Crop Modeling and Applications: A Cotton Example

K. Raja Reddy\textsuperscript{1}, Harry F. Hodges\textsuperscript{1}, and James M. McKinion\textsuperscript{2}

\textsuperscript{1}Department of Plant and Soil Sciences
Mississippi State University
Mississippi State, Mississippi 39762

\textsuperscript{2}USDA-ARS Crop Simulation Research Unit
Mississippi State, Mississippi 39762

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I. INTRODUCTION

One of the unusual features of agricultural production is the uniqueness of every season. Each year is unique in the timing of the rain, temperature regimes, etc., and when the uniqueness of the weather is combined with the individuality of cultural practices, soils, and variety characteristics, the crop production manager has more variables to consider than the human mind can reasonably organize. Resource managers need information organized within some sort of theoretical framework that can assist decision-making processes. They do not want to be confronted by a huge body of research data. With the availability of computers and a comprehensive knowledge of how crops respond to weather variables, mechanistic crop models can be developed to assist in making production-management decisions.

The purpose of this chapter is to describe the type of information useful for developing a physiologically based crop simulation model using cotton (*Gossypium hirsutum* L.) as an example. This report brings together data from experiments designed for a crop model, and it provides a general description of how a crop model can be developed, calibrated, validated, and used. It also shows how crop models may be used for technology transfer, including use in combination with precision agriculture and other forms of new technologies. Application of geographic information systems (GIS), global positioning satellites (GPS), and related improvements in field equipment monitoring and delivering devices to agriculture production systems will generate information not previously available. Simulation methodologies combined with expert systems technologies will close the gap between the GPS, GIS, and intelligent implements (II) and precision agriculture. That information will spawn a need for new and more powerful diagnostic tools to identify crop production problems and their solutions. Crop models that have physiological processes realistically incorporated into them, along with appropriate expert systems, may be integrated with these new technologies to provide such diagnostic tools.

Others have done considerable work on photosynthesis (Baker et al., 1983; Acock, 1991; Bonte and Loomis, 1991; Evans and Farquhar, 1991; Gutschick, 1991; Harley and Terhune, 1991; Norman and Arkebauer, 1991; Sinclair, 1991) so that will be discussed in only a limited way here. Similarly, root-zone processes and the topic of abscission are avoided. Those topics need to be developed and reviewed, but we cannot do so here.

Growth and development of plants in the natural environment are the result of the interactions of two major regimes; the genetic potential of individual plants and the external environment. Potential growth and developmental rates for a particular genotype are defined as the maximum rates achievable at a given temperature. These rates will be expressed as functions of temperature under optimum water and nutrient conditions. These potential rates may be decreased by stress factors. A stress factor is defined as any factor that reduces organ growth and/or developmental rate below its genetic potential at a given temperature. Controlled-environment facilities are necessary sources of process-rate data because they allow varying one environmental factor while maintaining other factors in nonlimiting conditions. Crop data obtained in this manner are less ambiguous and allow understanding of the responses to environmental variables and nutrient status. After potential rates of development or growth for a particular genotype have been established, the actual rates may be delayed or reduced by environmental and nutritional (including carbon) stresses. If major changes in genetic potential occur, then the model needs to be adjusted to reflect those changes. Typically small differences due to cultivar changes that are unique to the cultivar can be simulated with minor calibration adjustments to potential rates of the given species.

The minimum, optimum, and maximum temperatures at which plants grow and develop vary among species (Kiniry and Bonhomme, 1991). Although cotton is produced worldwide, it is grown in a relatively narrow temperature range compared to other species. For example, the minimum temperature threshold for cotton is 12–15°C, whereas for maize, pearl millet, rice, sorghum, soybean, and sunflower it is 7–9°C. The optimum and maximum temperatures also vary among species and are poorly defined and quantified. Planting dates of the crops are varied from year to year and among locations depending on temperature conditions. The suitability of a crop to a new location depends not only on the threshold temperatures but also on the length of growing season. Long-term average daily temperature is shown for several U.S. cotton-producing regions and Moro, Indonesia, a maritime equatorial region of the world (Fig. 1).

These long-term temperatures illustrate that several days per year can be ex-
The atmospheric concentration of CO₂ and other "greenhouse gases" has increased globally during the past 200 years. Recent CO₂ measurements at Mauna Loa, Hawaii show a 12% increase in the mean annual concentration in 32 years, from 316 μmol·l⁻¹ in 1959 to 354 μmol·l⁻¹ in 1990 (Keeling and Whorf, 1991). That increase, and the continuing rise at the rate of 1.8 μmol·l⁻¹ per annum, are likely to cause a change in climate (Roty and Marland, 1986; IPCC, 1990). Global circulation models predict a 1.5–5.9°C rise in global surface temperature, change in precipitation patterns, and cloud cover in the next 50–70 years (Washington and Meehl, 1984; Manabe and Wetherald, 1987; Hansen et al., 1988; Wilson and Mitchell, 1987; Schneider, 1989; Adams et al., 1990). Agricultural productivity is very sensitive to these climate change variables, and understanding their effects on major agricultural crops would allow lead time in adjusting to these changes.

If there is a rise in average global temperature, as has been hypothesized based on global circulation models, a 5°C increase would cause most areas where cotton is currently grown to have above-optimum temperatures during much of the summer. If such temperature changes occur, temperature will surely hamper production of cotton and other seed-bearing crops (Baker and Allen, 1994; Corroy et al., 1994; Rawson, 1995; R. Reddy et al., 1995c). It will also increase our need for understanding and predicting crop responses to temperature and other environmental factors.

A 5°C increase in daily temperatures at Stoneville, Mississippi, would bring temperatures to what we now consider acceptable cotton planting temperature about
45 days earlier in the year. If cotton planting occurs 45 days earlier than is normally practiced today, and if other production practices remain the same, then harvest would begin about August 15. Such production practices would allow much of the cotton growing season to occur in a higher solar radiation environment than is experienced today; however, a major portion of the flowering and boll growth period would occur during the period when temperatures are predicted to be above optimum. Environmental factors are often covariants resulting in several interacting changes occurring simultaneously, e.g., more rain is usually associated with less solar radiation. Crop responses to changing weather conditions also involve covariants, e.g., higher temperature increases transpiration. These crop- and weather-related changes quickly become too complex to accurately analyze by conventional ways and allow one to find the most appropriate combination of management practices to utilize the new conditions. A crop model that simulates plant responses to its physical world provides quantitative information needed to predict the effect of new management practices on crop performance.

It is difficult to build process-level simulation models from data collected in the field because many factors often simultaneously affect these processes; and because many environmental and biological factors are covariants. This makes it literally impossible to reasonably assess the causes and effects with accuracy. We have conducted numerous experiments in sealed, naturally lit plant growth chambers in which temperature, atmospheric [CO₂], water, and nutrients were varied independently while other factors were maintained at nearly optimum conditions (K. R. Reddy et al., 1992a,b, 1993a,b, 1995d, 1996a,b). This allowed us to determine the relationships of the varied factor with crop response(s). These experiments were conducted in environments in which major efforts were made to allow only the variable being tested to be limiting. Plants were typically grown in well-watered sand and adequately fertilized with all known mineral nutrients. Plants were also grown in higher [CO₂] to enhance photosynthesis to avoid carbon deficits, and the plants were not subjected to disease or insect infestations. Thus, the plants were grown at their potential rates and limited only by the variable being tested. Potential rates may be estimated from relationships developed in this manner and then corrected by stress factors known to occur in the natural environment. Thus, potential rates may be estimated from the temperatures that occurred and actual rates simulated by reducing the potential rates with "stress factors."

Cotton belongs to the genus *Gossypium* of the Malvaceae family. Of the 39 species of the genus that are diverse in habitat, only 4 produce commercial lint. The upland and acala varieties belong to *G. hirsutum* L., and extra-long staple pima and sea island or Egyptian varieties (G. barbadense L.) are grown commercially throughout the world. Upland cotton is grown on more than 5 million hectares in the United States and more than 34 million hectares worldwide (USDA, 1989). Much of the world’s production is in arid and semiarid climates and must be irrigated for commercial production.

To comprehend a plant’s responses to its environment, one needs to understand the morphological characteristics of the crop and its responses to temperature, water, and nutrient supply. It is necessary to describe the plant as a whole and each facet of growth at the organ level. The growth and development of each plant organ are also influenced by competition from other organs as well as by environmental conditions. Mauney (1968) described the anatomy and morphology of cultivated cotton. The primary axis of the cotton plant results from elongation and development of the embryo. In the dormant seed, the primary axis consists of a radicle, a hypocotyl, and a poorly developed epicotyl. The epicotyl contains one true leaf initial and a dome of meristematic cells. The growing cotton plant actively proliferates new cells on many fronts. Thus, all the differentiation of the vegetative framework above the cotyledons takes place after germination.

Cotton is indeterminate in growth habit in that the mainstem apex continuously initiates leaves and axillary buds. The axillary buds on the lower nodes develop into vegetative or monopodial branches if conditions are favorable. The axillary buds in the upper nodes, normally above node 5, develop into fruiting or sympodial branches. Vegetative branches behave much like the mainstem in that they produce both vegetative and fruiting branches. Fruiting branches, on the other hand, initiate one true leaf and then terminate as a flower. Branch elongation is accomplished by growth of axillary buds producing a sympodial zigzag structure (Mauney, 1984; Mutsaers, 1983a).

The phylloxy (arrangement of leaves on the stem) is spiral in cotton, with each leaf being 90° above the last. A stem may have either a counterclockwise or a clockwise phylloxy. Mauney (1968) stated that half of the stems tend to spiral to the right and half to the left, and occasionally a stem may be seen in which the phylloxy has reversed direction. Thus, potential patterns of growth are determined by the apical and axillary meristems.

**II. PHENOLOGY**

Crop growth and development are driven by canopy temperature and will be modulated by water and nutritional supply (Gupta, 1987; Hodges, 1991). Plant phenology is the study of the time between like events, dissimilar events, or the duration of a process. Like events include the time intervals between mainstem leaves or branch leaves on a plant. Unlike events include the intervals between plant emergence and formation of a flower bud, flower, or mature fruit. Duration of a process might include the period between unfolding of a leaf, or the appearance of an internode, and the time the leaf or internode reaches maximum size. Potential developmental events were defined as the genetic potential of a species at a given temperature where the plants are grown in a stress-free environment. These
rates were obtained from experiments conducted in controlled environmental facilities (K. R. Reddy et al., 1992a,b, 1993a,b, 1995a,b,c, 1996a,b; V. R. Reddy et al., 1994a,b). It is nearly impossible to determine potential process rates with any other known techniques. The important periods in the life of most plants can be distinguished and are predictable. Phenological information is essential for the analysis and understanding of source-sink interactions in plants.

Hesketh and co-workers performed a series of experiments in the late 1960s and early 1970s on many phenological events of cotton cultivars (Hesketh and Low, 1968; Moraghan et al., 1968; Low et al., 1969, Hesketh et al., 1972). K. R. Reddy et al. (1993b, 1996a,b) have studied the phenological rate functions for modern upland and pima varieties. They also added duration of expansion or elongation functions for leaves and internodes that were not previously available. The data of K. R. Reddy et al. (1993b, 1996a) are in the form of daily developmental rates. This is the form needed by modelers for building process-level dynamic simulation models. The data of K. R. Reddy et al. (1993b, 1996a) were collected in a wide range of temperatures and in both ambient and twice-ambient carbon dioxide levels. Compared to the earlier data on phenology (Hesketh and Low, 1968; Hesketh et al., 1972), this has broader applicability for model development. Genetic improvements that occurred in recent years resulted in cultivars that are earlier in maturity than cultivars grown 25–30 years ago (Wells and Meredith, 1984; K. R. Reddy et al., 1993b, 1996a). Models developed from such a database may be useful both in present-day crop production environments and in the future hypothesized warmer environments with higher CO₂.

