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Weather and Cotton Growth: Present and Future

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K. Raja Reddy
Plant Physiologist
Department of Plant and Soil Sciences

Harry F. Hodges
Professor of Agronomy
Department of Plant and Soil Sciences

William H. McCarty
Extension Agronomist
Department of Plant and Soil Sciences

James M. McKinion
Research Leader
USDA-ARS Crop Simulation Research Unit

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Introduction

Weather is one of the most important factors that affects crop growth and yields. Although information about the average climate of Mississippi has often been described (Boykin et al., 1995), relatively few attempts have been made to relate the specific effects of weather factors to crop growth and yield. After decades of agronomic research, little quantitative information is available on how major crops respond to weather variables. Crop production is directly influenced by temperature, photoperiod, total radiation, and precipitation. Temperature determines the duration of a crop's growing season. With cotton, temperature controls development and, indirectly, water requirements. Some crops are sensitive to photoperiod and will not flower in extremely long days or flower prematurely when exposed to an inappropriate photoperiod relative to its stage of growth. However, modern cotton cultivars are not photoperiod sensitive even though their ancestors were. Temperature controls cotton development and indirectly its water requirement. Total radiation is an important environmental factor, as it directly drives crop photosynthesis, growth, and indirectly controls all plant processes.

Although we know water is critically important, we do not have good quantitative knowledge of the relationships among water supply, other weather factors, and plant water status. Therefore, plants growing in the natural environment are often prevented from expressing their full genetic potential for yields. With irrigation, attempts are made to optimize moisture conditions by controlling amounts and timing of water application. Within the United States, for example, yields in the irrigated Southwest are approximately double those of the nation as a whole. Such high yields are the result of growing crops in a high radiation environment and correcting the most limiting environmental constraint, water deficits.

Long-term Temperature Patterns for U.S. Cottonbelt

Long-term averages of weather parameters are defined as the climatology of those factors for a region. Although each crop is controlled by the physical environment to which it is exposed, one can learn whether a particular crop is suitable for a given location or region by studying the long-term weather records. Inasmuch as the weather is repeatable from year to year, we can learn what weather conditions to expect by examining long-term averages.

Long-term average daily temperatures are shown for three important cotton-producing regions of the United States (Figure 1). The 42-year average daily temperature at Stoneville, Mississippi never exceeded the optimum temperature for cotton production (82 °F). However, at Phoenix, Arizona, long-term average daily mean temperatures exceeded 86 °F for 88 days per year.

Although such high temperatures would be expected to prevent commercial production of cotton, evaporation from the leaves of well-watered plants has an important cooling effect on the crop canopy. This is particularly true in a desert environment where the humidity is low and evaporation is high. There is a linear relationship between leaf water potential and leaf temperature minus air temperature (Figure 2). Leaf water potential is a measure of plant water status. Well-watered plants on a clear summer day have about -1.5 to -1.7 megapascal (MPa), a measure of pressure, at solar noon and about -0.1 to -0.4 MPa at dawn. Seriously stressed plants at noon might have -2.5 to -3.50 MPa, and if watered would require several days to recover. The relationship between leaf water potential and the difference between leaf and air temperature shows that as water deficit (stress) becomes more severe (-2.0 to -3.0 MPa), the leaf temperature becomes warmer. This indicates that plants close their stomata in stress conditions. Such a process conserves the moisture within the plant when the soil water supply is limited, but also results in warmer leaves causing modification and, in extreme cases, heat damage to various growth processes.

Long-term records at Corpus Christi, Texas illustrate that even though average daily temperatures in midsummer exceed the optimum temperature for cotton growth, producers can manage to successfully grow cotton there by planting early. By planting early, the crop escapes the midsummer temperature extremes many years.

Growing Degree Days

Growing degree days (GDD's) are sometimes used to predict crop growth and developmental events, because cotton growth increases linearly as temperature increases between 60 and 88 °F. Since cotton does not grow at 60 °F or cooler, growing degree days 60 (GDD_{60}) are calculated from the positive difference between the average daily temperature and the base temperature (60 °F)

$$\mathrm{GDD} = \frac{(\mathrm{Tmax,\ ^\circ F + Tmin,\ ^\circ F})}{2} - 60\ ^\circ\mathrm{F}$$

where GDD_{60} is growing degree day accumulation for a day with maximum (Tmax), minimum (Tmin), and the base temperatures.

The GDD_{60} can be added to and accumulated as the season progresses from planting or day of emergence. Figures 3 and 4 illustrate the Stoneville, MS 42-year average daily GDD_{60} additions and cumulative growing degree days. Growing degree days with a base of 50 or 40 °F are also included because they are sometimes used for other crops. Long-term weekly summaries of GDD_{60}, GDD_{50}, and GDD_{40} are also provided in Appendix Tables 1-3. Growing degree days are a useful way of summarizing temperature effects on crop growth and development. Temperature is the most limiting variable for the crop much of the season, and the crop developmental and growth responses are quite linear. If conditions are dry or nutrients are limiting, then crops do not respond directly to temperature in a predictable manner like they do in nonlimiting conditions, and GDD's accumulate without the usual advance in growth and development. Therefore, GDD's are not useful for predicting crop development in stress environments. This becomes particularly important in midsummer when other environmental stresses frequently limit crop growth. More information is needed to understand crop development in stress conditions. That, however, is beyond the scope of the this bulletin.

