CARBON DIOXIDE ENRICHMENT AND TEMPERATURE EFFECTS ON ROOT GROWTH IN COTTON

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REDDY V.R., REDDY K.R., Acock M. C. and TRENT A. *Carbon dioxide enrichment and temperature effects on root grouth in cotton.* BIOTRONICS **23**, 47–57, 1994. Understanding crop response to climate change requires knowledge of how roots respond to changes in the aerial environment. Changes in rate and amount of root growth could affect the root distribution in the soil profile and absorption of water and nutrients. Root growth and distribution in cotton (*Gossypium hirsutum* L.) were examined at day/night temperatures of 15/7, 20/12, 25/17, 30/22, and 35/27°C and at CO_2 concentrations of 350 and 700 μL L^{-1}. Plants were grown in controlled–environment chambers with a perspex top under nearly natural daylight. At least twice each week root observations were made on one 2 m^2 glass side of the soil bin. Root weight was significantly greater in the 700 μL L^{-1} CO_2 treatment at all depths and at all temperatures. Number of roots increased with increasing temperature up to 25/17°C but was not affected by the CO_2 treatment. Roots in the 350 μL L^{-1} CO_2 treatment were longer (root length per root axis) and penetrated the soil profile faster at the lower temperatures. In the 700 μL L^{-1} CO_2 treatment, roots were more evenly distributed down the soil profile than in the ambient [CO_2] treatment. Root growth was depressed 63 days after emergence (DAE) in virtually all treatments when fruits (bolls) were developing. The optimum temperature for root growth was also the optimum temperature for shoot growth (30/22°C). The effect of elevated [CO_2] was to make roots heavier, but there was no evidence that this translated into a root system with increased length. Roots were shorter in elevated [CO_2], penetrating the soil profile less rapidly but perhaps more thoroughly.

Key words: carbon dioxide; temperature; root growth; cotton; *Gossypium hirsutum* L.

INTRODUCTION

The increase in Earth's atmospheric carbon dioxide concentration $[CO_2]$ and associated climatic changes are a major concern to agronomists all over the world. The effect of climate change on crop production has been a major interest to crop physiologists. Presently there is an enhanced interest within the scientific community in how the projected increases in carbon dioxide concentration and the associated increase in atmospheric temperature will affect crop production (*4, 7, 9, 15, 16, 25*).

Enhancement of canopy photosynthesis is one important direct effect of rising $[CO_2]$. Increase in $[CO_2]$ has been shown to increase photosynthesis in cotton (*2, 6, 11*) and enhance growth and yield of above-ground plant parts (*6, 10, 12*). The studies conducted under controlled-environment conditions in recent years (*17, 18, 19, 20*) and the earlier work of Hesketh et al. (*8*) and Mutsaers (*13*) established a comprehensive database on the effects of temperature, including extreme low and high temperatures, on above-ground plant parts of cotton, which included stem elongation, node initiation, leaf expansion, branching, fruiting, and square and flower abscission.

Research on the effects of CO_2 concentration on root growth is very limited, with the exception of the work of Tognoni et al. (*29*) on bean and tomato, Chaudhuri et al. (*3*) on winter wheat, and Del Castillo et al. (*5*) and Rogers et al. (*23*) on soybean. To date we have not found any data on the effects of temperature and $[CO_2]$ and their interactions on cotton root growth. This lack of data is partly due to the difficulty involved in measuring root growth non-destructively. Studies on the effects of $[CO_2]$ and temperature on root growth and development are needed, and a strong recommendation has been made to this effect (*26*). The response of root systems to CO_2 and temperature is highly significant because of their role in mining water and nutrients, and manipulating the plant's ability to withstand water and nutrient stress. Changes in root growth also affect carbon partitioning by the plant, as well as the role of the soil as a sink in the global carbon budget and its potential to modify soil characteristics and water holding capacity. The objective of this study was to evaluate the interactive effects of temperature and $[CO_2]$ on cotton root growth, root initiation rate, depth of root penetration, and root dry weight under optimum water and nutrient conditions during the prefruiting period.