CROP SIMULATION MODELS

Crop simulation models that were developed to study global climate (Wall et al., 1994) or used to study the possible impacts of climate change on crop production (Curry et al., 1990; Fisher et al., 1995; Adams et al., 1999) did not use data that were collected in potential growing conditions. These studies, however, should be considered somewhat preliminary because the crop models used were based on a much narrower temperature range and the phenological information was collected at present-day atmospheric [CO₂] or at slightly lower levels.

A. REPRODUCTIVE INITIATION

Temperature and photoperiod are the two main environmental factors that determine flowering in young and established plants. Commercially grown cotton cultivars are very sensitive to temperature but not sensitive to photoperiod, so floral formation and floral development in these cultivars are relatively simple to understand. The formation of squaring marks the beginning of the reproductive phase in cotton. The rate of the first flower bud, or square formation, is very temperature dependent. The time from emergence to observance of first square, 3 mm in length which coincidences with the unfolding of the subtending leaf, is expressed as the reciprocal of days (Fig. 3A). That allows one to use the information by simply adding daily developmental rate at any temperature and predicting square formation when the sun equals one or greater (K. R. Reddy et al., 1993b). The base temperature, below which no progress occurred toward flower bud formation in cotton, was 15°C, the maximum rate of progress occurred at about 30°C, and progress at temperatures above 30°C was slower than that at 30°C.

One of the primary ways cultivars differ in maturity is determined by the time from emergence to first square (K. R. Reddy et al., 1993b). Cotton breeders have successfully shortened this developmental phase, and many of the modern upland

![Diagram](image)

**Figure 3** The role of temperature on daily progress of various phenological events: (A) from cotton plant emergence to first flower bud formation (square), (B) square to flower, and (C) flower to open boll (K. R. Reddy et al., 1993b).
and pima cultivars produce squares a few days earlier than cultivars used three to four decades ago (K. R. Reddy et al., 1993b; Moraghan et al., 1968). For example, at 27°C, the plants used by Moraghan et al. (1968) required 38 days to square for cv. M-8, the plants in Hesketh et al. (1972) took about 34 days, whereas the modern upland cultivars took only 25 days at the same temperature (K. R. Reddy et al., 1993b). The cultivars were different in all three studies.

Baker et al. (1983) developed a cotton model, GOSSYM, that simulated this phenological response based on the temperature-response data of Moraghan et al. (1968). When this model was first tested, they found that the model predicted 20% more time to reach first square than was observed in field conditions. They calibrated their model by introducing multipliers into the temperature response function for this phenological event. This adjustment improved the predictions at near-optimum temperature, but predicted rates were still too fast at both below- and above-optimum temperatures.

We found a modern pima cotton cultivar decreased its rate of progress toward first square more than a modern upland cotton cultivar at temperatures above 27°C, suggesting that it was more sensitive to high temperature than upland cotton (Fig. 3A). The modern cultivar took 18% less time to reach first square at 20 and 25°C than the cultivar reported by Moraghan et al. (1968), but 36% less time to form first square at 30°C. This suggests that modern pima cultivars are not only earlier but are also more heat tolerant than those pima cotton cultivars grown four decades earlier (Lu et al., 1994).

There are several reasons for the differences between our results and the earlier published work. One is differences among cultivars (Wells and Meredith, 1984), and another is uncertainty of the environments from which the developmental rates in the earlier work were determined and the definition of square formation. Our data show that modern cultivars of both cotton species formed squares much earlier and produced squares or other fruiting structures at higher temperatures than cultivars grown several years ago. Such data are needed to improve the predictive capabilities for crop management and yield forecasting models.

The effect of temperature on development rate has often been described by using a thermal time concept. The most widely used thermal time method is the growing degree days procedure, which relates developmental rate linearly to temperature above a species- or cultivar-specific base temperature at or below which developmental rate remains zero (Hedges, 1991; Ritchie and NeeSmith, 1991). The growing degree days concept has been used for simulating days to first square in cotton and several other developmental events (Jackson, 1991; Hearn, 1994). This procedure has been only moderately successful because of the variability in plant responses, but may be satisfactory if above-optimum and low-temperature thresholds are adequately considered in developing the relationships. The reason for variability in numbers of heat units required to reach first square in different weather conditions is apparent from Fig. 3A. The response curves are nearly linear to about 27°C, but at higher temperatures the rate of progress toward squaring is slower. This results in accumulating degree days very rapidly on hot days, but phenological progress is in fact slower at high temperatures than at 27°C. K. R. Reddy et al. (1993b) and Cognée (1988) found that a quadratic function was superior to any other form to describe the relationship of developmental rate to temperature in cotton.

Because we need to predict crop performance in a range of temperatures (Fig. 1), it was important to know the appropriate response functions at all meaningful temperature conditions. The rate functions describing the reciprocal of days from emergence to first square (1/duration, day−1) for upland and pima cotton cultivars are as follows:

\[
\text{Upland, } Y = -0.1265 + 0.01142X - 0.0001949X^2; \quad r^2 = 0.98 \quad (1)
\]

\[
\text{Pima, } Y = -0.1593 + 0.01473X - 0.0002749X^2; \quad r^2 = 0.99, \quad (2)
\]

where X is average temperature for that period.

Above-optimum temperatures delayed progress toward fruiting and extended the vegetative period. In the natural environment, high temperatures are often associated with water deficits, which result in partially closed stomates and even higher leaf temperatures (Fig. 2).

B. Square Maturation Period

The interval from square formation to flowering is presented in the same way as square formation (Fig. 3B). Rate of progress toward flowering was equally sensitive to temperature throughout the temperature range except at the above-optimum temperature for growth (27°C). Daily progress from squaring to flowering at above-optimum temperature did not decrease as rapidly as formation of squares. Similar temperature response functions were published by Hesketh and Low (1968) for the cultivars used two or three decades ago. At 27°C, the plants of Hesketh and Low (1968) required 20 days from square to bloom, whereas plants in Hesketh et al. (1972) took about 26 days. The modern cultivars reported by K. R. Reddy et al. (1993b) required about 24 days. The pima cotton cultivars required more time to form flowers from squares at all temperatures. After flowering begins, the plants are more subject to source/sink imbalance because bolls are major photosynthetic and mineral nutrient sinks in cotton plants. As fruit load increases, the rate of vegetative growth and development decreases because carbon becomes limited, fruit loss increases, and vegetative growth eventually stops completely. This process is often described as "cutout" in cotton (Guinn, 1986; Sadras, 1995). If insects or environmental conditions cause boll abscission, vegetative growth will resume. Vegetative growth will also begin, if weather is suitable, when bolls
mature and are no longer energy sinks. The daily developmental rates for square 
maturation period (1/duration, day\(^{-1}\)) as functions of temperature for upland and 
pima cotton cultivars are as follows:

\[
Y = -0.1148 + 0.009570X - 0.0001432X^2; \\
\text{Upland, } r^2 = 0.94 
\]

\[
Y = -0.06096 + 0.001817X - 0.00009917X^2; \\
\text{Pima, } r^2 = 0.94, 
\]

where \(X\) is average temperature for that period.

### C. Boll Maturation Period

Daily progress from flower to mature fruit (open boll) was nearly linear through- 
out the temperature range tested (Fig. 3C). Progress to mature fruit showed no 
evidence of slowing at temperatures above 30\(^\circ\)C as had the earlier-formed repro- 
ductive structures. The boll maturation period of these modern upland cultivars 
was slightly faster at low temperatures, but relatively slower at high tempera- 
tures, than those reported by Hesketh and Low (1968). The difference between pima 
and upland cotton cultivars for boll maturation period was about 2–5 days at tem- 
peratures above 25\(^\circ\)C, and the regression lines are not parallel. As the bolls matured 
and opened, the carbohydrate stress was slowly alleviated and regrowth occurred 
if conditions were favorable. The daily developmental rates from bloom to open 
boll or boll maturation period (1/\text{duration}, day\(^{-1}\)) as functions of temperature for 
upland and pima cotton cultivars are as follows:

\[
Y = -0.02610 + 0.002159X - 0.00001528X^2; \\
\text{Upland, } r^2 = 0.99 
\]

\[
Y = -0.01863 + 0.001803X - 0.00001368X^2; \\
\text{Pima, } r^2 = 0.99, 
\]

where \(X\) is average temperature for that period.

### D. Leaf Unfolding Interval Rates

Developing mainstem and fruiting branch nodes are important aspects of cot- 
ton development because these processes determine the number of leaves pro- 
duced and thus canopy development and interception of photosynthetically active 
radiation before the canopy closure in cotton. The rate of leaf formation was de- 
fined as the time required from the day the leaf unfolded until the next leaf un- 
folded on the mainstem. In cotton, we assumed a leaf unfolded the day three main

veins were clearly visible. Defined in this way, leaf appearance can be used as a 
discrete event. Others have used the Haun scale of leaf emergence over short peri- 
ods, but that method estimates leaf emergence by comparing the size of the 
emerging leaf relative to the preceding leaf.

The rates of leaf unfolding on the mainstem and on fruiting branches were func- 
tions of temperature (Fig. 4A). Daily developmental rates were accumulated until 
the summed value was equal to one or greater, which predicts a new leaf should 
be initiated either on the mainstem or on the fruiting branches. Developmental 
rates were not linear over the biologically meaningful temperature range. Leaf un- 
rolling rates of both mainstem and fruiting branch leaves increased with increasing 
temperature. At 30\(^\circ\)C, only 2.2 days were required to produce a new leaf on 
the mainstem, whereas at 20\(^\circ\)C, 5 days were needed to produce a mainstem leaf.

![Figure 4](image)

Figure 4. The role of temperature on daily developmental rate of phytochron intervals: (A) main- 
stem and fruiting branch nodes (Reddy et al., 1996a) and (B) days required to produce a leaf at each main- 
stem node at an optimum temperature (26.4\(^\circ\)C). Arrows identify the node of first fruiting branch and 
the node of unfolding leaf at first flower (R. R. Reddy et al., 1995a).
Fruiting branches, on the other hand, required 6 days at 30°C and 9.5 days at 20°C to produce a leaf. The rate of leaf formation on fruiting branches is considerably slower than that on the mainstem because the branch primordium develops a flower. An axillary meristem then forms from which the next leaf and internode and a flower are produced. Thus, the ratio of mainstem and fruiting branch leaf unfolding interval was not constant at different temperatures as assumed by others (Heath, 1969; Mutsaers, 1983a).

The most important differences between the two data sets and the data we obtained were decreased rates of leaf formation at higher temperatures found in our data and that our conditions also included a wider temperature range. Consequently, the growing temperature alters the architectural form of the plant. Leaf unfolding intervals and flower appearance intervals were not different from each other. Similar results were reported by Hesketh et al. (1972). Their plants required 2.4 days at 27°C to produce a leaf on the mainstem, whereas modern upland cultivars required 2.7 days (K. R. Reddy et al., 1996a).

