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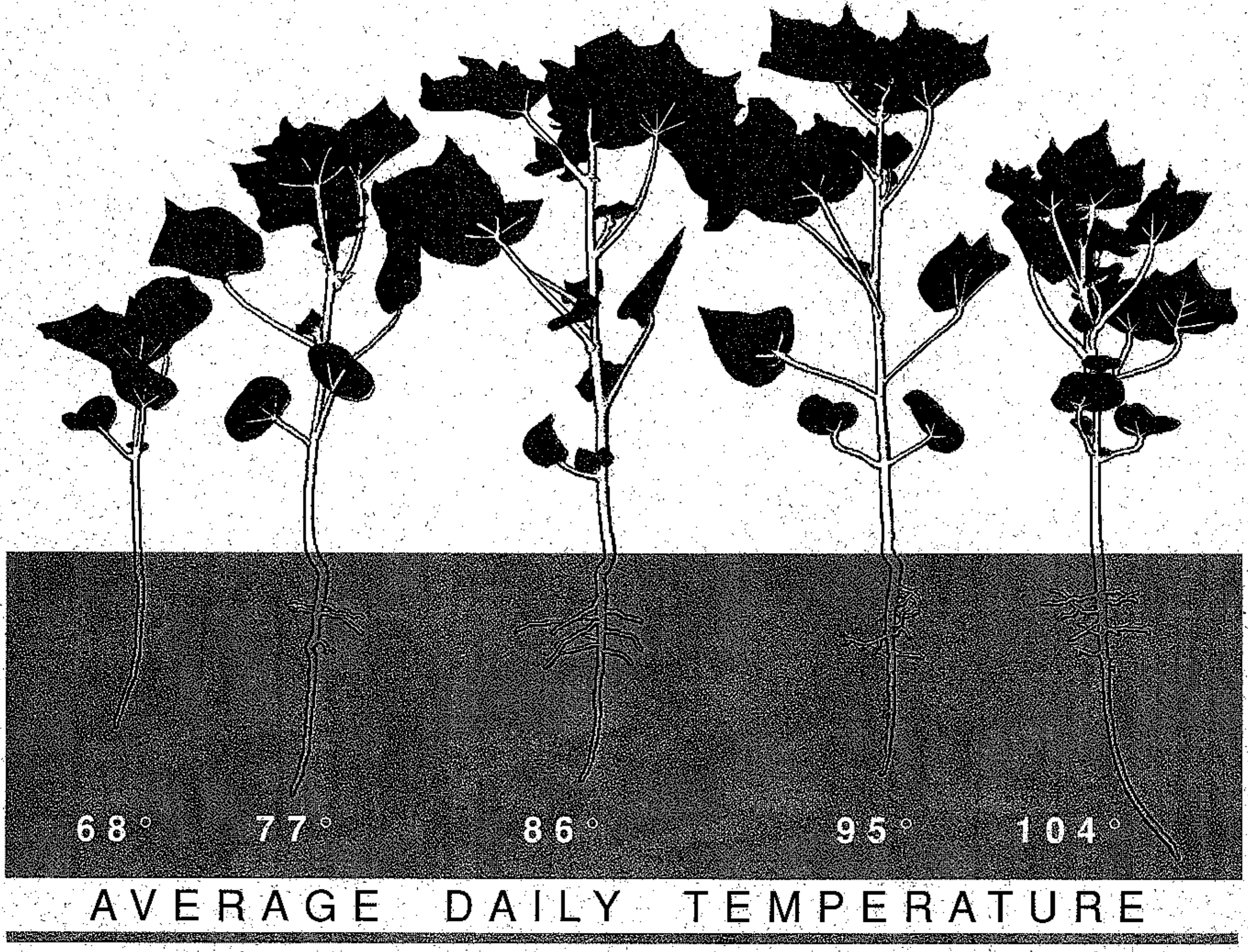
Temperature Effects on Cotton



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Temperature Effects on Cotton

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Temperature Effects on Cotton

Introduction

Cotton is sensitive to numerous environmental factors. Years of keen observation, experience with production practices, and weather allow producers to synthesize what seem to be optimum cultural practices. However, weather, soil, cultivars, and cultural practices affect crop growth interactively, sometimes resulting in plants responding in unexpected ways to their conditions.

The primary factor affecting crop development is temperature. But temperature is modulated by other factors, such as day length, water, or nitrogen stress. Plants at different growth stages, different species, and cultivars within a species have different responses to temperature and those factors affecting temperature responses. In addition, many environmental factors vary simultaneously, causing associations between individual weather variables and plant responses to be confounded, and thus impossible to determine "cause and effect relationships." These complexities make it impossible for any individual to know all the conditions in the field on a dynamic basis, let alone make reasonable estimates of their effects on the crop.

In recent years, there has been an increasing effort to integrate knowledge from various scientific disciplines into coordinated whole-crop responses to physical environment. To relate crop growth to physical conditions, one needs much detailed information about the way plants respond to a wide range of each important environmental variable.

Temperature is one of the most important variables controlling plant developmental and growth process. Thus, in this report, we show the results of several experiments in which temperature was varied independently of other growth conditions. We attempted to always keep other factors constant, e.g., an adequate supply of water and nutrients, so that the tests were determining potential growth and developmental rates at each temperature. Excellent insect control was also maintained so that insect damage was not a factor in these experiments. Water and nutrient deficit environments will be studied and reported later.

The computer-based crop model and expert system GOSSYM-COMAX is the first crop simulator that calculates specific cotton crop responses to weather, soils, and management conditions. It provides the producer with quantitative estimates of crop responses within the growing season to specific real or hypothesized management practices within the context of his particular soil, weather, and crop. Cotton producers have generally found this to be a helpful management tool (McKinion et al., 1989). Producers have credited GOSSYM-COMAX for helping make several types of management decisions resulting in added economic value from the crop. An independent evaluation by Texas A&M University found the average producer-user of GOSSYM-COMAX attributed $55 acre net return to the crop model when used in his cotton management.

One of the opinions producers and other users have unanimously expressed about GOSSYM-COMAX is its value as a teaching tool. Users of the model find that they learn more about their crop and its responses to soils, weather, and management practices than they had previously been able to understand.

Improvements and enhancements for quality of simulation, the variables GOSSYM-COMAX can address, as well as ease and convenience to the user, are under continued development. In the course of developing more detailed information for that model, experiments were conducted with plants growing in controlled conditions to provide detailed growth and development responses to temperature. The resulting data are being used to expand the temperature range over which the crop model is sensitive, and to improve the body of knowledge on modern cultivars. These experiments show several inter-relationships of growth of plant organs and some of the interlinkages between growth and photosynthesis and respiration.

It is the purpose of this bulletin to show producers and others interested in cotton growth and physiology: **(1)** responses of cotton to temperature, **(2)** the competition of different organs within a plant, and **(3)** the relationship of photosynthesis and respiration with growth. Hopefully, such information will be useful to those using a crop model to better understand their crops, as well as to those who are not using the model.

Materials and Methods

Experiments described here were generally of two types. One type was conducted with plants grown from seeds planted directly into plant growth chambers called SPAR (Soil-Plant-Atmosphere-Research) units (Phene et al., 1978; Acock et al., 1985). The main advantage SPAR units have over most other types of growth chambers is that they utilize natural radiation and thus have essentially full sunlight on the plants. They have an advantage over the natural environment since many of the weather elements that are covariants of one another can be controlled.

Additionally, for specific experiments, the atmospheric carbon dioxide level may be maintained higher than normal to avoid internal plant carbon deficiency. Although such a high CO_2 condition does not normally exist in nature, controlling CO_2 levels allows for more definitive causes for a particular plant response such as fruit shedding.

The SPAR units allow us to impose treatments from the seedling stage to maturity, to initiate treatments at later specific developmental stages, or to move potted plants into the units to answer specific questions. As an example, Figure 1 shows the daily time courses of air temperatures, dewpoint temperatures, and solar radiation on July 15, 1990 for five of the SPAR units. The day/night air temperatures were maintained within ± 0.9 °F of the treatment set points. Dewpoint temperatures were not controlled but resulted from the dynamic interaction between transpiration and condensate removal rate of the system. The dewpoint temperatures were slightly lower at higher radiation levels during midday than either morning or evening hours at all temperatures. The lower dewpoint temperatures, and thus lower relative humidity, were caused by more cooling required near midday to maintain the intended temperatures. During the nighttime hours, the values were very stable. This pattern was consistent throughout the growing season.

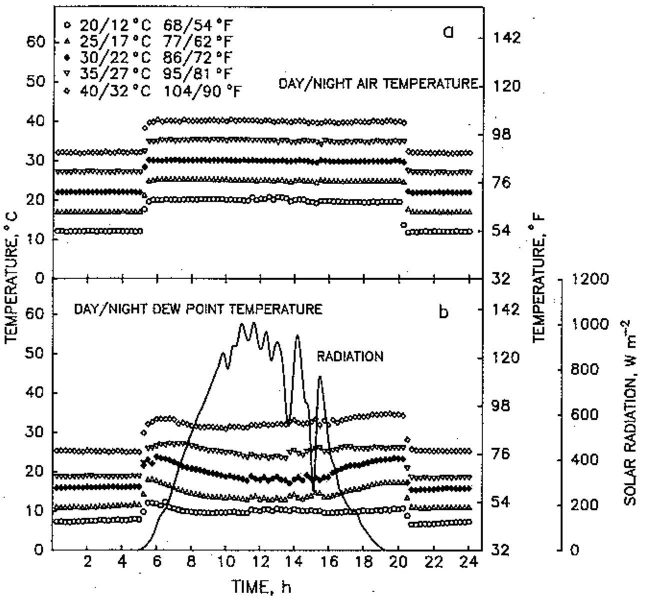

Figure 1. Daily time course of (a) five cabinet temperatures, and (b) dewpoint temperature measurements at various treatment conditions along with solar radiation measurements on a typical summer day. Dewpoint temperature was not controlled, but was the consequence of other factors in the cabinets.

