PHOTOSYNTHESIS AND ENVIRONMENTAL FACTORS

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Abstract

The relation between photosynthesis and environmental factors is presented. Here, we report the results from cotton plants grown in naturally-lit plant growth chambers in which temperature, CO_2, water, and nutrients were controlled and varied systematically. Photosynthesis of crop canopies was measured continuously along with other related vegetative growth parameters and abiotic variables. Photosynthesis is the driving process of dry matter production, but factors affecting vegetative growth and development are important aspects of cotton production. Canopy photosynthesis is not light saturated in Midsouth radiation environments. Present-day cropping practices allow the crop demand for photosynthates to occur during declining solar radiation. Current atmospheric CO_2 levels are limiting cotton production, and rising CO_2 will benefit cotton growth and yield. Temperature has a small effect on canopy photosynthesis and thus primary production is sustained in a wide range of temperatures. Temperature however, strongly influences vegetative growth and development and thus light capture during the vegetative period, and light conversion efficiency during much of the boll-filling period. Temperature above 28°C limits both vegetative growth and more importantly boll retention or sink capacity. Water, nitrogen and potassium deficits decrease leaf growth more than photosynthesis. Thus, crop production is a function of many processes from cellular to canopy levels. Increasing production and yield requires knowledge of processes at all levels.

Introduction

The U. S. cotton industry is under increasing pressure to survive competition from world supplies. The price of cotton is continuously hitting a ceiling above which causes millers to switch to other fiber sources. Production costs continue to increase, and producers are in a never-ending battle to contain or reduce expensive economic inputs. These forces, containing upper limits on the price producers can receive for their cotton crop and growing production costs, squeeze the profitably from cotton production. They cause the producer to examine all aspects of production and try to determine a more efficient way.

More efficient production methods may lie in the area of increasing crop yields rather than hammering production costs even more. We should examine the production potential of the crop and then attempt to determine the reasons that potential is not being met. It may even be possible to increase production without necessarily increasing costs by identifying the causes of potential yield losses and eliminating those causes. Recent studies have examined the cotton production potential and found some unexpected results.

Are Temperature and Solar Radiation Coupled in the Midsouth?

The long-term daily average temperature and total solar radiation received at Stoneville, MS is shown in Fig. 1 to illustrate the seasonal trends of these weather variables as they relate to cotton growth requirements. From previous controlled-temperature studies, we know that the minium temperature for cotton growth is about 15°C, and the optimum temperature for growth is about 28°C. The long-term daily average temperatures do not exceed the optimum temperature for cotton growth. It appears that we may need a modified production scheme that provides a well-developed canopy earlier in the season to utilize the available solar radiation that is associated with the solar solstice. That might be attained by having varieties that would tolerate and grow as seedlings at cooler temperatures or a modified planting environment that provides warmer early-season conditions.

A production problem in the Midsouth is having sufficient length of growing season. Both the beginning and ending of the growing season are limited by low temperatures. Planting cannot begin until soil temperatures are sufficiently warm that seedlings will emerge rapidly. At the end of the season, temperatures typically decline as illustrated in Fig. 1. Essentially no growth or development occur at temperatures below 15°C (Reddy et al., 1996a, 1997a). Some producers have attempted to provide a more suitable environment for planting earlier by covering seedlings with plastic. This practice has not been researched in the USA, but it is being used advantageously to extend the front-end of the growing season in other places.

What Is the Genetic Potential of Cotton and How Can We Estimate the Potential?

Research in the USDA-ARS crop simulation unit at Mississippi State University set out to determine potential cotton yields several years ago by eliminating many of the usual limits to production. Cotton was produced in closed, transparent chambers that kept insects and diseases out and provided an abundant supply of nutrients and water. Unexpectedly high production can occur in such an environment (Reddy et al., 1995, 1997b).

The chambers are clear Plexiglas so natural radiation is similar to that received by field-grown crops. An experiment in 1995 controlled temperatures to match outdoor

temperatures in one set of chambers, while other chambers were controlled at the outdoor temperatures minus 2°C, or plus 2, 5 or 7°C. This resulted in a series of diurnally and seasonally varying temperatures that matched in parallel the naturally occurring field temperatures. The cotton crop produced 9 bales per acre in the chambers maintained at the 1995 temperatures with other variables not limiting. This is approximately 3 times the yields we can obtain in Mississippi under good field production situations. Therefore, it deserves some analysis of the causes for the differences between production potential and actual field production. We place emphasis on photosynthesis in this report because it is the primary process driving production, although we will discuss other factors that may limit growth.

Materials and Methods

Climatology Data

Long-term (42-year) average daily temperatures were obtained by summing daily maximum and minimum temperature and dividing by two and long-term mean solar radiation were extracted from Boykin et al. (1995) for Stoneville, MS.

