

①

Author
Preprint

Simulation Models of Growth of Crops, Particularly under Nutrient Stress

I.P.I. colloquium
1980

Dr. F.W.T. Penning de Vries, Department of Theoretical Production Ecology, Agricultural University, Wageningen/The Netherlands

Summary

This paper considers the development of crop growth modeling, and analyzes some current models of crop growth under non optimal supply with nutrients.

Modeling of growth and production in agricultural situations without any nutrient stress received most attention till now, and models have been developed that predict growth and transpiration for those conditions fairly reliable. Some of their aspects, though, still need much improvement, such as plant morphology and assimilate distribution.

As more knowledge about availability of nitrogen and minerals in the soil becomes operational, modeling in this field is becoming more relevant for growth and production studies. Some aspects of crop production in these conditions are discussed. It appears that models of growth and production still need considerable strengthening by experimentation and modeling before they will be fairly predictive.

1. Introduction

This paper presents a brief overview of the modeling of crop growth, with an emphasis on growth and production under nutrient stress. Two viewpoints will be taken: a historical one to follow the development of models and modeling, and an analytical one to describe contemporary models at different levels of crop production.

Before these viewpoints are given, it is useful to repeat briefly the definition of some terms, and to structure the broad field of modeling by distinguishing 4 levels of crop production and by characterization of 3 levels of development of models.

A 'model' is defined as a schematic representation of a 'system', the latter being a 'coherent part of the real world'. 'Simulation' is the 'building and utilisation of models'.

Many types of models can be distinguished. Only the most important group of tangible models, that of explanatory, dynamic simulation models, will be considered in this paper. In such models, processes are described by mathematical equations. With the proper combination of those equations growth can be calculated. Such calculations are performed for relatively short time intervals, *e.g.* of 1 day, after which the computed increase in dry matter is added to the biomass already present. Changes in the leaf surface area and in stocks of soil water and soil nutrients can be computed similarly. For the next day, all calculations are repeated, accounting for the changes in biomass, leaf surface and stocks that took place and for changes in the plant environment (*e.g.* radiation) that may have taken place. Cycles of such calculations are repeat-

ed until the growing season is completed. Such models are explanatory in the sense that the simulated growth is calculated from, and hence based on, underlying physiological, physical and biochemical knowledge. Models are then used to integrate knowledge of processes fundamental to crop growth in order to compute the increase in crop biomass, and thus help to bridge levels of knowledge and fields of science (*De Wit [60]*). The models are called 'dynamic' because the growth rate throughout the growing season can be simulated with them, and not only the final production, and because the final production of the crop is not a complex, though static regression of yield to weather and soil variables. It is the resultant of interacting processes and of environmental conditions whose effects depend on their timing with respect to the current state of the crop and of the soil. The above terms and concepts are extensively discussed and elaborated by *De Wit [60]*, *De Wit and Goudriaan [62]*, *Brockington [8]* and *Penning de Vries [47]*.

For agricultural production, an elegant and practical delimitation of systems is proposed by *De Wit [63]*. He distinguishes 4 levels of plant production, ignoring diseases, weeds and pests. The systems of plant growth and crop productivity at each of these levels can be considered as belonging to one broad class. Those levels are:

Production level 1: Growth in conditions with ample plant nutrients and soil water. The crop growth rate is then determined by weather conditions and amounts to 100–350 kg dry matter ha⁻¹ day⁻¹; crop production depends on the growth rate and the duration of the growing season. This situation is sometimes realized in field experiments and in glasshouses. Major elements of this type of system are the dry weight of leaves, stems, reproductive or storage organs; major processes are photosynthesis, growth and maintenance, biomass distribution and leaf area development.

Production level 2: Plant growth is limited by water shortage part of the time and the duration of the growing season may also depend on soil water availability. This occurs on heavily fertilized soils in semi arid regions and in temperate climates. The situation is neither very common in agriculture, nor in natural ecosystems. The extra elements in this class of systems are the plant and soil water balances; crucial processes are transpiration and other processes of loss or gain of water from the soil.

Production level 3: Plant growth is limited by shortage of nitrogen (N) most of the time and sometimes by water shortage. This is quite a common situation in agricultural systems and is also normal in nature. Important elements of this class of systems are the N in the soil and in the plant; important processes are the transformation of nitrogenous compounds in the soil and other processes of the N-balance, absorption by roots, growth-availability interactions and redistribution within the plant.

Production level 4: Plant growth is mainly limited by the availability of other elements of which shortage of phosphorus (P) is most common. Growth rates are 10–50 kg dry matter ha⁻¹ day⁻¹ over a growing season of about 100 days. This situation occurs in heavily exploited areas where no fertilizer is used, such as in the poorest areas of the world. Important elements of this class of systems are the P and N contents of the soil and plants, and important processes are their transformations in the soil, absorption by roots and the response of plant growth to their absolute and relative availabilities. Though it is rare to find cases that fit exactly into any of these production levels, it

is a very practical simplification in the beginning of a study to reduce specific cases to one of them. Only in more detailed studies, the complex situation in which different limitations intertwine during growth, earns consideration.

Three stages of development of models can be distinguished in each of these situations (*Penning de Vries [47]*): preliminary, comprehensive and summary models. During its development, a model moves gradually from one stage into the next. All of these 3 stages do exist at the 1° and 2° level of crop production, but only preliminary models are developed at the levels 3 and 4.