A second type of experiment was conducted by planting seed in polyvinylchloride (PVC) tubing filled with sand or a sand:vermiculite mixture. These tubes were 6 inches in diameter and 26 inches deep. The bottoms of the tubes were sealed except for a 0.5-inch hole at the bottom to allow drainage. Plants grown in pots were arranged in a row configuration. Plants could be moved into the SPAR units where temperature treatments were imposed. Each pot was watered with a "dripper" irrigation system that was connected to a tank of complete nutrient solution. Irrigation was controlled with a computer that opened and closed valves and controlled pumps so that water and nutrients were not limiting. As a result, extremely uniform plants were produced that were transferred into the SPAR units at first flower. Specific measurements and conditions will be described in the context of individual experiments.

Plant Culture and Measurements

Cotton seeds (cv. DES 119) were pre-germinated in moistened paper towels at 82 °F for 48 hours. The imbibed seeds, with radicals emerging, were selected for uniformity and planted in the SPAR units. The seeds were planted in 11 rows of five plants per row in each SPAR unit on July 17, 1989. Fifty percent emergence was observed 4 days later. Six rows of plants were harvested 15 days after emergence (DAE) and two rows were removed at 27 DAE to avoid competition for light and to obtain plant growth measurements, leaving three rows with 15 plants m^{-2} until 56 DAE. Harvested plants were dissected, dried, and weighed to provide short-term dry matter accumulation rates. At each harvest, lengths and areas of all mainstem leaves, and total branch leaf areas were measured. Leaf area measurements were made using an automatic leaf area meter (Hayashi Denko Co., Tokyo, Japan). Individual mainstem leaf areas were estimated nondestructively during the experiment by measuring the distance from the point of petiole attachment to the leaf tip of the center lobe. These values were correlated with measured leaf areas taken on leaves of different ages at each harvest with an automated leaf area meter. The relationship between leaf length and area was determined and nondestructive measurements were converted to leaf areas. At the final destructive harvest, 56 DAE, the rooting medium in the soil bins was removed, and the roots were washed, dried, and weighed.

Plant heights, node numbers, and leaf lengths were measured or counted on nine plants at daily or weekly intervals, depending on the experiment. Stem lengths were estimated as the distance between the cotyledonary node and mainstem apex. Days from emergence to squaring and flowering were determined by tagging squares and flowers at their appearance. Square appearance was determined when they were about 3 to 4 mm (1/8-inch) in length.

Stoneville 825 (ST 825) seeds were planted outdoors in PVC pots containing a sand-vermiculite mixture. The plants were well watered and provided adequate nutrients three times a day with an automated dripper irrigation system. Five days prior to blooming, plants were selected for uniformity and placed in the SPAR units. At initial bloom, the SPAR units were set for 20/10 °C, 25/15 °C, 30/20 °C, 35/25 °C, and 40/30 °C, approximately equivalent to 68/50 °F, 77/59 °F, 86/68 °F, 95/77 °F, and 104/86 °F, (day/night) and maintained at those temperatures for 49 days. Other measurements and conditions were similar to those described previously. The growing conditions before and during the experiment are shown in Figure 2.

Results and Discussion

Plant Height and Mainstem Development

Figure 3A shows plant heights of cotton (cv. DES 119) seedlings from emergence to 56 days after emergence (DAE) grown at different temperatures. The average solar radiation during this experiment was 485 Langleys per day. Typical monthly average daily

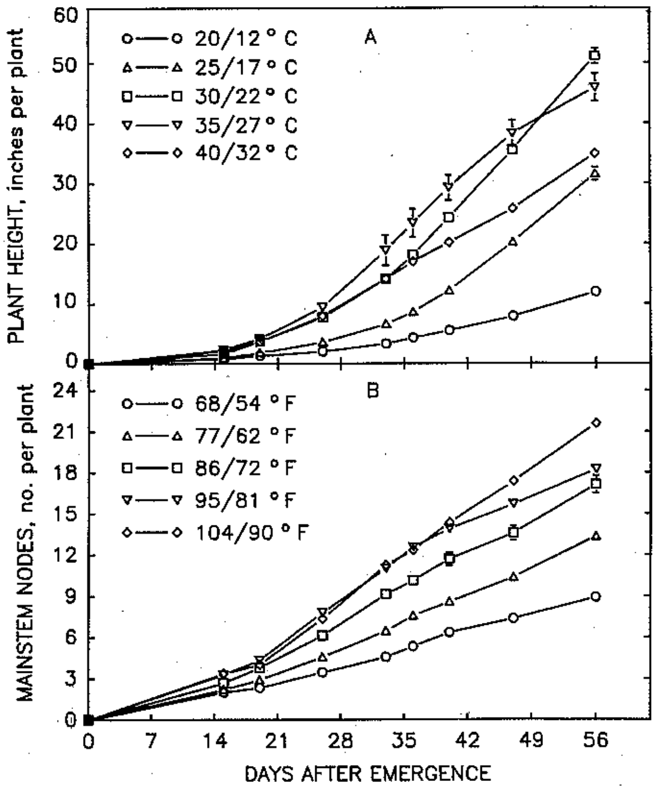

Figure 3. Effect of temperature on cotton (a) plant height and (b) mainstem nodes during early season growth. Standard errors of the means are provided where they are larger than the symbol size.

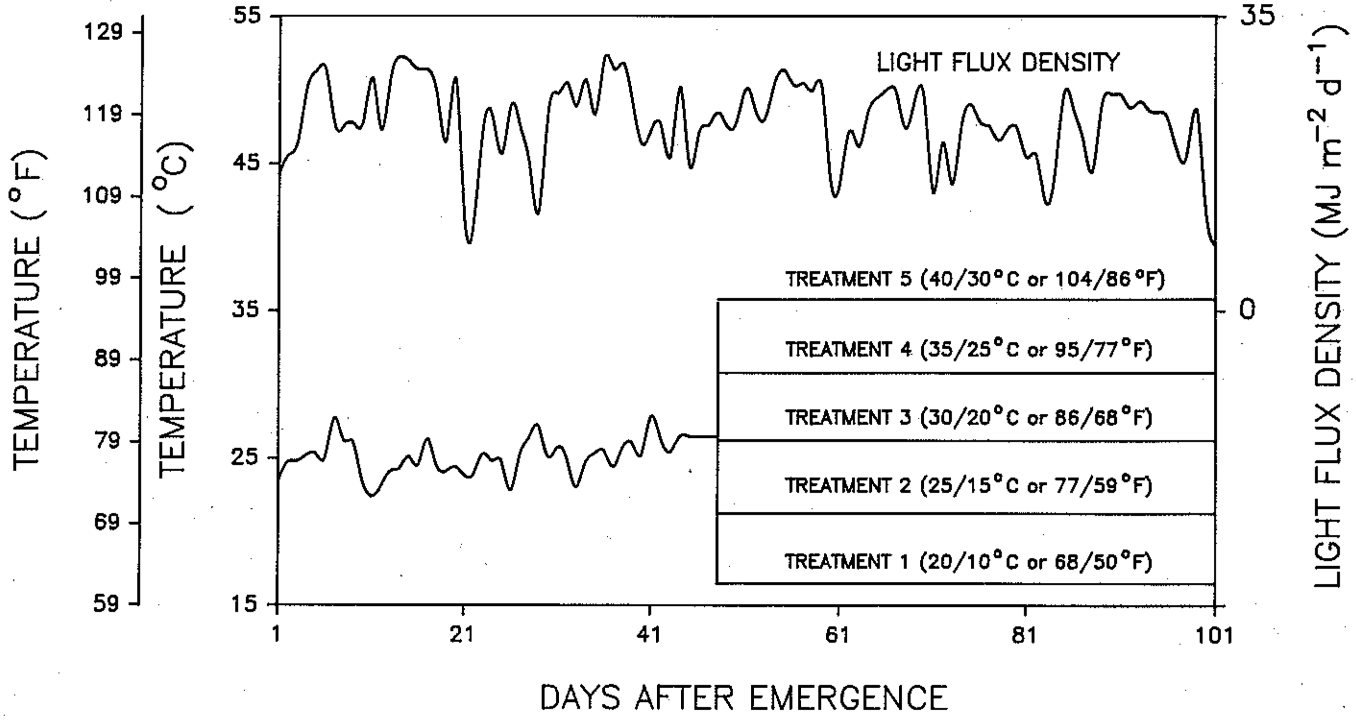

Figure 2. Average daily temperature and solar radiation levels on experimental cotton plants (cv. ST 825) before and during the course of the experiment.

