Chapter 9

PHYSIOLOGY AND MODELLING— PREDICTING THE "UNPREDICTABLE LEGUME"

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INTRODUCTION

It is clear that there have been major advances over the past decade in both the knowledge of peanut physiology and in the application of this knowledge to resolving crop improvement and production problems. The adverse perception of physiology by other peanut scientists as an "academic" discipline rather than an applied and applicable science has been (we hope) remedied. Peanut physiologists have been able to draw substantially on the developments and innovations made on other crops, since it is now evident that peanut is more similar to, than distinct from, the majority of other legume crops in its basic physiology. Thus, much basic legume physiology applies to peanut.

The greatest emphasis over the past decade has been on increasing the understanding of the role of environmental and genetic factors in modifying phenology and growth. To some extent these advances have occurred because of the decreasing levels of research resources for empirical experimentation over larger numbers of sites. Another factor contributing to these changes has been the increasing complexity of the problems that other disciplines have now to resolve. As other disciplines have found knowledge of crop processes to be important to their progress, physiologists have become integral parts of many multi-disciplinary research efforts.

Crop physiology has also been 'internally' influenced by the requirements of simulation modelling. The construction of simulation models has pointed to areas where increased knowledge has been necessary; particularly where models have been based on unrealistic, or empirical methods. This has been a very significant motive for basic research on peanut physiology.

The advances in peanut physiology will be described under three main sections—(a) normal growth (including basic processes, phenology, resource capture and use-efficiency aspects, growth distribution); (b) stress responses with particular reference to the genetic variation for these; and (c) applications of existing models. These sections will include examples of applications of physiological methods and knowledge to practical problems.

Physiology—A Study of Processes Rather Than Results

Physiology has always been defined as the study of processes. However, physiology has gained greater recognition because many more phenomena are now being considered from a process perspective. As a general rule, any

discipline adopts a physiological approach when the interest changes from the empiric result to the process(es) by which that result was obtained. This concept implicitly establishes a model relating to that result. For example, varieties may differ in their yield under drought conditions. The differences may be identified as having derived from differences in their growth (biomass accumulation) during the drought. Greater water extraction would result in these differences being due to variation in duration and amount of transpiration. However, they could arise also from differences in the carbon fixed per unit of water transpired—that is, in their water-use efficiency (WUE). Knowledge about the process basis for a result may allow varieties to be better matched with other known environments and become easier to exploit in other contexts, such as a breeding program.

Simulation modelling has been an important driving force in this change of emphasis. Reflecting the greater emphasis on physical environmental aspects of physiology, numeric modelling (as a mathematical expression of crop processes) has also found greater acceptance and significance as a tool for physiologists. Fundamental to these developments is the description of any result or change as the outcome of a process occurring at a rate for a given duration.

Although much of the research embraced by this definition of physiology has been focused on physical environment factors, there has also been considerable crop physiological efforts looking at the role of the biological environment on crop growth and development. Typical of this has been the investigation of the effects of foliar pathogens on peanut growth and development (Subrahmanyam et al., 1984; Pixley et al., 1990; Nokes and Young, 1991), and the research investigating the physiology of aflatoxin development in peanut (Sanders et al., 1993).

In crop physiology the desire to know the reason for empiric results often prompts a growth analysis linked to detailed environmental measurement. Experimental treatments and measurements are designed to allow the processes of interest to be examined as a function of either time or some other (usually environmental) factor. As an example, in the case of drought research, investigation of varietal differences may be done by examining water capture and WUE as the basis for differences in the growth, and partitioning differences as the basis for differences in pod yield. To do this, water supply must be manipulated and the water use by the treatments measured. Growth and its distribution also must be quantified by samples taken at appropriate stages of the experiment. With this data, growth can be expressed either as a function of time or water transpired.

Physiological Models—The Representation of Processes

The definition, or explanation of a result in terms of processes (now most usually in mathematical terms) provides a physiological model. Thus, modelling has been an integral part of crop and plant physiology for a long time. Over the past decade the advances in computers have allowed most scientists to consider simulation modelling as a research approach, and simulation modelling has come to dominate the outsider's perception of the

use of models in crop physiology. The use of analytical model forms, however, remains a fundamental feature of crop physiology and an area where physiological models are being applied in other disciplines (Williams, 1992).

Model Forms—A Progression of Complexity

Models often follow an evolution in terms of complexity and form. The initial model is often developed in an analog form in which the main components are often represented graphically. This model then is represented algebraically with the process being described in terms of an equation, the terms of which could be used for analysis and evaluation against observations in nature (termed analytic models). Once a model of a process has been proven reliable, it often provides the basis for (or part of) a simulation model. The really significant development in the simulation modelling approach has been the ability to introduce the time domain as a factor in interrelated multi-process phenomena, and therefore predict the effects of short term environmental effects.

The need or desire to model processes mathematically has encouraged two fundamentally different approaches to modelling. First, with the reductionist approach the problem is reduced into its component processes, and the control of individual components and their interactions are described with the ultimate intention to reassemble the component processes. The second approach (integrative) seeks to identify and focus on the most easily measured major processes which integrate subprocesses.

Analytic Models. Over the past decade many physiological processes have been defined in terms of an analytic model to facilitate design of experiments, determine the measurements needed, and to guide interpretation of data. For peanut, a classic example of this approach is provided by the investigation of yield changes in response to breeding (Duncan *et al.*, 1978). This experiment set out to analyze the basis for differences in yield potential of peanut cultivars against the model:

$$Y = C \times D_r \times p \qquad \text{Eq. (1)}$$

where Y = pod yield, C = mean crop growth rate, D_r = duration of the reproductive phase, and p = a partitioning coefficient. The experiment used plant populations which maximized the radiation interception and regular destructive sampling to determine the growth of plant mass and the duration of the reproductive phases. The results showed that improvements in yield potential associated with successive releases from the breeding program were attributable only to differences in D_r and p, with little change in C. This same model has been exploited successfully in analyzing a number of experiments (e.g., Witzenberger *et al.*, 1988; Flohr *et al.*, 1990; Williams and Saxena, 1991; Greenberg *et al.*, 1992).

Simulation Models. The greatest advantage of simulation model development has been the ability to combine models of subprocesses to estimate dynamic plant and crop responses to environmental conditions over short time intervals and to allow these results to influence the processes

operating during the next time interval. For example, the amount of photosynthesis occurring during a day is influenced by the leaf area. The current leaf area is the result of past investments of assimilate in leaf tissue. In a simulation model, some fraction of any day's photosynthesis would be utilized to change the leaf area for the computation of the next day's photosynthesis. Models for the relevant processes are combined as components of the overall crop simulation model, and then this is used to simulate crop responses to real or hypothetical conditions. A number of models of this type have been developed for peanut (Young *et al.*, 1979; Boote *et al.*, 1986, 1987, 1992).

However, these simulation models have been controversial in the sense that often they have required more parameters or knowledge than is available. To make them work, the developers often have taken a pragmatic view of present deficient knowledge, and they filled gaps by creating controlling mechanisms for these processes based on likely responses or information originating from other species. The parameters controlling these processes are then "calibrated" against data. This approach incorporates empiricism into the model and limits the scope for transferring the model to other situations and environments without "re-calibration." While this empiricism has been a major cause of criticism, it also has permitted models to operate and predict peanut responses with results acceptable to the users. A good example of this was provided by the use of photoperiod responses established for soybean (Wilkerson *et al.*, 1984; Jones *et al.*, 1991) as the basis for including photoperiod effects in the PNUTGRO model (Boote and Williams, unpubl. data, 1988). To achieve good correspondence with actual data, it was only necessary to implement the soybean program code and adjust the parameters to those appropriate for the cultivars of peanut.

A Generalized Linear Approach

Because of the complexities of analyzing and manipulating curves it has been a common practice to resort to and use linear functions wherever possible for making models. In a number of cases this has provided the basis for complete models. The models defining growth as a linear function of the resource captured and a resource use efficiency term (e.g., Monteith, 1977; Tanner and Sinclair, 1983) have been particularly successful as analytic models, as have the models describing phenology as linear functions of thermal time. This approach is of particular value in simulation modelling when the given process is influenced by a number of factors. Once the dominant factor (usually temperature) is determined and the rate of the process as a function of that factor is established in optimum conditions, then adjustment for modifying factors can be a simple process because of the simplicity of linear functions.

Even when the responses observed in nature are curvilinear, it seems that reducing them to a series of linear functions between given ranges of the controlling factor (as indicated in Fig. 1) has advantage. Obtaining the points of a linear function or "look up" table is probably less costly than accurately defining a curve. This approach has allowed many processes to be successfully
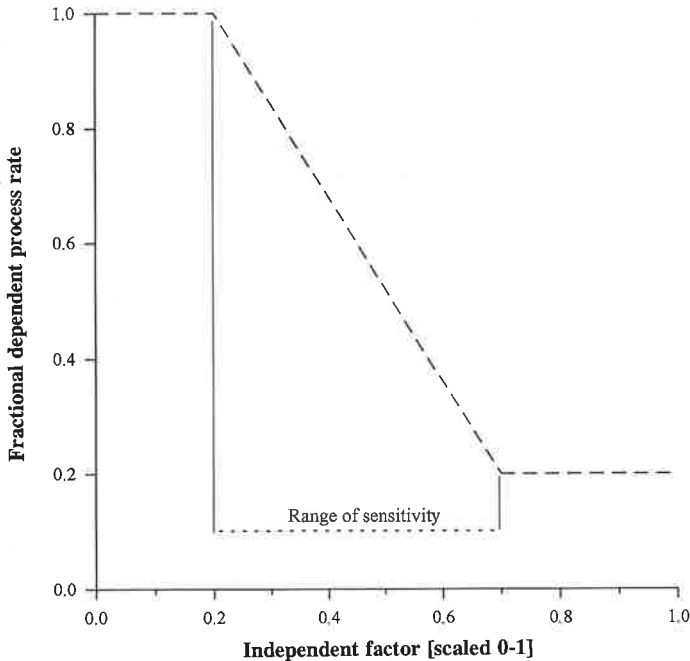
Fig. 1. A general linear model for controlling processes in response to environmental variables between two thresholds.

modelled without great discrepancies between actual and model simulated data.

While this exploitation of linear functions has been justified in the past, the advances in computer hardware and programming are such that this approach is likely to change as information and justification for other approaches increases. The conceptualization of processes and models as "objects" is likely to change approaches to simulation modelling substantially.

NORMAL, NONSTRESSED GROWTH

Basic Processes and Responses to Environment

Much of the increased knowledge about processes that determine peanut yield has occurred because of the commonality of basic plant processes across species. The physiology of peanut is very similar to that of many indeterminate legumes. Productivity is determined by the numbers of various plant structures developed, how fast they expand in size/mass, and the length of time this happens. Most processes are controlled by the same biophysical factors with results that are, in principle, similar to those observed in most plant species. For instance, the determinants of light interception are consistent across species, and species have common photosynthetic pathways (Boote and Loomis, 1991). Peanut usually varies from the general situation only in details.

Concepts of Time

Time is an abstract concept arising from observed change. Growth and development are changes over time. Therefore, concepts of time are of critical importance to physiology. Calendar time is determined by the rotation of the earth on its own axis and around the sun and is consistent relative to other experiences of man because of the constancy of our body temperature. In contrast, most plant processes are not consistent functions of calendar time. Plant change is determined by tissue temperature, which is not constant relative to the earth's rotation. Therefore, calendar time may be poorly related to plant changes and, if one uses this concept of time, then plant growth and development must be determined empirically for each environment. Despite the widespread recognition of the limitations of calendar time as a basis for phenology, this concept of time is still preserved in many current variety descriptions. Since the biochemical response of a plant is largely a function of temperature, it is more useful to examine processes as a function of thermal time (that is time conditioned by the prevailing temperature) than calendar time.

Temperature Responses

Biological processes have (a) a base temperature below which no activity occurs and no "time" occurs (T_b), (b) an optimum temperature (or temperature range) at which activity and time is maximized (T_o), and (c) a maximum temperature above which no time/activity occurs (T_m). These temperatures have been termed the cardinal temperatures and exist for both growth and developmental processes. Within species (including peanut), most plant processes have similar cardinal temperatures. Further, because of the role of temperature in determining respiration and the links between respiration and growth or development, most processes have similar temperature responses.

Base Temperatures. The most detailed information available on T_b of peanut is for phenological processes. Although earlier observations of time to flowering by Emery *et al.* (1969) fixed T_b at 13.3 C, work done in controlled environment facilities and glasshouses (Univ. of Nottingham, 1987) suggested a T_b consistently between 9 and 11 C for most peanut phenology (germination, leaf emergence, branch appearance, sowing to first flower, first peg, and first pod). Since the 9 to 11 C value for T_b coincided with that observed for other tropical species (Mohamed *et al.*, 1987), it is now widely considered a general T_b value for peanut. The T_b has always been considered to be constant for a given process. However, recent research (S. Nigam, unpubl. data, 1992) in varying photoperiods has supported the original values of $T_b = 13$ and has reopened the question of the constancy of T_b as will be discussed later.

Optimum Temperatures. The T_o for many processes lies somewhere between 27 and 33 C (Fig. 2; Fortanier, 1957), but only for a few processes has the optimum temperature been precisely determined. An interesting variation of this rule is the pod growth rate of crops. The rate of individual fruit growth conforms to this general rule (Fig. 2), but at the crop level the optimum is considerably lower, being between 20 and 24 C (Williams *et al.*,
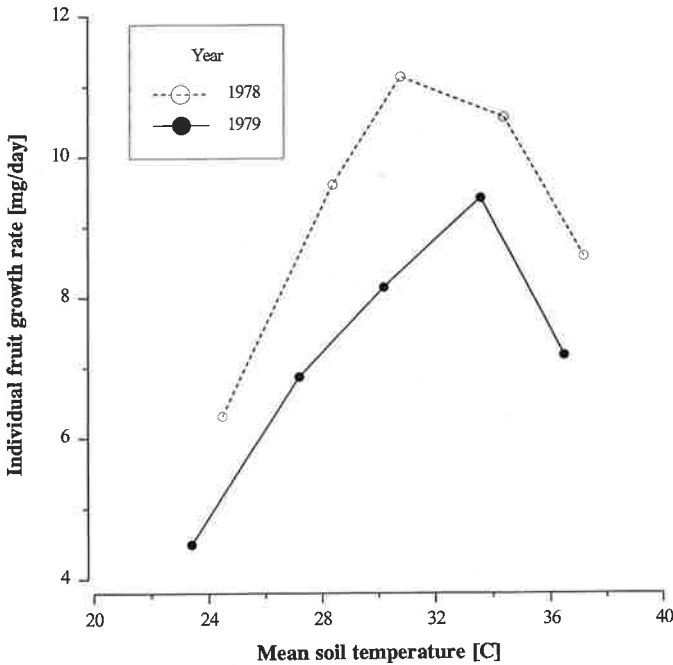
Fig. 2. Typical responses to temperature as demonstrated by individual pod growth rates (data derived from Dreyer, 1979).