Preliminary models have a structure and contain data that reflect current scientific knowledge about the modeled system, but they are simple because insight at the explanatory level is still vague and imprecise. As a consequence, the value of such models for prediction is quite limited. However, as modeling provides a means to make explicit and to quantify hypotheses about processes in a system, preliminary models can be useful for the development of science in showing the consistency of such hypotheses with other information. Moreover, preliminary models are a first step towards comprehensive models, which reflect systems of which essential elements are thoroughly understood and in which much of this knowledge is incorporated. Such models are often fairly good for predictive purposes, though they should be used with utmost precaution in situations that differ considerably from those in which the models were evaluated. Comprehensive models are typically intricate and little accessible for its potential users. Summary models should therefore be made of satisfactory comprehensive models. A summary model is a model of a comprehensive model: essential aspects are reproduced in a simple way, and aspects that are only marginally important are shedded. Its predictive value is about the same as that of its predecessor, but its simulated results contain much less detail and are thus more useful to non specialists.

2. A brief history of modeling growth and production

Since a little over a decade, modeling crop production and plant growth receives a fair amount of attention and had its share of publicity. At any time, models have been published that differ enormously in stage of evolution: some are well developed while others are still preliminary. This brief history emphasizes the most sophisticated models on a subject at any moment in time.

2.1 1953–1968: preliminary models

Regression models of crop productivity had been built for a long time to provide predictions of yields, and were usually based on rainfall. Scientists, seeking an explanation for such relationships, started to calculate potential and actual canopy photosynthesis on basis of the increasing operational knowledge of leaf photosynthesis. The first study was as early as 1953 by *Monsi* and *Saeki*. Preliminary growth models considered photosynthesis in detail, but calculated growth, very simple, by subtracting daily respiration from daily photosynthesis. These models were suitable for well developed leaf canopies and in good growth conditions, as leaf photosynthesis was measured in similar circumstances. Biochemical and physiological research had revealed in detail mechanisms of respiratory processes, but there was little understanding of how their rates were geared to processes in whole plants (*Beevers [6, 7]*). As

a result, crop respiration was modeled simply as a constant rate per unit plant weight or leaf area, taking care to arrive at an intuitively fair cumulative fraction of 20% (De Wit [57]), 33% (Loomis and Williams [32]) or 30% (De Wit [58]) of gross photosynthesis over the whole growing period. The limited understanding of metabolic activity and respiration restricted the predictive value of such models considerably.

Those early models did not simulate the distribution of new biomass over leaves, stems, reproductive organs and roots. Although its importance was well realized (Ross [48]), almost no mechanistic concept was available to simulate the patterns of growth of organs. Formation of plant organs was specified according to plant age or development stage. An exception was the distribution of new biomass over roots and shoots under mild waterstress, according to a 'functional balance'. This concept was included in Brouwer and De Wit's model [9] and its principle was adopted later in many other growth models.

Effects of moderate or severe water shortage on growth and production were not included in these models. Neither were effects of nutrient shortage. The leaf surface area of the crop, an important determinant of canopy photosynthesis, was not simulated but based on direct measurements. Finally lack of appropriate field observations made evaluation of these models, and the appreciation of their results, quite subjective.

Writing simulation models required considerable skill in using computers. The computer language *FORTRAN* was used predominantly for programming. Yet, simulation of micro-economic systems had already led to the development of the simulation language *DYNAMO* (Forrester [16]), that was remarkably suitable to crop physiologists.

2.2 1969–1976: comprehensive models at the production levels 1 and 2

2.2.1 Models

The models developed in agricultural research describe canopy photosynthesis, respiration and growth, and mimicked the distribution of biomass according to experimental results or attempted to simulate it. Transpiration was simulated in some of the models. Annual crops or vegetations were modeled almost exclusively, with particular emphasis on vegetative crops. Some models were set up to simulate types or crops (*ELCROS*, by De Wit et al. [59]; *SPAM*, by Sinclair et al. [54]; *ARID CROP* by Van Keulen [26]), but most were specific for certain species (such as: *SIMCOT* for cotton [1]; *SIMED* and *ALSIM* for alfalfa by Holt et al. [22] and Fick [14], resp.; *SOYMOD* for soybeans by Curry et al., [10]; *SUBGRO* by Fick et al. [13] for sugar beet.) Obviously, these models had much of their scientific content in common. *ELCROS*, *SUBGRO* and *SIMED* simulate plant growth in optimal soil nutrient and soil water conditions. *ARID CROP* and *SPAM* simulate growth at production level 2. Most other agricultural models were ment to simulate plant growth in actual field conditions, i.e. at production level 3 and in situations where also diseases and pests may play an important role. The results of such models seem of direct interest for application, but they require treatment of the whole gamma of interactions of growth with nutrient availability, water shortage and diseases. These aspects were not well understood, so that such models were necessarily inaccurate and hence difficult to evaluate. They could be extrapolated to conditions only slightly different from the one in which they originated.

In biological sciences, ambitious attempts were made to model parts of ecosystems, particularly in the Biome studies in the IBP programs in the United States of America. Examples are studies of desert ecosystems (*Goodall [17]*), tundra ecosystems (*Miller and Tieszen [38]*) and grassland ecosystems (*Innis [25]*). The Biome models had a wider scope than agricultural models, and conglomeration aspects as different as soil water and nutrients, weather, native plant species with different physiological and ecological characteristics, and species of herbivores and their predators. Consequently, plant growth received less attention, and its simulation lagged some years behind its formulation in agricultural models.

