Chapter 19

A CONCEPTUAL MODEL OF STRESS EFFECTS

Donald N. Baker and Basil Acock
USDA-ARS,
Mississippi State, Mississippi

INTRODUCTION

Optimum crop management requires an appropriate working definition of the term "stress." There are several kinds of stress, all of which affect yield by reducing the size and/or number of fruit produced. These stresses affect various physiological processes in different ways. A conceptual model relating plant processes to the external environment and to the various stress effects is presented here.

In most crops, including cotton, the number of plants per unit ground area, fruit size and the number of fruit per plant are the components of yield (Brevedan, *et al.*, 1978). In many species there are relatively narrow genetic limitations on fruit size. The maximum size often (as in the case of small grains and legumes) depends on the physical space available within the hull, and the minimum size is determined by seed viability considerations. On the other hand, plants generally initiate two to three times as many fruit as they can support. The remainder are aborted as a result of physiological stress. Thus, the number of fruit per plant is by far the most variable yield component.

Krizek (Chapter 17) notes that high photosynthetic rates alone may not be the crucial factor in determining yield. He cites several studies showing that the relationship between photosynthetic rate and yield depends on the developmental stage during which high photosynthesis occurs. In most cases increased yield is associated with enhanced photosynthesis during fruiting. Peet *et al.* (1977) found that photosynthetic rates at pod set in dry beans were positively correlated with yield in eight of nine varieties, but they found one variety in which high seed yield was associated with a very low photosynthetic rate. This variety happened to have a high harvest index. Evans (1975), in a careful consideration of carbon dioxide and other experimental variables, commented that there is little evidence of any positive relation between photosynthetic rate and yield, nor any instance where (cultivar) selection for a greater rate of photosynthesis has led to increase in yield. Any increase in photosynthate production must be accompanied by an adequate sink capacity, if it is to be beneficial. This may not always occur since plants have very sensitive mechanisms to abort fruit in response to short term deficits of photosynthate. This chapter examines the connection between physiological stress and fruit numbers. The rates of morphogenesis and the abortion of fruiting structures in cotton plants can be simulated as responses to imbalances in the metabolite supply:demand ratio (Baker *et al.*, 1973, 1976, 1979b). Baker *et al.* (1972), Boyer (1970) and many others showed that potential organ growth (and thus metabolite demand level) depend on temperature and plant turgor. Here, we consider two classes of metabolites: carbohydrates, derived from photosynthesis; and nitrogenous compounds, with nitrogen supply depending largely on the entrainment of nitrogen in the transpiration stream. During fruiting, there is usually a source/sink imbalance, and actual growth can be simulated (Baker *et al.*, 1979a) on the basis of the supply/demand ratio.

Most of the CO_2 fixed in photosynthesis and the water lost in transpiration pass through the stomata. Several climatic variables and metabolic inhibitors have direct and indirect effects on stomatal aperture and on the exchange rates of these gases between the plant and the surrounding atmosphere. Light intensity greatly modifies transpiration through its effects on stomatal opening (Kramer, 1959; Baker, 1966; Pallas *et al.*, 1962). Zelitch (1965) lists the following factors controlling stomatal behavior: light, temperature, atmospheric CO_2 concentration, leaf water status and a number of metabolic inhibitors. Meidner and Mansfield (1965) confirm this list, and in an effort to develop a theory of stomatal action, they cite literature showing that both temperature and water stress produce closing responses which are causally related to the internal CO_2 concentration of the leaf. They also suggest that metabolic inhibitors cause stomatal closure by modifying the internal CO_2 concentration, either by their effect on respiration or on photosynthesis, or both. However, they also show that temperature and leaf water potential have direct effects on the guard cells independent of their effects on internal CO_2 concentration. The work of Fisher (1970) suggests a mesophyll effect in the recovery of stomatal action after water stress, attributable to substomatal CO_2 concentration. Lange *et al.* (1971) and Cowan (1977) report a direct effect of humidity on stomatal action.

We have summarized these findings to provide a background for considering the effects (direct and indirect) of environmental factors on physiological stress.

Baker *et al.* (1973), in an analysis of the relationship of photosynthetic efficiency and yield in cotton, were able to simulate the delays in plant deveopment induced by metabolic stress. These delays were shown to cause the common sigmoid developmental pattern. They were also able to simulate the fruit abortion pattern of the crop. The variable used in indexing these morphogenetic delays and the fruit abscission rates was the ratio of carbohydrate supply to demand. This was, as far as we know, the first suggestion in the literature that both carbohydrate sink strength and carbohydrate supply levels are jointly involved in determining the growth and fruiting patterns of the plant. Although this model did not attempt to state explicitly the nature of the connection(s) between the metabolic

