

CENTRALE LANDBOUWCATALOGUS



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KUTUN

**A MORPHOGENETIC MODEL FOR COTTON**

*Gossypium hirsutum L.*

Proefschrift

ter verkrijging van de graad van doctor in de landbouwwetenschappen,  
op gezag van de rector magnificus,  
dr. C.C. Oosterlee,  
hoogleraar in de veeteeltwetenschap,  
in het openbaar te verdedigen  
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des namiddags te vier uur in de aula  
van de Landbouwhogeschool te Wageningen.

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# STELLINGEN

1. Het begrip plastochron, gedefiniëerd als het tijdsinterval tussen het bereiken van gelijke lengte of oppervlak van twee opeenvolgende bladeren en de daarvan afgeleide grootheid plastochron-index zijn morfogenetisch niet zinvol.

Erickson, R.O. and Michelini, F.J., 1957. The plastochron index. *Am. J. Bot.* 44, 297-305.

Pieters, G.A., 1974. The growth of sun and shade leaves of *Populus euramericana* 'Robusta' in relation to age, light intensity and temperature. *Meded. Landbouwhogeschool, Wageningen* 74-11, 1-107.

2. <sup>14</sup>C translocatie metingen aan intacte planten kunnen geen uitsluitsel geven over een eventuele voorkeursverdeling van assimilaten.

Constable, G.A. and Rawson, H.M., 1980. Carbon production and utilization in cotton: inferences from a carbon budget. *Austr. J. Plant Physiol.* 7, 539-53.

3. De gebruikelijke wijze van analyseren van de grootheden Leaf Area Ratio (bladoppervlak per eenheid plantgewicht) en Specific Leaf Area (bladoppervlak per eenheid bladgewicht) in groeidynamische studies vertoont teleologische trekken.

Evans, G.C., 1972. The quantitative analysis of plant growth. Blackwell Scientific Publications, Oxford. xxvi + 734 pp.

4. De hardnekkigheid waarmee in sommige landen katoen wordt bespoten met groeiregulatoren is een betere zaak waardig.

Khan, W.S. and Hanif, M., 1980. Shedding of buds, flowers and bolls of American cotton (*G. hirsutum*) as affected by Planofix (NAA) application. *Pakistan Cottons* 24, 299-305.

Malkani, T.J. and Asana, R.D., 1958. Effect of growth regulators on boll setting and yield of Punjab-American cotton, 216 F. *Indian J. Plant Physiol.* 1, 58-70.

5. De kwaliteit van een gewasmodel dient te worden beoordeeld naar de mate waarin het model het effect van morfologische veranderingen op gewasgroei en -ontwikkeling kan voorspellen.
6. De botanische tekeningen van *Gossypium hirsutum* L. in de monografie van Watt over het geslacht *Gossypium* tonen okselscheuten van prophyllen en zijn dus niet representatief voor de plant als geheel.

Watt, G., 1907. The wild and cultivated cotton plants of the world. Longmans, Green, and Co, London. 406 pp.

7. De mobiliteit en de kwaliteit van het personeel van de L.H. kunnen worden verbeterd door een samenwerkingsverband met de Landbouwinstituten met mogelijkheid van functieruil.
8. Het doelgroepenbeleid, waarbij de Nederlandse overheid voorschrijft aan welke groepen in een ontwikkelingsland hulp dient te worden gegeven is zowel arrogant als verkwistend.
9. Ontwikkelingsprojecten, door buitenlanders "geïdentificeerd", uitgewerkt en op gang gebracht zullen zonder buitenlanders mislukken.
10. Bij de huidige stand van zaken ten aanzien van het plagenprobleem dient introductie of uitbreiding van intensieve katoenteelt in ontwikkelingslanden te worden ontraden.
11. De gebrekkige belangenbehartiging door de gezamenlijke katoenindustrie in vergelijking met bijvoorbeeld de zuivelindustrie blijkt uit het ontbreken van een protest tegen de reclameactie voor Pampers luiers.

Proefschrift van H.J.W. Mutsaers

KUTUN, a morphogenetic model for cotton (*Gossypium hirsutum* L.)

Wageningen, 22 april 1982

## VOORWOORD

Dit proefschrift vormt de bundeling en synthese van onderzoek, verricht in twee periodes tijdens welke ik als medewerker verbonden was aan de vakgroep Tropische Plantenteelt van de Landbouwhogeschool.

Ik stel er prijs op een aantal mensen die een belangrijke rol hebben gespeeld bij het tot stand komen van deze dissertatie persoonlijk te danken.

Allereerst dank ik mijn promotor, prof. C.T. de Wit, die aanvankelijk de zaak op afstand en met kennelijke reserves aanzag, hetgeen echter eerder een prikkelend dan een ontmoedigend effect had. Dat was misschien de bedoeling. Vooral in de fase van synthese tot het definitieve groeimodel heeft hij door zijn scherpe inzicht, zijn vermogen tot stimuleren en door het stellen van hogere eisen op momenten dat ik het wel welletjes vond, een grote invloed gehad op het voorliggende eindresultaat.

Co-referent dr. J. Goudriaan dank ik voor zijn niet aflatende bereidheid mij te laten putten uit zijn kennis en ervaring en voor zijn vermogen om mijn ietwat duistere mathematische formuleringen tot iets begrijpelijks om te vormen.

Mijn collega's van de vakgroep Tropische Plantenteelt en met name co-promotor prof. J.D. Ferwerda dank ik voor de goede werksfeer en voor hun steun vooral bij het experimentele werk.

Bij de technische verwezenlijking van het experimentele werk en de publicaties waren vrijwel alle medewerkers van de vakgroep Tropische Plantenteelt in een of andere vorm betrokken, waarvoor ik hen allen dank. Zonder de anderen tekort te willen doen dank ik in het bijzonder de heer R. Boekelman die, ouderwets veelzijdig, zorgde voor zulke uiteenlopende zaken als de bouw van proefinstallaties alsmede voor uitstekend verzorgde tekeningen voor alle publicaties.

Wageningen, 15.02.82

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## KUTUN,

a morphogenetic model for cotton (*Gossypium hirsutum* L.)

### INTRODUCTION

Traditionally it has been the concern of crop research to understand how crops respond to environmental conditions and to develop methods to influence production through manipulation of crops and their environment. When yields are low and limited mainly by a few dominating factors like nitrogen supply or water availability, which influence overall growth of any plant, important yield increases may be obtained by simply adjusting these limiting factors, treating the different crops largely as black boxes. Similarly, plant breeding has been able to make large strides forward by selecting for such broad criteria as grain yield or disease resistance, even without much concern about the ways such results come about at the plant level.

For many crops the point has long been passed where such relatively simple approaches are adequate to generate significant advances. It has become increasingly clear that a more profound understanding of crops as complicated integrated systems is needed in order to find new ways to manipulate these crops to the advantage of their users. For that reason, over the past few decades, crop research has more and more shifted towards applied plant physiology, trying to integrate the vast body of knowledge about detail processes into whole plant and crop concepts. Such integration being a task too formidable for paper and pencil, the use of computerized systems analysis techniques, known as crop modelling, has become much *en vogue*. Basic to the systems analysis approach to crop physiology is the conviction, that a plant or crop may be represented by a set of well defined subsystems or separate processes, with the behaviour of the crop as a whole being the result of the interaction between these subsystems or processes.

The first models developed along these lines were static and



considered crops as structured leaf canopies. Potential crop photosynthesis was calculated from the light distribution inside the canopy and the photosynthesis function of single leaves. (de Wit, 1965; Duncan, Loomis, Williams and Hanau, 1967). The only subsystems considered in these models are the individual photosynthesizing leaves, interacting through shading due to leaf density and canopy geometry. Species differences consist of differences in the parameters of the photosynthesis function and canopy geometry. This approach was very successful in showing the limits to potential dry matter production due to the light factor.

Crop modelling efforts since have refined the calculations of light interception by leaf canopies (e.g. Mann, Curry, Hartfield and DeMichele, 1977), incorporated better data for the single leaf photosynthesis function into photosynthesis models (e.g. Goudriaan and van Laar, 1978), incorporated the effect of waterstress (e.g. de Wit et al., 1978) etc. In other cases, especially with cotton models, modellers have moved away again from the single leaf approach and treat a crop canopy as a black box with a known reaction pattern to environmental conditions represented by a multiple regression function (Baker, Hesketh and Duncan, 1972).

Quantification of the biochemical transformation of photosynthate into plant substances and maintenance respiration requirements have received considerable attention (McCree, 1974; Penning de Vries, 1974; Thornley, 1977). These efforts have resulted in much needed models for these processes, which are however to a large degree species independent phenomena. Little is learned from them about the typical growth behaviour of particular species. Differences do of course exist between species as to their rate of photosynthate production, transpiration etc., but they hardly influence the general appearance of the plant.

More profound differences exist between species as to their morphology: a cotton plant will be recognized as a cotton plant under almost any circumstances. These morphological peculiarities apparently mirror an underlying basic growth pattern which steers the plant during all of its development. This innate growth pattern will have a profound influence on crop growth in all its phases and will determine to a large extent the distribution of photosynthate within the plant, its branching pattern, the distribution of leaf sizes,

the balance between vegetative and reproductive growth etcetera. It will be clear that a crop model will only contribute to a more profound understanding of the typical growth behaviour of a species if this underlying morphogenetic template is adequately incorporated.

With cotton, the need to incorporate good morphological data into growth models has long been recognized. Hearn (1969<sup>a,b,c</sup>) for instance collected extensive field data on cotton morphogenesis in order to explain the field behaviour of the crop and to estimate its yield potential under different conditions. From the quantitative insight on the timing of events in the crop, gained in this way, combined with model calculations on crop photosynthesis, he concluded that boll growth and photosynthate production by the leaves, supposedly contributing to that boll, are out of phase. This would be the reason why yields obtained in the field lag far behind potential yield of cotton, defined as the yield which would be obtained if all leaves were assimilating at their full rate during the period of boll growth. This is an early creative attempt to combine model calculations on crop photosynthesis with details on the morphogenesis of cotton into an integrated crop concept.

Recent Australian studies on cotton performance (Constable and Rawson, 1980<sup>b</sup>) include more morphogenetic detail and arrive also at the conclusion that assimilate requirement of a boll and production by the adjacent leaves are out of phase. This conclusion again is arrived at by a reasoned reconstruction of crop development, in retrospect, as was the case with Hearn's analysis. The morphogenetic detail is not built into a dynamic model generating such development.

Research on the morphogenesis of cotton with the explicit objective of incorporation into the (American) model SIMCOT has been published by Hesketh and coworkers (Hesketh, Baker and Duncan, 1972; McKinion, Jones, Hesketh, Lane and Thompson, 1975).

The studies by Hesketh et al. (1972) and those by Constable and Rawson (1980<sup>b</sup>) present a fairly complete description of the growth of individual leaves after unfolding, the timing of appearance of successive leaves on the mainstem and sympodia, the succession of fruiting points etc. Although many useful detailed growth data, not available for cotton before are presented in these papers, funda-

mental questions on the internal plant organisation, which for instance gives rise to the typical succession of final leaf areas along the mainstem are not considered. Maximum potential growth rates for successive leaves, to be incorporated into the SIMCOT model are simply assumed to be those observed on plants growing under favourable conditions (McKinion et al., 1975). Such rigid growth procedures cannot account for instance for the strong dependence of the potential growth rate of a leaf after unfolding on its growth history before unfolding, including growth at the apex. They do not capture the underlying growth pattern nor the backfeeding mechanisms which lead to a particular outcome under real conditions.

Implementation for Californian conditions of the 1975 operational version of SIMCOT II (see McKinion, Baker, Hesketh and Jones, 1975), which contained an even more rudimentary morphogenetic section, led to the conclusion that that section had to be replaced by one which was based on a Californian data set, in order to yield satisfactory simulation results (Gutierrez, Falcon, Loew, Leipzig and van den Bosch, 1975). Such modelling techniques of course defeat their own purposes: a simulation model for cotton growth with more than local usefulness should contain a flexible morphogenetic routine which does justice to the impressive variability of the crop under field conditions, instead of incorporating such variability as data sets. Similarly, growth modelling in its proposed rôle as a guide to plant breeders can only successfully predict the impacts of plant modifications on whole crop performance if plant morphogenesis is adequately represented in the models.

It is therefore clear that there is scope for a more fundamental approach to cotton modelling which assigns a central rôle to the morphogenetic depth structure of the crop as a steering principle for growth and development. Much of the effort invested in the present model was taken up by the identification of this structure since an extensive literature search showed that published data were insufficient for these purposes. The work was reported in six publications, the outlines of which will be considered in the remainder of this section. The titles and summaries of these papers are presented in Annex II.

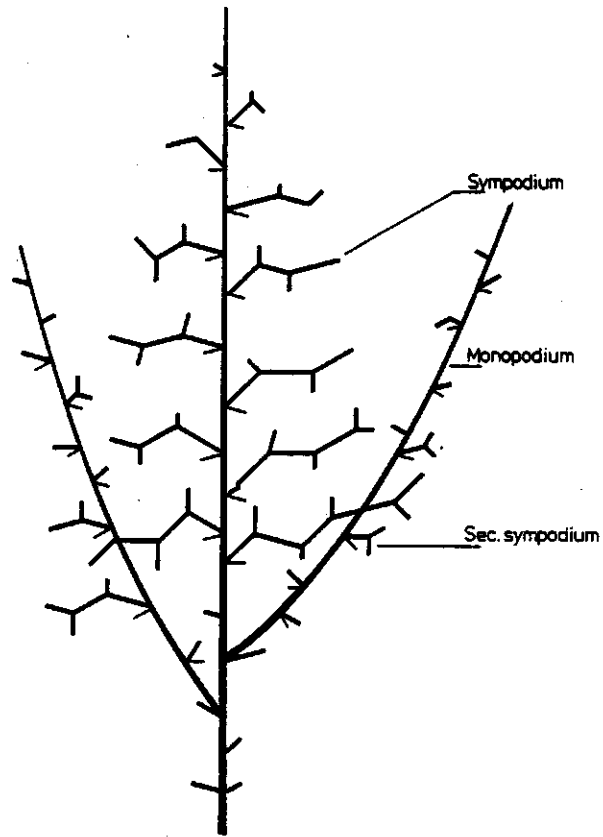


Fig. 1. A schematic representation of a cotton plant.

*The cotton plant.* Fig. 1 shows a schematical representation of a cotton plant. The mainstem apex initiates mainstem leaves and lateral buds in the axils of these leaves. On the lower nodes the buds may develop into vegetative branches (monopodia) of variable

vigour, while all higher nodes generally produce generative branches (sympodia). Monopodia replicate the mainstem and they may carry secondary sympodia. A sympodial apex initiates one true leaf and then transforms into a flower primordium. A visible flower bud is called a "square", a developing fruit is called "boll". The collective name used here for squares, flowers and bolls is "fruiting point". The branch is elongated by the axillary bud which leads to a typical zigzag structure. On any branch, prior to the initiation of the first (true) leaf a rudimentary prophyll and its accompanying axillary bud are initiated (Mauney, 1968). These buds often remain dormant but under favourable conditions, or after pruning of part of the branches (Mutsaers, 1982<sup>b</sup>) they may develop into (monopodial or sympodial) branches, adding to the high degree of flexibility of the species.

*Morphogenesis of cotton.* From a number of experiments under controlled conditions, in addition to various data sets from the literature a separate model for potential growth of cotton leaves was developed (Mutsaers, 1979, 1982<sup>b,c</sup>). For individual leaves the model describes the complete growth curve from initiation to maturity using a small number of parameters which govern the transition from exponential growth (associated with the phase of cell division between initiation and shortly after unfolding), through the phase of linear growth to the final phase when leaf blade expansion comes to a standstill.

Equally important, the model generates a succession of leaf primordia by a leaf initiation mechanism which invests a constant fraction of the apical dome into successive leaf primordia. The ratio between the initial size of two successive primordia then only depends on the growth rate of the apex, this ratio being maximal when the growth of the apex proceeds at its potential rate. The ratio decreases as the apical growth rate slows down due to substrate shortage but it is not allowed to fall below unity; if this would occur, leaf initiation rate slows down instead. Assimilate shortage acts upon leaf growth during all its phases and on growth of the apex and in this way leaf size at any instant reflects the integrated effect of crop history in term of substrate availability. The leaf growth model also generates a generative branch with each

mainstem leaf and the succession of leaves on these sympodia.

The direct effect of temperature on the succession and growth of leaves was shown to be completely characterized by a temperature effect on the time scale, since all rate parameters involved probably have the same temperature response.

Pruning experiments (Mutsaers, 1982<sup>b</sup>) showed that sympodial branches have preferential access to available assimilates over the mainstem apex. This can be explained by the more generalized hypothesis that any crop stratum has easier access to the assimilates produced in that same stratum than have other tissues. The surplus from an exporting mainstem leaf would then be easier available to its associated sympodial branch than to the mainstem apex. This conclusion agrees with frequent field observations on the imbalance of cotton growth under certain conditions, characterized by excessive vegetative growth and reduced boll set, especially in the lower crop strata (e.g. Anon., 1966; Hearn, 1975). Such excessive vegetative growth is associated with high night temperature, ample water supply and high fertility especially as regards nitrogen. The imbalance cannot be explained by an increased overall growth rate as this would not by itself give rise to a change in dry matter distribution. In a vigorously growing crop however, shading will build up quickly and assimilate production in the lower strata will decrease accordingly. As shedding of young fruiting points appears to occur in response to assimilate shortage (e.g. Goodman, 1955; Guinn, 1974), this phenomenon can also be explained by stratification of assimilate production and demand: increased shedding in the lower strata then is the result of low assimilate production in these same strata. These observations led to a modelling approach which treats the crop as a set of partly autonomous, interacting strata, with each stratum consisting of a mainstem leaf and its associated sympodial branch. Technical details will be treated below.

*Growth of cotton fruit.* In addition to cotton morphogenesis as discussed above, an adequate quantitative representation of the growth of fruits (called bolls) is essential for the model. Again it was tried to identify an underlying general growth pattern, characteristic for the species. Such a pattern emerged when dry weight increase as reported in a large number of publications was plotted

on relative scales with absolute dry weight and age after flowering being replaced respectively by weight as a fraction of final weight and age as a fraction of boll maturation period (BMP) (Mutsaers, 1976<sup>a,b</sup>). It was shown that, apart from a cultivar effect, BMP is practically only influenced by temperature through an exponential response pattern of boll development rate, between certain limits, i.e. a temperature effect on the time scale. Different final boll sizes result from different ovary sizes, at blooming, and ultimately from different sizes at initiation.

*Assimilate production.* A modelling method which treats a crop as a set of strata calls for a reliable calculation procedure for assimilate production by those strata in dependence of the sizes and ages of the leaves and their position in the canopy. An extensive literature review was therefore made on photosynthesis of individual cotton leaves, supplemented with a simple experiment on the effect of CO<sub>2</sub> concentration. The resulting photosynthetic parameters were used for the development of the photosynthesis routine of the model (Mutsaers, 1982<sup>a</sup>); which calculates carbohydrate production for each crop stratum. To account for the effect of lateral illumination in open canopies a simple calculation procedure for light interception by row crops was developed separately (Mutsaers, 1980).

In the following chapters the integrated whole crop simulation model, its procedures and simulation results are presented. First a general outline of the model is presented, followed by a more detailed description of the different routines for growth of plant parts, assimilate production and demand. Finally the behaviour of the model under different conditions is demonstrated. Since not all elements needed for the construction of this model were treated in the earlier work, some links will be added as their need shows up in the following systematic treatment of the model.

Two limitations of the model have to be mentioned here. Firstly, monopodial growth has not been incorporated yet and secondly, the model only considers carbohydrates and water as growth limiting substrates, assuming other growth substrates to be optimally available. The incorporation of monopodial growth and mineral nutrition will require additional research.

## OUTLINE OF THE MODEL

The guiding principle of the model is the idea that a cotton crop should be considered not simply as interacting sets of leaves, stems, roots and fruiting points, but that the positions of the different structures relative to each other are of utmost importance. The model therefore treats a cotton crop as a set of more or less horizontal, interacting strata, each stratum consisting of a mainstem leaf and the adjoining sympodium.

Vegetative growth and growth of fruiting points before flowering in any stratum is thought to depend to a large degree on assimilate production in the same stratum. Growth of bolls however, appears to have absolute priority for assimilates and each stratum contributes to boll growth in proportion to its production. This is equivalent to saying that for boll growth the assimilates constitute a common pool. The model first calculates assimilate production and potential growth of all plant parts for each stratum. Since potential growth is basically exponential, whereas assimilate production by a canopy approaches to a maximum, growth in a crop will ultimately be limited by assimilate production. The model therefore

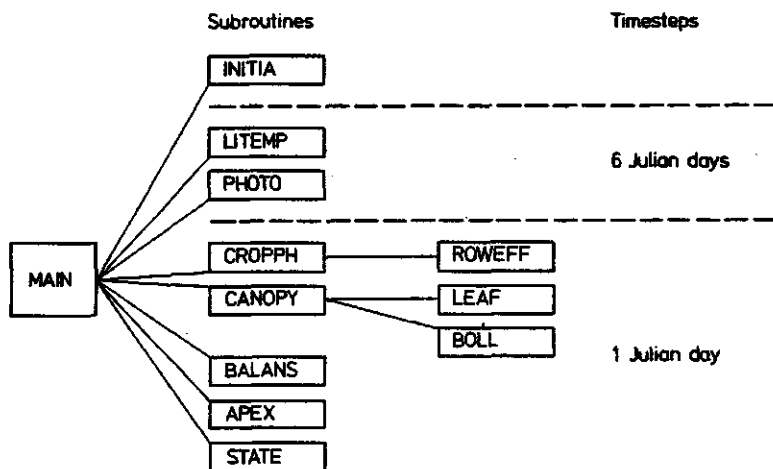


Fig. 2. Organizational diagram of the main program and subroutines.



contains a routine which adjusts growth to assimilate availability, taking stratification of assimilate production and demand into account.

The complexity of the system dictates a programming approach which captures most processes in separate subroutines, linked together by an operating routine which steps through these successive subroutines. Fig. 2 and table 1 show the subroutines and the way

TABLE 1. Summary of the procedures of the main program and subroutines of the cotton model KUTUN.

Name	Procedure
MAIN	Reads input files, advances calendar days and calls subroutines.
INITIA	Assigns initial values to variables and arrays.
LITEMP	Calculates environmental and crop parameters: daylength, daily temperature course, development rates, hourly and daily radiation, canopy light transmission.
PHOTO	Calculates daily net photosynthesis by layers of 0.5 LAI for a closed canopy.
CROPPH	Calculates net photosynthesis for each leaf and total assimilate production per stratum.
ROWEFF	Calculates row parameters for "equivalent crop" having the same light interception as the real crop.
CANOPY	Calls leaf and boll growth subroutines; calculates potential stem and root growth and assimilates required per stratum for potential growth and maintenance respiration of all plant parts.
LEAF	Calculates potential growth of mainstem and sympodial leaves.
BOLL	Calculates (potential) boll growth.
BALANS	Calculates actual growth for all plant parts in dependence of assimilate availability in each stratum.
APEX	Initiates leaves, branches and flower buds (squares).
STATE	Calculates quantities characterizing the state of the crop, outputs results.

they are linked up. The organisation of the model will be outlined summarily here while the subroutines will be treated in more detail in the following sections. A fully documented FORTRAN-listing of the model KUTUN is given in Annex I.

The MAIN section is simply an operating routine, which successively calls the different subroutines and counts the number of days elapsed since the start of the simulation. Each simulation cycle covers 1 calendar day. INITIA assigns initial values to a large number of variables, characterizing the initial status of the crop. If simulation starts from the seed, INITIA only assigns positive values to the areas of the cotyledons and the first true leaf, which are present in the ungerminated seed, and to the weight of the associated stem and root tissue. LITEMP derives radiation and temperature parameters from a set of environmental data, read from a data file. These derived parameters are used by other subroutines.