Table 1. Typical monthly average daily solar radiation values for Starkville, MS.

Month	Langleys
April	506
May	622
June	574
July	480
August	496
September	358
October	338
November	252

solar radiation values for Starkville, Mississippi, are shown in Table 1. The soil was a clay loam textured soil with approximately 1% organic matter that was sterilized with methyl bromide prior to placing it into soil bins to avoid nematode infection. Plants grown at 68/54 °F (day/night) reached only about 12 inches in the 56-day period. At 47 DAE the plants were progressively taller as temperature increased except for those grown in 104/90 °F.

Mainstem nodes and leaves were added progressively faster as temperatures increased to 104/90 °F (Fig. 3B). At 56 DAE, plants grown at 95/81 °F had twice as many mainstem nodes as those grown at 68/54 °F, and those grown at 104/90 °F had even more nodes. Average mainstem-node addition rate of early season cotton (Fig. 3B) increased in a linear fashion from 68/54 to 104/90 °F. Mainstem node additions during fruiting were similar to vegetating plants grown in similar temperatures to 95/81 °F, but their rates of node additions decreased at higher temperatures. Pima cotton (cv. S-6) was compared in a similar way and was found to add nodes even faster as temperature increased (Reddy et al., 1992b). Early-season Pima developmental rates responded to temperature very similarly to early-season Delta-type cotton. Average node addition rate varied during the time course of the experiment (data not shown). Nodes were added from 0.1 node per day at 68/54 °F to slightly more than 0.2 node per day at 95/81 °F, during the first 19 days after emergence. The other periods had node additions at about 0.2 node per day at 68/54 °F and about 0.4 node per day at 104/90 °F.

Mainstem elongation rates were summarized over several-day intervals and, plotted against weighted average daily temperature (Fig. 4A), showed only about 0.2 inch per day during the first 19 days. During the second 2-week period (20 to 33 DAE), the temperature optimum was about 82 °F. The temperature optimum decreased as the plants aged, with plants adding nearly 1.6 inches per day at 77 °F in the 34-47 DAE and 48-56 DAE periods. Plants growing at 77 °F and 82 °F developed more rapidly and were producing flowers and fruit during these measurement periods. The slower stem elongation rate at 82 °F compared with those at 77 °F during the 48-56 DAE period was the result of fruit competition with stems. Low rates of stem elongation at temperatures between 88 °F and 93 °F were due to high-temperature injury. This slower stem growth was not due to intra-plant competition with fruit, as essentially no fruit were produced at those high temperatures.

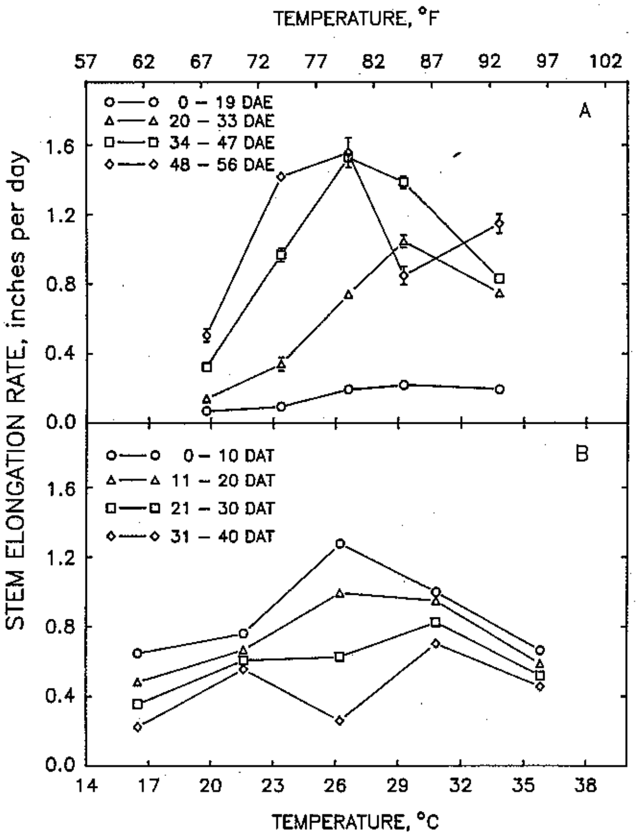

Figure 4. Effect of average daily temperature and age on stem elongation rate (a) cv. DES 119, days after emergence (DAE); and (b) cv. ST 825, days after temperature treatment (DAT); the treatments were imposed at emergence (a) or at first flower (b).

The stem elongation responses of plants introduced to different temperature treatments at the beginning of flowering (Fig. 4B) show that for the first 20 days, the maximum elongation was at about 79 °F. During that period, flowers were being rapidly produced and young growing fruit added. Stem elongation had decreased to about 0.2 inch per plant in plants growing at that temperature. By 31-40 DAT (days after treatment), intra-plant competition due to fruit load reduced stem elongation even more. Plants growing at the other temperatures were producing fruit more slowly and, thus, were less competitive with stem elongation.

Mainstem node additions were summarized for

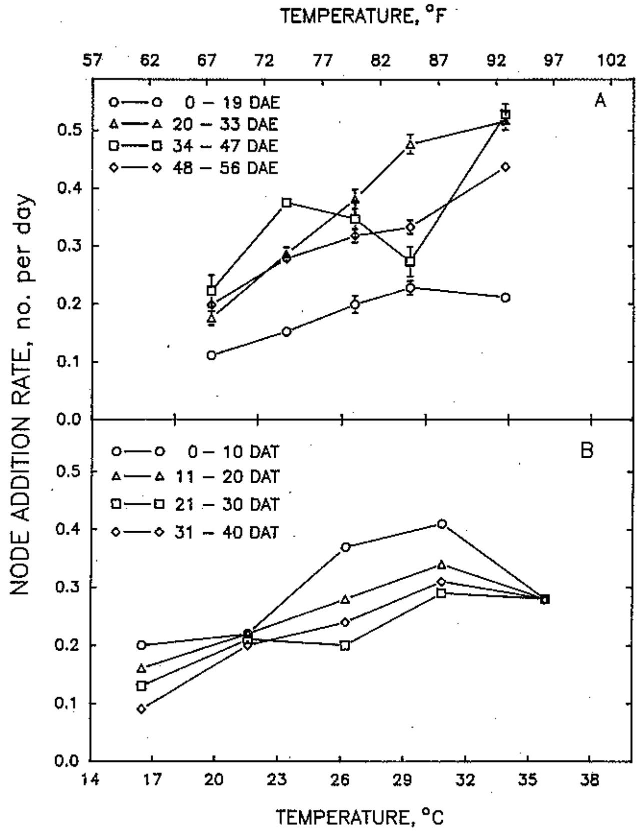

Figure 5. Effect of average daily temperature and age on mainstem node addition rate (a) cv. DES 119 days after emergence (DAE); and (b) ST 825, days after temperature treatments (DAT). The temperature treatments were imposed at first bloom.

plants grown in different temperatures from seedling emergence to early fruiting (Fig. 5A) and for plants grown in the natural environment until first bloom and then had temperature treatments initiated (Fig 5B). The reason for such comparisons is to determine the developmental or growth rates at different stages. Starting the experiment with uniform plants at first flowering allows one to avoid the drastically different growth stages that develop among plants grown at different temperatures from emergence.

Seedling cotton (Fig 5A) added mainstem nodes more rapidly as temperatures increased to about 86 °F during the 0 to 33 DAE period. The node additions were much slower in the 0 to 19 DAE period than in the 20 to 33 DAE period. Plants began flowering by the 34 to 47 DAE period causing node additions at the nearly optimum temperatures to be reduced. Node additions seemed less sensitive to high temperature than was stem elongation. The highest rate of node additions during the first 10 days after flowering occurred at 88 °F (Fig. 5B). The longer flowering plants were exposed to an average daily temperature of 62 °F, the slower they added nodes. Generally, as flowering plants aged, they produced nodes more slowly. However, at the highest temperature (97 °F), plants produced nodes at about the same rate regardless of length of time in that temperature. Most of the flowers aborted at 97 °F so fruit production was not a factor at that temperature.