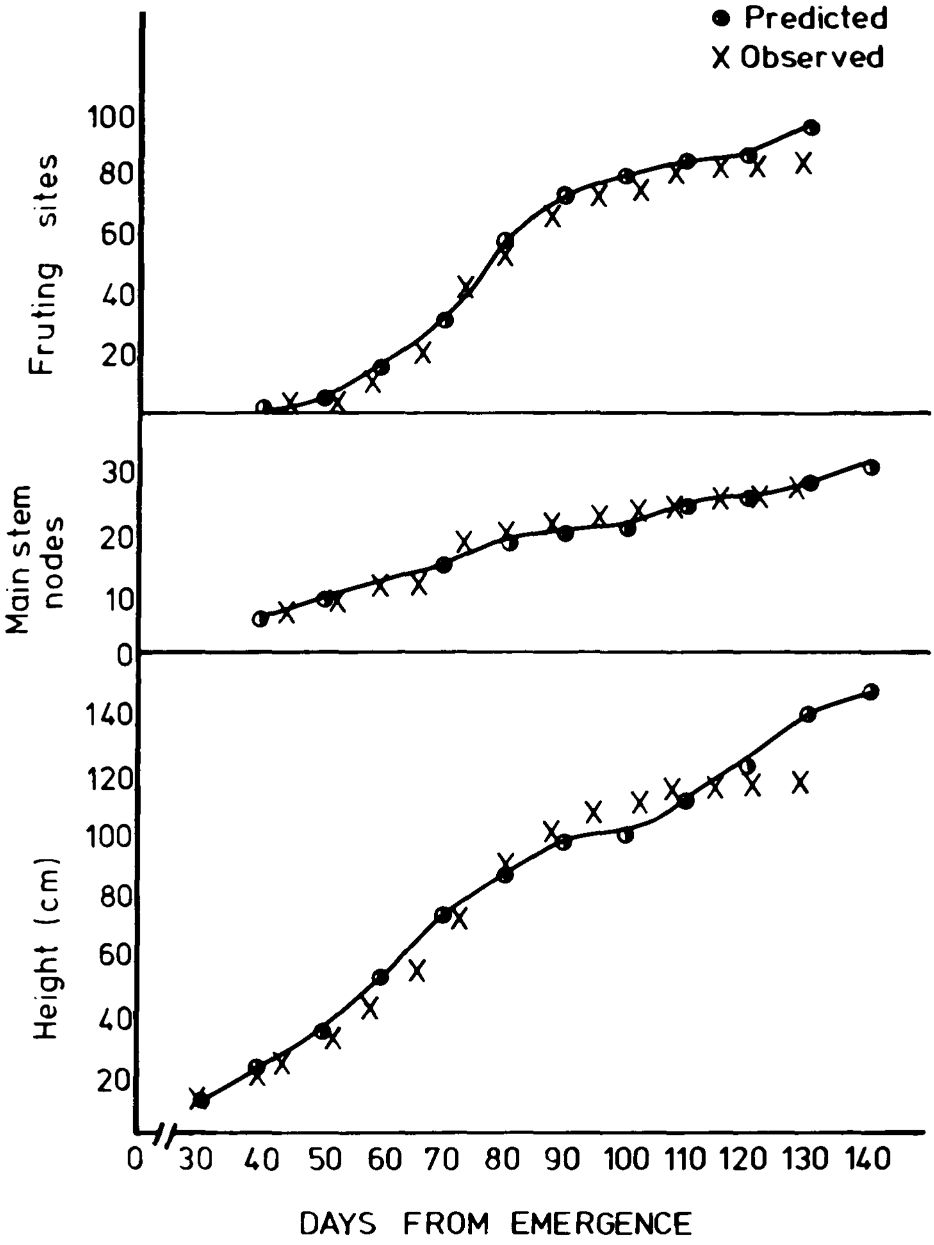

Figure 1. Field observations and model predictions of the seasonal time course of vegetative development in cotton.

pathways and the hormone systems within the plant, it did make the assumption that such connections exist and that they determine the balances of hormones in the plant. This concept was incorprated in a more advanced cotton simulation model, GOSSYM, (Baker *et al.*, 1976) along with a greatly improved data base for the physiological process rate equations (Baker *et al.*, 1972; Moraghan *et al.*, 1968; Hesketh *et al.*, 1972), as well as a detailed rhizosphere simulator, RHIZOS (Lambert and Baker, 1984). GOSSYM also has the capability to mimic the physiological effects of water stress and nitrogen stress in cotton. An example comparison of GOSSYM predictions and the field observations of fruiting sites, mainstem node numbers and plant height from Bruce and Römkens (1965) are presented in Figure 1. Similar comparisons for numbers of unpollinated flower buds (squares) and bolls are presented in Figure 2. The data in Figure 1 show the simulation of the sigmoid developmental curve of the crop. The data in Figure 2 depict the abortion of fruit.