PHOTO calculates daily assimilate production at successive levels of a closed cotton canopy, in dependence of daily radiation. The results from PHOTO are used by CROPPH to calculate daily net assimilation (i.e. gross assimilation minus dark respiration by the leaves) by different strata of the real crop. These calculations are complicated by the row effect which occurs in open canopies. This effect is accounted for by a separate subroutine ROWEFF, called by CROPPH.

CANOPY calculates potential assimilate demand for growth of all plant parts associated with each stratum. For that purpose the subroutines LEAF and BOLL are called to calculate potential growth of each leaf and fruiting point in the canopy. Potential growth of stems and roots is then calculated by CANOPY and finally potential growth is converted into assimilate demand.

The results from CROPPH and CANOPY are used by BALANS to adjust growth in each stratum to assimilate availability. Demand for growth of fruiting parts and maintenance respiration is first satisfied from a contribution by each stratum proportional to its production. Next, vegetative growth in a stratum gets partly preferential access to the remaining assimilates in the same stratum and leaf areas and weights of all plant parts are incremented accordingly. The load of fruiting parts is adjusted to assimilate availability in its stratum by partial shedding of flower buds (called squares) and young bolls.

Subroutine APEX initiates new leaf primordia and branches and new fruiting points with temperature dependent intervals. In case of assimilate shortage the initiation of mainstem leaves and branches is postponed until the apex has recovered its previous size. Finally subroutine STATE outputs various parameters that characterize the present status of the crop. Then the whole operation is repeated for the next day.

## DETAILED DESCRIPTION OF THE MODEL

### a. *Operation and initialisation (MAIN, INITIA)*

MAIN. The MAIN section reads data files containing various species and cultivar characteristic parameters, crop parameters like row spacing, row azimuth, number of plants per  $m^2$  and environmental parameters like latitude, date, temperatures etc. It calls upon the different subroutines and counts the number of days elapsed. INITIA is called only once, at the beginning of a run, LITEMP and PHOTO are called once every 6 days. All other subroutines, which represent the dynamic section of the simulation, are called each day.

The program keeps records (arrays) of the areas and specific weights of mainstem and sympodial leaves, weights of stems, roots and fruiting points, developmental age of leaves and fruiting points etc. These arrays are available to all subroutines that need them.

INITIA. Initial values of most variables are zero. Only area and weight of cotyledons and first mainstem leaf and weight of stem and root are given positive values. Specific leaf weight of all leaves is set to  $30 \text{ gm}^{-2}$ , which is the value at unfolding (cf. Constable and Rawson, 1980<sup>b</sup>). This value is assumed to hold also between initiation and unfolding.

### b. *Environmental and photosynthetic parameters (LITEMP, PHOTO)*

This program section calculates radiation and temperature characteristics of the environment and daily assimilation at different levels in a closed cotton canopy, corresponding with these characteristics. Average values for 6 days are produced. This program section operates independently from the dynamic crop simulation sections. The parameter values generated by these subroutines only depend on the physical environment (radiation, temperature) and not on the status of the crop. The parameters are used as fixed values by the dynamic sections.

LITEMP. The subroutine uses as input latitude, calendar day, average sky conditions and average maximum and minimum temperature.

The first part calculates a daily temperature course consisting of two sinus segments between minimum and maximum temperature. This temperature course is then used to calculate temperature dependent (relative) development rates for generative (Mutsaers, 1976<sup>b</sup>) and vegetative (Mutsaers, 1982<sup>c</sup>) growth, called RATE<sub>g</sub> and RATE<sub>v</sub> (day/day). These parameters are unity at a constant temperature of 25°C and increase with temperature. They are used in all growth sections and represent the advance in developmental (or physiological) age, corresponding with one Julian day.

The other part calculates various radiation characteristics like hourly and daily values for direct and diffuse incident radiation and light transmission to successive layers of a closed cotton canopy, based on Goudriaan and van Laar (1978) and Mutsaers (1982<sup>a</sup>). These figures are used as inputs for PHOTO and ROWEFF.

PHOTO. This subroutine yields three sets of data:

- potential net daily photosynthesis at 12 successive levels, 0.5 LAI units apart, for a closed canopy under a clear sky
- the same under an overcast sky
- daily dark respiration at the same levels.

Details on this photosynthesis procedure were published elsewhere (Mutsaers, 1982<sup>a</sup>). The input data needed are daylength and potential daily incident radiation (from LITEMP), a table relating maximum photosynthetic rate of single leaves to ambient radiation climate (defined in INITIA) and some environmental data (sky conditions and CO<sub>2</sub> concentration, read from a data file by MAIN). The method for treating the effect of waterstress on photosynthesis employed by the model is discussed in the section on subroutine LEAF. The three sets of data, which represent mean values for a 6 day period are used as an input for CROPPH.

#### *c. Assimilate production by canopy strata (CROPPH, ROWEFF)*

Assimilate production is calculated separately for each crop stratum (consisting of a mainstem leaf and a corresponding sympodium) by the subroutines CROPPH and ROWEFF. This is necessary, since growth

in each stratum is tightly linked to the amount of assimilates produced in that same stratum as will be seen in section d.

For a closed canopy, assimilation in a stratum is derived directly from the data produced by PHOTO by interpolation between the canopy layers. During much of its early development however the crop canopy will not be closed and the contribution from lateral illumination of the rows has to be taken into account. Since direct calculation of photosynthesis by row crops is complicated, an indirect method, based on a simple calculation method for light absorption by hedge row crops (Mutsaers, 1980, 1981<sup>a</sup>) is used.

Light absorption by a hedge row crop depends on LAI, relative leaf covered ground area or vertical canopy projection (RCG), canopy height (SL) and row orientation. LAI is available from BALANS, while RCG and SL are calculated by CROPPH itself. With these input data CROPPH calls subroutine ROWEFF, which calculates daily light absorption by the real crop. The real crop is then replaced by an "equivalent crop", which is defined as a closed canopy, covering part of the ground area and having the same daily light absorption as the real (row-)crop. The vertical projection of the equivalent crop will necessarily be greater than that of the real crop, which reflects the effect of lateral illumination. For each leaf in the real crop CROPPH then calculates the corresponding position in the equivalent crop and its assimilate production (in the equivalent crop a leaf will have less leaf area overhead than in the real crop). Finally leaf age is accounted for. Assimilation by each canopy stratum is found by summing for the individual leaf positions.

CROPPH. Prior to calling ROWEFF, CROPPH first has to calculate relative leaf covered ground area (RCG) and canopy height (SL) of the real crop. These calculations will be considered in some detail now.

Of necessity the relationship between LAI and RCG at not too wide row spacings will be a saturation type curve, with RCG approaching unity with increasing LAI. The rate of approach will however depend on rowspacing. Data from Mann, Curry, DeMichele and Baker (1980) on direct light absorption at noon by differently spaced and aged cotton crops with known LAI were used to estimate this relationship (fig. 3). It is assumed that for LAI above 1 the percentage

light absorption at noon approaches RCG, since the leaf canopy will then transmit only a small fraction of the intercepted radiation while all direct radiation falling over the uncovered path is not

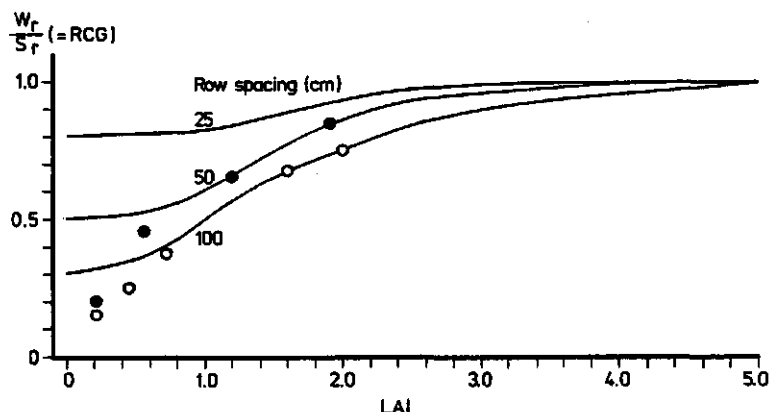


Fig. 3. Observed fraction of direct light absorbed at noon in dependence of LAI for field crops spaced (O) 100 and (●) 50 cms, and postulated relationships between LAI and relative leaf covered ground area (RCG) at 100, 50 and 25 cms rowspacing (drawn curves).

absorbed. At low LAI this does not hold as the canopy itself will also transmit radiation. Row effects however are only relevant when shading starts playing a role, i.e. when 2 or 3 mature leaves are present. The width of a widely spaced canopy with 2 mature leaves will be around 30 cms. Therefore, at a row-spacing of 100 cm the curve relating LAI and RCG may be initiated at  $RCG = 0.30$ . For spacings of 50 and 25 cm, initial values of 0.50 and 0.80 were chosen. The resulting curves, postulated for the relationship between LAI and RCG, at three row-spacings is shown in fig. 3. These curves, in a tabulated form, are used by CROPPH to calculate RCG in dependence of LAI.

As for stem length (SL) few data are available on the growth of internodes in cotton. Final lengths of successive mainstem internodes from 2 climate room and 1 greenhouse experiment are shown in

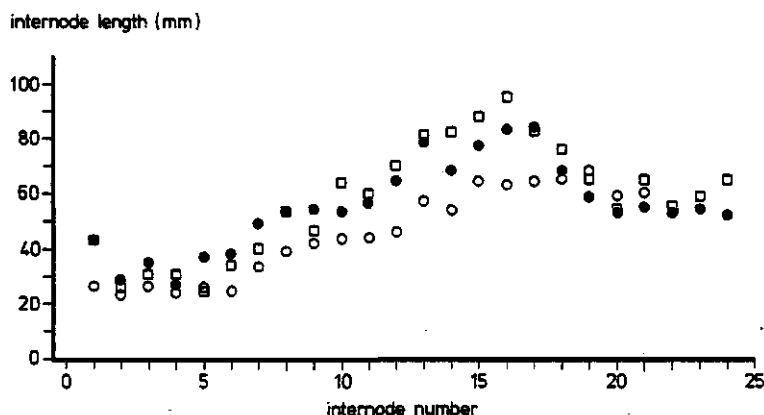


Fig. 4. Internode lengths along the mainstem of plants grown under (O,●) growth cabinet and (□) greenhouse conditions; averages of 4 plants.

fig. 4 and fig. 5 shows growth of some individual nodes from one of them. Maximum internode length was attained at a higher node than maximum final leaf area. This may be because apical size continues to increase up to much higher nodes than does final leaf area as discussed by Mutsaers (1982<sup>b</sup>). More detailed studies would be needed however for an adequate incorporation of this dynamics into growth models.

Fortunately light interception by row crops is not very sensitive to small variations in crop height and less so as the canopy approaches closure. Very accurate representation of stem growth is therefore not needed for these purposes. CROPPH simply uses the observed increase in total stem length with age from the top curve of fig. 4 as a forcing function. Length growth is reduced by water-stress in the model in the same way as leaf area growth.

CROPPH then calls ROWEFF, which calculates the relative leaf



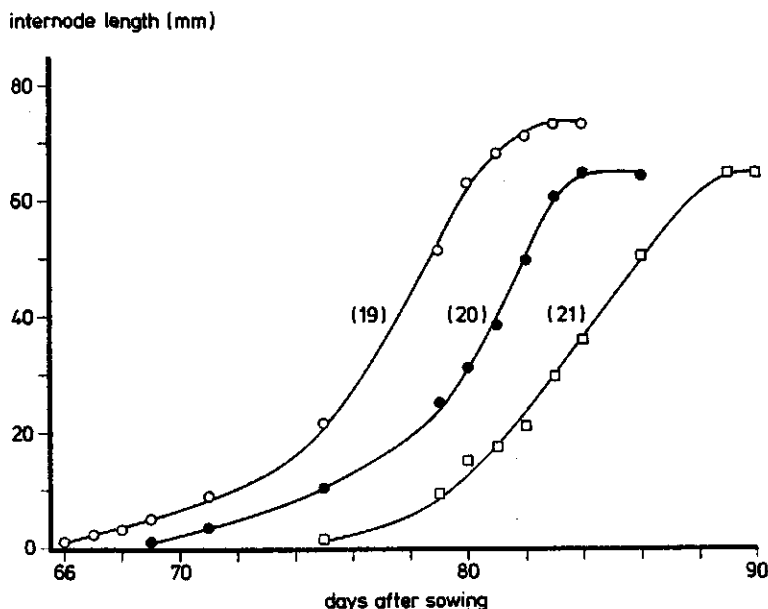


Fig. 5. Growth of some individual internodes; from exp. II in Mutsaers (1982<sup>b</sup>).

covered ground area (RCG) of the equivalent crop (see below). Assimilation by the real crop is equated to assimilation by the equivalent crop, which in turn is simply equal to assimilation by a closed canopy (calculated previously by PHOTO), covering only part of the ground area. For any leaf in the canopy CROPPH then calculates the corresponding position in the equivalent crop and calculates its assimilation by interpolation between layers.

Leaf age is accounted for as follows. Maximum photosynthetic rate of a leaf decreases with age but photosynthetic efficiency appears not to be affected (Constable and Rawson, 1980<sup>a</sup>). The effect of a leaf's age will therefore decrease with depth inside the canopy. For fully exposed leaves the subroutine simply multiplies photosynthesis by an activity factor, corresponding with age (Mutsaers,

1982<sup>a</sup>). This activity factor is corrected for depth inside the canopy in such a way that its influence decreases logarithmically until at LAI 5 it is 0.05 of what it would be for a fully exposed leaf of the same age.

ROWEFF. ROWEFF, called by CROPPH, first calculates daily light absorption by the real crop, treated as a hedge row (Mutsaers, 1980). Necessary input data are partly supplied by LITEMP (hourly incident radiation and sun angles, transmission characteristics of a cotton canopy), by BALANS (LAI) and by MAIN (row azimuth direction, read from the data file), partly calculated by CROPPH prior to calling ROWEFF (RCG and SL, see above).

After calculating light absorption by the real crop, ROWEFF calculates light absorption by an imaginary "equivalent crop", defined as a continuous canopy with the same LAI as the real crop, which covers only part of the ground area, while radiation falling over the non-covered area is lost. This calculation is done iteratively for successively wider continuous crops, until the same daily absorption is found as calculated for the real crop. The resulting relative leaf covered ground area (RCG) or vertical projection of the equivalent crop will always be greater than the vertical projection of the real crop due to lateral illumination. This RCG of the equivalent crop is fed into CROPPH.

c. *Potential growth of plant parts and assimilate demand (CANOPY, LEAF, BOLL)*

Potential growth of leaves, stems, roots and fruiting points is calculated by the program section consisting of the subroutines CANOPY, LEAF and BOLL.

CANOPY first calls subroutine LEAF, which calculates potential area and weight increments of each mainstem leaf. Next, subroutine BOLL is called for each sympodium, yielding (potential) weight increments for each fruiting point. LEAF is then called again for potential growth of sympodial leaves. Finally CANOPY calculates potential growth of stems and roots and assimilate demand for potential growth and maintenance respiration.

LEAF. LEAF is called separately for the mainstem and for each sympodium and calculates potential growth of all initiated leaves of the axis under consideration. (For a detailed treatment see Mutsaers, 1982<sup>b,c</sup>). Potential relative growth rate (RGR) of a leaf depends on its developmental age. With each Julian day this age is incremented with  $RATE_v$ , calculated by LITEMP in dependence of the temperature regime. The influence of temperature can be characterized completely by this effect on the development rate.

Potential RGR of the area of an individual leaf is constant between initiation and unfolding. After unfolding, which occurs at a fixed developmental age, potential RGR decreases with developmental age according to an inverse sigmoid pattern. This pattern and the parameters involved are described by Mutsaers (1982<sup>b,c</sup>). Potential absolute growth rate of leaf area ( $\Delta A$ ) over one calendar day is then calculated from

$$\Delta A = A(t) \{ \exp (RGR(t) \times RATE_v) - 1 \}$$

with  $A(t)$  = leaf area at developmental age  $t$

$RGR(t)$  = RGR in dependence of  $t$

(The model actually uses the RGR value applying to developmental age  $t + 0.5 \text{ } RATE_v$  to account for the change of RGR over the day under consideration.)

A leaf starts growth in thickness after unfolding. The initial specific leaf weight (SLW) is set equal to  $30 \text{ gm}^{-2}$  (cf. Constable and Rawson, 1980<sup>b</sup>). Maximum SLW is influenced by the amount of radiation the leaf is exposed to (e.g. Patterson, Bunce, Alberte and van Volkenburgh, 1977). This is treated as a morphogenetic response. The upper limit is set to  $65 \text{ gm}^{-2}$  for radiation above  $8.10^6 \text{ Jm}^{-2} \text{ day}^{-1}$  and  $SLW_{\max}$  decreases with decreasing radiation in the same way as maximum net photosynthesis (Mutsaers, 1982<sup>a</sup>). The "steady state" relationship between SLW and physiological age for a leaf growing at its potential rate is represented by

$$SLW = 30. + \frac{SLW_{\max} - 30.}{1 + ae^{bt}} \quad (1)$$

with  $SLW_{\max}$  = maximum SLW, depending on the light climate

$a, b$  = parameters

$t$  = physiological age after unfolding

Since growth in thickness is a dynamic phenomenon the subroutine actually operates with an expression for  $\frac{1}{SLW} \frac{dSLW}{dt}$  as a function of age from unfolding, derived from (1). This expression contains  $SLW_{max}$ , which is continuously adjusted in dependence of the light history of the leaf. (For convenience, this adjustment is actually done in CROPPH, where light penetration has to be calculated for other purpose as well.) The use of an expression for the relative rate of increase of SLW is also necessary in order to adjust growth in thickness to substrate supply as will be discussed below (BALANS). The parameter values (a,b) result from the conditions that the relative increase of SLW is maximum at 7 physiological days (cf. Maksymowitch, 1973) and SLW attains 99.9% of its final value at 20 physiological days (cf. Constable and Rawson, 1980<sup>b</sup>). Potential growth rate of leaf area and leaf thickness together determine potential growth of leaf weight.

Waterstress reduces the growth rate of all leaves through a multiplication factor ( $RED_{ext}$ ) operating on the RGR's. Advance of physiological age is however reduced as well but to a lesser degree (Baker, Landivar and Lambert, 1979; Mutsaers, 1982<sup>c</sup>) according to

$$RED_{tim} = RATE_v (0.2 + 0.8 RED_{ext})$$

In case of waterstress the term  $RED_{tim}$  acts as the development rate instead of  $RATE_v$ .

Apart from its effect on leaf expansion, waterstress also influences photosynthesis through a reduction of the maximum photosynthetic rate ( $NP_{max}$ ) of individual leaves. The following relationship between  $NP_{max}$  and daily leaf expansion rate in the linear phase of growth at different stress levels was estimated from data by Ackerson, Krieg, Haring and Chang (1977), Ackerson, Krieg, Miller and Zartman (1977) and Cutler and Rains (1977):

$$\frac{(NP_{max})_{stressed}}{(NP_{max})_{unstressed}} = 0.5 \left( 1 + \frac{\Delta A_{stressed}}{\Delta A_{unstressed}} \right)$$

In the linear growth phase, where RGR is small, the ratio  $\Delta A_{stressed} / \Delta A_{unstressed}$  approaches  $RED_{ext}$  as defined above. The

effects of waterstress on  $NP_{max}$  and on leaf expansion are therefore related through

$$\frac{(NP_{max})_{stressed}}{(NP_{max})_{unstressed}} = 0.5 (1 + RED_{ext})$$

This relationship operates on  $NP_{max}$  in the subroutine PHOTO. No attempt has been made yet to define  $RED_{ext}$  in terms of soil water potential and atmospheric conditions.

**BOLL.** Subroutine BOLL, which is called separately for each sympodium, calculates potential weight increase for each fruiting point, depending on its developmental age. Before flowering, which occurs at a developmental age of 44 physiological days after initiation (see APEX), fruiting points are assumed to grow exponentially at the same relative rate as meristematic leaf tissue. Developmental rate in dependence of temperature then equals  $RATE_v$ . After flowering, boll growth proceeds according to a fixed pattern described by Mutsaers (1976<sup>a</sup>) and confirmed experimentally by Marani (1979) and Constable and Rawson (1980<sup>b</sup>). This pattern emerges if the age of a boll is represented as a fraction of boll maturation period (BMP) and boll weight as fraction of final boll weight. The following, purely descriptive function for this growth pattern, based on Mutsaers (1976<sup>a</sup>) and Constable and Rawson (1980<sup>b</sup>) is used:

$$WB/WB_f = 0.03 + 0.97 [1 - \exp \{ -5 (t/BMP_{25})^2 \}] \quad (2)$$

with  $WB$  = boll weight

$WB_f$  = final boll weight

$t$  = developmental age (after flowering)

$BMP_{25}$  = BMP at 25°C constant temperature

The subroutine operates again with an expression for the relative increase of boll weight, derived from (2):

$$RGR = \frac{t/BMP_{25}}{0.1031 \exp \{ 5 (t/BMP_{25})^2 \} - 0.1}$$

With each calendar day developmental age is incremented with  $RATE_g$ , which is the development rate for generative growth, calculated by LITEMP. Absolute weight increase ( $\Delta WB$ ) over a day is now calculated with

$$\Delta WB = WB \{ \exp (RGR \times RATE_g) - 1 \}$$

CANOPY. After repeatedly calling LEAF and BOLL for the calculation of potential growth of all leaves and fruiting points, CANOPY enters a calculation procedure for stem and root growth based on the following analysis.

