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SOIL–PLANT–ATMOSPHERE–RESEARCH (SPAR) FACILITY: A TOOL FOR PLANT RESEARCH AND MODELING

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REDDY K. RAJA, HODGES H. F., READ J. J., MCKINION J. M., BAKER J. T., TARPLEY L. and REDDY V. R. *Soil–Plant–Atmosphere–Research (SPAR) Facility: a tool for plant research and modeling.* BIOTRONICS **30**, 27–50, 2001. Integration of a process–based crop simulation model with user–friendly expert systems has aided farm managers by facilitating the selection of optimal solutions to widely varying problems. As such systems are enhanced to further understand plant responses to environment, there is increased need for diagnostics and management–decision aids either in support of optimizing resources for efficient farm management in precision agriculture technologies, or global climate change research, or the use of plants for remediation of extreme environmental conditions. In regards to precision agriculture, most engineering and computing technologies are presently in reality or commercially available for variable–rate/site–specific management; whereas, the application of crop simulation models has been hampered by a lack of understanding of responses of several key physiological and developmental processes to environmental variation and the failure of many to conceptualize the opportunities to apply such technology to real–world agricultural and environmental problems. There are certainly a variety of approaches and facilities for investigating plant response to the environment. We have demonstrated the utility and value of a Soil–Plant–Atmosphere–Research (SPAR) facility, which comprises ten outdoor, naturally–lit chambers, in generating data useful for increased understanding of cotton growth and physiological responses to environment and for developing process–level physiological models. Operating a SPAR facility to acquire model data is often being more expedient and economical than field–plot experiments, because SPAR allows the scientist to minimize many of the covarying and confounding factors that occur in field experiments. As a result, basic plant

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processes investigated can be more directly related to the environmental variable(s) being studied. Also, the SPAR facilities are optimized for the measurement of plant and canopy-level physiological, growth and developmental processes under precisely controlled, but naturally lit, environmental conditions. This paper presents operational data and research results from a SPAR facility at Mississippi State University, Mississippi State, constructed in 1977 and still in use today. We describe herein how data obtained in the past and as well as data in future studies have features that are unique and instructive for both basic and applied plant biologists.

Key words: cotton; sunlit chambers; Soil-Plant-Atmosphere-Research(SPAR); simulation modeling; environmental factors; carbon dioxide; temperature; photosynthesis; growth; phenology

INTRODUCTION

A feature common to production agriculture is that every season is unique with respect to the timing of rainfall, temperature regimes and other weather variables. When a unique set of prevailing weather variables are combined with the various cultural practices, soils, and crop cultivars encountered during a growing season, farm managers may be faced with more variables than the human mind can easily manage. Consequently, resource managers need information organized within a theoretical (or predictive) framework to assist decision-making processes. With increased availability of computers and knowledge of crop responses to weather variables, decision-makers have benefitted from mechanistic crop simulation models designed as decision aids in crop production (*17, 24*). Because a number of cultural practices (e.g., rate and date of planting) affect the physical environment of a crop, simulation models can be used to predict changes in crop growth and productivity due to different cultural practices as well as to different weather conditions.

Our underlying hypothesis in prior experimental and modeling work is that growth and development of plants in field environments result from interactions between the genetic potential of individual plants to grow and various environmental limitations imposed on this growth potential. Here, the potential growth and developmental rates for a particular species or genotype are defined as the maximum rates achievable at given temperature under non-limiting nutrient and water conditions. This definition of growth potential has allowed the successful development of the cotton simulation model, GOSSYM (*6, 13*). A controlled-environment research facility realistically mimicking field-like environmental conditions is an essential tool for the acquisition of process-rate data because it allows manipulation of a single environmental factor while other factors are maintained in non-limiting conditions. Data obtained in this manner are far less ambiguous than those obtained in field experiments, allowing interpretation of specific crop responses across the range of the manipulated environmental variable. The actual rates may be delayed or reduced by environmental and nutritional (including carbon) stresses, and then compared

relative to the growth potential (e.g., rates of development or growth) established for a particular species/genotype. With this knowledge of process rates and stress responses, simulation models have been constructed to predict crop responses to various physical conditions and changes in cultural practices (*13, 24, 43*). Typically, differences unique to a newly released cultivar can be simulated with minor calibration adjustments to potential rates established for a previously studied cultivar (*7*).

There are several approaches and facilities available for investigating crop and ecosystem responses to environmental conditions. Allen et al. (*4*), reviewed the appropriateness of each of these facilities and the limitations of particular approaches, with emphasis on the physical comparisons of the facilities and the characteristics required to address plant or ecosystem to responses to environmental conditions. Additional development of facilities has occurred since then (*8, 57*).

Early work with controlled-environment growth chambers led some plant biologists to erroneous conclusions. As a result of low light intensities and poor light quality, plants grown in artificially lighted chambers did not satisfactorily represent plants grown in natural sunlit conditions. Also, small pots may restrict root growth and subsequently alter the root to shoot partitioning, introducing unintended experimental artifacts (*5*) even for plants well supplied with water and nutrients (*55*). Therefore, many biologists ceased using such chambers or information obtained from such studies for developing simulation models. Phene et al. (*26*) recognized the importance of unambiguously determining the role of specific environmental factors on plant growth and development, and were first to design naturally-lit plant growth chambers with realistic soil volume known as Soil-Plant-Atmosphere-Research (SPAR) units, which solved many of the problems of earlier chamber designs. A set of ten naturally-lit SPAR chambers, with computer control of environmental variables, was constructed at Mississippi State University in 1977 and has since been used for determining plant responses to a variety of environmental factors (*48, and references therein*). We have changed some design details to improve efficiency and reliability, but the basic design has remained essentially the same. These sunlit, controlled-environment chambers are uniquely useful for studying canopy and ecosystem or small-plot responses to several combinations of variables in controlled field-like environments (*43, 48, and the references therein*). The primary advantages of a SPAR facility for studying physiological processes in intact plants are repeatability (*37, 38*) and the ability to measure and control of environmental variables (*2, 15, 32, 33, 34, 35*). Similarly, the SPAR-like facilities have been used for plant physiological studies at the University of Florida, Gainesville, Florida (*3, 14, and the references therein*), the Battle Pacific Northwest Laboratory, United States Environmental Protection Agency facility, Corvallis, Oregon (*57*) and more recently at the Natural Resource Institute, United States Department of Agriculture, Beltsville, Maryland, USA.

Despite years of agronomic and crop science research, there exists still knowledge gaps, and a lack of quantitative information on crop responses to

physical environment. The purpose of this paper is to explicitly describe the control capabilities of SPAR and the different types of experiments that can be conducted with such equipment. Because our aim is to encourage the more widespread understanding of crop growth, development and yields in response to cultural practices and weather. To accomplish this, the crop production manager needs information on status of the crop and the factor(s) limiting growth at any given point in time. We present evidence and examples of how results can be used to develop process-level crop simulators that will provide such information. Here, we focus on our studies with cotton in the SPAR facility at Mississippi State University for developing a crop simulation model, and also discuss some relevant capabilities of SPAR facilities that are in use at other locations.

PHYSICAL AND ENVIRONMENTAL FEATURES OF THE SPAR FACILITY

The SPAR units are located outdoors on a 20×30 m concrete pad. Each unit has the capability for controlling air temperatures, and atmospheric composition (especially CO_2 concentration) at predetermined set points for studies of plant growth in natural solar radiation regimes (*33, 35*). The bottom third of each SPAR unit consists of a steel bin to contain rooting medium. The upper two-thirds is an airtight Plexiglas chamber of 2.5 m high and 2.0×1.5 m in cross-section to accommodate the aerial plant parts (Fig. 1). Variable-density shade cloths are positioned around the edges of a plant canopy inside each unit, and are adjusted manually to match plant heights, in order to simulate the presence of neighboring plants and eliminate the need for border plants.