Cotton is an indeterminate woody perennial. Typically, after fruiting begins, as each mainstem node is formed a fruiting branch begins development (see Chapter 2). At each node of the fruiting branch is a leaf in whose axil a fruit is initiated. This simple developmental pattern makes cotton an ideal subject for the identification of the time courses of stress effects. When measured as the number of mainstem nodes (Figure 1), plant development was simply a function of temperature out to about day 72 when the first boll appeared. The carbohydrate shortages began to develop, and the rate of new mainstem node formation was reduced. Fruiting site formation was exponential up to that time because, while temperature remained more or less constant, the number of fruiting branches increased as mainstem nodes were added. After first bloom, however, fruiting site formation became linear and then leveled off as the boll load became large. The number of flower buds (squares) increased as sites were formed until first bloom and then abortion began. Squares and young bolls were aborted in response to carbohydrate stress. In this way the time courses of fruit initiation and abscission are both determined by carbohydrate stress. GOSSYM contains similar logic in which a nitrogen source:sink imbalance also results in morphogenetic delays and fruit abscission.

The model calculates these effects of source:sink imbalance by performing the following operations daily: (a) photosynthesis, respiration, nitrogen uptake and reserves are calculated to estimate carbohydrate and nitrogen supplies; (b) the potential dry matter growth of all the organs is estimated from the age of the organs, temperature and turgor levels; (c) the product of the carbohydrate and nitrogen supply:demand ratios (with the variable name FSTRES) is calculated; (d) delays in the formation of new mainstem and fruiting branch nodes are calculated as functions of FSTRES; (e) the time of formation of each new node is calculated from temperature with these delays added; (f) the number of fruit per plant to be aborted each day (FLOSS) is calculated from FSTRES.

The delay functions (in days) are presented in Figure 3. Delays in mainstem

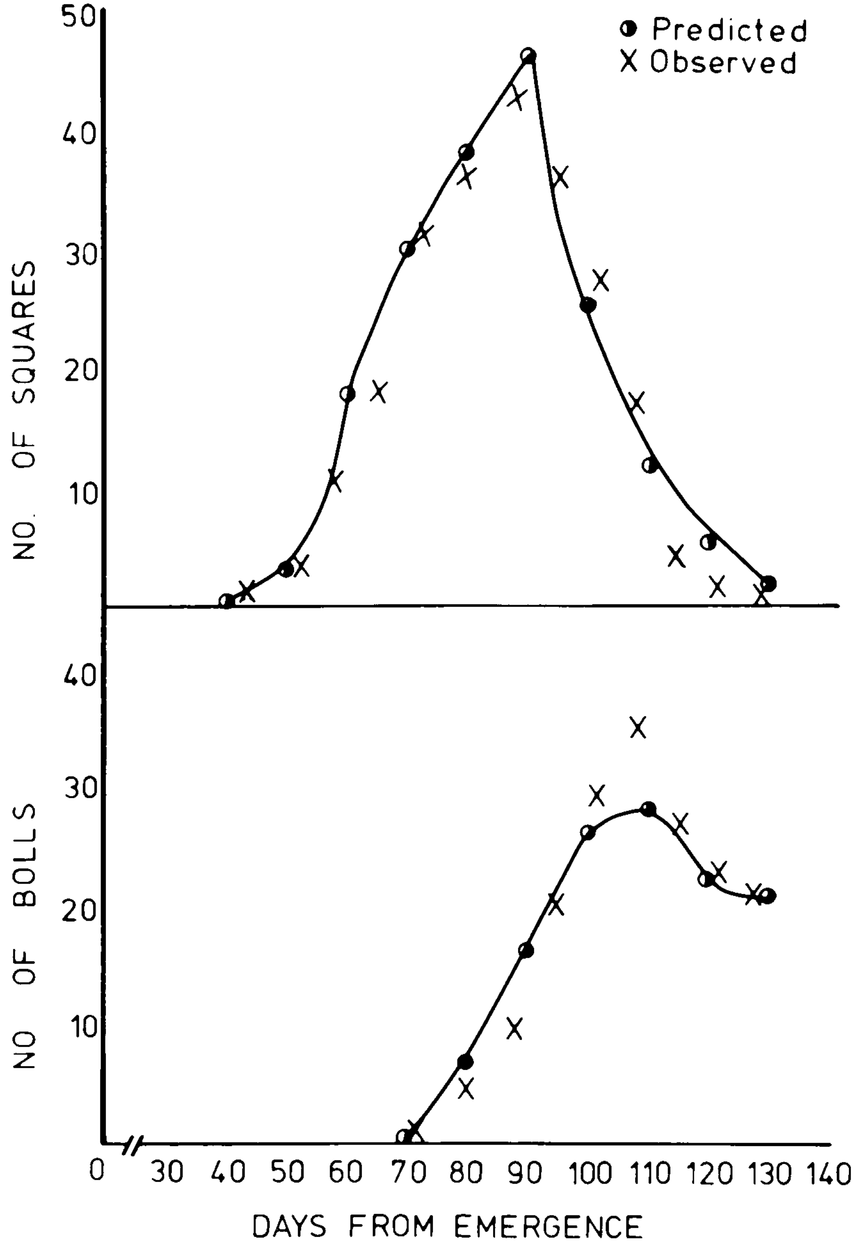

Figure 2. Field observations and model predictions of the seasonal time course of fruiting in cotton.