1976; Cox, 1979). The difference is probably due to competition between sinks and the resulting translocation patterns.

Accurately defining and measuring the optimum temperature is difficult because of the need to hold plant tissue at a constant temperature for a long time and enough steps in the treatment set to allow this cardinal temperature to be clearly defined. When significant diurnal variation in temperature exists, T_o cannot be precisely measured because at temperatures on either side of the optimum the rates of processes decline. Another difficulty is that only population level data can be obtained for some processes because of the subterranean nature of the fruit.

It is not clear if the fastest rate of development occurs at a sharply defined temperature or across a broader plateau through this range of temperatures. Only for seed germination has adequate peanut data around the T_o been collected. Mohamed et al. (1988) suggested that T_o for this process is sharply defined at 33 C. This distinct T_o for germination is supported by Ong (1986) and by observations in other crops (Garcia Huidobro et al., 1982). The extent of variation between peanut varieties for temperature responses has only been reported by Ong (1986), although evidence exists for differences in adaptation of varieties to different temperature conditions (Greenberg et al., 1992).

Maximum Temperature. Information concerning the T_m for peanut is

limited to a few processes. For germination, Mohamed *et al.* (1988) established a T_m of about 45 C. For other processes there is a dearth of data. Because better information is unavailable, the value of 45 C is used for T_m for almost all processes in the PNUTGRO model since this is the temperature at which protein is denatured. For both the T_o and T_m there is very little information concerning the extent of variations between genotypes.

Respiration

All growth and phenology depends on respiration; it is the price for changes in state and form. Unless differences in the efficiency of respiration exist, higher rates are usually advantageous and indicative of greater growth or developmental rates. It is generally accepted that many processes and phenomena are linked by common respiratory processes at the biochemical level and are, therefore, influenced by environmental factors, such as temperature, in the same manner. The two dominant determinants of respiration are temperature and substrate supply.

Little research has been conducted directly on the respiration of peanut. Generally, respiration in peanut is considered the same as other plants. The existing simulation models use generic respiratory coefficients to compute the respiration associated with the production of carbohydrates, proteins, and oils. There is no evidence for major differences in specific respiratory costs for any process within the species.

Peanut respiration responses to temperature are similar to those of most plants. Watterott (1991) observed that root respiration was influenced by both recent photosynthesis (an offset diurnal rhythm) and temperature. The Q_{10} for temperature was 2.07, which is similar to that observed for most plants (1.8 to 2.2), and the value $Q_{10} = 2.0$ is generally recommended for modelling of respiration (van Keulen *et al.*, 1982).

Limitations to respiration associated with substrate supply are more difficult to document at the biochemical level, but many processes have been successfully modelled using a substrate limitation hypothesis, providing circumstantial evidence that the underlying respiration has been limited by substrates. These aspects are discussed later in relation to phenology and partitioning. The direct evidence for substrate limitations to peanut respiration and respiration-related processes was shown by Watterott (1991) for roots. In this study the respiration was strongly influenced by the temperature and photosynthesis occurring over the preceding few hours. There were strong diurnal trends in respiration (after the effects of temperature had been taken into account), which imply that substrate limitations to root respiration occur during dark periods. Varieties had different respiration rates, but these were considered more a result of the growth differences than differences in maintenance respiration.

Photosynthesis

The photosynthesis of peanut is governed by the same processes as photosynthesis of other crops and has been reviewed earlier by Ketring *et al.* (1982). This chapter, therefore, focuses on the conceptual advances in

peanut photosynthesis. In summary, peanut photosynthesis is based on the C_3 pathway; the biochemical processes exploit standard enzymes and the gas exchange obeys accepted physical laws. Photosynthesis of individual leaves of peanut and other C_3 plants tend to saturate at somewhat less than full sunlight (Pallas and Samish, 1974; Trachtenberg and McCloud, 1976). However, peanut canopies have not been observed to saturate in full sunlight (Ketring et al., 1982; Boote, unpubl. data, 1987). The rate of photosynthesis for peanut crops is comparable with the best rate observed on other legume plants.

Although unproven, it seems likely that the active orientation of leaves in response to light intensity acts to optimize photosynthesis and to protect the photosynthetic apparatus. Paraheliotropism in peanut leaves has been manipulated by changing CO_2 levels (F. Lenz, pers. commun., 1992) and occurs in drought (Matthews et al., 1988b; Chapman et al., 1993b) and nutrient stress situations (J.H. Williams, unpubl. data, 1991). The full significance and understanding of the control of leaf movement is still to be established.

There are reported differences between the photosynthesis of peanut genotypes (Pallas and Samish, 1974; Bhagsari and Brown, 1976; Wright et al., 1994), and these differences relate to the amount of carboxylase enzyme present in leaves (Nageswara Rao et al., 1994). These differences in basic photosynthesis are thought to be responsible for the varietal differences in WUE (Wright et al., 1994). However, they do raise an interesting challenge for physiologists in relation to the common failure to observe comparable variations in radiation use efficiency (RUE) outside of stress conditions (Duncan et al., 1978; ICRISAT, 1983; Matthews et al., 1988a; Li, 1991; Bennett et al., 1993) despite frequent observations of WUE differences. [A possible reason for the difficulties in detecting RUE differences is in the choice of varieties for the comparison. Li (1991), the exception in the list above, compared unadapted lines such as Chico, with locally adapted lines.]

Translocation

While the short-term patterns of translocation of assimilates have received considerable attention (e.g., Stirling, 1988; Flohr, 1989), there have been few studies of the basic processes of translocation in peanut. This shortage of direct information is curious considering that translocation is the process underlying distribution of assimilates to the various structures and growth points, and differences result in variations in partitioning. It is assumed that translocation (being an active metabolic process) is influenced by the same factors that influence respiration. Thus, temperature is assumed to play a major role in determining the kinetics of translocation.

Source and particularly sink "strengths" apparently have a major impact on the rates of translocation. The research of Flohr (1989) suggests that translocation is influenced by gibberellic acid levels in the various competing sinks, while the work of Nageswara Rao et al. (1989) suggests that 'signals' from the roots may be involved in increasing translocation to roots during drought stress. Another aspect which may have significance to the patterns

of assimilate distribution is the distance between source and sink. Presumably this distance factor works to influence the "perceived" sink strength or by increasing the potential competition between the sink of interest and others. Although this aspect will be discussed further in the section on partitioning, it should be said here that translocation in peanut is an area where our direct knowledge is empiric. It seems likely that a better understanding of translocation will be needed to more accurately model some of the stress effects observed in this crop.

Transpiration

Transpiration is determined by the balance of water uptake relative to potential evaporative demand. In the event that the root is able to match evaporative demand, the rate of transpiration is determined by intercepted radiation and the dryness of the air. If the roots are not able to satisfy demand, then transpiration is determined by the extent and distribution of the root system, the soil physical properties and water content. When the soil within the extraction frontier is above a threshold water content, transpiration is closely related to the vapor pressure deficit (VPD) and the intercepted radiation flux. Below this soil water content, water supply factors such as root:shoot ratios (Simmonds and Azam-Ali, 1988) or soil water content (Erickson *et al.*, 1991) dominate the rate of transpiration.

Transpiration is a process that is controlled largely by physical processes. As such, it has been commonly modelled using the electrical resistance analog model. Thus, the rate of transpiration is determined by the differences in water vapor pressure between the leaf (v_i) and air (v_o) and the resistance of the stomata and canopy to diffusion. Stomatal resistance of peanut does increase progressively with imbalance between demand and supply as reflected in decreasing water potential (or leaf relative water content). But peanut is one of the more desiccation-tolerant legumes (Ludlow, 1989) and plants apparently make little effort to preserve hydration status by stomatal regulation.

Phenology

Phenology is the study of environmental influences on plant development. This includes the initiation of plant structures such as leaf, branch, flower, pod, and the progress from initiation to maturity and then death of these structures. Phenology has increased importance as an aspect of physiology because of its primary importance to adaptation of crops to different environments (Lawn and Williams, 1988) and its significance to understanding and simulation modelling of crop responses to environmental factors. Fundamental to the progress in this area has been the acceptance of the discrete event as the focus of interest. Single event phenology has attracted considerable research emphasis over the past 10 years, resulting in significant progress in knowledge. However, because of the indeterminate nature of peanut growth, we need to consider phenology at two levels, "discrete" and "population."

Phenological events/processes may be defined for many purposes, and no rigid classification is necessary. However, a detailed phenological description

(adapted from soybean phenology) has been defined for peanut (Boote, 1982). The purpose of this description (Table 1) was to define standard phases of peanut development relative to visually identifiable stages of the crop. This system describes a series of vegetative (V) and reproductive stages (R) and all stages are discrete population-based events which are mostly determined by field observation. This scheme is now an integral part of the PNUTGRO model and has the advantage of being a standard. The onset of each new stage depends on thermal time which is based on an empirical function of temperature with T_b = 11 C, T_o = 28 C and T_m = 45 C. This phenological description is employed and predicted in the PNUTGRO simulation model to control partitioning and other physiological processes. The environmental factors known to influence development of most crops are temperature, light, nutrients, water, and photoperiod.

Discrete structure phenology relates single events (such as the appearance of the first flower or a new leaf on a branch) to the environment. This aspect of phenology is determined mostly by direct environmental effects such as temperature, photoperiod and water. The transition between two states when expressed as a process is the rate of progress to that event (θ) (the

Table 1. Growth stage descriptions for peanut.

Stage no.	Stage title	Description
	Vegetative stage[a]	
VE	Emergence	Cotyledons near the soil surface with the seedling showing some part of the plant visible
VO		Cotyledons are flat and open at or below the soil surface
V-1	First tetrafoliolate	One to N developed nodes on the main axis, a node is counted when its tetrafoliolate is unfolded and its leaflets are flat
	Reproductive stages[a]	
R1	Beginning bloom	One open flower at any node on the plant
R2	Beginning peg	One elongated peg (gynophore)
R3	Beginning pod	One peg in the soil with turned swollen ovary at least twice the width of the peg
R4	Full pod	One fully-expanded pod to dimension characteristic of the cultivar
R5	Beginning seed	One fully expanded pod in which seed cotyledon growth is visible when the fruit is cut in cross-section with a razor blade (past the liquid endosperm phase)
R6	Full seed	One pod with cavity apparently filled by the seeds when fresh
R7	Beginning maturity	One pod showing visible natural coloration or blotching of inner pericarp or testa
R8	Harvest maturity	Two-thirds to three-fourths of all developed pods have testa or pericarp coloration. Fraction is cultivar-dependent, lower for virginia types
R9	Over-mature pod	One undamaged pod showing orange-tan coloration of the testa and/or natural peg deterioration

[a] For population, V stages can be averaged if desired. Reproductive stages should not be averaged. An R stage should remain unchanged until the date when 50% of the plants in the sample demonstrate the desired trait of the next R stage. The timing of a reproductive stage for a given plant is set by the first occurrence of the specific trait on the plant without regard to position (from Boote, 1982).

reciprocal of the time interval between two events). While the time to an event usually varies with temperature in a curvilinear fashion, the rate of progress is usually related in a linear fashion (Fig. 3) to environmental factors such as temperature and photoperiod (Summerfield and Roberts, 1987). This rate of progress to the event has been particularly effective in relating discrete events to environment.

Population phenology deals with successive, multi-site events, each having their own discrete phenology determined by one or more aspects of the environment (usually temperature), but often determined at the population level by environmental factors that apparently operate through substrate limitations. The environmental factors which dominate population phenology are often those that constitute or influence resources for growth. The difference between population and discrete event phenology is illustrated by leaf initation. On a single branch, it (the discrete event) is usually determined by temperature. However, for a crop (the population level), we may have the number of leaves being determined more by genotype, light, and mineral nutrition than by temperature.

The duration of the pod set phase of the crop and the associated time to optimum harvest serves as a second example. In the case of pod setting, temperature is the primary environmental factor determining the first pod and the rate of pod initiation on a branch; but the end of the process (when the last pod initiation process occurs) is determined largely by the plant's
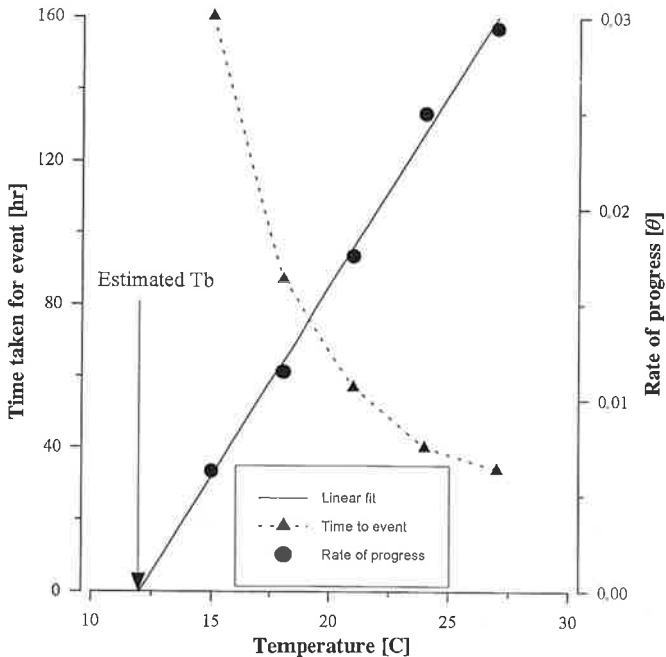

Fig. 3.   The linearization of phenology responses to temperature (hypothetical data).

source-sink relations and is therefore determined by factors such as light intercepted by that plant which can be varied by competition, defoliation (Williams, 1978) or water relations (Harris *et al.*, 1988).

Temperature. Because of the ease with which phenology can be measured, it has provided a convenient tool to examine general temperature effects on peanut and to estimate the cardinal temperatures for peanut. The cardinal temperatures have been generally accepted as constant for any given process (since they reflect temperature effects on respiration). The determination of cardinal temperatures has usually been done by linear regression of the rate of progress towards a phenological event against measured temperatures, either in the field or in controlled environments. The T_b and T_m have been taken as the temperature where the regression estimate for $Y = 0$ (Fig. 3). A major assumption in this approach has been that the response is linear between the T_b and T_o. Data for temperatures close to T_b are usually not available, the exception being for germinating seeds (Mohamed *et al.*, 1988). These data justify the use of a linear model, and this evidence has been used to support the general use of the linear regression method even when the data have been relatively distant from T_b.