A door in the bottom of the aerial portion of each chamber is hinged for access to the soil surface and the aboveground portions of the plants. Ducts on the northern face connect to the cooling system. Conditioned air is introduced at the top of the Plexiglas chamber, flows down through the plant canopy, and is returned to ducts just above the soil surface. A steel soil lysimeter contains the rooting medium, and measures 1.0 m deep×2.0 m long×0.5 m wide. The northern face of the lysimeter has many large holes closed with rubber stoppers to facilitate measuring soil environmental conditions. The southern face is constructed of reinforced glass to allow collection of data on root growth dynamics. Figure 1 is a picture of a SPAR unit showing the attributes mentioned. Construction details, operating parameters, data acquisition, and control capabilities of the SPAR/SPAR-like facilities are described in detail for the interested reader in Phene et al. (*26*), Parson et al. (*27*), McKinion (*18*), McKinion and Baker (*21*), McKinion and Bell (*22*), McKinion (*19*), McKinion (*20*), Jones et al. (*15*) Pickering et al. (*28*), Tingly et al. (*57*). With common equipment such as the secondary cooling system, the data acquisition and control system, the cost of a SPAR unit is approximately US$40,000, and includes the carbon dioxide gas analyzers, cooling system, data acquisition and control system, and associated gas pumps, instrumentation, sensors, and wiring which is comparable to most commercial plant growth chambers.

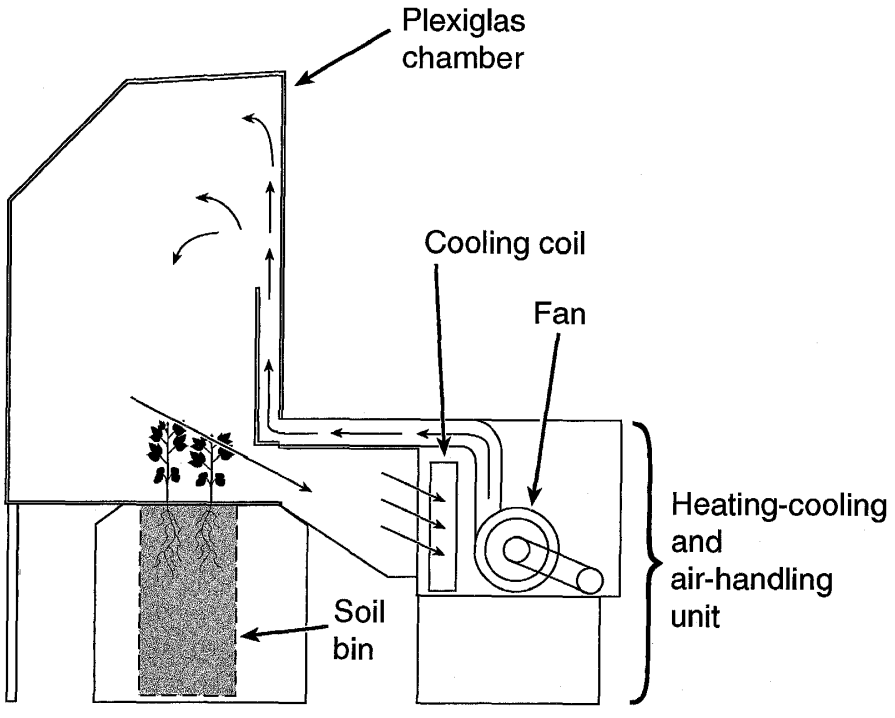

Fig. 1. Diagram showing a Soil–Plant–Atmosphere–Research (SPAR) unit at Mississippi State, Mississippi. The canopy volume including the air handling unit is 11.1 m^3. Conditioned air enters aboveground Plexiglas compartment about halfway between the bottom and the top of the unit and returns just above the soil level. The above–ground compartment is mounted on a steel frame, and a lysimeter. The air–handling unit accommodates a pressure pump to direct air from each chamber to the laboratory room for carbon dioxide analysis, two 11 kilowatt heaters on either side of the unit, a fan for air circulation, and a dew point sensor just inside the return airline.

The SPAR units provide a natural solar radiation environment (94% transmissive to photosynthetically active radiation) and have capabilities for controlling both the aerial and soil environment across a wide range of environmental set points. Controlled factors in each chamber include atmospheric carbon dioxide concentration ($[CO_2]$), dry–bulb air temperature, and dew point temperature. The environmental control system can be programmed to provide continuously changing values over a diurnal cycle to yield either a smooth sinusoidal or a square wave function. Similarly, a monitoring system provides accurate measurement of the environmental conditions throughout an experiment. Many season–long experiments have been conducted on cotton in which excellent environmental control was maintained for several months (*48, and references cited therein*). Set points also can be programmed to change for short–term periods so that plant responses to short–term environmental conditions can be investigated during critical stages of crop development. In addition, $[CO_2]$ can be maintained from subambient to superambient levels in the SPAR system in a manner not possible with other types of field exposure

systems. This capacity allows investigation of specific processes related to reduced carbon sources and sinks and their interactions that lead to widely varying patterns of growth, development, and fruiting in cotton. Because the SPAR units provide continuous measurement of canopy photosynthesis and transpiration throughout the experimental period, these biophysical processes can be determined under precisely controlled conditions. From these results, rate equations can be developed for building new mechanistic models of growth and development and/or improving the existing crop models.

Plant culture

Irrigation and nutrient media can be manipulated precisely to deliver the required amounts into each SPAR unit or pot by adjusting the provision of Hoagland's nutrient solution through a computer-controlled drip-irrigation system. Further, an adjoining nursery facility is available to grow plants in large pots and then move plants into the units following a predetermined period of growth to address short-term experimental objectives at specific growth stages.

Measurement and control of environmental variables

Temperature is monitored and adjusted automatically every 10 s throughout the day and night. Control of the dry-bulb air temperature is maintained using a dedicated computer that opens and closes a set of solenoid valves to a chilled water radiator and switches a heating system on and off. Heat is provided by two 11 kilowatt heating elements mounted on either side of the air circulation unit. Air temperature is monitored using an aspirated, shielded thermocouple and maintained within ± 0.5℃ of the treatment set points over a daytime range of 18℃ to 40℃ and a nighttime range of 12℃ to 32℃. The dew point temperatures are measured, but not controlled, with a gold mirror hygrometer ([1]Model Dew-10, General Eastern Instruments, Woburn, Massachusetts, USA) installed in-line the return airline. The dew point temperatures are collected at 10-s intervals and summarized over 900-s periods (*33*).

Canopy temperature of plants is monitored every 10 s using infrared thermometers ([1]Model 400AT, Everest Interscience Inc., Tucson, Arizona, USA) and the values averaged over 900-s intervals throughout the experimental period. In one of the ten units, photosynthetic photon flux density (PPFD) is monitored every 10 s using a pyranameter ([1]Model, LI-200SA, LI-COR Inc, Lincoln, Nebraska, USA) placed above the canopy. Similarly, canopy light interception is monitored using a dedicated line quantum sensor ([1]Model, LI-1000, LI-COR Inc, Lincoln, Nebraska, USA) placed just above the soil-level. Also, at an adjacent weather station, global radiation, PPFD is measured at 10 s intervals and those data are averaged separately over 900-s intervals. The $[CO_2]$ in each SPAR unit is monitored and adjusted every 10 s throughout the day and is maintained within $10\,\mu L\,L^{-1}$ of treatment set points during the day light hours by adjustment of controls consisting of a set of pressure regulator, calibrated rotometer, needle valve and solenoid valves. A mass-balance approach based on

the output from a dedicated CO_2 analyzer for each unit ([1]Model, LI 6200, LI-COR Inc, Lincoln, Nebraska, USA) is used to open and close the solenoid valves as needed. To maintain CO_2 in each chamber, pure CO_2 is injected through a system that includes a pressure regulator, solenoid and needle valves, and a