Fruiting or sympodial branch leaf unfolding interval at 27°C was 7 days for cultivars used by Hesketh et al. (1972), whereas the modern cultivars reported by K. R. Reddy et al. (1996a) required only 5.8 days. Unlike many other phenological events, there were no differences between upland and pima cotton cultivars for leaf developmental events. The daily developmental rates for mainstem and fruiting or sympodial branch leaf unfolding intervals (1/duration, day⁻¹) are as follows:

\[
\text{Mainstem plastochron, } Y = -0.6698 + 0.0570X - 0.0006765X^2; \ r^2 = 0.94
\]

\[
\text{Sympodial plastochron, } Y = -0.3645 + 0.03389X - 0.0005199X^2; \ r^2 = 0.84,
\]

where \(X\) is average temperature for that period.

Position on the plant also had some effect, probably indirectly, on rate of mainstem leaf development. For some unexplained reason, the rate of prefruiting leaf development was considerably slower than that of postfruiting branch leaf development (Fig. 4B). The prefruiting leaves were produced at progressively more rapid rates as plants added mainstem leaves. Because young plants partition a larger proportion of their photosynthates to roots, we hypothesized that prefruiting leaves were delayed due to carbohydrate deficits (Hodges et al., 1993). However, seedlings grown in twice-ambient \([\text{CO}_2]\) did not produce prefruiting nodes any more rapidly than plants grown in ambient \([\text{CO}_2]\). Because photosynthesis is more rapid in twice-ambient \([\text{CO}_2]\) (K. R. Reddy et al., 1995c; V. R. Reddy et al., 1995), one would have expected the additional carbohydrate to overcome the hypothesized carbon deficit if that was the rate-limiting factor.

Production of mainstem leaves or nodes after node 17 was probably slower due to carbohydrate deficits. The leaf at node 17 was produced when the first flower at node 6 was produced. After that time, flowers were added rapidly in the lower positions on the plant. The developing bolls soon became important sinks for all available metabolites and probably delayed vegetative growth (Sadras, 1995, and references cited therein).

Leaf unfolding intervals, generally referred to in the literature as plastochron intervals, were not different from the square appearance intervals in cotton (Hesketh et al., 1972; K. R. Reddy et al., 1993b, 1996a). Squares will normally appear when the leaf at a given node is unfolded with main veins visible from the top. Defined in this way, the same response rate functions can be applied for square intervals to mark the appearance of reproductive organs. Other researchers have distinguished between plastochron intervals, the time between two successive leaf primordium initiations that can be observed with a dissecting microscope, and plastochron intervals. Plastochron intervals may be more easily verifiable in the field than plastochrons.

E. Leaf Expansion and Internode Elongation Duration

The reciprocal of duration of leaf expansion and internode elongation is a measure of the rate at which these processes are completed (Fig. 5). Internodes typically took less time at all temperatures to reach final length compared to leaves.

![Figure 5](image_url) Role of temperature on duration of mainstem leaf expansion and internode elongation rates. Daily progress is the reciprocal of days to expand mainstem upland and pima cotton leaves. Expansion duration was similar regardless of position on the mainstem (K. R. Reddy et al., 1996a).
Leaf petiole elongation occurred simultaneously with lamina expansion. Leaf expansion duration at a particular temperature was similar despite leaf position on the mainstem (K. R. Reddy et al., 1993a). Leaf expansion duration and internode elongation duration data were not available for cotton prior to the reports of K. R. Reddy et al. (1993b, 1996a).

The equations describing the rate of leaf expansion duration (1/duration, day⁻¹) and internode elongation duration (1/duration, day⁻¹) are as follows:

Leaves, \[ Y = -0.09365 + 0.01070X - 0.0001697X^2; \]
\[ r^2 = 0.95 \]  (9)

Internodes, \[ Y = -0.04312 + 0.007383X - 0.0001046X^2; \]
\[ r^2 = 0.96 \]  (10)

where \( X \) is average temperature for that period.

III. GROWTH OF INDIVIDUAL ORGANS

A. LEAF AREA EXPANSION AND INTERNODE ELONGATION RATES

To mechanistically simulate plant height and leaf area development throughout the season, it was essential to simulate potential leaf and internode growth rates. The mechanism of internode elongation is similar in both dicots and monocots, although development is acropetal in dicots and basipetal in monocots because of the position of intercalary meristem (Evans, 1965; Kaufman et al., 1965; Sachs, 1965; Morrison et al., 1994). Growth is defined as increase in mass, area, or length. Because much of the plant is not growing, one needs to simulate the responses of the only growing organs. Such detail is necessary because the individual organs have a sigmoidal growth pattern. An internode just beginning to elongate has a different growth potential in a particular set of conditions than it has in its linear phase of expansion in the same conditions. Thus, to simulate plant height one should model the potential responses of the elongating internodes, including the duration of the elongation process, to the conditions that prevail during elongation. It is assumed that we are simulating plants grown in the natural environment, and the primary role of solar radiation is to drive photosynthesis and transpiration.

Rates of elongation were calculated by plotting relative leaf expansion rate (RLER) and relative internode elongation rate (RIER) as functions of days after leaf unfolding. These functions were calculated from daily measurements of leaf area and the subtending internode lengths for each leaf and internode on plants grown in a range of temperatures and \( \text{CO}_2 \) environments. The RLER and RIER decreased with age. The linearly extrapolated intercepts provided estimates of the maximum RLER (cm² cm⁻² day⁻¹) or RIER (cm cm⁻¹ day⁻¹) on Day 1. The slopes of the RLER or RIER with age for each leaf (cm² cm⁻² day⁻¹) or internode (cm cm⁻¹ day⁻¹) were also calculated. The maximum RLER or RIER and slopes are functions of temperature (Figs. 6 and 7).

The intercepts and slopes for leaves and internodes changed progressively with temperature, and the two were inversely related. The maximum RLER (Day 1) was 23% higher than the maximum RIER at all temperatures, whereas the slope, or the rate of growth reduction with age, was 5% lower for the leaves than for the internodes. The effect of temperature on final leaf area or final internode length is the net result of both temperature effects on duration (Fig. 5) and rates of growth
Figure 7. Influence of temperature on maximum relative internode elongation rate (RIER) and rate of reduction with age (Reduction rate or the slope, cm cm⁻¹ day⁻¹). The maximum RIER and slope were calculated by linear regressions fitted between internode age and relative internode elongation rate for each internode at each temperature and [CO₂] (K. R. Reddy et al., 1996a).

(Figs. 6 and 7). The equations describing these rate parameters for leaves as functions of temperature are as follows:

\[ Y = -0.03390 + 0.02041 \cdot X; \]
\[ r^2 = 0.95 \]

Slope (cm² cm⁻² day⁻¹), \[ Y = 0.01341 - 0.001879 \cdot X; \]
\[ r^2 = 0.98, \]

where \( X \) is average temperature for that period.

The equations describing the rate parameters for internodes as functions of temperature are as follows:

\[ Y = -0.001427 - 0.01665 \cdot X; \]
\[ r^2 = 0.97 \]

\[ \text{Slope (cm cm}^{-1}\text{ day}^{-1}), Y = 0.02479 - 0.001994 \cdot X; \]
\[ r^2 = 0.97 \]

where \( X \) is average temperature for that period.

B. LEAF AREA AND INTERNODE LENGTH AT LEAF UNFOLDING

Leaf area and internode length at leaf unfolding increased progressively at higher positions on the mainstem until first square (Fig. 8A) or first flower (Fig. 8B) were formed. After first square was initiated, the initial leaf area decreased at higher positions on the mainstem. The length of the internodes at leaf unfolding also decreased after the first flowers were formed. Mature leaf areas followed a similar pattern on the mainstem nodes as found for leaf areas at leaf unfolding (Fig. 9A). Mature leaf areas increased as mainstem node number increased until node 6 was produced, then succeeding mature mainstem leaves were progressively smaller with higher node position on the plant. The first square was produced when the flowering branch formed on node 6. A possible explanation is that initial leaf sizes

Figure 8. Profile of leaf areas (A) and internode lengths (B) at leaf unfolding on the mainstem at both CO₂ concentrations for plants grown at 37°C. Arrows and nodes 5 and 15 indicate appearance of a first square and first flower on the mainstem (K. R. Reddy et al., 1996a).
and leaf area expansion were competing with branches, roots, and reproductive structures for available photosynthates. Squares were formed when the leaf at nodes 5–7 unfolds; then, fruiting branches and other reproductive structures are initiated more rapidly with time and compete for the same resources.

Initial internode length, on the other hand, increased linearly as node number increased until the plants started producing bolls, and then each succeeding internode was shorter (Fig. 9B). Bolls were first produced when the leaves at nodes 15–17 were unfolded. Mature internode lengths also followed a similar pattern on the mainstem as found for internode lengths at leaf unfolding. Similar patterns in mature leaf areas were observed in the field (Constable and Rawson, 1980; Constable, 1985) and growth chamber studies (Mutasa, 1983a). Mutasa (1983a) found a positive relationship between leaf sizes and cell number. Mature internode lengths increased as mainstem node number increased until nodes 15–17, then subsequently produced internodes were progressively shorter. Again, the first flower was produced at the time the leaf on node 17 was unfolding. Mature internode lengths were correlated with internode lengths at leaf unfolding ($r^2 = 0.78$). It seems likely that potential internode lengths and leaf areas were determined by the time of leaf unfolding. Similar results were observed for mature internode lengths in growth chamber studies by Mutasa (1984). The equations describing initial leaf areas (cm$^2$) and internode lengths (cm) as functions of mainstem nodes are as follows (Fig. 8):

Leaves 1–6, $Y = 6.061 + 1.8069X; r^2 = 0.91$ \hspace{1cm} (15)

Leaves 7 and above, $Y = 18.3812 - 0.523X; r^2 = 0.95$ \hspace{1cm} (16)

Internodes 1–14, $Y = 0.05738 + 0.05605X; r^2 = 0.93$ \hspace{1cm} (17)

Internodes 15 and above, $Y = 1.5859 - 0.0407X; r^2 = 0.91$ \hspace{1cm} (18)

where $X$ is mainstem node number.

Leaf area and internode lengths at leaf unfolding for leaves 10–12 increased as temperature increased to about 27–30$^\circ$C and declined at higher temperatures (K. R. Reddy et al., 1995a). The equations describing these processes for leaves (cm$^2$) and internodes (cm) as functions of temperature are as follows:

Leaves, $Y = -18.599 + 2.186X - 0.0381X^2; r^2 = 0.62$ \hspace{1cm} (19)

Internodes, $Y = -0.06853 + 0.1077X - 0.002031X^2; r^2 = 0.11$ \hspace{1cm} (20)

where $X$ is average temperature for that period.

The initial branch leaf area decreased linearly with nodes on the branches. This was consistent with the change in mature leaf area by position on the branch (Mutasa, 1983a,b). This suggests that leaf area was largely determined by the number of cells formed before the leaf began to expand. The equation describing initial leaf area (cm$^2$) as a function of branch node number is as follows (K. R. Reddy et al., 1995a):

$Y = 13.457 - 1.179X; r^2 = 0.98$. \hspace{1cm} (21)

where $X$ is branch node number.

C. Specific Leaf Weight and Starch Accumulation

The specific leaf weight of the leaves on plants grown at 29/12$^\circ$C day/night temperatures was more than that of leaves produced at other temperatures, and the plants grown in the high CO$_2$ environments at that low temperature had significa-
Cotton growth rates were severely limited by 20/12°C day/night temperatures. Photosynthesis was affected less by temperature than by growth, resulting in the accumulation of nonstructural carbohydrates. The high CO₂ environment favored the production of additional carbohydrates, but temperature limited growth and thus carbohydrate utilization.

