

CAN COTTON CROPS BE SUSTAINED IN FUTURE CLIMATES?

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Abstract

Cotton producers in the 21st century will be farming crops in different climates than today. Atmospheric CO₂ will likely exceed 700 µl l⁻¹ by the latter half of the next century, and the mean global temperature has been predicted to be 1.5 to 5.9°C higher than today. Further, the incidence of extreme weather events within a growing season has been predicated to increase. Extreme-weather events often limit crop yields even in today's environment; e.g., late spring frosts may severely limit citrus or winter wheat crops. Agricultural productivity is extremely sensitive to changes projected in the environment, particularly where crops are produced in marginal areas.

We conducted two experiments in which plants were grown in controlled environments with natural solar radiation. Temperature was varied in one experiment based on temperatures of the ambient environment during the whole season. In a second experiment, temperatures were referenced to long-term average July temperatures at Stoneville, MS. These temperatures were imposed only during the fruiting period. In both the experiments, CO₂ was also a variable while water and nutrients were supplied in abundance. Growth, development, and fruit production and retention were measured.

Seedling growth was considerably below the maximum at ambient temperature (23°C). Maximum seedling growth was at 30°C. Doubling atmospheric CO₂ concentration caused about 20% more dry matter to be produced in seedlings grown at near optimum temperature, but there was less CO₂ effect on seedlings grown at other temperatures. Developmental events: days to first square, flower, and open boll were very sensitive to temperature, but not to atmospheric CO₂ concentration. Developmental events were disproportionately slower at temperatures below 23°C. Flower and fruit production increased slightly as temperature increased, but fruit retention was very low or none at ambient plus 5°C and 7°C (31.3°C and 33°C). Production of cotton, and probably other seed-bearing crops, are predicted to be strongly damaged by temperatures above those presently found in the cottonbelt during the midsummer.

Introduction

Climatic conditions in the later part of the 21st century are expected to be different from those of today. Currently, atmospheric carbon dioxide concentration [CO₂] is about 360 µl l⁻¹ (Fig. 1) (Keeling and Whorf, 1991), and there is general agreement now among climatic and atmospheric scientists that the atmospheric [CO₂] could be in the range of 510 to 760 µl l⁻¹ some time in the middle or later part of 21st century (Rotty and Marland, 1986; Trabalka et al., 1986). According to most climate models, a continued build up of [CO₂] and other radiative "greenhouse" trace gases are expected to warm the earth's surface air temperatures, change the patterns of precipitation, and cloud cover. It is expected that mean global surface air temperatures may be 1.5 to 5.9°C higher than the present (Table 1), and there may be more frequent occurrences of extreme climatic events of heat waves and/or drought (Adams et al., 1990; Manabe and Wetherald, 1987; Hansen et al., 1988; Washington and Meehl, 1987; Wilson and Mitchell, 1987; IPCC, 1990). For many farm managers this could be good or bad news as agricultural productivity is expected to be sensitive to global climate change. Increasing [CO₂] should cause increased productivity, at least in C₃ plants, and reduce soil-water use relative to the dry matter produced. Higher temperatures and periodic episodes of heat-stress and drought, however, could exacerbate the effect on many aspects of crop growth and development, reduce crop yields and affect quality of grain or seed and fiber.

Table 1. Annual temperature (°C) increase projected by Goddard Institute of Space Studies (GISS) and Geophysical Fluid Dynamics Laboratory (GFDL) global circulation models for doubled atmospheric carbon dioxide concentration scenario for major regions in U.S. (Adopted from Adams et al., 1990).

Region	GISS Model	GFDL Model
	°C	
Southeast	3.5	4.9
Delta	5.3	4.4
Northern Plains	4.7	5.9
Southern Plains	4.4	4.5
Mountain	4.9	5.3
Pacific	4.7	4.7

There are some environments in which cotton crops are commercially grown today where above-optimum temperatures occur for several days at a time during many growing seasons. We developed 40-plus year climatologies with average daily temperatures for Stoneville, MS, and Phoenix, AZ to represent major cotton growing regions of the US near 33° latitude. Long-term climatologies for Corpus Christi, TX (= 28° latitude) and a 15-year climatology of Maros, Indonesia, (a marine, equatorial environment less than 5° latitude) are also presented (Fig. 2.)

The average daily mean temperatures for Stoneville were less than 28°C, optimum for cotton growth and fruit retention. However, the midsummer temperatures in any given year, for example in 1995 for Stakville, MS, were

above optimum (28°C) for several hours per day during much of the fruiting period (Fig. 3). The long-term average daily temperatures at Lubbock, TX, were all slightly cooler than Stoneville (Reddy et al., 1995).

