SIMULATION MODELS FOR PLANT PRODUCTION.

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By

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#### INTRODUCTION

A generally accepted definition of simulation is: the building of a model and the studying of its dynamic behaviour. Simulation is a useful tool in plant production studies, if it increases insight in the relevant processes, when it leads to the design of new experiments or to extrapolate knowledge from investigated areas to areas where no experiments are available (De Wit, 1970).

A model is a simplified representation of a system. The relevancy of processes to be considered is determined by the boundaries of the system under consideration and the purpose of the simulation. The boundaries are preferably chosen in such a way, that there is no interaction between the system and its environment. In many cases, however, this is impossible and then the boundaries are chosen such, that the environment may influence the system in a known way, but not the reverse. In the crop growth model for example, the macro climate is a driving force and influences the micro climate and crop growth but these do have only small influence on the macro climate.

A model should account for most relevant phenomena and should not contain assumptions which are false. Although this seems obvious, many analytical models are based upon assumptions known to be wrong, to facilitate a solution. With proper simulation techniques, such limitations are mostly overcome and the efforts can shift from the technique to find a solution to the study of the model and hence of the system.

It may at first sight seem contradictory, to use a digital computer, in which all operations are discrete and take place in a fixed order, to simulate natural, continuous and parallel processes. The main aim of simulation languages is, to overcome these limitations of digital machines. For this purpose, it is recognized, that a system can be characterized by state variables and that all rates of change depend on the state of the system and are not mutually dependent. Thus, N equations with N unknowns do not occur in the structure of a simulation program. Therefore a routine may be introduced that sorts the given statements in computational order. Only after all rates of change have been calculated from the state at time t, the integration is performed in a semi-parallel fashion over a short time interval  $\Delta t$ , to arrive at the state at time  $t+\Delta t$ . The inevitable errors, introduced by the use of finite time intervals  $\Delta t$ , can be kept within reasonable limits by using proper numerical integration methods. Several of such methods are available. In simple systems, like the growth of two yeast species, in a mixed culture, which only interfere through the production of alcohol, it is fairly easy to define the relevant state variables and to specify the qualitative relationships. The definition of the exact mathematical relations between rates and state variables is another task (De Wit & Goudriaan, 1974).

It is no problem to make complicated models of complicated biological systems. However, such models are unwieldy, because the time constants of included processes may be a factor 10<sup>7</sup> apart and because proper validation soon becomes impossible. Moreover simplification is necessary because of lack of understanding of the relevant processes. It is prudent and more realistic to build only models with limited purpose, that can be evaluated with the experimental technique and equipment that is available. Of course it is always possible to study certain processes separately in models with higher resolution and to incorporate results of these in the main model. Examples of this hierarchical approach are the work of Penning de Vries (1973) on respiration and the micrometeorological work of Goudriaan (1972). Simulation without experimentation and validation is a waste of time.

#### DESCRIPTION OF THE PLANT GROWTH MODEL

In figure 1 a simplified relational diagram of the model is given. The model calculates the total dry matter production and the transpiration of a growing canopy in the vegetative stage from basic physical, physiological and chemical plant properties and macrometeorological data from standard weather stations. So far, not much attention has been paid to the distribution of dry matter between the various organs of the plant. The morphological properties of the crop are not simulated, but the leaf area index is given as a forcing function.

The basic data are determined from experiments under controlled conditions and then used to simulate the field situation. The field experiments are in principle not used to adapt parameters, but to validate the model.

#### Photosynthesis

The photosynthesis of the canopy is calculated by adding the photosynthetic rates of a number of leaf layers with known LAI. In the separate leaf layers, allowance is made to distinguish between leaves at different angles with the sun and between sunlit and shadowed leaves. The intensity of the visible light - divided into direct and diffuse - is calculated from the measured intensity at screen height, knowing the scattering coefficient of the leaves, and assuming an exponential extinction with depth in the crop, depending on the leaf angle distribution.

From this light intensity and a CO<sub>2</sub> assimilation lightresponse curve for individual leaves, characterized by the quantum efficiency at low light intensities and a saturation value at high intensities, the rate of photosynthesis is calculated. This rate is dependent on the internal resistance, the stomatal resistance, the resistance of the laminar layer above the leaves and a resistance for turbulent transport above the canopy. To calculate the internal resistance, the temperature and the age of the leaves is taken into account. Allowance is made for adaptation of the photosynthetic apparatus to different temperature regimes.

The stomatal resistance is derived from the water status of the canopy and the light intensity. At present a simple function is used, in which either of the two variables is limiting (experimental evidence has led to the working assumption that stomatal resistance is governed by the  $CO_2$  concentration in the stomatal cavity. The hypothesis is, that the plant regulates the resistance in such a way, that a constant internal concentration is maintained as far as possible). The laminar resistance above the leaf layer is derived from the windspeed and the average size of the leaves.

The resistance for turbulent transport from the canopy to the atmosphere is calculated from the windspeed, taking into account the height of the crop and the stability of the atmosphere.