MATERIALS AND METHODS

The plant growth chambers used in this study have been described by Acock et al. (*1*) and Reddy et al. (*19, 20*). Briefly, these chambers consisted of a steel soil bin containig rooting medium and measuring 1.0 m high, 2.0 m long, and 0.5 m wide. The southern face of the soil bin was covered with panels of wired safety glass, through which roots could be observed and measured non-destructively. The northern face had many large holes closed with rubber stoppers to facilitate the introduction of instruments to measure soil

environmental conditions. The entire soil bin, including the glass face, was surrounded by styrofoam insulation to reduce diurnal temperature fluctuations and to obstruct direct light on the glass face. A portion of the styrofoam insulation on the glass face of the soil bin could be detached for root observations. On top of the soil bin was an acrylic plastic box containing the aerial parts of the plants and measuring 2.0 m high, 2.0 m long, and 1.5 m wide. A door in the bottom of each box was hinged for easy access to the plants. The chambers were exposed to sunlight, and the sides were shaded to plant height with graded shades to eliminate the need for border plants. The soil bins of the growth chambers were filled with a mixture of sand and vermiculite (3:1 by volume) that was incorporated with slow-release micronutrients at the rate of 88 mg L^{-1} prior to filling the bins. Cotton 'Deltapine 50' seeds were pregerminated in moistened paper towels at 28/23°C day/night temperatures for 48 h. The germinated seeds were selected for their uniformity and planted on 22 March in the plant growth chambers. The seedlings were thinned to three rows of plants with a plant population of 15 plants m^{-2}.

The temperature- and CO₂-controlled chambers were all maintained at 28/23°C (day/night) during seedling emergence and until 14 days after emergence (DAE). On 15 DAE, temperature and CO₂ treatments were imposed, and the air temperatures in the growth chambers were maintained at 20/12, 20/12, 25/17, 30/22, and 35/27°C. The CO₂ concentrations were maintained at 350 and 700 μL L^{-1} for each temperature, utilizing a total of 10 controlled-environment cabinets. The daytime temperature was initiated at sunrise and returned to the nighttime temperature 1 h after sunset during the experimental period. On 24 DAE, the temperature treatments in two chambers were changed from 20/12 to 15/7°C to determine if we could measure root growth and development at such a low temperature. Since 20/12°C was a replicated treatment having two chambers at each [CO₂] and temperature, we were able to continue 20/12°C along with 15/7°C treatments at both CO₂ levels. However, 10 d later the plants at 15/7°C in both CO₂ levels had not grown and were found to be susceptible to disease. On 35 DAE, we changed the 15/7°C treatment back to 20/12°C. The average temperatures during the entire experiment were 17.8, 18.7, 22.7, 26.6, and 30.6°C for the day/night temperature treatments of 15/7°C with 20/12, 20/12, 25/17, 30/22, and 35/27°C at both CO₂ levels. The dewpoint temperatures were not controlled but were measured at 10-s intervals with gold mirror hygrometers. Data on the daytime and nighttime air temperatures, daily solar radiation, and dewpoint temperatures have already been presented (21). Soil temperatures were recorded at 10-s intervals throughout the experiment at depths of 25, 50, and 75 cm (Table 1). The soil temperature data show no dramatic influence of air temperatures on soil temperatures except at 25 cm soil depth, where a consistent increase in soil temperature was recorded with increases in air

Table 1. Seasonal mean soil temperatures at different depths of the soil during the experiment.

Soil depth, cm	Air Temperature Treatment, °C				
	17.8	18.7	22.7	26.6	30.6
25	19.43	19.57	20.02	21.27	22.08
50	21.68	21.76	22.32	23.04	23.11
75	21.17	21.33	21.75	22.13	23.10

temperature.

Carbon dioxide concentration, air temperature, and irrigation in the chambers were controlled by a computer (Digital, Pro 380,[1] Digital Equipment Corp., Maynard, MA), which also monitored other environmental and plant response variables (*21*). The temperatures in the growth chambers were maintained to within ±0.1°C of the set points for at least 95% of the time, using a secondary cooling system and resistance heaters. Continuous circulation of air maintained uniform temperatures throughout the chambers. The chambers were sealed, and the CO_2 concentration was monitored at 10–s intervals and averaged over 15–min period. Carbon dioxide was injected from a gas cylinder through a pressure regulator, solenoid valve, needle valve, and flow meter into the chambers as neccessary to maintain [CO_2] at 350 or 700 μL L^{-1} .

The plants were irrigated three times a day with a drip irrigation system with one emitter per plant. The daily amount of water was double the amount of pan evaporation from the previous day measured at an adjacent weather station. Drippers were calibrated prior to the start of the experiment, and those drippers that emitted more or less than 15% of the set point were replaced. The amount and timing of the irrigations were computer controlled. Insects were controlled as needed during the course of the experiment with proper insecticide applications.

