressed irrigation levels with added N (1984, 1985, 1986, and 1987)							
N^+	wet	ambient	435b	1069b	0.423a	0.079a	37.8a
N^+	wet	650	687d	1747d	0.403a	0.076a	38.3a
	% increase		(58)	(63)			
N^+	dry	ambient	311a	772a	0.397a	0.100b	38.1a
N^+	dry	650	540c	1290c	0.407a	0.096b	38.0a
	% increase		(74)	(67)			
	comments		A,B,C,D,E	A,B,C,D,E,G	A,C	A,B,C	A
c. Under well-watered and water-stressed irrigation levels and added and none-added N fertilizer levels (1986 and 1987)							
N^+	wet	ambient	388d	885c	0.419a	0.068a	0.390a
N^+	wet	650	531e	1295e	0.460a	0.064a	0.395a
	% increase		(37)	(46)			
N^+	dry	ambient	266ab	625ab	0.430a	0.067a	0.395a
N^+	dry	650	425d	1065d	0.400a	0.068a	0.393a
	% increase		(60)	(70)			
N^-	wet	ambient	309bc	700b	0.463a	0.056a	0.398a
N^-	wet	650	445d	1109d	0.421a	0.053a	0.385a
	% increase		(44)	(58)			
N^-	dry	ambient	233a	572a	0.441a	0.076a	0.395a
N^-	dry	650	351c	933c	0.396a	0.101a	0.403a
	% increase		(51)	(63)			
	comments		A,D,E	A,C,D,E,H,I,J	A		A

† There were no root data in 1987.

‡ Means not followed by the same letter are significantly different by at least the 0.05 probability level within the CO_2 groups (a), the CO_2–irrigation groups (b), or the CO_2–irrigation–N groups (c). For the $CO_2 \times H_2O \times N$ experiment (c; 1986, 1987) year was considered to be a repeated sample factor, whereas for the other experiments, it was considered to be a main effect.

§ % increase over the ambient value.

¶ Guide to comments A–significant effect of year; B–significant effect of irrigation; C–significant effect of year × irrigation interaction; D–significant main effect of CO_2; E–significant effect of year × CO_2 interaction; F–significant effect of irrigation × CO_2 interaction; G–significant effect of year × irrigation × CO_2 interaction; H–significant effect of N; I–significant effect of year × N interaction; J–significant effect of irrigation × N interaction; K–significant effect of year × irrigation × N interaction; L–significant effect of CO_2 × N interaction; M–significant effect of year × CO_2 by N interaction; N–significant effect of irrigation × CO_2 × N interaction; O–significant effect of year × irrigation × CO_2 × N interaction.

wood), and the accelerated photosynthesis caused by the high CO_2 (70% increase at 650 μmol mol^{-1}) is seldom inhibited (Radin et al., 1987). Also, orange trees (also woody perennials) growing in CO_2–enriched, open-top chambers in Phoenix respond even more to elevated CO_2 than cotton (Idso et al., 1991).

A second possible reason for the large CO_2 response we have observed with cotton is that the CO_2 × temperature interaction may be very important. Idso et al. (1987) found that the relative CO_2 growth stimulation of five plant species (including the cotton in these experiments appeared to increase by factors of −0.4 at 12 °C, 1.0 at 19 °C, and 2.3 at 34 °C. Therefore, the apparent large response of cotton to elevated CO_2 may be simply that we have conducted these CO_2-enrichment experiments under hotter conditions than anyone else.

Effect of Elevated Carbon Dioxide under Water-Stressed, Added-Nitrogen Conditions

Under water-stress (deficit irrigation regime) but with added nitrogen fertilizer in 1984 and 1985, concentrations of 500 and 650 μmol mol^{-1} CO_2 increased seed cotton yields significantly by 38 and 84% under the dry water-stress conditions (Table 3b). The comparable increases under well-watered conditions were 45 and 75%. Biomass was significantly increased 33 and 65% under dry conditions by the 500 and 650 μmol mol^{-1} CO_2 treatments, respectively, compared to 46 and 75% under the wet treatment. The year × CO_2 interaction was also significant with the increases in biomass and yield due to CO_2 from 500 μmol mol^{-1} to 650 μmol mol^{-1} being greater in 1984 and the increases from ambient to 500 μmol mol^{-1} being greater in 1985.

A 650 μmol mol^{-1} CO_2 treatment was imposed under water-stressed (dry), added-nitrogen conditions for 1984, 1985, 1986, and 1987 (Table 4b). The average increases in yield and biomass were 74 and 67%, respectively. The comparable increases for well-watered conditions were 58 and 63%. The interaction between year and CO_2 was again significant with generally larger responses to CO_2 in 1984 and 1985 than 1986 and 1987 under both wet and dry conditions.