In young plants the leaf to stem weight ratio is high but decreases as the plants grow older (Heath, 1937; Huxley, 1964; Marani

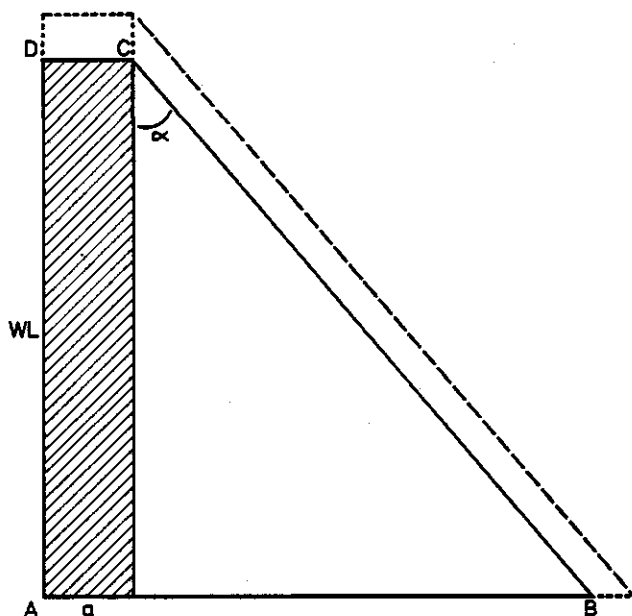


Fig. 6 Theoretical relationship between stem weight and leaf weight.

and Aharonov, 1964; Hearn, 1969<sup>b</sup>; Basset, Anderson and Werkhoven, 1970). With increasing number of leaves the supporting stem will grow accordingly, in order to maintain a sufficient two-directional flow of water and solutes. Therefore, apart from the amount of stem tissue formed directly under a growing leaf, lower down the stem additional tissue will have to be formed as well (cf. Splinter and Beeman, 1968). The addition of stem tissue for each addition of leaf tissue will therefore be greater as more leaf tissue is already present below the new leaf, resulting in an increasing stem to leaf weight ratio. This relationship between stem and leaf weight in its most simple form is visualized in fig. 6. The length of the vertical axis represents total leaf weight (WL). The area of the rectangle (aWL) represents the primary stem tissue associated directly with a new leaf, while the triangle stands for secondary stem tissue, associated with the leaves overhead. Total stem weight equals:

$$WS = a WL + \frac{1}{2} WL^2 \operatorname{tg} \alpha$$

The increase of stem weight with each increment of leaf weight then equals:

$$\frac{\Delta WS}{\Delta WL} = a + WL \operatorname{tg} \alpha$$

In fig. 7 the ratio between dry weight increase of stems and leaves ( $\Delta WS/\Delta WL$ ) is plotted against dry weight of leaves (WL) for two data sets, one from Israel (Kletter, unpublished results), the other from Arizona, USA (Butler, Henneberry and Wilson, 1969). The strongly fluctuating data points in the right hand part of the curve have little significance since the absolute weight increases involved are small and subject to large sampling errors (destructive sampling). The 3 open squares below the drawn curve to the left do not fall in line with the other points of the same data set, but they do have a similar slope. This deviation is probably due to irregularity of the sampling area. If these aberrant data points are ignored and if it is realised that destructive sampling in field plots will necessarily result in large sample variations, the remaining data may be satisfactorily described by the drawn curve in fig. 7. For young plants (with low total leaf weight) the linear

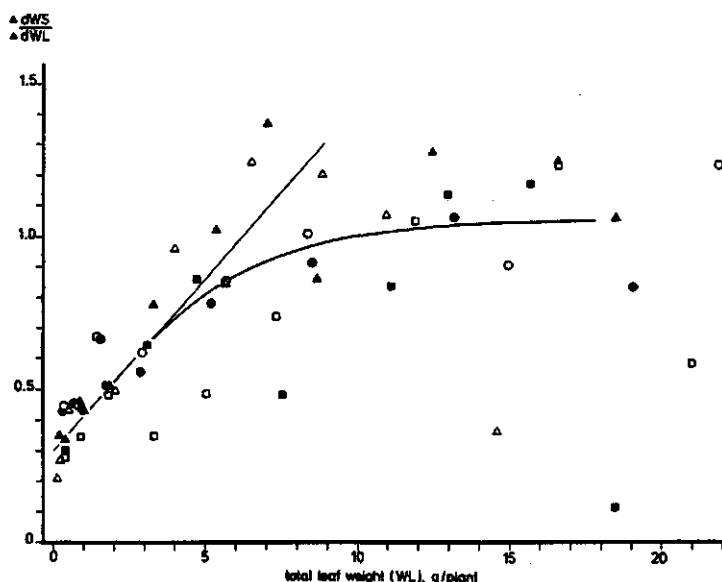


Fig. 7. Relationship between the ratio of dry weight increase of stems and leaves ( $\Delta WS/\Delta WL$ ) and dry weight of leaves (WL); data from (O,●) Butler et al. (1969), 2 different cultivars, and (□,■,△,▲) Kletter (unpublished results), 4 locations in 2 years.

relationship between  $\Delta WS/\Delta WL$  and WL, as suggested above by a theoretical argument is satisfactorily represented by the linear part of the drawn curve in fig. 7, or the equation:

$$\frac{\Delta WS}{\Delta WL} = 0.3 + 0.11 WL \quad (3)$$

The curve levels off as plants grow older, i.e. during the growth phase when the main contributors to leaf growth are the branches. This may be understood as follows. It was argued earlier that the total amount of new stem tissue, associated with new leaf tissue will depend on leaf weight already present below that leaf.



In young plants, consisting only of a leafy mainstem, this will be equal to all leaf tissue. For a new leaf on the branches, however, only the leaves present along the path between that leaf and the mainstem base will count, which will always be less than total leaf weight of the whole plant. The curve relating  $\Delta WS/\Delta WL$  to total plant leaf weight will therefore necessarily deviate from the linear as plants grow older. The model accordingly for each leaf calculates the associated stem weight increase from expression (3) but the variable WL is calculated for each leaf position separately in dependence of the leaf tissue below it.

Throughout simulation, the stem (and root) weight formed as a result of the growth of a given leaf, in the above sense, is treated as tissue, associated with that leaf. It is for instance assigned the same developmental age as that leaf.

Field data from Hearn (1969<sup>b</sup>) and greenhouse data from Cutler and Rains (1977) show that the ratio between leaf weight and stem weight at different growth stages was practically independent of water regime. The same was true for young cotton plants under different shading treatments by Huxley (1964). Expression (3) is therefore applied irrespective of water regime and incident radiation.

Data on cotton root weight are very scarce. Field samples of crudely removed roots yield 6-10% on a total dry weight basis for plants after the first bloom stage (McBryde, 1891; Armstrong and Albert, 1931; Marani and Aharonov, 1964). Root weight percentage of plants grown on sand culture by Huxley (1964) fluctuated between 15 and 20% from the first true leaf stage to a month later (plants in full sunlight) and the ratio between root weight and stem weight decreased from 1.0 to approximately 0.5. Cutler and Rains (1977) found a root to stem weight ratio of 1.0 for 55 days old plants, grown on sand culture and watered daily. This high ratio may be due to waterstress since even a frequency of 1 irrigation per day may lead to such stress in 12 liter pots filled with coarse sand (Steiner, pers. comm.). The ratio increased with decreasing irrigation frequency.

In the absence of waterstress the model invests an amount of dry matter in the roots equal to half the amount invested in stems. Waterstress however causes this ratio to increase. In the absence of

good data the model uses the following tentative relationship for the ratio of root to stem weight increase:

$$\frac{\Delta WR}{\Delta WS} = 1 - (\text{RED}_{\text{ext}} - 0.75) \times 2 \quad (4)$$

This relationship causes a progressively greater amount of root tissue to be formed for each unit of stem (or leaf) weight as water-stress increases. ( $\text{RED}_{\text{ext}}$  is treated in the section on subroutine LEAF).

CANOPY now proceeds to calculate assimilate demand for each crop stratum (mainstem leaf and adjoining sympodium). In addition to potential weight increase of all plant parts, just calculated, it also needs their chemical composition and conversion factors as calculated by Penning de Vries and co-workers (Penning de Vries, Brunsting and van Laar, 1974; de Wit et al., 1978). Composition of meristematic tissue is assumed to be equal for all plant parts but as the tissue ages the composition changes. Composition of meristematic, mature and senescent leaves, stalks and roots as used in the model is shown in table 2. For bolls the composition in dependence of developmental age is given by Mutsaers (1976<sup>a</sup>). The conversion factors of table 3 are used to calculate the "glucose-equivalent" of the tissue in dependence of composition.

The most elegant simulation method for the chemical composition of a tissue would be to assign a variable composition to each weight increment in such a way that the correct final composition of mature tissue would result. This procedure is adequate for bolls because they are assigned a fixed growth pattern. The model uses this procedure and reads the composition corresponding with each weight increment from a table. Growth of leaves, stems and roots however is subject to large variations due to waterstress and assimilate availability (see BALANS). This variability would strongly influence final composition if the above method were used. As little is known about the influence of growth conditions on chemical composition, it was preferred to adopt a simple method which always yields final composition as shown in table 2. This procedure works as follows: the composition of a leaf and its associated stem and root tissue (expressed in glucose equivalent) is kept equal to the composition

TABLE 2. Estimated composition <sup>1)</sup> of cotton leaves and "associated tissue" in stalks and roots, at different stages of development of a leaf.

Developmental stage of leaf	tissue	Composition in % of DM				
		organic N-compounds	carbohydrates, organic acids	lipids	lignin	minerals
meristematic	leaf	37.5	47.5	5.0	-	10.0
	stalk	37.5	47.5	5.0	-	10.0
	root	37.5	47.5	5.0	-	10.0
mature	leaf	20.0	61.0	8.5	0.5	10.0
	stalk	12.5	77.5	2.0	2.0	6.0
	root	10.0	79.0	2.0	2.0	7.0
senescent	leaf	12.5	68.0	8.5	1.0	10.0
	stalk	4.7	81.6	0.7	10.0	3.0
	root	3.7	81.6	0.7	10.0	4.0

<sup>1)</sup> Partly based on Fraps (1919), McHargue (1926), Armstrong and Albert (1931), Basset et al. (1970), Thompson et al. (1976).

TABLE 3. Amount of glucose needed for substrate uptake and synthesis of plant components, not including maintenance respiration (after Penning de Vries et al., 1974; de Wit et al., 1978).

	g glucose/g
carbohydrates	1.243
N-compounds	1.961
lipids	3.030
lignin	2.153
minerals	0.020

of meristematic tissue until 5 physiological days after unfolding of the leaf and then changes linearly to attain the composition of mature tissue at 20 days. At each time interval the tissue already present is assigned a new composition which corresponds with its developmental age. Since the glucose equivalent of the tissue decreases with age, a glucose surplus results, which is calculated and added to the assimilates being produced by the stratum. The dry weight increment is also assigned the composition corresponding to the developmental age of the tissue. By this method all tissue compositions are updated each timestep. Glucose equivalent of senescent tissue being very similar to that of mature tissue, further changes do not have to be accounted for.

Finally, CANOPY calculates total maintenance requirements ( $RSP_{mnt}$ ) for stems, roots and fruiting points ( $RSP_{mnt}$  of leaves is assumed to be accounted for by the dark respiration component of gross photosynthesis). For meristematic tissue at  $25^{\circ}C$ , a  $RSP_{mnt}$  of 0.04 g glucose/g dry matter/day is used, a figure calculated for very young bolls by Mutsaers (1976<sup>a</sup>). For mature and senescent tissue  $RSP_{mnt}$  is calculated from protein and minerals content as 0.0245 g glucose/g protein/day and 0.0326 g glucose/g minerals/day (de Wit et al., 1978). Intermediate values are calculated by linear interpolation.  $RSP_{mnt}$  requirements for growing bolls from Mutsaers (1976<sup>a</sup>) are represented as a tabulated input. The  $RSP_{mnt}$  requirements for (potential) weight increments are also calculated and added to total assimilate demand for potential growth in each stratum. The temperature response of  $RSP_{mnt}$  and vegetative growth being similar, both having a  $Q_{10}$  of around 2.2 between 20 and  $30^{\circ}C$ , the effect of temperature on  $RSP_{mnt}$  can be accounted for by multiplication by  $RATE_v$  (see LITEMP).

d. *The adjustment of growth to assimilate availability (BALANS)*

In the preceding sections the calculation of assimilate production and demand in each canopy stratum was discussed. The subroutine BALANS operates with these quantities to bring actual growth in correspondance with assimilate availability.

Maintenance respiration and growth of fruiting points have first priority (Mutsaers, 1976<sup>a</sup>). For these processes each stratum

contributes an amount proportional to its production and BALANS then calculates the remaining assimilate pool for each stratum, available for growth of vegetative structures. If each vegetative structure would have equal access to the remaining assimilates, then each of these structures should be assigned a share proportional to its demand. Mutsaers (1982<sup>b</sup>) argued that priority seems to exist for sympodial growth, irrespective of the presence or absence of fruiting points. Besides, simulation of cotton growth using this proportionality concept yielded very unrealistic results as will be shown below. The subroutine therefore assigns partial priority to vegetative growth in a stratum for assimilates produced in that same stratum. This is done as follows.

First the supply/demand ratio is calculated both for each stratum separately and for the whole crop. The whole-crop ratio represents the overall demand status of the crop. In case of completely proportional attribution, each stratum would satisfy its demand by a fraction equal to the supply/demand ratio for the whole crop. In a first round, the subroutine assigns this amount to those strata which have a higher ratio than the crop as a whole: these "surplus" strata first get their "fair share". The "deficit" strata with a less than average ratio keep their own production but they have a deficit relative to their fair share. These deficits are summed. A "surplus" stratum, in order to satisfy its remaining demand (above its fair share) then has the same relative claim to what remains of its own production as has this integrated deficit. This leads to a second assignment. What remains of the surplus thereafter forms a common pool of which all strata get a share proportional to their total remaining demand. After this redistribution of available assimilates over the strata the subroutine for each stratum calculates the new ratio between assimilates available and required for potential growth. Potential growth rates of all vegetative parts in each stratum are then multiplied by this ratio, yielding actual growth rates. As for the leaves, part of the potential weight increase is due to growth in area and part to growth in thickness. The subroutine reduces both by an amount proportional to their contribution to potential weight increase.

Reduction of generative growth only occurs through shedding of fruiting points. The model assumes that fruiting points are only

liable to be shed between 10 physiological days before (square shedding) and 2 days after flowering (shedding of young fruit). The fruiting points which are in the shedding age group are assumed to compete for assimilates at an equal footing with the vegetative structures in the same stratum. Since they are not sensitive to growth rate reduction, their shedding percentage will necessarily (in terms of the model procedures) also be equal to the ratio between assimilate supply and demand, after redistribution as treated above.

Young seedlings are assumed to obtain surplus assimilates from the seed up to unfolding of the first true leaf. Growth proceeds at its potential rate until that moment.

e. *Initiation of leaves and fruiting points (APEX)*

Initiation of new structures (leaves, sympodia and flower buds) is organized by subroutine APEX. The procedures used by this subroutine are based on a detailed analysis of initiation and growth of mainstem and sympodial leaves by Mutsaers (1982<sup>b,c</sup>). The subroutine needs information on a number of cultivar specific growth parameters, read from a data file by the MAIN program and data on the developmental status of the crop. The elements of this set of input data will be explained as they show up in the description of the subroutine.

The subroutine keeps track of the number of leaf intervals accumulated on mainstem and sympodia. At each timestep the leaf interval sum on the mainstem (LLI) is incremented by  $RATE_v / LI_b$ , with  $LI_b$  being the basic number of physiological days (at a constant temperature of 25°C) between initiation of successive mainstem leaves in case of unrestricted growth (Mutsaers, 1982<sup>c</sup>). Leaf initiation occurs each time LLI passes a whole number. Each time a new mainstem leaf is initiated, the next (yet uninitiated) leaf is attributed an area equal to 0.16 times the just initiated one. If growth were to proceed at its potential rate throughout, this would make the next leaf 1.38 times larger than the preceding one, both at initiation and at maturity (Mutsaers, 1982<sup>b</sup>). The uninitiated "leaf", which forms part of the apex, is treated by the subroutines LEAF and BALANS in the same way as the leaf primordia.

In case of less than potential growth due to assimilate shortage, a smaller area could result for a newly initiated leaf primordium, compared to its predecessor. This would involve shrinkage of the apex. In such case APEX postpones initiation until the new primordium has attained a size equal to its predecessor's (at initiation of that predecessor). The increase of LLI is of course slowed down as well.

Sympodial branches are issued from the first sympodium carrying node upward. This node number is sensitive to environmental conditions (e.g. Mauney, 1966) and shows some variation between individual plants (Jones, Hesketh, Colwick, Lane, McKinion and Thompson, 1975), but these aspects have not been incorporated yet. The program simply reads a value for the first sympodium carrying node from the data file. The interval between initiation of a mainstem leaf and the corresponding first sympodial leaf and the interval between two successive sympodial leaves on the same branch are set at 2.5 LI. Sympodial leaves are initiated at such an area that, at potential growth throughout, the ratio between final area of the first sympodial and the mainstem leaf becomes 0.75, and the ratio between two successive sympodial leaves 0.90. The actually realized final ratios depend on the carbohydrate status during development. Squares are initiated at the same time as sympodial leaves and at such a weight that final boll weight at first sympodial positions becomes 7 g. Each following square along a sympodium is initiated at a weight 0.9 times the preceding one.

## SIMULATION OF COTTON GROWTH

In a first evaluation round of a morphogenetic crop model one has to test the model's general ability to generate a crop which, under different conditions, shows the morphological features recognized as typical for the species. Such a test should also bring to light possible imperfections or too rigorous simplifications in the procedures applied in the model and show the way to improvements or additional research. If such tests do show that the model gives a realistic representation of the crop, more rigorous validation tests with independent field data sets have to be performed. At the present stage of the model, only the first type of testing can be done. Validation with field data will require further development of the model on such points as monopodial growth, variability of first sympodial position, and some other aspects which will show up in the following discussions.

In this first validation round, the present model will be shown to account for the following, well-documented, semi-quantitative growth phenomena. Some of these phenomena formed themselves part of the argument for the underlying morphogenetic template of the species, but they were never built directly into the model. For each one of them it will be indicated whether and to what extent they actually influenced the choice of simulation procedures employed by the model.

1. Cotton plants, whether grown as isolated plants or as a dense crop, show a typical succession of final leaf areas on the mainstem. These areas initially increase rather steeply with node number, to attain a maximum just above the first sympodium carrying node and decrease thereafter (Portsmouth, 1937; McKinion et al., 1975; Constable and Rawson, 1980<sup>b</sup>; Mutsaers, 1982<sup>b</sup>). The general occurrence of this phenomenon served as part of the argument for a stratification of assimilate supply and demand, which indirectly leads to a preferential access of a sympodium to the assimilates produced by the accompanying mainstem leaf.
2. Sympodial leaf areas and the area of the corresponding mainstem leaf are related. The ratio between the final area of a first sympodial leaf and the corresponding mainstem leaf ( $S_1/M$ ) is gener-



ally found to be between 0.5 and 0.6 (Horrocks, Kerby and Buxton, 1978; Constable and Rawson, 1980<sup>b</sup>; Mutsaers, 1982<sup>b</sup>). This relationship (in undisturbed plants) and the slight increase of  $S_1/M$  in partly pruned plants (Mutsaers, 1982<sup>b</sup>) led to the hypothesis of a fixed ratio of 0.75 between the size at initiation of a first sympodial and the corresponding mainstem leaf which was built into the model. The simulated ratio of final leaf areas is the combined outcome of this initial ratio and the assimilate allocation procedure operating during the long period between initiation and maturity of the leaves.

3. Under a constant temperature regime mainstem leaf unfolding proceeds at a constant rate at first, then slows down after a varying number of leaves, but always at a node far above the one which carries the largest mainstem leaf (Dale, 1959; Hearn, 1969<sup>b</sup>; Gutierrez et al., 1975; Mutsaers, 1982<sup>b</sup>). This decrease of unfolding rate can be, partly or wholly, counteracted by pruning of squares or sympodia (Dale, 1959; Mutsaers, 1982<sup>b</sup>). The model postulates a constant leaf initiation interval (at the apex) as long as the apex continues to increase in size. If the apex would shrink because of a reduced growth rate, mediated by assimilate shortage, the initiation interval is lengthened to avoid such shrinkage.

The non-coincidence of the node position of the largest leaf and the position where leaf unfolding rate starts decreasing, both in the model and in reality (Mutsaers, 1982<sup>b</sup>) was considered a strong argument for this hypothesis.

4. Field crops tend to show reduced boll set on the lower sympodia (e.g. Kerby and Buxton, 1981), which may be aggravated by vigorous vegetative development and/or a high population density (Anon., 1966; Brown, 1971; Johnson, Walhood and West, 1973; Hearn, 1975). Field observations on this phenomenon in Indonesian cotton actually formed the original motivation for the present work.

5. With increasing boll load, vegetative development including mainstem node production slows down and, in field crops, may eventually come to a complete standstill, called cut-out (e.g. Hearn, 1969<sup>b</sup>; McArthur, Hesketh and Baker, 1975; Mauney, 1979). Cultivars are very different as to their degree of cut-out which is even the criterion for the distinction between determinate and

indeterminate cultivar types. From the occurrence of cut-out and the fact that growing bolls are neither subject to shedding nor do they show much growth adaptability to changing substrate supply (Mutsaers, 1976<sup>a</sup>), it was concluded that growing bolls have absolute priority for assimilates.

6. As the load of growing bolls becomes heavier, the percentage of new fruiting points setting bolls decreases and shedding of squares and young bolls becomes heavier (e.g. Johnson and Addicot, 1967; Hearn, 1969<sup>b</sup>; Mauney, 1979). Cloudy spells often cause increased shedding of fruiting points a few days later (Goodman, 1955). These and similar observations (e.g. Guinn, 1974) form the basis for the "nutritional concept" on cotton fruit set regulation, which is also adopted in this model.

7. In field crops, planted at "normal" density (up to 10 plants per m<sup>2</sup>), bolls are practically only set at the first 3 sympodial positions, with 60-75% on the first position, 20-30% on the second and the remainder on the third position and on the monopodia (McNamara, Hooton and Porter, 1940; Munro, 1971; Mauney, 1979; Kerby and Buxton, 1981).

8. A crop which experiences light waterstress before the onset of flowering will respond with decreased vegetative development, better fruit set on the lower sympodia and a higher fruiting index, i.e. a better fruit-to-total top weight ratio (Miller and Grimes, 1967; Hearn, 1975).

The semi-quantitative phenomena, discussed above will be shown to be generated through the operation of the morphogenetic mechanisms incorporated in the model and their interaction with the environment. It has been made clear that some of them (1, 2, 3, 5, 6) actually formed part of the argument for important aspects of these mechanisms, particularly the stratification concept. The concepts derived from or supported by them however always operates at an explanatory level one step below that of the direct observations. The others (4, 7, 8) can be considered as fully independent and these represent a fairly severe test for the adequacy of the model procedures.

Simulation results will be presented for the growth of some

imaginary crops, with or without waterstress. In each run all environmental parameters are kept constant except calendar day and the corresponding potential radiation. They may however be varied at will, when simulating for actual conditions. The input data used in these runs are shown in table 4. The simulation results will be examined following the 8 points discussed at the beginning of this chapter. The central rôle, played by the allocation procedure for assimilates will be demonstrated by also presenting results obtained with the alternative allocation procedure which treats total assimilates produced as a common pool and assigns to each growing structure a share proportional to its demand. The numbers between parentheses in the following discussion refer back to the points mentioned above.

TABLE 4. Input data for simulation runs with (a) closely spaced plants under high irradiance and (b) widely spaced plants under low irradiance.

	a	b
row spacing (m)	-	1
row orientation	-	NS
plants per m <sup>2</sup>	1	10/20
latitude (°N lat)	12	12
day of unfolding 1st mainstem leaf	150	150
min. temperature (°C)	20	18
max. temperature (°C)	30	32
percentage overcast	80	20
RED <sub>ext</sub>	1.0	1.0/0.8

*Simulation for dense field crops.*

Fig. 8 shows simulated final areas of mainstem leaves for crops at a density of 10 plants/m<sup>2</sup> with or without fruiting points. The largest leaves in both cases are indeed encountered at node 6, just above the first sympodium carrying node (1). Absence of fruiting points has little influence on mainstem leaf areas but

total area on the sympodia at 120 days after sowing is about 50% greater with than without fruiting points. In both cases mainstem leaf unfolding slows down from around leaf number 17. (3)

The ratio between the final areas of the first leaf on a sympodial branch and the corresponding mainstem leaf ( $S_1/M$ ) fluctuates between 0.6 and 0.5 up to sympodium 9 (2) but decreases thereafter. This decrease will be explained below. These results, which are consistent with experimental data, are generated through the action of the allocation procedure for assimilates and its interaction with potential growth rates of the various tissues.

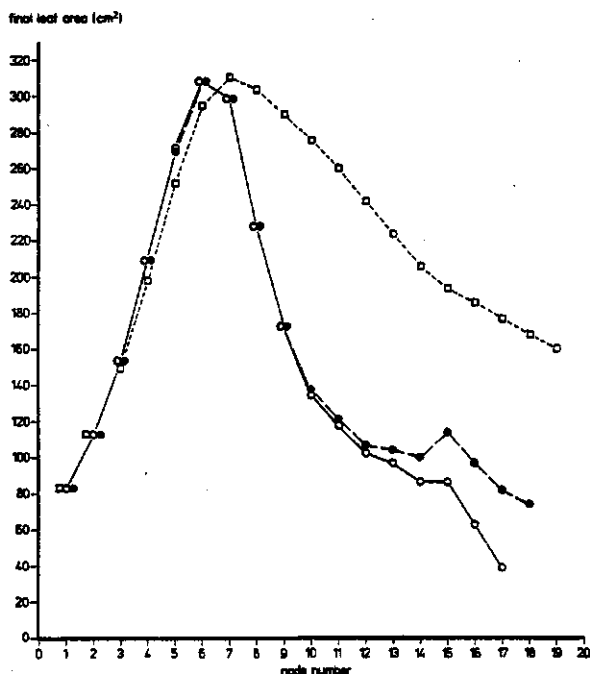


Fig. 8. Simulated final areas of mainstem leaves for crops with population density of 10 plants/m<sup>2</sup>; (O) with fruiting points; (●) without fruiting points; (□) with fruiting points and without stratification.