At least twice each week data were collected on new root growth appearing on the glass face of the soil bin. The root length was measured and marked with a wax pencil as described by Del Castillo et al. (*5*). In addition, at each measurement period the number of growing root tips and the depth of the root system were recorded. The quantity of root material and root elongation on the glass viewing surface was assumed to be representative of roots in bulk soil throughout the soil bin at the corresponding depth (*27, 28*). Taylor et al. (*28*) particularly tested this assumption at the Auburn rhizotron and found that the rooting density and growth at glass–soil interface was approximately equal to that in the rest of the soil bin. Because of the configuration of the cabinet soil bins, and the metal framing, the top 0.1 m of root medium was obscured. At the time of the final destructive harvesting (70 DAE), the rooting medium in the soil bins was washed of the roots using a metal screen. This destructive harvesting of the roots was accomplished separately for each 0.1 m layer of the root system in the soil bin. After they were washed, the roots were dried and weighed.

Statistical analysis was conducted by using procedures in the SAS General Linear Model (24). Dependent variables were regressed as linear functions of the independent variable. The regression coefficients were tested at the 0.05 alpha level for significance. The equalities of the regression lines were tested using the General Linear Test approach (14). The standard error of the mean was calculated and is presented whenever applicable.

RESULTS AND DISCUSSION

Root Weight and Distribution in the Soil

The increase in root dry weight with temperature was linear up to 22.7°C in both the 350 and 700 μL L^{-1} [CO_2] treatments. In higher temperature treatments, root dry weight remained stable in 350 μL L^{-1} [CO_2] but continued to increase in 700 μL L^{-1} [CO_2] (Fig.1). Results suggest that temperatures below 22.7°C control or limit root dry weight gain, but that at higher temperatures, root dry weight gain can be limited by aerial [CO_2]. The upper temperature limit on root dry weight gain for 700 μL L^{-1} [CO_2] is higher than 30.6°C, the highest temperature treatment in this study.

Root dry weight was consistently greater in 700 μL L^{-1} [CO_2] compared with 350 μL L^{-1} [CO_2] in all temperatures and at all soil depths (Table 2) (one–tailed paired t-test$=2.216$, $df=19$, $p<0.02$). Most of the root weight was found in the top 0.2 m layer of soil (78.5% of total root weight), with the tap root of the cotton plant contributing most to the total root weight. These results are consistent with reports on the effects of [CO_2] on the roots of other agronomic crops (3, 5, 23).
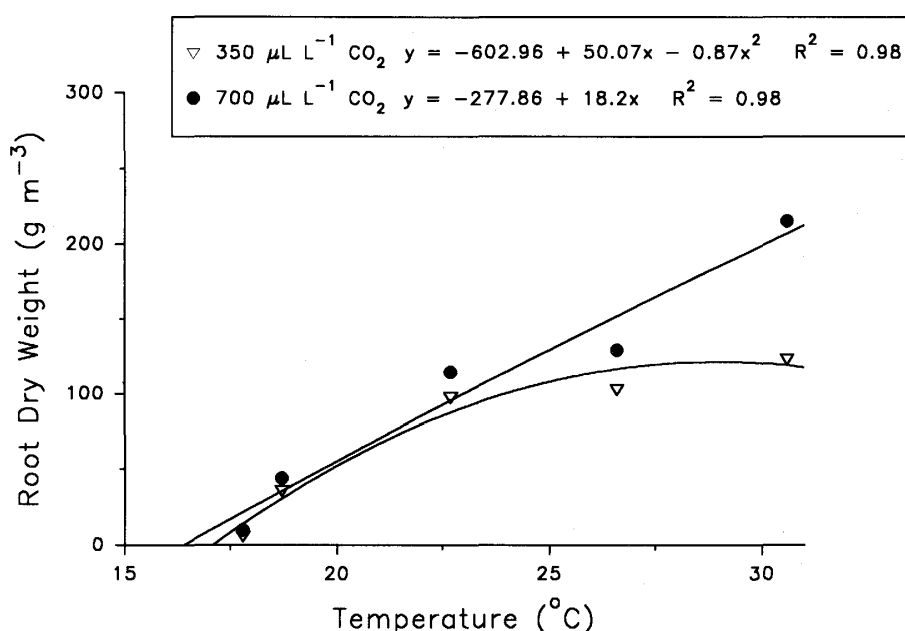

Fig. 1. Root dry weight of cotton plants as influenced by [CO_2] and temperature harvested at 70 DAE.