Branch Formation

The number of vegetative and fruiting branches produced per plant was strongly influenced by temperature (Fig. 6A). Vegetative branches were clearly favored by low temperatures. About five vegetative branches per plant were produced at 68/50 °F on early-season cotton DES 119 plants, while only one or two branches were produced on plants grown at 86/72 °F or above. We interpreted this effect to be the result of growth rate and available energy. At low temperatures, the growth and development rates are slower (Fig. 3A and 3B) allowing lower utilization of available energy. In such an environment, sugars accumulate in plant tissue and encourage or allow the growth of additional vegetative branches. Developing such additional vegetative branches occurs where

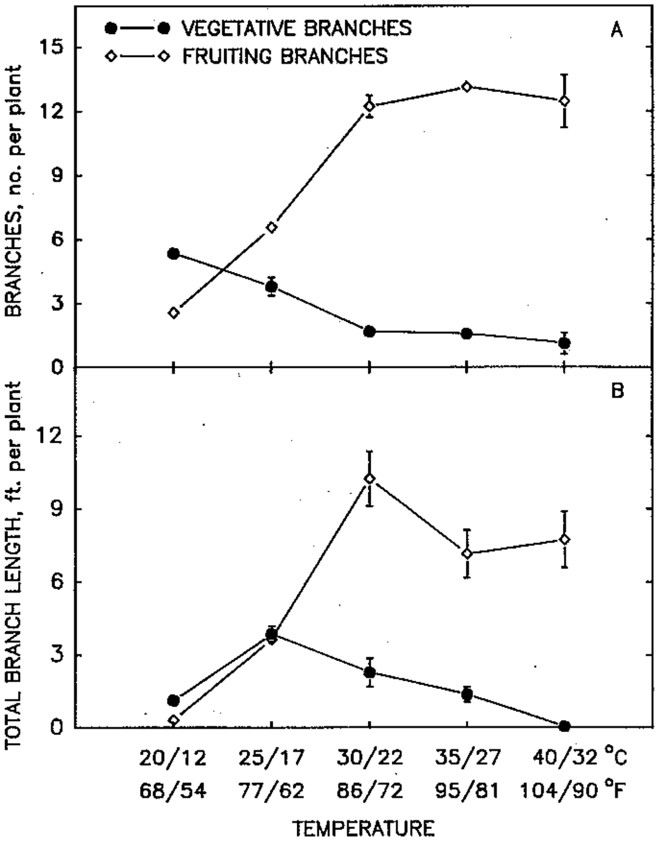

Figure 6. Effects of temperature treatments on vegetative and fruiting branch formation and growth, cv. DES 119, (a) number of branches per plant; (b) total branch length per plant.

stands are thin allowing more sunlight on some plants. Such an environment allows more favorable sugar supplies and consequently more vegetative branches to be produced.

Only about three fruiting branches per plant were produced at 68/54 °F, while 12 or more were produced at 86/72 °F or higher temperatures during a 56-day period. Total fruiting branch length per plant averaged 9 feet at 86/72 °F (Fig. 6B), while at 68/54 °F, total fruiting branch length averaged about 1.0 foot per plant. In a similar experiment, with cv. ST 825, plants were moved into the controlled temperature at first flower. The total fruiting branch length increased as temperature increased from 68/50 °F to 95/77 °F but was less at 104/86 °F (Reddy et al., 1990). Total number of fruiting branch nodes increased as temperature increased throughout the whole temperature range, but total branch length and number of nodes per branch were lower at 86/68 °F (Fig. 6, Reddy et al., 1992a). This was probably the result of more bolls produced on plants at 86/68 °F compared to other temperature regimes.

Leaf Growth

Cotton (cv. DES 119) grown from seedlings at various temperatures produced leaves at drastically different rates depending on temperatures and age of the plants (Fig. 7). We did not detect differences in leaf growth rates at different temperatures during the first 15 days after emergence. From 16 to 27 DAE, leaf growth at 86/72 °F and above was about 8 square inches per plant per day, but was lower at 68/54 °F. Leaf growth rate from 28 to 56 DAE increased linearly as temperature increased from 68/54 °F to 86/72 °F, then decreased linearly as temperature increased to 104/90 °F. About 40 square inches per plant per day were produced at 86/72 °F. During this rapid growth period, leaf growth rates were plotted against temperature for a single leaf of fruiting cotton, cv. ST. 825, (Reddy et al. 1991a). The shape of that curve was almost identical to leaf growth rate shown in Fig. 7. Similar data were obtained for Pima seedling cotton plants grown in a similar manner (Reddy et al. 1992b). Pima leaf growth rate of 40 square inches per plant per day was obtained at the highest rates, but the maximum growth rate obtained was at 95/81 °F instead of at 86/71 °F as for Delta-type cotton. Thus, Pima leaf growth responses to temperature were similar to those of Delta-type cotton except for that higher temperature optimum.

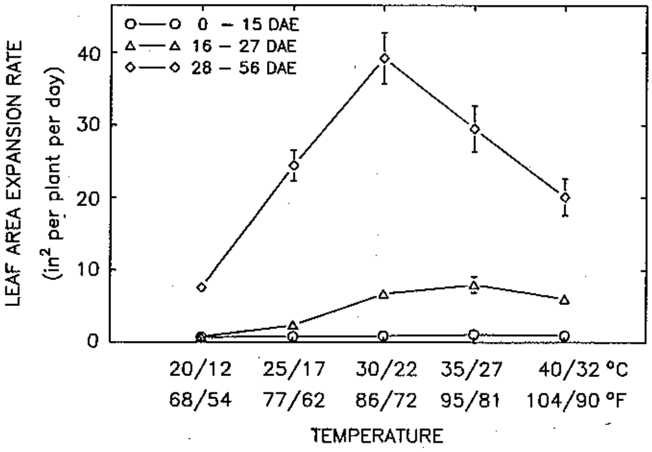

Figure 7. Effect of temperature and age on leaf area growth of cotton (cv. DES 119).

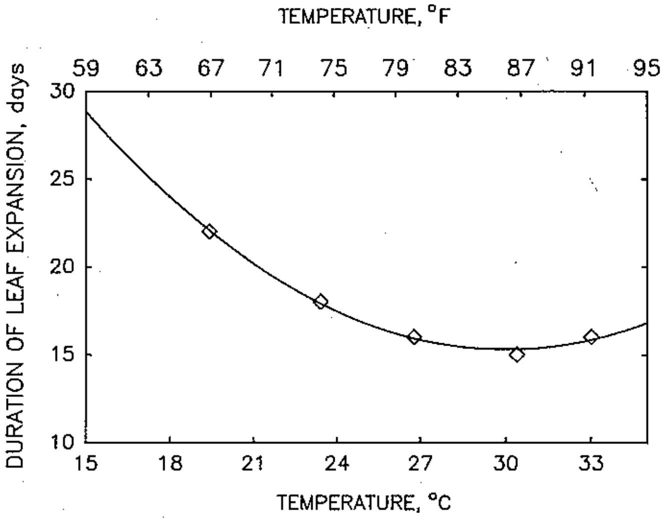

Figure 8. Effect of weighted average daily temperature on the days of linear leaf growth.

Duration of leaf expansion was also strongly influenced by temperature (Fig. 8). Leaf area was measured during the whole growth period, but duration of expansion was estimated during the linear growth phase as the period between 5% and 80% of full size. About 22 days were required for the leaves to pass through that "rapid" rate phase of expansion at 68 °F, but only about 15 days were required for similar leaves to expand at 86 °F.

At 56 DAE, only six leaves had been produced on the mainstems of DES 119 plants grown at 68/54 °F, while plants grown at 95/81 °F had produced 16 leaves on the mainstem (Fig. 9). The larger number of leaves produced at higher temperatures is consistent with the results shown in Fig. 3B and Fig. 5A that illustrate the effect of temperature on cotton mainstem nodes. The final leaf sizes were also affected drastically by the temperature at which the plants were grown. Maximum size of leaf three on plants grown at 68/54 °F was less than 23 square inches, while those grown at 104/90 °F were only about 15 square inches. Maximum leaf sizes were produced at 86/71

°F. Normally only three or four leaves were growing at one time so those data shown for the upper nodes represent immature leaves. Leaf growth rate and leaf size responses to temperature were very similar for Pima cotton (data not shown), except that the highest rate of growth and the most leaf area were produced on plants grown at 95/81 °F rather than at 86/72 °F.

Mature leaf sizes on the mainstem are controlled by the genetics of the plant, the temperature at which the plant is grown, and the availability of essential nutrients and water. In these experiments, all the minerals, nutrients, and water the plant could use were supplied. Mature leaf sizes at any temperature on the mainstem increased as node numbers increased to 9 or 10 and then decreased at higher nodal positions on the plants. Leaf sizes within that general context are also modified by available carbon or how the plant partitions carbohydrates, a limited resource, with other organs (roots, stems, or fruit). Early in vegetative development, more biomass was partitioned to roots than in later stages of development (Fig. 19). After fruit production becomes important, leaf expansion competes with those organs for available carbohydrates.

Reproduction Development

The days required to produce first square from emergence were both temperature- and cultivar-dependent (Fig. 10). The minimum time required to produce first square for DES 119 was about 82 °F (average daily temperature). The cultivar DPL 50 required 5 to 8 more days at all temperatures than DES 119 to produce the first square. Pima cotton, cv. S-6, has nearly equal response for this developmental event as that of DES 119 up to 80°F, but at higher temperatures, the differences between the two species become progressively greater. These data show that pima cotton is less heat-tolerant than Delta-type cotton cv. DES 119.

The equations selected to best fit the data suggested that plants grown at temperatures above optimum required longer to produce squares than at 82 to 86 °F. From these and other data, it seems clear that a major difference among cultivars is the time required to produce first square under uniform conditions.