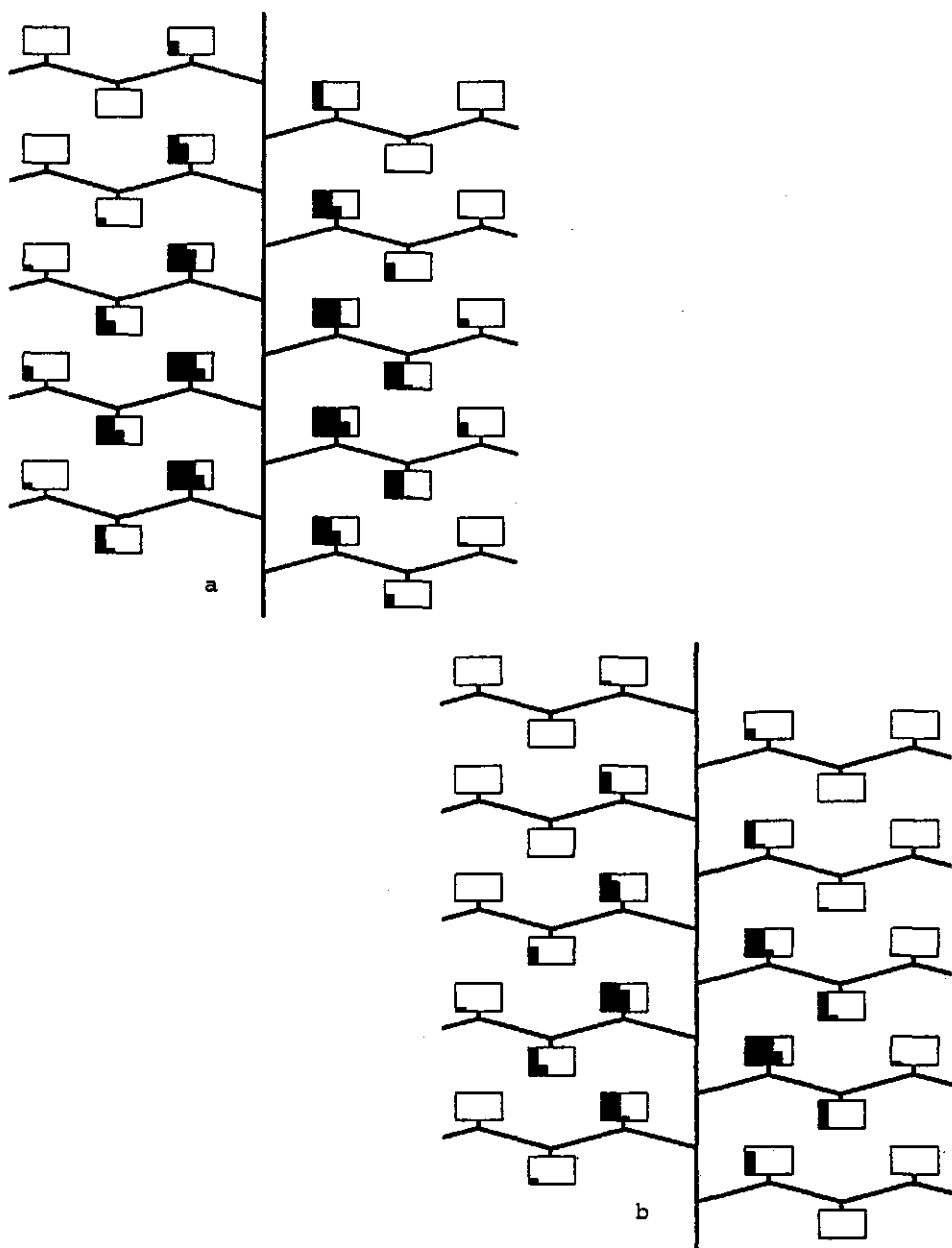


Fig. 9. Simulated fractions of fruit set (shaded areas) at the first 3 positions on the 10 lowest fruiting branches for crops with population density of (a) 10 plants/m<sup>2</sup>; (b) 20 plants/m<sup>2</sup>;

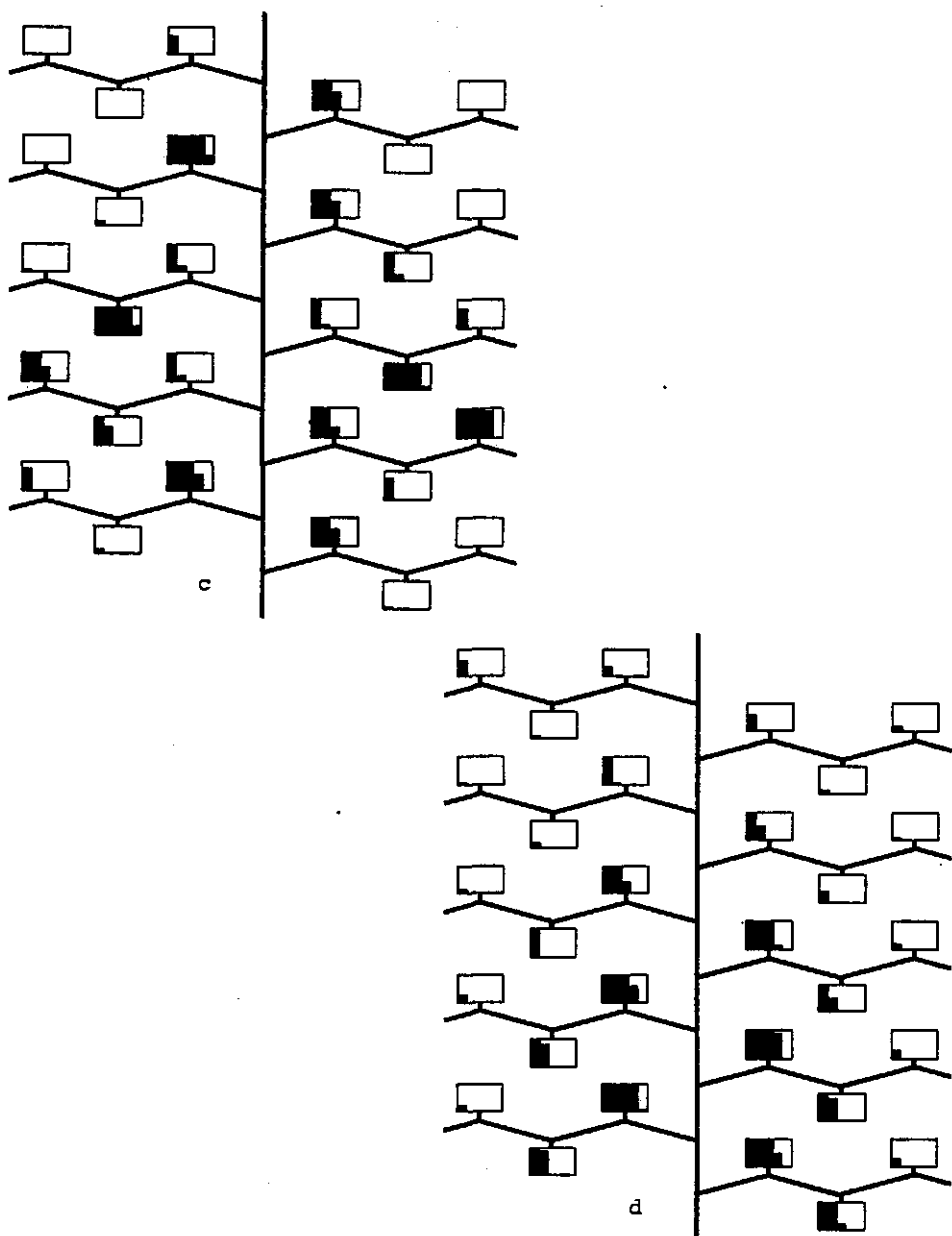


Fig. 9. Simulated fractions of fruit set (shaded areas) at the first 3 positions on the 10 lowest fruiting branches for crops with population density of (c) 10 plants/m<sup>2</sup>, with overcast weather between 72 and 78 days after sowing; (d) 10 plants/m<sup>2</sup>, with light permanent waterstress.

The simulated distribution of growing bolls at the first 10 sympodia at the start of boll opening, some 120 days after sowing, is shown in fig. 9a. All the important phenomena, associated with fruiting are present: 67% of all bolls are found on sympodial position 1, 29% on position 2 and only 4% on position 3; fruit set on higher positions is negligible (7); the percentage fruiting points shed increases with node number, both in a horizontal and a vertical direction. (6).

In field crops planted at 10 plants/m<sup>2</sup> there normally is still some monopodial growth. This will contribute to the early build up of internal shading, thereby intensifying the effect of reduced boll set on the lower sympodia. Increasing the population density has the same effect (4) and fig. 9b shows that this is correctly simulated as well.

Simulated vegetative growth and addition of new bolls practically stop at about a week before boll opening starts, through the dual effect of a heavy boll load and diminishing photosynthetic rate of the ageing leaves (5). After this cut-out, assimilate availability starts increasing again, due to diminishing demand from the growing bolls. The relative timing of these events compares well with published data (Bruce and Römken, 1965; Mauney, 1979).

An overcast spell of 6 days between 72 and 78 days after sowing was simulated by setting the parameter PERC<sub>ov</sub> (i.e. the overcast sky or day fraction, operating in PHOTO and CROPPH) at 0.6 instead of 0.2. This leads to increased shedding of fruiting points during that period, as may be seen from the altered distribution of growing and mature bolls after 120 days in fig. 9c as compared with fig. 9a (6).

Up to this point the simulated crop behaves very realistically. The reaction to renewed assimilate availability after cut-out however shows an anomaly in the behaviour of the model. In field crops some late boll set and some renewed vegetative growth take place after cut-out. In the model however vegetative growth at this stage responds with an appreciable time lag. Due to lack of competition from new vegetative tissue in the model, the fruiting points which come to the boll setting stage at that time are not shed. However, when this simulated late burst of fruit reaches its top demand, the photosynthetic activity of the crop has become insufficient to supply this.

# ERRATA

page 55, add:

CONSTABLE, G.A. and RAWSON, H.M., 1980<sup>b</sup>. Carbon Production and utilization in cotton: inferences from a carbon budget. *Austr. J. Plant Physiol.* 7, 539-53.

page 83, correct:

C ~~xxxx~~ R2XF1 REPRESENTS THE RGR OF A LOGISTIC WITH RATE PARAMETER R2.

ental aspect of the response of vegetative  
hortage which comes into play here. In the  
of vegetative tissue is reduced in response  
ut the advance of developmental age is left  
l load builds up, vegetative growth decreases  
mately grinds to a complete stop. Even then  
crementing developmental age of all initiated  
l and unfolded unhamperedly, which generates  
leaves of minute size in the top of the  
sponsive to renewed assimilate availability.  
alling ratio  $S_1/M$  after sympodium 9 as stated  
however a stock of leaf primordia appears to  
n case of severe assimilate stress (cf. Mauney,  
pable of growth and may build up a new demand  
model predicts. This potential growth stock  
and young bolls, thereby probably preventing a  
ng set. Besides, after cut-out, leaves of a  
t. In modelling terms this means, that the  
ricted advance of developmental age is too  
n in a situation of strong assimilate stress.  
i, operating in case of severe assimilate  
hat for waterstress: a slowing down of the  
al age, but less so than the reduction of  
owever be necessary to study in more detail  
mordia and their response to assimilate stress  
r this phenomenon.  
ive growth associated with high fertility and  
can at least partly be avoided by water  
y before flowering (e.g. Miller and Grimes,  
ch a restriction was simulated for a field  
vironmental conditions as used for the un-  
erstress parameter  $RED_{ext}$  was set at 0.8 to  
permanent waterstress. Fig. 9d shows the  
of growing bolls at 120 days after sowing.  
e lower sympodia has largely disappeared and  
120 days is 0.51 as compared with 0.38 for the  
these fruiting indices are in the right order



of magnitude for field crops (Hearn, 1969<sup>b</sup>; Hesketh, Lane, Alberte and Fox, 1975; Gutierrez et al., 1975). Incidentally, an increase of fruiting index as a result of waterstress is also predicted by the SIMCOT II model (Baker, Lambert and Jenkins, 1975).

An interesting point, not mentioned yet, is the well-known increase of shedding after release of waterstress through irrigation (Baker et al., 1979). When waterstress occurs the model accumulates some vegetative growth potential, due to the slowing down of physiological ageing, which was built into the model independent of this phenomenon (Mutsaers, 1979; 1982<sup>b</sup>). This accumulated growth potential is unchained by irrigation and an increased demand for assimilates results. In the model this increased demand correctly generates increased shedding shortly after stress release. Independently, Baker et al. (1979) decided to incorporate a similar mechanism into the SIMCOT II model, when this model in its original version predicted an increased boll set instead of increased shedding in response to stress release. In their case the mechanism of partial slowing down of physiological leaf ageing was also shown to be sufficient to generate a realistic response to stress release.

The essential part played in the model by the stratification concept can be demonstrated by examining simulation results obtained when all assimilates are treated as a common pool and assigned to each growing tissue in proportion to its demand. In order to pass judgement it is sufficient to look at the resulting final mainstem areas as shown in figs. 8 and 10. Although final area does decrease after a while, neither the extent of this decrease nor the position of the largest leaf are consistent with experimental data. Besides, the ratio between the final areas of sympodial and corresponding mainstem leaves decreases steadily from the start which is also at odds with reality.

#### *Simulation for widely spaced plants.*

In widely spaced crops mutual shading builds up much later and most cultivars respond to this lack of competition by a proliferation of secondary growth on the sympodia (Mauney, 1979). This effect is intensified by removal of the squares or part of the sympodia (Mutsaers, 1982<sup>b</sup>). The model does not have a provision as yet to

account for such secondary growth and this simplification is bound to show up in the simulation results for widely spaced plants. That this is indeed the case is shown in fig. 10 which presents final mainstem leaf areas for undisturbed plants and for plants with all squares removed. The pattern of change with node number is correctly generated for undisturbed plants up to leaf 10 but between leaf 10 and 15 a plateau shows up which did not occur in the experiments (see fig. 11 in Mutsaers, 1982<sup>b</sup>). With all squares removed, the model even simulates a slight increase of final areas between nodes 10 and 15 and a slow decrease thereafter. In real plants assimilate surplusses at a stratum induce the development of secondary buds, thereby leaving less to the mainstem apex than in the model.

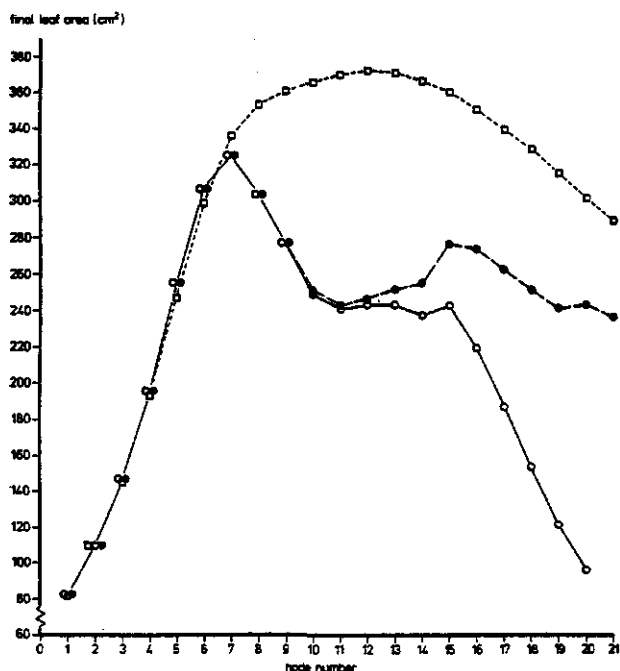


Fig. 10. Simulated final areas of mainstem leaves for crops with population density of 1 plant/m<sup>2</sup>; (O) with fruiting points; (●) without fruiting points; (□) with fruiting points and without stratification.

Although secondary growth is much reduced in dense field crops, due to more rapid build up of competition, such growth may be triggered by insect infestation, which adds to the species' potential for recovery from insect damage. Besides, there are indications that proliferation of secondary growth may become an important feature in newer, early maturing cultivars (Mauney, 1979). Ultimately, in order to obtain reliable simulation results for a wide range of conditions, it will therefore be necessary to include procedures in the model to generate secondary growth.

One property of the model, which adds a general argument to the detailed ones presented before has not been mentioned yet. In all growth stages simulated potential crop growth never exceeds actual growth by more than 25%. This means that at any moment the crop's growth potential does not much exceed the limits dictated by assimilate availability. Suddenly increased substrate supply can therefore not lead to a sudden growth explosion but produces a gradual increase until a new semi-equilibrium between potential growth and assimilate availability is attained at a higher level. This of course is the way real plants behave.

## CONCLUDING REMARKS

It has been argued in the introduction that successful growth simulation for any crop will depend on the adequate representation of the innate morphogenetic pattern of the species, which under a wide range of conditions results in a plant recognizably a representative of its species. The simulation model presented here demonstrates the feasibility of such an approach: it has the capability to generate a great number of well known and essential growth features of cotton observed both in the field and the laboratory, doing justice to the great variability of the crop within the limits of the basic pattern.

Stratification of assimilate production and demand was shown to play a central rôle in the model procedures: it has a great influence on the simulated distribution of leaf sizes and on the boll setting pattern in the crop. There is a large amount of experimental data on the fate of assimilates from different sources, which show that the distance travelled in the plant by assimilates is limited for the most part (e.g. Ashley, 1972; Brown, 1973). It is tempting to use this kind of experimental results as an argument for the stratification concept. This was not done, since it is not considered a valid argument: even without any priority for assimilate allocation a growing tissue would receive most of its assimilates from nearby sources through a simple redistribution mechanism. The experimental arguments that were used were based on simple pruning experiments, which show that nothing but complete removal of the sympodia can annihilate the priority of these branches over the mainstem apex (Mutsaers, 1982<sup>b</sup>). In any case, deleting the stratification concept from the model procedures completely ruins the simulation. This of course is not a real proof for its validity, but the faithful generation of a great number of well-known growth phenomena when the concept is included at least gives strong support to the idea that the plant operates along these lines.

In order to simulate growth over the whole imaginable range of conditions it will be necessary in the future to include monopodial growth and growth from secondary and higher order buds on the sympodia. This, and the modification of too simple a representation of vegetative growth under strong assimilate stress are the most immediate lines for further development of the model.

## SUMMARY

A whole crop model for growth and development of cotton (*Gossypium hirsutum* L.) is presented. The model is based on previous extensive studies on plant morphogenesis, growth of fruits and canopy photosynthesis. The crop model basically is a carbohydrate budget, but all processes are regulated by an underlying morphogenetic template, derived from the previous studies on plant morphogenesis. A cotton crop is considered as a set of partly autonomous, interacting strata, each consisting of a mainstem leaf and the adjoining sympodial branch, with their associated stem (and root) tissue. Growth of fruits and maintenance respiration have absolute priority for the allocation of assimilates but vegetative growth and growth of squares in any stratum depend to a large extent on the assimilates produced in that stratum. This stratification concept, together with the potential growth rates of all tissues in dependence of their developmental age and assimilate production, calculated for each stratum separately are the core of the simulation procedures. The crop model is shown to accurately generate a large number of well-documented semi-quantitative growth phenomena of cotton. Some lines for further research and development of the model are indicated.

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## SAMENVATTING

Het onderzoek waarvan deze dissertatie het verslag vormt, betreft de ontwikkeling van een simulatie model voor groei en ontwikkeling van katoen (*Gossypium hirsutum* L.). In de inleiding wordt een kort historisch overzicht geschetst van elders ondernomen pogingen om tot een integrale groeibesrijving van o.a. katoen te komen, waarbij in toenemende mate gebruik gemaakt werd van computer simulatie technieken. De tot nog toe ontwikkelde meer universele modellen voor katoen, d.w.z. modellen die in principe in staat zouden moeten zijn de groei onder uiteenlopende omstandigheden te voorspellen, blijken nogal onbetrouwbare resultaten op te leveren indien ze worden toegepast voor andere omstandigheden dan die waarvoor het model oorspronkelijk was ontwikkeld. De belangrijkste oorzaak hiervan is dat deze modellen het onderliggende, genetisch vastgelegde groeipatroon van de soort te weinig in rekening brengen.

Het doel van het hier beschreven onderzoek was het construeren van een nieuw groeimodel voor katoen waarbij de groeiverschijnselen van de plant mede worden gereguleerd door dit genetisch vastgelegde grondpatroon, met als resultaat een onder uiteenlopende omstandigheden herkenbaar katoengewas, met tevens de grote flexibiliteit die binnen de beperking van dit patroon mogelijk is.

Na een korte beschrijving van de katoenplant worden de resultaten samengevat van het voorbereidende onderzoek dat was gericht op het analyseren van de groei van vruchten en bladeren en de gewas-fotosynthese van de katoen onder uiteenlopende omstandigheden. De resultaten van dit onderzoek werden afzonderlijk gepubliceerd (zie annex II). Op grond van deze resultaten werden deelmodellen opgesteld die belangrijke schakels vormen in het hier beschreven integrale groeimodel.

In het tweede hoofdstuk wordt een overzicht gegeven van de opbouw en de interne organisatie van het model. Een katoengewas wordt beschouwd als een verzameling van gedeeltelijk autonome lagen, elk bestaande uit een hoofdstengel segment met één blad en de bijbehorende generatieve tak (sympodium). Het model wordt gestuurd door

een hoofdprogramma, dat met tijdstappen van één dag de verschillende routines aanroept welke de detailprocessen in het gewas berekenen. De eerste stap in de dagelijkse berekeningen is het bepalen van de assimilaten produktie in de verschillende gewaslagen. Vervolgens wordt de potentiële groei van alle bladeren, bloemknoppen, vruchten, stengels en wortels berekend, benevens de onderhoudsademhaling.

Op een bepaald moment in de gewasontwikkeling wordt de assimilaten produktie ontoereikend om potentiële gewasgroei mogelijk te maken. Vanaf dat moment treedt een regelingsmechanisme in werking dat de groei afstemt op de beschikbaarheid van assimilaten. Vruchtgroei en onderhoudsademhaling hebben daarbij absolute prioriteit. Bij de toewijzing van de resterende assimilaten geniet elke gewaslaag een gedeeltelijke voorkeur voor de assimilaten welke in diezelfde laag geproduceerd zijn. De hoeveelheid werkelijke groei wordt dan voor elke laag berekend in afhankelijkheid van het assimilatenaanbod.

Nadat op deze wijze de werkelijke groei is vastgesteld treedt een routine in werking die nieuwe bladeren, zijtakken en bloemknoppen aanlegt, deels in afhankelijkheid van niet-variabele plant parameters, deels in afhankelijkheid van de werkelijke groei. Vervolgens keert het programma terug naar het begin en start een nieuwe simulatie-cyclus voor de volgende dag.

In het derde hoofdstuk worden technische details van de verschillende routines behandeld, waarbij tevens een aantal niet eerder behandelde morfogenetische verschijnselen, o.a. de stengelgroei in relatie tot de bladgroei, wordt geanalyseerd en ingebouwd in het model.