An important development in modeling crop growth was the quantification of energy requirements for growth and maintenance processes, to both of which respiration is related. *McCree [35]* quantified experimentally respiration coefficients for both processes in white clover plants, and determined subsequently such coefficients for other species and for other temperatures (*McCree [36]*). *Penning de Vries and co-workers*, prompted by inadequacies of the *ELCROS* model, published a study of plant metabolism [*41, 42, 43*] that showed how respiration coefficients for growth processes can be derived by straight forward stoichiometry from the biochemical composition of the biomass. Insight into maintenance processes was improved, but its quantification remained essentially experimental. This approach to metabolism and respiration has been adopted since in most crop growth models (*Penning de Vries [47]*).

The model *ARID CROP* (*Van Keulen [26]*) linked successfully the soil water balance with growth of the vegetation on well fertilized soils in semi arid regions. This comprehensive model simulated in detail water transport in the soil, and used a summary of C-balance processes and of potential canopy transpiration from *ELCROS* to calculate the transpiration coefficient of the canopy. Division of the crop transpiration rate by this coefficient gives crop growth. This principle has been applied since in other models at this production level.

2.2.2 Modeling

The *Trebon Conference* in 1969, organized by the *International Biological Program* (*Setlik [53]*), marked the beginning of development of comprehensive growth models. This development resulted from advances in the knowledge about the subject and by advances in modeling techniques.

A major paper in Trebon was given by *De Wit [60]* about concepts in modeling, and was followed by an excellent discussion about merits of simulation (*Waggoner [56]*). The main points of those papers are the distinction between demonstrative and explanatory models, the idea that models can serve to integrate knowledge from different levels of biological organization, and a discussion of limitations to modeling of physiological processes. The conference, and many following ones, showed a large interest in modeling and considerable optimism about its future. The latter was based, among others, on the large success of canopy photosynthesis models in the preceding years (*Farquhar [12]*). In addition, suitable computer facilities appeared to be ready for use in this field, at least in some situations. As a result, this period witnessed the proliferation of extensive and complex models.

The frequent comparison of simulation results and field data upgraded the quality of model prediction considerably. Disagreement between experimental and simulated results led sometimes to discarding the experimental results, but caused usually

reconsideration of model parameters and design of new experiments. The danger that adjusting parameters to a particular situation results in a curve fitting procedure of little value is clearly recognized (e.g. *De Wit [60]*) but not always resisted.

As a result, not all scientists were impressed by these development. *Hesketh and Jones [21]* express concern about the superficiality with which, they claim, many models were built. *Passioura [40]*, reflecting on a developing fashion of modeling, stated that 'there is a much quicker way of getting... a framework in which to hang ones research... than spending a year to create a comprehensive simulation model'. *Seligman [51]* comparing grasslands models, saw the future value of such models rather than their actual performance as a justification for modeling, and the lack of an alternative integrative approach strengtened his conclusion.

On the technical level, many modelers continued to write their simulation programs in *FORTTRAN*. It has the important advantage of being widely available but large programs are often difficult to read. Others preferred user oriented simulation languages like *DYNAMO*, or *C.S.M.P.*, (*IBM [24]*) that require less programming skill. In the *U.S. Grassland Biome*, the simulation language *SIMCOMP* (*Gustafson [19]*) was developed and intensively used.

2.3 1977-?: Comprehensive and summary models at the production levels 1 and 2, and preliminary models at the level 3

2.3.1 Modeling

Evaluation is an important issue in this period. Some important papers were written around 1977 (*Baker and Curry [2]*, *Penning de Vries [44]*, *Innis [25]*) about concepts, terminology and procedures of evaluation. It is this point in time that has been taken as the benchmark for the beginning of this period. Its end cannot yet be indicated. In theory, evaluation is treated very seriously indeed. In practice, under the pressure for quick results and due to sloppiness of modelers, only a few models are thoroughly evaluated. In fact, experiments that are only used for evaluating model behaviour and not for derivation of one or more parameters are still rare. Still, the emphasis on evaluation is quite a healthy one.

Some models grow considerably in size and complexity. Particularly models that integrate many disciplines increase in size and maintain all known detail. Their growth suggest that its users are satisfied with their behaviour, at least to a certain extent. One should keep in mind, however, that if the scope of the model increases but its transparency decreases, the advantage of modeling can turn into a disadvantage by disorienting and misleading its user. The fact that this occurred quite a few times made some modelers and many non-modelers shy away from large simulation models. This leads to an important question: how to deal with very large models? Is increasing complexity inevitable in the process of model development? Technical limitations are sometimes also a reason for this concern, but they are generally offset by technical developments. One route leading away from the dilemma of further development that brings unmanagable complexity can be the use of summary models of well studied aspects. Summary models can be a suitable replacement for comprehensive models if less detail is needed than the large model can provide. But a summary can only be made when the subject is really well understood, and as yet, few summary models of crop growth have been published (*Penning de Vries [47]*).

Many comprehensive models are published in this period. However, it is alarming that these publications are usually too brief to get a good impression of the model. Fairly complete descriptions are sometimes given in little available internal reports or uncitable literature.

2.3.2 Models

A few generalities of the developments of models are presented here; some examples of the most sophisticated models will be discussed in the next chapter. Not much progress has occurred in the last few years in modeling the C-balance processes, which are of principal interest at production level 1. Further developments are still needed in the understanding of the dry matter distribution over the organs of plants, and that of the development of the surface area of the leaves. Such improvements are necessary to make models more versatile and to predict better the yields of economic products rather than total dry matter production. The reader is referred to *Loomis et al.* [33] and *Penning de Vries* [47] for further detail.