Transmission electron micrographs of leaf chloroplasts grown in high and ambient CO₂ at various temperatures also illustrate the previous result (K. R. Reddy et al., 1996b). When leaf cross sections were examined at lower magnification, chloroplast starch grains were conspicuous and copious in all the leaves except those in which growth was rapid. Starch grains were more abundant in the chloroplasts of leaves grown in high CO₂ environments and the most abundant in plants grown at low temperatures, where growth was slowest.

The equations describing these processes for specific leaf weight (g dm⁻²) and total nonstructural carbohydrate contents (%) as functions of temperature are as follows:

Specific leaf weight:

\[ Y = 2.050 - 0.0101X + 0.00159X^2; \quad r^2 = 0.95 \]  \hspace{2cm} (22)

\[ Y = 3.884 - 0.0240X + 0.000369X^2; \quad r^2 = 0.94 \]  \hspace{2cm} (23)

Total nonstructural carbohydrate content:

\[ Y = 78.79 - 5.2919X + 0.0887X^2; \quad r^2 = 0.91 \]  \hspace{2cm} (24)

\[ Y = 129.272 - 8.3081X + 0.1348X^2; \quad r^2 = 0.84 \]  \hspace{2cm} (25)

where X is average temperature for that period.

**D. INTERNODE MASS ACCUMULATION RATE**

Internode mass accumulation of cotton plants grown in optimum water and nutrient conditions increased as a function of internode age (Fig. 11). Unlike elongation duration (Fig. 5) and rate of elongation (Fig. 7), internode growth rate (g day⁻¹) continuously increased throughout the growing season. The growth rate followed two distinct patterns, one during the expansion phase (0–20 days) and the other during the rest of the growth period (20+ days). The growth rate from 20 days onwards was 338% more than the growth rate during the expansion phase.
(0–20 days). Thus, internode growth rate, along with internode elongation patterns, was an important factor in determining sink strength.

The equations describing potential internode growth rate (g cm\(^{-1}\) day\(^{-1}\)) as functions of age (days) are as follows:

\[
0\text{--20 days}, \ Y = 0.005032 + 0.002692X; \ r^2 = 0.46 \\
21\text{+ days}, \ Y = -0.01828 + 0.01178X; \ r^2 = 0.91,
\]

where \(X\) is the age of the internode after initiation.

**E. Root Growth**

In our growth chambers, the aboveground cabinet temperatures are controlled within ±0.5°C, but root environment temperatures are not controlled. Therefore, the soil surface temperature reflects the effects of the aerial chamber temperature, but only small or no differences caused by chamber air temperature occur in soil temperature at 25 cm or deeper (V. R. Reddy et al., 1994a). The soil bins have one face (1 x 2 m) that is glass. This allows observation of root growth on regular intervals and the estimation of root growth activity by treatment. It appears that root numbers were limited by temperature when the aboveground parts were below 22°C, but differences in root numbers were not found at higher temperatures (Fig. 12). The temperature response curves of the data on root length were similar to those of root numbers. Root length per axis increased as temperature increased throughout the temperature range tested. If conditions prevailed that caused flower

or fruit abscission, then greater root growth occurred, apparently because of less competition for available nutrients. The most root growth occurred at the temperature optimum for vegetative shoot growth. Apparently, if temperature caused fruit abscission, additional root growth occurred because of sparing nutrients that might have been used for fruit growth. Without the fruit, those nutrients, presumably carbon, were available for additional vegetative growth, including roots (Pearson et al., 1970). The experiments were not designed to determine the effect of temper-
F. SQUARE AND BOLL GROWTH

The data for square and boll development were collected from plants grown in both ambient and twice-ambient [CO₂] to derive potential growth rates. Potential growth of developing squares was temperature dependent and had a curvilinear response; growth rate increased to 22°C but did not grow more rapidly at higher temperatures (Fig. 13A). Square growth rate was low and less sensitive to high temperature than boll growth (Fig. 13B). Boll growth was much more rapid, had a distinct optimum temperature at about 28°C, and declined rapidly at higher temperatures. Boll mass increased with age of the bolls, but no difference in weight per boll occurred due to different CO₂ environments \( (P = 0.05) \) (Fig. 14). Plants grown in elevated [CO₂], however, produced more fruiting mass per plant and the differences in total fruiting structure mass were the result of more bolls and squares produced rather than boll size (K. R. Reddy et al., 1995d).

With increasing temperature, there was a shortening of duration of boll filling and slowing of the rate of filling at temperatures above 28°C (Fig. 3C and 13). Faster crop developmental rates resulted in less time available for the process or event to occur. Above-optimum temperature caused less time to be available for a fruit to develop, and it also reduced the rate of growth per day. Thus, any fruit grown at high temperatures was smaller than a similar fruit grown at optimum temperatures. This result was also true in rice (Baker et al., 1992), wheat (Wardlaw and Wrigley, 1994), as well as in cotton.

The square and boll growth rate \( \text{g d}^{-1} \) as functions of temperature are as follows:

Square: \[ Y = -0.010168 + 0.001253 \cdot X - 0.0000195 \cdot X^2; \quad r^2 = 0.98 \] (28)

Boll:

\[ 0-28.5^\circ C, \quad Y = -0.0508125 + 0.003125 \cdot X \] (29)

\[ 28.5^\circ C \text{ and above}, \quad Y = 2.73285 - 0.08285 \cdot X \] (30)
where $X$ is average temperature for that period.

**G. Whole Plant Leaf Area Development**

Whole plant leaf area development depends on the summation of all the leaves growing on the plant at any one time and their respective growth rates. This was obviously controlled by temperature when other factors were not limiting. Whole plant leaf area expansion rate was plotted for plants of different ages that were grown at different temperatures (Fig. 15A). Obviously, the smaller young plants had much slower rates of leaf tissue addition because fewer leaves were growing. Optimum temperature for whole plant leaf area development was 27°C, and leaf development decreased at other temperatures.

**H. Whole Plant Growth Rate**

Whole plant growth rate responses to temperature were similar to those of many of the previously mentioned plant parts (Fig. 15B). The maximum growth rate was at 27°C with lower growth rates at other temperatures higher than 27°C. This response to temperature was quite similar to whole plant leaf area response to temperature (Fig. 15A).

**IV. Partitioning Biomass**

The apparent priority for organs receiving available nutrients varies with growth stage. The specific factors controlling an overall priority system are not well understood; therefore, a general mechanism (if it exists) controlling the allocation of nutrients among competing plant organs is not known. The controlled environment studies, in which potential growth rate conditions were maintained, may be used to draw some inferences concerning resource partitioning.

Early in the growing season, in the natural environment, survival is often de-
depending on the ability of plants to extract water and nutrients from the soil. In our experiments, a large proportion of the available carbon was used for root growth early in the life of the plant and proportionally less was allocated for roots as the season progressed (Fig. 16). In environments in which the temperature caused fruit growth to slow, it was not produced, or to be abscised soon after flowering, plants allocated much of their resources to stems, leaves, and roots (Fig. 17). In growing environments in which the temperature is favorable for fruit growth, nearly 50% of the total biomass produced was in the fruit. Expansion of leaves and stems was delayed during the fruit-growing period, and new leaves and internodes developed because of the in planta competition (Figs. 4B, 9A, and 15). However, even during the fruit-growth period, when internode competition for nutrition was important, dry matter accumulation in the stems continued (Fig. 11) and root growth probably continued, but slowly. Recent field observations using a maturation technique found root growth recovered quickly as bolls matured (data not shown). Sadras (1995) reviewed and proposed a framework for compensatory growth in cotton due to fruit loss.

In other experiments (Ben-Porath and Baker, 1990), in which root volume was very restricted but 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 larger numbers of fine roots were 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 produced in the roots enhance aboveground growth and play a role in regulating source-sink interactions. Such interactions of growth

![Percent of Plant in Different Parts vs Temperature](image_url)

**Figure 17** The role of temperature on cotton plant partitioning among different organs (V. R. Reddy et al., 1991).

**CROP MODELING AND APPLICATIONS**

Rates among different plant parts, and therefore different partitioning coefficients, have caused some to hypothesize that plant growth regulators, such as PIB, an antiguibelin type plant growth regulator, or herbicides may be used to manage stem growth (K. R. Reddy et al., 1995b; Hodges et al., 1991, and references therein).

**V. HIGH-TEMPERATURE EFFECTS ON FRUITING STRUCTURES**

Baker and Landivar (1991) described a method for modeling abscission of fruiting structures in cotton. Basically, their method estimated the amount of carbohydrate produced plus any available from previous reserves, which they called C supply, and they estimated sink-demand potential based on the number of growing sites. They also estimated respiratory requirement, which was added to the carbon demand. When their supply-demand ratio became less than 1, they assumed that there was a carbon stress and the youngest reproductive organs (squares and bolls less than 7 days old) were subject to abscission. The supply-demand method has provided a relatively effective way to predict fruit abscission when other factors are not complicating the crop performance. With the recognition and partial quantification of high-temperature injury, which also causes square and young boll abscission, a more complicated mechanism for predicting fruiting structure abscission is needed. The observation of Constable (1991) that there is shedding of very small squares at the beginning of the season also complicates the issue, although Constable acknowledges that squares do compete with vegetative growth for available carbohydrates. The fact that mature leaf areas and areas at unfolding (Figs. 8A and 9A), and mature square lengths (Holt et al., 1994), follow the same trend on the mainstem nodes suggests that they both compete for available carbohydrate. Thus, the concept of supply-demand may adequately explain early square loss in cotton. The physiological mechanism responsible for high-temperature injury is not known and the process is not modeled. However, such a model is needed because crops frequently experience above-optimum temperatures in today’s crop production environments; such conditions will be more frequent and severe if global warming occurs as predicted (K. R. Reddy et al., 1995b; Adams et al., 1990; Fisher et al., 1995). Neither of the crop models described by Wull et al. (1994) and Fisher et al. (1995) has any mechanism to predict this injurious aspect of high temperature on food and fiber production.

K. R. Reddy et al. (1992c) found flower retention was negatively associated with the number of hours per day the plants were exposed to 40°C. Several other studies indicated that square and fruit abscission increased when average daily canopy temperature during the square- or fruit-formation period was above 30°C (V. R. Reddy et al., 1991; K. R. Reddy et al., 1992c; Hodges and Reddy, 1995).
As temperature increased, upland cotton produced more fruiting sites, but fewer squares and bolls were retained (Fig. 18A). Pima was even more high-temperature sensitive than upland cotton. It failed to produce fruiting branches and therefore fruiting sites when the average daily temperature was 36°C (Fig. 18B).

These results occurred in well-watered and fertilized plants in which insects or diseases were not a problem. In other experiments in which atmospheric [CO₂] was varied, and high atmospheric [CO₂] increased total photosynthesis, similar responses to temperature were observed (Fig. 19). Thus, high-temperature effects must be the result of temperature injury or physiological damage that is not affected by carbohydrate supply. Preliminary studies of flowers produced on plants grown in 42-year average daily July temperatures at Stoneville, Mississippi, plus 5 or 7°C found that pollen produced was viable if the plants had been exposed to high temperatures no more than 8 days. Almost no seeds were produced on flowers grown at ambient temperature, but that were pollinated with pollen from plants exposed to high temperature for 12 or more days. All parts of the flowers produced in the high-temperature treatments were smaller than flowers produced in 42-year average daily July mean temperature (data not shown). Thus, high-temperature effects on reproductive development are not clearly understood. Future studies should address reproductively developmental responses to environmental variables, particularly high-temperature and water-deficit conditions.