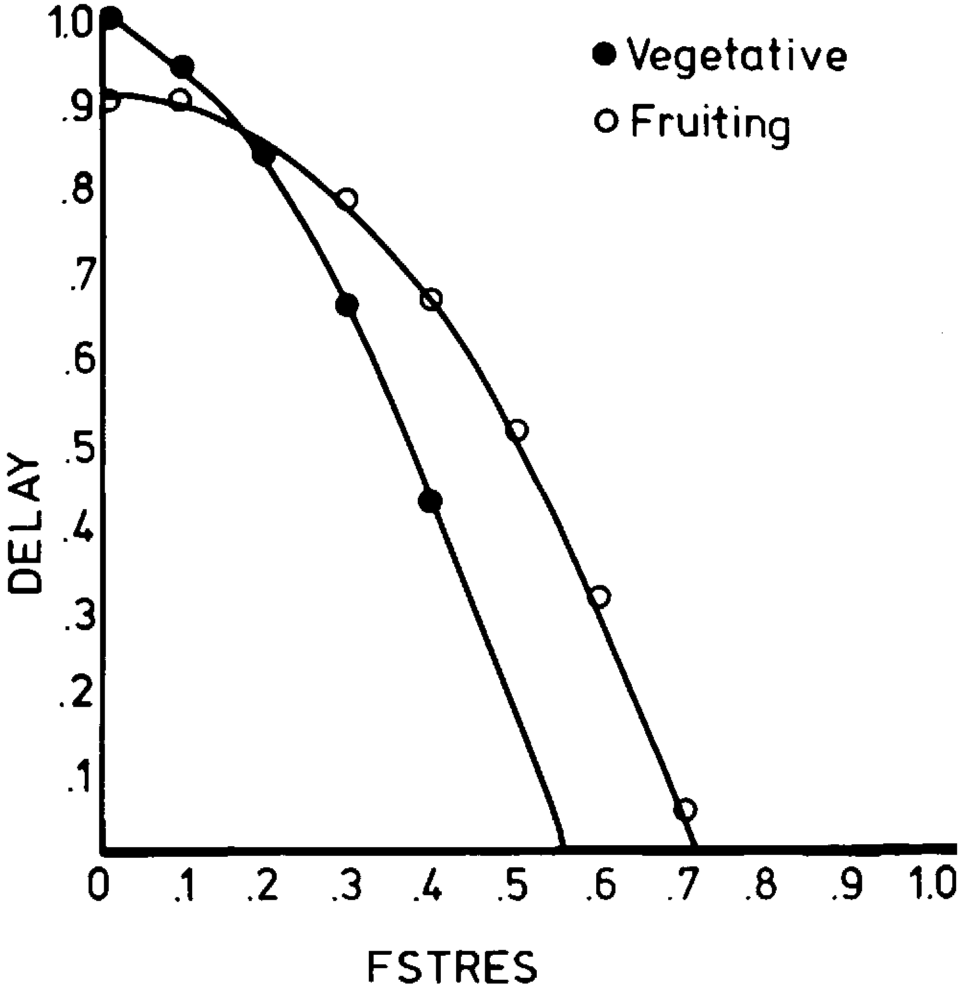

Figure 3. Morphogenetic delay functions (in days) in the cotton simulation model GOSSYM.

node formation only seem to occur under severe carbohydrate stress, and then they build rapidly. Delays in fruiting branch formation are noticeable when the metabolite supply:demand ratio is about 0.7. The fruit loss function (FLOSS) is graphed in Figure 4. This relationship provides the numbers of fruit per plant marked for abortion each day.

The GOSSYM model has now been validated with over 50 data sets from Israel, covering a wide range of climatic conditions and management practices, and with several data sets from Mississippi and Arizona (Marani and Baker, 1981; Reddy, 1981). The success of this model, using the carbohydrate supply:demand ratio to calculate developmental delays and "natural" fruit abscission, over the time course of crop growth under such a wide range of conditions, has reinforced our conviction that both the carbohydrate sink strength and the concentration of soluble carbohydrates in the system are involved in the determination of the plant's hormone balances and its decisions to delay morphogenesis and abort fruit. However, the biochemistry of this decision-making process is not clear in the literature, nor is it clear how the effects of drought and nitrogen shortage operate on growth, morphogenesis and fruit abscission (see Chapter 10). The GOSSYM model handles these effects, but probably with some unnecessary empiricism and redundancy. We know that research is needed to characterize the relative changes in photosynthesis and nitrogen uptake along with potential and actual organ growth and changes in hormone concentrations in various tissues under water stress. We are finding that comparable mechanisms explain tillering, fruiting and fruit abortion in wheat and fruiting and fruit abortion in soybean. We believe that we are approaching the point where we can advance an hypothesis about these interactions.

