

## Carbon dioxide and temperature interactions on stem extension, node initiation, and fruiting in cotton

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### Abstract

Understanding the response of agricultural crops to rising carbon dioxide concentration (CO<sub>2</sub>) and temperature is critical for modeling the effects of future climate change on crop productivity. The objective of this study was to evaluate the direct and interactive effects of temperature and CO<sub>2</sub> on mainstem and branch expansion rates, node initiation rates, and fruiting in cotton to be used for the development of a cotton simulation model. Cotton plants (*Gossypium hirsutum* L., cv. DPL 50) were grown in plant growth chambers exposed to natural light levels with temperature and CO<sub>2</sub> as treatments. The average temperatures were 17.8, 18.7, 22.7, 26.6, and 30.6°C during a 70 day experimental period with CO<sub>2</sub> treatments of 350 and 700 μl l<sup>-1</sup> at each temperature. Plant height and number of mainstem nodes increased with increase in temperature and CO<sub>2</sub>. A nine-fold increase was observed in number of fruiting branches with increase in temperature from 17.8 to 30.6°C, however, no significant differences were observed in fruiting branch number due to doubling of CO<sub>2</sub> except at 30.6°C. The number of days from emergence to first square was strongly influenced by temperature, and CO<sub>2</sub> had no effect on this process. The number of squares and bolls were increased at higher temperatures, and the rate of increase was greater at 700 μl l<sup>-1</sup> CO<sub>2</sub>.

### 1. Introduction

The increase in concentration of global atmospheric carbon dioxide, CO<sub>2</sub>, is expected to result in a CO<sub>2</sub> level of 600 μl l<sup>-1</sup> sometime between 2030 and 2070 (Schneider, 1989). The effects of increased CO<sub>2</sub> on agriculture have been a major concern in recent years (Kimball, 1983; Cure and Acock, 1986; Enoch and Zieslin, 1988; Smit et al., 1988; Post et al., 1990; Newton, 1991).

The continuing increases in concentration of CO<sub>2</sub> and other "greenhouse gases" should have two major consequences: earth's climate may change and plant growth may be stimulated. The primary effect of ele-

vated CO<sub>2</sub> on well watered plants with the C<sub>3</sub> carbon fixation pathway is an increase in net photosynthesis (Jones et al., 1984; Baker et al., 1990). The increased levels of CO<sub>2</sub> and other greenhouse gases are expected to increase global air temperatures. An increase in CO<sub>2</sub> tends to partially close stomata in plant leaves, resulting in reduced transpiration per unit leaf area (Jones et al., 1985) and increased tissue temperatures (Idso et al., 1987a). This direct effect of CO<sub>2</sub> on canopy temperature, in addition to a 3–6°C rise in global surface air temperature predicted by atmospheric general circulation models (Grotch, 1988), may have a significant effect on agricultural crops.

The beneficial effects of increased CO<sub>2</sub> on growth and productivity of crops and pasture plants have been well documented by the reviews of Kimball (1983),

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Cure and Acock (1986), and Newton (1991). The effects of long-term elevated CO<sub>2</sub> and temperature on productivity of crop plants are poorly understood (Bazzaz, 1990). Cure and Acock (1986) reported that temperature × CO<sub>2</sub> interactions on seed yield were unavailable in their survey of ten major crops. They found only three studies of CO<sub>2</sub> × temperature interaction on biomass. The work of Idso et al. (1987b) showed that growth stimulation caused by CO<sub>2</sub> enrichment increases with increase in air temperature during vegetative growth. However, Baker et al. (1989) reported a decrease with temperature in yield and harvest index for soybeans (*Glycine max* (L.) Merr.) grown at 330 and 660 μl l<sup>-1</sup> of CO<sub>2</sub>. Rawson (1992) showed that interactive effects of CO<sub>2</sub> enrichment and temperature on plant development and growth cannot

be interpreted within a simple framework. Plant response to temperature and other environmental factors is remarkably dynamic and can be expressed in multiple ways and differs depending on species and stage of plant development (Idso and Kimball, 1989; Bazzaz, 1990; Rawson, 1992). Recently, we characterized growth and developmental rates of cotton at a range of temperatures and ambient CO<sub>2</sub> level during the fruiting period (Reddy et al., 1991a; Reddy et al., 1991b), and prefruiting period (Reddy et al., 1992b). The effects of long-term CO<sub>2</sub> and temperature are interactive in some studies, and literature on them is very limited. Temperatures of 15–40°C are frequently observed in cotton producing areas, and periods with even greater temperature extremes will likely be more frequent and detrimental to cotton production (Reddy