The Naturally-Lit Plant Growth Chambers

The results described in this paper 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, yet 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. These chambers provide canopy growth rates by continuously monitoring and integrating CO_2 and water fluxes to explore the limits cotton productivity.

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 (Reddy et al., 1995).

Temperature Studies

This temperature experiment was conducted to determine the effect of temperature on flower production, retention, and growth. 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 2°C (3.6°F), (b) 1995 ambient, (c) 1995 ambient plus 2°C (3.6°F), (d) 1995 ambient plus 5°C (9°F), and (e) 1995 ambient plus 7°C (12.6°F). 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.

Although atmospheric CO_2 concentration is not a variable that growers can manage, it is increasing in the atmosphere over time due to the burning of fossil fuels and other activities. Carbon dioxide is presently a small part of the atmosphere (about 0.036%) and is expressed as 360 micro liters per liter (µL L^{-1}). Carbon dioxide in the atmosphere has increased about 12.7% during the past 30 years. It is a major nutrient for the crop and the concentration available affects crop growth and production efficiency. That should result in increased photosynthesis, growth, and yields. However, there may be a negative side to increasing CO_2.

Water Deficit Studies

In experiments in which water deficits were imposed, complete nutrient solutions were provided, and plants were grown at near optimum temperature (30/22°C, day/night) and in ambient and twice ambient atmospheric CO_2 levels. 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.

Nutrient Deficit Studies

The nitrogen deficit experiment was conducted by growing plants at near-optimum day/night temperatures (30/22°C) throughout the experimental period. 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 cultural practice. Unfortunately, measures of leaf N are not routinely available, but chlorophyll meters are available, and they 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 and other growth processes were measured throughout the period and subsequently related to leaf N content.

Potassium deficit studies were conducted in a similar manner as that of nitrogen deficit study. Plants were grown until first square with a complete nutrient solution. Then, the solution was modified with one supplying different concentrations of K while still providing a full compliment of the other essential nutrients. Leaf K was determined weekly. Photosynthesis and other growth processes were monitored throughout the period.

Results and Discussion

How Does Cotton Canopy Photosynthesis Respond to Daily Solar Radiation and Atmospheric Co_2?

We monitored the photosynthetic rate of the crop throughout each day. A typical day's CO_2 fixation rates just after the canopy began intercepting essentially all the light are shown in Fig. 2. The photosynthetic rate was tightly linked to the solar radiation received. In chambers with twice the atmospheric CO_2 concentration (720 µL L^{-1}), the maximum rates were about 6 mg CO_2 m^{-2} s^{-1}; while the maximum rates in today's ambient CO_2 concentrations were about 4 mg CO_2 m^{-2} s^{-1}. These photosynthetic rates are high rates, but are similar to those found for soybeans, eggplant, Bermuda grass and pigweed (Hand et al., 1993). The point is that in good growth conditions the primary process is sufficient to produce yields well above any that we experience today. Figure 3 illustrates the same point by expressing photosynthetic rates as a function of photosynthetically active solar radiation and CO_2 concentration for plants grown in 1995 ambient temperature on the same day. Canopy photosynthetic rates did not appear to light saturated even at high radiation levels in present-day atmospheric CO_2 environments when water and nutrients were provided optimally. Doubling CO_2 concentration in the atmosphere increases the initial slope when light is limiting and the asymptote of the light response curve.

Does Canopy Photosynthetic Efficiency Change with Season?

Daily photosynthesis rates at 1200 µmoles^{-2} s^{-1} were plotted throughout the growing season for plants grown in 1995 ambient temperature and CO_2 environments in Fig. 4. The maximum rate was reached soon after flowering and then decreased as the season progressed. One should question the reasons photosynthesis decreases during the important fruit-growth period. The apparent reasons include decreasing solar radiation as the season progresses, but that must be excluded from this data set, because all the data were normalized to PPFD 1200 µmoles^2 s^{-1}. This relatively low radiation value for natural radiation received was selected so that more days could be included in the seasonal data set, and because the photosynthetic rates of the crops at different temperatures are parallel with increasing light (data not shown). Photosynthesis was estimated for any days that did not have sufficient radiation to be included in the data set by using the measured radiation on those days and the average light-use efficiency factor measured for the days before and after those cloudy days. Therefore one must conclude that these plants decreased their light-use efficiency as the season progressed after flowering.

How Does Boll-load Influence Vegetative Growth? Does this Source/sink Alteration Affect Canopy Photosynthesis over the Season?