The irrigation × CO_2 interaction for yield was not statistically significant for either the data subset of Table 3b or that of Table 4b. However, it was significant for biomass in Table 3b with the averages across years suggesting that the biomass response of CO_2 was slightly smaller under the water-stress conditions. However, the effects of year and of year × CO_2 interaction were also significant in Tables 3b and 4b. Yield and biomass increases due to CO_2 were about 70% under the dry treatment compared to 45% under the wet in 1985, 1986, and 1987 when we had good control of the water applications with the drip irrigation system. In contrast, in 1984 when the untimely rains and the poor flood irrigation system prevented a sustained water-stress treatment, the yield and biomass increases due to CO_2 were about 61% under the dry treatment compared to 95% under the wet. Considering all 4 yrs, we conclude that the yield and biomass responses to CO_2 were practically the same under both wet and dry treatments, but when the dry treatments were well maintained, it appears that the yield and biomass responses to CO_2 were greater under the dry conditions.

No effect of CO_2 was observed on harvest index, root/shoot ratio, or lint percentage (Tables 3b and 4b). However, the dry irrigation regime did cause significant increases in root/shoot ratio.

Literature reviews by Cure (1985) and Kimball (1985) tabulate studies which suggest that the growth stimulation of C_3 plants due to elevated CO_2 can be greater, unchanged, or reduced under water-stress conditions compared to well-watered conditions. Nor have more recent data established a trend [e.g. Wray and Strain (1986), greater; Chaudhuri et al. (1990), unchanged; Bhattacharya et al. (1990), reduced]. As discussed by Cure (1985), the partial closing of stomates in high CO_2 might impart an improved internal water status of the plants. On the other hand, greater leaf area could increase the water requirement of CO_2–enriched plants. Perhaps greater root proliferation at high CO_2 enables the plants to more fully mine a volume of soil for water. Thus, reasons exist for hypothesizing that elevated CO_2 should enable plants to better withstand moisture stress. On the other hand, when plants are limited by moisture, the concept of limiting factors says there should be no response to increasing CO_2.

Our overall data support neither hypothesis. Averaged over all 4 yrs, there was about a 65% increase in growth with a near-doubling of CO_2 under both well-watered and water-stress conditions. However, for those years when the water stress treatment was best maintained, it appears that there was somewhat greater stimulation of growth by CO_2 under the dry conditions than under the wet.

Effect of Elevated Carbon Dioxide under Low-Nitrogen Conditions

The no-added N significantly reduced yields an average 11% in 1986 and 26% in 1987 (Table 4c). Biomass was similarly reduced by 6 and 30%. Nevertheless, no significant CO_2 × N or year × CO_2 × N interactions were detected. The year × CO_2 interactions were significant, with the effects of CO_2 being somewhat larger in 1986 than in 1987.

In spite of the N levels being low enough to limit growth and yield, there were large responses to CO_2. The 650 μmol mol^{-1} CO_2 treatment increased yields 44 and 51% with no added N for the wet and dry conditions, respectively. The comparable increases with added N were 37 and 60%. Biomass was similarly increased by 58 and 63% at low N for wet and dry conditions, respectively. The comparable increases under added N were 46 and 70%. No significant effects on harvest index, root/shoot ratio, or lint percentage were found.

These results showing a large growth response to CO_2 for C_3 non-N_2–fixing plants even under N-limiting conditions conflict with several nutrient-solution and small-pot studies which reported reduced CO_2 response under low N or P concentrations (Kimball, 1986a). Yet some studies have found similar or even larger growth responses to CO_2 at limiting nutrient levels (e. g. Norby et al., 1986). We can speculate that a larger mass of roots growing in soil under high CO_2 can take up correspondingly larger amounts of N. On the other hand, a certain proportion of a plant's mass is N, and as the plants grow larger, more N and other essential nutrients will be required. Therefore, if this experiment were continued for many years, one can speculate that eventually the soil N level might become sufficiently low that the response to CO_2 would be reduced. In the present study, growth increases of about 60% were observed with a near-doubling of CO_2, even as growth was reduced up to 30% by a lack of N.

CONCLUSIONS

There was a consistently large growth response of the cotton to CO_2 enrichment throughout the 5-yr experimental period. No significant effects on harvest index, root/shoot ratio, or lint percentage were found. Also, no statistically significant interactions of CO_2 with irrigation level or with N fertilizer levels were found, although under a well-maintained water stress, the growth responses to CO_2 tended to be larger than under well-watered conditions. Overall, therefore, the large CO_2 response was practically the same whether or not the plants were growing in soil sufficiently low in water or in N that growth was limited by these variables. Averaging over all the irrigation and N treatments but weighting for the number of years a particular treatment combination was administered, the mean increases in seed cotton yield and in aboveground biomass were 60 and 63%, respectively, for CO_2 enrichment to 650 μmol mol^{-1}.

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