The cardinal temperatures based on seed germination (10 or 11 C) have been accepted as general for the species, despite the higher values of $T_b = 13$ C observed for progress to flowering (Emery *et al.*, 1969) and $T_b = 17$ C for first pods (Campbell, 1980). However, two experiments provide data which raise doubt about the constancy of T_b or the linearity of the response. First, a phytotron study conducted (S. N. Nigam, pers. commun., 1992) in North Carolina found that a model using $T_b = 10$ C did not account for all the temperature effects on flowering phenology. T_b was recalculated (using linear regression) as 13.1 C (averaged over varieties) which is very close to the value obtained by Emery *et al.* (1969). Individual variety x photoperiod treatments showed small (statistically insignificant) differences in T_b between varieties and that T_b for photoperiod-sensitive varieties was similarly influenced by photoperiod (Table 2). While these differences are not statistically significant and are based on small temperature treatment numbers, the indications of photoperiod effects are supported by independent data where photoperiod was manipulated in the field (Flohr, 1989), which also indicate a higher T_b for pod development of photoperiod-sensitive varieties in long days. While observations of T_b changing in response to photoperiod

Table 2. Estimations by linear regression of rate of progress toward flowering on temperature for Tb from phytotron data of S. N. Nigam (pers. commun., 1992) in phytotron-controlled temperatures with varied daylength.

	Estimated base temperature (C)	
	Short day	Long day
VA 81B	13.30	13.70
TMV 2	12.54	14.50
NC Ac 17090	11.65	12.94

are not numerous and differ strongly from the general view of a consistent base temperature, they point to the need to improve knowledge in this area.

Some of the variations observed for T_b can be reconciled by examining the basic processes and the assumptions about them. First, the strongest evidence for a base temperature near to 10 C comes from germinating seeds. Second, most data sets for other processes do not have large amounts of data, particularly in the temperature range close to T_b. Therefore, there may be errors due to extrapolation or due to the assumption of a linear response over the full temperature range.

Photoperiod. The photoperiod is an environmental factor influencing phenology of many crops (Summerfield and Roberts, 1987). In the case of peanut, photoperiod was initially considered a phenologically insignificant factor (Fortanier, 1957; Bunting and Elston, 1980). However, this view has been revised during the decade following observations of photoperiod effects on yield (Wynne et al., 1974). Photoperiod does have significant effects on the post flowering phenology of many genotypes (Flohr et al., 1990).

Effects of photoperiod are not very evident in preflowering phenology where long days may cause a delay of only a few days in flowering. However, the subsequent phenology of sensitive varieties is strongly affected. The intervals between flower to resulting peg and pod to mature pod may be increased by long days in photoperiod-sensitive varieties (Flohr et al., 1990; S. N. Nigam, pers. commun., 1992). These effects are clearly genotype-specific and are modified by temperature (Bell and Harch, 1991; Bell et al., 1991).

Flohr (1989) found that the photoperiod effects in peanut were reversible by the manipulation of gibberellic acid levels in the plant. In short days, the application of GA_3 to the shoot had the same effect as long days—*viz.*, slower phenological development for fruit. In long days the phenology could be accelerated towards the rates operating in short days by decreasing shoot growth by the application of a GA-inhibiting compound (P333). If these manipulations with GA and its inhibitors are operating to change carbon distribution to the sinks, then the suggestion of a substrate limitation to phenology is justified.

Water. Both excess and deficient water in the atmosphere and soil have significance to phenology, most particularly at the population level. Most research has focused on the consequences of water-deficit situations, but excess water in combination with optimum temperature has been shown to be important in a few cases (Williams et al., 1976; Ong et al., 1988), particularly in deciding the initiation of pods on bunch-type peanuts.

Dry conditions (both atmosphere and soil) limit most phenological processes. However, for discrete events on existing structures the effects are less pronounced than at the population level. The differences in sensitivity according to level are best illustrated by the examples of flower and leaf initiation.

At the discrete level, rate of leaf appearance on the mainstem is slower during soil water stress than when water is not limiting (Harris et al., 1988).

But with the release of stress, there is rapid appearance of the leaves indicating that the leaves had been initiated but had failed to expand. However, the impact of water stress at the population level is also influenced by the impact of stress on the initiation of branches. Water deficit also rapidly changes the initiation of branches. Thus, dry air or soil may result in a small reduction in leaf initiation rate on a branch but have substantial impact on the same process for the canopy.

In the case of flower initation, the evidence is that water stress operates more by preventing expansion of flowers than by preventing flowers from being initiated. This is suggested by the flush of flowers associated with the release of drought stress. As for leaves, Harris *et al.* (1988) observed that flower emergence was reduced by low water potential but, when the stress was released, the "flush" of flowers rapidly returned the total number to a value comparable with that of the control treatment. Thus, the initiation of floral primordia was apparently continued despite stress, but their expansion was delayed until water relations returned to normal. However, the impact of water stress also may be permament because of a rapid translation of stress to population level phenology. Water deficit rapidly changes phenology of branch appearance. The attendant 'down stream' effects on the initiation of structures such as leaves, flowers, etc. can be substantial.

There are major differences between genotypes in the recovery response after stress (Harris *et al.*, 1988; Nageswara Rao *et al.*, 1989). These seem to relate to tolerances of phenological processes at the level of primordia which suspend expansion growth rather than ceasing or dying. Despite our lack of knowledge of the physiological basis for differences between varieties, these seem the largest source of genetic variation to drought stress (Nageswara Rao *et al.*, 1989) and are being currently exploited in selection by breeders and physiologists at ICRISAT. Clearly there is need to further study the phenomenon.

Fertility and Light. Although nutrients and light have an influence on phenology, particularly so for branch initiation, there are no clear indications of how these factors influence discrete event processes in peanut. Phosphorus deficiency and aluminum toxicity seem to influence branch production substantially (J.H. Williams, unpubl. data, 1991).

Nutrients and light are important because of their role in determining assimilates which often determine the end of phenological processes at the population level. Bagnall and King (1991a, b) reported that the rate of progress towards flowering and pod formation was retarded as irradiance was decreased below a critical level [<500 μmol photon flux /m²/s].

Genetics

Although genetics also plays a role in creating differences in phenology, there has not been much progress in understanding the biochemical basis for phenological differences between varieties. The majority of the information generated over the past decade has described genetic effects in terms of modifying the parameters of general models. Thus, varieties have been described as differing in the thermal time requirements (using the 'standard'

cardinal temperatures), but not in terms of the differences in biochemical process that cause this difference. Data relating to genetically determined differences in base temperature are scarce. Ong (1986) reported differences of 5 C in T_o between cvs. Natal Common and Robut 33-1 with attendant differences in T_m.

One obvious effect of genotype on the phenology of branching and reproductive structures lies in the inherent differences in the sequence of branches and reproductive nodes on plants of different subspecies of *A. hypogaea* (Gregory *et al.*, 1980). For the ssp. *hypogaea*, the branch number at the crop level may increase exponentially as a function of time, while the ssp. *fastigiata* group have much less flexibility, since the majority of nodes on the primary branches subtend inflorescences.

Agronomy

Among other environmental factors, agronomic management plays a part in determining the end of pod setting by varying the light resources available to individual plants. In low partitioning varieties grown at low plant population densities, pod initiation may continue indefinitely. This is possible because the initiation of a pod is dependent on the chain of events (starting with leaf and node initiation) which increases resource capture while there are unexploited resources. Continued stem growth that increases light capture also increases the nodes available for flower initiation, and this can continue indefinitely with the indeterminate peanut when there is no competition for light and water. However, higher populations do not progressively reduce the duration of pod-setting. The pod-setting phase seems to become constant once canopy closure occurs close to the start of flowering (J.H. Williams, unpubl. data, 1974).

Modelling Discrete Event Phenology

Most evidence suggests that temperature is the dominant influence for many discrete phenological processes. This has been reflected in the available models which seek first to take into account the temperature effects on development and deal with other environmental factors as modifiers of the temperature determined rate. This is clearly a sound strategy since most phenology is a linear function of thermally conditioned time within the temperatures prevailing in practical production environments. We know of no cases where, in conditions of less than optimal temperature, discrete events have occurred faster as a result of a varied environmental factor—thus temperature determines the boundaries to phenological progression.

Two essentially similar approaches have been employed to adjust thermal time to calendar time. The first expresses time as degree days (day C) and the second convention adjusts time to physiological days/calendar day (a physiological day is 24 hr at T_o). Common to both of these schemes is the concept that the rate of phenological processes increases linearly between T_b and T_o and then decreases linearly between T_o and T_m. A variation to this response is where T_o may be considered as either a precise temperature or as a plateau. Whether there is a plateau or a peak to the response function apparently has little practical impact on the outcome of predictions because

of compensating differences in the variable environments of the real world. Both models provide estimates of thermal time that relate well to empiric data.

Modeling Responses to Multiple Factors

As stated earlier, the responses to temperature between the cardinal temperatures are usually considered to be linear. A clearly defined optimum may exist (Fig. 4a), as for seed germination (Mohamed *et al.*, 1988). If the cardinal temperatures remain constant and the responses are linear, the effects of other environmental factors influencing phenology must reflect a decrease in the rate of progress at optimum temperature (Fig. 4b). This
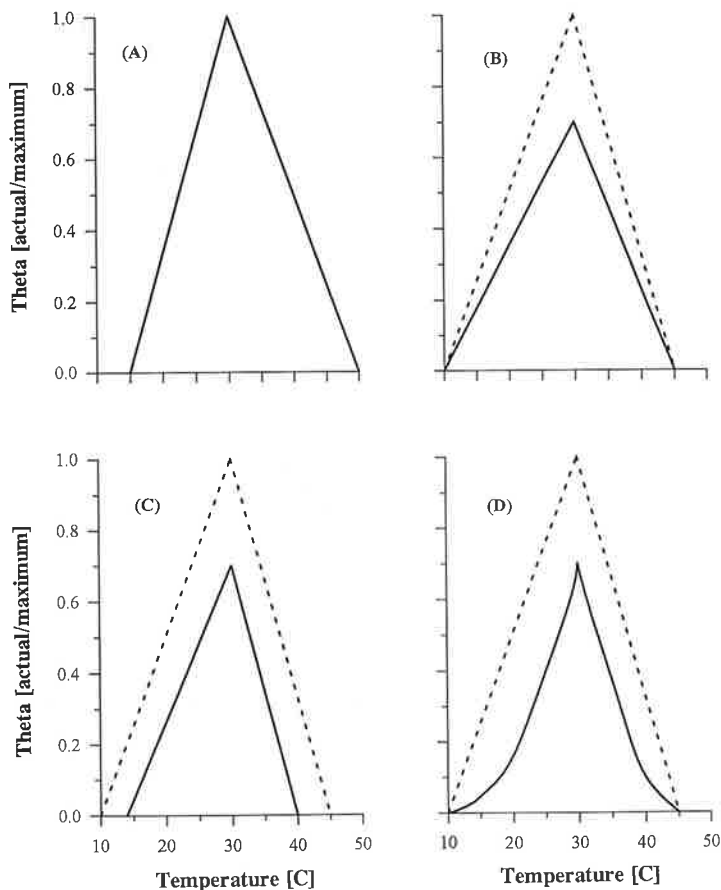
Fig. 4.   Models for the effect of temperature on phenology. (A) Linear model between three cardinal temperatures, no other factor limiting development. (B) Linear model with a factor limiting the maximum rate, but with no change in the base temperature, or in the maximum temperture. (C) Linear model with reduced maximum rate, and changes in upper and lower cardinal temperatures. (D) Nonlinear model for a limiting factor which reduces maximum rate, with apparent shift in cardinal temperatures as measured by linear regressions extrapolated to q = 0 but maintaining constant upper and lower cardinal temperatures.

approach has been very successful, accounting for most compound environmental effects. It also has the advantage of being conceptually and mathematically easy to deal with for both data validation and simulation purposes. However, the assumption is that the responses are linear between constant cardinal temperatures.

The challenge to these assumptions is recent and comes from a number of relatively small discrepancies, which individually have been discounted, but in concert should not be ignored. One of the observations which suggests that our model can be improved is the variation in T_b for different processes (germination 10-11 C; first flowers 13-14 C; first pods 17 C). These changes in apparent T_b occur despite the commonality of the underlying respiratory responses to temperature ($T_b = 10.7$ C; Watterott, 1991). Another discrepancy is the apparently higher T_b in photoperiod-sensitive varieties in long days (S. N. Nigam, pers. commun., 1992). These "discrepancies" all result in the estimated T_b being higher than T_b for respiration, but never lower.

The data from the photoperiod studies suggest that a change in T_b (Fig. 4c) or dropping the concept of linear responses over the full temperature range may be necessary to improve our model. This latter option is also necessary to arrive at a constant T_b for all processes. Given that the biochemical processes are determined by both temperature and substrate factors, a more appropriate model may be a curvilinear model driven by substrate and temperature—such that in the range, where most data are available, the response is linear but passing through the common T_b. A model like the expolinear model (Goudriaan and Monteith, 1990) (Fig. 4d) may be appropriate.

Whether these effects are proved or not, it is clear from the photoperiod effects that T_b may not be constant or the response may not be linear. Comparison of Fig. 4b and 4c indicates the extent of errors in prediction associated with choice of assumptions according to the prevailing temperature.

Modelling Population Phenology

Strong circumstantial evidence from simulation modelling indicates that the availability of assimilates is more important than temperature in determining many of the "population" phenology timings. Light, mineral nutrition, and water may influence population phenology mostly through carbon availability feedback mechanisms. These aspects of the environment seem to influence phenology mostly by delaying, or preventing, the expansion of new sites for phenological activity. Direct evidence for the assimilate feedback mechanism controlling the initiation of new pods is provided by a study of the rate of new pod initiation in relation to the stem growth rate. Williams (1978) observed that the rate at which growing pods were initiated was maintained through time until the assimilate supply (as measured by the stem growth rate) declined to a threshold value (Fig. 5). Mechanisms such as this are employed to regulate pod setting in most models. The pod setting routine of the PNUTGRO model establishes pods at an empirically determined maximum number per day until the carbon assimilates required to satisfy the pod growth requirements of existing pods exceeds a defined fraction of the

daily carbon assimilate. At this time the pod initiation ceases. This mechanism corresponds well with the data shown in Fig. 5.