Short-term Temporal Patterns in Temperatures

Daily and yearly temperature variability is another environmental factor that impacts crop growth and development. Long-term average daily temperature provides some understanding of the average conditions, but individual years obviously vary (Figure 5). Springtime planting is usually determined by temperature and rain. Seedling establishment and the prevalence of early-season diseases and insects are strongly influenced by temperature. Below-optimum temperatures cause slow cotton growth and favor pest development. We seldom have above-optimum temperatures before flowering, however, after flowering begins, high temperature may cause flower retention problems. Therefore, growers must manage their crops each year and deal with the unique combination of conditions provided by nature.

The data in Table 1 show the number of times the average daily temperature at Stoneville exceeded several selected values in each of the 31 years between 1964 and 1994. This illustrates the year-to-year variability in temperature, with 1980 being the hottest year on record at that location and 1976 and 1992 being the coolest years.

Diurnal Patterns in Temperatures

Figures 6 and 7 show the uniqueness of individual days relative to optimum or minimum temperatures at which cotton grows. It should be remembered that environmental conditions determine growth and survival of organs on individual days, and ultimately determine yield. Extreme conditions for a few hours will cause vulnerable tissues or organs to die and subsequently abscise from the plant. In addition, at low but nonlimiting cool temperatures below 60 °F, cotton metabolism is so slow that essentially no growth or development occurs. So, on days such as May 2 or September 23, 1995, much of the time no progress occurs (Figure 6). During 1995, approximately half the days during July the temperature at Starkville was above optimum for cotton (Figure 7) and, as we will see from the data in this bulletin, resulted in abscission of many young bolls. Such abscissions reduce yield, delay maturity, and favor rank growth.

Temporal Patterns in Solar Radiation

Another factor of the environment that dramatically influences other elements of the environment, and directly impacts crop processes, is the amount of solar radiation. In spite of its importance, solar radiation is not well understood by most people. Solar radiation is a continuous spectrum of electromagnetic radiation varying from very short to longwave rays. These wavelengths have different energy levels and do different things to the environment. The shortwave radiation has high energy per unit wavelength. It includes the ultraviolet radiation, that is best known as the portion of the solar radiation that causes sunburn on human skin, free radicles in cells, and cell mutations, sometimes resulting in skin cancer. Even shorter and higher-energy rays (x-rays, gamma rays, and cosmic rays) are present in very small quantities. Such short, high-energy wavelength radiation will do even more damage to both plants and animals. There has been considerable concern in recent years about the decrease in the density of atmospheric ozone layer. Ozone is found high in the atmosphere, and it filters much of the ultraviolet radiation, which damages plants by destroying chlorophyll and other pigments.

The radiation between 400 and 700 micrometers in wavelength is what we know as the visible portion of the solar spectrum. It is visible to the human eye, is responsible for photosynthesis, and is the driving energy force for most living organisms, either directly or indirectly. This solar energy is sometimes called photosynthetically active radiation. It is measured with a radiation sensor that has filters, which exclude the shorter or longer wavelengths. The units of measure may be expressed as microeinsteins per square meter (m^{-2}) per second or micromoles per square meter per second.

Radiation from about 700 to 2,000 micrometers in wavelength is known as infrared radiation. It is not visible to the human eye and is the primary energy we feel as heat on a hot summer day. The infrared radiation constitutes slightly more than half the total solar energy. We seldom see the amount of infrared radiation reported directly, but may find total solar radiation reported as megajoules per m^2 per day, or calories per cm^2 per minute. On a clear summer day near noon, the Earth's surface receives about 1.5 calories per cm^2 per minute. Radiation wavelengths even longer than infrared rays in the spectrum are known as radio waves and these include wavelengths that transmit radar, television, and sound. The total radiation received at the outer edge of the Earth's atmosphere is relatively constant throughout the year. The amount received at any site on the Earth's surface depends on the angle of the Earth to the Sun and the absorption of the radiation by the atmosphere. Absorption by the atmosphere is primarily caused by humidity, smog and dust. So in a dry, dust free atmosphere the Sun's rays are much more intense than in a humid, dust free atmosphere.

The data in Figure 8 show Stoneville long-term average daily seasonal trends in solar radiation and temperature, along with the minimum and optimum temperatures at which cotton grows. That figure illustrates the obvious seasonal trends in solar radiation that we experience, but such data are not widely published and most people do not understand it. It also emphasizes the limits we have for cotton production management. Shifting a production season to earlier in the year would be advantageous in some environments to escape excessively high mid- to late-summer temperatures; however, such a shift will always be somewhat limited by the availability of early-season solar radiation and cool temperatures.

Objectives

In this bulletin, we will show the effect of several environmental factors, varied singly while the other factors are held in sufficient supply, on cotton growth and development. Many of the experiments were conducted with more than one concentration of atmospheric carbon dioxide (CO_2). That was done to determine whether cotton is typically limited by the products of photosynthesis, since additional atmospheric CO_2 increases photosynthesis. Carbon dioxide is presently a small part of the atmosphere (about 0.036%) and is expressed as 360 microliters per liter ($\mu l\ 1^{-1}$). Plants convert incident solar radiation to chemical energy by synthesizing organic compounds from carbon dioxide and water.