The influence of boll-load on vegetative growth was illustrated in Fig.5. As the boll load increased, stem growth rates decreased. Stem growth is a function of both the addition of new nodes and internode elongation. New leaves are produced at each node, so as stem growth slows the addition of new leaves slows. When the crop is producing few or no new leaves, the average age of light intercepting leaves on the plant increases. Also, as leaves become older, they become less efficient photosynthetically (Fig. 6). It takes about 16 days after a leaf unfolds for it to reach maximum size in optimum conditions and longer under less suitable or cooler conditions. A leaf is most effective as a producer of plant food stuffs when it first reaches its maximum size. From that point onward, the efficiency of each leaf decreases linearly with age so that by 34 days of age (after unfolding) the leaf is only about half as effective as it was at 16 days. Leaf aging becomes an important factor affecting canopy photosynthesis. Similar patterns were observed in green-house and field grown cotton by Constable and Rawson (1980) and Wullschleger and Oosterhuis (1992), respectively.

Does Elevated Atmospheric CO_2 Increase Canopy Photosynthetic Efficiency over the Season?

By growing plants in twice the ambient concentrations of atmospheric CO_2, the canopy photosynthetic rate did not decrease with age (Fig. 7). The stems of both vegetative and fruiting branches continued to grow and produce 30% more new nodes and leaves on plants grown in 720 µL L^{-1} CO_2 than plants grown in 360 µL L^{-1} CO_2. There was also

22% more living leaf area at the end of the season on plants grown in the high CO_2 environment. This indicates that in the twice ambient CO_2 environment carbohydrates were available to support new stem and leaf growth, but not in the ambient CO_2 environment. Therefore, in the high CO_2 environment, new leaves continued to be produced throughout the season. Since young leaves are more efficient, the photosynthetic efficiency of high CO_2 grown plants continued throughout the season. As a result of this vegetative growth in the high the CO_2 environments, more fruiting sites were produced. About 40% more bolls and squares were produced and about 20% more bolls were retained in the high CO_2 environment.

What Is the Influence of Temperatures on Photosynthesis and Fruit Production Efficiency?

The effect of temperature on cotton photosynthesis is further illustrated by the results shown in Fig. 8. At cooler than ambient temperatures, the plants grew more slowly and there was less photosynthetic response to high CO_2. The crop took longer to mature at low temperatures. Fifty percent open bolls occurred at 162 days after emergence in plants grown at 1995 minus 2°C. At ambient temperatures and ambient plus 2°C, the photosynthetic response to twice normal CO_2 was consistently greater than at the 360 µL L^{-1} CO_2. The relative response of photosynthesis to high CO_2 was greater at 1995 plus 2°C than at the 1995 ambient temperatures. Apparently, growth during this period was limited by low temperatures and this resulted in higher photosynthetic rates of plants grown at warmer temperatures. Plants growing at increasingly higher temperatures also flowered and reached maturity at increasingly earlier dates (Table 1). The declining photosynthetic rates that occurred after flowering, observed in 1995 ambient temperatures, were not observed at the higher temperatures. In fact, photosynthesis in the plants grown at 1995 plus 5°C increased as the season progressed showing no indication of lower efficiency associated with canopy aging.

Table 1. Days from emergence to the appearance of first flower, and average temperatures from first flower to first flower plus 30 days at five temperature regimes maintained continuously relative to the outside air of Starkville, MS 1995.

Treatment	Days to First Flower	Average Temperature from First Flower to First Flower Plus 30 Days, °C
1995 minus 2°C	65	24.1
1995 plus 0 °C	51	26.8
1995 plus 2°C	48	28.7
1995 plus 5°C	42	32.0
1995 plus 7°C	49	33.6

The greatest boll weight was produced by plants grown at 1995 temperatures. Plants grown at 1995 plus 5° C and 1995 plus 7°C did not produce open bolls because the fruiting structures abscised within 3 to 5 days after flowering (Fig. 9). This loss of fruiting structures resulted in the lack of fruiting structure sinks in the plants and that allowed the vegetative mass to continue to grow. i.e., there was no cutout typically observed in cotton plants with a meaningful fruit load. Since vegetative growth continued, there was a continuing supply of new and photosynthetically more efficient leaves that replaced the aging leaves. Therefore, those canopies did not experience the declining rate of photosynthesis and radiation use efficiency associated with time after flowering (Fig 9) as did the canopies grown at 1995 ambient temperatures.

In a separate study we examined the effects of high temperatures on flower production and early embryo development. In that study we observed that pollen produced by plants grown at high temperatures was abnormal and failed to fertilize flowers of plants grown at optimum temperatures. Also, the female portion of cotton flowers produced by plants grown at high temperatures were not receptive to pollen provided by plants grown at optimum temperatures (data not shown). The degree of sterility was closely correlated with hours of exposure to high temperature. Thus, temperature from 20 to 40°C, has a relatively small influence on short-term photosynthetic rate, but it has a large influence on both vegetative development such as production of new mainstem and branch leaves and rate of crop maturity. If photosynthates are available as caused by high CO_2 environments, new leaves continue to be produced throughout the reproductive period. Temperatures above 32°C cause fruit abscission (Table 1and Fig. 9; Reddy et al., 1997b).