Table 2. Root dry weight (g m^{-3}) by temperature, soil depth, and [CO_2] at 70 DAE.

| Soil Depth, cm | 350 μL L^{-1} CO_2 | | | | | 700 μL L^{-1} CO_2 | | | | |
| | Temperature, ℃ | | | | | Temperature, ℃ | | | | |
	17.8	18.7	22.7	26.6	30.6	17.8	18.7	22.7	26.6	30.6
0–20	4.86	24.15	81.72	86.01	94.56	7.77	30.66	96.09	109.20	157.14
20–40	0.72	6.45	8.88	8.94	20.70	0.96	6.96	9.63	11.28	25.20
40–60	0.66	4.05	4.80	5.55	5.64	0.69	4.35	5.61	5.67	16.20
60–100	0.27	1.92	2.94	2.97	2.88	0.39	2.04	3.0	2.97	16.83
Total (g m^{-3})	6.51	36.57	98.34	103.43	123.78	9.81	44.01	114.33	129.12	215.37
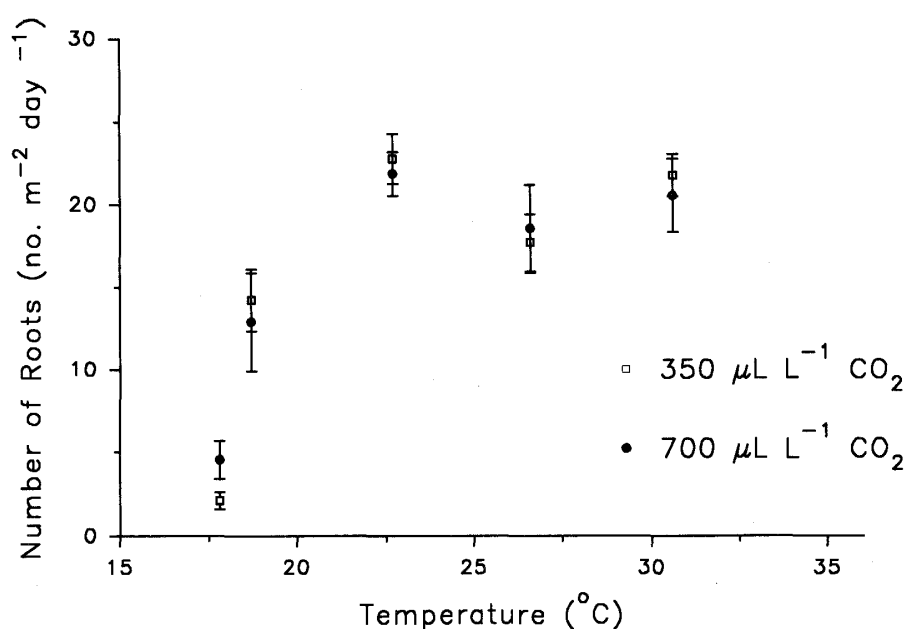
Fig. 2. The average number of roots produced on the glass face over the season as influenced by [CO_2] and temperature treatments.

Root Number

Root numbers increased dramatically with temperature up to 22.7℃, declined from that maximum in the 26.6℃ treatment, then showed an upswing at 30.6℃ (Fig. 2). This decline and upswing in root numbers may not be a direct effect of temperature on the root system but rather an indirect effect. Temperatures that favor shoot development, particularly fruit formation, may reduce the assimilate supply to the root, leading to a decline in root numbers. On the other hand, temperatures high enough to cause fruit (boll) abortion may actually favor root development. Reddy et al. (*22*) found that fruit abortion occurred at 30.6℃, which could explain why root numbers declined at 26.6℃ then increased again at 30.6℃.