Transpiration and soil water balance models are reviewed by *Hall* [20], *Hsiao et al.* [23] and *Fischer and Turner* [15]. Basic concepts changed little recently, and fair simulation models for growth at production level 2 are available. Models to simulate the daily course of carbon and water balances produce the effect of water stress always through stomatal closure. Some growth models that use time steps of 1 day reduce photosynthesis by a factor that depends on the average waterstress of the last day. Other models with 1 day time steps calculate growth by dividing daily transpiration by a transpiration coefficient (g water g⁻¹ dry matter). This approach seems indeed superior due to the constancy and predictability of this coefficient, particularly when transpiration is expressed relative to potential evapotranspiration (*Doorenbos and Kassam* [11]). This constancy is brought about by 1. gross photosynthesis and transpiration are almost proportional throughout the day, because stomata offer the largest diffusion resistance to both, particularly under water stress; 2. the efficiency of the growth process is unaffected by water stress; 3. the rate of maintenance respiration diminishes probably slightly as a result of the lower overall metabolic activity.

It has recently become evident that the transpiration coefficient of plants without water stress shows a similar constancy often, but not always. It is constant if stomata open and close in correspondence with the rate of photosynthesis, as the result of a regulating mechanism that maintains a constant CO₂-concentration within stomata over a wide range of photosynthetic rates (*Raschke* [48], *Goudriaan and Van Laar* [18], *Wong et al.* [64]). It has for consequence that the rate of canopy photosynthesis determines the rate of canopy transpiration under fixed atmospheric conditions, which leads to a transpiration rate in the field that is much lower than is often realized. This was shown with the model *BACROS*, that simulates such a mechanism [*Van Keulen et al.* [29)] and confirmed experimentally.

The effect of a sub-optimal N-supply to crops is studied increasingly with simulation models. Four of such models will be discussed in 3.3. Such models concentrate on the rate of absorption of N by the crop and on its concentration of N. In what way low or high N-concentrations modify the distribution of dry matter over organs, and how low concentrations reduce photosynthesis and growth is poorly understood. The problem of how the growth rate is related to the rate of uptake of N is confounded by the observation that tissues have maximum and minimum concentrations of N that diminish with age of the plant (e.g. *Penning de Vries et al.* [45]) and by fact that a part

of the absorbed N remains mobile and is translocated from old parts to growing tissues if the N-uptake by the root system becomes too low. Both aspects are not yet well-known, and the existing models of uptake, redistribution and growth are largely descriptive in nature, rather than explanatory. Examples of such models are given elsewhere [47].

Uptake of N by the crop under conditions of N-limitations is relatively fast and efficient, so that the question of uptake under conditions of N-limited growth becomes largely one of the availability of N in the soil. Reviews by *Beek* and *Frissel* [5], *Reuss* and *Innis* (in: [25]) and *Van Veen* [55] and further research by *Seligman* and *Van Keulen* [52] and *Krul* (in: [46]) showed considerable progress in the modeling of mineralization of N from soil organic matter and of immobilization back into it, and of the recovery of fertilizer N.

Modeling crop growth at production level 4 is still almost absent. The effect of P-shortage on growth and also the uptake of P by roots are even less known than those for N. One simulation model has been published for growth of a natural vegetation (*ELM*, *Sauer*, in: [25]) and it will be discussed in 3.3. It regards absolute concentrations of P in tissues. *Penning de Vries et al.* [45] suggested that the ratio of P to N in the plant may often be more relevant a variable than the absolute concentration of either of them, as these elements are functionally related in the metabolism of cells. They showed that the P/N ratio varies over a narrow range of 0.04 g P g⁻¹ N in P-starved plants to 0.15 g P g⁻¹ N in N-starved plants. This implies that the effect of P-shortage can be seen as a reduced availability of N to the crop. *Cole et al.* (in: [25]) presented an interesting preliminary model on transformations of organic P in the soil and on uptake by roots. It was coupled to the growth model of *Sauer* mentioned earlier. *Beek* [4] discussed transformations of forms of inorganic P in fertilized soils.

3. Some current crop growth models

Some examples of relatively advanced crop growth models at 3 of the 4 levels of production will be discussed. No models are published about growth limited by P-availability. For more detail, the reader is referred to the original papers and to recent reviews [33, 47].

3.1 Crop growth with ample nutrients and water

De Wit's [61] model *BACROS* may serve as an example of a comprehensive model. It simulates vegetative growth of crops at non limiting levels of soil water and soil nutrients (production level 1) on basis of standard meteorological observations. It considers neither germination nor the reproductive growth phase. It has been developed over more than a decade by *De Wit* and a team of co-workers, and was called *ELCROS* at an earlier stage. It comprises a thorough treatment of the processes of the C-balance and of transpiration. Laboratory research, literature study and frequent evaluations led to a model that simulates growth, yield and water use quite reliably over a wide range of environmental conditions for C₃ and C₄ crops. Its structure reflects cereal and grass crops, and small but specific sets of parameters and functional relationships specify the actual species under consideration. The model is adaptable to other types of species, but this has not yet been done. Like all models in this group

De Wit's model is particularly weak in the section regulation of distribution of biomass, and in the development of leaf surface area. The latter limitation is a serious handicap in simulation of the early stages of growth.