How Do Water Deficits Affect Canopy Photosynthesis and Vegetative Growth?

To estimate crop growth in the real world, one needs to adjust potential growth process rates with stresses to which the plants are likely to be exposed in field situations. Photosynthetic rates of cotton plants were reduced about 50% as the midday leaf water potential decreased from the well-watered condition, observed 1.4 to 1.5 MPa, to seriously wilted most of the day reaching a minimum at midday of -3.5 MPa (Fig 10). The photosynthetic rates of both ambient and twice ambient CO_2 grown plants decreased about equally under those drying conditions, but the plants grown in twice ambient CO_2 always had higher photosynthetic rates. Thus, we might conclude that plants grown in a high CO_2 environment will produce more photosynthates in a wide range of water deficit or drought conditions. The sensitivity of photosynthesis and stem elongation was compared by expressing the responses of those processes as percent of the maximum rates achieved (Fig. 11). Stem elongation was more sensitive to water deficit conditions than photosynthesis and reached zero expansion on days when the midday leaf water potential reached -2.5 MPa and about 50% maximum expansion rate at about -1.8 MPa. Such values are much lower than one might have predicted from the stem and leaf growth measurements of Boyer (1970); however one must realize that these leaf water potential measurements are not average

conditions but the extreme daily conditions. Obviously at other times during the day, the leaf water potential must have been much higher.

Leaf and stem expansion are more sensitive to leaf water deficits than photosynthesis. One of the earliest visual symptoms of drought conditions is reduced height and smaller leaves. Field environments vary dramatically from field to field and within seasons as to the extent of water deficit conditions. Even irrigated fields sometimes become too dry due to poor timing of irrigation and crop production is damaged from drought. Radin et al. (1989) found that heavy fruiting, mild water stress associated with long irrigation cycles triggers deterioration of root system that is very slow to repair. They concluded that high-frequency drip irrigation or modified conventional irrigation practices will favor sustained root growth during heavy fruiting and may benefit cotton production.

How Much Photosynthesis Is Lost in Nitrogen Deficit Environments, and Does Nitrogen Deficits Affect Vegetative Growth and Canopy Photosynthesis Differently?

Plants often experience nitrogen deficits in even well-managed field environments. The amount of N applied is usually determined to meet the crop requirements for expected yields. The producer does not provide more than the anticipated need to avoid wasted economic inputs and excessive vegetative crop growth, but this may result in insufficient N to meet the crop's potential needs. This is particularly true in seasons that have more than normal N losses due to unfavorable weather. Plant mineral status, particularly leaf N, can markedly affect photosynthesis and other growth processes. In this report, photosynthesis decreased about 25% as the leaf nitrogen decreased from the maximum leaf concentration achieved with the highest levels of N fertilization to 50% of maximum leaf N (Fig. 12). The response was nearly linear in both ambient and twice ambient CO_2 environments. Leaf growth also decreased as the leaf N decreased (Fig. 13). Leaf growth declined to nearly zero when the leaf N was 1.5 g m^{-2}, the minimum N concentration in cotton leaves. Leaf growth rate, expressed as a percent of the maximum rate achievable under optimum conditions, was only about 60% of the maximum when the leaf N was midway between its maximum and minimum leaf N concentration. This result is consistent with the observations of Radin and Mauney (1986) who concluded that N-deficits caused smaller leaves due to induced water deficits. Thus, the effect of nitrogen deficits on crop productivity is expressed by both lower photosynthetic rates and smaller leaves. Leaf growth is more sensitive than photosynthesis to nitrogen deficits.

How Much Photosynthesis Is Lost in Potassium-deficit Environments, and Do Potassium Deficits Affect Vegetative Growth and Canopy Photosynthesis Differently?

Potassium is the most abundant univalent cation in cell cytoplasm and regulates more than 50 enzymes of various physiological processes. It also plays an important role in the regulation of osmotic potential of plant cells. The development of mid-to late season K deficiency in cotton has become widespread in many cotton producing regions and attention is being refocused on the nutritional needs of cotton. A recent survey of the Mississippi State Soil Testing Laboratory tests found one third of the soil samples received during a recent 12 month period tested either low or medium for K.