In a separate analysis we added a 5°C to Stoneville average daily temperature (data not shown). Five additional degrees caused average daily temperature to exceed 30°C every day between June 21 and September 10. One of the warmest years on record at Stoneville was 1980. Only 20 days during that hot year did the average daily temperature exceed 30°C, whereas if 5°C was added to the long-term climatology 80 days had average temperatures above 30°C. Therefore, a 5°C increase in long-term average temperatures would be much more severe than even one of our hottest years in the Midsouth.

Phoenix, AZ represents the irrigated desert production region. Long-term average maximum daily temperatures approached or exceeded 40°C over 90 days per year, and long-term average daily mean temperatures exceeded 30°C 88 days (Fig. 2). However, canopy temperatures of well-watered crops in the irrigated desert may be cooler than air temperatures, so effective plant canopy temperature in that environment may be lower than measured shelter temperatures. There was a direct relationship between leaf water potential and canopy minus air temperature differential (Fig. 4).

The long-term average temperatures at Corpus Christi, TX were warmer in the early spring, but not so hot during the mid-summer period as Phoenix. Average mid-summer temperatures were quite similar to Stoneville, MS. Mean daily temperatures at Bakersfield, CA, were several degrees cooler (>5°C) throughout the spring and summer than Phoenix (Reddy et al., 1995). This irrigated desert environment has more favorable temperature for cotton production than that of Phoenix.

The temperatures at Maros, Indonesia are very constant throughout the year with average daily temperature about 28°C. Should environmental changes result in 5°C increases in these average daily temperatures, cotton and probably other crops will be grown at above optimum-temperature continuously throughout the season. These very stable and constant, above optimum temperatures leave essentially no flexibility for production management. In temperate-zone cotton producing regions of the world, producers may be able to modify planting dates as spring temperatures become warmer. By moving the planting date to an earlier period, cotton may be produced in a more favorable environment essentially escaping the highest temperature portion of the season. Such a shift in cultural practices is done today, and may be extended until the solar radiation becomes limiting due to early planting.

It appears that 5°C increased daily temperature at Stoneville will bring temperatures to what we now consider

acceptable cotton planting temperature about 45 days earlier in the year. If cotton planting occurs 45 days earlier than is normally practiced today, and if other production practices remain the same, then harvest would begin about August 15. Such production practices would allow much of the cotton growing season to occur in a higher solar radiation environment than is experienced today; however a major portion of the flowering and boll-growth period would still occur when temperatures are predicted to be super optimum (Fig. 2 and 3). Such high temperatures would be expected to hasten boll growth and reduce boll size (Hodges et al., 1993). In addition, the super-optimum temperature will likely cause considerable boll-retention problems (Reddy et al., 1991; 1992c).

As human activities continue to cause perturbations in climate, increasing world's population also puts pressure on agriculturists and sets new challenges for agronomists and crop physiologists to help achieve feeding the larger world population. The world's population is forecast to increase from 5.4 billion in 1990 to 8.5 billion by the year 2025. World food production must increase by 60 to 70% to keep pace. By the year 2050, experts believe that an additional 4 billion people will be added, 95% of whom are predicted live in the developing countries. As there is very little new arable land that can be added to meet the demand, the supply must come primarily from more intensive cultivation of the existing arable land. This may be impossible. For example, the average cereal yields were about 2,973 kg ha⁻¹ in 1992 that must increase to 4, 215 kg ha⁻¹ by the year 2025 simply to maintain 1992 status quo on a per capita basis. To illustrate the magnitude of the task, the upland-cotton lint yields increased only 13% over 30-year period in a high-radiation and irrigated desert region of Arizona (Kittock et al., 1988). During that period, the atmospheric [CO₂] also increased by 12% (Fig. 1). That 13% increase in yield must have been the result of increasing atmospheric CO₂ during that period plus other improvements in cotton production technologies. In addition, farmers in the 21st century will also be under increased pressure to produce more fiber, fuel and construction materials on these finite resources to meet the demands of an increasing population. As agriculture becomes more intensive, soil degradation will become a matter of major concern. Apart from the above changes, the world's water resource is also finite, and changing climate and increasing population demands will allow less water available for agricultural use. In many highly populated countries, food and fiber needs are being met by irrigating up to 75% of the arable land (Hoffman et al., 1990). It will be a major challenge for agronomists and other agriculturalists to produce enough food and fiber to satisfy the increasing world's population in an environmentally sustainable manner if a major climate change occurs as forecast.

This paper addresses some of the issues of how global climate change variables will affect cotton growth and

development, particularly the reproductive development. Understanding their potential effects, on major agricultural crops in general and cotton in particular, in advance would allow lead time for adjusting agronomic practices and genetic alternatives to meet these changes. As there have been few long-term studies on the interactive effects of atmospheric CO₂ and other environmental variables on crops in general and cotton in particular (Baker and Allen, 1994; Conroy et al., 1994; Rawson, 1995; Reddy et al., 1995), our discussion on the cotton crop will help to find alternative strategies to identify new research strategies to mitigate the food and fiber production problems for the 21st century.