Resource Capture and Growth

The primary resources of interest for growth are light, water, and nutrients which are captured by either the canopy or the root systems. Resource capture is dynamic and needs to be considered in both the domains of time and space. Therefore, it is common to consider resource capture both over short time intervals and cumulatively. In this section much of the discussion is structured around the components of a general, simple analytic model (Eq. 2) showing that growth over time (dM/dt) is the product of resources (X) captured/exploited over time (dX/dt) and the efficiency with which those resources are converted to dry matter (e). This model is appropriate for the discussion of light and water. While appropriate for nutrients, it has not been widely applied in that context.

$$dM/dt = (dX/dt) \times e \qquad \text{Eq. (2)}$$

General Resource Capture Considerations. The amount of resources captured by the root and shoot systems is inevitably determined by their size and their distribution and by the available amounts of the resource within their resource capture boundaries. The size and distribution of structures associated with resource capture through both time and space are intimately related to phenology (Eq. 3) which determines the numbers of each organ available at any given time. In the case of leaves, the size of a resource
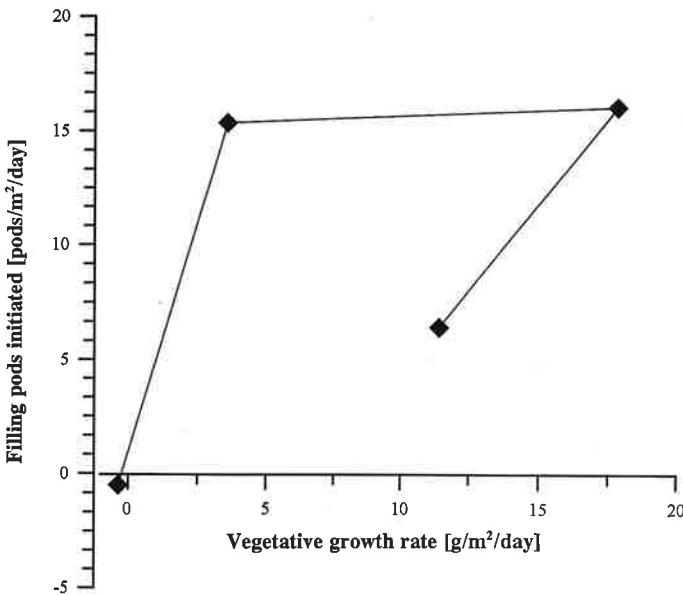

Fig. 5.   Relationship between pod initiation and carbon supply as indicated by stem growth rate for Valencia R1 peanuts grown at Harare Research station (from Williams, 1978).

capture apparatus is a function of the numbers of constituent units and their mean size. Thus, the leaf area index (L) for light interception is:

$$L = N_p \times N_L \times A_L \qquad \text{Eq. (3)}$$

where N_p = plant number per unit land area, N_L = mean leaf number per plant, and A_L = mean area per leaf.

However, equally successful at describing the size of the resource capture system (Eq. 4) is information on the mass and the surface area per unit mass for the organ involved. With this approach, L is the product of leaf mass per unit land area (M_L) and specific leaf area (s_L):

$$L = M_L \times s_L \qquad \text{Eq. (4)}$$

Both solutions to the determination of the size of a resource capture system are equally valid. However, they are not particularly valid in the event of stress when distribution of organs relative to resources plays an important role in their ability to capture resources.

Light Capture and Light Use. The past decade has seen considerable progress in understanding of light interception and its exploitation for growth. This knowledge has been exploited in refining simulation models and in interpreting experiments. The light intercepted by peanut is a function of the leaf area, distribution of leaves, and their orientation relative to the sun.

a. Canopy size and distribution considerations. When leaves are distributed uniformly over the ground surface, the basic relationships between leaf area index, leaf orientation, and sun angle apply. In these conditions, light interception by plants is generally complete (>95% of incident radiation) once the leaf area index exceeds 3 to 3.5. With complete interception (and other conditions not being limiting), the crop growth rate of peanut ranges between 15 and 25 g/m²/calendar day depending on the radiation flux (ICRISAT, 1983). However, the leaves of a peanut crop are not usually uniformly distributed across the ground surface. This introduces more complex geometry into the process of light interception. Between emergence and the complete cover stage it is normal for the crop to go through two phases with distinctly different geometric characteristics (Matthews *et al.*, 1988b). First, as individual plants (before the canopies of individual plants within the row merge), the canopy approximates a series of hemispheres. In the second phase (after adjacent plants merge), the canopy approximates to a horizontal hemi-cylinder (hedge-row), which passes to a uniform canopy once the canopies of adjacent rows merge. How long the canopy approximates to each of these forms depends on the planting geometry and population density. For the typical U.S. production system with rows 91 cm apart, the hedge-row form exists for a significant part of the season. In the PNUTGRO model, light interception is addressed in each of these phases by having the appropriate functions included (Boote *et al.*, 1992).

Within the boundaries of these geometric forms the radiation interception is generally high. Azam-Ali (pers. commun., 1985) found that within the boundaries of the geometric shape the fractional radiation interception was

usually in excess of 0.9 for the spreading bunch cultivar Kadiri 3. Thus, good estimates of radiation capture in unstressed conditions may be obtained by simple measurement of plant dimensions.

b. Para-heliotropism. The leaves of peanut are able to fold so the relationships between light interception and leaf area within the boundaries of the canopy are not constant. Leaf folding commonly occurs when stress occurs and then reduces the fractional radiation interception. Leaf folding has been observed in response to strong radiation in drought (Matthews *et al.*, 1988b; Chapman *et al.*, 1993b), heat, nematode injury (K.J. Boote, unpubl. data, 1989), and nutrient stress (J.H. Williams, unpubl. data, 1992). Research at the University of Bonn has shown that peanut leaf angle can be manipulated by variations of the atmospheric carbon dioxide concentrations and light intensity (F. Lenz, pers. commun., 1992).

Leaf folding diminishes the light intensity at the chloroplasts by changing the angle of incidence. This latter aspect seems valuable in protecting the photosynthetic system against long-term damage to the chloroplasts. D. Harris (pers. commun., 1983) observed differences in leaf greenness resulting from orienting the leaves at right angles to strong incident light while measuring photosynthesis. The nonutilized reduction potential resulting from electron excitation by photons in full sunlight apparently bleached the chlorophyll of these peanut leaves. Para-heliotropism is apparently an adaptation to stress conditions that can limit photo-inhibition of photosynthesis.

There may be genetic differences also in the predisposition or ability to exhibit para-heliotropism of the leaves. Although commonly observed in drought screening at ICRISAT, these differences rarely have been reported in the context of varietal attributes, perhaps because of the difficulty of quantifying them. However, Matthews *et al.* (1988b) showed that the extent of leaf folding was a single function of water potential across four cultivars. Chapman *et al.* (1993b) also noted that the cultivar McCubbin wilted when exposed to water stress while other virginia types displayed leaf folding, perhaps because of differences in water potential.

c. Radiation use efficiency. The efficiency with which radiation is converted to dry matter (RUE) has attracted considerable interest from physiologists. Studies have shown that the accumulation of biomass (or more usually shoot mass) is a linear function of the cumulative radiation intercepted by most crops (Monteith, 1977) when other factors are not limiting to growth. For peanut, this concept has been validated (Matthews *et al.*, 1988b; Azam-Ali *et al.*, 1989; Bennett *et al.*, 1993) with the range of RUEs between 0.75 and 1.4 g/MJ. This value is usually computed as the linear regression coefficient for the biomass as a function of cumulative intercepted radiation. Some of the differences in estimates for RUE can be accounted for by the higher energy content of the pods. Failure to adjust for differences in energy content of the pods relative to other structures (Duncan *et al.*, 1978) can result in low values of RUE (Bennett *et al.*, 1993). Another source of RUE variation lies in the N content of the leaves (Sinclair *et al.*, 1993). Theoretical calculations with more complex canopy photosynthesis models indicate that

RUE increases somewhat as the canopy closes and that RUE is higher with lower irradiance (also achieved by para-heliotropism) and cloudy conditions (Boote, unpubl. data, 1994).

Stresses tend to reduce the observed RUE. For instance, drought stress results in a decrease in RUE (Matthews *et al.*, 1988b; Chapman *et al.*, 1993b). However, the biomass observed in these experiments is usually the above-ground fraction, and there is evidence that water deficits promote root growth preferentially (Azam-Ali *et al.*, 1989) so the decline in radiation use efficiency observed may be actually less than usually documented for droughts.

Considerable evidence exists to suggest that conditions which prevent the utilization of photosynthates for growth result in reduced RUE through feedback inhibition. This has been proven for cool night effects (Bagnall *et al.*, 1988; Bell *et al.*, 1992).

Cultivars have shown very little difference in RUE in nonlimiting conditions at the crop level (Duncan *et al.*, 1978; ICRISAT, 1983; Bennett *et al.*, 1993). It is possible that this may occur because the variable leaf orientation helps decrease light intensity when the leaf cannot process the full light flux.

Water Capture and Use. The capture and use of water by peanut involves standard physical and plant processes and is determined by both the canopy and root systems. In the long term, the water use is the integral of the instantaneous transpiration. Since water use is so closely linked to photosynthesis by physics, it provides an attractive surrogate for photosynthesis and can be an excellent indicator of both the current and cumulative growth. For peanut, the biomass accumulation in a given environment has been shown to be usually a linear function of transpiration. In some very dry situations, even when no shoot growth is occurring, the observed transpiration is associated with biomass increases in the roots (Azam-Ali *et al.*, 1989).

a. Root systems as factors influencing water capture. When soil water capture is limiting to transpiration by the canopy, the attributes of the root system determine transpiration. Roots have received considerable research emphasis over the review period reflecting the fact that it is an area where our knowledge is limited. Much of this research has been driven by the need to evaluate root systems as a factor contributing to drought resistance of peanut cultivars (Ketring, 1984; Watterott, 1991; Kalfaoui and Havard, 1993). As with the canopy, the ability to extract water is determined by the size of the root system and its distribution relative to the available water. The concept of a frontier between exploitable and unexploitable areas is important.

b. Root distribution. In the time domain, the rooting/extraction front is an important aspect determining the changes in soil volume exploitable for transpiration and nutrient uptake, while the root profile is the appropriate measure in the spacial domain. Peanut has deeper roots than many other legumes (Pandey *et al.*, 1984) which provides (relatively) greater drought tolerance to this species. There are clearly substantial environmental (University of Nottingham, 1987; Simmonds and Williams, 1989) and cultivar effects on the rate of root extension (Ketring *et al.*, 1982; Kalfaoui and Havard, 1993).

Temperature must modify root extension because of the effects of temperature on respiration, and the evidence from simulation modelling supports this effect. The PNUTGRO model uses a maximum rate of root extension of 2.85 cm/physiological day. This model's root extension rate corresponds well with the values quoted for the velocity of the extraction front at 1.2 to 2.6 cm/calendar day (Boote and Ketring, 1990). Soil type is presumed from comparison of data to have a large effect on the rate of extension; however, no direct studies were made. The rate of root extension into wet soil also is strongly influenced by the water content of the atmosphere with dry air increasing the velocity of root extension (University of Nottingham, 1987).

Root extension is strongly influenced also by the availability of carbon to support extension growth with all the attendant complexities of assimilate distribution. The data of Watterott (1991) on respiration suggest that throughout plant life there is a carbon limitation to root activity. The root system continues to extend most rapidly while carbon is not being used for reproductive growth and decreases with the transition to reproductive growth. Thus, long-season varieties have greater opportunity to develop more extensive root systems than do short cycle lines. Cultivars with low partitioning are able to sustain root extension during reproductive growth while those with high partitioning are not able to expand the soil volume exploited during this phase (Nageswara Rao et al., 1993). While our knowledge in this area is not perfect, carbon partitioning has been used to control root extension and growth in simulation models with considerable success, providing circumstantial evidence for the key role of carbon assimilates in deciding root attributes and water capture capabilities.

   c. **Root densities and profile distributions.** Root distribution fundamentally follows that observed for most crops, with the greatest length, mass and density being in the upper horizons of the soil (Robertson et al., 1980; Gregory and Reddy, 1982; Devries et al., 1989a; Nageswara Rao et al., 1989; Simmonds and Williams, 1989). However, this general pattern may be influenced by soil texture and water distribution within the profile. Higher plant populations result in greater root densities in deeper soil horizons than do low plant densities (Simmonds and Williams, 1989). This phenomena probably is caused by the more rapid depletion of soil moisture in the upper soil horizons where the higher root density resulting from high density allows rapid exploitation of the available water.

   The ability of the peanut roots to extract water from the soil increases with root length density (University of Nottingham, 1987), reflecting the physics of water movement in soils. However, peanut roots seem less effective than millet roots, extracting at about half the efficiency of the latter. Perhaps this poor root uptake efficiency reflects the relative absence of root hairs, and this feature seems to relate to the strategy of dehydration tolerance (Ludlow, 1989), providing an alternate method of spreading the available water through time and allowing the plant time to adapt and respond to deficits by invoking mechanisms such as para-heliotropism.

   d. **Root system size**. The size of the root system is a function of the root

mass and specific root length. To increase the potential for water capture and therefore reduce the occurence of drought stress, there has been considerable effort investigating possibilities of developing bigger root systems. Root growth is influenced by the basic processes influencing respiration described earlier (Watterott, 1991) being kept in an approximate balance with the canopy. This probably occurs because of "signals" between the root and shoot and possible carbon assimilate feedback controlling mechanisms.

In unstressed conditions there is a progressive decrease in the fraction of assimilates allocated to root growth with time. Many of these effects are related to assimilate partitioning between the various structures competing for assimilates, and will be dealt with later in the section of this chapter dealing with assimilate distribution.

e. Specific root lengths. This aspect has received some attention from the point of view of energy costs of building and maintaining a water capture system relative to the returns to this investment in terms of extraction potential (Watterott, 1991). There are substantial cultivar differences in the mass per unit length; however, these may represent the outcomes of different strategies for coping with drought. Logically, if a large area per unit of carbon investment in roots were strategically desirable, then the plant should achieve this by having a greater number of root hairs, a feature that peanut does not have. A better understanding of the adaptive advantages of different investments in roots is needed, this being a problem for which a simulation model has a major advantage.

f. Shoot systems as factors in water use. When the root system is able to satisfy transpirational demand, the water use is determined by the amount of radiation intercepted and the vapor pressure deficit (VPD). Thus transpiration normalized for VPD is closely related to the radiation interception. When the supply is limiting, the stomatal resistance increases but not to a level that preserves hydration. This strategy is common to many of the drought-tolerant legumes (Ludlow, 1989).

g. Water use efficiency. Over the past decade there has been substantial research effort on the WUE of peanut. These efforts have indicated the potential for genetic exploitation of the greater WUE attributes found in some cultivars. Initially there was a strong feeling that WUE of peanut would be a conservative attribute and that changes in WUE would stem mostly from variations in the atmospheric vapor pressure (Tanner and Sinclair, 1983). This has been challenged by work at the biochemical level using the ^{13}C discrimination technique (Farquhar et al., 1982) and the early indications of differences in WUE between peanut cultivars in the drought screening effort at ICRISAT (Matthews et al., 1988a). The ^{13}C discrimination ratio is associated with WUE (Hubick et al., 1986; Wright et al., 1988) and studies of WUE show a twofold variation between cultivars.