Root numbers were not influenced by [CO_2] except in the lowest temperature treatment. Plants grown at the lowest temperature had more root
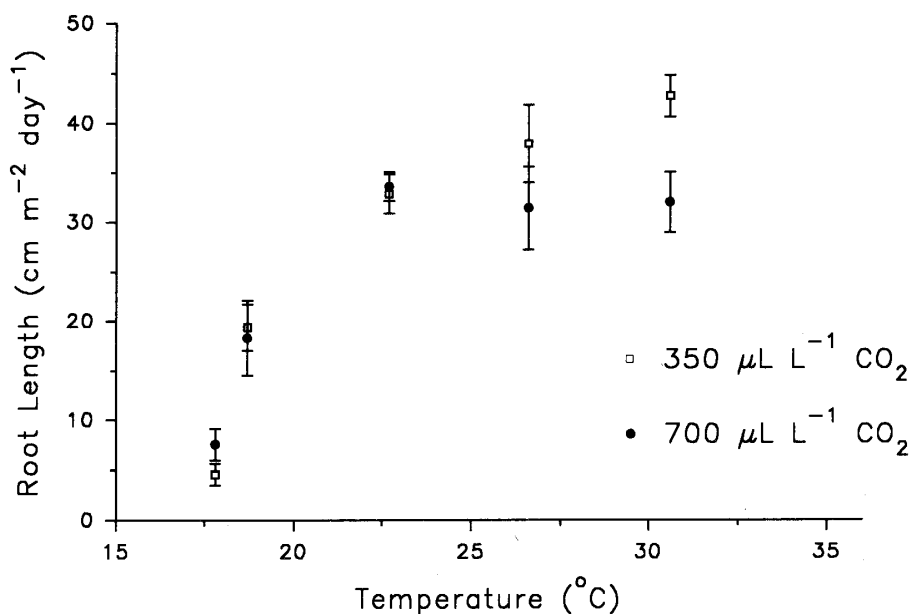
Fig. 3. The average root length visible at the vertical glass face over the season as influenced by $[CO_2]$ and temperature treatments.

tips if they were grown in $700\,\mu L\ L^{-1}$ $[CO_2]$ rather than in $350\,\mu L\ L^{-1}$ $[CO_2]$. Dry matter partitioning patterns change at low temperatures with proportionally more dry matter going into the root (20). This change in partitioning pattern along with the greater availability of carbohydrate in $700\,\mu L\ L^{-1}$ $[CO_2]$ could explain why more roots were observed in the $700\,\mu L\ L^{-1}$ $[CO_2]$ treatment compared with $350\,\mu L\ L^{-1}$ $[CO_2]$ at the lowest temperature.

Root Length

Root length increased sharply with temperature up to 22.7°C, and there was no distinction between $[CO_2]$ treatments at these lower temperatures. At temperatures above 22.7°C, root length of plants in $350\,\mu L\ L^{-1}$ $[CO_2]$ continued to increase, while root length of plants in $700\,\mu L\ L^{-1}$ $[CO_2]$ did not increase further (Fig. 3). At first glance, this result is difficult to explain. Why should root length be diminished by the $700\,\mu L\ L^{-1}$ $[CO_2]$ treatment ? Rogers et al. (23) found increased root length for soybean using the same $[CO_2]$ treatments. The explanation may lie, once again, in how the shoot is being affected. Rogers et al. (23) examined root growth in vegetative plants grown for 18 days. Our study examined root growth for 70 days including the early reproductive period. Under elevated $[CO_2]$, cotton plants initiate and retain more bolls (22). These additional bolls may compete with roots for assimilates. If the plant has sufficient water and nutrients, as in this experiment, assimilates can be diverted to bolls without consequence to the plant as a whole. Under water and nutrient stress conditions, root growth might be very different.

Because root numbers were similar for the two $[CO_2]$ treatments but root lengths were not, it follows that plants in $700\,\mu L\ L^{-1}$ $[CO_2]$ had shorter roots
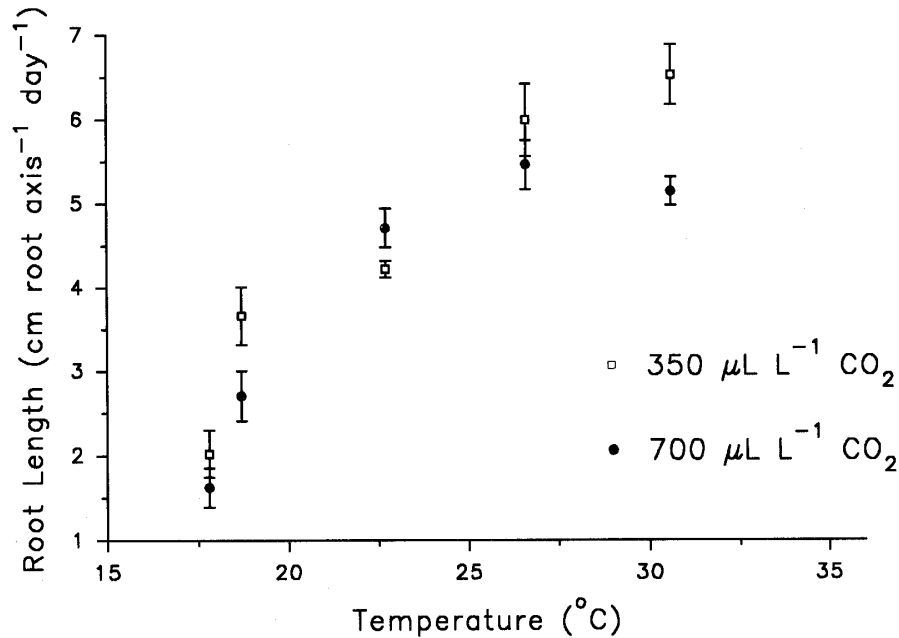
Fig. 4. The average root length per root axis at the vertical soil/glass interface over the season as influenced by [CO_2] and temperature treatments.