Materials and Methods

Soil-Plant-Atmospheric-Research (SPAR) units

The closed environment plant growth chambers used for this study were described in detail by Acock et al. (1985) and Reddy et al. (1992a; 1992b). The SPAR units are located outside and can control temperature and CO₂ concentration at predetermined set points for plant growth studies in natural solar radiation regimes. Each SPAR unit consisted of a steel soil bin (1 m tall by 2 m long by 0.5 m wide), and a plexiglass chamber (2.5 m tall by 2.0 m long by 1.5 m wide) to accommodate aerial plant parts, a heating and cooling system, and environmental monitoring and control system. The plexiglass allows 98% of solar radiation to pass without spectral variability in absorption.

Variable-density shade cloths around the edges of plants were adjusted regularly to match plant heights simulating the presence of other plants and eliminating the need for border plants. Air ducts located on the northern side of each SPAR unit connected heating and cooling devices to each unit. Conditioned air was passed down through the plant canopy with sufficient flux to cause leaf flutter and returned to the ducts just above the soil level.

Chilled ethylene glycol was supplied to the cooling system via several parallel solenoid valves that were opened and closed depending on the cooling requirement. An electrical resistance heater provided short pulses of heat, as needed, to fine tune the air temperature control. A dedicated computer (Digital, Pro 380, Digital Equipment Corp., Maynard, MA) controlled air temperature, CO₂ concentration, and soil watering in each SPAR unit. The computer also conducted continuous monitoring of all important environmental and plant gas-exchange variables.

Air temperature in each SPAR unit was monitored and adjusted every 10 s throughout the day and night. Air temperatures were maintained within $\pm 0.5^{\circ}\text{C}$ of treatment set points. Average daily temperature was calculated by summing the average temperatures for each 900 s period during the day and dividing by 96 periods.

We conducted two experiments to quantify cotton plant responds to increases in CO₂ concentrations and projected

changes in temperatures by global circulation models. In experiment I, plants were grown from seed to maturity (planted 6 June, 1995) in these chambers. The chambers were temperature controlled using the previous 15-minute average outdoor temperature called ambient. Five temperature treatments were used throughout the growing season including the 1995 ambient, ambient minus 2°C, and ambient plus 2, 5, and 7°C. The mean daily temperatures for all the temperature treatments were presented in Fig. 5. For experiment II, plants were grown outside in 66 cm deep pots until first flower, then uniform plants were moved into the SPAR units. The sinusoidal daily temperature in the various treatments averaged -2°C, 0°C, +2°C, +5°C, and +7°C from the long-term daily average July temperatures for Stoneville, MS. The plants were exposed to these daily diurnal temperatures for 28 days (Fig. 6). This experiment was replicated over time.

The CO₂ concentration in each SPAR unit was also monitored every 10 s and integrated over 900 s intervals throughout the day. The CO₂ concentration was maintained at 360 or 720 $\pm 10 \mu\text{l l}^{-1}$ in experiment I from planting to maturity and 350 or 700 $\pm 10 \mu\text{l l}^{-1}$ in experiment II during the daylight hours from the beginning of flowering. A computer-controlled timing device applied a complete Hoagland's nutrient solution (Hewitt, 1952) to each row of plants via a drip irrigation system in both the experiments. The total solution added each day was twice the previous day's evaporation from a standard evaporation pan located about 50 m from the site. Excess water was allowed to drain from a small opening in the bottom of each soil bin or pot.

Plant culture and measurements

Cotton, cv. DPL 51, seed were pregerminated in moistened paper towels at 28°C and 48 h. The imbibed seeds, with radicles emerging, were selected for uniformity and planted in the ten SPAR units on 6 June 1995 in experiment I. The soil bins were filled with pure fine sand. The seeds were planted in 11 rows of five plants per row, with rows 167 mm apart. Fifty percent emergence occurred four days later. Six rows of plants were harvested 14 days after emergence (DAE) and two rows were removed at 20 DAE to avoid competition for light. This left three rows of 15 plants m⁻² to final harvest which was about the time 50% of the harvestable bolls were open. These rows were 667 mm apart. Node numbers were counted and plant heights were measured on nine plants in each unit at weekly intervals. Observations were made daily for appearance of first squares, first flowers, and first open bolls. Flowers were tagged on the date of their appearance and the abscised parts collected daily. Leaf areas and the total shoot dry weights were determined on each plant part at each harvest. Leaf area was measured with an automatic leaf area meter (Hayashi Denko Co., Tokyo, Japan). In experiment II, dry matter produced before and at the end of the experiment was measured. Flowers were tagged on the date of their

appearance and the abscised parts collected daily as described in experiment I.