In het vierde hoofdstuk wordt de gesimuleerde gewasgroei vergeleken met de werkelijke groei van katoen. Aan het begin van het hoofdstuk wordt een groot aantal typische groeiverschijnselen van katoen besproken, die door een goed groeimodel gegenereerd dienen te worden. Deze verschijnselen betreffen vooral de verdeling van bladgroottes en de vruchtbezettingsgraad op verschillende plaatsten in het gewas en de invloed daarop van groeiomstandigheden zoals plantdichtheid, straling en vochtvoorziening. Met sommige van deze verschijnselen werd weliswaar rekening gehouden bij het afleiden van het morfogenetisch basispatroon, doch steeds indirect: ze vormden mede een argument voor dieper liggende mechanismen, die deze ver-

schijnselen zelf kunnen opleveren, maar werden niet als zodanig in het model ingebouwd. Een deel van de besproken verschijnselen werd niet eerder in beschouwing genomen en vormt een onafhankelijke toetssteen voor de kwaliteit van het model. Het model blijkt in staat te zijn zowel de "afhankelijke" als de "onafhankelijke" aspecten van de groei zonder uitzondering te genereren.

Wel blijken uit de simulatieresultaten enige onvolkomenheden van het model, die te wijten zijn aan een te sterke vereenvoudiging van de reactie van de bladgroei op extreme assimilaten tekorten, zoals die optreden wanneer de vruchtzetting van het gewas zijn top bereikt. Voor het (modeltechnisch eenvoudige) verhelpen van deze onvolkomenheden zijn aanvullende experimentele gegevens nodig betreffende de reactie van de bladgroei op zulke extreme omstandigheden.

Het is echter duidelijk, dat dit groeimodel dat recht doet aan het morfogenetische basispatroon als regulerend mechanisme voor de assimilatenstroom, de vertakking, de aanleg van groeipunten en bloemknoppen etcetera, in staat is om betrouwbare voorspellingen van de gewasgroei op te leveren.

## **ANNEX I**

**Listing, relation matrix and legend of the fortran simulation program**

LISTING OF COTTON SIMULATION PROGRAM "KUTUN"  
=====

COMMON STATEMENTS  
=====

-----  
THE FOLLOWING SET OF COMMON BLOCKS HAS TO BE PLACED AT THE HEAD  
OF THE MAIN PROGRAM AND ALL SUBROUTINES WITH THE EXCEPTION OF LEAF  
AND BOLL. LEAF AND BOLL ARE PRECEDED ONLY BY THE COMMON BLOCK:  
COMMON/RATE/RATEV, ----ETC.  
-----

COMMON/PARAM/PI, RAD, A1, A2, A3, A4, ALAT, PLM2, ROW, RAZ, CO2, TMIN, TMAX  
COMMON/GEOMTR/RCG, RCGC, RCGO, ALAIT, ALAIDL, ALAI, SL  
COMMON/TIME/DAY, DEC, FYSDA, REALDA, SLI, SLIS(30), FYSAGE(0/30),  
1FYSAGS(10,26), FINTIM  
COMMON/LITE1/DAYL, DAYLE, DRC, DIFCLT, SUNDCT, PERCOV, SUNDCL(24),  
1DIFCL(24), HSUN(24), REDLI, PNREL(0/21), SLWMAX(0/26)  
COMMON/LITE2/CONTR(9), DKV(0/19), TRANS(24), EDIFV(0/12), EFRIV(0/12)  
COMMON/FOTO/PNC(0/12), PNO(0/12), RD(0/12)  
COMMON/RATE/RATEV, RATEVD, RATEG, R1, R2, BLI, RLIS, BMP, REDEXT, REDTIM,  
1RGRM(0/30), RGRS(10,26)  
COMMON/LEAV/NRLM, NRLS(30), AIO, AREAM(0/30), ARDLTM(0/30),  
1AREAS(10,26), ARDLTS(10,26), LOWSYM  
COMMON/WEIGHT/SLWM(0/30), WLDLTM(0/30), WLTM(0/30), SLWS(10,26),  
1WLDLTS(10,26), WLTS(10,26), WSDLTM(0/30), WSTM(0/30), WSDLTS(10,26),  
2WSTS(10,26), WRDLTM(0/30), WRTM(0/30), WRDLTS(10,26), WRTS(10,26)  
COMMON/BOLLS/BNR(5,26), WB(5,26), WBDLT(5,26), FYSAGB(5,26)  
COMMON/PRODEM/PROD(0/30), ASDEM(0/30), ASDEMG(26), PRODT, ASSDV,  
1ASSDG, RSFMNT

PROGRAM KUTUN

```

C-----C
C      MAIN PROGRAM, OPENS INPUT FILES, READS PLANT, CROP AND ENVIRON-  C
C      MENTAL PARAMETERS, ADVANCES DAYS AND CALLS SUBROUTINES.        C
C      THE UNIT OF TIME IS 1 DAY, THE UNIT OF CROP AREA IS 1 M2.        C
C      FOR INSTANCE: AN INCREASE OF LEAF AREA FOR MAINSTEM LEAF K      C
C      (ARDLTM(K)) BY X M2 MEANS THAT THE TOTAL AREA OF THE LEAVES     C
C      ON NODE K OF THE MAINSTEM OF THE PLANTS OCCUPYING 1 M2 GROUND-   C
C      AREA (PLM2) INCREASES BY X M2.                                    C
C-----C
      OPEN(UNIT=1, ACCESS='SEQIN', FILE='PARAM.DAT')
      OPEN(UNIT=20, ACCESS='SEQIN', FILE='ENVIRM.DAT')
50     READ(1,100,END=40) R1,R2,BLI,RLIS,BMP,AREAM(1),A1,A2,A3,A4,LOWSYM
      READ(1,101,END=40) ALAT,DAY,PLM2,ROW,RAZ,CO2,FINTIM,IPRINT
      PRINT 102,ALAT,PLM2,ROW,RAZ
100    FORMAT(5F,5E,1)
101    FORMAT(7F,1)

```

```

102  FORMAT(1H-.30X,'RUN OF THE SIMULATION PROGRAM KUTUN FOR A
1  COTTON CROP'/31X,53('='))//31X,'LATITUDE : ',F5.1,' DEGREES NL
2;' /31X,27('-')/31X,'DENSITY : ',F4.0,' PLANTS PER M2;ROW DIS
3TANCE : ',F4.2,' M;/31X,54('-')/31X,'ROW ORIENTATION : ',F4.0,
4' DEGREES RELATIVE TO THE NORTH-SOUTH DIRECTION.'/31X,
571('-')/)
CALL INITIA
1  DO 21 J=1,IPRINT

C  -----
C  STATIC PROGRAM SECTION.READS 6 DAY MEAN VALUES FOR ENVIRON-
C  MENTAL PARAMETERS AND CALLS SUBROUTINES PHOTO AND LITEMP
C  ONCE EVERY 6 DAYS.
C  -----

JJ=J
IF(SLI+6./BLI.LT.5.) GO TO 6
24  READ(20,101,END=25) TMIN,TMAX,PERCOV,REDEXT
GO TO 30
25  BACKSPACE 20
GO TO 24
30  DAY=DAY+6.

C  **** SLI IS INITIATED BY INITIA AND INCREMENTED BY APEX;BLI AND DAY
C  **** ARE READ FROM THE DATA FILE.

CALL LITEMP
CALL PHOTO

C  -----
C  DYNAMIC PROGRAM SECTION.CALCULATES DAILY INCREMENT OF DEVELOP-
C  MENTAL AGE (REDTIM) IN DEPENDENCE OF VEGETATIVE DEVELOPMENT
C  RATE (RATEV) AND WATERSTRESS (REPRESENTED BY REDEXT);CALLS
C  DYNAMIC SUBROUTINES EACH DAY.
C  -----

6  DO 20 I=1,6
IF(SLI.LT.5.) REDEXT=1.
REDTIM=RATEV*(.2+.8*REDEXT)
IF(SLI+REDTIM/BLI.LT.5.) GO TO 5
CALL CROPPH
5  CALL CANOPY
CALL BALANS
CALL APEX
IF(REALDA.GT.FINTIM) GO TO 50
REALDA=REALDA+1.
20  FYSDA=FYSDA+REDTIM
21  CALL STATE(JJ,IPRINT)

C  **** IF JJ EQUALS IPRINT, SUBROUTINE STATE OUTPUTS DETAILED INFORMATION
C  **** ON THE CROP STATUS, INCLUDING LEAF AREAS, RGR'S, SLW'S, BOLL NUMBERS
C  **** AND WEIGHTS FOR EACH POSITION ETC.; OTHERWISE ONLY A SUMMARY OF
C  **** DATA IS OUTPUT.

GO TO 1
40  STOP 1000
END

```



# SUBROUTINE INITIA

```

C-----C
C      CALCULATES RELATIVE TRANSMISSION OF DIFFUSE LIGHT TO 12 CANOPY C
C      LEVELS(EDIFV);ASSIGNS INITIAL VALUES TO VARIOUS VARIABLES AND C
C      ARRAYS. C
C-----C
      DATA(DKV(I),I=0,18)/3.2069,3.2069,2.2311,1.2552,1.0260,.9268,
      1.8610,.8159,.7928,.7716,.7623,.7530,.7488,.7445,.7426,.7404,
      2.7394,.7384,.7384/
      DATA(CONTR(I),I=1,9)/.030,.087,.133,.163,.174,.163,.133,
      1.087,.030/
      DATA NRLM/1/,RATEV/1./,RATEG/1./,PI/3.1415927/,SL/.01/,
      1FYSDA/.0/,REALDA/.0/,SLI/1./,SLWMAX(0)/65./,RCGC/.1/,RCGO/.1/
      DATA(PNREL(I),I=0,20)/.0,.14,.225,.3,.37,.42,.48,.535,.585,.63,
      1.675,.72,.765,.805,.84,.875,.91,.94,.96,.98,1./
      RAD=PI/180.
      DAY=DAY-3.
      EDIFV(0)=1.
      DO 3 I=1,12
3      EDIFV(I)=.0
      DO 2 I=1,9
      DO 2 J=1,12
2      EDIFV(J)=EDIFV(J)+CONTR(I)*EXP(-DKV(2*I-1)*(FLOAT(J)-.5)/2.)
      AREAM(1)=PLM2*AREAM(1)
      AIO=AREAM(1)
      AREAM(0)=3.133E+03*AREAM(1)

C      **** THE FACTOR 3.133E+03 ACCOUNTS FOR THE DEVELOPMENTAL AGE DIFFER-
C      **** ENCE BETWEEN COTYLEDONS (AREAM(0)) AND FIRST TRUE LEAF
C      **** (AREAM(1)) IN THE SEED AND CAUSES THE FIRST LEAF TO ATTAIN A
C      **** FINAL AREA,1.7 TIMES LARGER THAN THE COTYLEDONS TOGETHER
C      **** IN CASE OF UNRESTRICTED GROWTH.

      AREAM(2)=A1*AREAM(1)
      DO 4 I=0,30
      WSTM(I)=.0
      SLWM(I)=30.
      RGRM(I)=R1
      FYSAGE(I)=.0
4      PROD(I)=.0
      DO 8 I=1,26
      NRLS(I)=0
      SLIS(I)=.0
      DO 8 J=1,10
      WSTS(J,I)=.0
      SLWS(J,I)=30.
      RGRS(J,I)=R1
      FYSAGS(J,I)=.0
      IF(J.GT.5) GO TO 8
      FYSAGB(J,I)=.0
      BNR(J,I)=PLM2
8      CONTINUE

```

```

FYSAGE(0)=4.*BLI
WSTM(0)=1.251E+07*AREAM(1)
WRTM(0)=6.83*WSTM(0)

C **** THE FACTORS 1.251E+07 AND 6.83 GENERATE A DRY MATTER DISTRIBUTION
C **** BETWEEN LEAVES,STEMS AND ROOTS (IN CASE OF UNRESTRICTED GROWTH),
C **** AS REPORTED BY HUXLEY(1964) FOR A PLANT JUST AFTER UNFOLDING
C **** OF ITS FIRST TRUE LEAF.

RETURN
END

```

```

SUBROUTINE LITEMP
-----C
C      CALCULATES TEMPERATURE AND RADIATION PARAMETERS.      C
C-----C

  DIMENSION FRDIF(0/19),TEMP(48),RRATEV(40),RRATEG(40)
  DATA(FRDIF(I),I=0,18)/1.,1.,.6615,.323,.271,.219,.1975,
  1.176,.168,.16,.1525,.145,.1405,.136,.1354,.1348,.1342,
  2.1336,.133/
  DATA(RRATEV(I),I=13,40)/.09,.18,.27,.36,.45,.53,.61,.68,.74,
  1.80,.86,.93,1.,1.08,1.16,1.25,1.35,1.44,1.52,1.58,1.62,1.64,
  21.65,1.65,1.62,1.50,1.13,.00/
  DATA(RRATEG(I),I=13,40)/.12,.22,.31,.38,.45,.51,.58,.63,.69,
  1.76,.83,.91,1.,1.1,1.2,1.32,1.44,1.52,1.56,1.58,1.58,1.59,
  21.59,1.59,1.59,1.58,1.57,1.55/
  SOLC=640.

C      -----
C      CALCULATES DAYLENGTH (DAYL) IN DEPENDENCE OF LATITUDE AND DAY.
C      CALCULATES DAILY TEMPERATURE COURSE (TEMP) FROM TWO SINOIDS
C      BETWEEN THE MAX. AND MIN. TEMPERATURE (READ FROM THE DATA FILE)
C      AND TAKING DAYLENGTH INTO ACCOUNT.
C      -----

  DEC=-23.45*COS(2.*PI*(DAY+10.)/365.)*RAD
  SSIN=SIN(DEC)*SIN(RAD*ALAT)
  CCOS=COS(DEC)*COS(RAD*ALAT)
  DAYL=12.*(PI+2.*ASIN(SSIN/CCOS))/PI
  HSRISE=(24.-DAYL)/2.
  AMPL=(TMAX-TMIN)/2.
  DO 20 I=1,48
    HOUR=FLOAT(I)/2.
    IF(HOUR.GE.HSRISE.AND.HOUR.LT.14.) GO TO 5
    IF(HOUR.LT.HSRISE) HOUR=HOUR+24.
    TEMP(I)=TMIN+AMPL*(1.+SIN((HOUR-14.)*PI/(HSRISE+10.))+PI/2.))
    GO TO 20
  5  TEMP(I)=TMIN+AMPL*(1.+SIN((HOUR-HSRISE)*PI/(14.-HSRISE)-PI/2.))
  20  CONTINUE

```

```

C -----
C CALCULATES DAYTIME (RATEVD) AND 24 HRS (RATEV) VEGETATIVE
C DEVELOPMENT RATE AND 24 HRS GENERATIVE DEVELOPMENT RATE (RATEG).
C -----

RATEV=.0
RATEVD=.0
RATEG=.0
DO 1 I=1,12
RRATEV(I)=.0
1 RRATEG(I)=.0
DO 2 I=1,48
II=INT(TEMP(I))
XX=RRATEV(II)+(RRATEV(II+1)-RRATEV(II))*(TEMP(I)-FLOAT(II))
YY=RRATEG(II)+(RRATEG(II+1)-RRATEG(II))*(TEMP(I)-FLOAT(II))

C ***** THIS INTERPOLATION PROCEDURE IS EQUIVALENT TO THE CSMP PROCEDURE
C ***** XX=AFGEN(RRATEV,TEMP)

IF(FLOAT(I).LE.24.-DAYL+.5.OR.FLOAT(I).GE.24.+DAYL)GO TO 7
RATEVD=RATEVD+XX/AINT(DAYL*2.)
7 RATEV=RATEV+XX/48.
2 RATEG=RATEG+YY/48.

C -----
C CALCULATES SUNANGLES (HSUN) AND DIRECT(SUNDCL) AND DIFFUSE
C (DIFCL) RADIATION FOR SUCCESSIVE HOURS ON A CLEAR DAY AND TOTAL
C DIRECT LIGHT TRANSMITTED TO SUCCESSIVE CANOPY LAYERS(EFRIV),
C TO BE USED BY ROWEFF;CALCULATES CORRECTED DAYLENGYH(DAYLE)
C AND TOTAL DAILY RADIATION ON A CLEAR DAY(DRC) WITH TIME-
C STEPS OF 15 MIN.,TO BE USED BY PHOTO.MAINLY BASED ON
C GOUDRIAAN AND VAN LAAR(1978)
C -----

DAYLE=43200.*(PI+2.*ASIN((-SIN(8.*RAD)+SSIN)/CCOS))/PI
SUNDCT=.0
DIFCLT=.0
EFRIV(0)=1.
DO 30 I=1,11
30 EFRIV(I)=.0
DRC=.0
DO 10 J=0,23
DO 10 K=1,4
HSUN(J+1)=.0
I=4*J+K
HOUR=FLOAT(I)/4.
SNHSS=SSIN+CCOS*COS(RAD*(HOUR+12.)*15.)
IF(SNHSS.LE..001) GO TO 10
HSUN(J+1)=ASIN(SNHSS)
DSUN=HSUN(J+1)/RAD
IH=INT(DSUN/5.)
FFRDIF=FRDIF(IH)+(FRDIF(IH+1)-FRDIF(IH))*(DSUN/5.-FLOAT(IH))
TRAT=EXP(-.1/SNHSS)
SUNDCL(J+1)=SOLC*SNHSS*(1.-FFRDIF)*TRAT*900.
DIFCL(J+1)=SOLC*SNHSS*FFRDIF*TRAT*900.
DRC=DRC+SUNDCL(J+1)+DIFCL(J+1)
IF(K.NE.4) GO TO 10

```

```

TRANS(J+1)=DKV(IH)+(DKV(IH+1)-DKV(IH))*(DSUN/5.-FLOAT(IH))
SUNDCT=SUNDCT+SUNDCL(J+1)*4.
DIFCLT=DIFCLT+DIFCL(J+1)*4.
DO 10 L=1,11
  EFRIV(L)=EFRIV(L)+SUNDCL(J+1)*4.*EXP(-TRANS(J+1)*
1 (FLOAT(L)-.5)/2.)
  CONTINUE
RETURN
END

```

# SUBROUTINE PHOTO

```

C-----C
C CALCULATES DAILY NET PHOTOSYNTHESIS AND DARK RESPIRATION C
C BY LAYERS OF .5 LAI AT CLEAR AND OVERCAST SKY FOR A CLOSED C
C CANOPY(MUTSAERS,1982 A). C
C-----C

```

```

C-----C
C CALCULATES PHOTOSYNTHETIC EFFICIENCY (EFFE);A REDUCTION FACTOR C
C (REDLI) OPERATING ON PNMAX IN CASE OF DAILY INCIDENT RADIATION C
C BELOW A THRESHOLD (8.0E+06 JM-2DAY-1);MEAN HOURLY INCIDENT C
C RADIATION (RADC) AND MAX. NET PHOTOS. AS A FUNCTION OF CO2 C
C AND WATERSTRESS (PNMAX),ALL FOR SINGLE LEAVES. C
C-----C

```

```

EFFE=(15.+2.35E-02*(CO2-300.))*85E-06
REDLI=DRC*(1.-.8*PERCOV)/8.E+06
RADC=DRC/DAYLE
PNMAX=(CO2-65.)/(300.-65.)*.5*(1.+REDEXT)*1.2E-03

```

```

C-----C
C CALCULATES DAILY PAR RECEIVED AT SUCCESSIVE LAYERS AS PERCENT- C
C TAGE OF THRESHOLD (PER) AND CORRESPONDING MAX.GROSS C
C PHOTOS. (AMAX) AS THE SUM OF NET PHOTOS. AND DAYTIME DARK C
C RESPIRATION. C
C-----C

```

```

PERO1=AMIN1(100.*EXP(-.25*.806)*REDLI,99.9999)
PERO5=100.*EXP(-2.25*.806)*REDLI
PER10=100.*EXP(-4.75*.806)*REDLI

```

```

C **** .806 STANDS FOR EXTINCTION COEFFICIENT OF DAILY PAR.
C **** .25,2.25 AND 4.75 STAND FOR LAI OVERHEAD.

```

```

IO1=INT(PERO1/5.)
IO5=INT(PERO5/5.)
I10=INT(PER10/5.)
AMAXO1=((1.+0.347*RATEVD)*PNMAX*(PNREL(IO1)+(PNREL(IO1+1)-
1PNREL(IO1))*(PERO1/5.-FLOAT(IO1)))+12.5E-06*RATEVD)
AMAXO5=((1.+0.347*RATEVD)*PNMAX*(PNREL(IO5)+(PNREL(IO5+1)-
1PNREL(IO5))*(PERO5/5.-FLOAT(IO5)))+12.5E-06*RATEVD)
AMAX10=((1.+0.347*RATEVD)*PNMAX*(PNREL(I10)+(PNREL(I10+1)-
1PNREL(I10))*(PER10/5.-FLOAT(I10)))+12.5E-06*RATEVD)

```

```

C **** THE QUANTITY .0347*PNMAX+12.5E-06 REPRESENTS DARK RESPIRATION
C **** AT 25C CONSTANT TEMPERATURE.MULTIPLICATION BY DAYTIME DEVELOP-
C **** MENT RATE (RATEVD) YIELDS ACTUAL DARK RESPIRATION.