An example of a summary model at this production level is that by *Van Keulen* [27] for potential rice production. It is based on structure, data and concepts of *BACROS*. Its basic growth equation can be given as:

$$\text{growth} = (\text{GP} \times 0.68 - \text{MC} \times \text{DW}) \times \text{CE}$$

GP stands for gross photosynthesis (in $\text{kg CO}_2 \text{ m}^{-2} \text{ day}^{-1}$; 0.68 converts it to $\text{kg glucose m}^{-2} \text{ day}^{-1}$), DW for total dry weight ($\text{kg dry matter m}^{-2}$), MC for the maintenance coefficient ($\text{kg} \cdot \text{kg}^{-1} \text{ day}^{-1}$) and CE for the conversion efficiency of the growth process ($\text{kg} \cdot \text{kg}^{-1}$). *Van Keulen* distributes biomass formed over roots, leaves, stems and, after flowering, to inflorescences plus seeds in predetermined proportions and related to the physiological age of the crop. GP is calculated from standardized data. The leaf surface area, required in the photosynthesis calculation, is found by dividing the leaf weight by $0.1 \text{ kg} \cdot \text{m}^{-2}$. MC is 0.02–0.015; the effect of temperature on MC could be neglected as this model was applied in a fairly constant environment. CE depends only on the chemical composition of the biomass formed, and a value of about 0.7 is common. Final yield is calculated by proceeding with time steps of 10 days. The structure of this summary model is correct for many other crops with a determinate growth pattern; parameters and functions might need adjustment. The model is also principally correct at lower levels of productivity. However, the equation focusses on photosynthesis as the limiting factor for growth, which is then not correct. Only very cautiously may thus the above summary growth model be applied to other productivity levels.

3.2 Crop growth with ample nutrients

An example of a comprehensive model at production level 2 is *ARID CROP* by *Van Keulen* [26] and *Van Keulen et al.* [28]. It simulates the growth of annual vegetations of natural pastures in semi-arid regions with winter rains, and has also been applied to wheat. The model *SORGF* for simulation of growth of sorghum (*Maas and Arkin* [34]), designed for optimization of growth and water use during the season, has much in common with *ARID CROP*, scientifically spoken. Both simulate the water balance of a number of soil layers by accounting for rain and drainage from one layer into the next, for evaporation from the surface and for extraction of water from the rooted layers, due to transpiration. Run off of water from surfaces with a slope under intensive rain and interception were added to *ARID CROP* for its use in a summer rainfall area (*Stroosnijder*, in: [46]). Canopy transpiration is close to the potential evapotranspiration when the soil is well covered. The transpiration rate is reduced if soil water runs low in one or more rooted layers. Daily growth equals daily transpiration divided by the transpiration coefficient. The latter is equal to the ratio of the transpiration rate and the growth rate with ample water but otherwise in similar conditions. The transpiration coefficient is lower when photosynthesis determines the rate of transpiration through the regulation of the internal CO_2 -concentration in stomata [2.3.2] than when the regulation is absent. Effects of severe water stress on development, growth and death of tissues are included in *ARID CROP*, although little physiological basis exists for their actual formulation. *ARID CROP* simulates

growth and the soil water balance in winter and in summer rainfall areas fairly reliably [28, 46].

A summary model of a soil water balance and the growth of a vegetation of annuals with ample nutrients in semi-arid regions has been described by *Stroosnijder* (in: [46]). It is based on concepts and data of ARID CROP. It presents a calculation of the amount of soil water that is available to the plants over time intervals of 10 days, and computes growth by dividing the transpired water by the transpiration coefficient.

3.3 Crop growth under conditions of N- or P-limitation

Given the large amount of field experimentation and also the numerous measurements of ion uptake by plant roots, the number of simulation models that try to combine, or even to make use of all this information is still amazingly small. Only a few models for growth at this level of production were found: *GOSSYM+RHIZOS* (*Baker et al. [3]*, *Lambert et al. [31]*) for cotton, *PAPRAN* (*Seligman et al. [50]*, *Seligman and Van Keulen [52]*) and *ELM* (*Sauer, in: [25]*) for natural pastures in semi-arid regions, and *SOYMOD/OARDC* (*Meyer et al. [37]*) for soybeans. The approaches in these models differ considerably. However, there are many parameters and even processes that are poorly known in such systems so that there is sufficient freedom in the choice of parameters to let all models show a fairly realistic behaviour. This remark is not to criticize these models, as for each choice good arguments are presented, but it underlines the preliminary stage of these models. As these models are much larger than the growth-nutrients interactions discussed, their value should not be inferred from the description below.

The *ELM* model harbours the simplest description of the reduction of the growth rate by N-shortage: a reduction factor between 1 and 0 with which the potential growth rate is multiplied. The factor depends on the current N-concentration in the plants, but young plants are more reduced at any concentration than old plants are. N in tops and roots and the translocation of N from one to the other are simulated. The supporting sub-models of N-transformation (*Reuss and Innis, in: [25]*) and of P-transformations (*Cole et al., in: [25]*) in the soil and of N and P uptake are sophisticated and thoughtfully developed. The rate of uptake of nitrate ha^{-1} is a function of root biomass, the nitrate concentration in the soil solution, and of the soil water potential. The uptake of P depends on similar factors, plus on the concentration of N in the roots. Too high concentrations in the plants are avoided by reducing the rates of uptake.