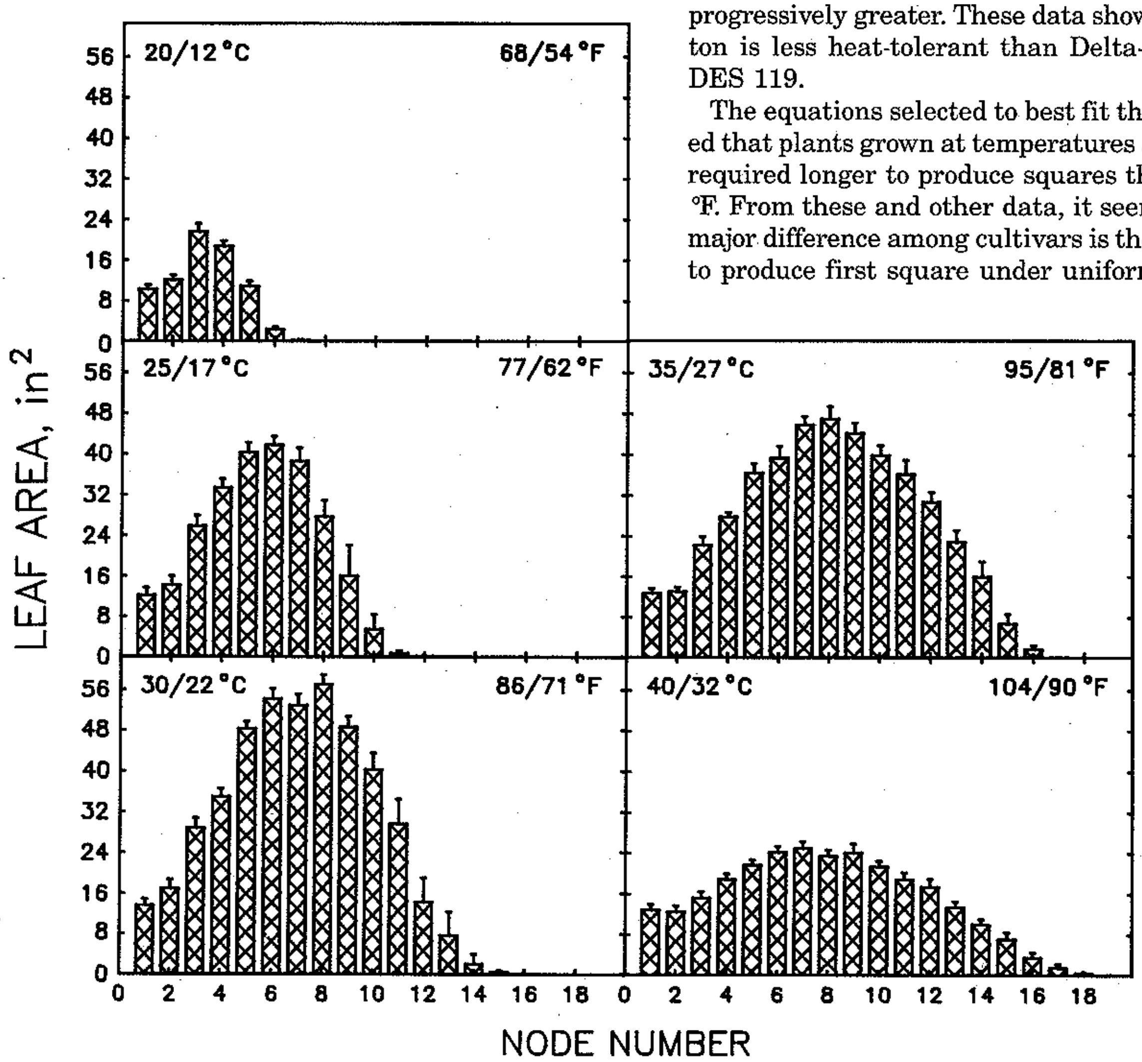

Figure 9. Effect of temperature and mainstem nodal position on leaf size. Standard errors of the means are shown.

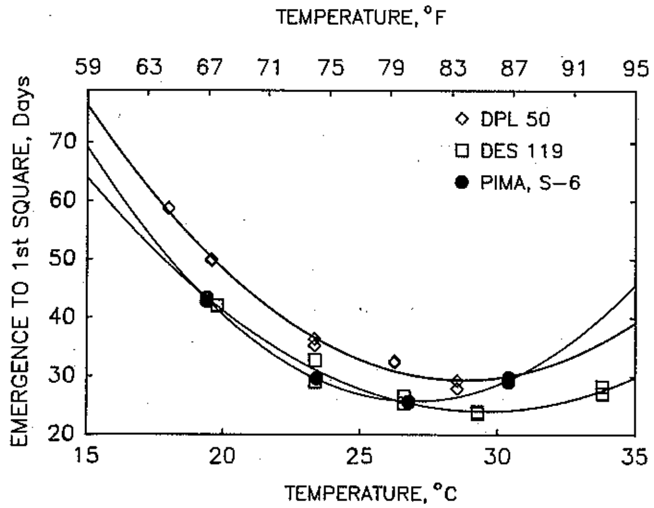

Figure 10. Effect of weighed average daily mean temperature and variety on days from emergence to first square.

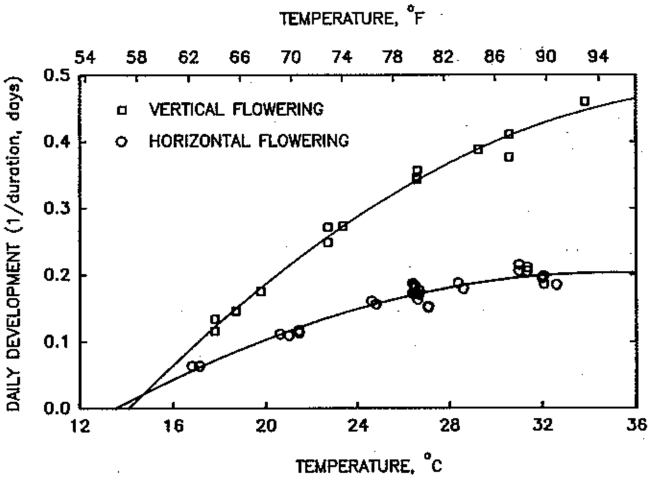

Figure 12. Effect of weighted average daily temperature on the daily development toward the next flower vertically and horizontally. Data include cv. DPL 50, DPL 51, DES 119, and Pima S-6. (Daily development is the number of days required at a particular temperature divided into one.)

Days from first square to first bloom and from bloom to open boll are presented in Figure 11 for several cultivars grown at different average daily temperatures. The solid symbols illustrate the days required from bloom to open bolls at different temperatures. Boll maturation period is strongly influenced by temperature, with the fastest rate of maturation occurring at about 91 °F. Pima requires a slightly longer period from flowering to open bolls. As the average daily temperature decreases below 77 °F, the time required for boll growth increased dramatically. The time between squaring and flowering, or between flowering and open boll, has much less variability among cultivars within species than time for developing first square. Thus, data from several varieties could be pooled to show the temperature responses of time required to advance from square to flowering and from flowering to open boll (Fig. 11).

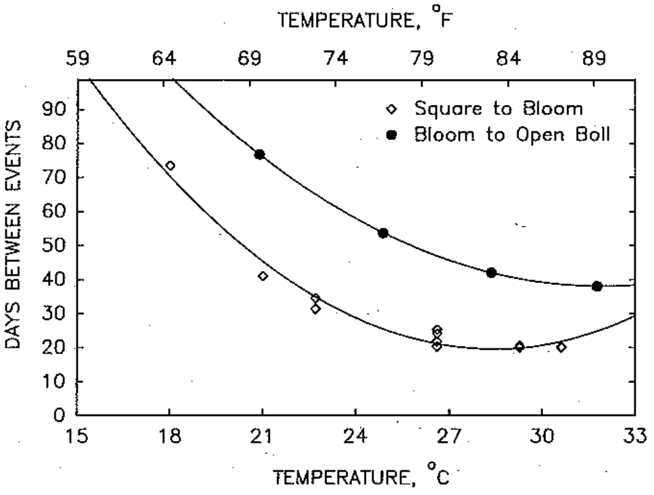

Figure 11. Effect of weighted average daily temperature on days required from square to bloom and from bloom to open boll.

The vertical flowering data (Fig. 12) show the rate of flower additions up the mainstem vs temperature, while the horizontal flowering rates show time between flowers on fruiting branches. These data illustrate the different responses of these processes to temperature, including the curvilinear characteristic of the responses.

The differences among cultivar responses to temperature for these traits were small. Even Pima (cv. S-6) was not different from the three Delta cotton cultivars for which data were available. The differences in daily rates of vertical and horizontal progress toward the next flower were relatively small at low temperature, but the differences were much greater as temperature increased. About 5 days (0.2 daily development) lapsed between flowers on fruiting branches at 86 °F, whereas only about 2.5 days (0.4 daily development) was required between vertical flowers.

Such nonlinear responses point out a serious problem with the use of growing degree days (GDD) to predict biological events. In nonlinear responses, a few days above optimum temperature for a particular process generate many degree days with a relatively small amount of progress toward the biological event (in this case the next flower up the plant or out the branch). A second problem with GDD is illustrated by differences in rates of progress of the two processes at a similar temperature. Obviously, it takes much longer to produce a new flower in the next horizontal position than it does to produce the next flower in the vertical direction.

The use of GDD has been a useful tool to predict certain biological processes and thus identify a time for management decisions. Its limitations should be recognized by users to avoid being misled by the technique. Those limitations are primarily the curvilinear nature of most biological processes and the limited domain in which the process may be safely used.