Results and Discussion

Average daily temperatures plus 5°C and 7°C were much closer to the optimum temperatures than ambient temperatures for cotton growth early in the season for Midsouth during 1995. The higher temperature conditions (ambient plus 5° or plus 7°C) resulted in seedlings, at 20 days after emergence, that were about 10 times taller than plants grown at 21°C, or ambient minus 2°C (Fig. 7). The effect of double-ambient CO₂ concentrations on plant height was small and not significant. Only 3.9 mainstem nodes per plant were produced in 20 days at ambient temperature and CO₂ conditions. That number increased 130% at plus 2°C, 167% at plus 5°C, and 182% at plus 7°C relative to the plants grown in ambient conditions. Atmospheric CO₂ concentrations did not affect the number of mainstem nodes at any temperature. Leaf area, and dry weight of plants grown for 20 days at 30°C (ambient plus 7°C) were also much larger than those parameters on plants grown at 21°C. Atmospheric CO₂ increased the leaf area produced on seedling cotton plants. Dry weight of seedlings was about 20% more on plants grown in ambient temperature plus 5°C at 720 µl l⁻¹ CO₂ than seedlings grown at 360 µl l⁻¹ CO₂ (Fig. 8). Plants grown in less favorable temperatures responded even less to CO₂ enrichment. Seedlings grew much faster and accumulated more dry weight at 28°C and 30°C than seedlings grown at 21°C. Growth, both leaf area and dry matter accumulation, for the first 20 days was very sensitive to temperature. When expressed as a percentage of growth at ambient temperature, growth was linear to 30°C. The plants grown in 1995 ambient or cooler temperatures, when planted June 6, was much less favorable than ambient temperatures plus 5°C or 7°C.

The days required to produce first flower bud (square), flower or mature, open boll were very temperature sensitive (Table 2). Days from emergence to first square decreased 1.09 days for each degree C average daily temperature increased during this period from 23°C to 29.4°C. A decrease of only 1.18°C below ambient temperature caused an additional 7 days to be required to produce first square. Thus, the time required for the appearance of first square from emergence was disproportionately delayed below 23°C. This is consistent with previous observations in which we found no development at about 15°C (Reddy et al., 1993). The days to produce first flowers decreased similarly as temperature increased. Between 25.1°C and 31.1°C, the days required to produce the first flower from emergence decreased about 2 days per degree temperature increased. However, fourteen more days were required to produce a flower when the temperature averaged only 1.6°C below ambient. The point is that seedling cotton plants are typically grown at temperatures too cool for optimum growth in the Midsouth area. Increased

temperatures above 25°C up to 31°C results in much faster developing plants. First flowers were produced on plants grown in the ambient plus 7°C and ambient plus 5°C on July 19 and 22, respectively. Those are the days of the year 200 (19 July) and 203 (22 July) (Fig.5). First open boll was produced 101 (19 September) days after emergence in ambient temperature conditions, but 43 more days were required to produce first open boll in plants grown in ambient minus 2°C. Days required to produce first open boll decreased only 7 days for plants grown in ambient plus 2°C, and 34 days for plants grown in ambient plus 5°C. Plants grown in ambient plus 7°C did not retain any fruit. Ambient temperatures from about day of the year 190 until about day 240 were near optimum for satisfactory cotton growth. Ambient plus 5°C and 7°C resulted in rapid flower production, but abscissions occurred 2 to 4 days after flower opening resulting in essentially no mature fruit being produced in either high-temperature condition. After day 240 (28 August), the temperatures decreased considerably and fruit produced after that time did not abscise, but the remaining season was too short and the temperatures were too cool for fruit to mature. The effect of CO₂ was not significant on days to first square, first flower, or first open boll. Neither did it affect the abscission due to high temperatures. More bolls were produced, however, on the high-CO₂ grown plants at temperatures where abscission was not a problem.

Table 2. Projected temperatures and cotton development. There were no significant differences between the CO₂ levels. The data are means of both CO₂ treatments.

Treatment	Days and average temperature (°C) in parenthesis to the event		
	Square	Flower	Open Boll
1995 minus 2°C	33 (21.9)	65 (23.5)	144 (21.5)
1995 plus 0°C	26 (23.0)	51 (25.1)	101 (25.5)
1995 plus 2°C	24 (24.7)	48 (26.9)	94 (27.4)
1995 plus 5°C	21 (27.6)	42 (29.3)	77 (30.5)
1995 plus 7°C	19 (29.4)	39 (31.1)	No fruit (32.4)

In a second experiment, the number of bolls produced by cotton plants increased within days after the treatments were initiated, and more bolls were produced at higher temperatures up to the average July mean temperature plus 2°C for plants grown in twice ambient CO₂ concentrations, 29.6°C (Fig. 9). Temperatures higher than 2°C above the daily July average caused the plants to produce slightly fewer flowers and bolls. The number of bolls retained was also strongly influenced by time of exposure and by temperatures higher than July average plus 2°C. The number of bolls retained was drastically reduced at July average plus 5°C (32.6°C) and none were retained at July average plus 7°C (34.6°C).