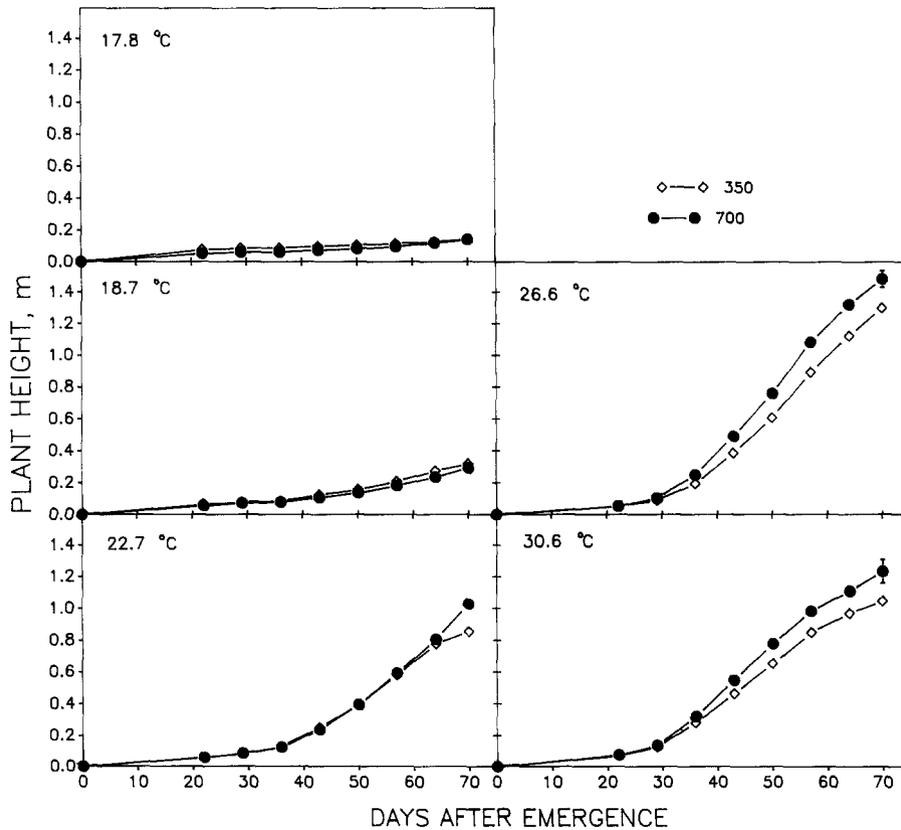


Fig. 1. Influence of temperature and CO<sub>2</sub> on plant height of cotton. Bars indicate standard errors of the mean, and are shown when greater than the symbol size.

et al., 1992a), if predicted global warming occurs.

The objective of this study was to evaluate the interactive effects of temperature and CO<sub>2</sub> on mainstem and branch expansion rates, node initiation rates, and fruiting in cotton. Additionally, this database can be used for improved estimates of growth and developmental rates for modeling the growth and productivity of cotton.

## 2. Materials and methods

The plant growth chambers used in this study have been described by Acock et al. (1985) and Reddy et al. (1991b). In brief, the chambers consisted of a steel bin containing the rooting medium and measuring 1.0 m high by 2.0 m long by 0.5 m wide. An acrylic base

Table 1  
Parameters for quadratic equations regressing plant height ( $y$ ) and number of mainstem nodes ( $y$ ) as functions of days after emergence ( $x$ ) at various temperature regimes and CO<sub>2</sub>. ( $y = b_0 + b_1x + b_2x^2$ )<sup>a</sup>

Temperature (°C)	CO <sub>2</sub> μl l <sup>-1</sup>				
		$b_0$	$b_1$	$b_2$	$r^2$
<i>Plant height (cm)</i>					
17.8	350	5.71	-0.002	0.001	0.447
18.7	350	9.44	-0.376	0.009	0.740
22.7	350	22.13	-1.612	0.039	0.969
26.6	350	11.439	-1.404	0.047	0.981
30.6	350	-27.894	1.145	0.013	0.967
17.8	700	6.819	-0.126	0.0026	0.518
18.7	700	8.404	-0.305	0.0075	0.706
22.7	700	29.114	-2.021	0.044	0.988
26.6	700	-3.545	-0.752	0.045	0.985
30.6	700	-41.01	1.76	0.01	0.974
<i>Mainstem nodes (no. per plant)</i>					
17.8	350	5.123	-0.133	0.0025	0.611
18.7	350	0.905	0.1007	0.00036	0.845
22.7	350	-1.796	0.240	0.0008	0.959
26.6	350	-5.493	0.430	-0.0009	0.980
30.6	350	-9.58	0.689	-0.0034	0.967
17.8	700	5.563	-0.148	0.0026	0.694
18.7	700	1.269	0.065	0.0008	0.873
22.7	700	-1.169	0.193	0.0007	0.938
26.6	700	-6.118	0.482	-0.0018	0.984
30.6	700	-9.924	0.702	-0.0032	0.977

<sup>a</sup>Regression lines for each temperature are significantly different ( $P=0.05$ ) from preceding temperature treatment for plant height and mainstem nodes. The regression lines are significantly different only at 26.6°C and 30.6°C owing to CO<sub>2</sub>.

on top of this soil bin holds the aerial parts of the plants and measures 2.0 m high by 2.0 m long by 1.5 m wide. A door in the bottom of each base is hinged for easy access to the plants. The growth chamber soil bins were filled with a mixture of sand and vermiculite (3:1 by volume) to which was added a mixture of slow-release micronutrients at the rate of 88 mg l<sup>-1</sup> prior to filling the soil bins. At the bottom of each soil bin, a 150 mm layer of washed gravel and water outlets allowed good drainage.