VI. NITROGEN-DEFICIT EFFECTS

Growth and nutrient uptake by plants have been the subjects of numerous studies. Crop yields are much higher now than they were several years ago probably because of improved fertility practices. Nitrogen (N) fertility practices, in particular, have resulted in dramatically improved crop yields. Crop responses to additions of N have resulted in such gains that excesses in its application have sometimes occurred, and even been encouraged, because of the economic advantage. As a result, streams and aquifers have sometimes been contaminated by nitrate leached from the soil. In addition, it is now recognized that excessive nitrogen applied to cotton can sometimes cause lower fruitfulness. The relative amounts of vegetative to reproductive growth are modified by the plants' environment, including nitrogen fertility.

The function of N in crop growth and development has been studied extensively. The underlying assumption is that N deficiency causes several often related, yet discrete and identifiable, effects. These effects are integrated at the whole plant level to produce systematic alterations in growth, altered ratios of plant parts to one another, yield, and earliness. These effects are also dependent on environmental and genetic factors. Although crop plants interact with the environment in
a complex way, a careful understanding must be developed if reliable predictions of growth are to be made. Such predictions will help to enable the most productive farming and environmental quality to be maintained.

In an excellent review, Radin and Mauney (1986) described many of the responses of plants to N deficiency. They described the effects of low N nutrition of plants as causing (i) lower photosynthetic rates, (ii) slower leaf expansion resulting from lower hydraulic conductivity, and (iii) altered responses (largely stomatal) to water stress. They argued convincingly, and are supported by the results of Wong (1979), that although photosynthesis has received the most attention, it is probably the least important effect of N deficits in agricultural production situations.

Leaf size is a primary visual symptom of N deficiency. Smaller leaves are produced by plants grown in low N (Radin and Mauney, 1986, and references cited therein). Radin and Parker (1979a) showed that N effects on leaf area were caused largely by differences in leaf cell expansion. Those differences were apparently the result of decreased root hydraulic conductivity in low-N grown plants (Radin and Boyer, 1982). Their work was extended to show that the increased resistance occurred in the cortical root cells (Radin and Matthews, 1989). The lower root conductivity resulted in sufficiently lower leaf cell turgor to reduce expansion during the day but not during the night when water potential was higher. Cell wall softening was not affected by low N. Thus, these data, and those of Radin and Parker (1979b) and Radin (1983), show that N deficiency mainly inhibits leaf expansion by altering plant water relations. Probably for this reason, N deficiency causes many symptoms that are similar to plant responses to water deficits. Water deficits cause an earlier leaf-expansion response than photosynthesis response, which results in more carbon being available for other purposes (root growth, osmotic adjustment, cell wall thickening, etc.).

The stomata of N-deficient cotton plants are more sensitive to water deficits and close long before wilting occurs (Radin and Parker, 1979b). This characteristic has ecological significance in that it allows N-deficient plants to essentially slow water use during periods of moderate stress. Slower water use and enhanced root growth allow greater exploitation of soil water and nutrients, effectively delaying the impact of drought (Shimshi and Kafkafi, 1978).

Despite enormous amounts of research on plant nutrition during the past several decades, many of the specific relationships required for modeling appear to be totally missing or not quantified in many crops including cotton. For example, the relationship between leaf N and many physiological responses is not known, and the interaction of leaf nitrogen and growth in high-CO2 grown plants is not clear. How plants respond to nitrogen as carbon becomes more readily available is not well known. Results from fertility experiments and nutrient uptake studies often do not provide relationships between tissue N and plant growth or development processes. The rate of appearance of both vegetative and reproductive organs is primarily governed by canopy temperature modulated by water and nutrient deficiencies. Some researchers have found no effect of nitrogen supply on the rate of leaf emergence (Davidson and Campbell, 1983; Banor et al., 1984). Others have observed a decreased leaf emergence rate in response to low N supplies (Single, 1964; Terry, 1970; Dale and Wilson, 1978; Radin and Mauney, 1986; Boquet, 1989; Longnecker et al., 1993; Gerik et al., 1993; Parker et al., 1993). The discrepancies in these observations have several reasons: the different intensities of N-deficiency stress, growth stages, the methods used in the calculation of developmental events, and poorly controlled temperature conditions.

It was unclear from the literature how severely N-starved plants must be before there is an effect on leaf emergence. Therefore, we conducted experiments in which plants were grown in naturally lit chambers at optimum temperature, water, and nutrient conditions until the plants had first squares. Various N treatments were imposed at 17 days after emergence. Growth, development, and photosynthesis were measured frequently along with leaf nitrogen. The data were used to generate the rate functions in response to leaf N content.

A. Leaf Nitrogen and Phenology

The rate of cotton leaf development increased as leaf N increased (Fig. 20). There was no difference in N response between plants grown at twice-atmospheric CO2 (700 μl liter−1) and ambient atmospheric CO2; therefore, the data from both CO2 levels were combined to generate the relationship. A quadratic equation fit the data better than any other form. The results show that the formation of new leaves or other organs was considerably slowed as leaf nitrogen diminished. To our knowledge, there are no reports directly dealing with leaf N and morphogenetic delays.

The relationship describing this developmental rate (1/duration, day−1) as a function of leaf N (g N m−2) is as follows:

\[ Y = -0.805 + 0.856\cdot N - 0.160\cdot N^2; \]
\[ R^2 = 0.86 \quad (30) \]

The maximum rate of node development was achieved at about 2.5 g N m−2, and development was projected to stop at about 1.25 g N m−2, although leaf N never reached that low of a concentration. In the natural environment, plants nearly always function under somewhat nutrient-deficit conditions and canopy development is restricted by the nutrient concentrations in the tissue.

The rate of development from square to flower was not affected by nitrogen nutrition. Several others have reported no differences of nitrogen treatments for time to first flower or time between flower and open boll (Waldeigh, 1944; Towelde et al. 1993; Gerik et al., 1989). This suggests that once the organs are formed the
The relationship between leaf nitrogen (g N m\(^{-2}\)) and rate of node development is governed by canopy temperature, and canopy nutrient status rarely gets so low that rates are not directly altered.

The number of bolts and squares produced may be limited by nitrogen effects on node development and the initiation of both vegetative and fruiting branches. Median nitrogen concentration up to 2 m\(\text{D}\) caused more fruiting sites to be produced, but at higher concentrations additional increases were very small. Similar results were observed by several others concerning the effects of N deficits on the fruiting sites produced (Jackson and Gerik, 1990; Gerik et al., 1989). They, too, concluded that the number of fruiting sites was probably controlled by plastochron intervals and other developmental events such as branch development.

B. LEAF NITROGEN AND LEAF AND STEM EXPANSION

Nitrogen-deficit effects on the processes underlying leaf area expansion rates are only occasionally documented in mathematical terms in the literature. Leaf growth parameters, such as initial leaf sizes, relative leaf expansion rate, and leaf appearance rates, are essential information for modeling canopy development in field situations in which leaf N content varies. Leaf area at leaf unfolding was greater in plants with more leaf N, and plants grown in high [CO\(_2\)] had significantly bigger leaves at unfolding than plants grown at ambient [CO\(_2\)] (Fig. 21). The fact is that any parameter that affects leaf area will cause variation in initial leaf sizes (Terry, 1970; Dale, 1972; Robson and Deacon, 1978; Tolley-Henry and Raper, 1986; Gerik et al., 1993).

The equations describing these initial leaf sizes (cm\(^2\)) as a function of leaf N (g N m\(^{-2}\)) are as follows:

$$\text{350 \, \mu\text{D liter}^{-1} \, \text{CO}_2, \, Y = -6.5774 + 13.4476 \cdot \text{N}}$$

$$-2.8023 \cdot \text{N}^2, \, r^2 = 0.81$$

$$\text{700 \, \mu\text{D liter}^{-1} \, \text{CO}_2, \, Y = -4.8437 + 12.1494 \cdot \text{N}}$$

$$-2.4555 \cdot \text{N}^2, \, r^2 = 0.69$$

The RLER increased as the leaf N concentration increased (Fig. 22) with the maximum RLER obtained at the highest leaf N concentration. Similar increases in leaf area have been observed with increased N (Radin and Sell, 1975; Oosterhuis et al., 1983; Jackson and Gerik, 1990; Gerik et al., 1989; Fernandez et al., 1993).
The RLER was not different between CO₂ treatments; therefore, the data were combined to generate the rate parameters. The RLER (cm² cm⁻² day⁻¹) and leaf N (g N m⁻²) relationship is expressed as follows:

\[ Y = -0.5374 + 0.5063 - 0.0981 - N^2; \quad r^2 = 0.84. \]  \(33\)

Stem elongation rate increased as leaf N increased (Fig. 23). Stem elongation rate followed a quadratic trend similar to that of leaf expansion rate. Plants grown in high-CO₂ environments had consistently higher stem elongation rates at all N levels compared to plants grown in ambient CO₂ environments. The shapes of the curves in both CO₂ levels, however, were similar. These data suggest that stem elongation was also carbohydrate limited and was consistent with the sensitivity of stem growth to boll load. Rates of stem elongation (cm day⁻¹) as a function of leaf N (g N m⁻²) are as follows:

- 350 μl liter⁻¹ CO₂: \[ Y = -10.967 + 11.633 - X - 2.389 - X^2; \quad r^2 = 0.91 \]  \(34\)
- 700 μl liter⁻¹ CO₂: \[ Y = -10.238 + 11.20 - X - 2.282 - X^2; \quad r^2 = 0.90. \]  \(35\)

C. LEAF NITROGEN AND SPECIFIC LEAF WEIGHT

Specific leaf weight was maximum when leaf N concentration was low and decreased as leaf N increased. Specific leaf area (cm² g⁻¹), the inverse of specific leaf weight as a function of leaf N (g N m⁻²), is as follows:

\[ Y = -0.946 + 1.438 - N - 0.264 - N^2; \quad r^2 = 0.80. \]  \(36\)

D. LEAF NITROGEN AND PHOTOSYNTHESIS

The rate of photosynthesis was uniquely related to leaf N both in ambient and twice ambient [CO₂] (Fig. 24). Plants grown in twice-ambient [CO₂] had consistently higher photosynthetic rates at all N levels compared to plants grown in ambient [CO₂]. Such a relationship between leaf N and photosynthetic rates has been observed in several other species, including soybean (Boote et al., 1978; Sinclair and Horie, 1989), rice (Cook and Evans, 1983; Yoshida and Cornel, 1976), corn (Ryle and Haslinton, 1969; Wong et al., 1988); wheat, grasses (Osman et al., 1977; Evans, 1983), sunflower (Goudriaan and Van Keulen, 1979; Connor et al., 1993) and Eucalyptus spp. (Reich and Walters, 1994).