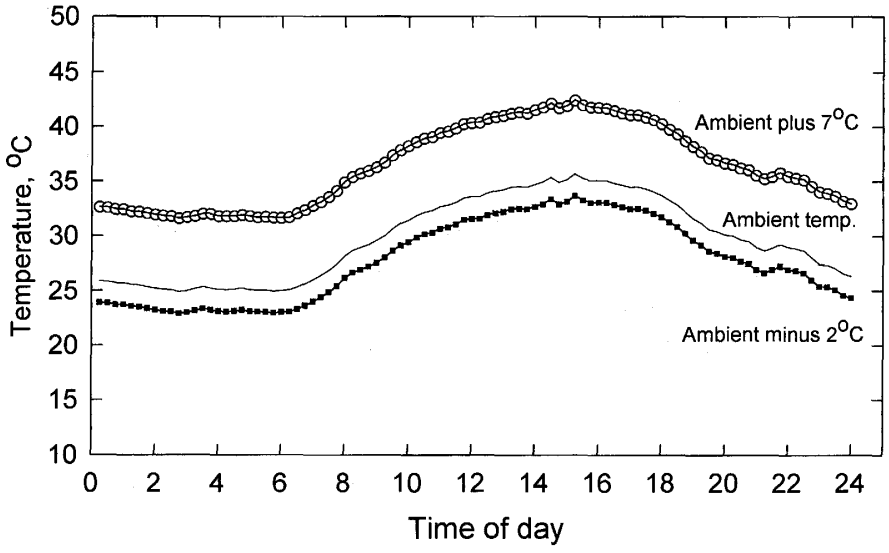

Fig. 2. A typical diurnal period of temperature control for three SPAR units programmed to control at current ambient temperature, ambient minus 2℃, and ambient plus 7℃.

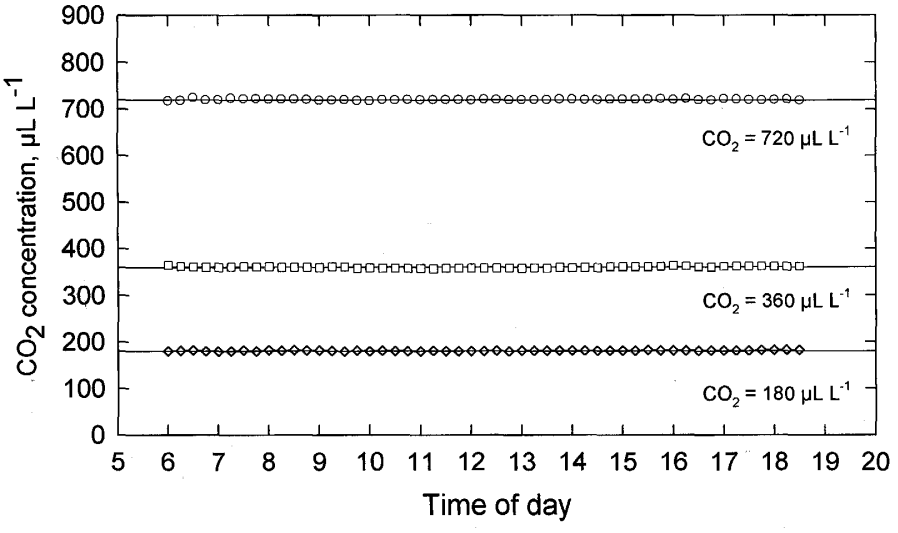

Fig. 3. A typical day of CO_2 control for three SPAR units programmed to control at subambient ($180\,\mu L\,L^{-1}$), ambient ($360\,\mu L\,L^{-1}$), and elevated ($720\,\mu L\,L^{-1}$) levels.

[1]Mention of this and other proprietary products is for convenience of the readers only, and does not constitute endorserment or preferential treatment of these products by Mississippi State University, USDA-ARS or Texas A&M University.

flowmeter. The flowmeters are calibrated with a gas displacement meter at the beginning and end of each experiment. Figures 2 and 3 illustrate typical temperature and [CO_2] control during one day.

Measurement of photosynthesis and respiration

Each SPAR unit's growth chamber and fan-coil box form a semi-closed system for measurement of canopy CO_2 and water vapor exchange (Fig. 1). The Plexiglas chamber containing the plants, ducts, and cooling system are nearly airtight. A mass balance approach is used to calculate net CO_2 exchange rates (P_n) of the plant canopies per unit ground area throughout the experiment. Precise control of the [CO_2] at $\pm 10\,\mu L\,L^{-1}$ of the treatment set point is achieved by using a dedicated infrared gas analyzer, calibrated weekly. Carbon dioxide flow rates are recorded three times a day and converted into mass quantity via gas law correction for temperature and pressure. The time intervals during which the solenoid valves are open are monitored by a computer, and thus the amount of CO_2 injected is known. A leakage test is performed each night to derive the plant growth chamber leakage rate and to correct canopy gas measurements (*1*).

Using values for the mass of CO_2 injected to maintain a treatment set point, and the mass of CO_2 lost via leakage, one can calculate net canopy photosynthesis per unit ground area, P_n (mg $CO_2\,m^{-2}\,s^{-1}$). Rates of CO_2 fixation for cotton at a full canopy are shown for a typical diurnal cycle (Fig. 4 and 5), and are closely coupled to the amount of solar radiation received. In chambers with $720\,\mu L\,L^{-1}$ [CO_2], the maximum rates were about 6 mg $CO_2\,m^{-2}\,s^{-1}$, while the maximum rates in plants at ambient [CO_2] about 4 mg $CO_2\,m^{-2}\,s^{-1}$. "Dark"

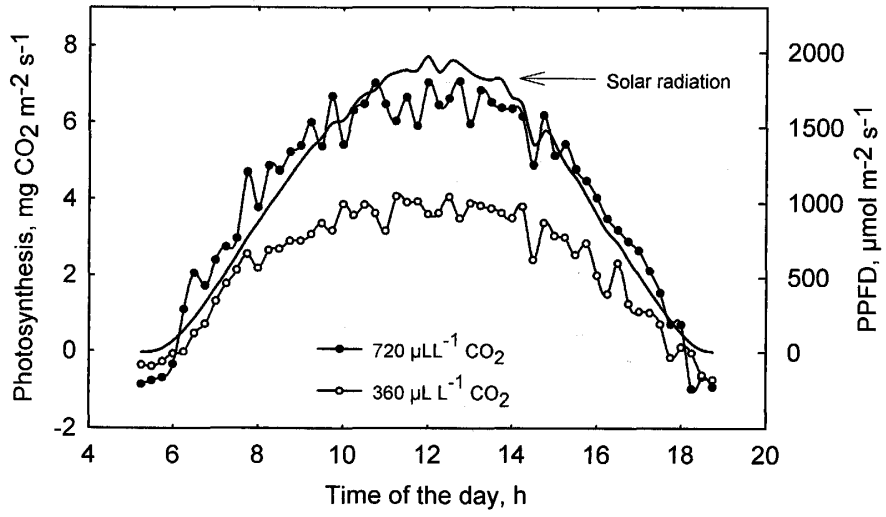

Fig. 4. Net photosynthesis of cotton canopies at 80 days after emergence grown in 360 and $720\,\mu L\,L^{-1}$ CO_2 and at ambient temperatures. Variation in solar radiation, expressed as photosynthetic photon flux density, on that day is also shown. Data for both photosynthesis and solar radiation were collected at 10-s intervals and averaged over 900 s.