Cotton 'Deltapine 50' (DPL 50) seeds were germinated in moistened paper towels at 28/23°C day/night temperatures for 48 h. The germinated seeds were selected for uniformity and planted in naturally lighted plant growth chambers in 11 rows of five plants per row on 22 March. Full strength Hoagland's nutrient solution (Hewitt, 1952) was applied daily to provide the macro- and micronutrients. Six rows of plants were harvested at 23 days after emergence (DAE) and two more rows were harvested at 35 DAE to avoid competition for light, leaving three rows of five plants each for final harvest on 70 DAE with 15 plants m<sup>-2</sup>. The initial thick planting was needed to get a canopy large enough to measure photosynthesis from the seedling stage. However, we harvested these extra rows at canopy closure, once at 23 DAE and again at 35 DAE. These harvested rows were used to provide short-term dry matter accumulation rates and total leaf area of the plants. The data collected on canopy photosynthesis and dry matter accumulation rates are not presented, as they are outside the scope of this paper.

The temperature and CO<sub>2</sub> controlled chambers were all maintained at 28/23°C (day/night) during seedling emergence and until 14 DAE. On 15 DAE temperature and CO<sub>2</sub> 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 CO<sub>2</sub> concentrations were set at 350 and 700 μl l<sup>-1</sup> during the day for each temperature, utilizing a total of ten controlled environment cabinets. The daytime temperature was initiated at sunrise, and the nighttime temperature was started 1 h after sunset during the experimental period. On 24 DAE, at the time of first destructive harvest of extra rows, the temperature treatments in two of the cabinets were changed from 20/12 to 15/7°C to see if we could measure growth and development at that low a temperature. As 20/12°C was a replicated treatment having two cabinets at each CO<sub>2</sub> and tem-

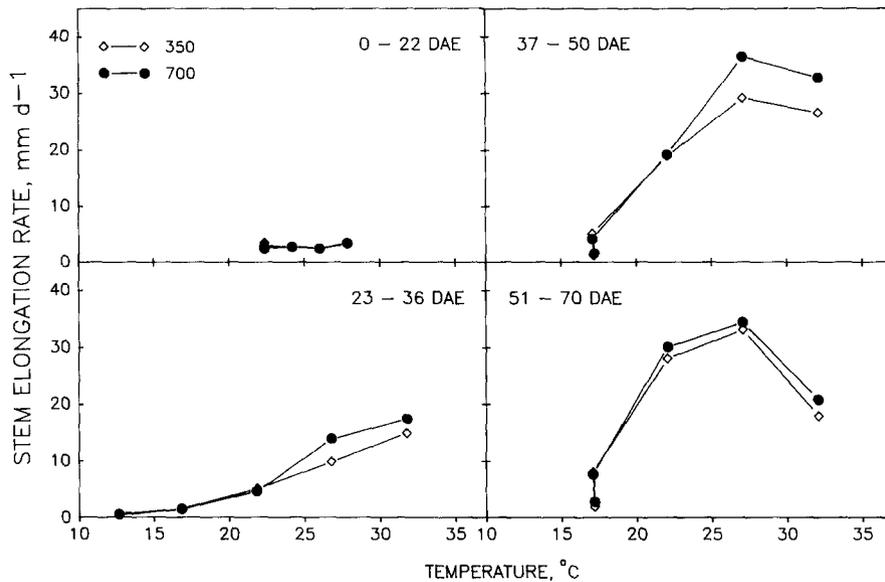


Fig. 2. Influence of temperature and CO<sub>2</sub> on cotton stem elongation rate during various periods after emergence. The double points at the same temperature are the result of changing the 15/7°C treatment to 20/12°C during 37-50 and 51-70 DAE. Bars indicate standard errors of the mean, and are shown when greater than the symbol size.

perature, we were able to continue the 20/12°C treatment along with the 15/7°C treatment. However, after 10 days the plants in 15/7°C had not grown and were found to be disease prone. On 35 DAE, we changed the 15/7°C treatment back to 20/12°C and completed the second destructive harvest. During the entire experimental period, the average temperatures were 17.8, 18.7, 22.7, 26.6, and 30.6°C for the temperature treatments of 15/7°C with 20/12, 20/12, 25/17, 30/22, and 35/27°C at both CO<sub>2</sub> levels. The dewpoint temperatures were not controlled but measured at 10 s intervals with gold mirror hygrometers installed inside the return air line. Data on air temperatures in the chambers, daily solar radiation, and dewpoint temperatures for this study have already presented (Reddy et al., 1994).

Carbon dioxide concentration, air temperature, and irrigation in the chambers were controlled by a computer (Digital, Pro 380,<sup>1</sup> Digital Equipment, Maynard,

<sup>1</sup> Trade name and company name are included for the benefit of the reader and do not imply any endorsement or preferential treatment of the product by USDA/ARS or Mississippi State University.

MA), which also monitored other environmental and plant response variables. The temperatures in the growth chambers were measured at 10 s intervals and maintained to within  $\pm 0.1^\circ\text{C}$  of the set points for 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<sub>2</sub> concentration and temperature were monitored at 10 s intervals and averaged over 900 s periods. Graded shade cloths were adjusted around the cabinet sides to plant height to simulate shading effects of adjacent plants in a field crop. The plants were irrigated with a drip irrigation system three times a day.