Fruit Retention

High temperature environments have sometimes been associated with cotton sterility and boll retention problems; however, there is little specific information available on cotton sensitivity to high temperatures. A series of experiments was conducted in the SPAR units where temperature was accurately controlled and its effects on fruiting-site production determined. Also, abscission of squares, flowers, and bolls was observed. In each of these studies, the plants were always well watered and fertilized. The CO_2 in the chambers was kept at 600 $\mu L.L^{-1}$ (well above normal atmospheric concentration) in order to avoid carbohydrate stress, and insects were completely controlled. Thus, the usual factors that are attributed to fruiting structure retention problems were eliminated.

Number of fruiting sites per plant increased approximately 50% as temperature increased from 86/71 °F to 104/90 °F (Fig. 13). The number of bolls and squares retained per plant was essentially the same between 86/71 °F and 95/81 °F, but dropped to nearly zero at 104/90 °F. Very immature squares dropped from their sites of attachment at early pinhead size. This occurred very early in the reproductive period when boll load was essentially zero so carbohydrate was not a factor causing square abscission.

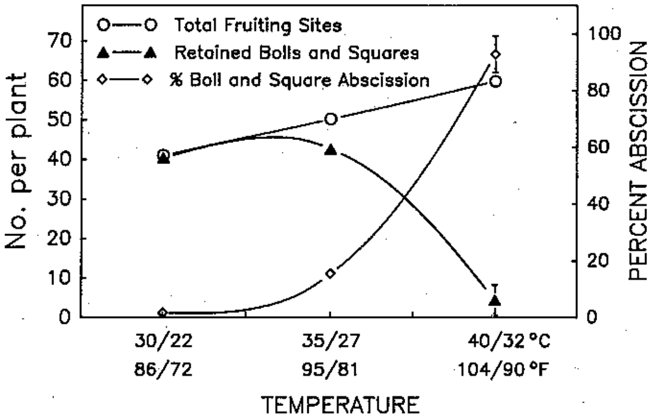

Figure 13. Effect of day/night temperature on fruiting sites produced, bolls and squares retained, and percent boll and square abscission (cv. DES 119).

In other studies, McKinion et al. (1992) and Reddy et al. (1992d) found Pima cotton did not produce fruiting branches or any fruiting organs at 104/90 °F with either ambient (350 $\mu L.L^{-1}$) or double (700 $\mu L.L^{-1}$) CO_2, providing additional evidence that carbohydrates were not limiting.

Reddy et al.(1992b) found Pima cotton plants grown at 104/90 °F did not produce either fruiting branches or squares while plants grown at 95/81 °F retained only about one third as many bolls and squares as plants grown at 86/72 °F. This supports field observations that Pima cotton is more high-temperature sensitive than Delta-type cotton.

It appears that more heat-tolerant Pima cultivars are being developed. Some so-called heat tolerance may be heat escape by fruiting earlier, while other heat-tolerant types have greater transpiration in well-watered environments and maintain an even cooler leaf canopy than the air temperature than other cotton plants. If heat-tolerant types have greater transpiration, as suspected, it would reduce their real plant temperatures in damaging hot environments, but such types would also require more water.

In the experiment in which temperature treatments were imposed at first flower formation, Stoneville 825 plants grown at 86/68 °F produced 36% more dry weight than those grown at 68/50 °F (Table 2). Weight gain was only 52% as much at 104/86 °F compared to plants growing at 86/68 °F. Boll weight was greatest at 86/68 °F. Boll growth was drastically more temperature sensitive than vegetative growth. The low boll weights produced at 68/50 °F and 77/59 °F reflect slower development and fruit growth rates at those low temperatures; however, low boll weights at 95 °F and 104 °F (day time) were due to low boll retention.

Table 2. Effect of temperature on cotton growth, cv. Stoneville 825, harvested 49 days after initiation of temperature treatments. Treatment was imposed at first flower. Standard error of the mean values are shown.

	Day/Night Temperature, °F				
	68/50	77/59	86/68	95/77	104/86
	.... g per plant				
Total weight	242±10.0	320±3.6	330±14.8	293±4.9	225±3.1
Weight gain during experiment	133	211	221	184	116
Bolls	17.4±2.4	62.7±26.5	143.3±2.4	16.7±11.3	0.8±0.1

Meyer (1969) reported that homozygous male-sterile cotton plants produced nearly 100% sterile anthers if maximum temperature exceeded 90 °F each day. However, this was a Mississippi Delta field study in which there was considerable day-to-day variability in conditions and the length of period at high temperature was not reported. Apparently, Meyer found that some of the genetically homozygous male-sterile plants produced some fertile anthers in cooler environments. She reported that the heterozygous plants became sterile in some, but not all, cytoplasmic backgrounds near 100 °F maximum daily temperature. She also found a negative relationship between maximum daily temperatures and plant fertility with an interval of 15 to 16 days between the time of high temperature and the expression of fertility.

In one of our experiments, plants were exposed to 95 °F for 12 hours at several different times of the day to determine if high temperature at the time of pollen shed was causing sterility. The time of day at which the plants were exposed to 95 °F did not influence boll retention.

In another experiment, plants were exposed to 104 °F for different periods per day. The hours of the high temperature treatment were equal on either side of solar noon. Both boll number and boll mass were dependent on the length of time per day to which the plants were exposed to 104 °F (Fig. 14). All the bolls and flowers were removed from the plants on the day the plants were first treated with 104 °F conditions, so the numbers represent the total bolls produced and retained during the experiment. These plants were grown at lower temperatures prior to imposition of the 104 °F for some portion of the day so fruiting branches and squares of various ages were on the plants at the start of the high temperature treatments.

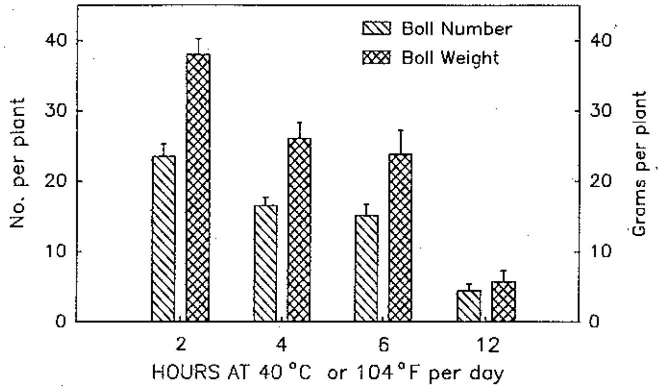

Figure 14. Effects of time per day at 104 °F on boll number and total boll weight after 21 days. Temperature was at 80.6 °F except when at 104 °F.

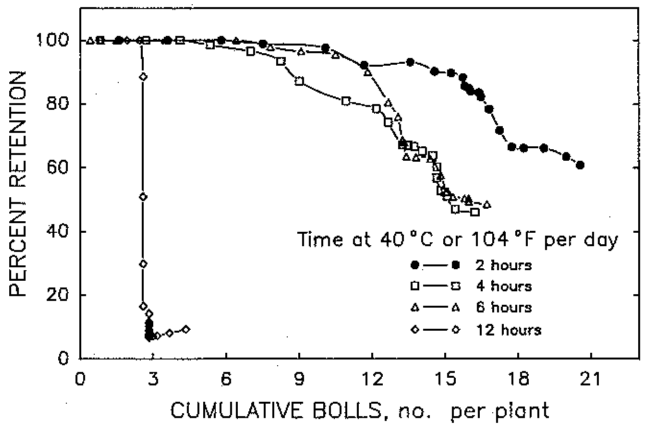

Figure 15. Effects of time per day at 104 °F on boll retention. Temperature was 80.6 °F except when at 104 °F.

Bolls abscised within 3 days after flowering if plants were exposed to 104 °F for 12 hours per day, while bolls exposed to the high temperatures for only 2 hours per day remained on the plants for about 6 days (data not shown). There was a linear decline in the time bolls remained on plants after flowering as the length of exposure to 104 °F increased.

Exposure of cotton plants (cv. DPL 50) to 104 °F for 2 hours per day resulted in plants retaining essentially 100% of their bolls until approximately 10 or 11 bolls were on the plants (Fig. 15). Percent boll retention then decreased rapidly to about 60% by the time 20 bolls per plant had been set. Plants exposed to 104 °F for 4 and 6 hours per day began having a lower retention rate when fewer bolls were on the plants. By the time 15 bolls per plant were set, those plants treated at 104 °F for 4 to 6 hours per day retained only about 50% of the new bolls produced.

Plants treated with 104 °F for 12 hours per day retained no bolls. The data as presented show three bolls per plant remaining, but in fact those were the last bolls formed before the experiment was terminated and they simply had not been present long enough (3 days) for abscission to occur.

The effect of high temperature on cotton flowering and boll retention has been observed for several years, but no one has attempted to quantify the impact of specific high-temperature conditions. Causes of boll abscission are often confounded with other factors, such as insect damage, boll load, or water and nutritional stresses. These factors were essentially removed as uncontrolled variables in these studies. The biological causes of reproductive failure in high temperature are still not known, but the consequences are clear and quantifiable. Surely this is an area of research that needs further study, and selection for heat-tolerant types is a desirable objective in plant breeding programs.