Numbers in the following discussion refer to the line numbers in Figure 5. Virtually all of the linkages presented here can be documented in the literature.

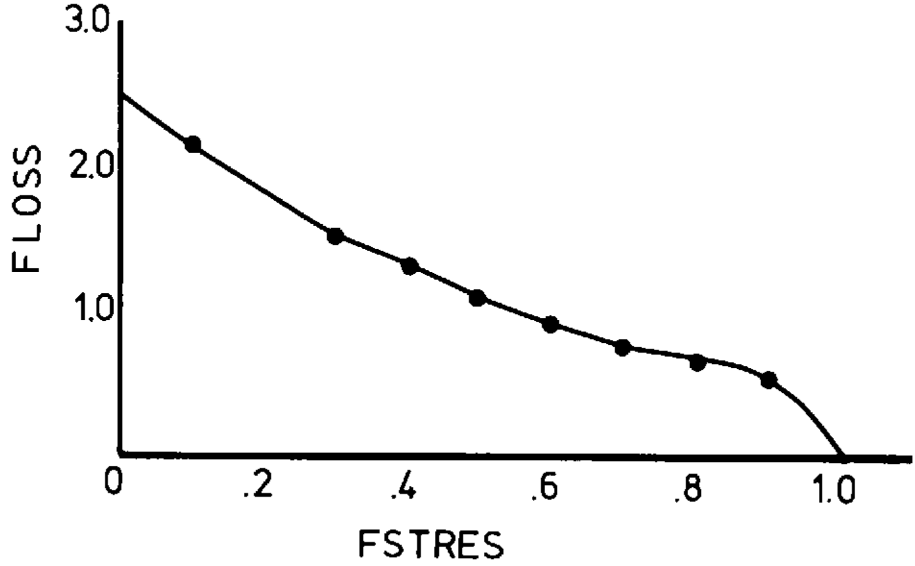

Figure 4. The fruit abortion function (fruit per plant) in the cotton simulation model GOSSYM.

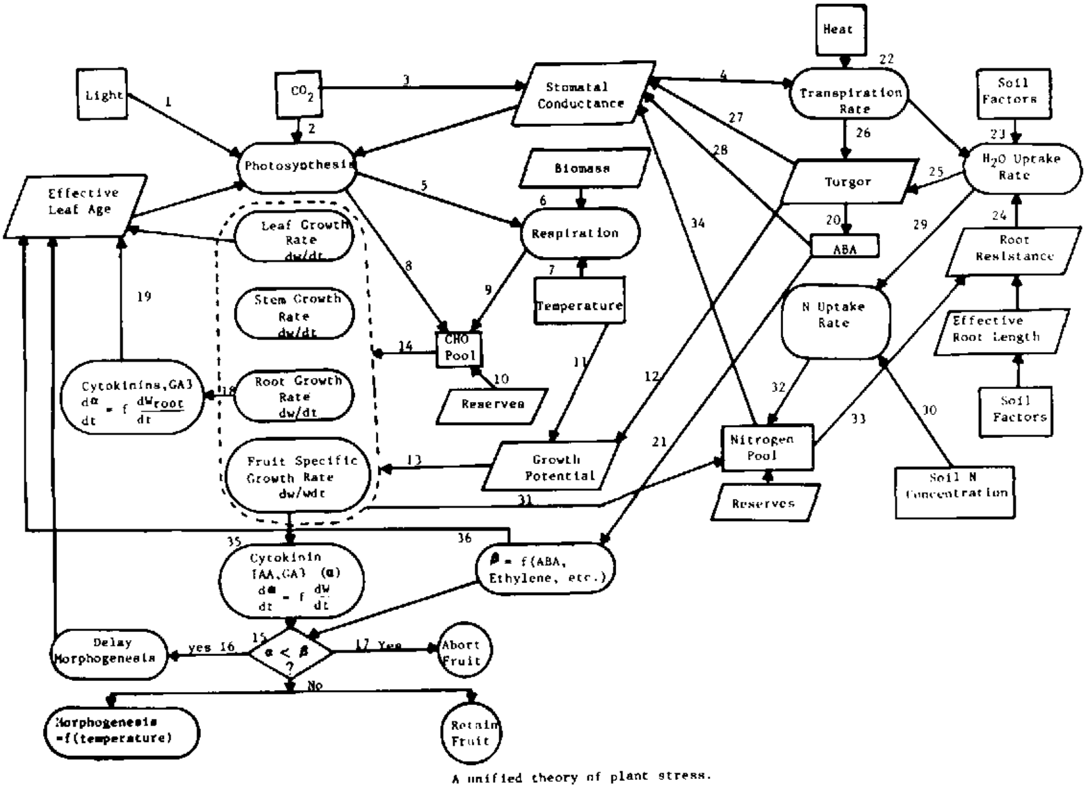

Figure 5. The major elements of a unified theory of plant stress.