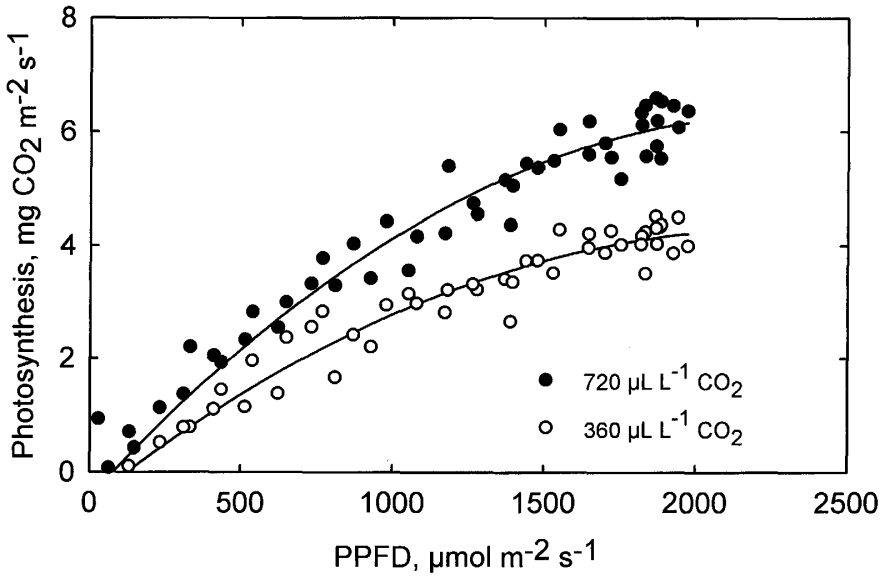

Fig. 5. Net photosynthesis of cotton canopies 80 days after emergence grown in 360 and 720 μL L^{-1} CO_2 environments and at 1995 temperatures as a function of solar radiation. Data were collected at 10-s intervals and averaged across 900 s.

respiration rates (mg CO_2 m^{-2} s^{-1}) are calculated in a similar manner by maintaining daytime temperatures one hour into the nighttime period. Consequently, gross canopy C exchange rate, P_g, is calculated and used to correct P_n data for daytime "dark" respiration rates. We have routinely used these data to quantify the photon flux density vs. P_n or P_g of cotton canopies, and have found a close relationship (r^2=0.97) between seasonal P_n and biomass (*11*). V. R. Reddy et al. (*54*) reported a close relationship between CO_2 fixed by soybean grown at four [CO_2] (350 μL L^{-1} to 900 μL L^{-1}) and the estimated cost of biomass synthesis.

Measurement of transpiration

Canopy transpiration rates expressed on a ground area basis (g H_2O m^{-2} s^{-1}) throughout the growing season is measured as the rate at which condensate is removed by the cooling coils at 900-s intervals (*23*) by measuring the mass of water in collecting devices connected to a calibrated pressure tranducer. The soil surface is sealed from gaseous exchange with the aerial environment using plastic sheeting. Data on diurnal trends in radiation and transpiration for flowering cotton plants grown at two [CO_2]'s for a typical clear day are presented in Fig. 6. From measurements of photosynthesis and transpiration, water-use efficiency (g CO_2 fixed per unit of water transpired) of crop canopies can be estimated as functions of various environmental conditions.

Measurement of crop growth and development

Crop phenology or development can be precisely measured in predetermined environments with the SPAR system. For cotton, these processes are: 1) emergence to first square (cotton floral buds); 2) squaring to flowering (anthesis); 3) flowering to open bolls (dehiscence of the many-carpellate fruits); 4) open bolls to crop maturity or termination; 5) duration of the growth of a leaf or an internode; 6) leaf area development, 7) stem and root elongation rates; and 8) abscission rates of leaves, squares, and bolls. When these measurements are obtained with manipulation of $[CO_2]$ from subambient to superambient levels, one can precisely estimate the C source and sink relations and identify causes for fruit-shed or delays in plant development. As the ratio of supply to demand for C or other nutrients decreases due to C or other nutrient deficiencies growth becomes limited by the respective nutritional deficiency. Therefore, the causes for fruit shedding in flowering plants can be more easily investigated using the SPAR system than through any other known means.

QUANTIFYING GROWTH, DEVELOPMENT AND PHYSIOLOGICAL PROCESSES

During the past several years, SPAR experiments were conducted to answer many questions regarding cotton growth and developmental rates, and rates of specific processes, in response to several environmental factors. These experiments, summarized in Table 1, serve to illustrate the potential of the SPAR facility for systematically providing mechanistic explanations of the response of diverse plant processes to environment. A criticism of these experiments is the limited number of replicates available when examining interactions of treatment variables due to a limited number of experimental units (10 at the Mississippi State facility). The median variance of eight diverse measurements of plant growth and development within a single SPAR unit often exceeds by fivefold the variance among the units treated alike. We attribute this low variability between similarly treated SPAR units to the precise, computerized control of the environmental variables possible in the SPAR chambers.

The SPAR facility has supplied many of the model parameters and process-level rate equations used by the mechanistic cotton-crop simulation model, GOSSYM (*6, 13*). Model validation studies can also be conducted to examine the reliability of SPAR data. For example, K. R. Reddy et al. (*39*) used SPAR data in order to provide inputs to the model from a subroutine that describes the effects of a commonly used plant growth regulator in cotton, mepiquat chloride. With the aid of the subroutine, GOSSYM/COMAX was used to predict several growth parameters for making comparisons to actual values in 50 field cropping systems. The linear regressions of model predictions vs. the observed values with a zero intercept yielded slopes near 1.0, and r^2 values ranged from 0.95 to 0.99.

Examples of gas exchange measurements

Canopy daytime photosynthesis in cotton during the fruiting period

Table 1. Treatment structures for experiments conducted on cotton in naturally sunlit environment chambers (SPAR units) during 1988 to 1998.

Year	Cultivar	Temperatures, ℃ Day/Night	[CO_2] μmol mol^{-1}	Comments and references
Expt. 1-1988	DPL 50	25/15, 30/20, 35/25	350	Flowering to end-season, and three PREP®[1] treatments
Expt. 2-1989	DPL 50	15/7, 20/10, 25/15, 30/20, 35/25	350, 700	70 days from emergence, well-watered and fertilized (*12, 49, 50, 51, 52*).
Expt. 3-1989	DPL 50	30/22	Several [CO_2]	Short-term, few weeks during flowering, well-watered and fertilized (*38*).
Expt. 4-1989	DPL-50	Several high air temperatures	600	4-weeks during the fruiting period, Flower abscission study (*49, 50, 51*).
Expt. 5-1990	Pima-S-6	20/12, 25/17, 30/22, 35/27, 40/32	350, 700	64 days after emergence, well-watered and fertilized (*37, 38*).
Expt. 6-1990	Pima-S-6	25/17, 30/22, 35/27	350, 700	Flowering to maturity, well-watered and fertilized (*37, 38, 39*).
Expt. 7-1990	Pima-S-6	Four high temperatures	700	Flowering to end of season, fruit retention study (*30, 36*).
Expt. 8-1991	Pima-S-6	30/22	350, 450, 700	95 days after emergence, 3 drought stress levels (*42*).
Expt. 9-1991	DES 119	30/22	350	Four N levels (*45, 53*).
Expt. 10-1992	DPL 5415	26/18, 31/23, 36/18	350, 450, 700	60 days after emergence, well-watered and fertilized (*31*).
Expt. 11-1992	DPL 5415	26/18, 31/23, 36/18	350, 450, 700	Flowering to maturity, well-watered and fertilized (*39, 41*).
Expt. 12-1993	DES 119	30/22	350, 700	49 days after emergence, 5 N levels (*44*).
Expt. 13-1993	DES 119	30/22	350, 450, 700	80 days after emergence, 3 drought stress levels (*45*).
Expt. 14-1993	DES 119	Several PIX®[2] levels	Out-of-doors	Short-term, 30 days from squaring, 5 PIX®[2] treatments (*29, 40*).
Expt. 15-1994	Acala Maxxa HS-26, DPL 51	20/12, 25/17, 30/22, 35/27, 40/32	360, 720	46 days after emergence, well-watered and fertilized (*47*).
Expt. 16-1994	DPL 51	Temperatures: Long-term Mississippi July mean minus −2, and. July mean plus 2, 5 and 7℃	360, 720	4-weeks, flowering period, well-watered and fertilized (*44*).
Expt. 17-1995	DPL 51	Temperatures: 1995 ambient, 1995ambient −2℃, and 1995 ambient plus 2, 5 and 7℃.	360, 720	Full-season, well-watered and well-fertilized (*44*).
Expt. 18-1996	NuCot33	30/22	360, 720	84 days, 5 K levels (*48*).
Expt. 19-1996	NuCot33	26/26	360	Manual de-leafing and de-fruiting study, well-watered and well-fertilized.
Expt. 20-1997	Nucot33	30/22	360, 720	Several water-deficient studies (*48*).
Expt. 21-1997	NuCot33	Several short-term temperatures	Several [CO_2]	Short-term, few days to treatments weeks, well-watered and well-fertilized (*48*).
Expt. 22-1998	NuCot33	30/22	360, 720	Water and CO_2 interactive study (*56*).