Photosynthesis and Respiration

The solar radiation and average temperature conditions prevailing during the growth of plants for which photosynthetic measurements are discussed are shown in Figure 2. Plants were grown in the natural environment until nearly first bloom, then placed in the SPAR units where various day/night temperature treatments were imposed. The average daily temperatures are shown as straight lines in the figure indicating the average daily temperatures inside the cabinets. Plants were maintained in a well-watered and fertilized status during the entire growth period. Plants were kept at 340 μL.L^{-1} CO$_2$ while in the SPAR units. Radiation was measured above and below the crop canopy continuously in each SPAR unit and those values summarized over 15-minute intervals. This allowed us to estimate light interception by the plants each day. There was a full canopy from the beginning of the experiment, with 98% of the visible light intercepted by the crop. Plants' photosynthesis process is sensitive to essentially the same wave lengths of the solar radiation spectrum as is the human eye.

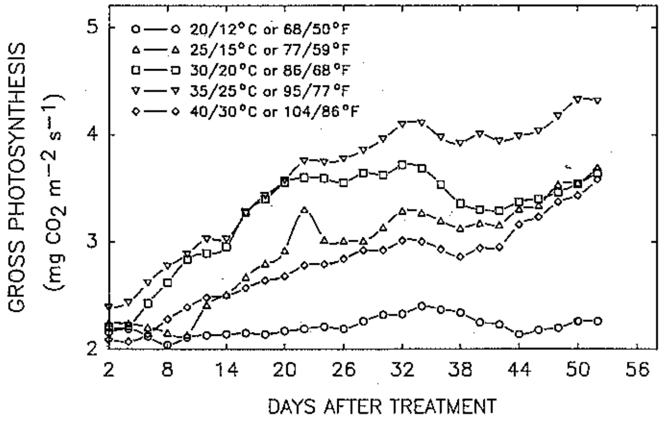

Figure 17. Effect of temperature and days of temperature treatment on gross photosynthesis calculated at near midday summer sun (1,600 μmol per m^2 per second).

Plant responses to temperature, light, and age are shown in Figure 16. Two days before the treatments were imposed, essentially all the plants responded to light in the same way. As the plants remained in the temperature treatments for a longer period, the pho-

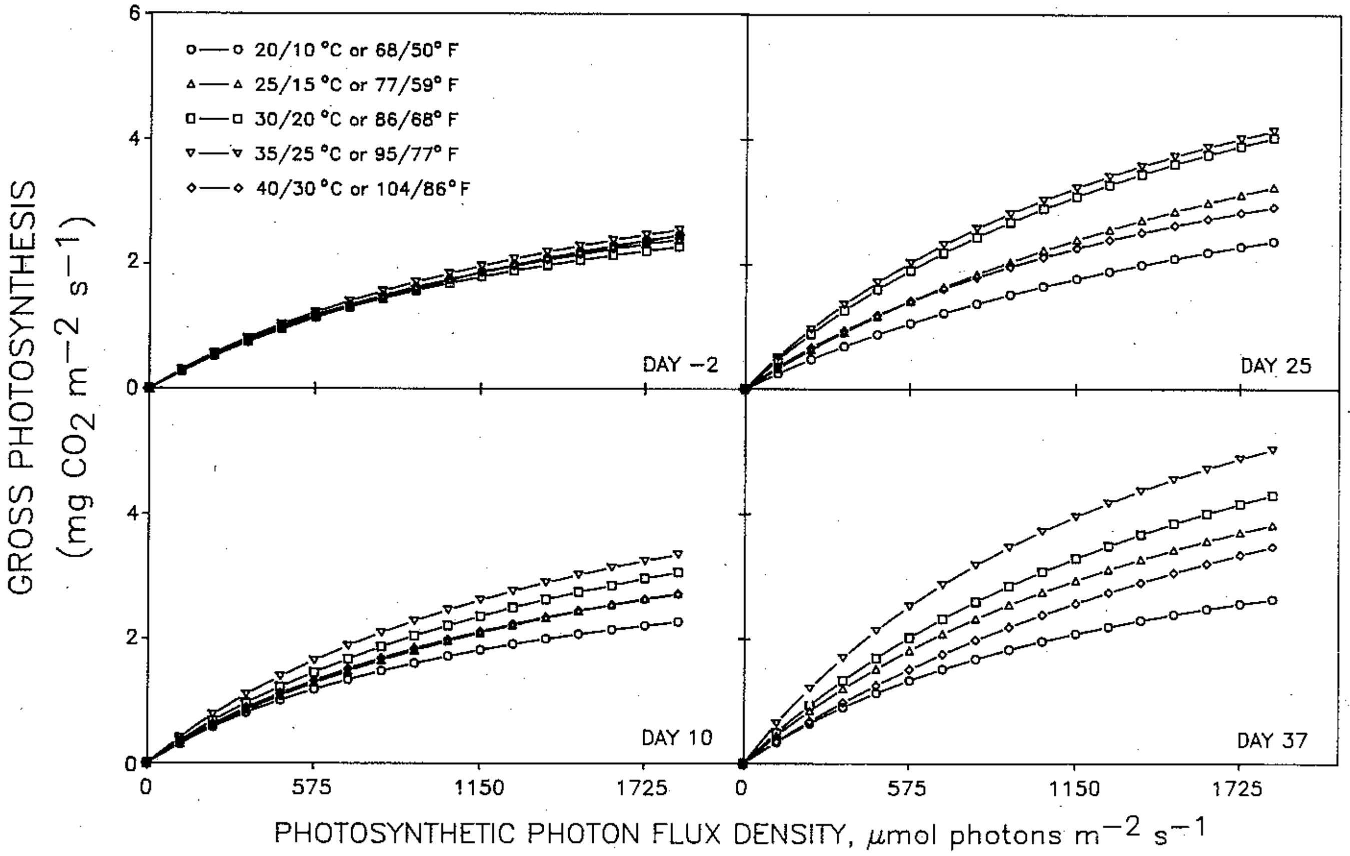

Figure 16. Effect of temperature, time of plant exposure to particular temperature after flowering, and light level on gross photosynthesis of cotton plants. Gross photosynthesis = New Photosynthesis + Respiration.

tosynthetic responses became greater. Plants growing at 68/50 °F consistently had the lowest rates of photosynthesis. The highest rates of photosynthesis measured were by plants grown at 95/77 °F. Plants growing at 104/86 °F typically fixed CO_2 more rapidly than plants growing in 68/60 °F, but less rapidly than plants growing at any of the other temperatures. These results are consistent with the dry matter accumulation results (Table 2).

If the photosynthetic rates were normalized by expressing the average rate of CO_2 fixed at 1,600 μmol photosynthetically active radiation per m^2 per second (a value close to maximum midsummer daily radiation values) for each day (Fig. 17), one can see that photosynthesis increased with age during the fruiting period; except for those plants growing at 68/50 °F. Plants at 68/50 °F grew so slowly that the average age of the leaves in the upper canopy was becoming older. In the other temperatures, however, the rate of leaf additions was sufficiently rapid that the upper portion of the canopy continually had young leaves intercepting the major portion of radiation.

The reason for continually increasing rates of photosynthesis by plants in the four highest temperatures is subject to speculation. We believe that photosynthesis rate is controlled, in part, by internal plant factors related to growth, as well as by environmental factors. The SPAR units each had a full plant canopy at the beginning of the experiment so the increasing rates of photosynthesis were not a function of light interception.

The notion that growth partially controls photosynthesis is important in order to understand the overall crop responses to environmental conditions. Clearly, temperature, radiation, water, and nutritional status of the crop are all important elements controlling photosynthetic rates; however, the rapidly growing crops in similar conditions on day 2 had only about 50% as much photosynthesis as on day 37 (Fig. 16). This idea is fairly well documented in the literature for other species; but it is not understood by many people, nor has it been documented prior to these studies that cotton has this characteristic.

Respiration, the energy plants use to drive various growth and metabolic processes, varied from about 6% to 17% of the photosynthesis rates. The lowest respiration rate occurred at low temperatures because respiration is clearly a temperature-sensitive process, and because at low temperatures there is slower growth resulting in less respiring biomass. Respiration that occurred at nighttime temperature was consequently lower than that which occurred at daytime temperature (measured immediately after sunset). The amount of sugar available to support respiration of leaves and other organs is considerably greater early in the evening than later in the night (Hendrix and Granger, 1991). The availability of more sugar seems to control respiration rate and probably impacts growth rate. Thus, the control of growth, photosynthesis, and respiration is complex with one plant process impacting the other processes. Environmental conditions may limit one process, which indirectly results in other processes also being affected. This will be illustrated more clearly later.

Roots

Cotton seedlings typically grow very slowly. This low rate of growth is considered a production problem. Therefore, to compensate for low crop vigor, experienced producers use cultural practices, such as waiting to plant until the soil is warm, until the probability of low temperature is suitably low, and until preparation for good early-season weed control is com-

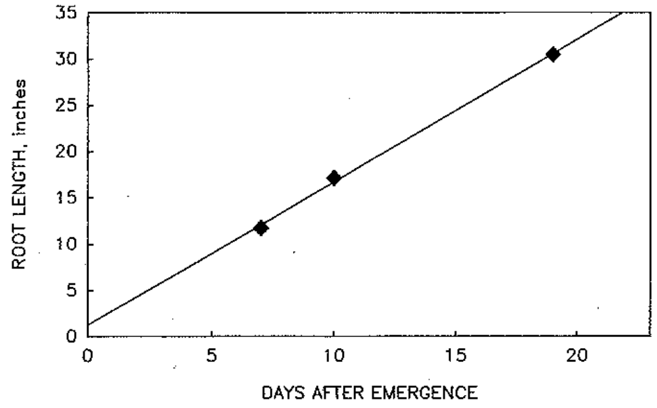

Figure 18. Effect of age on taproot length in a sandy, well-watered soil.