```

```

C -----
C ESTIMATES GROSS PHOTOS. FOR 3 LAYERS USING CORRECTIONS TO
C COUNTERACT SOME SIMPLIFYING ASSUMPTIONS.
C -----

RED10=.5-(1.-SIN(PI*.5+DEC-ALAT*RAD))*1
REDO5=1.-RED10*1.0000000001
XCO1=EFFE*RADC/AMAXO1
XCO5=REDO5*EFFE*EXP(-.806*2.25)*RADC/AMAXO5
XC10=RED10*EFFE*EXP(-.806*4.75)*RADC/AMAX10
XOO1=.2*XCO1
XOO5=.2/REDO5*XCO5
XO10=.2/RED10*XC10
GPCO1=.5*DAYLE*AMAXO1*XCO1/(XCO1+1.)
GPCO5=.5*DAYLE*AMAXO5*XCO5/(XCO5+1.)
GPC10=.5*DAYLE*AMAX10*XC10/(XC10+1.)*(1.+(108.7E-06-AMAX10)*
14.5E+02)
GPOO1=.5*DAYLE*AMAXO1*XOO1/(XOO1+1.)*(1.+(1189.2E-06-AMAXO1)*
11.2E+02)
GPOO5=.5*DAYLE*AMAXO5*XOO5/(XOO5+1.)*(1.+(510.4E-06-AMAXO5)*
11.5E+02)
GPO10=.5*DAYLE*AMAX10*XO10/(XO10+1.)*(1.+(108.7E-06-AMAX10)*
14.3E+02)

C ***** THE TERMS (1.+(108.7E-06-AMAX10)*4.5E+02) ETC. CORRECT FOR A
C ***** SLIGHT BUT SYSTEMATIC DEVIATION OF THE FIRST PARTS OF THESE
C ***** EXPRESSIONS FROM THE CROPPHOT RESULTS. (SEE BELOW)

C -----
C LINEAR REGRESSION OF THE "EXACT" RESULTS CALCULATED BY
C CROPPHOT (GOUDRIAAN AND VAN LAAR, 1978) ON RESULTS AS CALCULATED
C ABOVE. (LOGARITHMS ARE TAKEN FOR CONVENIENCE IN FOLLOWING
C SECTIONS).
C -----

GPCO1=ALOG(.44164+1.00495*GPCO1)
GPCO5=ALOG(-.074295+1.01904*GPCO5)
GPC10=ALOG(.010734+1.019087*GPC10)
GPOO1=ALOG(-.65003+1.037088*GPOO1)
GPOO5=ALOG(-.074855+1.058391*GPOO5)
GPO10=ALOG(-.007224+1.014189*GPO10)

C -----
C CALCULATES DARK RESPIRATION PER LAYER (RD).
C -----

DO 20 I=0,12
FI=FLOAT(I)
PER=AMIN1(100.*EXP(-(FI*.5-.25)*.806)*REDLI,99.999999)
IO=INT(PER/5.)
IF(I.EQ.0) PER=AMIN1(100.*REDLI,99.999999)
RD(I)=(.5*.0347*PNMAX*(PNREL(IO)+(PNREL(IO+1)-PNREL(IO))*
1(PER/5.-FLOAT(IO)))+12.5E-06)*RATEV*86400.
20

```



```

1      SL=SL+SLDLT
      RCGC=AMAX1(.99,RCGC)
      RCGO=AMAX1(.99,RCGO)
      IF(ALAI.LT..25.OR.ALAIT.GE.5..OR.(RCGC.GE.1..AND.
1      1RCGO.GE.1.)) GO TO 3
      KK=INT(4.*ALAIT)
      LL=INT(ROW*3.+51)
      RCG=FROW(KK,LL)+(FROW(KK+1,LL)-FROW(KK,LL))*(4.*ALAIT-
1      1FLOAT(KK))
      CALL ROWEFF

C      -----
C      CALCULATES MAX. SPECIFIC LEAF WEIGHT (SLWMAX) FOR MAINSTEM
C      LEAVES IN RELATION TO AVERAGE DAILY INCIDENT RADIATION.THE
C      SAME RELATIONSHIP IS USED AS FOR DEPENDENCE OF MAX. NET
C      PHOTOS. ON AVERAGE DAILY INCIDENT RADIATION (SEE PHOTO).
C      -----

3      PER=AMIN1(100.*REDLI,99.999999)
      KK=INT(PER/5.)
      SLWMAX(0)=35.*(PNREL(KK)+(PNREL(KK+1)-PNREL(KK))*(PER/5.-
1      1FLOAT(KK)))+30.
      ALAIR=.0
      DO 8 I=0,NRLM
      II=NRLM-I
      PROD(II)=.0
      IF(FYSAGE(II).LT.5.*BLI) GO TO 8

C      -----
C      CALCULATES NET DAILY ASSIMILATE PRODUCTION ON CLEAR AND
C      OVERCAST DAY (PPNC,PPNO;G GLUCOSE M-2 LEAFAREA) IN A LEAF
C      STRATUM,BASED ON THE EQUIVALENT POSITION IN THE EQUIVALENT
C      CROP (CALCULATED BY FUNCTION ALAYER).
C      -----

      PPNC=ALAYER(RCGC,PNC(0),ALAIR)
      PPNO=ALAYER(RCGO,PNO(0),ALAIR)

C      -----
C      CALCULATES NET DAILY ASSIMILATION BY A MAISTEM LEAF (ASS)
C      IN DEPENDENCE OF AVERAGE SKY CONDITIONS (PERCOV) AND AN AGE
C      DEPENDENT CORRECTION FACTOR (ACT).THE INFLUENCE OF THIS FACTOR
C      IS TOO STRONG FOR SHADED LEAVES AND IS CORRECTED FOR DEPTH
C      IN THE CANOPY BY ACTCOR.
C      THE PRODUCTION IS ADDED TO STRATUM PRODUCTION (PROD).
C      -----

      PPR=(1.-PERCOV)*PPNC+PERCOV*PPNO
      ACTCOR=1.-EXP(-.599*ALAIR/RCGC)

C      **** THIS EXPRESSION REPRESENTS ACTCOR AS A FUNCTION OF LAI OVERHEAD.
C      **** THE FACTOR .599 SIMPLY CAUSES ACTCOR TO BECOME .95 WHEN LAI=5.

35     IF(FYSAGE(II)-5.*BLI.GT.80.) GO TO 10

C      **** A LEAF BECOMES INACTIVE AND IS SHED AT AN AGE OF 80 PHYSIOL.
C      **** DAYS AFTER UNFOLDING.

```

```

ACT=1.
IF(FYSAGE(II).LE.5.*BLI+20.) GO TO 45
ACT=AMAX1(.0,1.-(FYSAGE(II)+REDTIM/2.-5.*BLI-20.)/60.)
ACT=ACT+(1.-ACT)*ACTCOR
45 ASS=(AREAM(II)+ARDLTM(II)/2.)*ACT*PPR
IF(ASS.LE.0) FYSAGE(II)=5.*BLI+81.

C ***** THE AGE OF A LEAF WITH ZERO OR NEGATIVE ASSIMILATION IS SET
C ***** TO 81 PHYSIOL. DAYS (AFTER UNFOLDING),WHICH IS EQUIVALENT
C ***** TO SHEDDING.

PROD(II)=AMAX1(.0,ASS)
ALAIR=ALAIR+AREAM(II)+ARDLTM(II)/2.
10 III=II-LOWSYM+1
IF(III.LE.0) GO TO 8

C -----
C CALCULATES SLWMAX FOR SYMPODIAL LEAVES,AS ABOVE,TAKING INTO
C ACCOUNT AVERAGE DAILY LIGHT PENETRATION.
C -----

PER=AMIN1(100.*REDLI*EXP(-.806*ALAIR/RCGC),99.999999)
KK=INT(PER/5.)
SLWMAX(III)=35.*(PNREL(KK)+(PNREL(KK+1)-PNREL(KK))*(PER/5.-
1.FLOAT(KK)))+30.

C -----
C CALCULATES NET DAILY ASSIMILATE PRODUCTION BY SYMPODIAL
C LEAVES (ASS) IN DEPENDENCE OF SKY CONDITIONS AND AGE.ADDS
C THIS PRODUCTION TO STRATUM PRODUCTION (PROD).
C -----

DO 6 J=1,NRLS(III)
IF(FYSAGS(J,III)-5.*BLI.GT.80.OR.FYSAGS(J,III).LT.5.*BLI)GO TO 6
ACT=1.
IF(FYSAGS(J,III).LE.5.*BLI+20.) GO TO 50
ACT=AMAX1(.0,1.-(FYSAGS(J,III)+REDTIM/2.-5.*BLI-20.)/60.)
ACT=ACT+(1.-ACT)*ACTCOR
50 ASS=(AREAS(J,III)+ARDLTS(J,III)/2.)*ACT*PPR
IF(ASS.LE.0) FYSAGS(J,III)=5.*BLI+81.
PROD(II)=PROD(II)+AMAX1(.0,ASS)
ALAIR=ALAIR+AREAS(J,III)+ARDLTS(J,III)/2.
6 CONTINUE
8 CONTINUE
RETURN
END

FUNCTION ALAYER(RCG,PN,ALAI)

C -----
C CALCULATES NET ASSIMILATION IN G GLUCOSE/M2/DAY FOR A LEAF IN
C DEPENDENCE OF ITS POSITION IN THE EQUIVALENT CROP CANOPY.
C -----

DIMENSION PN(0/12)
ALAER=2.*ALAI/RCG+.5
KK=INT(ALAER)

```



```

IF(KK.EQ.O)ALAER=4.*ALAI/RCG
IF(PN(KK).LE..O.OR.PN(KK+1).LE..O) GO TO 1
POS=ALOG(PN(KK))-(ALOG(PN(KK))-ALOG(PN(KK+1)))*
1 (ALAER-FLOAT(KK))
ALAYER=EXP(POS)*2.
RETURN
1 ALAYER=(PN(KK)-(PN(KK)-PN(KK+1))*(ALAER-FLOAT(KK)))*2.
RETURN
END

```

#### SUBROUTINE ROWEFF

```

C-----C
C   CALCULATES RELATIVE LEAF COVERED GROUNDAREA (RCG) FOR   C
C   EQUIVALENT CROP HAVING EQUAL LIGHT INTERCEPTION AS THE  C
C   REAL CROP (MUTSAERS,1980;1982 A).                        C
C-----C

```

```

C-----C
C   CALCULATES SUN'S AZIMUTH (SAZ), DIFFERENCE IN AZIMUTH BETWEEN  C
C   DIRECT SUN RAYS AND ROWS (DAZ) AND EFFECTIVE ROWHEIGHT (FROW),  C
C   ALL PER HOUR.                                              C
C-----C

```

```

DIRABS=.0
ABSDIF=.0
SUNCLT=DIFCLT+SUNDCT
DO 10 I=1,24
IF(HSUN(I).LT.1.E-06) GO TO 10
HO=2.*PI*(FLOAT(I)+12.)/24.
ARCSAZ=SIN(HO)*COS(DEC)/COS(HSUN(I))
SAZ=ASIN(AMIN1(1.,ARCSAZ))
DAZ=ABS(SAZ-RAZ*RAD)
SINDAZ=SIN(DAZ)+.000000001
FROW=SL/ROW*SINDAZ
FWPATH=1.-RCG

```

```

C-----C
C   CALCULATES VERTICAL TRAJECTORY OF SUNRAYS (TH) FOR 20 HORIZONTAL  C
C   SECTIONS COVERING ONE ROW DISTANCE, PER HOUR, AND AMOUNT OF DIRECT  C
C   LIGHT INTERCEPTED OVER A DAY (DIRABS).                  C
C-----C

```

```

DO 5 J=1,20
F=.05*(FLOAT(J)-.5)
TH=VTFUNC(F,RCG,FWPATH,FROW,HSUN(I))
5 DIRABS=DIRABS+SUNDCL(I)*4./20.*(1.-EXP(-TRANS(I)*ALAI/RCG*
1 TH/FROW))
10 CONTINUE

```

```

C-----C
C   THE SAME CALCULATIONS FOR DIFFUSE LIGHT COMING FROM 9 SKY  C
C   SECTORS, YIELDING INTERCEPTION PERCENTAGE OF DIFFUSE LIGHT  C
C   (ABSDIF). CALCULATES TOTAL DAILY INTERCEPTION PERCENTAGE  C
C   (ABSTOT) FOR A CLEAR DAY.                                  C
C-----C

```

```

DAZ=30.*RAD
SINDAZ=SIN(DAZ)+.0000001
FTHROW=SL/ROW*SINDAZ
DO 15 K=1,9
HHSUN=(FLOAT(K)*10.-5.)*RAD
DO 15 J=1,20
F=.05*(FLOAT(J)-.5)
TH=VTFUNC(F,RCG,FWPATH,FTHROW,HHSUN)
15  ABSDIF=ABSDIF+CONTR(K)/20.*(1.-EXP(-DKV(2*K-1)*ALAI/
1RCG*TH/FTHROW))
ABSTOT=(DIRABS+ABSDIF*DIFCLT)/SUNCLT
RCGC=RCG

C -----
C CALCULATES DAILY LIGHT INTERCEPTION PERCENTAGE ON A CLEAR DAY
C (ABSTOE) BY SUCCESSIVELY WIDER EQUIVALENT CROPS WITH CONSTANT
C LAI.RCG OF THE EQUIVALENT CROP ON A CLEAR DAY (RCGC) IS
C FOUND WHEN ABSTOE=ABSTOT.
C -----

DO 30 I=1,100
RCGC=RCGC+.01
KK=INT(2.*ALAI/RCGC+.5)
ALDIF=ALOG(EDIFV(KK))+(ALOG(EDIFV(KK+1))-ALOG(EDIFV(KK)))*
1(2.*ALAI/RCGC-FLOAT(KK)+.5)
DIFABE=(1.-EXP(ALDIF))*RCGC*DIFCLT
ALDIR=ALOG(EFRIV(KK))+(ALOG(EFRIV(KK+1))-ALOG(EFRIV(KK)))*
1(2.*ALAI/RCGC-FLOAT(KK)+.5)
DIRABE=(SUNDCT-EXP(ALDIR))*RCGC
ABSTOE=(DIRABE+DIFABE)/SUNCLT
IF(ABSTOT.LT.ABSTOE) GO TO 35
30 CONTINUE
35 RCGO=RCGC
IF(DIFABE/DIFCLT.GT.ABSDIF) RCGO=RCG

C -----
C SAME CALCULATIONS FOR OVERCAST SKY,YIELDING RCG OF EQUIVALENT
C CROP FOR OVERCAST DAY (RCGO).
C -----

DO 40 I=1,100
RCGO=RCGO+.01
KK=INT(2.*ALAI/RCGO+.5)
ALDIF=ALOG(EDIFV(KK))+(ALOG(EDIFV(KK+1))-ALOG(EDIFV(KK)))*
1(2.*ALAI/RCGO-FLOAT(KK)+.5)
ABSDIE=(1.-EXP(ALDIF))*RCGO
IF(ABSDIF.LT.ABSDIE) GO TO 45
40 CONTINUE
45 RCGC=AMIN1(1.,RCGC)
RCGO=AMIN1(1.,RCGO)
RETURN
END

```

FUNCTION VTFUNC(F,RCG,FWPATH,FHROW,HSUN)

C -----  
C CALCULATES VERTICAL CANOPY DISTANCE PASSED THROUGH BY  
C A SUN RAY.  
C -----

FA=.0  
IF(F.GE.FWPATH) FA=1.  
BASE=AMAX1((FHROW\*COS(HSUN)/SIN(HSUN)-(FA+FWPATH-F)),.0)  
BNR=AINT(BASE)  
TFH=BNR\*RCG\*SIN(HSUN)/COS(HSUN)  
HFIRB=FA\*AMIN1(((1.-F)\*SIN(HSUN)/COS(HSUN)),FHROW)  
HFINB=AMIN1((RCG\*SIN(HSUN)/COS(HSUN)),((BASE-BNR)\*  
1SIN(HSUN)/COS(HSUN)))  
VTFUNC=TFH+HFIRB+HFINB  
RETURN  
END

#### SUBROUTINE CANOPY

C -----C  
C CALLS LEAF AND BOLL GROWTH SUBROUTINES FOR POTENTIAL C  
C GROWTH OF LEAVES AND BOLLS,CALCULATES POTENTIAL STEM AND C  
C ROOT GROWTH AND ASSIMILATES REQUIRED PER STRATUM FOR MAINTEN- C  
C ANCE RESPIRATION AND POTENTIAL GROWTH OF ALL PLANT PARTS. C  
C ADJUSTS "GLUCOSE EQUIVALENT" OF ALL TISSUES IN DEPENDENCE OF C  
C AGE. C  
C -----C

DIMENSION BEQ(0/21),BMNTN(0/20)  
DATA(BEQ(I),I=0,21)/1.675,1.628,1.5,1.333,1.275,1.28,1.33,  
11.388,1.465,1.544,1.65,1.773,1.952,2.178,2.353,2.513,2.251,  
21.94,1.89,1.885,1.882,1.882/  
DATA(BMNTN(I),I=0,20)/.04,.04,.0398,.0389,.0335,.0265,.0175,  
1.0095,.0076,.0072,.0069,.0068,.0068,.0068,.0068,.0068,  
2.0068,.0068,.0034,.0/

C -----  
C CALLS SUBROUTINES LEAF AND BOLL,THE FORMER BOTH FOR MAINSTEM  
C AND SYMPODIA.  
C -----

KK=30-NRLM  
NR=NRLM+1  
CALL LEAF(AREAM(0),ARDLTM(0),SLWM(0),WLDLTM(0),FYSAGE(0),NR,  
1SLWMAX(0),KK)  
IF(NRLM.LT.LOWSYM) GO TO 2  
DO 5 I=LOWSYM,NRLM  
II=I-LOWSYM+1  
IF(NRLS(II).GT.0)CALL BOLL(NRLS(II),WB(1,II),WBDLT(1,II),  
1FYSAGE(1,II))  
KK=10-NRLS(II)  
CALL LEAF(AREAS(1,II),ARDLTS(1,II),SLWS(1,II),WLDLTS(1,II),  
1FYSAGS(1,II),NRLS(II),SLWMAX(II),KK)  
CONTINUE

5

```

2      WLACC=.0
      ASSDV=.0
      ASSDG=.0
      PRODT=.0
      RSPMNT=.0
      DO 10 I=0,MINO(30,NRLM+1)
      ASDEMV(I)=.0

C      -----
C      CALCULATES POTENTIAL STEM (WSDLTM) AND ROOT GROWTH (WRDLTM),
C      ASSOCIATED WITH EACH MAINSTEM LEAF IN DEPENDENCE OF THE WEIGHT
C      OF LEAF TISSUE PRESENT BELOW THAT LEAF (WLTM).
C      -----

      WLTM(I)=WLACC+AREAM(I)*SLWM(I)
      WLACC=WLTM(I)
      WSDLTM(I)=(.3+.11*WLTM(I)/PLM2)*WLDLTM(I)
      WRDLTM(I)=(1.-(REDEXT-.75)*2.)*WSDLTM(I)

C      -----
C      ADJUSTS GLUCOSE EQUIVALENT OF ALL TISSUES ACCORDING TO AGE AND
C      ADDS GLUCOSE "RELEASED" TO THE PRODUCTION TERM (PROD).CALCULATES
C      GLUCOSE REQUIRED FOR MAINTENANCE RESPIRATION (RSPMNT) BY STEM AND
C      ROOT TISSUE ALREADY PRESENT.CALCULATES GLUCOSE REQUIRED FOR
C      MAINTENANCE RESPIRATION AND DRY MATTER ACCUMULATION OF THE
C      POTENTIAL WEIGHT INCREMENT OF VEGETATIVE TISSUE (ASDEMV).
C      -----

      AGEUNF=FYSAGE(I)-5.*BLI
      IF(AGEUNF.LT.5..OR.AGEUNF-REDTIM.GT.20.) GO TO 30
      DAE=AMIN1(AGEUNF-5.,REDTIM)
      IF(AGEUNF.GT.20.)DAE=AGEUNF-20.
      PROD(I)=PROD(I)+DAE/15.*(AREAM(I)*SLWM(I)*.059+WSTM(I)*.167+
30      1WRTM(I)*.196)
      RSP=RSPVEG(AGEUNF,REDTIM,WSTM(I),WRTM(I),RATEV)
      RSPMNT=RSPMNT+RSP
      IF(AGEUNF.GT.30.) GO TO 15
      RED=AMAX1(AGEUNF-5.,.0)/15.
      IF(AGEUNF.GT.20.) RED=1.
      GLEQLF=1.48-.059*RED
      GLEQST=1.48-.167*RED
      GLEQRT=1.48-.196*RED
      RSP=RSPVEG(AGEUNF,REDTIM,WSDLTM(I)/2.,WRDLTM(I)/2.,RATEV)
      ASDEMV(I)=GLEQLF*WLDLTM(I)+GLEQST*WSDLTM(I)+GLEQRT*WRDLTM(I)+RSP

C      -----
C      SAME PROCEDURES FOR SYMPODIAL GROWTH.TOTAL AMOUNT OF GLUCOSE
C      REQUIRED FOR A SYMPODIUM IS ADDED TO AMOUNT REQUIRED
C      FOR POTENTIAL GROWTH OF MAINSTEM LEAF AND ASSOCIATED TISSUE
C      IN THE SAME STRATUM(ASDEMV).GLUCOSE "RELEASED" (SEE ABOVE)
C      BY THE SYMPODIUM IS ADDED TO THE PRODUCTION TERM.
C      -----

15      II=I-LOWSYM+1
      IF(II.LE.0.OR.I.EQ.NRLM+1) GO TO 20
      WLACCS=WLACC
      ASDEMG(II)=.0

```

```

DO 1 J=1,MINO(10,NRLS(II)+1)
WLTS(J,II)=WLACCS+AREAS(J,II)*SLWS(J,II)
WLACCS=WLTS(J,II)
WSDLTS(J,II)=(.3+.11*WLTS(J,II)/PLM2)*WDLTS(J,II)
WRDLTS(J,II)=(1.-(REDEXT-.75)*2.)*WSDLTS(J,II)
AGEUNF=FYSAGS(J,II)-5.*BLI
IF(AGEUNF.LT.5..OR.AGEUNF-REDTIM.GT.20.) GO TO 35
DAE=AMIN1(AGEUNF-5.,REDTIM)
IF(AGEUNF.GT.20.) DAE=AGEUNF-20.
PROD(I)=PROD(I)+DAE/15.*(AREAS(J,II)*SLWS(J,II)*.059+
1 WSTS(J,II)*.167+WRTS(J,II)*.196)
RSP=RSPVEG(AGEUNF,REDTIM,WSTS(J,II),WRTS(J,II),RATEV)
RSPMNT=RSPMNT+RSP
IF(AGEUNF.GT.30.) GO TO 25
RED=AMAX1(AGEUNF-5.,.0)/15.
IF(AGEUNF.GT.20.) RED=1.
GLEQLF=1.48-.059*RED
GLEQST=1.48-.167*RED
GLEQRT=1.48-.196*RED
RSP=RSPVEG(AGEUNF,REDTIM,WSDLTS(J,II)/2.,WRDLTS(J,II)/2.,RATEV)
ASDEMV(I)=ASDEMV(I)+GLEQLF*WDLTS(J,II)+GLEQST*WSDLTS(J,II)+
1 GLEQRT*WRDLTS(J,II)+RSP
25 IF(J.EQ.NRLS(II)+1.OR.J.GT.5.OR.FYSAGB(J,II)-44.-RATEG.GE.BMP)
1GO TO 1

```

```

C -----
C CALCULATES ASSIMILATES REQUIRED FOR MAINTENANCE AND GROWTH OF
C FRUITING POINTS AND TOTAL ASSIMILATES REQUIRED PER STRATUM FOR
C GENERATIVE GROWTH (ASDEMG).CALCULATES TOTAL GLUCOSE REQUIRED BY
C THE CROP FOR VEGETATIVE (ASSDV) AND GENERATIVE GROWTH (ASSDG).
C -----

```

```

BMNT=.04
GLEQB=1.48
IF(FYSAGB(J,II).LT.44.) GO TO 22
PER=AMAX1(FYSAGB(J,II)-RATEG/2.-44.,.0)/BMP*20.
KK=INT(PER)
BMNT=BMNTN(KK)+(BMNTN(KK+1)-BMNTN(KK))*(PER-FLOAT(KK))
GLEQB=BEQ(KK)+(BEQ(KK+1)-BEQ(KK))*(PER-FLOAT(KK))
22 RSPMNT=RSPMNT+(BMNT*(WB(J,II)+WBDLT(J,II)/2.))*RATEV
ASDEMG(II)=ASDEMG(II)+GLEQB*WBDLT(J,II)
1 CONTINUE
ASSDG=ASSDG+ASDEMG(II)
20 PRODT=PRODT+PROD(I)
10 ASSDV=ASSDV+ASDEMV(I)
RETURN
END

```

FUNCTION RSPVEG(AGE,REDTIM,ST,RT,RATE)

```

C -----
C CALCULATES MAINTENANCE RESPIRATION OF VEGETATIVE TISSUE.
C -----

```

```

IF(AGE-REDTIM/2..GT.20.) GO TO 2
RED=AMAX1(AGE-REDTIM/2.-5.,.0)/15.
RSPVEG=((-.04-.0339*RED)*ST+(-.04-.0343*RED)*RT)*RATE
RETURN

```

```

2      RED=(AGE-REDTIM/2.-20.)/60.
      RSPVEG=((0.0061-.0035*RED)*ST+(.0057-.003*RED)*RT)*RATE
      RETURN
      END

```

```

      SUBROUTINE LEAF(AREA,ARDLT,SLW,WDLDT,FYSAGE,NRL,SLWMAX,KK)
C-----C
C      CALCULATES POTENTIAL GROWTH OF LEAVES ON MAINSTEM OR SYMPODIUM C
C      (MUTSAERS,1982 B,C). C
C-----C
      DIMENSION AREA(31),ARDLT(31),SLW(31),WDLDT(31),FYSAGE(31)
      IF(KK.LE.0) GO TO 5

C-----C
C      CALCULATES POTENTIAL INCREASE OF AREA (ARDLT) AND WEIGHT C
C      (WDLDT) OF UNINITIATED LEAF PRIMORDIUM. C
C-----C

      ARDLT(NRL+1)=AREA(NRL+1)*(EXP(R1*RATEV)-1.)
      WDLDT(NRL+1)=ARDLT(NRL+1)*30.
5      IF(NRL.EQ.0) RETURN

C-----C
C      CALCULATES PARAMETERS (A,B) FOR FUNCTION F3 (SEE BELOW) C
C      REPRESENTING THE RELATIVE RATE OF INCREASE OF SLW. C
C-----C

      SLWMAX=AMAX1(30.,SLWMAX)
      A=(41.93*SLWMAX)**(1./1.3)
      B=ALOG(A/SQRT(SLWMAX/3.))/7.

C ***** THE PARAMETERS A AND B CAUSE THE POTENTIAL RELATIVE RATE OF
C ***** INCREASE OF SLW (SEE BELOW) TO BE MAXIMUM AT 7 PHYSIOLOGICAL DAYS
C ***** FROM UNFOLDING AND 99.9 % OF THICKNESS GROWTH TO BE COMPLETED
C ***** AT 20 PHYS. DAYS FROM UNFOLDING.