The physiological basis for differences in WUE of cultivars apparently lies in their ability to generate lower internal leaf CO_2 concentrations due to either greater mesophyll thickness or greater photosynthetic capacity. Observations that WUE was related to leaf thickness (J.H. Williams, unpubl. data, 1988) have been confirmed by research in Australia and India (Nageswara

Rao and Wright, 1994; Nageswara Rao *et al.*, 1994). This provides a possible simple screening method (currently being investigated in India) for application in breeding programs aimed at increasing productivity in situations where water is a limiting factor. However, the situation is complex because the additional investment in leaf tissue to create the high WUE decreases either (a) the amount of leaf available per unit leaf mass, with attendant consequences to light resource capture; or (b) the amount of carbon available for the growth of other competing processes—i.e., pod initiation and growth.

These options are complicated further by the probabilities of either water capture or light being the limiting factor to yield determination in the variable real world situation. Clearly, research on this issue is best done using a simulation modelling approach, as is done in the section on applications of models in this chapter. The cost of empirically determining the optimums would be very high.

Nutrient Uptake and Use Efficiency. Nutrient capture and use efficiency by peanut has not attracted much emphasis from a model perspective. Indeed, nutrient uptake by peanut has attracted significant physiological research attention only for three elements—nitrogen, iron, and calcium. For the other elements, agronomic trials have determined application levels necessary to prevent deficiencies or toxicities.

a. Nitrogen. The greater part of the research emphasis on nitrogen physiology has focused on N_2 fixation aspects, with not much effort to follow up the suggestion of Sinclair and de Wit (1975) that N was limiting to yield. The peanut can assimilate nitrogen as either mineral N or exploit the N_2 fixation process associated with symbiotic rhizobia. Fortunately, the peanut is promiscuous in its nodulation, doing so with the many strains that constitute the widely spread cowpea group. The details of new knowledge of nodule formation and fixation are covered in Chapter 8 of this book.

At the end of the 1970s, the prospects for manipulating nitrogen fixation appeared to be good. The motives for this were both to increase the contribution of this legume to the nitrogen balance of farming systems and to increase yield of the crop since it was considered likely that peanut may experience N limitations to yield (Sinclair and de Wit, 1975). There were reports of yield increases in response to specific strains of bacteria (Nambiar *et al.*, 1982) and reports of varietal differences in fixation giving rise to hopes of improving nitrogen fixation by breeding (Arunachalam *et al.*, 1984; Nutman, 1984). Both these aspects have provided interesting physiological insights into peanut physiology and provide good case studies for the application of physiology to practical problems.

The crop physiological interest in N_2 fixation arose from inconsistencies between experiments which required explanation. The reported differences in the fixation among cultivars (Nambiar *et al.*, 1982) were not reflected in differences in their crop growth rates (ICRISAT, 1983). This problem was resolved by using a resource capture/resource use efficiency model as an analytic tool.

Fixation was measured (using the acetylene reduction technique) in a range of cultivars with reputed differences in fixation, each being grown at

a range of plant spacings. Fractional radiation interception (f) was also measured. The statistical analysis then utilized f as a covariate and showed that differences in fixation were associated with energy interception per unit land area rather than other cultivar effects (Williams *et al.*, 1990). Since the N_2 fixation process is dependent on current photosynthesis or leaf area (Wynne *et al.*, 1982; Osman *et al.*, 1983), this should have been anticipated. The reported differences in fixation, therefore, were due to canopy differences rather than differences in the efficiency of N_2 fixation per unit light (or carbon). Since it is much easier to manipulate canopy by agronomy than by genetics, peanut breeding for higher N_2 fixation is not an attractive improvement option.

A second nitrogen fixation physiology investigation centered around the observed responses of peanut plant to the *Bradyrhizobium* strain NC92 and demonstrated a truly serendipitous research result. In this case, the agronomic yield responses anticipated as a result of increased fixation were observed, but inconsistently across sites. Growth studies were undertaken to put the variable yield responses within a physiological context, but they failed to reproduce higher yields. The enigma was solved by the discovery that NC 92 produced a siderophore which improved iron nutrition (Nambiar *et al.*, 1990). All the trials where positive yield responses had been observed were on high pH soils where peanut was prone to iron chlorosis. Where luck played a powerful role in this advance was that the ridge and furrow irrigation system being used in the initial experiments created local concentrations of alkaline salts by the capillary movement of water to the top of the ridge which matched soil conditions at other locations. The physiology studies which failed to observe the effect were conducted with sprinkler irrigation and rainfall which did not have this localized pH change. Subsequently, there has been a major research effort into the iron nutrition of peanut and the bacteriological manipulation of this aspect of nutrition (Terry *et al.*, 1988; Sahrawat *et al.*, 1990).

b. Iron. Iron nutrition of peanut has attracted considerable research interest for a number of reasons. There is increased peanut production on calcareous or alkaline soils; there is increasing pH in many irrigated soils; and there have been varietal changes to shorter season, Fe-inefficient cultivars. Where iron chlorosis occurs, it can result in up to 40% yield reductions (Potdar and Anders, 1992) associated with reduced photosynthesis.

Two situations have been observed in relation to the occurrence of Fe chlorosis. First, there is the situation where the uptake process is prevented by the nonavailability of Fe^{++} in the soil. The second situation is more complex since iron is present in the leaves but, due to the presence of the bicarbonate ion, is not available for chlorophyll synthesis. Apparently, bicarbonate accumulates in leaves when there is reduced aeration of the soil due to short-term water-logging. Strong interactions of iron nutrition, nitrogen nutrition, and rhizobial symbiosis have been observed (Sahrawat *et al.*, 1990; Tang *et al.*, 1991). It is not clear whether these effects are more than the result of reduced photosynthesis associated with the interruption of chlorophyll synthesis.

c. **Calcium.** The one aspect of nutrient uptake which is unique in peanut is the uptake of calcium and boron by the pod. These elements are taken up by the roots in a normal manner. However, since these elements are transported in the transpiration stream, root uptake is not available to the pods which do not transpire.

The most common approach to problems of calcium deficiency in pods in the U.S. is to apply landplaster (gypsum) (Cox et al., 1982). However, particularly in Africa, calcium deficiencies in peanut remain a problem since inputs such as gypsum are not used and genetic solutions are more attractive. In the early 1980s, it was recognized that the pod size was a factor in determining the soil levels needed for adequate calcium nutrition. But it was clear that the basis for genetic differences was not fully understood. At that time it was hoped that the breeders could "transfer the Ca-efficient character of small-seeded cultivars to large-seed cultivars" (Cox et al., 1982). Kvien et al. (1988) reduced the problem to a physiological basis, examining the calcium uptake both in terms of (a) the surface for resource capture relative to the pod's calcium requirements and (b) the resistance to the movement of calcium by the shell and soil.

The pod size is a major factor because the ratio of surface area to volume is dictated by the geometry of cylinders or spheres (Fig. 6). Larger pods, therefore, must have a larger flux of calcium across the surface to provide the same calcium concentration in the pod tissues (Keisling et al., 1982). The remaining aspects of the pod which can influence the ease with which the kernel's calcium need can be satisfied is the resistance to transport, either in the soil (Rajendrudu and Williams, 1987) or the shell. Kvein et al. (1988) showed that shell thickness was inversely related to proneness to calcium
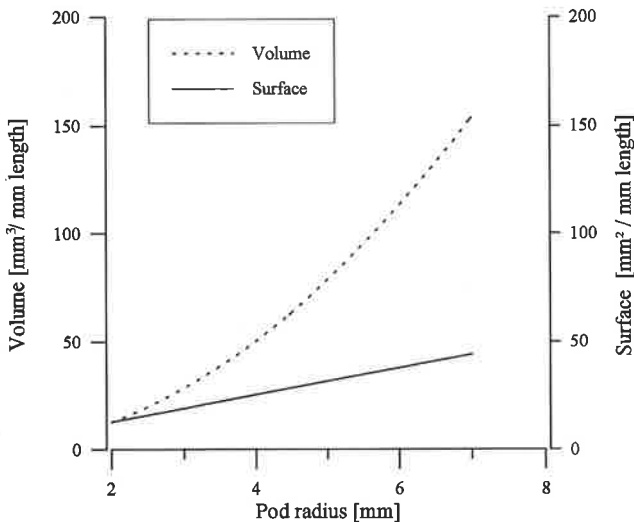

Fig. 6.   Relative changes in pod surface and volume according to pod radius.

deficiency. A further development of this theme has been the exploration of plant habit as an exploitable trait to reduce the dependence of pods on high calcium levels in the soil. Hartmond *et al.* (1994) reported that the pods of runner types are more widely and uniformly distributed. Examination of a range of varieties for the contributions of pod size, plant habit, and other factors (including shell thickness) to the variation in shelling percentage is shown in Table 3. The differences in pod dispersal result in bunch types having higher calcium requirements than runners and the shelling percentage of runners being less influenced by pod size than is that of the bunch type (Hartmond, 1991). Interestingly, the majority of breeding efforts for the African continent where calcium defficiency is a major problem have focused on breeding bunch types.

Assimilate Use and Distribution—Partitioning

The products of photosynthesis need to be moved from leaves to other structures and used there for the (a) maintenance of those structures; (b) increase of resource capture capabilities; (c) storage (either long or short term); (d) biochemical transformation of other compounds, including nitrogen fixation, protein, and oil synthesis; (e) establishment; and (f) growth of reproductive structures. These uses constitute "sinks" for assimilates. Only those uses resulting in change of mass are reflected as distributed growth, and the amounts used in respiration can be very substantial. Failure to move photo-assimilates from the leaf can result in end-product inhibition of photosynthesis (Bagnall *et al.*, 1988).

The processes that regulate the distribution of the assimilates are complex and poorly understood. Since structures decided by phenology are the recipients of this assimilate (sinks), there inevitably are strong links between phenology and assimilate distribution. Both the numbers and the potential durations of growth by any given organ are determined by phenology. There is much empiric data that documents the outcome of these processes, but control of the processes is less easily established by direct evidence.

Table 3. Analysis of variance for factors contributing to variations in shelling percentage across experiments, calcium and irrigation environments (Hartmond *et al.*, 1994).

Factor/variable	d.f.	S.S.	M.S.	V.R.
Pod volume	1	6315.11	6315.11	142.44
Habit	1	1147.86	1147.86	25.89
Volume x habit	1	672.34	672.34	15.17
Other variety effects[a]	11	3119.17	283.56	6.40
"Environments"	8	2232.91	279.11	6.30
Residual	37	1640.35	44.33	
Total	59	15127.73	256.40	

[a]Includes all other varietal attributes.

Source-Sink Proximity Effects. The assimilates are used by those sinks available to accept them in a manner analogous to fluid mechanics. Thus, the "suction" generated by respiration and transformation, combined with the distance and flow capacity, apparently form the dominant controls of distribution. Second, the ability of sinks to accept the materials is determined by the factor most limiting to the biochemical processes occurring. Thus, when protein supply in a pod is limiting, carbon assimilates from the nearest leaf tend not to be used directly by that organ. As a result, the assimilates bypass the pod and are available for use by other structures and processes, such as the nodules. Nitrogen fixation is thus supported as a sink to the extent that the carbon assimilation exceeds the balanced growth requirements of other organs. These analog models of distribution seem to provide a good process-based explanation for many of the distribution phenomena observed. In dealing with the distribution of assimilates, there are two major areas of interest—the control of distribution between the shoots and roots and that between vegetation and fruit.

Root vs. Shoot. With time there is normally a progressive shift in the distribution of mass between the roots and shoots. Roots as sinks were investigated by Watterott (1991) using respiration as an integrated measure of root growth and maintenance costs. He showed that respiration associated with the root system was much greater than that evident from measurements of mass. Substantial root respiration was maintained throughout the study period (20-75 days after sowing), but the fraction of net photosynthesis apparently respired by roots decreased progressively from about 80 to 30%.

Although root:shoot ratios are normally conservative, there is good evidence that the distribution of assimilates between root and shoot is strongly influenced by the environment (University of Nottingham, 1987; Watterott, 1991). The balance of investment in these resource capture systems is modified towards the most limiting system. This generalization is apparently conditioned by the established reproductive sinks which seem to often have priority for assimilate over either resource capture apparatus. Thus, dry conditions shift the balance from stem and leaf towards roots, humid conditions towards the shoots. There are substantial differences in genotypes in the partitioning to the roots in response to drought. Rodrigues (1984) observed that the drought-susceptible cultivar Pearl Early Runner wilted before other cultivars because it partitioned less to roots and had slower root depth progression. Nageswara Rao *et al.* (1993) showed that the drought-resistant cultivar ICGS 86707 sustained root growth during drought (as measured by the changes in the extraction front) while other varieties were much less able to do so; and Watterott (1991) showed that this was reflected in higher root respiration by this cultivar in water stress conditions. These differences in root growth response seem to be inversely related to the genetic disposition to establish a powerful reproductive sink in favorable conditions. Cultivars which do not establish a major pod sink seem to be those able to continue root expansion in the event of a drought.

Watterott (1991) found that drought reduced the root respiration of all cultivars (reflecting the decreased photosynthesis), but root respiration of

lines with "low" partitioning to pods in nonstressed conditions are less influenced by drought than lines with "high" partitioning. These lines also have higher root respiration rates than other "drought-susceptible" cultivars (Watterott, 1991) in dry conditions, reflecting sustained root growth.

The actively growing roots are the organs most distant from the sinks and may be expected to be most sensitive to competition from other sinks. How they continue to attract carbon assimilates is not clear. If one accepts the "most limiting element" hypothesis, then other organs must be limited by mineral nutrient supply until near maturity. There is some evidence (Williams, 1978) that during pod filling the roots exploit carbohydrate reserves accumulated in roots during earlier phases of growth.

Shoot vs. Reproductive Mass. The partitioning of material between the shoot and the fruit is a point of great practical interest and the subject of much study. It determines the pod yield and, in optimized agronomic management, determines the yield potential of cultivars. Duncan et al. (1978) showed that the pod:shoot partitioning of assimilates was the major change affected by the Florida peanut improvement program by selecting for increased yield. In the "Duncan" model (Eq. 1), partitioning was taken as the fraction of the mean crop growth rate (C) used for reproductive growth (R). Both growth rates were derived from measured growth under optimum conditions where both C and R were observed to be effectively linear. In reality, partitioning is seldom a constant fraction (Harris et al., 1988).