Non-destructive data were collected at daily, 3 day, or weekly intervals on all the shoot and root growth parameters of nine plants in each chamber. Plant height, number of nodes, and leaf area were measured or counted on the nine plants at weekly intervals. Plant height was measured from cotyledonary node to the stem apex. Time of squaring was defined as the time of appearance of flower buds 3-4 mm in length. At 70

DAE, at the time of final harvest, stem and branch lengths were recorded and the plants were mapped.

Statistical analysis was conducted by using procedures outlined in the General Linear Model (SAS Institute Inc., 1987). 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 (Neter and Wasserman, 1974). The standard error of each mean was calculated using data from 15 plants and is presented wherever appropriate.

### 3. Results and discussion

#### 3.1. Plant height and stem elongation rate

Plant height increased significantly with increase in temperature (Fig. 1; Table 1). Cotton plants grown at a mean temperature of 17.8°C reached a height of 0.14 m by 70 DAE compared with 0.33 m, 0.96 m, 1.29 m, and 1.04 m at 18.7°C, 22.7°C, 26.6°C and 30.6°C, respectively, when exposed to 350  $\mu\text{l l}^{-1}$  CO<sub>2</sub>. Similar increases in plant height with temperature were observed for cotton cultivar DES 119 (Reddy et al.,

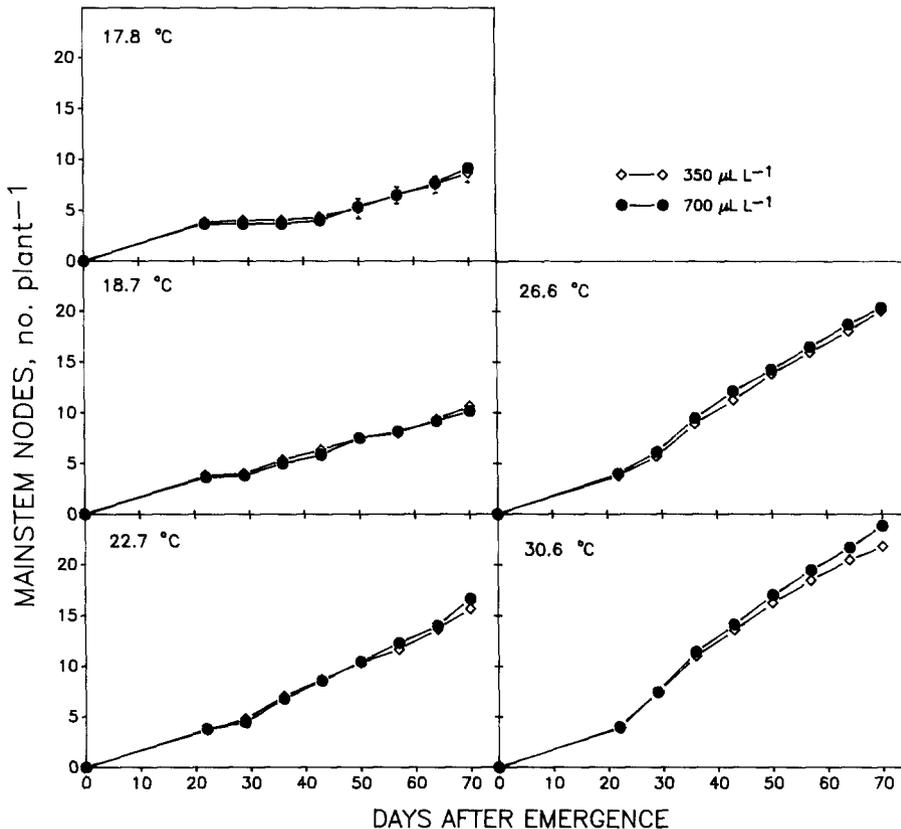


Fig. 3. Influence of temperature and CO<sub>2</sub> on mainstem node number in cotton. Bars indicate standard errors of the mean, and are shown when greater than the symbol size.