The photosynthetic rates (mg CO₂ m⁻² sec⁻¹) and leaf N (g N m⁻²) relationships are as follows:

- 350 μl liter⁻¹ CO₂: \[ Y = -1.6642 + 2.0116 - N - 0.3172 - N^2; \quad r^2 = 0.88 \]  \(37\)
- 700 μl liter⁻¹ CO₂: \[ Y = -1.7204 + 2.1967 - N - 0.3092 - N^2; \quad r^2 = 0.90. \]  \(38\)

E. LEAF NITROGEN AND TRANSPIRATION

The potential transpiration rate of a canopy is dictated by meteorological conditions, but it also depends on the availability of water in the root zone. Nitrogen
The factor limiting growth response to multivariables is not always readily indisputable, nor can one always be confident of the most appropriate way to model the stress results. Azcock (1990) discussed several processes that may control partitioning of photosynthates and other plant growth resources into different plant parts. For an extended discussion of how plants respond to two or more simultaneously varying limiting factors see Sinclair (1982). Compensation occurs in plants when an apparent single-most limiting nutrient, e.g., nitrogen, is supplied with an additional nutrient, e.g., carbon. The results from this experiment are consistent with the hypothesis proposed by Bloom et al. (1985). They proposed that when simultaneously limiting factors that control plant growth are increased, then growth is also increased in proportion to the extent the deficit of either nutrient was overcome.

VII. WATER-DEFICIT EFFECTS

Plants growing in the natural environment are often prevented from expressing their full genetic potential for yields. Environmental stresses have been estimated to reduce crop yields in the United States by about 71% compared with maximum achievable yields (Boyer, 1982). Similar problems are encountered worldwide because much of the world’s cotton production is in arid or semiarid climates. With irrigation, attempts are made to optimize moisture conditions by controlling amounts and timing of water application. Within the United States, for example, yields in the irrigated Southwest are approximately double those of the nation as a whole (USDA, 1989). Such high yields are the result of growing crops in a high-radiation environment and correcting the most limiting environmental constraint—water deficits.

When a plant experiences a shortage of water, its water content decreases and tissue water potentials become more negative. The negative tissue water potentials cause reduced tissue expansion, lower photosynthetic rates, and closed stomata, and proportionally more dry matter is partitioned to roots. In extreme conditions, the leaves wilt, senesce prematurely, and abort; ultimately, the whole plant dies. Plants that are exposed to relatively long cycles between irrigation are less able to extract water from the soil than frequently irrigated plants (Radin et al., 1989). This is particularly true during the fruiting period when intraplant competition is strong between fruiting structures and roots for limited supplies of carbohydrates.

Increased hydraulic resistance of root systems of water-deficit-exposed plants and intraplant competition for resources limits root growth and delays recovery of plants after watering. Such delayed recovery extends the negative effects of drought on crop productivity.

Leaf water potential is commonly accepted as an index of plant water status and deficiency causes stomata to partially close because of greater resistance in root cortical cells (Radin and Boyer, 1982) and thus affected transpiration (Fig. 25). Nitrogen deficit causes reduced leaf growth, in both size and number, as well as stomatal opening and closing. Therefore, studies in which N is a variable are always confounded with water relations. Transpiration increased linearly with increased leaf N in both CO₂ levels in well-watered conditions, but the rates of increase were not parallel. The equations describing transpiration rates (mg H₂O m⁻² sec⁻¹) and leaf N (g m⁻²) are as follows:

\[ Y = -278.218 + 250.22 \cdot N; r^2 = 0.92 \] (39)

\[ Y = -120.552 + 171.43 \cdot N; r^2 = 0.91 \] (40)

F. MODELING THE EFFECTS OF N DEFICITS

Potential growth, development, and photosynthetic rates were calculated as functions of canopy temperatures under optimum water and nutrient conditions. Reduction or delay factors were calculated by assigning maximum growth, development, or photosynthetic rates at maximum leaf N, and the values at leaf N below the maximum were expressed as a fraction of the maximum rate. The new scaled values range from 0, where no growth or development occurred, to 1, where potential growth or development occurred at maximum leaf N. The relationships calculated in this way can be used as multiplication factors to decrease the potential growth and developmental rates in nitrogen-deficit environments.

![Figure 25](image)

Figure 25: The relationship between transpiration (mg H₂O m⁻² sec⁻¹) and leaf nitrogen (g N m⁻²).
is relatively easy to measure. It is a function of both availability of water in the root profile of the soil and prevailing atmospheric demand. It is also influenced by the hydraulic conductivity of the system, which may be influenced by the age of the plants and their previous environmental conditions.

A. TISSUE EXPANSION

Water deficits have very large effects on tissue expansion in both stems and leaves. Rates of increase in plant height are plotted against midday leaf water potential (Fig. 26). Stem elongation rate declined in response to leaf water potential. Stem growth was maximum when midday leaf water potential was $-2.2$ MPa; it decreased to zero at $-2.4$ MPa. Stem elongation rate (cm day$^{-1}$) as a function of midday leaf water potential (MPa) is as follows:

$$Y = 4.2904 - 0.6491X - 0.9737X^2; \quad r^2 = 0.77,$$

where $X$ is midday leaf water potential (MPa).

Water deficits also had a very large effect on the expansion of leaves that was similar to that found for stem elongation (Fig. 26). Leaf growth rate was maximum ($m^2$ day$^{-1}$) at about $-2.4$ MPa and decreased to zero at $-2.4$ MPa. The relationship describing leaf expansion rate ($m^2$ day$^{-1}$) as a function of midday leaf water potential (MPa) is as follows (Marani et al., 1985):

$$Y = 44.89 + 33.98X + 6.36X^2; \quad r^2 = 0.73,$$

where $X$ is midday leaf water potential (MPa).

![Figure 26](image)

Figure 26  The relationship between midday leaf water potential (MPa) and the rates of canopy photosynthesis (mg CO$_2$ m$^{-2}$ sec$^{-1}$), and stem elongation (cm day$^{-1}$).

B. PHOTOSYNTHESIS

Photosynthetic rate reduction in cotton as a result of moisture deficits is well documented (Hsiao, 1973; Ackerson and Krieg, 1977; Sung and Krieg, 1979). There is a close relationship between photosynthetic rate and leaf water potential (Fig. 26). Several others observed similar results both in the growth chambers and in field-grown cotton (Ackerson and Krieg, 1977; McMichael and Hesketh, 1982; Marani et al., 1985; Radin, 1992; Turner et al., 1986). The photosynthetic reduction rate (mg CO$_2$ m$^{-2}$ sec$^{-1}$) as a function of midday leaf water potential (MPa) is as follows:

$$Y = 4.7929 - 0.1318X - 0.3319X^2; \quad r^2 = 0.63,$$

where $X$ is midday leaf water potential.

The inhibition of photosynthetic rate was assumed to be caused by both stomatal closure and nonstomatal factors when the plant experienced water deficits (Hutmacher and Krieg, 1983; Farquhar and Sharkey, 1982; Jordan and Ritchie, 1971).

C. MODELING THE EFFECTS OF WATER DEFICS

In order to apply the functional relationships between leaf water potential and various growth and photosynthetic processes in any environmental situation and in different plant growth stages, the data on the effect of leaf water potential on stem and leaf growth and on photosynthesis had to be reanalyzed assuming that maximum growth potential occurs at the minimum midday leaf water potential. At the minimum midday leaf water potential the midday water potential was no less than $-1.0$ MPa, the growth potential of the process is given a value of 1, and the rest of the values are expressed as a fraction of that minimum. The new scaled value now ranges from 0 at no growth to 1 at the potential or the maximum growth. For simulation purposes, these values are used as multiplication factors to decrease the potential growth, development, and process rates that were calculated as functions of temperature.

VIII. MODEL DEVELOPMENT

A physiologically based crop model can be assembled using the equations previously described. The equations were based on the data collected from controlled-environment studies with only the limiting variable being tested. Therefore, the equations provide a basis to model potential crop growth and development rates. The quantitative information introduces only briefly how one might model water- and nutrient-deficit conditions.
The step-by-step model development and applications are as follows:

1. The time required to produce the first square from emergence can be calculated by summing the daily developmental rates from Eq. (1) for upland cultivars and Eq. (2) for pima cultivars until the summed value equals 1 or greater.

2. Once the squares are formed, their potential developmental rates to become flowers can be calculated from Eq. (3) for upland and Eq. (4) for pima cotton cultivars.

3. The bolt maturation period, or the time from flower to open boll, can be calculated from Eq. (5) for upland and Eq. (6) for pima cotton cultivars similar to the procedure used in the calculation of time to first square by summing the daily developmental rates.

4. Cotton potential leaf unfolding interval rates on the mainstem and on fruiting branches can be described with Eqs. (7) and (8), respectively. Vegetative branch leaf unfolding intervals follow the mainstem axis. Nutrient-deficit effects may be added to account for morphogenetic delays. Equation (30) is used to simulate N effects on leaf development.

5. Once leaves and internodes are initiated, their potential growth can be simulated with three rate functions: growth duration, maximum RIER or maximum RIER, and rates of growth reduction with age [Eqs. (9)-(14)].

6. Variable internode lengths or leaf areas on the mainstem and on branches can be simulated by using initial values, size at the time of leaf unfolding, from Eqs. (15)-(21) assuming ontogenetic patterns seen in the mature internodes and leaves are set at or before leaf unfolding.

7. Potential growth of plant height or whole plant leaf area simulation can be predicted by integrating the growth rates of successive internodes on the mainstem or all the leaves both on the mainstem and on the branches capable of growth.

8. Nitrogen-deficit effects on leaf and stem growth can be added with Eqs. (31)-(35). These growth processes can be decremented by water-deficit effects on stem elongation and leaf area development based on Eqs. (41) and (42).

9. Potential leaf weight per unit area increase can be calculated from Eqs. (22) and (23). The effect of nutrient status on specific leaf weight can be calculated with Eq. (36).

10. Potential internode growth rate can be calculated from Eqs. (26) and (27), and total mainstem weight can be calculated by summing growth rates of all internodes. A similar approach can be employed for fruiting branch internodes.

11. Potential canopy photosynthetic rates in the model from Baker et al. (1983) and water- and nutrient-deficit effects on photosynthesis could be calculated from Eqs. (37), (38), and (43).

12. The effect of high temperature on fruit and square abortion needs much more attention in the future to develop models in that area. The data available in the literature are not adequate for developing models for fruit abscission in response to short- or long-term high-temperature stress.

From these equations, a crop model can be developed that describes the responses of cotton to many aspects of its physical environment. The data from which these equations were derived represent conditions in which a concerted effort was made to obtain potential rates. It is also shown how potential morphogenetic rates may be delayed or how growth rates may be reduced by water and nutrient deficits. These potential growth and developmental rates, and the effects of water and nitrogen deficits on these potential growth and developmental rates, have been incorporated into a comprehensive simulation model for cotton, GOSSYM/COMAX/WHIMS, which will be discussed briefly later.

A cotton crop simulation model was developed in the mid-1980s by several collaborators (Baker et al., 1983; Whisler et al., 1986). This model, called GOSSYM/COMAX, was the first of its kind available for assisting agronomic production-type decisions. It is a materials-balance model that simulated the location of water, nitrogen, and carbon in the plant and soil system. It simulates the soil processes, including roots, using two-dimensional geometry. The concept of simulating potential growth and developmental rates allowed model developers to incorporate growth reduction and organ abscission factors into the model. For the first time, this provided a vehicle to simulate deficits of water and nutrient factors and relate those deficits to the plant's potential growth requirements. They used a supply-demand ratio concept to reduce the growth rates of particular organs in water- and nutritional-deficit environments. This concept proved to be a useful mechanism to simulate plant responses to environmental-stress conditions (Baker and Aoeck, 1986). The GOSSYM/COMAX model expert system has been used commercially by cotton producers and consultants to assist management decisions since 1984 (McKinnon et al., 1989). It has undergone many changes as new information has become available (K. R. Reddy et al., 1993a, 1995a,b,d; K. R. Reddy, 1995) for producers and consultants (Ladewig and Thomas, 1992; McKinnon et al., 1989) and for scientists to study and identify the principles of plant-environment interactions (V. R. Reddy et al., 1989a,b; Landivar et al., 1983; Whisler et al., 1982, 1993).