Potassium deficiency symptoms first appeared in young and expanding canopy during fruiting. The deficiency symptoms first appeared as mottled leaves followed by marginal necrosis and curling, then crinkling and severe necrosis. Visual K symptoms can only be detected at about 1 to 1.5% of leaf K. Severe K deficiency symptoms occurred at about 1% and below. Visual diagnosis or chlorophyll meter readings are not sufficiently sensitive to detect critical K values. Cotton seems to accumulate luxuriant amounts of K when available and will use that K in periods of insufficient supply. Potassium levels varied among organs in well-fertilized plants, but at low fertility more K was partitioned to bolls and squares.

Potassium deficits cause distinct cotton leaf mottling characteristics. Photosynthesis and leaf growth are sensitive to potassium deficiency, but stem elongation is not. Photosynthesis showed little or no reduction due to leaf potassium content above 2% K (Fig. 14). Below 2% K, the rate of photosynthesis declined sharply as leaf potassium content decreased. The response of potassium to twice atmospheric CO_2 concentrations was similar to the response in ambient CO_2 concentrations, but photosynthesis was greater in high concentrations of CO_2. The response of cotton plant leaf growth to low levels of leaf K was gradual over a wider range of leaf K. i.e., leaf growth was less when only slightly lower concentrations of leaf K occurred (Fig. 15).

Availability of nutrients in the field is influenced not only by supply of the various essential nutrients, but also by the water supply. The supply of essential nutrients is reduced during droughts because less water is available for dissolving the minerals and therefore crop growth potential is lower because of both lower plant water potential effects and less nutrient availability.

Conclusions

Photosynthesis is the driving force for primary production. In environmental controlled chambers where insects and diseases are not factors limiting production, cotton plants are capable of producing much more photosynthesis and thus more dry matter and lint than we normally experience in field environments. Some of the differences in the field and controlled chamber environments were examined to determine what causes these differences.

Field production must always be tuned to the weather conditions available. In the Midsouth, planting time is determined by the advent of sufficiently warm conditions to support cotton growth. Cotton does not grow below 15°C and only to a very limited extent below 20°C. Temperatures in both the spring and fall are usually well below optimum for cotton production. In the experiment reported here, the crop was planted late relative to the usual planting date, and ambient temperatures early in the season were well above the minimum for cotton growth, but early season growth was limited by low temperatures (data not shown). The fall of the year was considerably below the minimum temperature for cotton growth after the first open boll in the ambient-temperature grown crop. The 1995 plus 5°C and plus 7°C crops matured early and escaped the low temperature fall temperatures.

Crops grown in the ambient-temperature conditions flowered at about the highest temperature period in the year. Thus, ambient plus 5°C or 7°C caused all the flowers to abscise. During the first 30 days of the flowering period the average daily was 24.1, 26.8 (ambient), 28.7, 32.0, and 33.6°C respectively for each treatment. The apparent variation from the previously mentioned set points was caused by the differences in the weather during the flowering period. The high temperature grown plants grew more early in the season, flowered earlier (Table 1) and reached maturity earlier (Reddy et al., 1997b). Ambient temperature plus 7°C grown plants flowered 49 days after emergence while plants grown in ambient minus 2°C conditions flowered 64 days after emergence. This resulted in the flowering period (first flower to first flower plus 30 days) occurring at different times for each treatment and thus each condition experienced different temperatures.

Thus, photosynthesis is the driving force for primary production, but factors affecting leaf area duration and development are important aspects of cotton production. Canopy photosynthesis is not light saturated. Current atmospheric CO_2 levels are limiting cotton production, and rising CO_2 will benefit. cotton growth and yield.. Temperature has a small effect on canopy photosynthesis and thus primary production is sustained in a wide range of temperatures. Temperature however, strongly influences vegetative development and thus light capture during much of the vegetative period and light conversion efficiency during fruiting period. Temperature above 28°C limits both vegetative growth and more importantly sink capacity. Water, nitrogen and potassium deficits decrease leaf growth more than photosynthesis. Thus, crop production is a function of many processes from cellular to canopy levels. Increasing production and yield requires knowledge of processes at all levels.