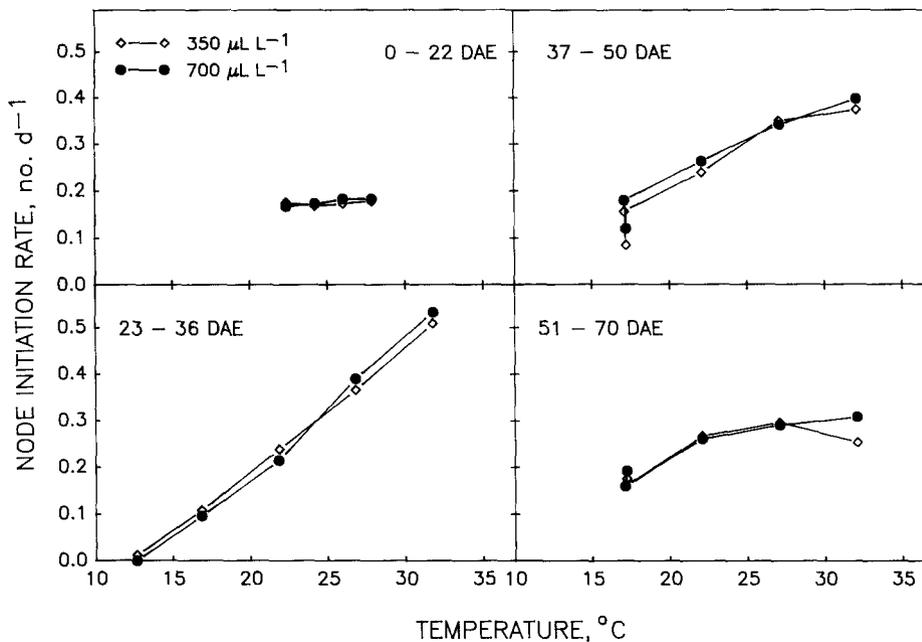


Fig. 4. The rate of node initiation in cotton as influenced by temperature and CO<sub>2</sub> during various periods after emergence. The double points at the same temperature are the result of changing the 15/7°C treatment to 20/12°C during 37–50 and 51–70 DAE. Bars indicate standard errors of the mean, and are shown when greater than the symbol size.

1992b), but the rate of growth for DES 119 was found to be higher by 40–50% at different temperature treatments. In both these studies the highest plant height was recorded at 30/22°C. Plant height was also increased by CO<sub>2</sub> enrichment but only in the higher temperature treatments, the increase was significant (Table 1). On 70 DAE the cotton plants grown at the three higher temperature treatments were 7, 14, and 18% taller at 700 μl l<sup>-1</sup> than those grown at 350 μl l<sup>-1</sup> CO<sub>2</sub>.

Stem elongation rates plotted for short time intervals against running average temperature are presented in Fig. 2. The stem elongation rate of cotton seedlings during the first 3 weeks of growth (0–22 DAE) did not respond either to temperature or CO<sub>2</sub> levels. However, the stem elongation rate was influenced by both temperature and CO<sub>2</sub> levels later in the season. A large increase in stem elongation rate with increase in temperature occurred during the period 23–36 DAE. The stem elongation rate increased from 0.57 mm day<sup>-1</sup> at 12.5°C to 17.4 mm day<sup>-1</sup> at 32°C at the 700 μl l<sup>-1</sup>

CO<sub>2</sub> level, and from 0.66 mm day<sup>-1</sup> at 12.5°C to 14.91 mm day<sup>-1</sup> at 32°C at the 350 μl l<sup>-1</sup> CO<sub>2</sub> level. The rate of stem elongation increased to higher levels during 37–50 and 51–70 DAE compared with 23–36 DAE in response to temperature at both CO<sub>2</sub> levels. However, stem elongation rate from 37 to 70 DAE was significantly lower for plants exposed to 15/7°C for 2 weeks, i.e. from 23 to 36 DAE, than for plants grown continuously at 20/12°C. Stem elongation rate declined slightly at the highest temperature treatment during the later part of the season (37–50 and 51–70 DAE) because the formation of squares and flowers resulted in slower vegetative growth. A similar decline in stem elongation rate was observed for DES 119 at higher temperatures due to the formation of fruiting organs (Reddy et al., 1992b). The highest effect of CO<sub>2</sub> concentration on stem elongation rate was observed during 37–50 DAE at the two highest temperature treatments, showing a 26.6 and 23.0% increase at the 700 μl l<sup>-1</sup> CO<sub>2</sub> level (Fig. 2).

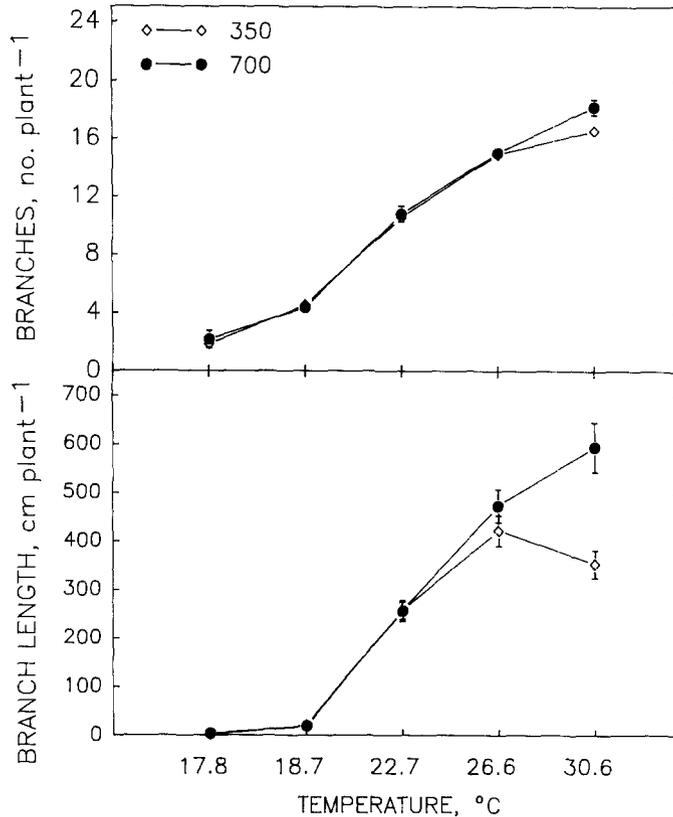


Fig. 5. The influence of temperature and CO<sub>2</sub> on the number of fruiting branches and mean length of the fruiting branches in cotton at 70 DAE. Bars indicate standard errors of the mean, and are shown when greater than the symbol size.