A constant  $CO_2$  concentration in the air is assumed throughout the crop. The primary photosynthetic products are accumulated in the reserves, which consist of soluble carbohydrates.

#### Transpiration

Analogous to the photosynthesis, the canopy transpiration is calculated by adding the transpiration rates of individual leaf layers. In each layer this rate is derived from the absorbed radiation, the vapor pressure deficit in the ambient air and the resistance for vapor transport to the atmosphere. This includes the same elements as in the photosynthesis except for the internal resistance.

The heat balance of the leaves provides also the leaf temperature, used in the photosynthesis calculation. From this, an average crop temperature is calculated used in the temperaturedependent growth processes.

Crop water status

The water status of the crop is calculated from the balance between transpiration and water uptake from the soil. The uptake is dependent on the difference in water potential between the soil and the plants, and on the resistance of the roots (the resistance of the stem for water flow is of minor importance). The root resistance is calculated from the amount of roots and the degree of suberization. Soil temperature is taken into account. In this model optimal soil water conditions are assumed. A somewhat different approach is used to calculate the productivity under conditions where water may be a limiting factor.

### Crop growth

Growth is defined as increase in dry weight of the structural material. The growth rate of the canopy is calculated on basis of a constant relative consumption rate of the reserves and is dependent on the temperature and the crop water status.

The respiratory losses, both due to growth respiration and to maintenance respiration are taken into account. Both processes are temperature dependent and allowance is made for the chemical composition of the material. The division of the newly formed material between shoot and root is governed by the functional balance principle of Brouwer (1963) and depending on the water status of the canopy and the temperature of the roots.

Roots

The roots give many problems. A study of their lifetime, their suberization rate and decay rate is at present part of a project in our department. Until now, intelligent guesses for these variables are used, where these processes are depending on the soil temperature.

Experimental evaluation

Some of the above described processes are fast and require short term experiments with a high resolution in time to be validated, while others have a much longer time constant and must be validated in long term experiments.

The short term experiments are carried out with crop enclosures in the field, using a mobile equipment (Louwerse & Eikhoudt, 1974). Especially the rate of  $CO_2$ -assimilation and respiration and the transpiration rate are evaluated. The long term experiments, validating the above ground dry matter production are carried out with periodic harvests.

#### **RESULTS AND DISCUSSION**

Experiments with the crop enclosure were carried out last spring and summer in The Netherlands.

The first figures refer to an experiment on May 22, in a field of winter wheat, variety Orca. The development stage was boot stage while the leaf area index was  $\pm$  4.5. In figure 2 a comparison is shown between the measured and simulated CO<sub>2</sub> concentration of the air, leaving the enclosure. The concentration of the incoming air is given for comparison. In figure 3 these data are converted into net photosynthesis rates.

In general, the simulated and measured values agree within 15 %. The biggest deviations occur when the sun is low, probably because part of the canopy surrounding the chamber is damaged by installing the measuring equipment. It is difficult to calculate the exact radiation climate in such a stand. In this case it was assumed that the enclosure was not surrounded by plants at all, which is an oversimplification, causing an overestimation of photosynthesis.

During daytime the rate of respiration is measured by covering the enclosure with a black cloth. The observed and simulated rates are in close agreement, both during day and night. It is worthwhile to note, that recent work of Penning de Vries (1974) indicated that the cost of maintenance in a fast growing canopy like this, may amount to 3-4 % of the dry matter present. As shown this experiment supports this view.

Figure 4 shows the result of a temperature experiment under otherwise the same conditions. At the lower temperature  $(15^{\circ}C)$ , the rate

of photosynthesis is higher than at  $\pm 23.5^{\circ}$ C. Here we face another problem: the data collected under controlled conditions show hardly any influence of temperature on photosynthesis of wheat between 15 and 25°C. Apparently in the field situation this does not hold. The inverse phenomenon is observed in maize experiments. This may be due to the fact that the pretreatment of field plants is different and that the plants have an ability to adapt to such circumstances. Another possibility is, that these relations depend on the development stage of the plant. Both these factors are not included in this model. This part thus leads to the design of experiments in which the temperature reactions are investigated more thoroughly.

In figure 5 the measured and simulated transpiration rates are compared. Because of the rather inaccurate way of measuring, this is done in hourly periods. Here again the values are within 15 %. Some bigger deviations occur here, mainly because measurement by water collection from the condenser reacts slowly to sudden changes in conditions.

A second set of measurements was carried out on June 20, in a field of summer wheat, variety Fundus; stage of ear emergence. In figure 6 the measured and calculated rates of photosynthesis are compared. It is obvious that the discrepancies are here larger than in the first example. Comparison of the rates of transpiration shows that here the deviations are in the same order of magnitude as in the previous experiment. It seems justified therefore to attribute the differences in photosynthesis mainly to differences in photosynthetic capacity. Figure 7 shows the relative importance of the saturation value of photosynthesis of the individual leaf. A decrease of  $\pm 30$  % in the saturation rate of photosynthesis - here from 40 kg ha<sup>-1</sup> hr<sup>-1</sup> in the dashed line, to 28 kg ha<sup>-1</sup>hr<sup>-1</sup> with the solid line - causes a reduction in net photosynthesis of  $\pm 15$  % over a daily period with high radiation.