Acknowledgments

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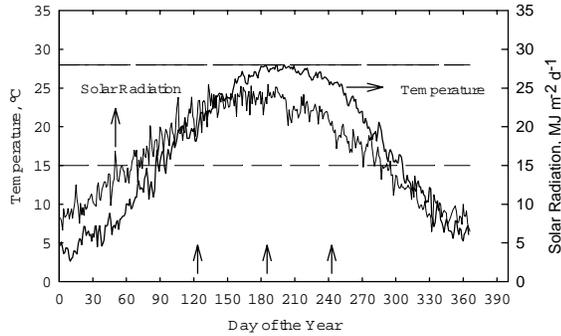
Figure 1. Forty-year average daily temperature and solar radiation at Stoneville, MS. The arrows indicate approximate cotton planting, beginning of flowering, and open boll dates.
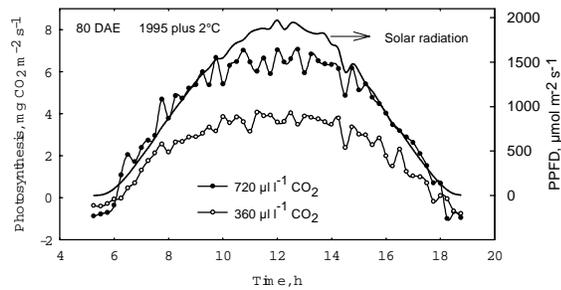
Figure 2. Net photosynthesis of cotton canopies 80 days after emergence, DAE, grown in 360 $\mu L\ L^{-1}\ CO_2$ at 1995 ambient temperatures. Solar radiation, expressed as photosynthetic photon flux density (PPFD), on that day is also shown. Data for both photosynthesis and solar radiation were collected at 10-s intervals and averaged over 900 s periods.
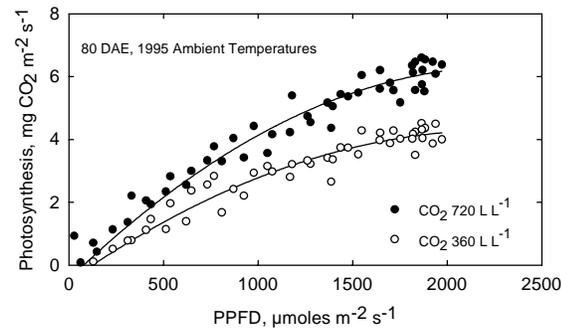
Figure 3. Net photosynthesis of cotton canopies, 80 days after emergence, DAE, grown in 360 and 720 $\mu L\ L^{-1}\ CO_2$ environments at 1995 temperatures as a function of solar radiation. Data were collected as in Fig. 2.
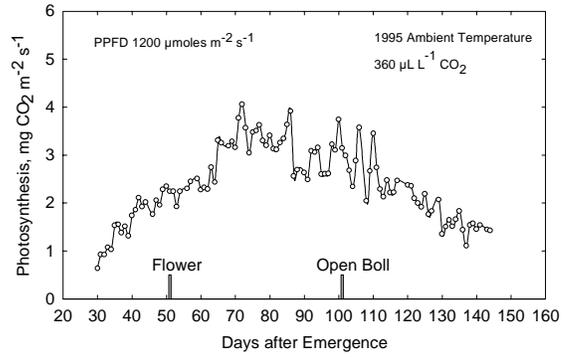
Figure 4. Net photosynthesis of cotton canopies grown at 1995 ambient temperatures and 360 $\mu L\ L^{-1}\ CO_2$. Photosynthesis at 1200 μmoles $^{-2}\ s^{-1}$ was calculated daily from the 900-s average values regressed against solar radiation (PPFD) at each 900 s interval. Beginning of flowering and boll opening are indicated by small bars.
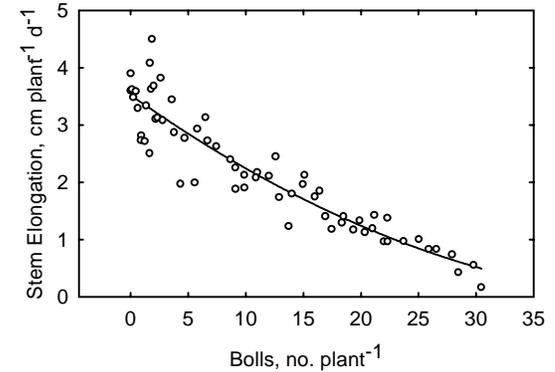
Figure 5. Mainstem elongation rates of cotton plants grown at 30/22°C, day/night, in 350 $\mu L\ L^{-1}\ CO_2$ as a function of bolls numbers. These plants were grown at optimum water and nutrient conditions throughout the period.