### 3.2. Mainstem nodes and node addition rate

The number of mainstem nodes increased significantly with increase in temperature, and the increase was slightly higher in high CO<sub>2</sub> treatments (Fig. 3; Table 1). At 70 DAE the numbers of mainstem nodes were 8.67, 10.67, 15.67, 20.0, and 21.78, respectively, showing an increase of 23.1%, 80.7%, 130.7% and 151.2% at 18.7°C, 22.7°C, 26.6°C and 30.6°C, respectively, over the 17.8°C temperature treatment in 350 μl l<sup>-1</sup> CO<sub>2</sub>. In 700 μl l<sup>-1</sup> CO<sub>2</sub>, the increases were 10.9%, 81.8%, 121.7% and 159.3%, respectively. The high CO<sub>2</sub> level increased the number of mainstem nodes moderately, but the effect was significant only at 26.6°C and 30.6°C.

The node addition rate segmented over various intervals is presented in Fig. 4. During the first 22 DAE there were no differences in node addition rate over the temperature range tested in either CO<sub>2</sub> level. The node addition rate increased with increase in temperature at both CO<sub>2</sub> levels during 23–36 DAE. The rate of node addition ranged from 0.0 to 0.508 day<sup>-1</sup> over the temperature range tested. As the season progressed, the node addition rate increased at the lower temperatures, whereas the rate decreased at higher temperatures (26.6 and 30.6°C), possibly because of formation of fruiting organs and associated competition of fruiting organs for carbohydrates with vegetative growth (Fig. 4).

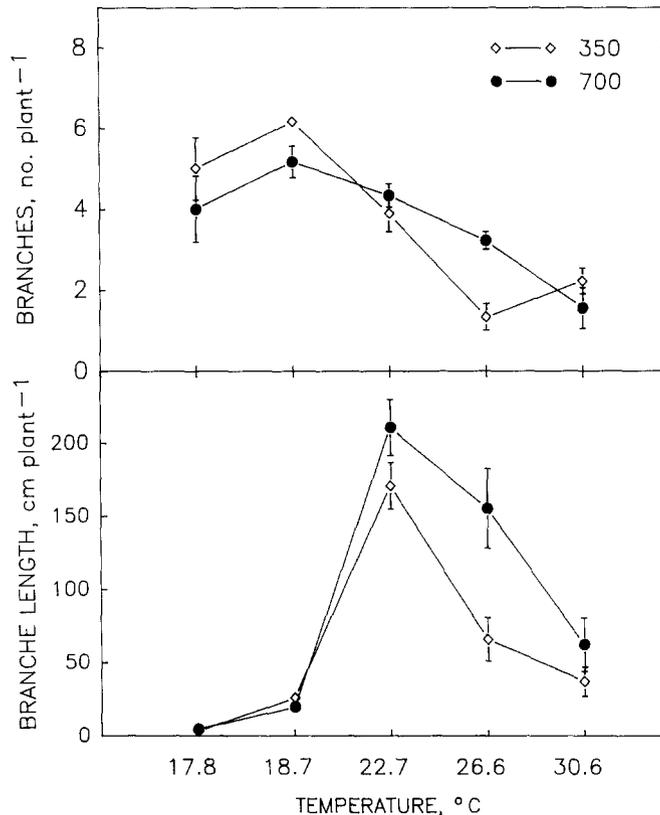


Fig. 6. The influence of temperature and CO<sub>2</sub> on the number of vegetative branches and mean length of vegetative branches in cotton. Bars indicate standard errors of the mean, and are shown when greater than the symbol size.

### 3.3. Branch growth and development

The number of fruiting branches per plant increased more or less linearly with increase in temperature to 30.6°C (Fig. 5). No significant differences in the fruiting branch number owing to doubling of CO<sub>2</sub> were observed except at 30.6°C, where there was an increase of 10.0%. At both CO<sub>2</sub> treatments there was a nine-fold increase in the number of fruiting branches with increase in temperature from 17.8 to 30.6°C.

The fruiting branch length also increased rapidly with increase in temperature at both CO<sub>2</sub> levels except for a slight decline in the length at 30.6°C when exposed to 350  $\mu\text{l l}^{-1}$  CO<sub>2</sub> (Fig. 5). This decline is probably due to carbohydrate stress caused by the demand created by the high growth rate (Reddy et al., 1991a).

However, at the high CO<sub>2</sub> level the plant was able to meet the demand for carbon due to higher photosynthesis levels. Carbon dioxide did not affect branch length significantly at lower temperatures, but at the two higher temperatures doubling CO<sub>2</sub> caused a significant increase (Fig. 5).

The number of vegetative branches was higher at the lowest two temperatures (17.8 and 18.7°C) at both CO<sub>2</sub> levels (Fig. 6). At lower temperatures phenological development rate was very slow, possibly resulting in higher amounts of carbon being available to produce more vegetative branches. The total vegetative branch length increased with increase in temperature up to 22.7°C and then declined. Vegetative branch lengths were significantly increased by high CO<sub>2</sub> treatment at temperatures of 22.7, 26.6, and 30.6°C. This was prob-

ably because, at higher temperatures, growth was suppressed by carbohydrate stress, and a high CO<sub>2</sub> level decreased stress, causing significant increases in branch lengths.