```

```

1      DO 4 J=1,NRL
      RGR=R1*REDEXT
      F2=.0
      ARDLT(J)=.0
      WDLDT(J)=.0
      SLWDLT=.0
      IF(FYSAGE(J).GT.5.*BLI+30.)GO TO 20
      IF(FYSAGE(J)+REDTIM.LT.5.*BLI) GO TO 3
      IF(FYSAGE(J).GT.5.*BLI+20.) GO TO 2

```

```

C-----C
C      CALCULATES POTENTIAL RGR OF THE AREA OF EACH LEAF IN DEPEN- C
C      DENCE OF ITS DEVELOPMENTAL AGE (FYSAGE);CALCULATES POTENTIAL C
C      INCREASE OF SLW (SLWDLT), LEAF AREA (ARDLT) AND LEAF C
C      WEIGHT (WDLDT).INCREMENTS DEVELOPMENTAL AGE. C
C-----C

```

```

      F2=1./((1.+9.**((FYSAGE(J)+REDTIM/2.-5.*BLI-.77*9.)/(.23*9.)))

```

```

C **** F2 GOVERNS THE (INVERSE SIGMOID) TRANSITION OF RGR FOR A LEAF
C **** FROM PRIMORDIAL (EXPONENTIAL) GROWTH TO LOGISTIC GROWTH, WHICH
C **** IS 90 % COMPLETED (.9) AT 9 PHYSIOL. DAYS FROM UNFOLDING.
C **** THE PARAMETER .77 (AND 1.-.77=.23) DETERMINES THE POSITION OF
C **** THE POINT OF INFLEXION OF THIS SIGMOID TRANSITION (MUTSAERS, 1982 A).

```

```

2      F1=1.-1./(1.+EXP(-R2*(FYSAGE(J)+REDTIM/2.-5.*BLI-9.)))

```

```

C **** F1 REPRESENTS THE RGR OF A LOGISTIC WITH RATE PARAMETER 1.
C **** AND WITH ITS POINT OF INFLEXION AT 9 PHYSIOL. DAYS FROM UNFOLDING.

```

```

      PP=A*EXP(-B*(FYSAGE(J)+REDTIM/2.-5.*BLI))
      F3=(SLWMAX-30.)*B*PP/((SLWMAX+30.*PP)*(1.+PP))
      RGR=(R1*F2+R2*F1*(1.-F2))*REDEXT
      IF(FYSAGE(J).LT.5.*BLI) SLW(J)=SLW(J)*EXP(-F3*REDEXT*
1      1(5.*BLI-FYSAGE(J)))
      SLWDLT=SLW(J)*(EXP(F3*REDEXT*RATEV)-1.)
3      ARDLT(J)=AREA(J)*(EXP(RGR*RATEV)-1.)

```

```

C **** INTEGRATION PROCEDURE FOR LEAF AREA.

```

```

      WDLT(J)=ARDLT(J)*(SLW(J)+SLWDLT)+AREA(J)*SLWDLT
      IF(FYSAGE(J).LT.5.*BLI+25.) GO TO 10
20     FYSAGE(J)=FYSAGE(J)+RATEV
      GO TO 4
10     FYSAGE(J)=FYSAGE(J)+REDTIM
4      CONTINUE
      RETURN
      END

```

```

      SUBROUTINE BOLL(NRL,WB,WBDLT,FYSAGE)

```

```

C-----C
C      CALCULATES GROWTH OF FRUITING POINTS.      C
C-----C

```

```

      DIMENSION WB(1),WBDLT(1),FYSAGB(1)
      EXC=RATEG
      DO 3 I=1,MINO(5,NRL)
      WBDLT(I)=.0
      WBDL1=.0
      IF(FYSAGB(I)-44..GT.BMP) GO TO 3
      IF(FYSAGB(I)+RATEV.LT.44.) GO TO 2
      IF(FYSAGB(I).GT.44.) GO TO 1

```

```

C-----C
C      CALCULATES WEIGHT INCREASE OF FRUITING POINTS ON DAY OF
C      FLOWERING.
C-----C

```

```

      WBDL1=WB(I)*(EXP(R1*(44.-FYSAGB(I)))-1.)

```

```

C **** INTEGRATION PROCEDURE FOR WEIGHT OF FRUITING POINTS.

```

```

      EXC=(FYSAGB(I)-44.+RATEV)*RATEG/RATEV
      FYSAGB(I)=44.

```

```

C -----
C CALCULATES WEIGHT INCREASE OF FRUITING POINTS AFTER FLOWERING.
C -----

```

```

1  T=(FYSAGB(I)-44.+EXC/2.)/BMP
   RGR=T/(.1031*EXP(5.*T*T)-.1)
   WBDL2=(WB(I)+WBDL1)*(EXP(RGR*EXC/EMP)-1.)
   WBDLT(I)=WBDL1+WBDL2
   FYSAGB(I)=FYSAGB(I)+EXC
   GO TO 3

```

```

C -----
C CALCULATES WEIGHT INCREASE PRIOR TO FLOWERING.
C -----

```

```

2  WBDLT(I)=WB(I)*(EXP(R1*RATEV)-1.)
   FYSAGB(I)=FYSAGB(I)+RATEV
3  CONTINUE
   RETURN
   END

```

#### SUBROUTINE BALANS

```

C -----C
C CALCULATES ACTUAL GROWTH FOR ALL PLANT PARTS IN DEPENDENCE C
C OF ASSIMILATE AVAILABILITY. C
C -----C

```

```

   ALAI=.0
   ALAIT=.0
   ALAIDL=.0
   DEM=.0
   SRPLUS=.0
   DEF=.0

```

```

C -----
C ALLOCATES ASSIMILATES TO FRUITING POINTS AND MAINTENANCE
C RESPIRATION AND REDISTRIBUTES REMAINING ASSIMILATES TO STRATA
C FOR VEGETATIVE GROWTH.
C -----

```

```

   PPROD=PROD-RSPMNT-ASSDG
   IF(SLI.LT.6..OR.PPROD.GT.ASSDV.OR.PPROD.LT..0) GO TO 50
   FS=AMAX1(.0,PPROD/ASSDV)
   DO 11 I=0,MINO(30,NRLM+1)
   PROD(I)=PROD(I)-PROD(I)/AMAX1(1.E-25,PROD)*(RSPMNT+ASSDG)
11  DEF=DEF+AMAX1(.0,FS*ASDEMV(I)-PROD(I))
   DO 1 I=0,MINO(30,NRLM+1)
   AS=FS*ASDEMV(I)
   IF(PROD(I).LT.AS) GO TO 1
   ADD=(ASDEMV(I)-AS)/(DEF+ASDEMV(I)-AS)*(PROD(I)-AS)
   SRPLUS=SRPLUS+PROD(I)-AS-ADD
   PROD(I)=AS+ADD
1  DEM=DEM+ASDEMV(I)-PROD(I)
   DO 45 I=0,MINO(30,NRLM+1)
45  PROD(I)=PROD(I)+(ASDEMV(I)-PROD(I))/DEM*SRPLUS

```



```

C -----
C CALCULATES ACTUAL GROWTH OF VEGETATIVE PARTS IN DEPENDENCE
C OF ASSIMILATE AVAILABILITY AND DEMAND IN EACH STRATUM. UPDATES
C WEIGHT OF PLANT PARTS AND AREAS OF LEAVES.
C -----

```

```

50 DO 3 I=0,MINO(30,NRLM+1)
   IF(PPROD.LE..0) PROD(I)=.0
   GRFRAC=AMIN1(1.,PROD(I)/AMAX1(1.E-25,ASDEMV(I)))
   IF(SLI.LT.6..OR.PPROD.GT.ASSDV) GRFRAC=1.
   WSDLTM(I)=WSDLTM(I)*GRFRAC
   WRDLTM(I)=WRDLTM(I)*GRFRAC
   WSTM(I)=WSTM(I)+WSDLTM(I)
   WRTM(I)=WRTM(I)+WRDLTM(I)
   SLWDLT=(WDLTM(I)-ARDLTM(I)*SLWM(I))/(AREAM(I)+ARDLTM(I))
   ARDLTM(I)=GRFRAC*ARDLTM(I)/(1.-(1.-GRFRAC)*SLWDLT/
   1(SLWM(I)+SLWDLT))
   SLWDLT=SLWDLT*GRFRAC
   SLWM(I)=AMAX1(30.,SLWM(I)+SLWDLT)
7   RGRM(I)=ALOG(1.+ARDLTM(I)/AREAM(I))/(RATEV*REDEXT)
   IF(I.EQ.NRLM+1)RGRM(I)=RGRM(I)*REDEXT
   AREAM(I)=AREAM(I)+ARDLTM(I)
   IF(FYSAGE(I)-5.*BLI.LE.80.) ALAI=ALAI+AREAM(I)
   ALAIT=ALAIT+AREAM(I)
   ALAIDL=ALAIDL+ARDLTM(I)
60  II=I-LOWSYM+1
   IF(II.LE.0.OR.SLIS(II).EQ..0) GO TO 3

```

```

C -----
C SAME PROCEDURES FOR SYMPODIAL BRANCHES.
C -----

```

```

DO 3 J=1,MINO(10,NRLS(II)+1)
   WSDLTS(J,II)=WSDLTS(J,II)*GRFRAC
   WRDLTS(J,II)=WRDLTS(J,II)*GRFRAC
   WSTS(J,II)=WSTS(J,II)+WSDLTS(J,II)
   WRTS(J,II)=WRTS(J,II)+WRDLTS(J,II)
   SLWDLT=(WDLTS(J,II)-ARDLTS(J,II)*SLWS(J,II))/
1(AREAS(J,II)+ARDLTS(J,II))
   ARDLTS(J,II)=GRFRAC*ARDLTS(J,II)/(1.-(1.-GRFRAC)*SLWDLT/
1(SLWS(J,II)+SLWDLT))
   SLWDLT=GRFRAC*SLWDLT
   SLWS(J,II)=AMAX1(30.,SLWS(J,II)+SLWDLT)
   RGRS(J,II)=ALOG(1.+ARDLTS(J,II)/AREAS(J,II))/(RATEV*REDEXT)
   IF(J.EQ.NRLS(II)+1)RGRS(J,II)=RGRS(J,II)*REDEXT
   AREAS(J,II)=AREAS(J,II)+ARDLTS(J,II)
   IF(FYSAGS(J,II)-5.*BLI.LE.80.) ALAI=ALAI+AREAS(J,II)
   ALAIT=ALAIT+AREAS(J,II)
   ALAIDL=ALAIDL+ARDLTS(J,II)
65  IF(FYSAGB(J,II)-44..GE.BMP.OR.J.GT.5.OR.J.EQ.NRLS(II)+1) GO TO 3

```

```

C -----
C CALCULATES BOLL WEIGHTS (WB) AND BOLL NUMBER (BNR) FOR EACH
C POSITION AFTER ACCOUNTING FOR SHEDDING.
C -----

```

```

      WB(J,II)=WB(J,II)+WBDLT(J,II)
      IF(FYSAGB(J,II).LT.34..OR.FYSAGB(J,II).GE.46.) GO TO 3
      WB(J,II)=WB(J,II)*GRFRAC
      BNR(J,II)=BNR(J,II)*GRFRAC
3     CONTINUE
      RETURN
      END

```

#### SUBROUTINE APEX

```

C -----
C INITIATES LEAVES, BRANCHES AND FRUITING POINTS.
C -----

```

```

C -----
C INCREMENTS LEAF INTERVAL SUM OF THE MAINSTEM (SLI), CALCULATES
C DEVELOPMENTAL AGE IN EXCESS OF WHOLE SLI-NUMBER IF SUCH NUMBER
C IS CROSSED DURING THE PRESENT TIME STEP. IN THAT CASE THE "AREA"
C AT INITIATION OF THE NEW LEAF PRIMORDIUM (AI) IS CALCULATED.
C IF AI IS GREATER THAN AI OF THE PRECEDING LEAF (AIO), THEN THE
C LEAF IS INDEED INITIATED. OTHERWISE INITIATION IS POSTPONED.
C -----

```

```

      SLI=SLI+RATEV/BLI
      IF(INT(SLI).EQ.NRLM.OR.NRLM.GE.30) GO TO 3
      EXCDAY=(SLI-AINT(SLI))*BLI
      AI=AREAM(NRLM+1)*EXP(-RGRM(NRLM+1)*EXCDAY)
      IF(AI.GE.AIO) GO TO 2
      TT=(ALOG(AIO)-ALOG(AI))/AMAX1(1.E-25,RGRM(NRLM+1))
      IF(TT.LT.EXCDAY) GO TO 1
      SLI=AINT(SLI)-1.E-06
      GO TO 3
1     EXCDAY=EXCDAY-TT
      AI=AIO
      SLI=SLI-TT/BLI
2     NRLM=NRLM+1
      IF(NRLM.GE.30) GO TO 20
      AREAM(NRLM+1)=AREAM(NRLM)*A1
      RGRM(NRLM+1)=RGRM(NRLM)
      AIO=AI
      IF(NRLM.GT.3) GO TO 20
      AREAM(NRLM)=AREAM(NRLM)*EXP(-RGRM(NRLM)*1.)
      AREAM(NRLM+1)=AREAM(NRLM+1)*EXP(-RGRM(NRLM)*1.)
      FYSAGE(NRLM)=-1.
      SLI=SLI-1./BLI
20    FYSAGE(NRLM)=FYSAGE(NRLM)+EXCDAY
      IF(NRLM.LT.LOWSYM) RETURN

```

```

C -----
C INITIATES NEW SYMPODIAL BRANCH.
C -----

AREAS(1,NRLM-LOWSYM+1)=AIO*A2*EXP(RGRM(NRLM)*EXCDAY)
SLIS(NRLM-LOWSYM+1)=(EXCDAY-RATEV)/(BLI*RLIS)
3 IF(NRLM.LT.LOWSYM) RETURN
DO 5 I=LOWSYM,NRLM
II=I-LOWSYM+1
SLIS(II)=SLIS(II)+RATEV/(RLIS*BLI)
IF(INT(SLIS(II)).EQ.NRLS(II).OR.NRLS(II).GE.10) GO TO 5

C -----
C INITIATES NEW LEAF ON A SYMPODIUM.
C -----

EXCDAY=(SLIS(II)-AINT(SLIS(II)))*BLI*RLIS
NRLS(II)=NRLS(II)+1
IF(NRLS(II).GE.10) GO TO 10
AREAS(NRLS(II)+1,II)=A3*AREAS(NRLS(II),II)
RGRS(NRLS(II)+1,II)=RGRS(NRLS(II),II)
10 FYSAGS(NRLS(II),II)=EXCDAY
IF(NRLS(II).GT.5) GO TO 5

C -----
C INITIATES NEW FRUITING POINTS.
C -----

WB(NRLS(II),II)=.797E-13*PLM2*.9**AMAX1(.0,FLOAT(NRLS(II))-1.)*
1EXP(EXCDAY*R1)

C ***** THE FACTOR .797E-13 CAUSES A FINAL BOLL WEIGHT OF 7 GRAMS AT
C ***** FIRST SYMPODIAL POSITIONS.

FYSAGB(NRLS(II),II)=EXCDAY
5 CONTINUE
RETURN
END

SUBROUTINE STATE(JJ,IPRINT)
C -----C
C OUTPUTS INFORMATION ON THE STATUS OF THE CROP. C
C -----C

NRLVS=-1
TLW=.0
TDLW=.0
TSW=.0
TRW=.0
TBW=.0
TNSQ=.0
TNGB=.0
TNMB=.0
YLD=.0
DO 5 I=0,MINO(30,NRLM+1)
IF(FYSAGE(I).GE.5.*BLI) NRLVS=NRLVS+1

```

```

IF(FYSAGE(I)-5.*BLI.LE.80.) GO TO 1
TDLW=TDLW+AREAM(I)*SLWM(I)
GO TO 2
1 TLW=TLW+AREAM(I)*SLWM(I)
2 TSW=TSW+WSTM(I)
TRW=TRW+WRTM(I)
II=I-LOWSYM+1
IF(II.LE.0.OR.SLIS(II).EQ..0) GO TO 5
DO 5 J=1,MINO(10,NRLS(II)+1)
IF(FYSAGS(J,II)-5.*BLI.LE.80.) GO TO 3
TDLW=TDLW+AREAS(J,II)*SLWS(J,II)
GO TO 4
3 TLW=TLW+AREAS(J,II)*SLWS(J,II)
4 TSW=TSW+WSTS(J,II)
TRW=TRW+WRTS(J,II)
IF(J.GT.5.OR.J.EQ.NRLS(II)+1) GO TO 5
TBW=TBW+WB(J,II)
IF(FYSAGB(J,II).LT.22.) GO TO 5
IF(FYSAGB(J,II).LT.44.) TNSQ=TNSQ+BNR(J,II)
IF(FYSAGB(J,II)-44..LT.BMP.AND.FYSAGE(J,II).GE.44.)
1TNGB=TNGB+BNR(J,II)
IF(FYSAGB(J,II)-44..LT.BMP) GO TO 5
TNMB=TNMB+BNR(J,II)
YLD=YLD+WB(J,II)*.73
5 CONTINUE
PRINT 100,REALDA,TMIN,TMAX,ALAI,TLW,NRLVS,PERCOV,PRODT,TDLW,
1TNSQ,REDEXT,ASSDV,TSW,TNGB,RATEG,ASSDG,TRW,TNMB,RATEV,AIO,
2TBW,RATEVD,YLD
IF(JJ.NE.IPRINT) RETURN
PRINT 103,(I,AREAM(I),RGRM(I),SLWM(I),I=0,NRLM+1)
DO 6 I=1,MINO(10,NRLM-LOWSYM+1)
IF(NRLS(I).EQ.0) RETURN
PRINT 101,I,(J,AREAS(J,I),RGRS(J,I),SLWS(J,I),WB(J,I),BNR(J,I),
1FYSAGB(J,I),J=1,MINO(5,NRLS(I)))
6 IF(NRLS(I).GT.5)PRINT 102,(J,AREAS(J,I),RGRS(J,I),SLWS(J,I),
1J=6,NRLS(I))
100 FORMAT(1H-,'CROP AGE : ',F6.1/18('='))//12X,'ENVIRONMENTAL
1AND CROP PARAMETERS',18X,'WEIGHTS OF PLANT PARTS(G/M2)',17X,
2'NUMBERS/M2'/X,57('-'),3X,33('-'),3X,32('-')/' TEMPS ',F4.1,
3'/' ,F4.1,28X,'LAI ',E8.3,12X,'ATTACHED LEAVES ',E8.3,5X,
4'UNFOLDED MAINSTEM LEAVES ',I6/' PERCOV ',F9.3,11X,'ASSIM.PRODU
5CED(G/M2) ',E8.3,13X,'DROPPED LEAVES ',E8.3,14X,'VISIBLE SQU
6ARES ',F6.1/' REDEXT ',F9.3,' ASSIM.DEMAND VEG.GROWTH(G/M2)
7 ',E8.3,22X,'STEMS ',E8.3,16X,'GROWING BOLLS ',F6.1/' RA
8TEG ',F9.3,' ASSIM.DEMAND GEN.GROWTH(G/M2) ',E8.3,22X,'ROOTS ',
9E8.3,19X,'OPEN BOLLS ',F6.1/' RATEV ',F9.3,' INITIAL SIZE
1 LAST LEAF(M2/M2) ',E8.3,12X,'FRUITING POINTS ',E8.3/' RATEVD ',
2F9.3,45X,'HARVESTABLE SEEDCOTTON ',E8.3//)
101 FORMAT(' '//' SYMPODIUM NR ',I2/1X,15('-')//20X,'LEAVES',24X,'BOL
1LS'/20X,6('='),24X,5('='))/' POSITION AREA/M2',5X,'RGR',6X,
2'SLW',6X,'WEIGHT/M2 NUMBER/M2 PHYS.AGE '/X,8('-'),2X,26('-'),
33X,30('-')/(I7,4X,E8.3,2X,F5.3,5X,F5.2,5X,E8.3,3X,F5.2,6X,F4.1))
102 FORMAT(I7,4X,E8.3,2X,F5.3,5X,F5.2)
103 FORMAT(1H0,48X,'MAINSTEM LEAVES'/49X,15('-')//3(' LEAF NR
1 AREA/M2',5X,'RGR',4X,'SLW',7X)/1X,3(32('-'),7X)/(3(3X,I2,3X,
2E10.3,3X,F5.3,3X,F4.1,6X)))
RETURN
END

```

TABLE OF MAIN INFORMATION EXCHANGE BETWEEN SUBROUTINES OF PROGRAM KUTUN.  
DATA READ FROM DATA FILES AND TABULATED INPUTS ARE NOT MENTIONED.