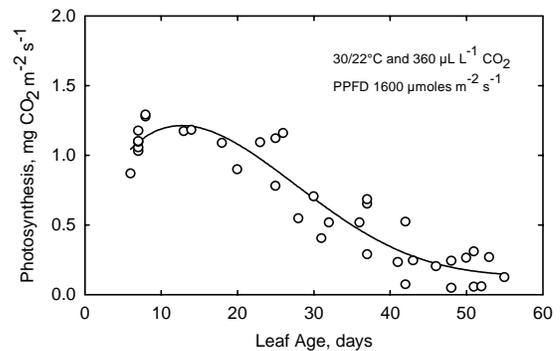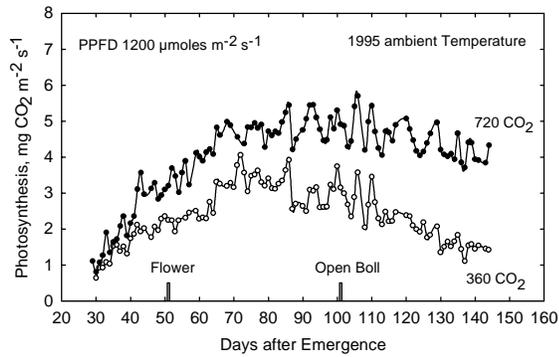Figure 6. Photosynthesis of individual cotton leaves grown at 30/22°C, day/night, and in 350 $\mu L\ L^{-1}\ CO_2$. Photosynthesis was measured at 1600 μmoles $^{-2}\ s^{-1}$ photon flux density.

Figure 7. Net photosynthesis of cotton canopies grown at 1995 ambient temperatures and 360 and 720 µL L^{-1} CO$_2$. Photosynthesis was measured at 10-s intervals and averaged over 900 s intervals. The 900-s photosynthetic values were regressed against radiation for the same 900 s intervals and daily values at 1200 µmoles m^{-2} s^{-1} are shown. Time of beginning of flowering and boll opening are indicated by small bars.
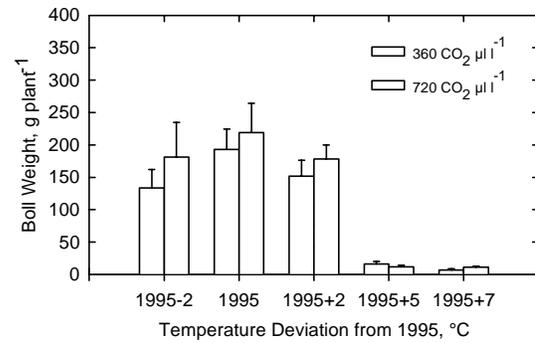

Figure 9. Boll weight per plant produced at 360 and 720 µL L^{-1} CO$_2$ at five temperature regimes as described in figure. 7. Standard error of the means are shown.
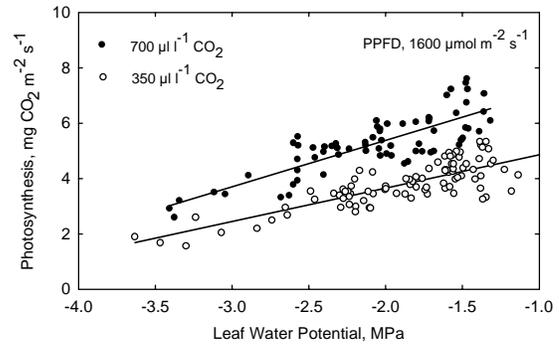
Figure 10. Net photosynthesis of cotton canopies grown at 350 and 700 µL L^{-1} CO$_2$ for plants grown at a range of water deficit conditions and expressed as a function leaf water potentials measured midday. Measurements were taken when the canopies were intercepting more than 95% of the incoming solar radiation. Photosynthesis was measured at 10-s intervals and averaged over 900 s intervals. The 900-s photosynthetic values were regressed against radiation for the same 900 s intervals and daily values at 1600 µmoles m^{-2} s^{-1} are shown.
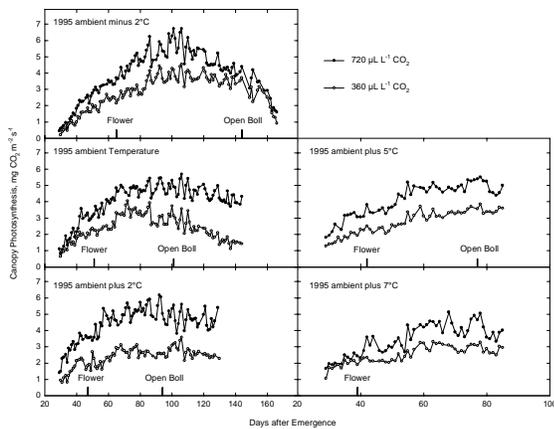