It has been suggested that because we are using large amounts of fossil fuels, Earth's atmosphere is increasing in CO_2. Carbon dioxide in the atmosphere has increased about 12.7% during the past 30 years. That should result in increased photosynthesis, growth, and yields. However, there may be a negative side to increasing atmospheric CO_2. Carbon dioxide does not absorb visible radiation, but it does absorb infrared radiation. Therefore, the incoming solar radiation passes through the atmosphere without the visible portion of the spectrum being absorbed, but after it strikes Earth or solid objects on Earth, it is reflected back into the atmosphere as the longer, lower-energy wavelengths, infrared radiation. That infrared radiation may be absorbed by the CO_2 and water vapor in the air, increasing the heat around the Earth somewhat like a glasshouse accumulates heat while in the sun (visible rays in solar radiation pass readily through glass, but longer infrared wavelengths are reflected and re-emitted from solid objects inside glasshouses and cannot pass through glass, so glasshouses accumulate heat on a bright day). Some meteorologists have speculated that the increasing CO_2 in the atmosphere will cause global warming by trapping the infrared wavelengths in the atmosphere. It is expected that average global surface air temperature may be 2.7 to 10.6 °F higher than the present sometime during the latter part of the next century (Table 2).

However, there is considerable debate whether the increasing atmospheric CO_2 will cause average global temperatures to increase. We want to determine what role these environmental changes would have on cotton production as cotton is sensitive to both magnitude and the rate of climate changes (increasing CO_2 and warmer temperatures).

Specifically we will report the effects of:

- Temperature and atmospheric CO_2 on seedling growth when other factors are not limiting.
- Temperature and atmospheric CO_2 on photosynthesis.
- Light intensity and atmospheric CO_2 on photosynthesis.
- Leaf nitrogen and water deficits on photosynthesis.
- Temperature and atmospheric CO_2 on the rate of crop development.
- Temperature, water deficits, and CO_2 on water use.
- Temperature and atmospheric CO_2 on fruit production and retention.
- Temperature and atmospheric CO_2 on growth of bolls and various vegetative structures.

Data Collection

Climatology Data

Long-term (42-year) average daily temperatures were obtained by summing daily maximum and minimum temperature and dividing by two and by the length of the record at each respective location (Boykin et al., 1995). Hourly records are the summation and averaging of essentially a continuous recording of temperature over each hour. Cotton leaf and air temperatures were determined with a hand-held infrared thermometer. The thermometer was held about one foot from the upper part of the canopy. Air temperature was determined with an automatic monitoring of a thermocouple on the instrument.

Naturally-Lit Plant Growth Chambers

The results described in this bulletin were from several experiments conducted in naturally-lit plant growth chambers. Agronomists have largely discounted data from plant growth chambers because they recognized that plants grown in most chambers did not represent the plants they saw in the field. The energy from artificial light provided by most growth chambers does not adequately represent the solar spectrum nor have enough total radiation for suitable plant growth. Phene et al. (1978) recognized the problem, but identified the need for unique data that could be obtained with growth chambers. They designed chambers that utilize radiation from the sun and still controlled several aspects of the environment. This solved many of the problems associated with unique and atypical appearing plants often produced in artificially-lit plant growth chambers.

Similar naturally-lit chambers have since been built and modified several times to improve operational details and efficiency, but the primary characteristics have been kept. These chambers are known as Soil-Plant-Atmosphere-Research (SPAR) units. These are located outdoors and can accurately control temperature and CO_2 at predetermined set points for plant-growth studies in natural solar radiation regimes.

Each SPAR unit consists of a steel soil bin (3.25 feet tall by 6.5 feet long by 1.5 feet wide), and a plexiglass chamber (8 feet tall by 6.5 feet long by 4.75 feet wide) to accommodate aerial plant parts, a heating and cooling system, and an environmental monitoring and control system. Canopy photosynthesis is calculated by summarizing the amount of CO_2 added to the chambers over each 15-minute period and correcting for dark respiration and chamber leakage (Acock et al., 1985; Reddy et al., 1995b).

Nutrient Deficit Studies

A computer-controlled timing device applied a complete nutrient solution to each row of plants via a drip irrigation system in each SPAR unit. When nitrogen was a variable in the experiment, selected treatments provided an altered solution in which calcium chloride was used to replace varying amounts of calcium nitrate (Reddy et al., 1996b). Cotton plants were grown until first square with all nutrients provided in sufficient quantities. Then the solutions were changed so that some plants received none and other plants provided varying percentages of sufficiency of N.

Leaf N was determined weekly. Plant responses are expressed as functions of leaf N as determined by the microkjeldal technique, not the amounts of nitrogen fertilizer applied. Thus, the data should be relevant to crops grown on any soil or with any cultural practice. Unfortunately, measures of leaf N are not routinely available, but chlorophyll meters are available that provide reasonable estimates of leaf greenness. There are several reasons for lack of green color in cotton leaves, but the lack of leaf N is one of the more important reasons. Photosynthesis was measured throughout the period and subsequently related to leaf N content.

Water Deficit Studies

In experiments in which water deficits were imposed, complete nutrient solutions were provided and plants were grown at near optimum temperature (81 °F). Water was provided as a function of evaporative demand (120, 60, or 40% of the previous day's evaporation from the plants in the well-watered SPAR units). Excess water was allowed to drain from the fine sandy soil. Leaf water potential was determined near solar noon from recently expanded, mature, sunlit leaves using the Scholander pressure chamber technique.

Leaf water potential is a suction that occurs in the leaf because of evaporation of water from the leaves. That suction, caused by the loss of water from the relatively rigid plant-cells, causes tension to be placed on water in the plant vessels. That tension is transmitted all the way to the roots, and is the force that pulls water from the soil. It pulls water to the leaves somewhat like one can suck water from a glass through a straw.

A pressure chamber technique that measures the water suction in the leaf was discovered several years ago by Scholander. We sampled leaves at noon for several days on many plants that were in varying degrees of water deficit (water stress). The measured leaf water potential was related to the amount of photosynthesis that occurred on that day by the appropriate cotton canopies. Water use was also measured by continuously collecting the water from the cooling coil and weighing it at 15-minute intervals. Growth and development of various organs were monitored along with square and boll abscission rates. Abscission anytime after flowering was considered boll abscission.