The number of bolls retained increased slowly, but the percent bolls retained dropped as days after first flower occurred when the plants were grown at 29.1°C or higher temperatures (Fig. 10). The percent bolls retained declined after first anthesis due to the progressively greater boll load on the plants. High concentrations of CO₂ should increase the photosynthetic capacity of the plants and the overall

productivity. There were 15% more bolls retained on plants grown in high CO₂ than at ambient CO₂ concentration at 29°C and lower temperatures as expected. However, the percent bolls retained dropped to nearly zero on plants grown at 33.3°C. Essentially all the bolls abscised at 33.3°C regardless of CO₂ concentration. It is apparent that such high temperatures critically damaged the reproduction process. The number of bolls produced and retained are presented Fig 11 at range of temperatures for plants grown ambient and twice ambient CO₂ concentrations. Number of bolls produced increased with temperature up to 29.1°C, and declined slightly at two higher temperatures. Increasing atmospheric CO₂ had no effect on flower production rate and thus the total number of bolls produced at the end of four week experimental period. Boll retention was not different between 25 to 29°C, but declined sharply at the two higher temperatures. Increasing atmospheric CO₂ did not ameliorate the fruit abortion problem at the two higher temperatures.

Fruit production efficiency increased as temperatures increased to 29°C, then it declined rapidly as temperature increased above 29°C (Fig. 12). The amount of vegetative biomass did not change as temperature increased (data not shown). Since the rate of fruit retention dropped so dramatically at temperatures above 29°C, the fruit production efficiency also dropped at those high temperatures. The number of bolls retained was strongly influenced by temperatures higher than July average plus 2°C. At the two higher temperatures, the number of bolls retained was drastically reduced. The upper limit for cotton fruit survival is about 32°C or July average plus 5°C. Such a statement may be misleading as the survival and growth of bolls are not equally sensitive to high temperature throughout their development. Bolls usually abscised within 2 to 4 days after flowering when exposed to high temperatures. In experiment I, there were a few times when the temperature was not damaging for a few days and flowers produced during that period survived to maturity for plants grown in 1995 plus 2°C and even for plants grown in 1995 plus 5°C. Apparently, there is a short period associated with flowering when the reproductive processes is most vulnerable to high temperature. If the fruit escapes high temperature during that time, it can survive those unfavorable conditions during the rest of its growth period. We do not have an exact definition of the vulnerable period. Response of rice to growing temperatures was similar to that of cotton (Baker et al., 1990). Rice grain production appears to be slightly more high-temperature tolerant than does cotton, with minimum grain produced at about 36°C (Fig. 12). Rice flowering and reproductive parts also appear to be most sensitive to high temperature. Increasing CO₂ did not ameliorate the heat-sensitive process at the high temperatures both in rice and cotton. Breeding both high- and low-temperature tolerant cultivars will be beneficial in future warmer world. Efforts to reduce the impact of high temperatures on cotton production have been recognized (Kittcock et al., 1988;

Reddy et al., 1992c; Lu and Zeiger, 1994; Lu et al., 1994), and additional research is needed to reap the benefits of rising atmospheric CO₂ levels and the anticipated increase in global surface air temperatures.

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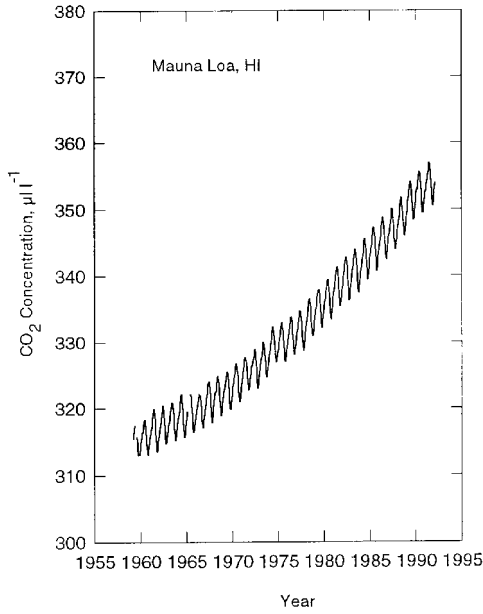


Figure 1. Monthly atmospheric CO₂ concentrations at Mauna Loa, HI, since 1958. Each year, the highest concentration was observed in May, just before the growing season in the northern hemisphere, and the lowest concentration was in October (Adopted from Keeling and Whorf, 1991).