The uptake of N in *RHIZOS* equals the amount of nitrate dissolved in the transpiration stream. This view neglects the contribution of diffusion to the N-supply of roots, which can be substantial (*Van Keulen, [30]*). *GOSSYM* is coupled to *RHIZOS* and calculates the potential growth rates of the organs of the cotton plant and the corresponding demands for C and for N. The actual growth rates are found by multiplication of these maximum rates by reduction factors due to C-stress and to N-stress. These factors are numerically equal to the current reserves of carbohydrates and of N divided by the demands for them, a formulation that resembles the transpiration coefficient concept. The pool of labile N is filled by uptake by roots and by 'mining' for N in older organs. In addition to growth rates, the C-stress and N-stress factor modify the morphogenetic development of the plants and control the rate of abortion of flowers.

PAPRAN computes also the growth rate by multiplication of the potential rate, derived from *ARID CROP*, by a reduction factor. This factor depends on the difference between the actual N-concentration in the tissues and the minimum concentration. The latter diminishes as the plant ages from about 2.5% to 1%. At any moment, its optimum concentration is about 2× its minimum value above which there may still be some luxurious consumption of N. The daily uptake of N by the crop is essentially equal to half its demand for N (the current weight of its biomass times the difference between its current maximum and actual N-concentration), limited only by a maximum rate of N-absorption by the crop and not exceeding the amount of N available in the soil. Redistribution of N from vegetative parts to grain occurs up to a maximum seed yield or until the minimum N-concentration of the straw is attained, and as long as weather conditions permit. The amount of N available in the soil is computed as the resultant of mineralization and immobilization of N in 10 soil layers, in which inorganic N, and N in fresh and 'stable' organic matter are considered (*Seligman and Van Keulen [52]*). The rates, efficiencies and regulations of these processes are simulated according to current knowledge. From comparisons of simulations and experiments the authors conclude that the model provides a good framework for further investigations but also that more physiological and soil micro-biological information is required before the model can be applied more widely.

SOYMOD/OARDC represents a particular case: that of a legume which assimilates N only as N_2 in its root nodules. The growth of N-free material and of proteins are simulated basically independent, but their ratios are not allowed to exceed the limits of 2% N and of 6% (8% in the seed). The rate of N-assimilation is controlled by the average level of N in the plant. Photosynthesis and growth are simulated for each node separately; both rates become reduced at all N-levels below the maximum concentration, and are 0.0 at 2% N. The basic limitation to crop growth remains thus canopy photosynthesis.

The direct effect of water shortage at these production levels is the reduction of photosynthesis and growth in all models, except in *ELM* where a direct relationship between the growth rate and the soil water potential is programmed. An indirect effect of water stress results from a reduced uptake of N, and is related to the soil water potential in *ELM* and to the transpiration rate in *RHIZOS*. This indirect effect is small in *PAPRAN* as diffusion of nitrate towards the roots is fast and plays an important role in the N-supply (*Van Keulen [30]*). (There is no N-uptake in *SOYMOD*). Both effects of water shortage reduce the final yield most when the crop was relatively well supplied with N. The reduction is only small if the final yield was limited by the small amount of N absorbed by the crop and the minimum concentration of N was attained. It is interesting to note that the transpiration coefficient of vegetation of annuals of natural rangelands in the Sahel, where production is limited by N or P, was observed to be as low as that of crops under optimal growth conditions. This is ascribed to the functioning of the stomatal internal CO_2 -concentration regulating mechanism (2.3.2, *Penning de Vries and Djiteye [46]*). Annual grasses of rangelands in the mediterranean zone do not regulate their stomata in this way (*Van Keulen, pers. comm.*), which leads to a less efficient water use. This feature of stomatal regulation has not yet been included in models at this production level.

The differences between those models indicate that modeling at the levels of crop production 3 and 4 still need considerable strengthening by research involving experimentation and modeling before they will be fairly predictive and more widely applicable.

Acknowledgements

This paper is heavily based on work from colleagues in the *Department of Theoretical Production Ecology* of the *Agricultural University*, Wageningen, The Netherlands. The authors familiarity with their work may have caused too large an emphasis on it. Mrs. *Merkelijn* helped to trace many publications on models.