Temperature Studies

Two experiments were conducted to determine the effect of temperature on flower production, retention, and vegetative growth.

Fruiting Period Experiment

Experiment one was conducted by placing cotton plants in the plant-growth chambers at the beginning of flowering. The plants had been grown from seedlings to beginning flowering in 12-liter pots maintained outside in the natural environment. The chambers were set to control temperature relative to a long-term average maximum and minimum daily July temperatures at Stoneville.

To some chambers, temperatures 3.6 °F less than the average daily maximum and minimum temperature were maintained, while in other chambers 3.6 °F, 9 °F, or 12.6 °F were added to the average maximum and minimum July Stoneville temperatures. A sinusoidal curve fit between maximum and minimum temperatures provided typical diurnal daily pattern for each temperature condition. Plants at each temperature regime were grown in ambient CO_2 (350µl l^{-1}) or twice ambient CO_2. This experiment was maintained for 28 days. Flowers were tagged daily and fallen plant parts were collected daily, dried, counted, and weighed. Dry weights of various plant components were also measured at the end of the experiment.

Whole Season Experiment

Experiment two was conducted by imposing temperature treatments from planting. The SPAR units were kept at 1995 outdoor air temperature or some constant variation from that temperature. As the outdoor air temperature changed, so did the temperature in each chamber. Five different temperature treatments were imposed: (a) 1995 ambient minus 3.6 °F, (b) 1995 ambient, (c) 1995 ambient plus 3.6 °F, (d) 1995 ambient plus 9 °F, and (e) 1995 ambient plus 12.6 °F (see Figure 15). Temperature control was maintained from crop emergence to maturity (lint could be seen in the sutures of 50% of the bolls). Plants were grown at ambient (360 µl l^{-1}) or twice ambient CO_2 throughout the growing season. Water and nutrients were supplied abundantly. Insects were not a problem since the chambers were sealed.

Days to first square, first flower, and open boll were recorded. The initial planting was with narrow rows, and, at 20 days after emergence, selected rows of plants were removed to avoid competition. Plant heights, leaf areas, number of nodes, and dry weights were determined on the plants removed. Final row spacing was 26 inches with 4 inches between plants in the row. Flowers were tagged daily and abscised bolls and squares collected. At final harvest, the numbers of bolls and squares were counted. Weights of bolls and total vegetative parts were determined.

Results and Discussion

Photosynthesis

Solar Radiation and Photosynthesis

Photosynthesis of fruiting cotton plants increased as CO_2 and solar radiation increased (Figure 9). There were differences in canopy light-utilization efficiency (initial slopes of curves when light was limiting). Photosynthesis did not appear to light saturate even at high radiation levels; however, from this and from a similar study with even higher CO_2 concentrations, cotton response to increasing CO_2 appeared to reach a maximum at 700 $\mu l\ l^{-1}$ CO_2 or slightly higher. Also (not shown here), there is considerable variation among crop species.

Canopy photosynthesis increased throughout the boll-filling period with the increases being greater in high CO_2 environments. The average photosynthesis of cotton canopies was determined at nearly full sun on bright days (1,600 $\mu mol\ m^{-2}\ s^{-1}$ photosynthetic photon flux density, Reddy et al., 1995C). Those data were collected on days when natural radiation exceeded 1,600 $\mu mol\ m^{-2}\ s^{-1}$ during the boll-filling period. Plants grown in 700 $\mu l\ l^{-1}$ CO_2 fixed 34% more carbon than plants grown in ambient CO_2 environments. Thus, any change in weather or cultural practices that increases the amount of solar radiation available to cotton will increase the potential yield of that crop. This assumes that water and other nutrients would not be limiting. On the other hand, any change in weather or cultural practices that decreases the amount of solar radiation available to the crop would be expected to decrease cotton yields.

Temperature and Photosynthesis

The photosynthetic response of plants to increased atmospheric CO_2 and temperature (Figure 10) is quite similar to vegetative-growth responses to temperature (Reddy et al., 1992a, 1992b). The response of photosynthesis to increasing CO_2 was smaller at the lowest (63 °F) and at the highest temperatures (97 °F) compared to the responses at temperatures more favorable for cotton growth. The optimum temperature for vegetative structures, particularly leaf growth, both pima and upland cotton is slightly higher than the optimum temperature for producing fruiting structures. The higher photosynthetic rates at both ambient CO_2 and twice ambient CO_2 are likely because of the continued addition of new leaves at those high temperatures.

Previous work also found that temperatures above optimum for fruiting result in fruit abscission and, therefore, less intra-plant competition for carbohydrates. Normally cotton, being an indeterminate-flowering type plant, slows the addition of leaves and fruiting sites as the boll load increases, resulting in what is commonly called "cutout." As bolls mature and no longer require nutrition, photosynthetic products accumulate and encourage vegetative growth commonly known as "regrowth." If the bolls prematurely abscise, the intra-plant competition for nutrients does not occur, and more new leaves continue to be produced throughout the fruiting period. Bolls may abscise prematurely because of injury by insects, nutritional deficits, or injury by environmental factors.