[1]PREP® is Ethephon, (2-Chloroethyl) phosphonic acid
[2]PIX® is Mepiquat Chloride, N, N-dimethylpiperdinium chloride

expressed as a function of photosynthetically active solar radiation and [CO_2] are presented in Fig. 5. The canopy was closed, intercepting about 95% of the incoming solar radiation. Plants were grown in optimum temperature, water, and nutrient conditions, but in varying CO_2 environments. Unlike data obtained in indoor, light-limited plant growth chambers, cotton canopy/leaf photosynthetic rates did not appear to light-saturate even at high radiation levels in present-day [CO_2] environments (*30, 58*). Doubling [CO_2] in the atmosphere increased both the initial slope of the diurnal light response curve and the estimated maximum light-saturated rate. Using the SPAR system, we have calculated the initial slopes and the maximum rates of canopy light response curves as functions of various temperature, atmospheric [CO_2], water, and nutrient regimes by manipulating these environmental conditions. From these physiological response functions, and knowledge of canopy light interception, it is possible to develop a functional model of canopy carbon exchange rate for a faield-grown crops.

From light response curves of the type depicted in Fig. 5, the daily net photosynthetic rates at a specific radiation level can be estimated and the values plotted throughout the growing season to compare environmental conditions (e.g., Fig. 7). Under ambient temperature of 30℃ and atmospheric [CO_2] of 360 μL L^{-1} CO_2, the maximum photosynthetic rate at 1200 μmol mol^{-1} s^{-1} PPFD was reached about 30 days after flowering, and then gradually decreased as the season progressed. In cotton, fruit-set (boll number) increases rapidly after first flower stage until the size of the fruit load (a major sink for C) reaches the maximum the plant can support. Actually, the maximum number of fruits a

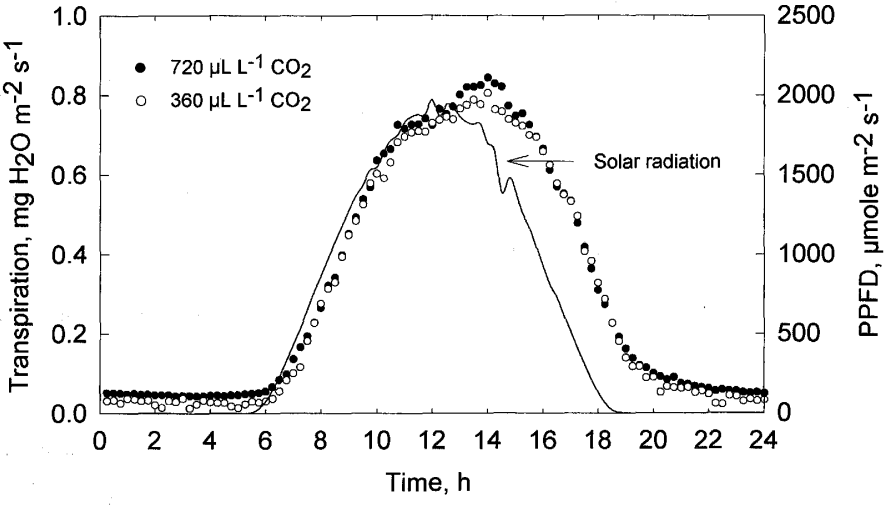

Fig. 6. Transpiration of cotton canopies 80 days after emergence grown in ambient (360 μL L^{-1}) or twice ambient CO_2 concentrations and at 1995 ambient temperatures. Solar radiation, expressed as photosynthetic photon flux density (PPFD), and air temperature on that day are also shown. Data for transpiration were collected at 900-s intervals while data for solar radiation and air temperatures were collected at 10-s intervals and averaged over same 900 s periods.

cotton plant can support varies daily, depending on the amount of photosynthate production, respiration rate, and limitations due to nutrients and water. In cotton, as in most other indeterminate plants, some or all young fruit within a certain maturity class may abscise on certain stressful days, but when conditions improve later an even larger number of fruits might be added and subsequently supported to maturity.

It is interesting to find a decrease in canopy photosynthesis in cotton during the important fruit-growth period (Fig. 7). Among possible reasons for this decline is a decrease in solar radiation as the season progresses in the midsouthern USA; however, this can be excluded in the present SPAR study because the data were normalized to a PPFD of 1200 μmol $^{-2}$ m $^{-2}$ s $^{-1}$. Therefore, one must conclude that radiation-use efficiency decreased in these plants as the season progressed following flowering. Regressing photosynthetic rates as a function of days after emergence (DAE) from DAE 80 to maturity yielded a slope of -0.032 mg CO_2 m $^{-2}$ s $^{-1}$ d $^{-1}$ for 360 μmol CO_2 mol $^{-1}$ air and -0.015 mg CO_2 m $^{-2}$ s $^{-1}$ d $^{-1}$ for 720 μmol CO_2 mol $^{-1}$ air (Fig. 7). The ratio of these diurnal slope values indicates P_n was enhanced about 46% by doubled [CO_2], as compared to plants grown in ambient [CO_2]. This reflects a 47% greater rate of canopy photosynthesis in plants grown at twice-ambient [CO_2] on 80 days after emergence compared to plants grown in ambient [CO_2]. The net effect was an approximate doubling (99% increase) of cumulative seasonal net photosynthesis estimated using the regression parameters from each day's net photosynthesis

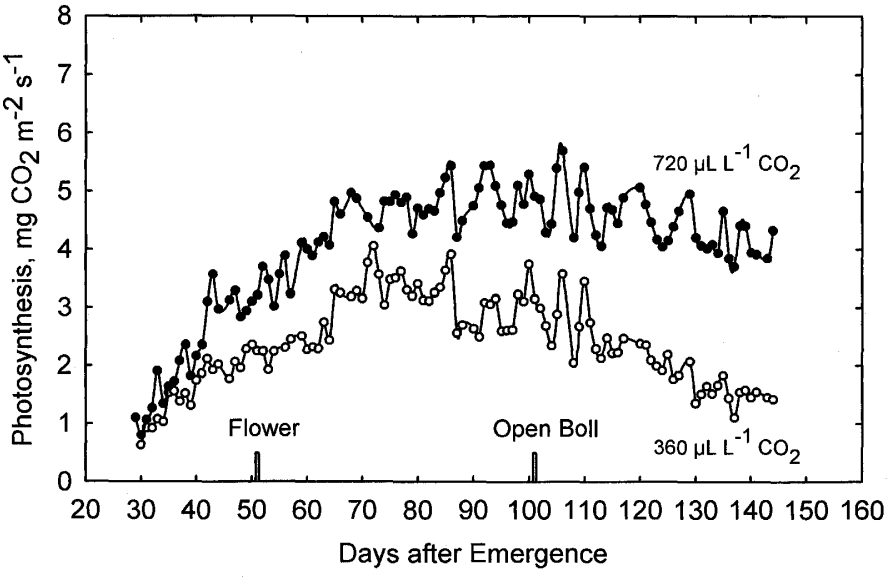

Fig. 7. Net photosynthesis of cotton canopies grown at 1995 ambient temperatures, and 360 or 720 μL L $^{-1}$ CO_2. Photosynthesis was measured at 10-s intervals and averaged over 900-s intervals. The 900-s photosynthetic values were regressed against radiation for the same 900-s intervals, and daily values at 1200 μmol m $^{-2}$ s $^{-1}$ PPFD are shown. Initiations of flowering and boll opening in 50% of the plants are indicated by small vertical bars from left to right, respectively.

values, due to doubling CO_2 levels, from 7.25 kg CO_2 assimilated in ambient air to 14.49 kg CO_2 assimilated in elevated [CO_2]. Higher photosynthesis in elevated CO_2 environments may be due to both the direct effects of higher [CO_2] in the atmosphere and thus a CO_2 steeper gradient between atmosphere and the chloroplasts and the indirect effects of carbon on sustaining more vegetative growth longer into the fruiting period thus causing a younger canopy of leaves in the high-CO_2-grown crop.