4. Literature cited

1. *Anonymus*: Computer simulation of a cotton system. ARS-S-52. Agric. Res. Service, USDA, POB 5465, Mississippi State, Miss., 39762, USA, 1975
2. *Baker, C.H. and Curry, R.B.*: Structure of agricultural simulators: a philosophic view. *Agricultural Systems*, 1, 201-218 (1976)
3. *Baker, D.N., Lambert, J.R., Phene, C.J. and McKinion, J.M.*: GOSSYM: a simulator of cotton crop dynamics. In: *Computers applied to large scale agricultural enterprises*. Proc. U.S.-U.S.S.R. seminar, Moscow, Riga, Kishinev, pp. 100-133, 1976
4. *Beek, J.*: Phosphate retention by soil in relation to waste disposal. Ph. D thesis Agricultural Univ., Wageningen, The Netherlands, 1979
5. *Beek, J. and Frissel, M.J.*: Simulation of nitrogen behaviour in soils, PUDOC, Wageningen, The Netherlands, 1973
6. *Beevers, H.*: Respiratory metabolism in plants. Row, Petersen and Company, New York, 1961
7. *Beevers, H.*: Respiration in plants and its regulation. In: *Setlik*, 1970
8. *Brockington, N.R.*: Computer modeling in agriculture. Oxford Univ. Press, London, 1979
9. *Brouwer, R. and Wit, C.T. de*: A simulation model of plant growth with special attention to root growth and its consequences. Proc. 15th Easter School Agric. Sci., Univ. of Nottingham, 224-242, 1969
10. *Curry, R.B., Baker, C.H. and Streeter, J.G.*: SOYMOD I, a dynamic simulator of soybean growth and development. *Trans. ASAE*, 18 (5), 963-974 (1975)
11. *Doorenbos, J. and Kassam, A.H.*: Yield respons to water, FAO irrigation and drainage paper 33, FAO, Rome, 1979
12. *Farquhar, G.D.*: Modeling of photosynthetic reponse to environmental conditions. Vol. 14, chapter 16, *New Encyclopedia Plant Physiology* (in press). Springer Verlag, 1981
13. *Fick, G.W., Williams, W.A. and Loomis, R.S.*: Computer simulation of Dry Matter Distribution during sugar beet growth. *Crop Sci*, 13, 413-417 (1973)
14. *Fick, G.W.*: The mechanism of alfalfa regrowth, a computer simulation approach. *Search, Agriculture* 7 (3), 1-26, 1977. Cornell Univ. New York
15. *Fischer, R.A. and Turner, N.C.*: Plant productivity in the arid and semiarid zones. *Ann. Rev. Plant Physiol.* 29, 277-317 (1978)
16. *Forrester, J.W.*: *Industrial Dynamics*. MIT Press, Boston, USA, 1961
17. *Goodall, D.W.*: Ecosystem simulation in the US/IBP Desert Biome. Summer Computer Simulation Conference, Montreal, 777-780, 1973
18. *Goudriaan, J. and Van Laar, H.H.*: Relations between leaf resistance, CO₂-concentrations and CO₂-assimilation in maize, beans, Lalang grass and sunflower. *Photosynthetica*, 12 (3), 241-249 (1978)
19. *Gustafson, J.D.*: SIMCOMP 3.0. In: *Innis*, 1978 (1978)
20. *Hall, A.E.*: Mathematical models of water loss and plant water relations. Vol. 14, chapter 7, *New Encyclopedia Plant Physiology* (in press). Springer Verlag, 1981
21. *Hesketh, J.D. and Jones, J.W.*: Some comments on computer simulators for plant growth-1975. *Ecol. Model.*, 2 (3), 235-247, 1976
22. *Holt, D.A., Bula, R.J., Miles, G.E., Schreiber, G.E. and Peart, R.M.*: Environmental physiology, modeling of alfalfa growth. 1. conceptual development of SIMED. Res. Bull. 907, Purdue Univ., Indiana, USA, 1975
23. *Hsiao, T.C., Fereres, E., Acevedo, E. and Henderson, D.W.*: Waterstress and dynamics of growth and yield of crop plants. In: *Ecological Studies* vol. 19, *Lange, Kappen and Schulze*, eds. Springer Verlag, Berlin. pp. 281-305, 1976