The number of fruiting branches produced and fruiting branch length at various temperature treatments were higher for DPL 50 compared with the early season cultivar DES 119 (Reddy et al., 1992b). A similar response to temperature was observed for vegetative branches; however, the vegetative branch length was much lower for DES 119 (Reddy et al., 1992b).

### 3.4. Reproductive growth and development

Floral induction, measured as days from emergence to first square, was strongly influenced by temperature but not by CO<sub>2</sub> treatments (Fig. 7). This suggests that floral induction in cotton is not limited by carbon supply in our ambient CO<sub>2</sub> environment and that increasing photosynthesis with CO<sub>2</sub> enrichment will not speed this developmental process. Rawson (1992) surveyed the available literature on the effects of CO<sub>2</sub> on flowering of wheat, soybean, sunflower, rice, cotton, cowpea, and maize. He concluded from this survey that the results varied depending on environmental conditions, particularly light levels. Reddy et al. (1992b) observed a

similar response to temperature for an early maturing upland cotton cultivar, cv. DES 119 grown at ambient CO<sub>2</sub>.

The number of fruiting sites on each fruiting branch at 70 DAE is presented for the two higher temperatures at both CO<sub>2</sub> levels (Fig. 8). Very few fruiting branches were present at the three lower temperatures because of slow growth and development. Doubling CO<sub>2</sub> increased the number of fruiting sites on each fruiting branch at both temperatures, but the effect was more consistent at 30.6°C than at 26.6°C. There was a CO<sub>2</sub> by temperature interaction where CO<sub>2</sub> increased fruiting site number more at high temperature than at low temperature. It appears that the initiation of fruiting points on the fruiting branches is source limited in ambient CO<sub>2</sub> at higher temperatures. This hypothesis is supported by the total number of fruiting sites observed on 70 DAE (Fig. 9). The numbers of bolls and squares produced increased linearly with increase in temperature at 700 μl l<sup>-1</sup> CO<sub>2</sub>, while at 350 μl l<sup>-1</sup> CO<sub>2</sub>, the numbers of total sites increased only up to 26.6°C, and there was no further increase in fruiting sites at the highest temperature. The number of bolls and squares that were retained increased with increase in temperature up to 26.6°C and decreased slightly at the highest temperature in both CO<sub>2</sub> levels. The dou-

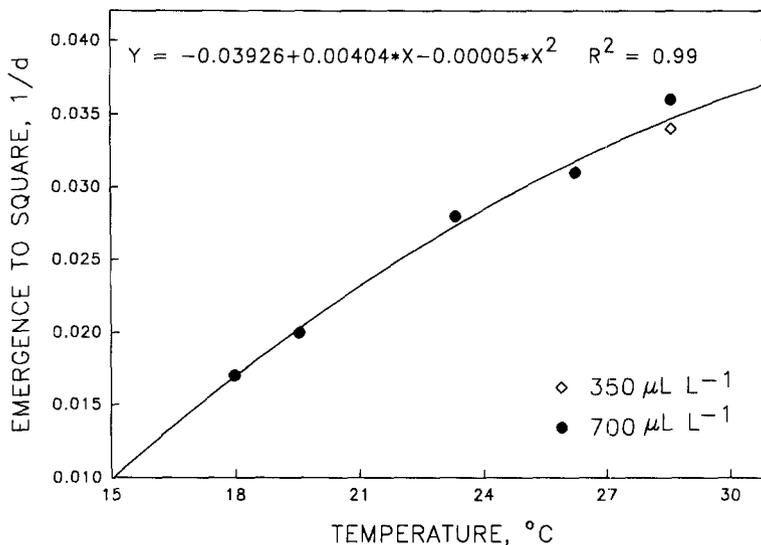


Fig. 7. The daily increment from emergence to first square of cotton as influenced by temperature and carbon dioxide concentration.