Crop developmental rates

Examples of classical growth analysis to determine changes in a developmental rate of a cotton crop are presented in Figs. 8 to 11 for plants grown under favorable water and nutrient conditions. It is practically impossible to obtain such data in field situations, because many physiological and environmental factors vary or interact in complex ways to affect cotton development. Even with suitable control of cultural practices, several experiments are needed from different geographic locations in order to generate valid crop development data. Using SPAR chambers, it is possible to describe the number of days between seedling emergence and first square, and calculate the daily rate of development (reciprocal of days) for this developmental process to occur (Fig. 8). Similarly, the rate of square (flower-bud) and boll development can be described (Fig. 9), as well as plastochrons for mainstem leaves and fruiting branches, as a function of temperature (Fig. 10). These processes are important for understanding growth and development in cotton, and in managing the crop, because it is tropical in origin, and very sensitive ambient temperatures.

In a field environment, variability in temperature within and between days

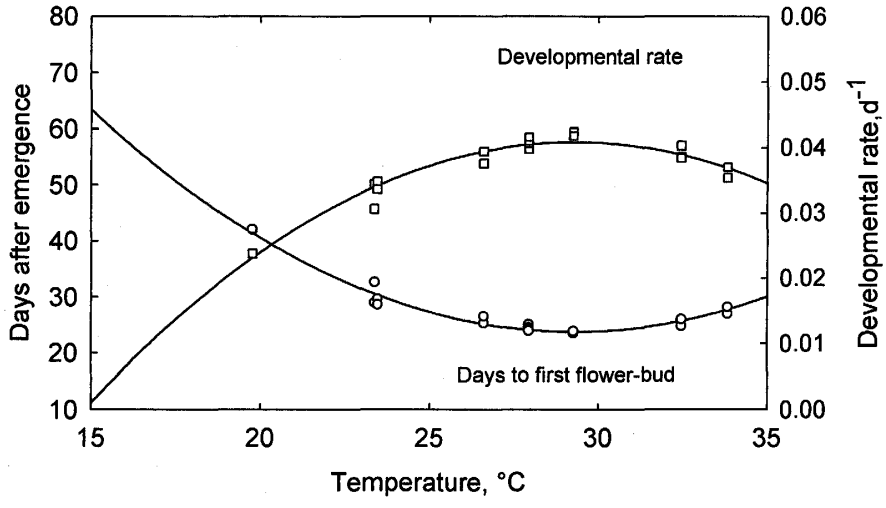

Fig. 8. Influence of temperature on the development of first flower bud in a cotton and/or rate of development. The rate of development was calculated as the multiplicative inverse of duration; i.e., one over days at a given temperature (*see 43 for details*).

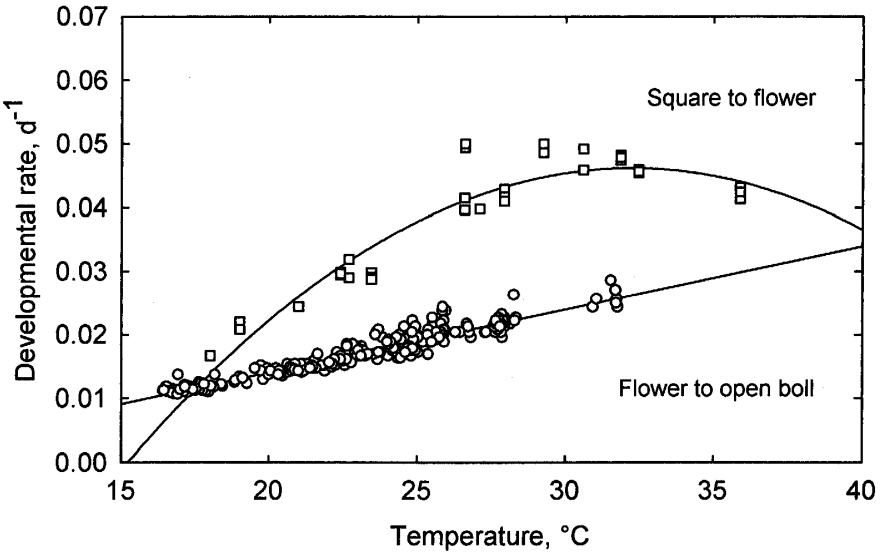

Fig. 9. Influence of temperature on the rate of crop development: first flower-bud to open flower and flower to open a boll in cotton grown either at ambient ($350\,\mu L\,L^{-1}$) or twice ambient CO_2 levels. The rate of development was calculated as the multiplicative inverse of duration; i.e., one over days at a given temperature (*43, 46*).

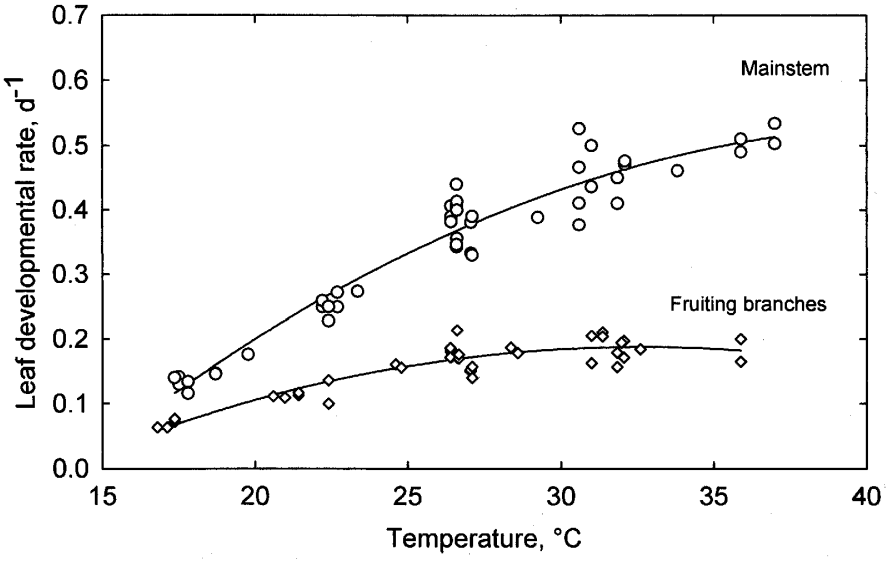

Fig. 10. Influence of temperature on the rate of mainstem leaf development and fruiting branches in cotton. The rate of development was calculated as the multiplicative inverse of duration; i.e., one over days at a given temperature (*46*).