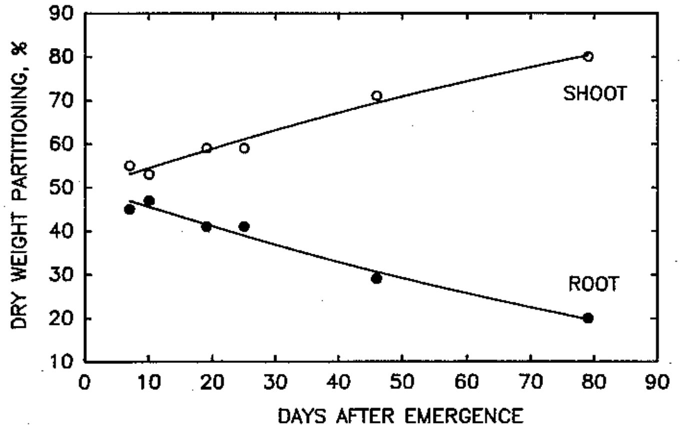

Figure 19. Effect of age on cotton plant partitioning of mass between the root and shoot.

pleted before planting. Part of the reason for slow apparent growth of cotton seedlings is the way the plant partitions early season growth.

Seedlings were planted in PVC pots filled with sand and growth was measured at different intervals after emergence. The plants were well watered and fertilized throughout the study. The growth of the taproot increased linearly from 7 to 19 DAE, (Fig. 18). At that time, the taproot reached the bottom of the containers so length measurements beyond that time were not meaningful. There were only two nodes on the plants at 19 DAE and the cotyledons were still the primary source of photosynthesis on the plants. The partitioning of dry matter between the roots and the above-ground parts was almost equal soon after emergence (Fig. 19). As the season progressed, a continually smaller proportion of the total plant dry weight was partitioned into the root fraction. At 80 DAE, the roots only represented about 20% of the total mass; whereas at 7 DAE, the roots represented about 45% of the total mass.

Root measurements of other crops have shown that most of the root growth occurs early in the growing season. Mengle and Barber (1974) found that corn roots increased length linearly from emergence until about 2 weeks after pollination (the time linear increase in grain dry matter accumulation began), then declined throughout the grain-filling period. That work has been interpreted to mean that grain production had priority for available carbon. Consequently, root length declined because of insufficient carbohydrate resources available to support root respiration and growth. Normal root sloughing, combined with low growth rates, resulted in an actual decline in root length during the grain-filling period. Other studies suggest that cotton plant roots are opportunistic. If conditions are favorable for growth and food resources are available roots grow rapidly, but if food resources are limiting root growth will be limited first.

Partitioning Biomass

Cotton plants are not only sensitive to their environment but also have intra-plant compensating factors controlling the way resources are used. It was previously shown that early in the season, nearly 50% of the plant's dry matter is found in roots, but as the season progresses, the percentage dry matter in the root decreases. At maturity, there is only about 10% in roots (Reddy 1991a).

The temperature at which plants grow also affects the ratio of material designated for different plant parts (Fig. 20). Plants (cv. ST. 825) that had been exposed to different temperatures for 49 days during their fruiting period allocated drastically different amounts of dry matter to fruiting structures. Plants grown at 95 °F and 104 °F (day) produced little fruit, presumably due to a small number of fruit set, and those grown at 68 °F and 77 °F (day) only allocated between 10% to 15% to fruiting structures. Similar plants growing at 86/68 °F allocated about 40% of their production to fruiting structures. Those same 86/68 °F grown plants produced less root, stem, and leaf mass. Plants growing in high temperatures allocated more biomass to stems, leaves, and roots because of fewer bolls retained at these high temperatures.

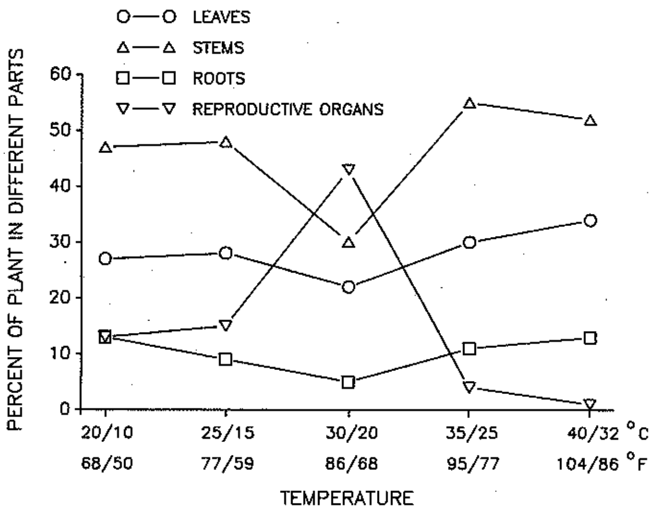

Figure 20. Effect of temperatures on mass partitioning among different plant parts.

In other experiments (Ben-Porath and Baker, 1990), where root volume was very restricted but where adequate nutrients and water were maintained, the total root mass was reduced. A compensatory amount of growth occurred in developing fruit, however. In that situation, less taproot was produced, but a larger number of fine roots was added to the plants growing in small containers. There is some evidence that extensive root growth is a vital part of overall plant development. The implication is that growth regulators produce in the roots enhance above-ground growth. Such an interaction of growth rates among different plant parts has caused some to hypothesize that plant growth regulators, such as PIX, or herbicides may be used to manage stem growth.

In addition to modifying the way available resources are allocated among different structures, rapidly growing plants produced more dry matter via greater photosynthesis (Fig. 16 and 17). Such an endogenous control of photosynthesis must have regulatory control by some means. It has been widely assumed that such control is mediated by the removal of recently produced products of photosynthe sis to support rapid growth. However, that is difficult to prove and is disputed by some.

Hendrix and Granger (1991) showed that nighttime exports of sugar from leaves and nighttime leaf respiration were closely correlated with leaf starch content at the end of the day. This suggests that nighttime respiration is dependent on starch accumulation during the day.

From other data (Coggeshall and Hodges, 1980) it seems reasonable to infer that nighttime respiration is also dependent on growth rate. Thus, it seems likely that linkages between growth, respiration, and photosynthetic rates exist causing complex interrelationships among these processes. Whether natural plant growth regulators are involved or not is still not clear.

Summary

Crops grow under diverse weather, soil, and cultural practices and it is often impossible to know what factor is limiting at any particular time. Many weather elements vary simultaneously, which further complicates interpretation of field conditions. Furthermore, after years of agricultural research and numerous field experiments, we still cannot quantify completely crop responses to various physical and soil variables, and to interactions between them.

Fortunately, now we have simulation models that incorporate our understanding of how each environmental and soil factor affects essential processes in the system. The rapid calculations made by modern computers make it feasible to more successfully estimate field conditions on a daily or hourly basis, and more importantly, to predict plant responses to those conditions. The cotton crop model, GOSSYM-COMAX is an endeavor in that direction and has proven a valuable tool for helping producers estimate their crop's condition and to predict the crop's responses to various real or hypothesized practices. By running the model with varying cultural practices, soil, and weather conditions, model users gain insight into the way crops respond to changing physical conditions. This additional understanding enables producers to become better crop managers.

As we extend the information on which the crop model is based, we also gain understanding of the crop's responses to various physical conditions. This report summarized several experiments in which the effect of temperature on cotton was the primary focus. In all cases, care was taken to avoid water and nutrient deficits or stresses caused by insects or diseases. In several experiments, the plants were grown in a high-CO_2 environment to avoid carbohydrate deficits and thus allow the data to be interpreted as purely potential plant responses to temperature.

The temperature optimum for stem and leaf growth is about 86 °F. Temperature responses of seedling and fruiting cotton are very similar. There is considerable information on developmental processes (as contrasted to growth) responses to temperature. These include rates of node formation, days to first square, first bloom, and open boll, as well as comparisons of flowering vertically and horizontally on the plant. Of the various developmental processes, there is more variation among cultivars for time required to form first square than for other traits.

The effects of high temperature on fruit abortion were quantified in the absence of water and nutritional deficits, and the damaging effects of insects. Fruit retention decreased rapidly as time of exposure to 104 °F increased. Evidence was presented that shows growth activity in one plant part strongly influences activity in other parts. Photosynthesis was much greater in rapidly growing plants. Respiration and growth appeared to be closely linked and mutually dependent. Emerging seedlings partitioned nearly 50% of their dry weight into roots, whereas mature cotton plants had only 5 to 10% of their dry weight in roots. Leaves and stems received most of the dry matter produced from 3 weeks after emergence until soon after first flower. After that, most of the growth was allocated to developing bolls with little going to the synthesis of new roots or leaves and stems. The amount of food allocated to these various plant parts was strongly influenced by temperature.

Hopefully, this report will provide better understanding of the growth and physiology of the cotton plant and help producers become better crop managers. The information is also being used to expand and enhance the value of the cotton crop model, GOSSYM-COMAX.

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