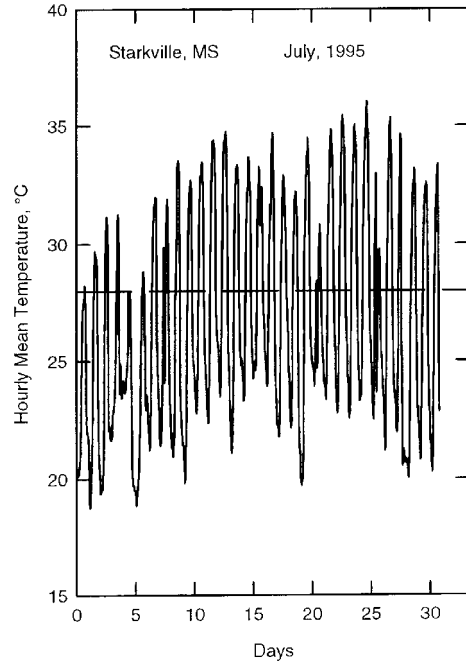


Figure 3. Hourly mean temperatures for July 1995 at Starkville, MS. The dashed line at 28°C represents the optimum temperature for cotton reproductive growth.

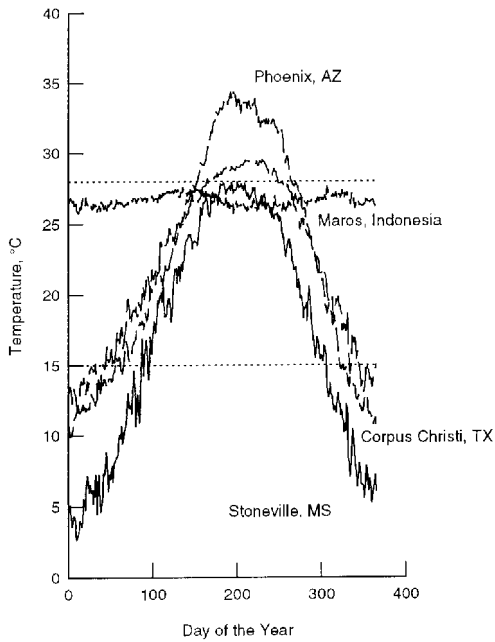


Figure 2. Long-term average daily mean temperatures for three major U.S. cotton producing areas and Maros, Indonesia. The temperatures were 40-plus years for U.S. and 15 year averages for Maros. The straight dotted lines at 15°C and 28°C represents the lower threshold and optimum temperatures for cotton growth and reproductive development (Adopted Reddy et al., 1995).

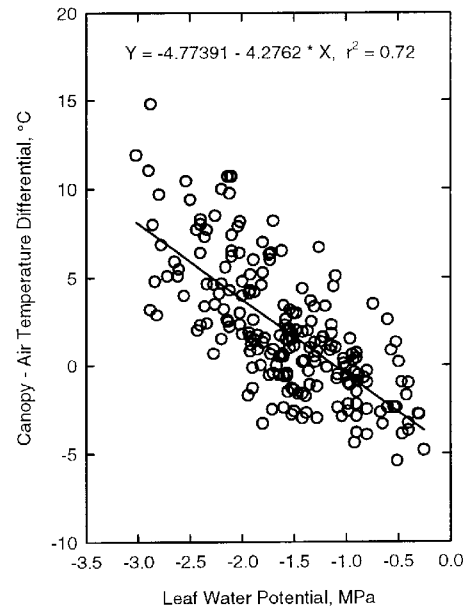


Figure 4. The relationship between leaf water potential and the difference in canopy and air temperature.

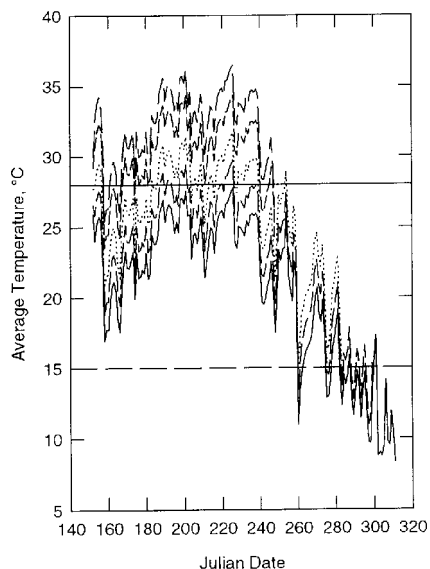


Figure 5. Treatment structure for the experiment in 1995. The lines from bottom up are 1995 minus 2°C, 1995 (ambient), 1995 plus 2°C, 1995 plus 5°C, and 1995 plus 7°C temperature treatments. Plants were grown in each of the temperature treatments in ambient ($360 \mu\text{l l}^{-1}$) and twice ambient CO_2 levels throughout the season. The temperature treatments resulted in different maturities; therefore the lengths of the growing season varied. The dashed and solid straight lines represent the minimum (15°C) threshold and optimum (28°) temperatures for cotton.