Young cotton leaves reach their maximum photosynthetic rates about 14 to 16 days after unfolding, then the photosynthetic rates of individual leaves gradually decline until leaf senescence. Therefore, the relatively higher rate of net photosynthesis that occurred at 80 °F or higher compared to that of plants grown at 63 °F was probably because of the younger population of leaves in the canopy of the high-temperature grown plants. More leaves were initiated on both the mainstem and branches at high temperatures than at low temperatures (Reddy et al., 1993, 1994, 1995a). Leaves also expanded more rapidly at 86 °F than at either 68 °F or 97 °F in those studies, resulting in a younger leaf population in a canopy grown at 86 °F. One would expect therefore, that in a warmer, high CO_2 climate, photosynthetic rates of plants will be greater because of both a steeper CO_2 gradient from the atmosphere to the CO_2 fixation sites inside the leaves and the younger, more efficient leaf population on canopies produced in that environment.

Water Deficits and Photosynthesis

There was little apparent interaction between photosynthetic rates of plants in varying degrees of water deficits and midday leaf water potentials (Figure 11). Photosynthetic rates decreased as the daily midday leaf water potentials declined (became more negative), and the rates of decrease of both the 350 (ambient) and 700 µl l^{-1} CO_2-grown plants were nearly parallel. Therefore, we expect that in a high CO_2 environment, photosynthesis will be greater even when water deficits occur.

Leaf Nitrogen and Photosynthesis

The maximum photosynthetic capacity of leaves depends on several factors, including nitrogen content (Figure 12). Doubling the atmospheric CO_2 caused plants supplied with excellent N fertility (2.25 g leaf N m^{-2}) to fix CO_2 about 40% more rapidly. Even plants that were severely N starved (1.5 g leaf N m^{-2}) increased their photosynthetic rate about 34% when the atmospheric CO_2 was doubled. The leaves of plants fertilized with adequate N did not light-saturate at 1,800 µmol m^{-2} s^{-1} of visible solar radiation (nearly the maximum radiation received at noon on clear summer days). Plants provided little N did light-saturate (more light did not increase photosynthesis) as expected (data not shown).

Stomatal conductance increased, and appeared to be primarily responsible for increased photosynthesis, as leaf N increased (Reddy et al., 1997). Increased stomatal conductances in high leaf N plants suggest that more healthy plants had more highly functional stomata that could open and close as needed.

We also found that leaf internal CO_2 increased in N-starved plants (Reddy et al., 1997). Lower internal leaf CO_2 values in plants that were fed adequate N are consistent with increased enzymatic efficiency in leaves containing sufficient N. Nitrogen starvation has been reported by others to cause less efficient photosynthesis in leaves of wheat and beans. Thus, it appears that low concentrations of leaf N cause photosynthesis to be reduced because of both greater stomatal resistance (less functional stomata) and less effective chloroplasts. The less effective chloroplasts were probably limited by the enzyme that first uses atmospheric CO_2.

Schulze (1986) reached a similar conclusion for the cause of lower photosynthesis in plants during a water-deficit condition. It seems likely from the these data that environmental stresses caused by water or nitrogen deficits will lower photosynthesis about equally in a high CO_2 environment as similar stresses in today's ambient CO_2 environment.

Respiration

Photosynthesis is the process of converting CO_2 and water into sugars. Cotton plants can store only very small quantities of sugars. These are therefore quickly converted to starch or translocated to growing organs anywhere in the plant. Each growing organ may use that sugar to support growth or some "work" activity. Approximately 50% of the sugar each growing organ receives is used as building blocks to form structural material, i.e., that portion of the sugar supply becomes incorporated into the cell walls as cellulose or other structural compounds. The remaining 50% of the sugar that arrives in a growing organ is used as an energy source for making the chemical conversions essential to create proteins, lipids, or other structures used to build cells; or it is used to do the other necessary work. Examples of the other work include providing the energy for mineral uptake by the roots, or transporting sugars and other nutrients throughout the plant. Energy for these activities, building new molecules and structures and providing the biochemical energy for other work, is obtained from a process called respiration.

Respiration is sensitive to temperature. As temperature increases so does respiration. Therefore, plants growing in a high-temperature environment require more sugars for respiration than similar plants in lower temperatures. Plants that are stressed because of inadequate water may also become warmer because their stomata close because of water loss. An indirect effect of the water deficit then causes a greater need for sugars because of the higher temperatures; a lower sugar supply also results because closed stomates reduce photosynthesis. A deficiency of leaf nitrogen also quickly results in a shortage of sugars required for respiratory-supported growth and other work. Plants stressed because of water or nutrient deficits, or plants simply stressed because of high temperatures, may have insufficient sugars to support all their structures. This may result in the death of tissues that were previously actively growing.

Crop Water Use

Plants grown in high CO_2 environments use water more efficiently than plants grown in ambient CO_2 environments (Figure 13). As plants develop lower leaf water potentials (become drier and leaf water is held with more tension), the stomata close and photosynthesis declines. The rate of water use by plants grown in ambient CO_2 decreased as the leaf water potentials became lower, to about -2.5 MPa., then the rate of decrease slowed; but the rate of water use by plants growing in the 700 $\mu l\ l^{-1}$ CO_2 chambers changed slowly and linearly as the water deficits became greater (more negative).

The stomata of plants growing in chambers maintained at high CO_2 are apparently partially closed even in well-watered conditions. Their water use per gram of CO_2 fixed (data not shown) did not change as the water deficits increased, but the plants grown in ambient CO_2 closed their stomata in response to midday leaf water potential. This resulted in less water transpired per gram CO_2 fixed by the plants growing in severe water-deficit conditions than by similar plants not water stressed. Thus, plants growing in a high CO_2 atmosphere are more efficient water users at all levels of water stress than plants growing in today's atmospheric environment.