A. The Cotton Simulation Model GOSSYM

The development, characteristics, and applications of GOSSYM/COMAX have been previously described (Baker et al., 1983; McKinnon et al., 1989; Baker and Landivar, 1991). Briefly, GOSSYM, an acronym from the word Gossypium, the genus of cotton, is a cotton crop simulation model that is linked to a rule-based expert system called COMAX (Crop Management Expert). GOSSYM simulates crop responses to environmental variables such as solar radiation, temperature, rain/irrigation, and wind, as well as variation in soil and cultural practices. Growth and development are estimated and a record is kept of leaf,
internode, square, and fruit age. GOSSYM estimates growth and development rates by calculating potential rates from daily temperatures assuming other conditions are not limiting; then it adjusts the potential rates by intensity of environmental stresses as discussed previously. GOSSYM provides users with the size and stage of the crop as well as its present growth rate and the intensity of the stress factors. Therefore, a grower can assume certain weather conditions (e.g., last year's temperature, rainfall, solar radiation, and wind speed) to determine yield estimates depending on the current maturity of the crop.

A flowchart of GOSSYM shows the general organization of the model and program flow (Fig. 27). GOSSYM is the main program from which all the subroutines vertically below it in the diagram are called. CLYMAt reads the daily weather information and calls DATES, which keeps track of both Julian day number and the calendar date being simulated; CLYMAt also calls TMSOL, which calculates the soil temperatures by soil layer. SOIL is a mini-main program, which calls the soil subprograms (Boone et al., 1995). The soil routines provide the plant model with estimates of soil water potential in the rooted portion of the soil profile, an estimate of the nitrogen entrained in the transpiration stream available for growth, and an estimate of metabolic sink strength in the root system.

The belowground processes are treated in a two-dimensional grid. The material balances of water and nitrate, ammonia, and organic matter are maintained and updated several times per day. FERTLIZ distributes ammonium, nitrate, and urea fertilizers in the soil profile. GRAFLO simulates the movement of both rain and irrigation water into the soil profile by gravitational flow. ET estimates the rate of evaporation from the soil surface and transpiration from the plant. UPTAKE calculates the amount of soil water taken from the soil region in which roots are present. CAPFLO estimates the rewetting of dry soil from wetter soil by capillary flow. NITRIF calculates the conversion of ammonium to nitrates by bacterial action in the soil medium. CHEM is also a mini-main program that calls subprograms, PIX (K. R. Reddy et al., 1995b) and PREP (V. R. Reddy, 1995), which calculate the effect of chemicals in plant physiological processes. PIX deals with the effects of the plant growth regulator, meipquat chloride, and PREP deals with the effect of a boll opener, Allephen, and defoliant chemicals.

In PNET leaf water potential, canopy light interception, photosynthesis, and respiration are calculated. Then, in GROWTH, potential dry matter accretion of each organ is calculated from temperature. These potential organ growth rates are adjusted for turgor and nitrogen availability. Photosynthates and any reserve carbohydrates are partitioned to the various organs in proportion to the total growth requirements. The partition control factor is the carbohydrate supply demand ratio. RUTGRO calculates the potential and actual growth rates of roots. RIMPED calculates the effect of increasing soil bulk density on the capability of roots to elongate. NITRO calculates the partitioning of nitrogen in the plant. MATBAL keeps track of the nitrogen and carbon material balance in all parts of the plant and soil complex. In PLTMAP, fruit loss and developmental delays are calculated using both carbohydrate and nitrogen supply: demand ratios. These developmental delays are used to allow the simulator to slow the plastochron intervals that are calculated as functions of temperature depending on the intensity of the stress. ABSCISE estimates the abscission rate of fruit, squares, and leaves caused by nutrient or water deficits. PMAPS, COTPLT, and OUTPUT print various user-selected reports from the model. The program cycles through these subroutines one day at a time from emergence to the end of the season. A more complete description of the subroutines and how GOSSYM works can be found in Baker et al. (1983).

B. Expert System COMAX

Briefly, COMAX is an expert system that was explicitly developed for working with the crop simulation model GOSSYM (Lemmon, 1986). Its organization and utility have changed considerably since its inception (McKinley et al., 1989). COMAX is a forward-chaining, rule-based system that contains an inference engine, a file maintenance system for the simulation model requirements, a database
C. Expert System WHIMS

Insect control for economical cotton production is consistently more critical than for any other major field crop. After testing and application of GOSSYM/COMAX as an agronomic management decision aid, it became apparent that many entomological decisions in cotton production were equally complex. A decision to spray an insecticide might control the problem, delay a problem, or kill beneficial insects and cause the problem to become worse. As a result of an untimely or inappropriate insecticide application, the producer might add both economic and environmental cost. Therefore, a rule-based expert system was developed to help control cotton-damaging insects in the mid-South that could be used in conjunction with GOSSYM/COMAX. This system is called rbWHIMS (rule-based W)Holistic Insect Management System. It makes recommendations on 13 arthropod pests. The insect-control expert system uses a Microsoft Windows graphical interface. A specifically designed scouting protocol was also developed to improve scouting efficiency and to provide the necessary data input for rbWHIMS (Olson and Wagner, 1992; Wagner et al., 1995a,b; Willers et al., 1992, 1995; Williams et al., 1991, 1995). The rbWHIMS is most useful when field conditions do not lead to definitive decisions or clear-cut actions on specific pests. The greatest possibility to waste or conserve resources directed to pest management occurs when such a condition exists, and it is at these times that the crop production manager needs a second opinion. The rbWHIMS is based on the combined judgment of several cotton insect-control specialists and may be used to provide the manager with such an opinion. However, insect-control situations are so unique that the rules may not be universal in application. Because we do not know much about the biology associated with insect control in a complex agricultural system, such rules and control strategy must be developed regionally.

IX. MODEL CALIBRATION AND VALIDATION

A. Model Calibration

The simulation model developed from the response rate functions collected from the controlled environment chambers needs to be calibrated against field data for each cultivar. Cultivars may have different rate functions to environmental variables. However, it is expensive and time-consuming to generate the process-rate data for all the cultivars used commercially (Curry and Feldman, 1987). Several methods have been proposed to calibrate the simulation models including iterative and heuristic approaches to applying genetic algorithm techniques (V. R. Reddy et al., 1985; Boone et al., 1993; Sequeira et al., 1994). Assuming that the cultivars of a particular species have similar response rate functions to the environmental variables, one can shift the function by moving either direction with multiplying factors. For example, daily developmental rates from emergence to first square are presented in Fig. 3 and the response functions for these rate functions can be calculated by Eq. (1) for upland cotton, by Eq. (2) for pima cotton as described by Boone et al. (1993), or by automating the techniques to parameterize the models as described by Sequeira et al. (1994). The data for upland cotton were collected for two cultivars and there were no differences between cultivars for this trait. Therefore, the data were pooled to generate the function. If different cultivars take more or less time for this particular response function, the function can be modified by multiplication factors: 1.1 for early season cultivars and 0.90 for late-season cultivars compared to that generated in the present study. However, it is not possible to accurately calibrate the model for pima cotton cultivars based on the response functions developed for upland cotton because the response functions are not parallel. Thus, a new response function had to be developed for pima cultivar in order to simulate its behavior.

B. Model Validation

Validation is a critical stage in model development if the models are intended for use as an on-farm decision-aiding tool. Validation data should be obtained from real-world field experiments. The data sets must include a wide range of soil and weather conditions with an array of cultural practices and genetic resources. Val-
CROP MODELING AND APPLICATIONS

1995b), for evaluating the performance of two similar models dealing with the same process, provide new techniques in evaluating the simulation model performances.

X. MODEL APPLICATIONS AND BRIDGING TECHNOLOGIES

Before we can discuss model applications, we need to discuss the types of bridging technologies that make additional use of a biological model possible. Members of the Crop Simulation Research Unit have had many years of experience in building crop models, insect models, and associated decision support systems. Simply building a crop decision support system is not enough. It must be easy to use. The user interface must be intuitive. The system must limit the requests made by the user to supply labor-intensive information. The system within its self-described limits must work successfully. The system must be thoroughly tested and debugged. Software used by consultants and growers for crop management decision support must be essentially bug free or the developers will face the unpleasant realization that users will say the system does not work, whether or not the bug affects system accuracy.

A. COMPUTER TECHNOLOGY

The advent of the personal computer, with increasingly more available memory, disk space, and computational power, starting in the mid-1980s, is largely responsible for the use of models and decision-support systems for cropping systems. This phenomenon was predicted by McKinnon and Baker (1983). They observed that computer technology, driven by the integrated circuit industry, had an orderly, predictable increase in computer speed and memory availability. This increasing computing power was making minicomputers competitive with mainframe computers for running software. Industry had published data showing that, over a 5-year period, users could expect memory costs to decrease by a factor of 90% and the cost of the central processing unit to likewise decrease by 75%. At the same time, the speed of the computer was doubling every 2 years while the price essentially remained constant. Integrated circuits were just then being developed to build the first desktop computers, i.e., the Altair microcomputer. Even then, it became apparent that the same process that made minicomputers competitive with mainframes would be at work to improve the microcomputer.

For the foreseeable future, computer capabilities will continue to increase while costs continue to decline. Computer capabilities doubled about every 2 years dur-
ing the period from 1960 to 1985. Since then, this rate of technology introduction has accelerated. From 1965 through 1992, the doubling period diminished from 24 months to 18 months. From 1992 to 1995, the doubling period was approaching 12 months. When technological change in the past has allowed an incremental (2 X 4 X) increase in computer capability over a 5-year period, software technology has followed a smooth evolutionary path. Now, with the order of magnitude change in computational power (not only just speed but also memory size, disk storage size, and high-speed access to the Internet) over a 5-year period, we face revolutionary changes in the way we do business with computers. These dramatic increases in computer technology will cause even more radical changes in the way information is handled and delivered to the user.

This discussion will not be concerned with many applications of computers on the farm. The list is endless and will continue to grow for the foreseeable future. We do, however, identify some developing technologies that we see as possibilities of facilitating major changes in crop production management and related activities.

B. OBJECT-ORIENTED SIMULATION

Advances in software technology will allow new computer programs to take advantage of increased computational capability. Foremost among these is the object-oriented programming paradigm. For the first time, it appears that a programming methodology will finally deliver on promises of code reusability. As part of its assignment in the U.S. Global Change Research Program, the Agricultural Research Service (ARS) recently identified the need for comprehensive process-level crop models. Such models should respond mechanistically to future high CO₂, climatic conditions for seven major crops: cotton, corn, wheat, soybean, rice, potato, and an unspecified forage legume. These crops constitute the great majority of tilled agricultural land, provide most of our food energy and protein either directly or indirectly, and should receive priority in model development. The construction of comprehensive, process-level models of these crops will require a significant modeling effort. In the past, models for different crops have been developed with varying levels of detail and capability. These models include relatively comprehensive, process-level models such as GOSSYM, COTCO2, OZCOT, and GLYCIM, less comprehensive models, such as SOYGRO, CERES-WHEAT, KUTN, and CERES-MAIZE, and finally the purely statistical regression models (Baker et al., 1983; Matassar, 1984; Acock and Trent, 1991; Hodges, 1991; Boote and Loomis, 1991; Hearn, 1994; Wall et al., 1994). Of these models, only two, GOSSYM and GLYCIM for cotton and soybean, respectively, have been field tested on commercial farms for use as decision-support systems in crop production. Research is currently under way to give SOYGRO and GOSSYM the
mechanisms necessary to respond to and predict the effects of a high-CO₂ future climate. However, these are only two of the targeted high-priority crop models.