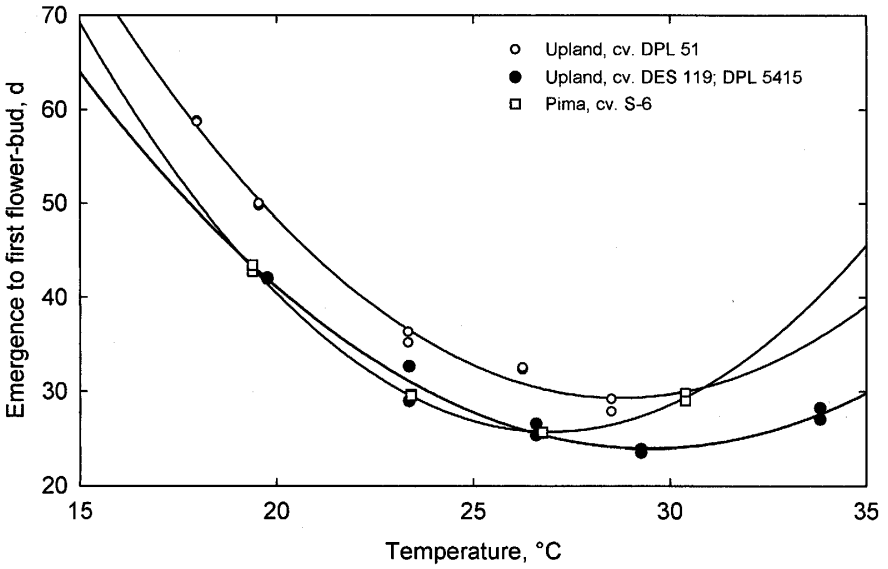

Fig. 11. Effect of ambient air temperature and cotton cultivars on days from emergence to first square for plants grown either at ambient (350 μL L^{-1}) or twice ambient CO_2 levels.

makes develop functions for plant phenology nearly impossible, but such functions can be developed in the SPAR units and applied effectively to predict growth and development in the natural world where variable conditions are paramount. Although one can estimate phenological development by using either hourly or daily developmental rates and either hourly or daily temperatures, the data can be more useful if one calculates the reciprocal of the number of days required to reach an event from the average temperature for each day. These daily reciprocal values can be added together until they total 1.0 or greater. At that time, the phenological event should be observed. Daily average temperature can be estimated by summing the maximum and minimum temperatures and dividing by two. When cotton plants were grown in continuously varying temperatures such as occurs in nature, we observed plants have responses similar to those of plants grown at the same average, but at constant day/night temperature conditions typical of SPAR units (*33, 44*).

We have incorporated a number of process-level rate equations and algorithms into the cotton simulation model, GOSSYM/COMAX (*13, 43*) and tested the predictive ability of these algorithms using independent data sets that measured plant height, mainstem node numbers, and yield collected across the U. S. Cotton Belt. The data sets comprise both irrigated and rain-fed conditions, with three or more cultivars, and with several different soils. The performance statistics for GOSSYM/COMAX model prove the applicability of the algorithms generated using the SPAR facility (Table 2).

One can use similar procedures to develop computer-assisted tools for estimating the time for other developmental events to occur, such as the addition of a new mainstem node that supports a leaf and sympodial branch of a fully

Table 2. Performance statistics of the simulation model GOSSYM/COMAX for plant height, mainstem nodes, and yields determined from indeperdent data sets between 1987 to 1992 across the U. S. cotton belt.

Variable	Number of management units	Number of observations	Slope	R^2
Plant height, cm	50	235	0.9420	0.96
Mainstem nodes, no.	50	235	0.9986	0.94
Yield, kg ha^{-1}	38	38	0.9523	0.94

expanded leaf. Such an exercise can be readily performed, but using records for dates of planting and emergence and daily temperatures. This calculation allows one to document an almost reasonably quantitative estimate of crop status that is almost independent of location or calendar dates. Water and nutrient deficits seem to have little effect on developmental processes in cotton unless the deficiencies are extreme. However, such deficiencies dramatically affect leaf and stem growth processes and thus alter canopy development.

We have found both species and cultivars have different temperature-response functions (Table 1). For example, the minimum number of days required for two Upland cotton cultivars, DES 119 or DPL 5415, to produce the first square was observed at 28℃ (Fig. 11). Another Upland cultivar, DPL 50, required 5 to 8 more days to produce the first square at all temperatures. A Pima cotton cultivar, S-6, had a response for this developmental event nearly equal to that of an Upland cultivar, DES 119, up to 27 to 28℃, but in higher temperatures, Pima development was delayed by about 8 days at 30℃, and 15 days at 35℃ compared to DES 119. Pima cultivar, S-6, failed to produce squares if the temperature was above 35℃. This knowledge helps to identify the level of heat tolerance in different species and varieties, and illustrates that certain varietal traits can be selected to fit a niche environment.

Examples of responses to specific deprivations

The relationship between midday leaf water potential and both canopy net photosynthesis and stem growth in cotton clearly illustrates the effects of a single, well-defined environmental variable on different plant processes (Fig. 12). Results demonstrate that stem elongation is more sensitive to water deficits than photosynthesis. The relationships between these two plant processes differ under different environmentally-induced stresses, but they are consistent and predictable. The relationship must be appropriately modeled to be usable for producers to manage cultural practice for optimum benefits and for those developing cultivars with adaptations to stressful environments. For instance, the relationship between different plant processes may shift under nutrient-stress conditions. In well-fertilized plants, both photosynthesis and leaf expansion proceed at their potential rates; however, in N-deficient environments leaf expansion is reduced more than photosynthesis (Fig. 13).

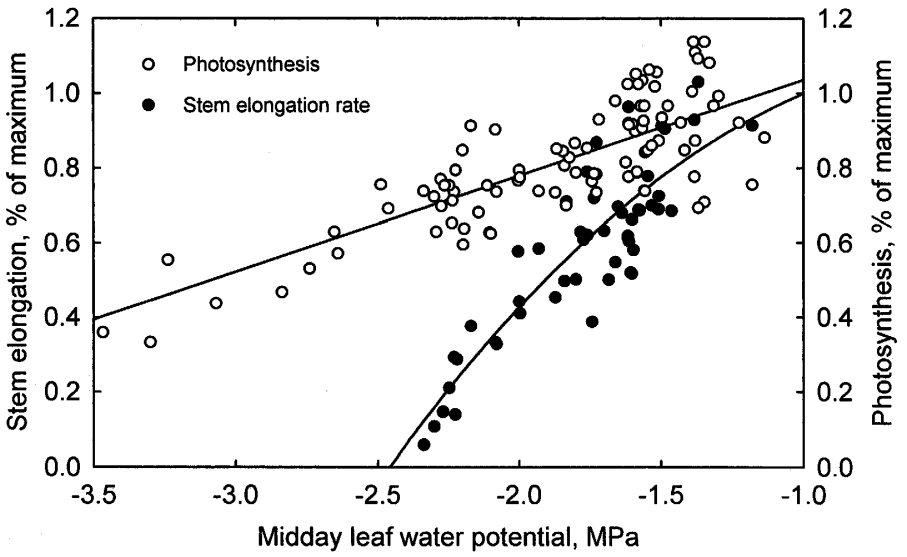

Fig. 12. Net photosynthesis and stem elongation during the linear growth phase (expressed as fraction of the maximum) as a function of midday leaf water potential for plants grown at a range of water deficit treatments. Photosynthesis was measured at 10-s intervals and averaged over 900-s intervals. The 900-s photosynthetic values were regressed against solar radiation for the same 900-s intervals, and daily values for photosynthesis at 1600 μmol m^{-2} s^{-1} are presented.

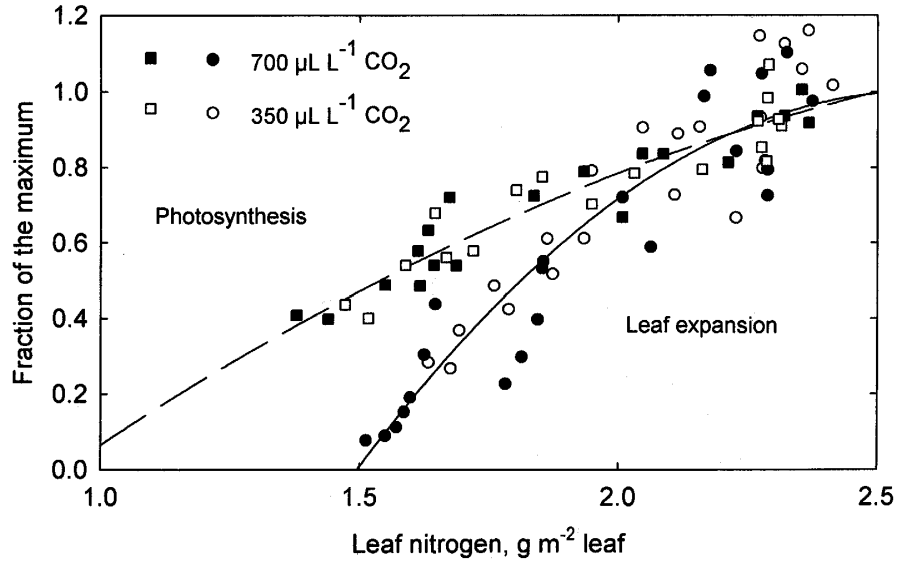

Fig. 13. Single-leaf photosynthesis and leaf area expansion in cotton grown in 350 and 700 μL L^{-1} air, and at 30/22℃ (day/night) as a function of leaf nitrogen. Photosynthesis and leaf area expansion are expressed as a fraction of maximum nitrogen levels. The uppermost fully expanded leaves were used for these measurements, as well as leaf nitrogen measurements.