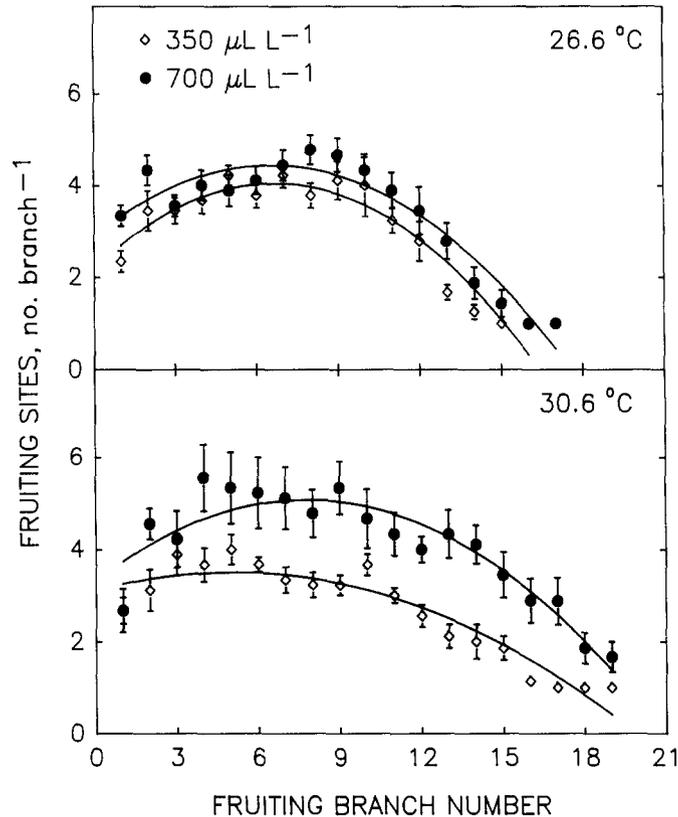


Fig. 8. The influence of temperature and CO<sub>2</sub> on the number of fruiting sites in cotton on various branches. Bars indicate standard errors of the mean, and are shown when greater than the symbol size.

bling of CO<sub>2</sub> significantly increased the total number of fruiting sites produced and retained at the two higher temperatures, 26% at 26.6°C and 67% at 30.6°C, showing an interaction between CO<sub>2</sub> and temperature.

#### 4. Conclusions

Based on our long-term CO<sub>2</sub> and temperature studies with cotton, it can be concluded that floral initiation, measured by days from emergence to first square, is temperature dependent and that doubling the CO<sub>2</sub> level has no effect on this process. Apparently, floral initiation is limited more by temperature than by carbon supply in our ambient CO<sub>2</sub> environment, and increasing carbon supply by doubling CO<sub>2</sub> does not speed this

process. The addition of nodes on the mainstem is also temperature dependent, and the node addition rate is not constant at any temperature during the entire growing season. Increasing CO<sub>2</sub> from 350 μl l<sup>-1</sup> to 700 μl l<sup>-1</sup> has no effect on node addition rate before flowering across a wide range of temperatures. However, two additional nodes are produced in the early reproductive period at the highest temperature tested. On the other hand, doubling CO<sub>2</sub> at higher temperatures increased the number of fruiting sites on each fruiting branch, resulting in a greater number per plant. This shows that the addition of nodes or fruiting sites in ambient CO<sub>2</sub> is source limited, particularly at higher temperatures. Growth processes like stem elongation on the mainstem and branches are also temperature dependent but are influenced by carbon supply to a limited extent. These

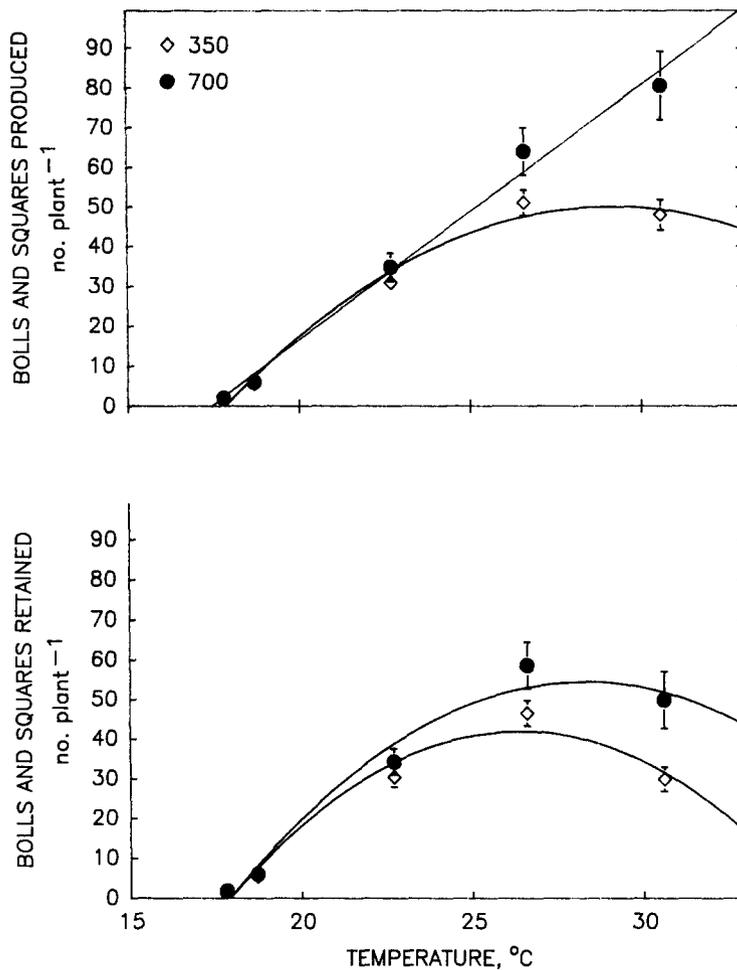


Fig. 9. The influence of temperature and CO<sub>2</sub> on cotton: (a) bolls and squares produced, (b) bolls and squares retained. Bars indicate standard errors of the mean, and are shown when greater than the symbol size.

results show that cotton plant responses to CO<sub>2</sub> are exhibited through a change in morphology, such as increased branching and addition of more leaves and fruiting sites. Plant species which are source limited, such as cotton, will benefit more due to a rise in CO<sub>2</sub> concentration.

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