ARS, in a national modeling effort encompassing multiple locations and research units, is attempting to develop a next-generation cotton crop model. At the same time, and complementary to that effort, standardized crop model components will be developed. An informal project of cooperating ARS and state research groups has been organized under the banner cotton production modeling. These groups have agreed to use object-oriented programming technology to develop interchangeable modules using a standardized model structure. Computer crop models have been written in the past using procedural languages, such as FORTRAN or PASCAL, or in computer simulation languages such as CSMP. The most comprehensive crop models consist of several thousand lines of computer code and have been built by teams of interdisciplinary research scientists. These models have been a barrier for nonmodelers, or even modelers of other crops, to understand. It may take as much as a year of training and examination of such a model before a scientist feels comfortable to modify it. Most researchers cannot afford to devote this much time to learning a crop model, particularly when they are interested in only certain subsystems. A potential answer to this problem has arrived in the form of object-oriented programming or, as applied to simulation, object-oriented simulation (OOS). The specifications and capabilities of OOS offer exactly what is needed to provide easy access to comprehensive crop simulators. Using OOS, models can be written so that modules correspond directly to objects found in nature, thus providing easy recognition of system components by nonmodelers. Ideally, modules communicate through carefully and completely specified interfaces, relieving the scientist concerned with only the operation of one module from being forced to know the details of the rest of the model. Modules or objects should contain all the code and data necessary to completely describe that object. Thus, if a scientist knowledgeable about photosynthesis wanted to use a particular photosynthesis module, he or she would simply replace the model's photosynthesis object. The user should not be concerned with the operation of other modules as long as the module responds correctly to the message-passing interface. Extensive and careful design early in the project is essential. To ensure that model hierarchy will easily accommodate such proposed changes as outlined previously requires extensive and careful design up front. For a good presentation of object-oriented programming, see Booch (1991), and for a discussion of OOS, see Segreteri et al. (1991).

The crop production modeling group has already spent several man months developing a generalized crop object-oriented model hierarchy. Perhaps even more design time must be allocated to object-oriented design than in top-down programming design efforts using structured systems design with the PASCAL or C programming languages. It has already been the experience of the Crop Simulation Research Unit at Mississippi State, Mississippi, with cotton and soybean models that there are a number of algorithms common among these models when writ-
C. Decision Support Systems

The GOSSYM/COMAX cotton crop management system is a simulation-based, decision support system that is widely used today in cotton production (McKinney et al., 1989). This system is currently used as a decision aid on a commercial basis for determining the (i) timing and amount of irrigation applications, (ii) timing and amount of fertilizer applications, (iii) timing and amount of plant growth regulators to be applied, and (iv) timing and amount of crop termination chemicals. The system is designed to be a process aid for the identification of pest management, GOSSYM/COMAX/WIM, is scheduled to be released in the mid-South area in 1996 as an integrated system.

All these decision aid questions involve agronomic and entomological issues that are weather dependent and have traditionaly been made by experienced managers for each management unit (often a field). Often, however, managers have limited information available on which to base decisions. This has resulted at times in misuse of chemicals, resulting in poor choices for both environmental and economic reasons.

Crop models also allow users to study the cropping systems. Users can specify soils and test cropping practices with multiple weather scenarios and ultimately make fundamental decisions on the basis of reasonable probabilities of weather. With a greater number of weather files, one can develop reasonable probabilities of simulated results and stronger risk management analysis. The use of expert system technology, coupled with detailed crop models, has already shown that a complex simulation system can be used by farmers as a crop management decision aid. These can and must be tested under current environmental conditions to establish validity.

D. Geographic Positioning System

The U.S. Department of Defense satellite navigation system was completed in the late 1980s and permits precise navigation and location of the receiving sensor. The space segment of the system consists of the GPS. These satellites send radio signals from space. The GPS Operational Constellation consists of 24 satellites and provides users with between five and eight position signals visible from any point on the earth. By using GPS sensors, which can receive the satellite signals, users can precisely compute their location and altitude on or above the surface of the planet. Using this technique, accuracies of ±5 cm have been achieved. This technology makes possible the concept known as precision agriculture.

E. Geographic Information Systems

GIS provide the integrating software technology in which the pieces of this concept are brought together. GIS allows the collection and display of megabytes of spatially registered data through a graphical user interface, but require large-capacity computers and data memory capability. GIS were only feasible for agricultural applications after such hardware became realistically inexpensive. GIS technology allows the coding of information, which is tied to spatial coordinates, and displays the information through maps. In agriculture, the basic map that a grower would use is the map of each management unit, which displays where each soil type is located. Not only could the soil type be known for each location, but also the soil physical properties such as bulk density, a soil water retention curve by horizon, sand, silt, and clay content, and percentage slope. Other data layers might include percentage organic matter, residual nitrate, ammonia content by horizon, preplant fertilizer content, and micronutrient content. After the crop is planted, additional data layers might include rainfall or irrigation amount, variety, plant population, tillage operations, and applied fertilizers, insecticides, herbicides, and plant growth regulators. Also, locations of historical hot spots for insect pests could be entered into the GIS system. When plant samples are taken or insect scouting information is gathered, all this information can be geo-referenced via the use of portable differential sensors. Thus, plant and insect information can be entered into the GIS database with precise location information. GIS can be defined with many layers of data, which can be specific to management units. When a crop model and expert system decision aid is interfaced to the GIS structure, users can activate the system by simply pointing and clicking with a mouse pointing device at the map location from which information is desired. Users will be able to simulate the growth of their crop, query the decision-support system for advice on crop management (both agronomic and entomological), and develop "control tapes" for use with farm implements coupled with harsh environment-tolerant microcomputers for applying seed and agrochemicals in a precise manner.

F. Intelligent Implements

Tractors, harvesters, airplanes, and other powered equipment used to apply seed and agrochemicals have high production costs, when equipped with powerful, harsh en-
vironment-tolerant microcomputers, differential global positioning satellite (DGPS) sensors, GIS software, and a control tape, can be called intelligent implements. The DGPS sensor tells the II where it is within a management unit. The GIS software with stored geographical databases provides the context within which the intelligent implements are working. The control tape gives the microcomputer instructions on rate of application of materials, depending on which operation is being performed. The control tape can be a 3½-inch diskette generated from the GIS-based GOSSYM/COMAX/WHIMS system. This diskette will contain the information on the rates by location within the management unit. For example, a user has a field with six different soil types. The GOSSYM/COMAX/WHIMS system then runs to develop first optimum planting densities by soil type. It then writes information to a diskette, which is then transferred to the intelligent implements, which are a tractor and variable-rate seed planter. As the tractor and planter travel across the management unit, the computer adjusts the seed planting rate for each of the six soil types. Similarly, as other production management operations are performed, the grower runs GOSSYM/COMAX/WHIMS to determine optimum application of fertilizer, plant growth regulators, water, herbicide, pesticides, and harvest-aid termination chemicals. The DGPS sensor tells the implement where its precise geographic location is. The GIS system provides the context of the operation by telling the intelligent implements which soil type they are on, etc.

G. SITE-SPECIFIC AGRICULTURE FOR FARM MANAGEMENT

With intelligent implements and GOSSYM/COMAX/WHIMS, cotton growers can literally "farm by the square foot." Precise applications of agrochemicals can be justified to potential regulators, and the growers can apply "what is right," "when it is needed," thereby becoming better stewards of the land. The model and expert system was developed from the beginning as a precision agriculture system, even before the term "precision agriculture" became popular. The model and expert system uses information on soil series type: soil water retention, sand, silt, and clay content, bulk density, initial nitrogen carryover from the preceding season, and percentage organic matter, all by soil horizon. These factors are by definition site specific.

The American Farm Bureau Federation recently completed a 2-year study (March 3, 1995) of precision agriculture and its implications in today’s—tomorrow’s production agricultural world. They concluded that the missing element was a way to incorporate the biologically important and dynamic information into the proposed precision agriculture system. The crop model and expert system can provide the knowledge-based system’s requirement identified as the missing part needed for effective precision agriculture. The American Farm Bureau Federation report said that all the key components for precision agriculture are now available.

These include variable-rate planters and chemical applicators. DGPS sensors with ±5-cm accuracy, and GPS software. In other words, by linking dynamic, physiologically sound crop models and expert system decision aids with GPS, GIS, and intelligent implements, the package becomes complete for applying appropriate agronomic and entomological site-specific production practices.

All extension recommendations from the experimental point of view were designed for general application on a wide area basis. Precision agriculture is the opposite extreme. Expert systems alone will not be able to help because they do not have predictive capability, and we do not have experts who can answer those questions on plant population, chemical application rate, etc. by soil type. Knowledge-based systems can provide those answers because they are a combination of a predictive model component of the system, which responds correctly to soil, weather, and cultural practice variation, and a rule-based expert system. The GIS software and DGPS provide location-based input information that, when combined with the GOSSYM/COMAX/WHIMS system, can generate the large quantity of information that will be needed by intelligent implements to carry out their operations.

Today, the model and expert system has DGPS input capability, is coupled to a GIS system and database, and generates site-specific recommendations. Cotton production equipment is available that has implement-mounted computers, DGPS sensors, and variable application rates of materials under computer control. The final loop is now being closed by making the site-specific output of GOSSYM/COMAX/WHIMS available to the intelligent implements for use as the control algorithm for precision application of seed and agrochemicals. The aerial pesticide industry is already using DGPS sensors in airplanes to precisely determine where the aircraft is and when to apply the pesticide. This technology has already reduced grower’s and applicator’s liability by eliminating ground personnel formerly used as flaggers to help the aircraft keep track of where it has been and by logging the time and place of application of pesticides to reduce liability exposure to charges of misapplication of chemicals by site or air drift errors on other crop producers adjacent land.

XI. SUMMARY AND CONCLUSIONS

In this chapter, we have attempted to bring together a unique data set appropriate for modeling cotton and to illustrate how it can be used to develop such a model. It is also suggested that models of other crop species can provide fundamental tools that can be useful for both in-season and preseason crop management decisions. Several additional crop management tools are becoming available that appear to provide additional impetus to allow precision agriculture to become feasible and real. As progress toward precision agriculture continues, the need for
yield-limiting diagnostic tools and other crop management decision aids will become more urgent. Mechanistic crop models and automated, user-friendly expert systems that can facilitate selection of the optimum and environmentally sound solutions to problems with many variables are a way to select best-management alternatives. The engineering and computing technologies that are needed to allow precision agriculture to evolve with many of its ramifications are essentially all now available. Unfortunately, our understanding of the biology of crop production is less well advanced, and currently the models are not perfect. There are many aspects of crop growth, crop interactions with other plants, insects, and diseases, and the responses of these organisms to their physical environment that are not properly understood. Modeling forces organization of known information and concepts. Although we may not know enough to develop a comprehensive model that includes all aspects of the farm or crop production system, modeling a meaningful portion of the system provides clarity. For a model to correctly predict plant responses to physical conditions, the concepts and the response functions must be appropriately modeled. When a crop model is built on appropriate concepts and processes, it has predictive capability in new environments and could be used either alone or with other emerging newer technologies to disseminate information to the end users.

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