This suggests that if the frequency and intensity of droughts do not change as atmospheric CO_2 increases, then irrigation of crops in the high CO_2 environment will be less important than it is in today's environment. However, it does not mean that plants grown in high CO_2 environments will need less water. They will still need water, but they are slightly more efficient in mild water stress conditions than plants growing in today's CO_2 environment.

The use of water (transpiration) was lower at all temperatures in the high CO_2 environments (Figure 14). As atmospheric CO_2 increased, transpiration decreased. Higher temperatures caused more rapid transpiration as expected, and water use was more in the higher temperature, low CO_2 environments.

Temperature and Cotton Development

Developmental events occur much more rapidly as temperature increases (Table 3). Number of days to the appearance of first square, first flower, and mature open boll decreased as the average temperature to the respective events increased. The plants growing in chambers in which average daily temperature was 91 °F or higher did not produce any mature fruit so those data points are not shown. The numbers of days required to produce squares, flowers, and mature fruit were reduced by 0.9, 1.7, and 3.8 days, respectively, per degree increase in temperature. Thus, assuming the temperature increase will be equally distributed throughout the growing season, a 9 °F increase in average global temperature will speed development from emergence to maturity by 24 days. Unfortunately, most of the shortening of developmental time occurs during the boll growth period and results in smaller bolls (Hodges et al., 1993). Bolls that mature rapidly because of high temperature have less time available to grow and reach their genetic potential size. Therefore, in years that are extremely hot during the flowering and boll-filling period, the crop matures earlier and has smaller bolls than in years in which the temperature during that period is cooler.

An examination of the GDD_{60} and these results illustrates the effects of seasonal changes in temperatures on the catchup of crop developmental events when planted at different times. Suppose one had planted so that the crop emerged April 20, May 10 or June 1. Using the data in Table 3 and the accumulation of GDD_{60} from Figure 4, we can estimate that first square would occur 34 days from emergence on April 20, 24 days from emergence on May 10, and only 19 days from emergence on June 1. Thus, there was a difference of 42 days in emergence dates of these crops, but if the average GDD_{60} occurred the dates of squaring were separated by only 15 days. We often see such a "catching up" of crops planted when the temperature is more favorable for growth and development.

Many flowers were produced on plants growing at 1995 plus 9 or 13 °F, but the fruits abscised soon after flowering. It is not clear whether fertilization occurred on those flowers or if abscission was caused by some other problem. There was not a loss of squares due to high temperature in any of the environments. More fruiting sites, and thus more squares and flowers, were produced in the high- CO_2 and high-temperature-grown plants. Doubling the atmospheric CO_2 did not affect the developmental rates or protect the plants from injury to the fruit-set process at high temperatures. Thus, cotton plants developed fruiting sites more rapidly in temperatures above 86 °F, but the young fruit abscised because of such high temperatures (Reddy et al., 1992, 1996). As a result, well-fertilized and well-watered crops continued producing additional flowers and leaves and maintained a canopy capable of rapid photosynthesis while in hot temperatures (average daily above 86 °F).

Variation in temperature in the natural environment allows some flowers to escape exposure to damaging temperatures so that some bolls are eventually produced. Unfortunately, long growing seasons resulting from such a scenario are expensive to sustain because of the long period the crop must be provided nutrients, water, and protection from pests.

Temperature and Early-season Vegetative Growth

The experiment conducted during the summer of 1995 was unique. The temperature control was set to maintain several constant variants from ambient conditions (Figure 15). This resulted in plants grown at all growth stages at temperatures that were real relative to natural conditions, and ± variants from that. We summarized the temperatures by averaging the values to the time of various events (Table 3). Days to first square ranged from only 19 days at 85 °F to 33 days at 71 °F. It took from 39 days at average daily temperatures of 88 °F to 65 days at 74 °F for cotton plants to reach first flower. It took 142 days at 71 °F, 101 days at ambient 78 °F, and only 77 days at 87 °F to produce open bolls. Unfortunately, essentially no bolls were retained at 87 °F and none were retained at 90 °F.

If days to the event were plotted against average temperature, all these events were linear, i.e. as temperature increased, the time required to produce squares decreased in a linear manner, as did flowering or open bolls. The rates of the processes (time to first square, first flower or first mature boll-time when lint can be seen through the cracked sutures) were different, but the responses to temperature were linear.

Temperatures during seedling establishment played an important role in cotton growth. The plant height of cotton plants growing at 70 °F was about 1 inch at 20 days after emergence, while plants growing at 82 °F averaged 7.6 inches tall and those growing at 86 °F were over 9 inches in height (Figure 16). There were small but not significant differences in the heights of plants in different CO_2 at the warm temperatures, but essentially no height differences in plants limited by low temperature.

Mainstem node formation in response to temperature was essentially the same as plant height (Figure 17). Dry matter (above ground) accumulation and leaf area at 20 days after emergence also increased similarly to plant height as temperature increased (Figures 18 and 19). There was a greater response of dry matter accumulation to elevated atmospheric CO_2. Again, the dry matter accumulation response to CO_2 was greater in plants growing at near optimum temperature.

Temperature and Balance Between Vegetative and Reproductive Growth

The numbers of bolls and squares produced by plants growing at these different temperature regimes are shown in Figure 20. Large numbers of squares were produced at all temperatures. More were produced at the high temperatures 1995 + 9 °F or + 12.6 °F than at the lower temperatures because the bolls abscised from plants growing at the two highest temperatures. Since the bolls abscised from plants growing at those high temperatures, the plants continued to produce new nodes and fruiting sites.