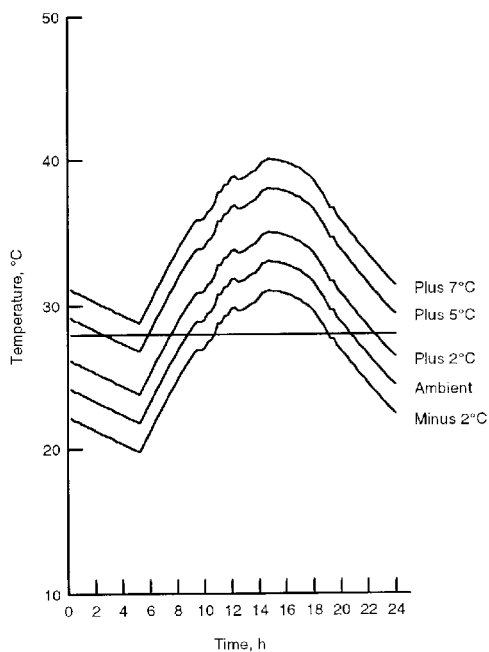


Figure 6. Treatment structure for the experiment in 1994. The treatments were imposed for four weeks during the flowering period. The solid straight line at 28°C represents the optimum temperature for cotton growth.

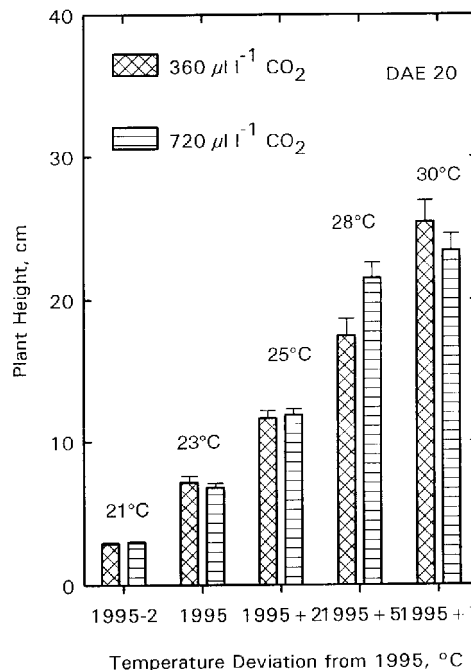


Figure 7. Influence of temperature and atmospheric $[\text{CO}_2]$ on plant height of seedling cotton. The average temperatures for each treatment are also presented in the figure.

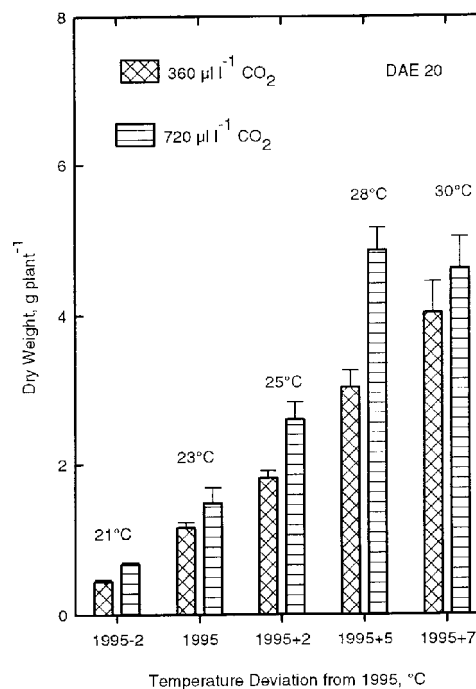


Figure 8. Influence of temperature and atmospheric $[\text{CO}_2]$ on dry weight of seedling cotton. The average temperatures for each treatment are also presented in the figure.