CARBOHYDRATE STRESS

Light intensity 1 and atmospheric CO_2 concentration 2 drive the photosynthetic process, with the latter directly affecting the CO_2 concentration gradient and the flux rate into the leaf. Also, CO_2 indirectly affects the flux rate by its effect on stomatal aperture 3. This latter effect also determines the transpiration rate 4. We might note here that other factors, including light, intensity and temperature also affect stomatal apertures.

Photosynthetic rate (in C_3 species))5, biomass 6 and temperature 7 determine the respiration rate. The pool of carbohydrates available for growth depends on photosynthesis 8, respiration 9 and the quantity of labile carbohydrates held in reserves 10. Temperature 11 and tissue turgor 12 determine the potential dry matter accretion rate (sink strength) in a particular organ. Actual organ growth rate depends on the sink strength of the organ 13 and the supply of carbohydrates 14.

Several excellent reviews of hormone physiology have been written recently. Here we rely extensively on Moore (1979), Cognée (1976) and Guinn (Chapter 12). Much of the material concerns organ abortion in cotton. Also, much is known about the sources of hormones and the nature of their effects in plants. Osborne (1974) states that there are five specific compounds or classes of compounds in plants which act as "effector" substances regulating metabolic processes. These are abscisic acid (ABA), auxin (IAA), gibberellic acid (GA), cytokinins and ethylene. She notes that they all are present in all parts of the plant and all are involved in the control of abscission. Little is known about the physiological factors which determine the balances of hormones in plants, and little has been done to relate the processes of organ growth to hormone action in plants. From the hormone literature it is difficult to determine cause and effect. The plant appears able to sense a balance 15 between certain combinations of hormones involved in the stress-induced triggering of morphogenetic delay 16 and fruit abortion 17. For example, ABA and ethylene are implicated in the abscission process. Davis (1968) proposed that the abscission of cotton fruit is triggered by ABA above a threshold concentration. The data of Rodgers (1980) indicate that the threshold may be between 75 and 90 μg equivalent ABA per 100g fresh weight of tissue. However, he suggests that in young fruit the amount of ABA available to the abscission zone is of less importance than its interaction with several growth hormones known to be present. He proposes a homeostatic mechanism. Davis and Addicott (1972) reported that young bolls abscising late in the season contained about twice as much abscisic acid as those abscising early in the season. The rate of ABA production is enhanced under conditions of low tissue turgor 20 (McMichael and Hanney, 1977). Guinn (1976) noted that the sensitivity of plant organs to ethylene varied with age, condition and the levels of other hormones. IAA and certain gibberellins seem to assure fruit retention. Because we are unsure of the hormone physiology here, for the sake of discussion, we refer to the factor contributing to fruit retention as α, and the factor contributing to abscission as β. The rate of α production is enhanced under conditions of rapid growth 35. Could it be that α is a by-product of the growth process?

As noted earlier, the above rationale has been used successfully to simulate the seasonal time course of fruiting and morphogenesis. Those efforts suggest that, in cotton at least, the whole system is very dynamic. The metabolite pools are highly mobile and the abscission zones are very sensitive to the relative concentrations of α and β. We have found that to simulate abscission and the developmental delays, it is necessary to assume that the carbohydrate reserves (up to 30 percent of leaf dry weight) are all available within a 24-hour period. Calculations show that with a heavy fruit load, demand always greatly exceeds supply. In other words, the plant is living on a single day's photosynthate production during much of the fruiting period. The trigger to abort may be reached over a very short time period, and is, of course, irreversible. Via this mechanism the plant balances fruit load against photosynthate supply. We assume that some background ABA level exists, and that a carbohydrate stress which reduces fruit growth rate reduces the α concentration and allows the ABA to trigger fruit abortion. ABA counteracts the effects of GA, auxin and cytokinin, probably by making the cell membranes permeable.

As Osborne (1974) noted, all of the five classes of hormones are found in all parts of seeds plants. However, there are large variations in concentrations between organs and between the major sites of production for the various hormones identified in Figure 5. Auxin is produced primarily by the shoot tips, but smaller amounts are found at all sites of meristematic activity (Moore, 1979). It is subject to basipetal polar transport in the plant. Its primary action is to loosen cellulose microfibrils in the cell wall so that cell expansion can take place (Moore, 1979). Cytokinin is produced primarily by root tips 18 and by young fruit (Sandstedt, 1971), but it is also found in all meristematic tissue. It is translocated in both xylem and phloem, but is immobilized in leaves and buds (Moore, 1979). Cytokinin enhances nucleic acid synthesis and protein synthesis. It, therefore, delays leaf senescence 19, presumably by maintaining the proteins in a good state of repair, and it facilitates cell division. Gibberellins also delay leaf senescence (Osborne, 1974). ABA (Radin, 1981; Friedrich and Huffaker, 1980) and the gibberellins have opposing physiological and biochemical effects, although gibberellins are synthesized in the chloroplasts (Moore, 1979), and ABA tends to accumulate there (Hartung *et al.*, 1981).