Plants growing at 1995 ambient temperatures plus 3.6 °F and minus 3.6 °F in 360 $\mu l\ l^{-1}$ CO_2 produced about equal number of bolls. They matured at different times (Table 3), so those growing at lower temperatures took longer to produce the same number. Plants grown at all three temperature regimes eventually stopped producing new fruiting sites because of boll load. The plants growing in higher CO_2 produced more sites and squares plus bolls, because additional vegetative growth was caused by greater photosynthesis (Figures 9, 10, 11, and 12).

The number of bolls retained was very strongly controlled by temperature regimes in which the plants were grown (Figure 21). This experiment was unique in that the temperatures were controlled from the emergence of seedlings, and the unique natural diurnal variation was maintained throughout the season. There was a distinct advantage to growing plants at the higher temperatures early in the season. At 20 days, the high-temperature-grown plants were 4 to 7 times larger than plants grown in 1995 temperatures. However, that advantage was lost because of failure of the high-temperature-grown plants to retain fruit.

Seedling responses to warmer temperatures than typically occur during seedling establishment period in the Midsouth suggest that any cultural practice that could be used to warm the seedling environment would be beneficial. The high-temperature-grown plants produced large numbers of squares, and those squares matured to produce flowers. The squares did not abscise or abscised in only very small numbers. The very young bolls (3 to 5 days after anthesis) abscised in the two highest temperature regimes. Irrigation during flowering can lower canopy temperatures and reduce high-temperature injury.

The total vegetative weight (leaves, stems, and roots) produced by plants grown at the various temperature regimes was not different (Figure 22). Plants grown in high CO_2 environments produced about 40% more vegetative mass than plants grown in ambient CO_2 environments. However, the plants grown in the high temperatures matured earlier and were harvested earlier than those grown in the cooler environments. Therefore, the rate (mass per day) of vegetative dry matter production was higher in the high temperatures.

Boll weights on the mature plants are shown (Figure 23). At the three lowest temperatures, doubling the atmospheric CO_2 consistently increased boll mass a small amount, but in each of the two highest temperature regimes, the boll mass was insignificant because of the abscission of young bolls. The small mass values shown are the green bolls that were initiated late in the season when the temperatures declined sufficiently so the 1995 + 9 °F and + 12.6 °F average daily temperatures were below 82 °F (Figures 15 and 23).

Temperature and Flower Production and Boll Retention

The bolls produced and retained on cotton plants growing in different temperature regimes for a 28-day period are shown in Figure 24. Hourly temperatures were generated from a sinusoidal fit of long-term average July temperatures for Stoneville. Similar sinusoidal temperature regimes were calculated by subtracting 3.6 °F or adding 3.6, 9.0, and 12.6 °F to those average July temperatures.

The number of bolls produced in these environments was not influenced much by these different temperature regimes. Approximately 200 to 250 bolls m^{-2} were produced in all temperatures over a 4-week period; however, the number retained was strongly controlled by temperature. About 200 bolls m^{-2} were retained when the average daily temperature was 85.6 °F or less. At 91.2 and 94.6 °F, the number of bolls retained by the cotton was negligible. When plants were grown at 85.6 °F (ambient plus 3.6 °F), all the flowers set for the first 5 days were retained (Figure 25A). After that, the percentage retained gradually declined as the boll load on the plants increased. The greater retention by plants grown in 700 $\mu l\ l^{-1}$ CO_2 demonstrates the effects of higher photosynthesis in those plants. All the bolls abscised within 5 days after flowering in the chambers kept at the long-term July mean temperature plus 9 °F or higher (Figure 25B).

Bolls produced and retained are also presented as a function of days after temperature treatment in Figure 26. From these data, it is clear that there is a very low probability of cotton production at such high temperatures in a humid environment where evaporation from leaves is low.

Fruit production efficiency, defined as dry weight of fruit per dry weight total mass produced, increased as average daily temperatures increased to 85 °F, then it declined rapidly as temperature increased above 85 °F

(Figure 27). Since the rate of fruit retention dropped so dramatically at temperatures above 85 °F, the calculated fruit-production efficiency also dropped at those high temperatures. The number of bolls retained was essentially eliminated by temperatures higher than Stoneville July average plus 3.6 °F (85 °F). At the two highest temperatures, the number of bolls retained was drastically reduced. The upper limit for cotton fruit survival is about 90 °F or long-term July average plus 9 °F for U.S. Midsouth Cottonbelt. Such a statement may be misleading, because 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 other experiments, we have observed that when the temperature was not damaging for a few days, the flowers produced during that period survived and bolls grew to maturity even though temperatures were above 90 °F for several days during the fruit-growth period.

Apparently, there is a short period associated with flowering when the reproductive process is most vulnerable to average daily temperatures above 91 to 94 °F. If the fruit escapes high temperature during that time, it can survive unfavorable, high-temperature conditions during the rest of its growth period. However, we do not have an exact definition of the vulnerable period. Such high temperatures cause rapid maturation of the bolls (Table 3) so that less time is available for seed and lint growth. Thus, even if the bolls escape average daily temperatures above 85 °F during flowering, which causes boll abscission, exposure to such high temperatures later in the boll growth period will cause smaller bolls.

A number of reciprocal crosses were made between plants growing at different temperatures, i.e., in some cases, pollen from high-temperature-grown plants was used to pollinate flowers produced at optimum temperatures, and, in other cases, pollen from optimum-temperature-grown plants was used to pollinate flowers produced at high temperatures. The high temperatures appeared to injure both pollen and the female flower parts, and the injury appeared to be progressive with time of exposure. In addition, preliminary experiments were conducted to determine the age of squares when high temperatures caused damage. It appears that fertilization and seed set were damaged by high temperature 10 to 12 days prior to flowering. The results were not conclusive because the number of crosses was low.