Examples of high temperature injury in cotton fruit

The effect of high temperature on cotton flower and boll retention has been previously documented (*9, 10, 16, 25*), but no one has attempted to quantify the impact of well-defined high-temperature conditions. The cause of boll abscission in field environments is often confounded with other factors, such as

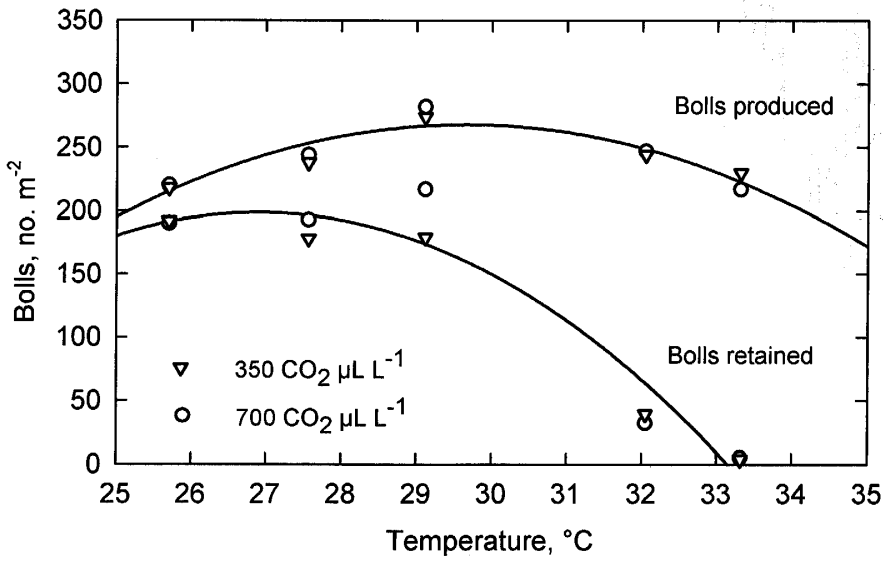

Fig. 14. Influence of temperature on fruit production and fruit retention for plants grown in ambient and elevated [CO_2]. Temperature treatments were imposed at initial flowering and the data were collected during 4 weeks of treatment (*42*).

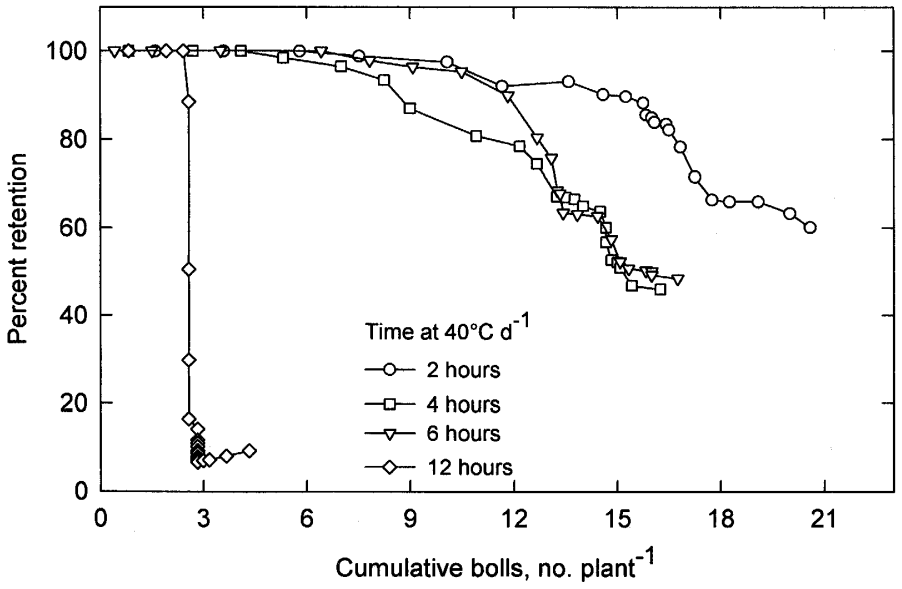

Fig. 15. Effects of hours per day at 40℃ on fruit retention. Plants were maintained at air temperature of 27℃, except for a few days when temperature was increased to at 40℃ (*see 34 for details*).

insect damage, boll load, or water and nutrient stresses. Figures 14 and 15 illustrate the effect of high-temperature injury on cotton fruit retention, as factors other than temperature were eliminated as uncontrolled variables. The mechanisms causing reproductive failure at high temperature are still not fully understood, but the consequences are clear and quantifiable. When plants were grown at 40℃, we observed injury to the developing ovules up to 12 days before pollination. Pollen was also damaged when plants were at 40℃ during development. Because, selection for heat-tolerant genotypes is an objective in both traditional breeding and biotechnology research programs, temperature-responses are certainly an area of research that needs further and more extensive study in many crops.

SUMMARY AND CONCLUSIONS

We have shown how controlled-environment facilities can be used to increase our knowledge of plant responses to individual environmental factors and how the information may be linked to a simulation model to predict crop responses in diverse and varying environments. The impact of cultural practices can be predicted with such information to further enhance management of the crop. Operating a SPAR facility to acquire such data will often be more economical than the use of field-plot experiments, because it allows the scientist to avoid many of the covarying and confounding factors that occur in field experiments. Thus, the basic processes can be related more directly to the environmental variables being studied.

As we progress in developing systems for understanding plant response to environment, whether in support of global climatic change research, the application of plants in the remediation of environmental conditions, or the increased application of precision agriculture technologies, the need for diagnostics and management decision aids will become more urgent. Mechanistic plant models and automated, user-friendly expert systems can facilitate selection of the optimum solutions to problems with many variables. Essentially all of the engineering and computing technologies needed to allow the use of variable and site-specific technologies, such as precision agriculture, are now available. However, our understanding of the plant ecophysiological responses to the environment as it relates to specific growth and developmental events require further development. Although comprehensive knowledge for developing a model for all aspects of plant growth and development may not be available, the ability to simulate some of the more significant and/or meaningful portions of the crop/ecosystem provides clarity and purpose to the research. For a model to correctly predict plant responses to environment, the crop and genotype-specific response functions must be realistically assembled. These relationships should include, but not be limited to, the phenological responses of specific genotypes to temperature and their responses to environmental stresses. We would, for example, expect to find quantifiable differences among genotypes in fruit-shed sensitivity to above-optimum temperature and to deficiencies of

water and/or nutrients. One might also find differences in sensitivity of fruit-shed to plant-C deficiency caused by an imbalance between photosynthesis, fruiting rate, and vegetative growth. These environment-genotype interactions can be measured and incorporated into a meaningful model. We have been able to demonstrate a model, GOSSYM/COMAX, that is based on appropriate concepts and processes, and has predictive capability in new environments. The simulation model can be used either alone or with other emerging newer technologies to display/disseminate useful plant growth and development information.

There are currently a variety of approaches and facilities to investigate plant responses to the environment. Among these, the SPAR facilities are optimized for the measurement of plant and canopy-level physiological responses to precisely controlled, but naturally lit, environmental conditions. The data that have been and will be obtained are unique and particularly instructive for applied and basic plant biologists.

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