WATER STRESS

As noted earlier, the CO_2 effect on stomatal aperture 3, together with the heat input to the leaf 22, at any specific humidity, determines transpiration rate, which along with soil water potential 23 and the hydraulic conductivity of the root system 24 determines the rate of water uptake by the plant (see Chapter 10). Any imbalance between water uptake rate and transpiration rate will reduce leaf turgor 25,26. The literature suggests that both turgor loss *per se* 27 and the increased ABA levels 28 associated with it will reduce stomatal apertures. However, Ackerson *et al.* (1977) reported numerous cases of visibly wilted leaves with reduced photosynthetic rates and little or no stomatal closure. We wonder if there is redundancy in the inclusion of the ABA stomatal closure connection 28 here. The feedback loop is closed in most cases, and the plant can conserve water. The suggestion of redundancy comes in the observation that if a plant is suddenly subjected to a high evaporative demand (little time for ABA buildup) turgor may be lost and the stomates may remain open.

The increase in ABA and ethylene associated with water stress seems to shift the hormone balance (α / β) toward fruit abortion and toward morphogenetic delay. This may be offset to some extent by the effect of turgor loss on potential growth rate 12 under conditions when growth is affected more than photosynthesis. Bruce and Römkens (1965) observed that rainout shelter plants, grown in clay soil, did not quickly resume vegetative growth and fruiting on rewatering after water stress treatments. In attempts to simulate the growth and development of these plants, we (Baker *et al.*, 1979a) found that the model GOSSYM, which predicted a restoration of photosynthate production and a relaxation of carbohydrate stress on rewatering, erroneously predicted a resumption of vegetative growth and a reduced rate of fruit abortion. We hypothesized that cell division and cell elongation were differentially affected by turgor loss, and we modified the model to accumulate the difference between potential (turgid) and actual organ growth under water stress conditions. This accumulated difference between actual and potential growth, during the drought, was added to potential growth on rewatering. Thus, in the model, on rewatering, an inordinate number of unexpanded cells contribute to the growth potential and to the total sink strength in the plant. This means that, even though rewatering may have enhanced photosynthate production, carbohydrate must be divided among more growing cells with the result that growth rate is curtailed in some. This offsets the enhancement of photosynthesis after rewatering and maintains the metabolic stress. With the inclusion of the logic, a good simulation of the Bruce and Römkens (1965) crops was obtained.

This rationale is somewhat controversial, and probably inadequate under conditions where osmoregulation occurs (Cutler and Rains, 1977). However, Radin and Parker (1979) have shown that growth can be inhibited by restriction in cell elongation while cell division continues, and Hsiao (1973) citing Slatyer (1967) and Slavik (1965) noted that it has often been stated that cell division appears to be less sensitive to water stress than cell enlargement. So there appears to be adequate justification for incorporation of this mechanism in a simulation model, at least under conditions of turgor loss.

An alternative explanation for the continued metabolic stress after irrigation, manifested in the Bruce and Römkens (1965) data, emerges from the experiments of Marani *et al.* (1984). They showed that when water stress develops over a considerable period of time, photosynthesis may not be fully restored for several days after rewatering. This effect may be mediated by root growth and cytokinin production. Apparently, cytokinin production is associated with root growth (Sitton *et al.*, 1967) in much the same way that IAA seems to be associated with shoot growth. Sitton *et al.* (1967) also have shown that the senescence rate of leaves is related to cytokinin levels. A powerful feedback effect may be set up in fruiting cotton subjected to water stress over a long period in which the reduction in root growth and the associated production of cytokinin enhances the rate of leaf sensecence, aggravating the reduction in photosynthesis. On rewatering, the plants may have a low photosynthetic rate until the old, senescent leaves are shaded by a layer of new leaves.

The experiments of Marani *et al.* (1984) document the connection between effective leaf age and canopy photosynthesis (37 in Figure 5). They showed that water stress, as it typically occurs in the field during a drying cycle, decreases photosynthesis through turgor effects on stomatal conductance, but it also affects leaf aging and the photosynthetic potential of the upper exposed leaves in the canopy in three ways. First, the rate of senescence of existing leaves is accelerated. Second, the rate of new leaf initiation is decreased. Third, the rate of growth and the ultimate size of new leaves is decreased. If the drought is long enough, these senescence effects on canopy photosynthetic efficiency may be quantitatively more important than the direct effects through leaf turgor and stomatal conductance. The effects are not simple, however. A vegetative plant may shift its dry matter partitioning to favor root growth. This tends to moderate the stress by allowing the plant access to more water, but also, if cytokinin production is associated with root growth, it may slow or moderate the drought effect on the leaf senescence rate. A fruiting plant, however, often lacks this option to shift partitioning in response to turgor loss in the leaves, and drought effects on canopy senescence and photosynthetic efficiency are profound. They can only be reversed with the initiation and growth of new leaves after rewatering.