Experiments conducted in Florida found the response of rice to temperatures was similar to that of cotton (Baker et al., 1990). Rice appears to be slightly more high-temperature tolerant than does cotton. The least grain was produced at about 97 °F (Figure 27). Rice flowers also appear to be the most sensitive plant structures to high temperature. Increasing CO_2 did not ameliorate the heat-sensitive condition in either rice or cotton. In a correlative field study, Seshu and Cady (1984) found rice yields were negatively correlated with increases in temperature. Their data included 40 field environments over a 5-year period from eight countries in Asia, two in Latin America, and one each in Africa and Oceanasia. Their experiments had good water control, optimal fertility, and adequate plant protection. They found 193 lb/acre lower yields with each degree increase in temperature ($r^2 = 0.71$), and the rice yields projected to zero at 91 °F.

The observed response functions derived from the data collected from those field experiments are similar to the response functions observed for rice and cotton in temperature-controlled naturally-lit plant growth chambers (Baker et al., 1990; Figures 24 and 27). If 9 °F were added to Seshu's and Cady's temperature data (simulating projected increases in temperature for the Midsouth by global circulation modelers), and if no changes occurred in cultural practices to alleviate the stresses, one would expect their crop yields to be reduced to unacceptable levels. A similar relationship was found between rice yields and temperature in a similar, but more recent study (Pandey, R. K., 1995, personal communication). Thus, both the field experiments with rice conducted over several years and with many different cultural practices and locations, and the controlled-environment studies with rice, lead to the same conclusions suggested from our cotton experiments.

Breeding both high- and low-temperature-tolerant cultivars will be beneficial in a future warmer world. Low-temperature tolerance in cotton would allow producers to plant the crop earlier and permit a crop canopy to develop earlier in the growing season. This would allow flowering to occur before the midsummer high temperatures that limit fruit set. The damaging effect of high temperature on cotton production in Arizona has been recognized (Kittock et al., 1988; Lu and Zeiger, 1994; Lu et al., 1994). They found that cotton yields in Arizona were limited by high temperatures especially if not planted early. Cotton cultivars tolerant to high temperature transpired more water than high-temperature-sensitive cultivars. The high-temperature-tolerant cultivars had cooler canopies because they transpired more; thus they essentially escaped the damaging high temperatures. They also found crops grown at lower elevations, where the temperature was higher, yielded less than similar crops grown at higher elevations and cooler environments.

Summary and Conclusions

Atmospheric scientists have studied global circulation of air and ocean currents and constructed models that describe weather. With the recognition of man's activities, including massive burning of fossil fuels, they have hypothesized that the average daily temperatures will increase from 5 to 9 °F, depending on the location, by the time the concentration of carbon dioxide in the atmosphere doubles. This has been forecast to occur by the middle to the latter part of the 21st century.

Controlled-environment studies have provided a technique to study the impact that such temperature and CO_2 changes would have on cotton production.

- Doubling the atmospheric CO_2 in the atmosphere would increase photosynthesis by about 40%. If other environmental conditions do not change, a major portion of that increase in photosynthesis would result in increased dry mass produced. This increase in biomass is not totally reflected in fruit production.
- Increased atmospheric CO_2 would result in increased plant growth even in dry and nutrient-deficit situations. However, plants grown in high CO_2 are also sensitive to water and other nutrient deficits.
- Rate of forming first square, flower, or first open boll is not enhanced by increasing atmospheric CO_2 but, these developmental rates are very temperature dependent.
- Atmospheric CO_2 does little to alleviate the adverse effects of high temperature.
- Early-season growth would be greatly enhanced by higher temperatures in many cotton-producing areas across the U.S. cottonbelt. In our studies, leaf area, plant height, and dry weight of plants grown 20 days at 82 °F (1995 ambient temperatures plus 9 °F) were 6 to 8 times more than those parameters of plants grown at 70 °F (1995 ambient temperatures).
- Increased temperature, hypothesized to occur because of increased CO_2, would result in increased seedling growth rate.
- Photosynthesis early in the season would be increased by higher temperatures, but would be lower during the midsummer when temperatures are projected to increase.
- Fruiting sites would be increased at higher temperatures. We found that 3 to 5 degrees increase in average temperature caused more rapid addition of fruiting sites. Squares and flowers were produced at those fruiting sites.
- Young bolls abscise when grown at 90 °F or higher average daily temperatures in humid environments. Mature bolls are not produced when grown at temperatures above 90 °F even in well-watered, fertilized situations and even higher atmospheric CO_2 concentrations. Vegetative growth was sustained even at these temperatures where fruits were totally abscised. Higher atmospheric CO_2 concentrations favored vegetative growth at all temperatures.
- Other mechanisms of heat tolerance in seed-bearing crops need to be identified.
- It appears likely that most grain and fruit-bearing crops are sensitive to high temperatures, and their production will be limited by increases in global temperature. If the hypothesized climate change occurs as forecast, and greater instability occurs as projected because of increased atmospheric CO_2 and other radiative greenhouse trace gases along with accompanying temperature increases, then our major food and fiber crops will be subject to more adverse weather. The world's food and fiber supply is largely provided by seed or fruit-bearing summer annuals that will be injured by seasonal increases in global surface air temperatures; and these crops are also vulnerable to periodic occurrences of heat and

drought stresses. On the other hand, the vegetative structures of plants are less sensitive to high temperature, and if global warming occurs, man's diet may shift so that more of his nutrition will be derived directly from leaves, stems, and roots or animals that consume these structures.

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