(Fig. 4). This was particularly true for the 30.6°C treatment, where plants in 700 μL L^{-1} [CO_2] had 66% more bolls to support than those in 350 μL L^{-1} [CO_2] (*22*).

Root Distribution Over Time

Root activity peaked twice during the growing season, the first peak at 35 DAE and the second one at 62–64 DAE (Fig. 5). The appearance of roots at the glass face was linked with plant development. The first flush of root activity occurred just prior to or during squaring (Fig. 5), which varied from 30 to 59 days depending on the temperature treatment.

Early Root Distribution Down the Soil Profile

The distribution of roots within the soil profile was bimodal with peaks in the top 0.2 m and at 0.5–0.6 m soil depth. The temperature in the upper portion of the soil profile was influenced more by aerial temperature and may have caused relatively more roots to be produced there.

Plants grown in 350 μL L^{-1} [CO_2] had root axes less uniformly distributed down the soil profile from 20 to 100 cm depth in the first half of the growing season (36 days) than plants grown in 700 μL L^{-1} [CO_2] (Fig. 6). This was determined by using a Chi–square test for uniformity of distribution.

Root Penetration into the Soil Profile

The minimum time for roots to penetrate halfway down the soil profile (0.5 m) was 35 DAE. This was achieved at a temperature of ≥22.7°C for 700 μL L^{-1}
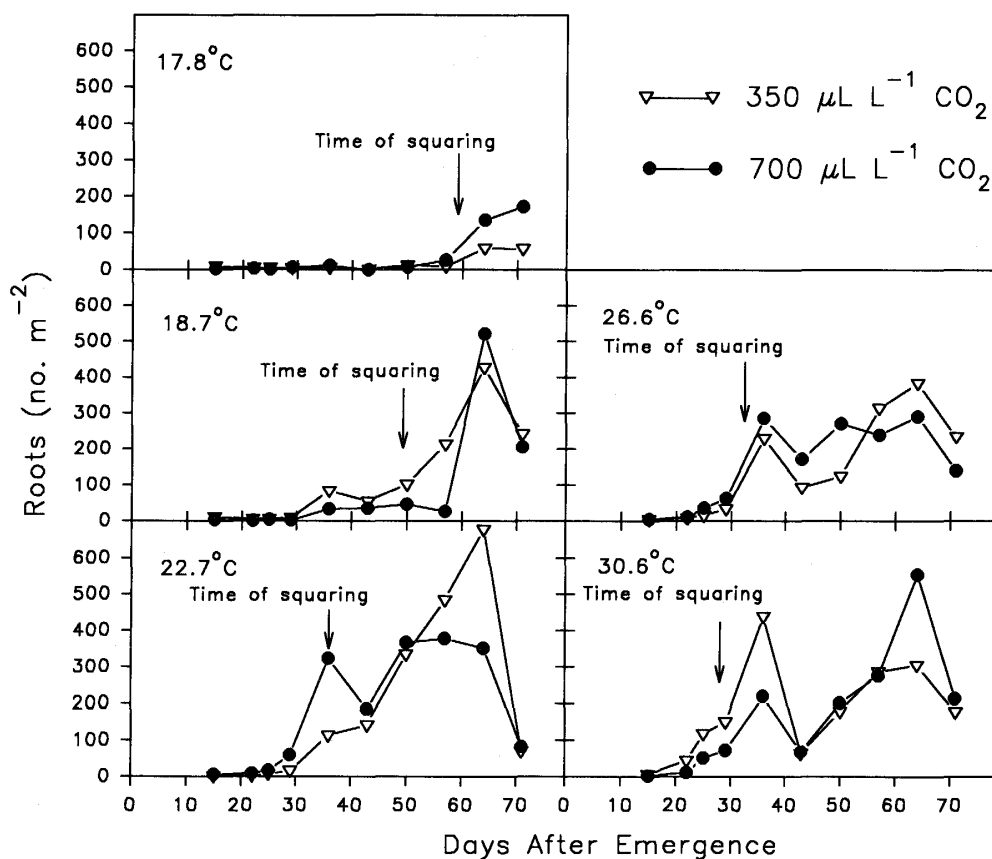
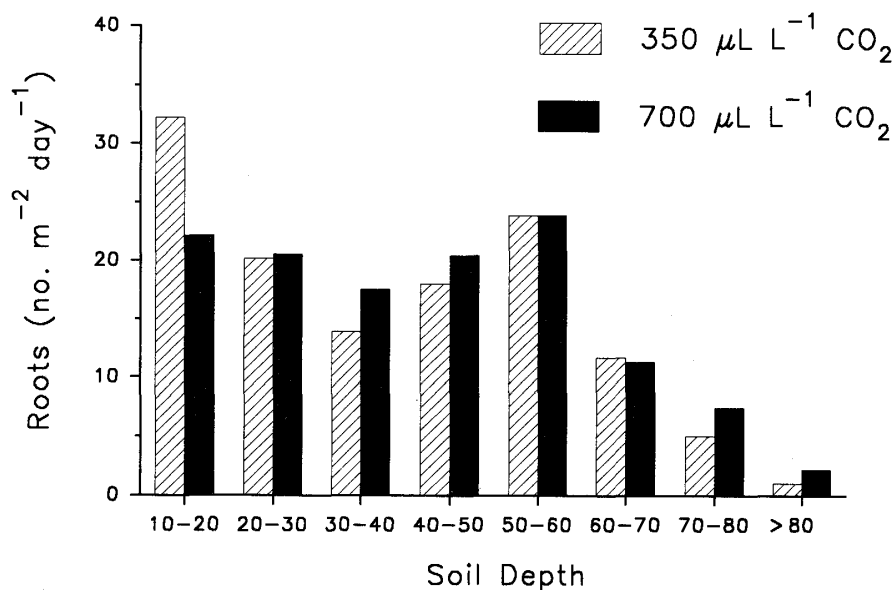Fig. 5. The number of new roots growing during the experiment as influenced by temperature and [CO₂] treatments.