The effects of distance or assimilate competition on assimilate distribution may provide an explanation for the unexpectedly low T_o = 21 C (Williams et al., 1976) or T_o = 24 C observed for fruit growth by crops (Cox, 1979) relative to that (T_o = 30 C) observed by Dreyer (1980) and Dreyer et al. (1981) (Fig. 2) for individual fruit. For the lowest T_o, the distance between the source and the sink of the bunch cultivar Makulu Red increased with temperature as the pod growth rate decreased. It is worth noting that Williams et al. (1976) found the optimum temperature for pod growth of a bunch cultivar (Makulu Red) was less than that observed by Cox (1979) for a more spreading type (Florigiant).

Modelling Growth Distribution. The first concerns for distribution of assimilate were reflected in the interest in harvest index (HI). In process terms, HI is the result of the mean reproductive growth rate and its duration relative to the mean crop growth rate and its duration. HI should be used with caution because it is determined by independent contributions of phenology, resource capture, and partitioning. Nevertheless, HI has been used extensively in models that have focused on resource capture, where it has been used to estimate a pod yield from the biomass (e.g., Azam-Ali et al., 1993). A more physiologically based parameter is partitioning (Duncan et al., 1978). While not totally accurate (Harris et al., 1988), it does provide a parameter in which differences associated with phenology do not greatly influence the values of the parameters.

In PNUTGRO, a cultivar attribute defines the maximum proportion of daily assimilate that can be utilized for reproductive growth. Within the limits of this maximum fraction, newly produced shells and seeds have

priority for assimilates over leaf, stem, and root growth. A most limiting factor approach is used to distribute the remaining assimilate pool between the various sinks according to a phenologically based empiric pattern.

RESPONSES TO MAJOR STRESSES WITH PARTICULAR REFERENCE TO GENETIC EFFECTS.

Stress occurs when the environment is limiting to growth or partitioning. All aspects of the environment are seldom optimum and therefore stress is a usual condition. However, the most common concerns for stress are those situations where there is unexpected variation of the environment, resulting in more than normal "stress" or a change in the nature of stress.

Drought

Drought is a complex stress which may occur at any time during the season or plant development stage, lasting for varying durations and reaching variable intensities. Droughts usually cause a combination of water, heat, and nutrient stresses. Heat stress will occur in association with drought if the air temperature is near or above the optimum. The decrease in evaporative cooling when water uptake is limited by root zone soil water content and the associated adjustment of the energy balance to dissipate intercepted radiation by other methods may increase plant temperature by up to 5 C above air temperatures.

Droughts are also usually associated with a nutrient stress, particularly so for calcium and nitrogen. Calcium uptake by the pods is very sensitive since the pods are in the first soil horizon to dry out. The N_2 fixation process also is highly susceptible to drought (Venkatswarlu et al., 1989), perhaps for the same reason since the majority of nodules also are distributed in the upper soil horizons. However, it should be noted that the N_2 fixation of peanut is less sensitive to drought than that of many other legumes (Devries et al., 1989a).

The main effect of water stress is always the same, regardless of cultivar, reducing the photosynthate by limiting gas exchange. The extent of the limitation in transpiration is determined by the factors covered earlier in the resource capture and resource use efficiency section.

Once the progress of phenology and the relationship between carbon assimilate availability and phenology are understood, then drought effects are more predictable. In the PNUTGRO model, once the parameters controlling the phenological development of a cultivar have been established, the consequences of drought are simulated in many circumstances via the reduction in carbon assimilates. This was clearly demonstrated by the ability to simulate the response of cultivar Robut 33-1 with PNUTGRO (V1.0) in long-term and end-of-season drought patterns, after only calibrating the model for unstressed growth (Williams, unpubl. data, 1987). However, the model failed to predict the responses of pod initiation in the recovery phase after a midseason drought. The model has now been modified to provide a mechanism which allows a variable recovery response.

Drought has received considerable research emphasis on the differences in response of cultivars to this stress. The greater part of the complexity of varietial drought responses seem to be in (a) the effects of reduced photosynthate at different stages of development on phenology, (b) the varietal differences in sensitivity of phenology (Harris *et al.*, 1988) to this decreased assimilate, and (c) varietal differences in response after the release of stress.

While there are a multitude of responses possible, we will explore the results of a series of drought experiments (Nageswara Rao *et al.*, 1989) as the basis for discussion of the major sources of genetic variation. The explanation of effects observed will illustrate the basics of physiology and phenology described in the preceding sections of this chapter.

The experiments in question examined the yield responses of 25 cultivars selected for contrasting drought susceptibilities from a large-scale drought screening trial involving 500 cultivars. The selected cultivars were subjected to 12 patterns (single and multiple) of drought occurring over different stages of development. Within each pattern of drought, eight levels of stress were created by varying the amount of water applied using the line source irrigation approach (Hanks *et al.*, 1976).

In all drought patterns the decrease in biomass was a linear function of the water applied, a result consistent with the resource capture model. However, the experiment was not able to compare cultivars for water capture and WUE differences because of limited plot size. In all the patterns involving either multiple phases of drought or drought over the pod-filling phase, the cultivars with high yield potentials in nonstressed conditions were the most susceptible to drought. This association was always very strong, apparently because high pod yield potential is dependent on high partitioning to the pods, which leaves little flexibility for buffering of the fruit growth process by reduced vegetative growth. For 11 of the 12 drought patterns, there was very little genetic variation detected among the 25 cultivars for the relationship between yield potential and drought susceptibility.

The one exception to the association of yield potential and drought susceptibility was where drought was imposed only over the pod-setting phase. In this case, even though yields were decreased by the drought, the cultivars differed substantially in the extent of this decrease. Subsequently, these differences were associated largely with variations in the speed of the recovery process. Upon the release of stress, some cultivars very rapidly established pods from flowers that must have bloomed before or during the drought while others had to recommence flowering to establish pods. Sexton (1992) confirmed this feature for one cultivar (Florunner) by tagging pegs formed just at the onset of drought. These pegs were found to arrest development until the drought ended (3 weeks), at which time the pegs rapidly expanded to produce pods. These differences in susceptibility of phenological processes to drought are reported in detail by Harris *et al.* (1988). They are particularly significant to crop improvement in that they can apparently be included as an attribute of a cultivar without a penalty to yield potential.

Subsequently, 10 selected cultivars were studied to resolve the uncertainties about water capture and WUE. The cultivars with normally low partitioning to the fruit achieve yield stability by having (a) the ability to continue root growth through the reproductive phase and/or (b) greater WUE (Watterott, 1991; Nageswara Rao et al., 1993).

Many other mechanisms, such as greater water-capture due to extensive root systems, provide drought tolerance/resistance but have a penalty to pod yield potential in nonstressed conditions. This effect is consistent with the concepts of Schulze (1988) which suggest that the investment of assimilates needed to support larger root systems pay a dividend in increased biomass production only in a few circumstances, and is supported by Waterott (1991). Therefore, their exploitation by breeding programs becomes more problematic and an area for which models can provide considerable guidance to research direction.

The exploitation of genetic differences for WUE are problematic also. There are two aspects to the problem. First, there is a close negative association between observed WUE and partitioning (Wright et al., 1994). Whether this association can be broken is not clear and the problem is receiving attention in Australia and India (R. C. Nageswara Rao, pers. commun., 1994). However, the association of WUE with high leaf rubisco and nitrogen contents suggests that this may be a physiological barrier. High partitioning is probably dependent on the export of nitrogen from the leaf and therefore the nitrogen needed for high WUE may depend on low partitioning of nitrogen to the pods.

The second problem in exploiting the genetic variation in WUE lies in the changeable nature of the limiting resource in most rainfed peanut production environments. If water is consistently the limiting factor, then the situation is relatively clear but, where the limiting factor alternates between light and water, then the solution is more uncertain. Carbon invested in the leaf maximizes radiation interception when the leaf is thin (a low specific leaf weight (SLW), which minimizes WUE.

Simulation models able to address strategic questions such as the value of traits (such as WUE) will become standard tools for breeders deciding on breeding options over the next 10 years, as is demonstrated in the section on applications of model. These models will replace the presently largely statistical models of relationships between traits and empiric results that is currently being used to guide many breeding programs.

Temperature

At present, high temperature stress is usually associated with the occurrence of drought. However, it is a stress for which there should be increased concern in the future, particularly if the predicted global warming changes the environment where peanut is traditionally important. Research at ICRISAT's Sahelian Center shows that temperature tolerance is the dominant attribute of the adaptation of peanut to the drought-prone Sahelian regions of West Africa (Greenberg et al., 1992). In this region there has been a history of breeding for drought tolerance (Gautreau, 1966; Bockelee-Morvan

et al., 1974). This has resulted in a number of "drought-tolerant" cultivars, most notably the cultivar 55-437. However, recent examination of a range of cultivars with varying responses to drought in this region show that they have no special advantage in the capture of water or in their WUE. There are very strong indications from current work at the ICRISAT Sahelian Center that the "drought tolerance" stems largely from the ability to maintain partitioning to the fruit despite above-optimum temperatures (Greenberg *et al.*, 1992). These above-optimum temperatures routinely occur in the event of a drought. There is, however, little information concerning these differences at the biochemical or mechanisms/process level which presents a gap in our knowledge which needs to be remedied.

Nutrition

Nutrition stresses operate mostly through limiting carbon fixation via the substrate limitation to biochemical processes. The exception to this is calcium and boron stress which can operate to limit pod filling.

The evidence for stress based on limitations to iron uptake and use efficiency similarly have been discussed earlier within the context of resource capture and nitrogen. While it is recognized that there are major differences in iron requirement/stress susceptibility between genotypes, the biochemical or genetic basis for these remains unclear. It is apparent that the earlier maturing types [particularly of the subsp. *fastigiata* var. *vulgaris* (Harz) types] are more prone to iron chlorosis than the longer season (subsp. *hypogaea* var. *hypogaea*) types. The physiological reasons for these differences have not been established. To some extent, the increased importance of iron nutrition stress is associated with the desire/need to fit short season peanuts into rice-based cropping systems in South-East Asia or to escape terminal droughts in areas such as Gujurat, India where the more iron-chlorosis-resistant *hypogaea* types traditionally have been grown.

Photoperiod

Photoperiod is not usually considered an environmental stress factor within the context of a single site breeding program since it is a requirement for adaptation to that environment. Thus, for a breeding program with a limited geographical mandate, photoperiod is not important since unadapted material will be discarded. The question of photoperiod is of particular relevance to the transfer of cultivars to new regions and new cropping systems. Changes in photoperiod across sites can be a major factor in changing the partitioning of growth between vegetative and pod components (Wynne *et al.*, 1974; Witzenberger *et al.*, 1988; Flohr *et al.*, 1990).

The past 20 years have witnessed major moves to exploit the world germplasm to provide resistances to pests and diseases, to reduce chemical inputs, to reduce costs of production, and to respond to increased environmental concerns about the use of chemicals in production. This increased interest has led to many germplasm lines being identified as sources of desirable attributes and used in crossing programs. Many of these germplasm lines and their progeny now have been shown to be photoperiod sensitive. Photoperiod has come into the picture since many of these hybrids

have been produced at one location (Hyderabad, India), and the products are being moved to many other locations.

In terms of the parameters of Duncan's model, photoperiod effects are integrated mostly in the partitioning factor (Witzenberger *et al.*, 1988). These effects were included in the PNUTGRO model simply by activating the photoperiod response mechanisms inherited from the soybean model (Jones *et al.*, 1991) on which it was based. There is a threshold photoperiod below which there are no photoperiod effects and a more or less linear response from the no-photoperiod effect to the maximum effect. The evidence for this comes directly from both growth analysis and modelling of a data set of six cultivars in five manipulated daylengths conducted at ICRISAT. Figure 7 demonstrates the nature of varietal photoperiod effects on partitioning for selected cultivars and shows the appropriateness of the generalized linear response modifying model described earlier (Fig. 1).

Photoperiod extension relative to normal winter daylengths
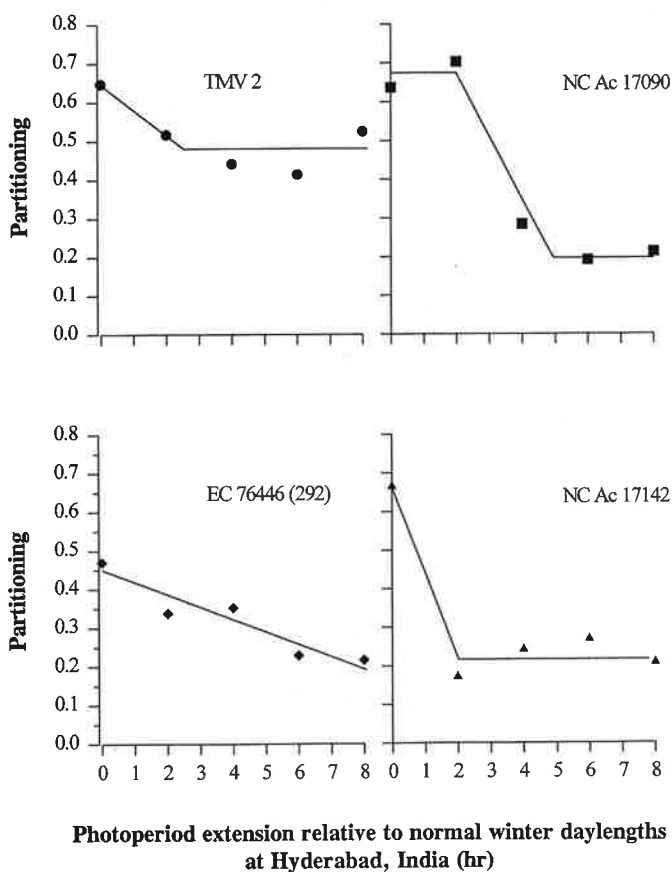at Hyderabad, India (hr)

Fig. 7.   Changes in partitioning for a range of varieties in response to a range of extensions to normal winter daylengths (11-12 hr) at Hyderabad, India.

Diseases and Pests

The main involvement of physiologists in the areas of plant protection has focused on the problems associated with loss of leaf area from various causes. There has been a concerted effort by scientists to put the problems of defoliation on a physiological basis. The problem is physiologically simple, the majority of disease effects being associated with resource capture (Bourgeois and Boote, 1992). Once the extent and pattern of defoliation is determined, the consequences to dry matter assimilation are covered mostly by the existing physiological models related to leaf area and light interception (Nokes and Young, 1991) and the algorithms for distribution of assimilates. In the case of leaf spots, only a minor component of yield loss need be attributed to the necrotic spot and halo area effects on photosynthesis.

The area where there has been some controversy is the interaction between yield potential and disease resistance. Most germplasm identified as resistant to the major foliar diseases has low yield potential based on low partitioning to the fruit (Subrahmanyam et al., 1984). Whether these resistances were physiologically associated with low partitioning or not has been the topic of considerable research. Pixley et al. (1990) concluded two phenomena were involved in resistance—(a) leaf spot resistance per se at the leaf level and (b) lower partitioning that caused higher yield by permitting sustained leaf growth and replacement of diseased leaves, providing a tolerance to the disease.