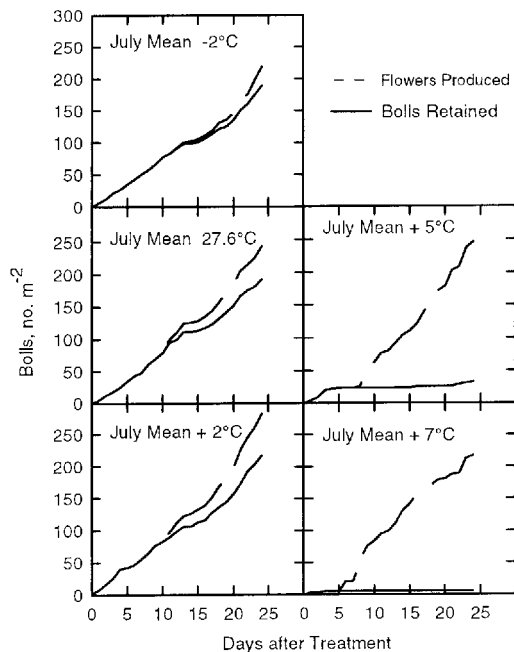


Figure 9. Effect of long-term July mean temperatures on the number of flowers produced and retained for plants grown in twice ambient CO_2 ($700 \mu\text{l l}^{-1}$) concentration. The temperature treatments were imposed at flowering as shown in Fig. 6.

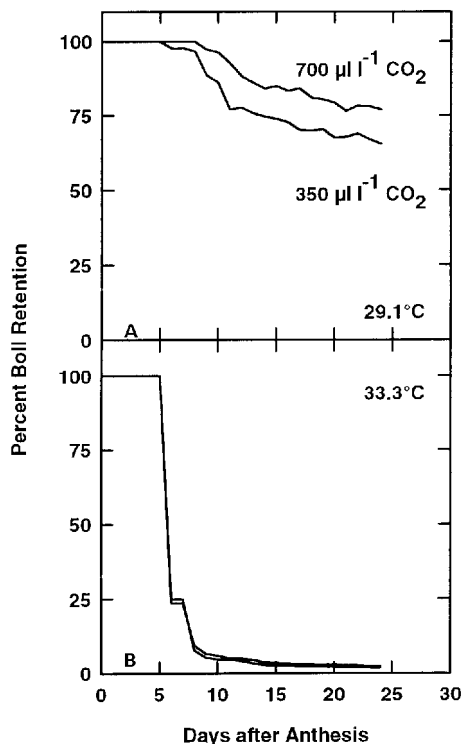


Figure 10. Effect of long-term July mean temperatures and carbon dioxide enrichment on percent boll retention at the two higher temperature treatments.

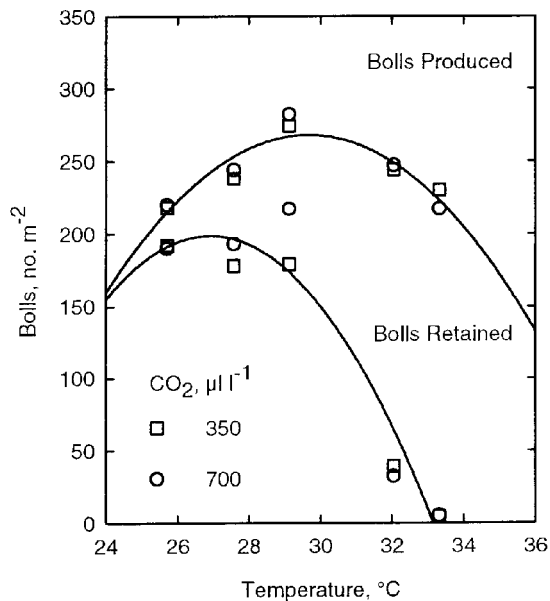


Figure 11. Effect of long-term July mean temperatures and carbon dioxide enrichment on bolls produced and retained. The temperature treatments were imposed at flowering as shown in Fig. 6.

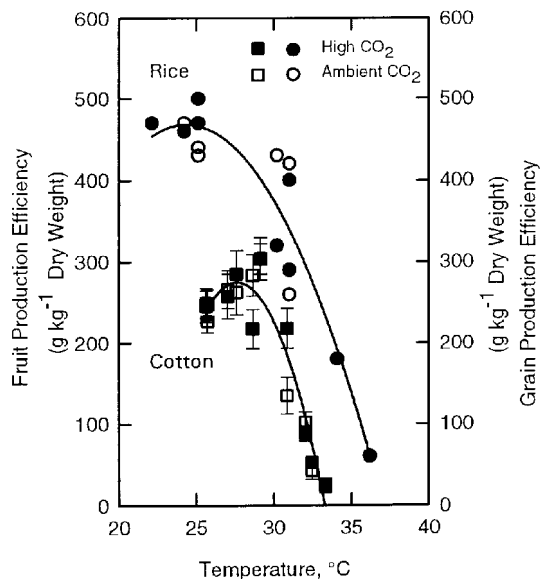


Figure 12. Effect of long-term July mean temperatures and carbon dioxide enrichment on fruit production efficiency of cotton. Also shown the temperature and CO_2 enrichment effects on grain production efficiency for rice (Adopted from Baker et al., 1990)