TO	FROM										
---	----										
	++ MAIN	+ INITIA	+ LITEMP	+ PHOTO	+ CROPPH	+ ROWEFF	+ CANOPY	+ LEAF	+ BOLL	+ BALANS	+ APEX
MAIN	++	+	+ RATEV	+	+	+	+	+	+	+	+
INITIA	++ DAY	+	+	+	+	+	+	+	+	+	+
LITEMP	++ DAY	+	+	+	+	+	+	+	+	+	+
PHOTO	++	+	+ DRC	+	+	+	+	+	+	+	+
	++	+	+ DAYLE	+	+	+	+	+	+	+	+
	++	+	+ RATEVD	+	+	+	+	+	+	+	+
CROPPH	++ FYSDA	+	+ RATEV	+ REDLI	+	+ RCGC	+	+ FYSAGE	+	+ ALAI	+ NRLM
	++ REDTIM	+	+	+ PWREL	+	+ RCGO	+	+ FYSAGS	+	+ ALAIDL	+ NRLS
	++	+	+	+ PFC	+	+	+	+	+	+ ALAIT	+
	++	+	+	+ PNC	+	+	+	+	+	+ AREAM	+
	++	+	+	+	+	+	+	+	+	+ ARDLTM	+
	++	+	+	+	+	+	+	+	+	+ AREAS	+
	++	+	+	+	+	+	+	+	+	+ ARDLTS	+
ROWEFF	++	+ CONTR	+ DIFCLT	+	+ RCG	+	+	+	+	+	+
	++	+ DKV	+ SUNDCT	+	+ SL	+	+	+	+	+	+
	++	+ EDIFV	+ HSUN	+	+ ALAI	+	+	+	+	+	+
	++	+	+ SUNDCL	+	+	+	+	+	+	+	+
	++	+	+ TRANS	+	+	+	+	+	+	+	+
	++	+	+ EPRIV	+	+	+	+	+	+	+	+
CANOPY	++ REDTIM	+	+	+	+ PROD	+	+	+ FYSAGE	+ FYSAGB	+ AREAM	+ NRLM
	++	+	+	+	+	+	+	+ FYSAGS	+ WBDLT	+ SLWM	+ NRLS
	++	+	+	+	+	+	+	+ WDLTM	+	+ AREAS	+
	++	+	+	+	+	+	+	+ WDLTS	+	+ SLWS	+
LEAF	++ REDTIM	+	+ RATEV	+	+ SLWMAX	+	+	+	+	+ SLW	+ NRL
	++	+	+	+	+	+	+	+	+	+ AREA	+
BOLL	++	+	+ RATEG	+	+	+	+	+	+	+ WB	+
	++	+	+ RATEV	+	+	+	+	+	+	+	+
BALANS	++ REDTIM	+	+ RATEV	+	+	+	+ PRODT	+ WDLTM	+ WBDLT	+	+ NRLM
	++	+	+	+	+	+	+ ASSDG	+ ARDLTM	+ FYSAGE	+	+ NRLS
	++	+	+	+	+	+	+ ASSDV	+ FYSAGE	+	+	+
	++	+	+	+	+	+	+ ASDENV	+ WDLTS	+	+	+
	++	+	+	+	+	+	+ PROD	+ ARDLTS	+	+	+
	++	+	+	+	+	+	+ RSPMNT	+ FYSAGS	+	+	+
	++	+	+	+	+	+	+ WSDLTM	+	+	+	+
	++	+	+	+	+	+	+ WRDLTM	+	+	+	+
	++	+	+	+	+	+	+ SLIS	+	+	+	+
	++	+	+	+	+	+	+ WSDLTS	+	+	+	+
	++	+	+	+	+	+	+ WRDLTS	+	+	+	+
APEX	++	+	+	+	+	+	+	+	+	+ AREAM	+
	++	+	+	+	+	+	+	+	+	+ RGRM	+
	++	+	+	+	+	+	+	+	+	+ AREAS	+
	++	+	+	+	+	+	+	+	+	+ RGRS	+

# LEGEND TO SIMULATION PROGRAM KUTUN

		UNITS -----
A1,A2,A3,A4	APICAL TISSUE FRACTIONS INVESTED IN MAINSTEM, FIRST AND NEXT SYMPODIAL LEAVES AND SQUARES.	
ABSDIE	FRACTION DIFFUSE LIGHT ABSORBED BY EQUIVALENT CROP.	
ABSDIF	IDEM BY REAL CROP	
ABSTOE	FRACTION OF TOTAL LIGHT ABSORBED BY EQUIVALENT CROP.	
ABSTOT	IDEM BY REAL CROP.	
ACT	"PHOTOS. ACTIVITY" OF AN EXPOSED LEAF IN DEPENDENCE OF AGE.	
ACTCOR	CORRECTION FACTOR FOR ACT IN DEPENDENCE OF DEPTH INSIDE CANOPY	
ADD	ADDITIONAL GLUCOSE ALLOCATION TO STRATUM HAVING SURPLUS PRODUCTION.	G GLUCOSE/M2 GROUND/DAY
AGEUNF	DEVELOPMENTAL AGE AFTER UNFOLDING	PHYS.DAYS
AI	INTERMEDIATE VARIABLE.	M2
AIO	AREA AT INITIATION OF YOUNGEST MAINSTEM LEAF.	M2
ALAER	NUMBER OF LAYERS OF LAI 0.5	
ALAI	LEAF AREA INDEX.	
ALAI DL	LAI INCREASE	
ALAIR	LAI RELATIVE TO LEAF COVERED GROUND AREA.	
ALAIT	LAI INCLUDING DROPPED LEAVES	
ALAT	LATITUDE	DEGR
ALDIF,ALDIR	LOGARITHMICALLY INTERPOLATED EDIFV,EPRIV.	
AMAXO1-AMAX10	MAXIMUM GROSS PHOTOSYNTHESIS OF INDIVIDUAL LEAVES AT DIFFERENT CANOPY LEVELS.	G CO2/M2 LEAF/SEC
AMPL	DAILY TEMPERATURE AMPLITUDE.	
ARCSA2	ARCSINE OF SAZ	
ARDLTH,ARDLTS	AREA INCREASE OF MAINSTEM AND SYMPODIAL LEAVES.	M2/DAY
AREAM,AREAS	AREA OF MAINSTEM AND SYMPODIAL LEAVES	M2
AS	GLUCOSE AVAILABLE FOR VEGETATIVE GROWTH IN CASE OF EQUITABLE ALLOCATION.	G GLUC./M2 GROUND/DAY
ASS	NET DAILY GLUCOSE PRODUCTION BY A LEAF.	G GLUC./M2 GROUND/DAY
ASDEMG,ASDEMV	GLUCOSE DEMAND FOR GEN.AND VEG.GROWTH AT A STRATUM.	G GLUC./M2 GROUND/DAY
ASSDG,ASSDV	TOTAL GLUCOSE DEMAND FOR GEN.AND VEG.GROWTH.	G GLUC./M2 GROUND/DAY
B	AUXIL.VARIABLE FOR F3.	
BASE	RELATIVE ROWWIDTH CROSSED BY A SUNRAY BETWEEN TOP AND BOTTOM OF THE CANOPY.	
BEQ	TABLE FOR GLUCOSE EQUIVALENT OF BOLL TISSUE.	G GLUC./G
BLI	BASIC LEAF INTERVAL (AT 25C CONSTANT TEMP.).	DAYS
BMP	BOLL MATURATION PERIOD AT 25C CONSTANT TEMPERATURE	DAYS
BMNT	MAINTENANCE RESP.FOR FRUITING POINTS.	G GLUC./G/DAY
BNR	BOLL NUMBER AT A POSITION.	
CO2	MEAN CO2 CONCENTRATION IN CANOPY	PPM
CONTR	CONTRIBUTION TO DIFFUSE RADIATION BY SKY SECTORS.	
DAE	DAILY PHYS.AGE INCREASE BETWEEN 5 AND 20 PHYS.DAYS AFTER UNFOLDING.	PHYS.DAYS
DAYL	DAYLENGTH	HOURS
DAYLE	CORRECTED DAYLENGTH.	HOURS
DAZ	DIFFERENCE BETWEEN ROW AND SUN AZIMUTH DIRECTION.	RADIANS
DEC	DECLINATION OF THE SUN.	RADIANS
DEF	GLUCOSE DEFICIT OF A STRATUM RELATIVE TO TOTAL PLANT AVERAGE.	G GLUC./M2 GROUND/DAY
DEM	ADJUSTED TOTAL GLUCOSE DEMAND FOR VEG.GROWTH.	G GLUC./M2 GROUND/DAY
DIFABE	AMOUNT OF DIFFUSE LIGHT ABSORBED BY EQUIVALENT CROP.	J/M2 GROUND/DAY
DIFCL	DIFFUSE VISIBLE LIGHT INCIDENT PER HOUR.,CLEAR SKY.	J/M2 GROUND/H
DIFCLT	DAILY INCIDENT DIFFUSE VISIBLE LIGHT,CLEAR SKY.	J/M2 GROUND/DAY
DIRABE	AMOUNT OF DIRECT LIGHT ABSORBED BY EQUIVALENT CROP.	J/M2 GROUND/DAY
DIRABS	IDEM BY REAL CROP	J/M2 GROUND/DAY
DKV	EXTINCTION COEFFICIENT FOR DIRECT VISIBLE LIGHT.	
DRC	DAILY INCIDENT VISIBLE LIGHT,CLEAR SKY	J/M2 GROUND/DAY
DSUN	SUN ANGLE	DEGR

EDIFV	FRACTION OF DIFFUSE LIGHT TRANSMITTED TO LAYERS.	
EPRIV	IDEM FOR DIRECT LIGHT.	
EPFE	PHOTOSYNTHETIC EFFICIENCY OF INDIVIDUAL LEAVES.	G CO2/J
EXC	FRACTION OF PHYS.DAY IN EXCESS OF START OF FLOWERING.	PHYS. DAYS
EXCDAY	FRACTION OF PHYS. DAY IN EXCESS OF BLI.	PHYS. DAYS
F1	RGR OF LOGISTIC/R2	DAY/DAY
F2	FUNCTION GOVERNING THE TRANSITION FROM EXPONENTIAL TO LOGISTIC GROWTH.	
F3	RGR OF SLW	
FFRDI	INTERPOLATED IN FRDI TABLE.	
PHROW	EFFECTIVE ROW HEIGHT	
F1	INTERMEDIATE VARIABLE	
FINTIM	LAST SIMULATION DAY	
FLI	CORRECTION FACTOR.	
FS	RATIO BETWEEN TOTAL GLUCOSE AVAILABLE AND DEMANDED FOR VEGETATIVE GROWTH (FAIR SHARE)	
FWPATH	NON-COVERED ROWFRACTION.	
FYSAGE,FYSAGE,	PHYSIOL.AGE OF FRUITING POINTS,MAINSTEM AND	PHYS.DAYS
FYSAGS	SYMPODIAL LEAVES.	
FYSDA	NUMBER OF PHYSIOL.DAYS ELAPSED.	PHYS.DAYS
GLEQLF,GLEQST	GLUCOSE EQUIVALENT OF 1G OF LEAF,STEM,ROOT AND	G GLUC./G
GLEQRT,GLEQB	FRUITING POINT TISSUE	
GPCO1-GPC10	DAILY GROSS PHOTOS.PER LAYER,CLEAR SKY.	G CO2/M2 GROUND/DAY
GP001-GP010	IDEM,OVERCAST SKY.	
GRFRAC	MULTIPLICATION FACTOR FOR WEIGHT INCREASE OF PLANT PARTS	
HFINB	VERTICAL DISTANCE PASSED THROUGH CANOPY IN LAST ROW TOUCHED BY SUNRAY	
HFIIB	IDEM IN FIRST ROW	
HO	HOURLY	HOURS
HSRISE	HOURLY OF SUNRISE	HOURS
HSUN	HOURLY SUNANGLE	HOURS
IH	INTERMEDIATE VARIABLE	
II,III	AUXILLIARY VARIABLES	
IO1-I10	INTERMEDIATE VARIABLE	
IPRINT	PRINT INTERVAL	DAYS
KK	INTERMEDIATE VARIABLE	
LL	IDEM	
LOWSYX	NUMBER OF LOWEST SYMPODIUM CARRYING NODE.	
NR	INTERMEDIATE VARIABLE	
NRIM,NRIS	NUMBER OF LEAVES ON MAINSTEM AND SYMPODIA.	
PER	AUXIL.VARIABLE,REPRESENTING PERCENTAGE	
PERO1-PER10	IRRADIANCE AS PERCENT.OF THRESHOLD AT THREE LEVELS	
PERCOV	AVERAGE FRACTION OF HOURS WITH OVERCAST SKY.	
PLM2	PLANTS PER M2	
PNC,PNO	MEAN DAILY NET GLUCOSE PRODUCTION PER M2 GROUND FOR CLOSED CANOPY UNDER CLEAR AND OVERCAST SKY,BY LAYER.	G GLUC./M2 GROUND/DAY
PNREL	REDUCTION FACTORS FOR PNMAX DUE TO LIGHT CLIMATE	
PPNC,PPNO	MEAN DAILY NET GLUCOSE PRODUCTION PER M2 LEAF IN DEPENDENCE OF LEAF POSITION IN EQUIVALENT CROP;CLEAR AND OVERCAST SKY	G GLUC./M2 LEAF/DAY
POS	INTERMEDIATE VARIABLE	
PP	AUXIL.VARIABLE FOR FUNCTION F3	
PPR	MEAN DAILY NET GLUCOSE PRODUCTION PER M2 LEAF,BY NODES	G GLUC./M2 LEAF/DAY
PPRODT	TOTAL GLUCOSE AVAILABLE FOR VEG.GROWTH	G GLUC./M2 GROUND/DAY
PROD	GLUCOSE AVAILABLE AT A STRATUM	G GLUC./M2 GROUND/DAY
PRODT	TOTAL GLUCOSE AVAILABLE FOR GROWTH AND MAINTENANCE	G GLUC./M2 GROUND/DAY
R1	RELATIVE GROWTH RATE OF MERISTEMATIC TISSUE	DAY-1
R2	RELATIVE RATE OF APPROACH OF FINAL INDIV.LEAF AREA	DAY-1
RAD	TRANSFORMATION COEFFICIENT	
RADC	MEAN HOURLY INCIDENT VISIBLE LIGHT	J/M2/H
RATEG	PHYSIOL.EQUIVALENT OF JULIAN DAY FOR BOLL GROWTH	PHYS. DAY/DAY
RATEV	IDEM FOR VEG.GROWTH	PHYS. DAY/DAY
RATEVD	IDEM DURING DAYTIME	PHYS. DAY/DAY
RAZ	ROW AZIMUTH DIRECTION	RADIANS
RCG	RELATIVE LEAF COVERED GROUND AREA OF REAL CROP	M2/M2

RCGC	IDEM OF EQUIVALENT CROP, CLEAR SKY	M2/M2
RCGO	IDEM OF EQUIVALENT CROP, OVERCAST SKY	M2/M2
RD	DAILY DARK RESPIRATION BY LAYER	G GLUC./M2 GROUND/DAY
REALDA	NUMBER OF JULIAN DAYS ELAPSED	
RED	AGE DEPENDENT CORRECTION FACTOR FOR GLUCOSE EQUIVALENT AND MAINTENANCE RESPIRATION OF TISSUES	
REDOS, RED10	CORRECTION FACTORS	
REDEX, REDEXT	REDUCTION FACTOR FOR WATER STRESS	
REDLI	INCIDENT LIGHT AS FRACTION OF THRESHOLD	
REDTIM	DEVELOPMENTAL AGE INCREMENT	PHYS. DAYS
RGR	RELATIVE GROWTH RATE	DAY-1
RGRM, RGRS	REALISED RGR FOR AREA OF MAINSTEM AND SYMPODIA	DAY-1
ROW	ROW SPACING	M
RRATEG, RRATEV	AS RATEG, RATEV; TABLE.	
RSPMNT	MAINTENANCE RESPIRATION	G GLUC./M2 GROUND/DAY
SAZ	SUN'S AZIMUTH	RADIANS
SINDAZ	SINE OF DAZ	
SL	MAINSTEM LENGTH	M
SLDLT	INCREASE OF SL.	M/DAY
SLI, SLIS	TOTAL NUMBER OF LEAF INTERVALS ACCUMULATED ON MAINSTEM AND SYMPODIA	
SLWDLT	SLW INCREASE.	G/M2/DAY
SLWM, SLWS	SPECIFIC LEAF WEIGHT OF MAINSTEM AND SYMPODIAL LEAVES.	G/M2
SLWMAX	MAX. SLW DUE TO LIGHT CLIMATE.	G/M2
SNHSS	SINE OF SUN HEIGHT	
SOLC	SOLAR CONSTANT	
SRPLUS	TOTAL GLUCOSE SURPLUS.	G GLUC./M2 GROUND
SUNCIT	DAILY INCIDENT VISIBLE LIGHT, CLEAR SKY	J/M2 GROUND/DAY
SUNDCL	DIRECT VISIBLE LIGHT INCIDENT PER HOUR	J/M2 GROUND/H
SUNCT	DAILY INCIDENT DIRECT VISIBLE LIGHT.	J/M2 GROUND/DAY
TEMP	TEMPERATURE AT SUCCESSIVE HOURS.	O C
TFH	RELATIVE VERTICAL DISTANCE PASSED THROUGH BY SUNRAY.	
TMIN, TMAX	MIN. AND MAX. TEMP.	
TBW	TOTAL WEIGHT OF FRUITING POINTS	G/M2 GROUND
TDLW	IDEM OF DROPPED LEAVES	
TLW	IDEM OF ALL LEAVES.	
TNGB	TOTAL NUMBER OF GROWING BOLLS.	
TNEB	TOTAL NUMBER OF MATURE BOLLS.	
TNSQ	TOTAL NUMBER OF SQUARES.	
TRANS	SAME AS DKV, INTERPOLATED.	
TRAT	TRANSMISSIVITY OF THE ATMOSPHERE.	
TRW	TOTAL ROOT WEIGHT	G/M2 GROUND
TSW	TOTAL STEM WEIGHT.	G/M2 GROUND
TT	TIME REQUIRED FOR LEAF INITIAL TO ATTAIN SIZE EQUAL TO PREDECESSOR'S.	PHYS. DAYS
WB	WEIGHT OF FRUITING POINT.	G/M2 GROUND
WBDLT	INCREASE OF WB.	G/M2 GROUND/DAY
WBDL1, WBDL2	INTERMEDIARY VARIABLES.	
WLACC, WLACCS	INTERMEDIARY VARIABLES	
WLDLTM, WLDLTS	INCREASE OF LEAF WEIGHT ON MAINSTEM AND SYMPODIA.	G/M2 GROUND/DAY
WLTN, WLTS	TOTAL LEAF WEIGHT BELOW A LEAF.	G/M2 GROUND
WRDLTM, WRDLTS	INCREASE OF WRTH, WRTS.	G/M2 GROUND/DAY
WRTH, WRTS	ROOT WEIGHT ASSOCIATED WITH MAINSTEM AND SYMPODIAL LEAVES.	G/M2 GROUND
WSDLTM, WSDLTS	INCREASE OF WSTM, WSTS.	G/M2 GROUND/DAY
WSTM, WSTS	STEM WEIGHT ASSOCIATED WITH MAINSTEM AND SYMPODIAL LEAVES.	G/M2 GROUND
XCO1-XC10	INTERMEDIARY VARIABLES.	
XCO1-XC10	IDEM	
XX	IDEM	
YY	IDEM	



## **ANNEX II**

### **List of publications and summaries**

## Growth and Assimilate Conversion of Cotton Bolls (*Gossypium hirsutum* L.) 1. Growth of Fruits and Substrate Demand

H. J. W. MUTSAERS<sup>1</sup>

Department of Tropical Crops, Agricultural University, Wageningen, The Netherlands

Received: 11 February 1975; Revised: 12 July 1975

### ABSTRACT

A generalized growth pattern of cotton bolls and their components is derived from data available in the literature. This pattern is used to calculate substrate requirements for dry matter accumulation and results in an estimated consumption of 138.5 g of (CH<sub>2</sub>O) and 15.4 g of amino acids per 100 g of mature boll dry matter omitting maintenance respiration. For maintenance respiration at 12 h day and 12 h night temperature of 30 and 20 °C respectively and a boll maturation period of 50 days, 26.9 g CH<sub>2</sub>O per 100 g of mature bolls is found. The rate is considerably higher in the earlier phases of boll development when primarily 'structural growth' occurs compared with later phases when 'storage growth' prevails.

## Growth and Assimilate Conversion of Cotton Bolls (*Gossypium hirsutum* L.). 2. Influence of Temperature on Boll Maturation Period and Assimilate Conversion

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Received: 11 February 1975; Revised: 12 July 1975

### ABSTRACT

A negative exponential relationship between temperature and boll maturation period (*BMP*), is hypothesized from published data. A crucial experiment was undertaken to test this hypothesis. Six groups of cotton plants were placed under different temperature regimes, half of these groups having a daily temperature amplitude of 4 °C, the remainder of 10 °C. The resulting *BMP* values showed good agreement with the hypothesis and a *Q*<sub>10</sub> of 2.46-2.56 was calculated. Since the *Q*<sub>10</sub> for maintenance respiration is about 2.2, the conversion efficiency of cotton bolls should increase slightly with increasing temperature. However, the measured increase of conversion efficiency with temperature cannot be explained from reduced maintenance respiration alone and this suggests a shift in boll composition as well. Bolls with a short *BMP* are produced at a lower cost per unit of mature dry matter than those having a long *BMP*.

## The effect of row orientation, date and latitude on light absorption by row crops

By H. J. W. MUTSAERS

*Department of Tropical Crops, Agricultural University, P.O. Box 341,  
Wageningen, Netherlands*

*(Revised MS. received 28 March 1980)*

### SUMMARY

A model study of light absorption by rectangular hedgerows with different row orientations was made.

The effect of row orientation on daily light absorption is greatest around 25° latitude. North-south orientation gives highest absorption for most of the year near the equator. At higher latitudes, up to 55°, absorption is highest with N-S orientation during the summer months and with E-W orientations for the rest of the year, but the magnitude of the difference between orientations decreases with increasing latitude. From 65° upwards, E-W orientation gives highest absorption all the year round, but the difference among orientations is minor. The effect of orientation will be smaller as cloudiness is greater.

The results of this study are wholly consistent with yield differences due to different orientations, reported in the literature.

*Field Crops Research*, **5** (1982) 000-000

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## PHOTOSYNTHESIS OF COTTON CANOPIES (*GOSSYPIMUM HIRSUTUM* L.)

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(The Netherlands)*

*(Accepted 8 September 1981)*

### ABSTRACT

Mutsaers, H.J.W., 1982. Photosynthesis of cotton canopies (*Gossypium hirsutum* L.). *Field Crops Res.*, **5**: 000-000.

An analysis is presented of single leaf photosynthesis of cotton as influenced by plant and environmental factors. The results are incorporated into a canopy photosynthesis model, which takes leaf ageing, azimuth preference, effect of open canopy and row orientation into account. Simulation results show good agreement with two sets of data from the literature, one for a closed and one for an open canopy.

Ann. Bot. (in press).

LEAF GROWTH IN COTTON (*Gossypium hirsutum* L.)

I. Growth in area of mainstem and sympodial leaves.

H.J.W. Mutsaers

Dept. Tropical Crops, Agric. Univ., P.O. Box 341, Wageningen, Netherlands.

ABSTRACT

A model is presented for growth of individual and successive mainstem leaves of cotton, based on a series of indoor experiments and data sets from the literature. Three variable parameters are used to describe individual leaf growth: Relative Growth Rate of meristematic tissue ( $R_1$ ), Relative rate of approach of final area ( $R_2$ ) and a 'position parameter' ( $t_{0.5}$ ) which governs the transition from meristematic to extension growth. Final area of a leaf does not occur in the model as a deterministic quantity but it is a result of the processes during growth. The model generates successive mainstem leaves and sympodial leaves as an integrated system. Assimilate shortages occurring in the plant operate on  $R_1$  leading to the characteristic change of final leaf area along the mainstem.

Ann. Bot. (in press).

LEAF GROWTH IN COTTON (*Gossypium hirsutum* L.)

II. The influence of temperature, light, waterstress and root-restriction on the growth and initiation of leaves.

H.J.W. Mutsaers

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ABSTRACT

The rate parameters  $R_1$ ,  $R_2$ ,  $1/LI$  and  $1/t_{0.5}$ , which characterize the growth in area of successive mainstem leaves (see preceding paper), probably all have the same temperature response. Temperature therefore only operates on the time scale. Waterstress reduces both the relative growth rate and the advance of developmental age, the latter however to a lesser extent than the former. The effect of root-restriction is explained as resulting from mineral shortage.

## CURRICULUM VITAE

H.J.W. Mutsaers werd geboren op 21 juni 1940 te Tilburg, bezocht het St. Odulphuslyceum aldaar vanaf 1953 en behaalde het einddiploma gymnasium B in 1959. Hij studeerde aan de Landbouwhogeschool te Wageningen van 1959 tot 1967 en legde in 1967 het ingenieursexamen af in de studierichting Tropische Landbouwplantenteelt met als keuzevakken Wiskundige Statistiek, Algemene Bodemkunde en Bemestingsleer, en Erfelijkheidsleer.

Hij was werkzaam als ingenieur buitenland bij de N.V. Ilaco, gestationeerd bij het Landbouw Ontwikkelingsproject Lombok in de periode 1968 tot 1971. Vervolgens was hij van 1971 tot 1974 als wetenschappelijk medewerker verbonden aan de vakgroep Tropische Plantenteelt van de Landbouwhogeschool en aanvaardde in 1975 een functie als docent aan de Ecole Nationale Supérieure Agronomique in Yaoundé, Cameroun. Na terugkeer in 1978 was hij wederom, tot oktober 1981, als wetenschappelijk medewerker werkzaam aan de vakgroep Tropische Plantenteelt.