The first cultivars resulting from crosses of genotypes with low yield potential but with resistance crossed with high partitioning but susceptible types are now available (Gorbet et al., 1987; Reddy, 1989; Nigam et al., 1992). In environments where heavy late leaf spot infestations occur, Knauft and Gorbet (1990) have shown that simultaneous selection for resistance and yield can produce lines with moderately high partitioning and foliar disease resistances. For resistances to rust (F. Waliyar, unpubl. data, 1988), data show that lines with resistance also may have high partitioning.

The extent of disease resistance and the microclimate interacting with disease epidemiology has a number of interesting consequences. In West Africa the existing cultivars are all susceptible to foliar diseases and yield is optimized at low plant populations (<10 plants/m^2). This optimum is well below that needed to maximize light interception in the absence of disease, but is the outcome of population effects on the microclimate-mediated variations in disease pressure, as suggested by Alderman et al. (1987) and Nokes and Young (1991). Control of the pathogens by fungicide results in yield increases until there are about 30 plants/m^2, while the optimum population detected for resistant cultivars is near 20 plants/m^2 (ICRISAT, 1993).

Defoliation by insects, while influencing biomass production according to the principles determined by resource capture, has another interesting side effect of stimulating leaf regeneration. Williams et al. (1976) found that defoliation increased leaf growth but, from the data, it was not clear whether the effect was due to regeneration of leaf area or increased specific leaf weight associated with greater light penetration into the lower layers of the

canopy. The evidence of Wilkerson *et al.* (1984) shows that defoliation by leaf removal (as opposed to abscision) stimulates renewed leaf expansion/growth. However, in both reports the renewed leaf growth was highly dependent on reproductive stage.

APPLICATIONS OF PHYSIOLOGY AND MODELS

Models as Research Tools

Some of the applications of models in the analytical role have been described earlier (nitrogen fixation, temperature tolerance, yield potential). We will therefore concentrate on a more speculative application of resource capture models to breeding and the interpretation and correction of empiric experimental data in agronomy trials. This area is of interest because methods have been developed (Williams and Saxena, 1991; Nageswara Rao *et al.*, 1992; Williams, 1993; J.H. Williams and R.C. Nageswara Rao, unpubl. data, 1994) which allow largely nondestructive growth analysis and which make possible traditional growth analysis on the scale necessary for breeding. These models can then be expanded to improve selection efficiency (for attributes such as yield) by separating the phenotype into its components with the attendant benefits to progress.

For application to breeding, two models (one breeding and one physiological) combine to provide a powerful tool. Because the parameters of Duncan's model (Eq. 1) integrate families of processes and can now be estimated nondestructively with reasonable accuracy, the model has substantial merit as a simple analytical model of yield that can be combined with the traditional and equally simple phenotype model described in Eq. 5.

The phenotype model defines Y as the result of the additive contributions of genotype (G), environment (E), and their interaction (GxE).

$$Y = G + E + GxE \qquad \text{Eq. (5)}$$

These models combined become:

$$Y = C(G + E + GxE) \times D_r(G + E + GxE) \times p(G + E + GxE) \quad \text{Eq. (6)}$$

Because C is determined by the resource capture and resource use efficiency of a crop and the latter is conservative between cultivars, variations in C are dominated by environmental and management aspects. Variations in D_r are associated with both components of the phenotype model but, since D_r is very easily observed in experiments, all components can be easily quantified for analysis and interpretation. Evidence from numerous trials suggests that within a single experimental environment, p is determined largely by G and GxE.

Evidence to support the above statement and define the limitations to it as a generalization are still being produced. The evidence available so far (B.R. Ntare and J. H. Williams, unpubl. data, 1994) is that these distributions of sources of variation are largely correct and suggest that improvement in breeding, selection, and statistical analysis can be achieved by the cautious

application of these models. Nondestructive growth analysis (Williams and Saxena, 1991; Greenberg *et al.*, 1992; Ntare *et al.*, 1994) has been used to analyze agronomic and cultivar trials, but the number of cases for which data have been reduced to all the components of the model (Eq. 6) is still very limited.

The traditional method of nondestructive growth analysis has been to estimate whole plant/crop gas exchange. This clearly has major limitations to application in plant breeding because very large numbers of individual plants (or single rows) must be evaluated. The new approaches being developed use the resource capture models that have been validated over the past decade. These have shown that RUE and WUE are conservative (Monteith, 1990); therefore, measurements of light interception (Nageswara Rao *et al.*, 1992) and/or transpiration to determine the pattern of resource capture provide a reasonable estimation of the distribution of growth through time (Williams and Nageswara Rao, unpubl. data, 1994).

A possible variation of this is provided when measurements of resource capture/use are not accurately recorded. In the case of transpiration, the measurement of $\Delta^{13}C$ combined with the biomass allows an estimate of transpiration. This has been exploited to correct for water extraction that could not be adequately measured (Nageswara Rao *et al.*, 1993). Although this approach makes some assumptions, it provides a very powerful avenue for cost reduction in the study of total transpiration.

Use of Models and Physiology as a Basis for Research Direction

In the future, we believe that models like these discussed will play a major role in deciding research priorities between the management and crop improvement approaches to a problem. Both simulation and analytic models will be employed to analyze diagnostic trials. The sensitivity of results to changes in crop attributes controlled by either genetic or management domains will then provide policy makers with the most probable solution and allow them to focus resources into the most appropriate areas.

Within crop physiology it is clear that models have been responsible for a large amount of physiological research. Validation of both the simulation and the resource capture models has absorbed a major fraction of the research effort by physiologists over the past decade. The second thrust has been the application of these models to applied problems. An important aspect of physiology research and modelling has been the impact of physiological study on research in other disciplines, for example breeding.

As described earlier, the substantial effort to select for greater N_2 fixation in peanuts at ICRISAT was stopped by the demonstration that the majority of variation for this attribute was associated with the interception of radiation rather than differences in efficiency of fixation.

Another area where physiology has played a major role in breeding decisions and emphasis has been in the area of breeding for drought tolerances and resistances. The major emphasis has been placed on drought recovery since this has no obvious penalties to yield potential. Although end-of-season drought is the most common problem, it is the area where there is

least genetic variation independent of yield potential. Models to decide the appropriate trade-off between resistance and potential already have been exploited (Bailey, 1989). Data from the experiment on cultivar response to drought pattern (Nageswara Rao et al., 1989) were used to evaluate the consequences of using high yield potential/drought-susceptible lines or using low potential/drought-tolerant lines in Indian situations using a modelling approach. Experimental yields were related to applied water and linked to climatic data. Yields then were estimated for the available meteorological history in a number of growing areas. These simulated results showed that on average (across past seasons), the high yield potential drought-susceptible lines did better than low yielding resistant lines.

For the Sahelian areas, the demonstration of heat tolerance as a dominant attribute for adaptation (Greenberg et al., 1992) has influenced the direction of the breeding program at the ICRISAT Sahelian Center. Since heat screening is conducted more easily than drought screening, the present assessment is that only those lines with high partitioning in hot conditions should be investigated further for drought responses. However, this leaves a problem which will need to be addressed in the future where simulation models linked to geographic information systems can delimit areas where cultivars with heat tolerance could be beneficial. The temperatures at which these attributes cease to be the dominant response factor in droughts needs to be established.

Model simulations can be used to test the value of genetic traits for improving yield potential of peanut grown in specific regions if long-term historic weather data are available. Such analyses were performed by Boote and Jones (1988) using the PNUTGRO V 1.0l model to evaluate genetic traits for a short-season spanish-type cultivar (like Starr) grown under rainfed conditions in Gainesville, FL (Table 4). Simulations were performed with 21 years of weather data using three sowing dates (15 April, 15 May, and 15 June) to create 63 "crop-weather combinations." In the genetic sensitivity analysis, individual traits were varied by 10%, and percentage yield response to a 10% change in trait computed. Rooting traits, life cycle traits, and podding/partitioning attributes were evaluated. Yields were compared to the mean yield (3.475 t/ha) of the existing genotype which had a mean life cycle of 117.3 days.

For the first of the rooting traits, increasing the rate of root depth progression increased yield by 2.4% when averaged over all simulations (Table 4). The enhanced trait increased simulated transpiration by 1.7% and increased biomass and leaf area index (LAI). Altering the shape of the rooting profile (increasing roots below 30 cm by 10% and decreasing roots above 30 cm by 10%) increased yield 2.9% because of improved water uptake. Similarly, increasing the root length to mass ratio allowed more water uptake and increased yield 1.6%. These three root traits not only increased yield but resulted in a lower coefficient of variation (CV) for yield. The model did not charge any cost for making thinner roots or shifting the root profile to deeper layers. Real plants may suffer a penalty such as greater resistance to water flow (for thin or deep roots) or decreased nutrient uptake

Table 4. Percentage pod yield response to 10% changes in crop and genetic characteristics in PNUTGRO, simulated with 21 years of weather at Gainesville, FL (adapted from Boote and Jones, 1988).

Characteristic[a]	Pod yield		Change in pod yield		
	Mean	CV	Mean	Min.	Max.
	t/ha	%	------- % -----		
Standard run	3.475	19.6			
Rooting/drought traits					
Rate of root depth increase	3.550	18.4	2.42	-0.45	8.39
Root profile[b]	3.571	18.8	2.92	-0.14	9.36
Root length to mass ratio	3.527	19.1	1.61	-0.43	4.56
Partitioning to root	3.426	19.7	-1.43	-5.22	2.15
Partition to root vs. turgor	3.481	19.5	0.17	-0.62	1.22
Leaf loss vs. turgor	3.467	19.9	-0.31	-2.55	0.00
Life cycle traits					
Vegetative phase (V1-R4)	3.648	17.9	5.38	-3.30	16.05
Reproductive phase (R4-R8)	3.858	19.2	11.14	0.95	18.98
Total life cycle (V1-R8)	3.991	18.1	15.41	-2.49	31.67
Same R8, 10% change in reproductive phase	3.408	22.6	-2.54	-20.81	5.29
Podding/partitioning					
Maximum partition to pods	3.658	20.9	4.97	-0.40	8.11
Pod addition rate	3.515	20.4	0.95	-3.71	3.55
10% decrease in shelling percent[c]	3.392	20.3	-2.55	-11.75	0.86

[a]10% increase except as noted.

[b]Same total root length, but 10% more below 30 cm and 10% less in 0-30-cm depth.

[c] Maximum shelling percentage was decreased from 78 to 71.8%.

if there are fewer roots in the topsoil. A 10% increase in partitioning to roots did not increase pod yield; rather, average yield was reduced 1.4% primarily because assimilate was diverted from producing leaf area (for light capture) needed to support pod production. The ability to shift partitioning to roots in response to turgor deficiency improved yield slightly (0.2%), whereas more rapid leaf loss under turgor deficiency was detrimental to yield (0.3% decrease).

For a short-season cultivar like Starr, traits that increased the life cycle were generally beneficial to yield (Table 4). Increasing the vegetative phase (V1 to R4) by 10% increased yield by 5.4% primarily because it allowed an increase in leaf area index (LAI). Increasing the reproductive duration (R4 to R8) or the total life cycle by 10% resulted in 11.1 and 15.4% yield increases, respectively. Early maturity is a trait desired by breeders and producers, so a simulation was attempted with a 10% longer reproductive phase (R4 to R8) within the same total life cycle. This combination reduced

yield by 2.5% and increased yield variability (CV increased from 19.6 to 22.6%). The earlier onset of pod formation limited the LAI (14.8% less) which limited light capture and biomass production (8.3% less). Two traits to improve reproductiveness—10% increase in partitioning or a 10% faster pod addition rate—increased yield 5.0 and 1.0%, respectively, but also increased yield variability. Thus, it appears that determinacy traits that improve yield, particularly in good weather years, may reduce yield stability. A lower shell-out decrease from 78 to 71.6%, typical of large-seeded confectionary cultivars, also reduced yield. Specific genetic applications of these simulations need to be taken with a "grain of salt" for several reasons— first, they were computed for one particular environment and should be validated much more broadly and, second, this simulation was done using an early version of PNUTGRO (models, even improved ones, are fallible because they represent how the model developers "see" and "program" the traits).

Improvement in WUE is a highly desirable goal for crop improvement because many crops are grown under rainfed conditions and irrigation supplies are often limiting. Farquhar et al. (1982) suggested, based on theory, that WUE and ^{13}C isotope discrimination ratio should be correlated, given their common linkage to the ratio of C_i/C_o [intercellular CO_2 concentration (C_i) to ambient CO_2 concentration (C_o)]. This theory was shown to be generally true by the discovery of negative correlations of WUE and $\Delta^{13}C$ isotopic discrimination for genotypes of peanut (Hubick et al., 1986, 1988; Wright et al., 1988). They found negative associations between specific leaf weight (SLW) and $\Delta^{13}C$, and between HI and $\Delta^{13}C$. Simply stated, lines with high WUE had thick leaves and low HI.

The CROPGRO peanut model was used to study transpirational WUE. The model has hourly hedgerow canopy photosynthesis with energy balance being solved for foliage temperature iteratively in conjunction with leaf photosynthesis and stomatal conductance (Pickering et al., 1993; Boote and Pickering, 1994). Leaf-level photosynthesis is modeled after Farquhar and von Caemmerer (1982), and photosynthesis controls stomatal conductance via the present assumption of constant slope of C_i/C_o. Other features of the CROPGRO model and its simulation of nitrogen uptake and N_2 fixation are described by Hoogenboom et al. (1992, 1993).