Fig. 6. Variation in the number of roots produced with depths for cotton as influenced by [CO₂] treatments at 70 DAE.

$[CO_2]$ and at $\geq 18.7°C$ for $350 \mu L$ L^{-1} $[CO_2]$. The roots of plants grown in $700 \mu L$ L^{-1} $[CO_2]$ may have taken longer to penetrate halfway down the soil profile at the lower temperatures because root elongation was limited by these lower temperatures and roots in $700 \mu L$ L^{-1} $[CO_2]$ were shorter.

The dynamic response of the root system to temperature and CO_2 cannot be understood without knowing how those same factors affect shoot and fruit development. Flushes in root growth appear to be related to shoot activity. Roots flourish when flowers and fruits abort or when shoot growth declines. Extreme temperatures can limit shoot or fruit growth and favor root development (*19*). The greatest increase in root activity has occurred at temperatures optimum for shoot growth (*22*). Proliferation of roots coincides with specific stages in plant development. The location of roots in the soil profile depends on how far they have penetrated into the soil profile when certain plant development stages are reached.

In this study, the effect of elevated CO_2 on roots was to make them heavier, but there was no evidence that this translated into a root system with more absorbing power for water and nutrients. There was no increase in the number of roots. Those roots observed were shorter, and they penetrated the soil profile less rapidly. However, root distribution through the soil profile was more uniform under elevated CO_2.

The effect of temperature on roots was to increase the numbers of roots and root length up to $22.7°C$. Further increases in root activity depended on how temperature affected the competition between the root and the shoot.

REFERENCES

1. Acock B., Reddy V. R., Hodges H. F., Baker D. N. and McKinion J. M. (1985) Photosynthetic response of soybean canopies to full-season carbon dioxide enrichment. *Agron. J.* **77**, 942–947.

2. Baker D. N. (1965) Effects of certain environmental factors on net assimilation in cotton. *Crop Sci.* **55**, 53–56.

3. 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.

4. Cure J. D. and Acock B. (1986) Crop responses to carbon dioxide doubling: A literature survey. *Agric. Meteorol.* **38**, 127–145.