Figure 8. Net photosynthesis of cotton canopies grown at 360 and 720 µL L^{-1} CO$_2$ in 1995 temperatures, a. 1995 minus 2°C, b. 1995, c. 1995 plus 2°C, d. 1995plus 5°C and e. 1995 plus 7°C. Photosynthesis was measured at 10-s intervals and averaged over 900 s intervals. The 900-s photosynthetic values were regressed against radiation for the same 900 s intervals and daily values at 1200 µmoles m^{-2} s^{-1} are shown. Time of beginning of flowering and boll opening are indicated by small bars in each of graph. Plants grown at 1995 ambient plus 7°C did not retain bolls.
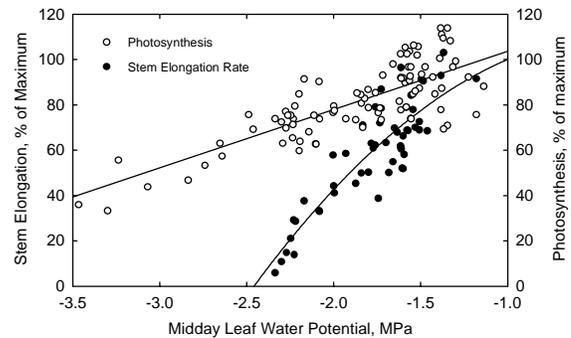

Figure 11. Net photosynthesis as shown in figure 10, and stem elongation of main axis during linear growth phase expressed as percent of maximum for plants grown at a range of water deficit treatments as a function midday leaf water potentials.
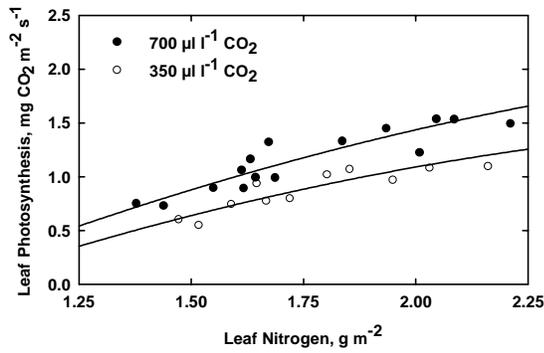
Figure 12. Cotton leaf photosynthesis of plants grown in 350 and 700 μL L^{-1} CO$_2$, and at 30/22°C (day/night) as a function of leaf nitrogen. Photosynthesis was estimated as indicated in Figure 7 at 1600 μmoles $^{-2}$ s^{-1} PPFD. The upper most fully expanded leaves were used for these measurements as well as leaf nitrogen measurements.

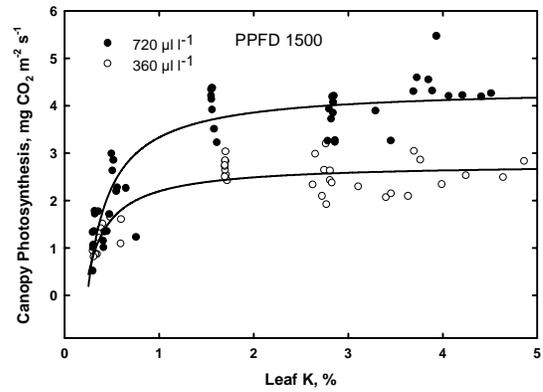Figure. 14. Cotton canopy photosynthesis at 1500 μmoles m^{-2} s^{-1} of PPFD as a function of leaf K. Plants were grown in 350 and 700 μL L^{-1} CO$_2$, and at 30/22°C (day/night). Photosynthesis was calculated as described in figure 7.
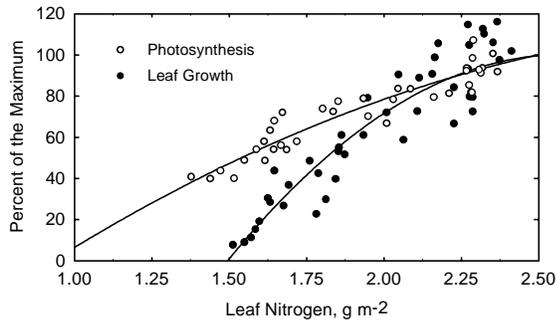

Figure 13. Cotton leaf photosynthesis and pre-fruiting mainstem elongation rates of plants growing in 350 and 700 μL L^{-1} CO$_2$, and at 30/22°C (day/night). Photosynthesis was calculated as described in figure 12. Data are expressed as percent response of the unstressed plants.
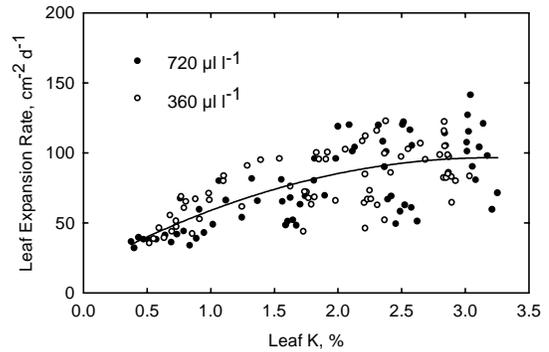

Figure 15. Cotton prefruiting leaf growth rates as a function leaf K. Plants were grown in 350 and 700 μL L^{-1} CO$_2$, and at 30/22°C (day/night) condition.