NITROGEN STRESS

The rate of nitrogen uptake by the plant depends on the water uptake rate 29 and the soil nitrogen concentration 30. The pool of available nitrogen depends on withdrawal by the plant in the growth process 31, the nitrogen uptake rate 32 and the reserves available. The GOSSYM model simulates nitrogen stress by reducing potential growth, *i.e.* the sink strength, on the assumption that if a certain minimum of nitrogen is not available for the elaboration of new tissue, the new tissue will not be elaborated.

It is possible that the mechanism of action of nitrogen stress on the rate of morphogenetic development and fruit abortion is through the same route as the effect of water stress. Radin and Mauney (Chapter 10) showed that a nitrogen-starved plant has a large resistance 33 to the radial flow of water through the root. This tends to unbalance the transpiration rate:water uptake rate to the detriment of plant turgor. This balance is restored to some extent, however, by the fact (Radin and Parker, 1979) that stomatal conductance in cotton is more sensitive to water stress 27 under nitrogen stress conditions. In many species there is a good relationship between leaf nitrogen concentration and photosynthetic efficiency (Boote *et al.*, 1978). It might be supposed that this is mediated by reduced stomatal conductance and that observed fruit abortion and morphogenetic delay, especially in indeterminate fruiting plants, is through reduced photosynthate supply. Thompson *et al.* (1976) reported that late season cotton leaf nitrogen concentrations fell below two percent under a range of nitrogen fertilizer application rates. We have conducted numerous full season canopy photosynthesis experiments (Baker, 1965; Baker *et al.*, 1972) in crops fertilized at rates in the range of the Thompson *et al.* (1976) experiments, and never observed any decline in photosynthetic efficiency until cold weather occurred. Thus, this mechanism appears to operate only when leaf nitrogen concentrations fall below two percent.

We have proposed that cytokinins and gibberellins, which delay leaf and fruit senescence, are produced in the root system as by-products of root growth, and that IAA, cytokinins and perhaps, gibberellins are produced in the fruit as by-products of growth there. This hypothesis should be tested in experiments in which growth rates of these organs are varied in several ways while recording hormone concentrations in the organs. Root and fruit growth rates should be varied by adjusting photosynthate supply (atmospheric CO_2 concentration), temperature and turgor (water stress).

SUMMARY

We have outlined the linkages between the major plant processes in a model which can mimic the whole plant responses to various types of stress by describing the various influences on carbohydrate, nitrogen and water supply and demand. We believe that the plant physiological processes and the linkages between them vary little among species. All fruiting plants seem to have the capability to adjust morphogenesis and fruit set to establish a balance between demand for and supplies of water, photosynthate and nutrients in a way that will ensure the development of viable seed. By constructing this model we hope to provide a conceptual framework for the dynamic simulation of whole plant growth and development. *The model defines stress as a imbalance within the plant which results in reduced growth rates.* The model predicts that stress delays morphogenesis, speeds senescence and causes fruit abortion. The model is capable of describing variations in dry matter and nutrient partitioning, and it provides an interpretation of observations of stomatal responses to water stress, photosynthetic responses to nitrogen stress, and the effects of these stresses on plant senescence. These shifts in hormone balances trigger premature senescence, delays in morphogenesis and organ abortion.

The simulation of plant stress requires a whole system model with soil and climate variables as inputs. Such a model must account for the fact that a plant grown in an elevated CO_2 atmosphere has an enhanced rate of photosynthesis which may increase organ growth rates, the cumulative (over the period of plant growth) indirect effects of which may go far beyond the immediate effects on photosynthesis and transpiration. For example, the model must account for the fact that an enhanced leaf growth rate will exponentially increase light capture and photosynthesis in many young crop canopies. It must account for the fact that a more rapidly growing root system will help the plant to escape drought, and if, as we have proposed here, cytokinin production is a by-product of this root growth, leaf senescence will be delayed, and the leaves will retain their photosynthetic efficiency longer. Such positive feedbacks can amplify the direct effects of enhanced photosynthesis. Simultaneously, the model must account for the higher fruit set resulting from the enhanced fruit growth rate. Finally, the model must

account for the partitioning of more dry matter into fruit and the effect of this on vegetative (especially root) growth.

The ability of this dynamic crop simulation model to predict crop growth should be tested by comparing its predictions with crops grown under controlled conditions in which photosynthesis, transpiration and growth can be varied independently.