Analyses with the CROPGRO peanut model indicates that it is possible to mimic increase in transpirational WUE as a function of increased SLW. Light-saturated leaf photosynthesis was allowed to increase linearly with increasing SLW, and the C_i/C_o ratio was allowed to vary from 0.9 at zero SLW to 0.5 at SLW = 90 g/m^2. For typical SLW of upper leaves, the ratio would be 0.7. The slope of biomass accumulation versus transpiration increased 22 and 42%, respectively, as canopy-average SLW increased from 15 to 30 to 60 g/m^2 (Fig. 8A). To examine the consequences of the varied SLW, different seasonal transpirations were obtained by progressively reducing rainfall for the 1987 season with planting on 2 June at Gainesville, FL. The soil water profile was initialized at 50% of available water. Because the model increases SLW with simulated drought, drought has feedback
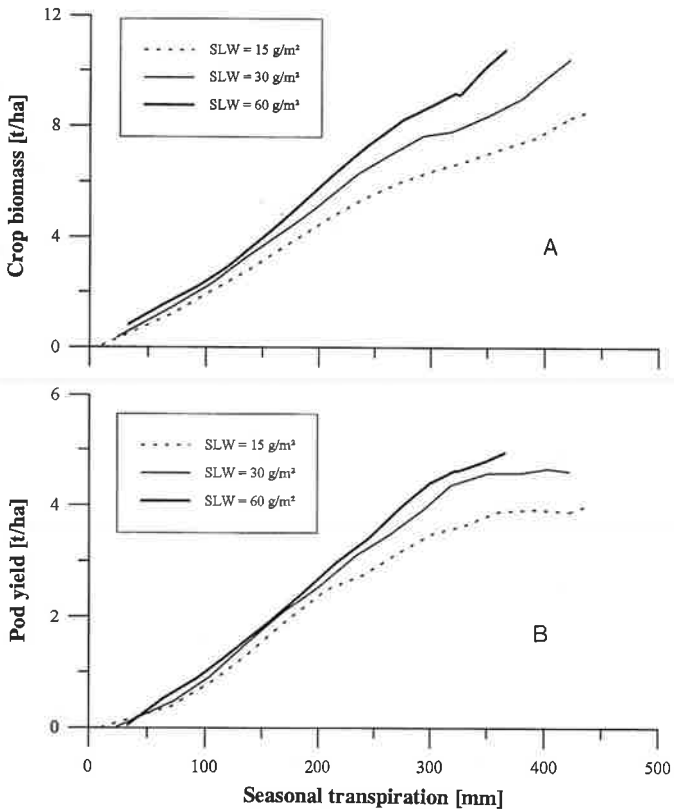
Fig. 8.   Simulated biomass (A) and pod yield (B) versus seasonal transpiration of Florunner peanut as a function of hypothetical variation in SLW where light-saturated leaf photosynthesis increases linearly with SLW and the C_i/C_a ratio decreases linearly with SLW. Simulation was performed with the hourly energy balance version of the CROPGRO model using 1987 weather at Gainesville, with rainfall varied from 0.1 to 1.4 of actual, and initial soil profile at 50% available water.

effects to increase SLW and influence WUE. As expected, pod yield was increased with increasing transpiration; however, the effects of increased SLW (and improved WUE) on pod yield were small (Fig. 8B).

Yield and biomass initially increased as SLW was increased; however, there was a simulated optimum SLW for yield, as also suggested for soybean by Boote and Tollenaar (1994). Creating greater SLW resulted in lower LAI and decreased light interception and, beyond a critical LAI, reduced pod yield (Fig. 9). Under very deficient rainfall conditions (10 to 20% of evaporative demand), pod yield and biomass increased up to SLW of 60-70 g/m^2. Between 30 and 80% of adequate rainfall, SLW of 25-30 g/m^2 was optimum for pod yield and, at better water supply, SLW of 40-50 g/m^2 was optimum for yield. Figure 9 shows that the optimum SLW is influenced by the relative water supply in a systematic manner. One of the reasons pod
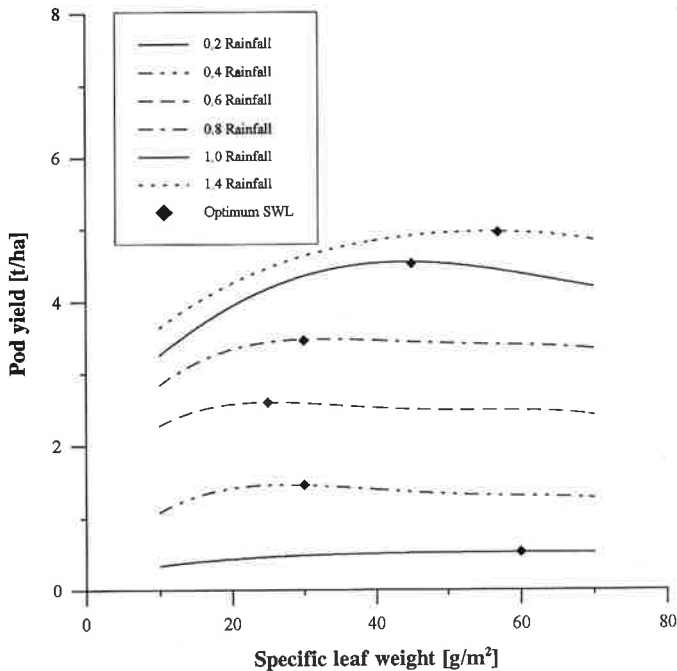
Fig. 9.   Simulated pod yield of Florunner peanut versus SLW at different water supply levels where light-saturated leaf photosynthesis increases linearly with SLW and the C_i/C_o ratio decreases linearly with SLW. Simulation was performed with the hourly energy balance version of the CROPGRO model using 1987 weather at Gainesville with rainfall at 0.2, 0.4, 0.6, 0.8, 1.0 of actual and 1.4 (plus irrigation), and initial soil profile at 50% available water.

yield showed an optimum response to SLW, but biomass did not, is that simulated pod HI decreased as SLW increased. Because the LAI is lower for the higher SLW crop, the plants were later in setting a full pod load and matured later. Harvested on a given date, the crop with greater SLW had lower HI and lower shell-out (% seed). Low HI and late maturity are reportedly associated with high SLW, high WUE genotypes (Nageswara Rao *et al.*, 1994) and low HI was reported associated with high WUE genotypes (Wright *et al.*, 1988). It is interesting that these features were output consequences of the model without explicit "programmed" connections.

The above simulations are very preliminary and need to be verified further. Nevertheless, it appears that, if improved WUE is associated only with increased SLW, then benefits of increased WUE are offset by lost opportunity of light capture during brief rainy seasons. Thus, high SLW may not be that beneficial for yield in drought-prone regions, particularly if low light capture leads to slow pod set and low harvest index. Note that it may be possible to offset low light capture problems by increased planting density. Even through computed transpirational WUE was substantially increased, the model energy balance simulations indicated that reduction in LAI (with high SLW) decreased total transpiration and allowed more energy

for soil evaporation and soil heating (even total evapotranspiration was reduced up to 5 or 10% for the highest SLW). A different and more beneficial scenario is likely if increased WUE is associated with lower C_i/C_o caused by greater photosynthesis (but at the same SLW).

Model Simulations as a Management Tool

Simulation models can be a powerful tool for assisting management decisions, both preplant and during the season. The limit to this type of application is dictated by the limits to the questions being asked. Guidance for decisions on many inputs—such as whether to apply fungicide for control of foliar diseases (Nokes and Young, 1991; Batchelor *et al.*, 1993) or when to harvest relative to potential pod losses (Batchelor *et al.*, 1994)—and other investments can be obtained by asking the right questions of simulation models. These are already being applied extensively in agriculture of the advanced farming systems of the U.S. To apply these models, the approach of calibrating the model to a given location and cultivar is appropriate. The farmer then can evaluate responses to decisions given a range of scenarios with increased confidence.

A good example is the decision to invest (or not) in irrigation equipment. This was examined from the point of view of a farmer in the Gainesville, FL area. The yield response to irrigating when the top 50 cm of the soil had been depleted to 50% of available water on Lake fine sand soil was simulated for 25 years. On average, the yield response was about 0.5 t/ha for a 130-day cultivar. There were years in which the response to irrigation was very substantial (Fig. 10). The benefit from irrigation would be expected to be larger in an environment with less rainfall. The model also indicates the amount of irrigation to be applied when there has been drought. Thus, the data allow the farmer to examine the costs and benefits that may be anticipated from such an investment. The timing of stress in the drought years is provided also by the model and may be used further to guide the farmer in
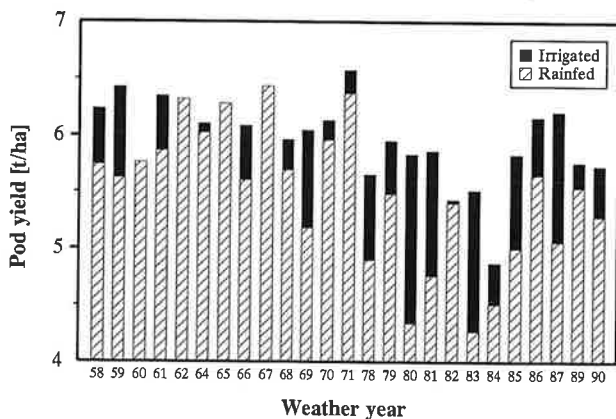

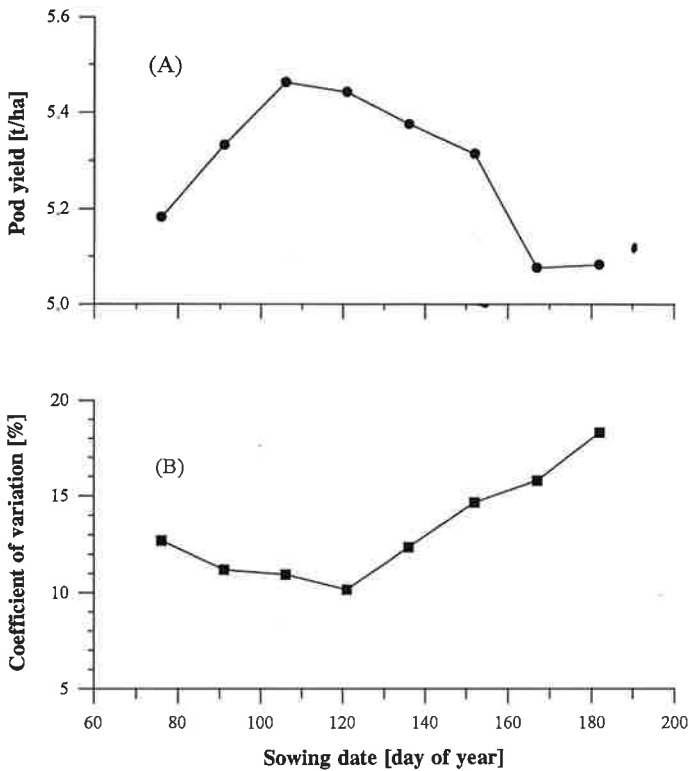Fig. 10.   Simulated yield responses to irrigation at Gainesville using PNUTGRO V1.01 model.

Fig. 11.   (A) Simulated yield response to planting date at Gainesville using PNUTGRO and (B) simulated coefficient of variation for yield versus planting date.

his decision process. Since the occurrence of water stress over the last days of growth has a very substantial influence on the occurrence of problems from aflatoxin contamination, the risks from this aspect to the equation can be evaluated from the simulation data. In 3 years (1959, 1981, and 1983), the irrigation would have added value to the crop by modifying the occurrence of stress over the last 30 days of growth and so decreasing the risk of aflatoxin (Mehan *et al.*, 1988; Sanders *et al.*, 1993). For this production system, aflatoxin contamination has major market value considerations, and preventing this risk is a very real factor. In the other years, the response to irrigation was primarily associated with stresses which occurred during pod setting and these could be expected to result in a decrease in pod uniformity with the attendant impact on market grades (simulated shelling percentage was decreased). Given the likely outcomes and the cost of irrigation, farmers can make informed decisions on appropriate investments and insurance policies.

Other preplant decisions include decisions on planting date, row spacing, plant population, and choice of cultivar. If long-term weather data are available, one can run the model to evaluate the optimum planting date

relative to rainfall, temperature, and end-of-season frost hazards. Figure 11 illustrates, for the Gainesville area weather, that producers have a broad planting window from the end of March to the first of July. The optimum yield was simulated for planting 16 April to 1 May, with good results from 1 April to 1 June. The CV for yield was clearly the lowest at the optimum yield dates. Plantings in mid-July risked frost damage.

Similarly, yield response to row spacing can be evaluated. The hedgerow version of the PNUTGRO model shows that narrow rows (0.45 to 0.75 m) are optimum for the cultivar Florunner and that, as row spacing becomes wider than 0.9 m, pod yield drops off significantly (Fig. 12). The reason for the broad shoulder at about 0.9 m is that the Florunner canopy generally closes in 0.9-m rows. For shorter-season spanish-type cultivars like Tamnut, the response to narrow row spacing is greater. The generally lower yield of Tamnut is caused by 2-week shorter life cycle, earlier pod set, and thus lower LAI, smaller plant size (relative width of 0.85), and somewhat lower partitioning than Florunner. Choice of cultivar also can be simulated relative to long-term weather, planting date, row spacing, and plant population; however, this assumes one has information on life cycle, canopy architecture (partitioning intensity), and yield potential of such cultivars.

In-season decisions can be made also with a peanut growth model; for example, to help schedule irrigation, to schedule management relative to peanut growth stage, and to help predict harvest maturity. However, in-season decision-making requires weather data (maximum and minimum temperature, rainfall, and irrigation) up to the current date. Five-day future weather forecasts would be helpful. Then the model makes multiple runs to finish out the season with multiple (good, moderate, and adverse) weather
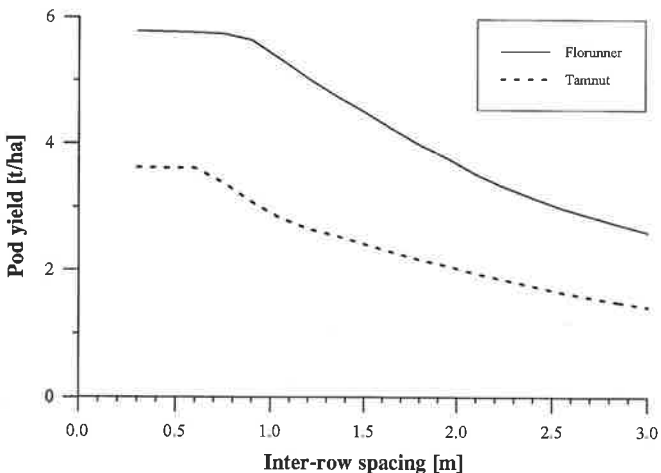
Fig. 12.   Simulated yield response to row spacing for Florunner and Tamnut cultivars at Gainesville using PNUTGRO. Florunner and Tamnut differ in life cycle traits, podding/partitioning, and in relative canopy width (Tamnut canopy assumed 85% as wide as Florunner). Tamnut planting density was 50% greater than Florunner.

years to project yield to the end of the season. The model also requires solar radiation but that is fairly easily generated. Another feature, recently added to the new CROPGRO peanut model, is the ability to input pest damage based on scouting inputs on diseases, insects, and other injury conditions (Batchelor *et al.*, 1993). With pest damage inputs, producers can project to the end of the season with and without control of pest damage to determine economic thresholds for pest control. Efforts are also being made to use the CROPGRO peanut model to predict pod losses and optimum harvest date relative to past weather, crop, and pest conditions (Batchelor *et al.*, 1994). A version of the model predicts the pod maturity profile to compare with the field-measured pod maturity profile (Williams and Drexler, 1981; Williams *et al.*, 1987). Likely, these newly developed model features will enhance the future use of peanut growth models as decision-making tools, both for preseason and in-season purposes.

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