24. *I.B.M.*: Continuous System Modeling Program III, General system information manual (GH19-7000) and Users manual (SH19-7001-2). IBM data processing div., 1133 Westchester Avenue, White Plains, NY 10604, USA, 1975
25. *Innis, G.S.*: ed. Grassland simulation model. Springer Verlag, New York, 1978
26. *Keulen, H. van*: Simulation of water use and herbage growth in arid regions. Simulation Monograph, PUDOC, Wageningen, The Netherlands, 1975
27. *Keulen, H. van*: A calculation method for potential rice production. Contr. Centr. Res. Inst. Agric. Bogor 21, Central Research Institute for Agriculture, Bogor, Indonesia, 1976
28. *Keulen, H. van, Seligman, N.G. and Benjamin, R.W.*: Simulation of water use and herbage growth in arid regions; a reevaluation and further development of the model ARID CROP. Agric. Systems (1980)
29. *Keulen, H. van, Van Laar, H.H., Louwerse, W. and Goudriaan, J.*: Physiological aspects of increased CO₂-concentration. *Experientia* (1980)
30. *Keulen, H. van*: Modeling the interaction of water and nitrogen. Proc. ICARDA symposium 'Increasing the effectiveness of water and nitrogen in rainfed farming systems in mediterranean type environments., *Webb, ed.* (1980)
31. *Lambert, J.R., Baker, D.N. and Phene, C.J.*: Dynamic simulation of processes in the soil under growing row crops: RHIZOS. In: Computers applied to the management of large scale agricultural enterprises. Proc. U.S.-U.S.S.R. seminar, Moscow, Riga, Kishinev, 1976
32. *Loomis, R.S. and Williams, W.A.*: Maximum crop production, an estimate. *Crop Sci.*, 3, 67-72 (1963)
33. *Loomis, R.S., Rabbinge, R. and Ng E.*: Explanatory models in crop physiology. *Ann. Rev. Plant Physiol.* 30, 339-367 (1979)
34. *Maas, S.J. and Arkin, G.F.*: Users guide to SORGF, a dynamic sorghum growth model with feed back capacity. Program and model documentation 78-1. Texas Agric. Exp. Station, Texas A+M Univ. Texas, USA, 1978
35. *McCree, K.J.*: An equation for the rate of respiration for white clover plants under controlled conditions. In: *Setlik*, pp. 221-231, 1970
36. *McCree, K.J.*: Equations for the rate of dark respiration of white clover and grain sorghum as functions of dry weight, photosynthetic rate and temperature. *Crop Sci.*, 14 (4), 509-514 (1974)
37. *Meyer, G.E., Curry, R.B., Streeter, J.G. and Mederski, H.J.*: SOYMOD/OARDC, a dynamic simulator of soybean growth, development and seed yield, I. Res. Bull. 1113, Ohio Agric. Res. Devel. Center, Wooster, Ohio, USA, 1979
38. *Miller, P.C. and Tieszen, L.L.*: A preliminary model of factors affecting primary production in the arctic tundra. *Arct. Alp. Res.*, 4, 1-18 (1972)
39. *Monsi, M. and Saeki, T.*: Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Jap. J. Bot.*, 14, 22-52 (1953)
40. *Passioura, J.B.*: Sense and nonsense in crop simulation. *J. Aust. Inst. Agric. Sci.*, 39, 181-183 (1973)
41. *Penning de Vries, F.W.T., Brunsting, A.B. and Van Laar, H.H.*: Products, requirements and efficiency of biological synthesis, a quantitative approach. *J. Theor. Biol.* 45, 339-377 (1974)
42. *Penning de Vries, F.W.T.*: The cost of maintenance processes in plant cells. *Ann. Bot.* 39, 77-92 (1975)
43. *Penning de Vries, F.W.T.*: Use of assimilates in higher plants. In: *Photosynthesis and productivity in different environments. Cooper, ed.* Cambridge Univ. Press, Cambridge, UK, pp. 459-480, 1975
44. *Penning de Vries, F.W.T.*: Evaluation of simulation models in agriculture and biology: conclusions of a workshop. *Agricultural Systems* 2, 99-107 (1977)
45. *Penning de Vries, F.W.T., Krul, J.M. and Van Keulen, H.*: Productivity of Sahelian grasslands and the availability of nitrogen and phosphorus from the soil. In: *Nitrogen cycling in West African ecosystems. Proc. SCOPE-UNEP Nitrogen Unit Workshop, Ibadan. Rosswall ed.* Roy. Swed. Acad. Sci. 1980
47. *Penning de Vries, F.W.T.*: Modeling growth and production. Vol. 14, chapter 17. *New Encyclopedia Plant Physiology* (in press). Springer Verlag.
48. *Raschke, K.*: Stomatal action. *Ann. Rev. Plant Physiol.* 26, 309-340 (1975)
49. *Ross, Y.R.*: Mathematical description of plant growth. *Doklady Akademii Nauk. SSSR* 17, 481-483 (1966)

50. *Seligman, N.G., Keulen, H. van and Goudriaan, J.*: An elementary model of nitrogen uptake and redistribution by annual plant species. *Oecologia* 21, 243-261 (1975)
51. *Seligman, N.G.*: A critical appraisal of some grassland models. In: Critical evaluation of systems analysis for research and management. *Arnold and De Wit*, eds.: Simulation Monograph, PUDOC, Wageningen, The Netherlands, 1976
52. *Seligman, N.G. and Van Keulen, H.*: PAPRAN, a simulation model for annual pasture production limited by rainfall and nitrogen supply. In: Models for behaviour of nitrogen in soils and uptake by plants. Frissel and Veen eds., PUDOC, Wageningen, The Netherlands (in press)
53. *Setlik, I.*: Prediction and measurement of photosynthetic productivity. Proc. IBP/PP Tech. meeting Trebon, PUDOC, Wageningen, The Netherlands, 1970
54. *Sinclair, T.R., Allen, L.H. and Stewart, D.W.*: A simulation model for improving crop productivity. Summer Computer Simulation Conference, Boston, 784-794, 1971
55. *Veen, J.A. van*: The behaviour of nitrogen in soil. Ph. D. thesis Agricultural Univ., Wageningen, The Netherlands, 1977
56. *Waggoner, P.E.*: Consultation on how models are made, how they are tested and what they tell us of experiments to be done. In: *Setlik*, 1970, pp. 575-579
57. *Wit, C. T. de*: Potential photosynthesis of crop surfaces. *Neth. J. Agric. Sci.* 7, 141-149 (1959)
58. *Wit, C. T. de*: Photosynthesis of leaf canopies. Agr. Res. Rep. 663, PUDOC, Wageningen, The Netherlands, 1965
59. *Wit, C. T. de, Brouwer, R. and Penning de Vries, F. W. T.*: The simulation of photosynthetic systems. In: *Setlik*, 1970, pp. 47-70
60. *Wit, C. T. de*: Dynamic concepts in biology. In: *Setlik*, 1970, pp. 17-23
61. *Wit, C. T. de*: Simulation of assimilation, respiration and transpiration of crops. Simulation Monograph. PUDOC, Wageningen, The Netherlands, 1978
62. *Wit, C. T. de and Goudriaan, J.*: Simulation of ecological processes. Simulation Monograph, PUDOC, Wageningen, The Netherlands. (Japanese edition from: Kodansha Ltd., Tokyo), 1978
63. *Wit, C. T. de*: In: Production primaire au Sahel. *Penning de Vries and Djiteye*, eds., Agric. Res. Rep. (in prep.), PUDOC, Wageningen, The Netherlands, 1980
64. *Wong, S.C., Cowan, I.R. and Farquhar, G.D.*: Stomatal conductance correlate with photosynthetic capacity. *Nature* 282, 424-426 (1979)