5. 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.

6. DeLucia E. H., Sasek T. W. and Strain B. R. (1985) photosynthesis inhibition after long –term exposure to elevated levels of atmospheric carbon dioxide. *Photosynthesis Res.* **7**, 175–184.

7. Enoch H. Z. and Zieslin N. (1988) Growth and development of plants in response to carbon dioxide concentrations. *Appl. Agric. Res.* **3**, 248–256.

8. Hesketh J. D., Baker D. N. and Duncan W. G. (1972) Simulation of growth and yield in cotton. II. Environmental control of morphogenesis. *Crop Sci.* **12**, 436–439.

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

10. Mauney J. R., Fry K. E. and Guinn G. (1978) Relationship of photosynthetic rate to growth and fruiting of cotton, soybean, sorghum, and sunflower. *Crop Sci.* **18**, 259–263.

11. Mauney J. R., Guinn G. E., Fry K. E. and Hesketh J. D. (1979) Correlation of photosynthetic carbon dioxide uptake and carbohydrate accumulation in cotton, soybean, sunflower and sorghum. *Photosynthetica* **13**,260–266.

12. Morison J. I. L. and Gifford R. M. (1984) Plant growth and water use with limited water supply in high CO_2 cocentrations. I. Leaf area, water use and transpiration. *Aust. J. Plant Physiol.* **11**, 361–374.

13. Mutsaers H. J. W. (1983) Leaf growth in cotton. II. The influence of temperature, light, water stress, and root restriction on growth and initiation of leaves. *Ann. Bot.* **51**, 521 –529.

14. Neter J. and Wasserman W. (1974) *Applied linear statistical models.* Richard D. Irwin, Inc., Homewood, IL.

15. Newton P. C. D. (1991) Direct effects of increasing carbon dioxide on pasture plants and communities. *New Zealand J. Agric. Res.* **34**, 1–24.

16. Post W. M., Peng T. –H., Emanuel W. R., King A. W., Dale V. H. and DeAngelis D. L. (1990) The global carbon cycle. *Am. Scientist* **78**,310–326.

17. Reddy K. R., Hodges H. F. and Reddy V. R. (1992a) Temperature effects on cotton fruit retention. *Agron. J.* **84**, 26–30.

18. Reddy K. R., Reddy V. R. and Hodges H. F. (1992b) Temperature effects on early season cotton growth and development. *Agron. J.* **84**, 229–237.

19. Reddy V. R., Reddy K. R. and Baker D. N. (1991a) Temperature effect on growth and development of cotton during the fruiting period. *Agron. J.* **83**, 211–217.

20. Reddy V. R., Baker D. N. and Hodges H. F.(1991b) The effects of temperature on cotton canopy growth, photosynthesis, and respiration. *Agron. J.* **83**, 699–704.

21. Reddy V. R., Reddy K. R. and Acock B. (1994) Carbon dioxide and temperature effects on cotton leaf initiation and development. *Biotronics* **23**, 59–74.

22. Reddy V. R., Reddy K. R. and Hodges H. F.(1994) Carbon dioxide enrichment and temperature effects on cotton photosynthesis, transpiration and water use efficiency. *Field Crops Res.* (*in press*).

23. Rogers H. H., Peterson C. M., McCrimmon J. N. and Cure J. D. (1992) Response of plant roots to elevated atmospheric carbon doixide. *Plant, Cell Environ.* **15**, 749–752.

24. SAS Institute. (1987) *SAS users' guide: Statistics.* Version 5.18. SAS Inst., Cary, NC.

25. Smit B., Ludlow L. and Brklacich M. (1988) Implications of a global climatic warming for agriculture: A review and appraisal. *J. Environ. Qual.* **17**, 519–527.

26. Strain B. R. and Cure J. D. (*eds.*). (1985) Direct effects of increasing carbon dioxide on vegetation. DOE/ER 0238. The Office of Energy Research, U.S. Dept. of Energy.

27. Taylor H. M. and Böhm W. (1976) Use of acrylic plastic as rhizotron windows. *Agron. J.* **83**, 693–694.

28. Taylor H. M., Huck M. G., Klepper B. and Lund Z. F. (1970) Measurement of soil–grown roots in a rhizotron. *Agron. J.* **62**, 807–809.

29. Tognoni F., Halevy A. H. and Witter S. H. (1967) Growth of bean and tomato plants as affected by root absorbed growth substances and atmospheric carbon dioxide. *Planta* **2**, 43–52.