The variety Orca (figures 1-4) would produce about 250 kg dry matter ha<sup>-1</sup>day<sup>-1</sup>. The variety Fundus under the same conditions + 190 kg dry matter ha<sup>-1</sup>day<sup>-1</sup>. Unfortunately no photosynthesis-light response curves of this particular variety were available.

It should, however, be noted, that if differences in this order of magnitude exist, between different varieties, it would be possible to find considerable differences in dry matter production in the field, which is as yet not the case.

It is concluded that simulation applied in studies of crop productivity has great advantages. It pinpoints to areas where our understanding is limited or where knowledge is lacking. Furthermore it shows the quantitative consequences of new opinions in a very lucid manner.

However, without proper experimentation and evaluation the technique leads to futile number shuffling.

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### LITERATURE

between overground and underground plant parts. Jaarboek I.B.S., 31-39. Goudriaan, J. and P.E. Waggoner 1972 Simulating both aerial microobservations above the foliar canopy. Neth. J. agric. Sci. 20, 104-124. Louwerse, W. and J.W. Eikhoudt 1974 A mobile laboratory for measuring photosynthesis, respiration and transpiration of field crops (in press). Penning de Vries, F.W.T. 1973 Use of assimilates in higher plants. In: Photosynthesis and productivity in different environments. I.B.P. Photosynthesis Meeting. Aberystwyth, 1973. Penning de Vries, F.W.T. 1974 The cost of maintenance processes in plant cells. Annals of Botany (in press). 1970 Dynamic concepts in biology. In: Prediction and measurement of photosynthetic productivity. Proceedings IBP/PP Technical Meeting, Trebon, Pudoc, Wageningen.

Pudoc, Wageningen.

Brouwer, R.

- Wit, C.T. de
- Wit, C.T. de and J. Goudriaan
- 1974 Simulation of ecological processes.

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- - 1963 Some aspects of the equilibrium
  - climate and soil temperature from

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### CAPTIONS

# Fig. 1

Simplified relational diagram of the crop growth model.

# Fig. 2

Comparison between measured (VPMO) and simulated (VPMUT) concentration of  $CO_2$  in the air leaving the enclosure. VPMCO<sub>2</sub> indicates the  $CO_2$  concentration in the incoming air.

# Fig. 3

Comparison between measured (NPHOTM) and calculated (NPHOTH) net photosynthesis rates of Fundus wheat on May 22.

# Fig. 4

The influence of the temperature inside the enclosure on the  $CO_2$  concentration of the outgoing air. Concentration in the incoming air is the same.

# Fig. 5

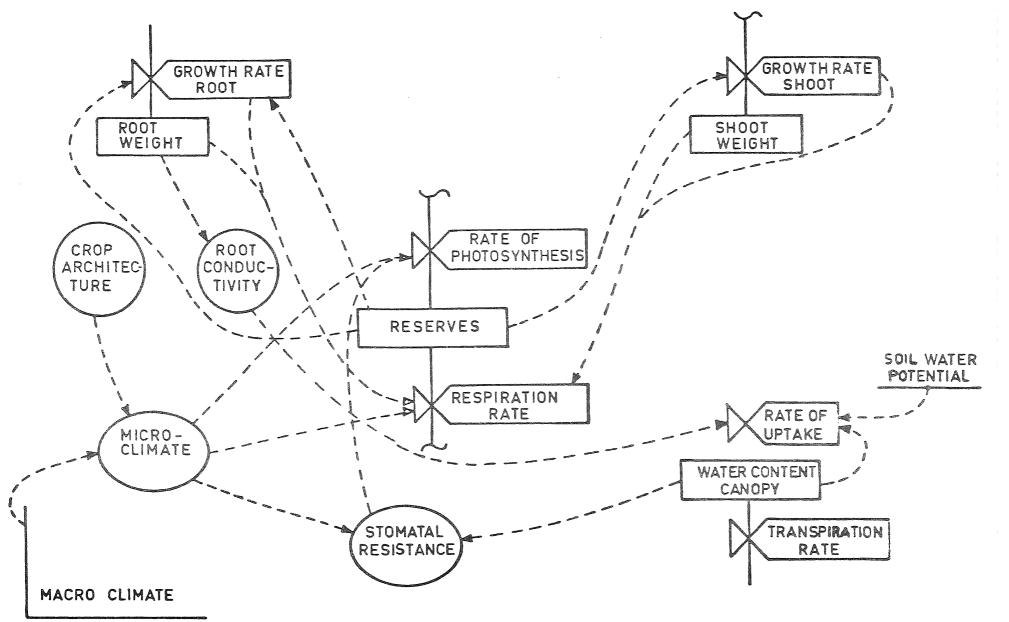
Comparison between measured (WLOSSM) and calculated (TRANSO) transpiration rates of Fundus wheat on May 22.

# Fig. 6

Measured (NPHOTM) and calculated (NPHOTH) net photosynthesis rate of Orca wheat on June 20.

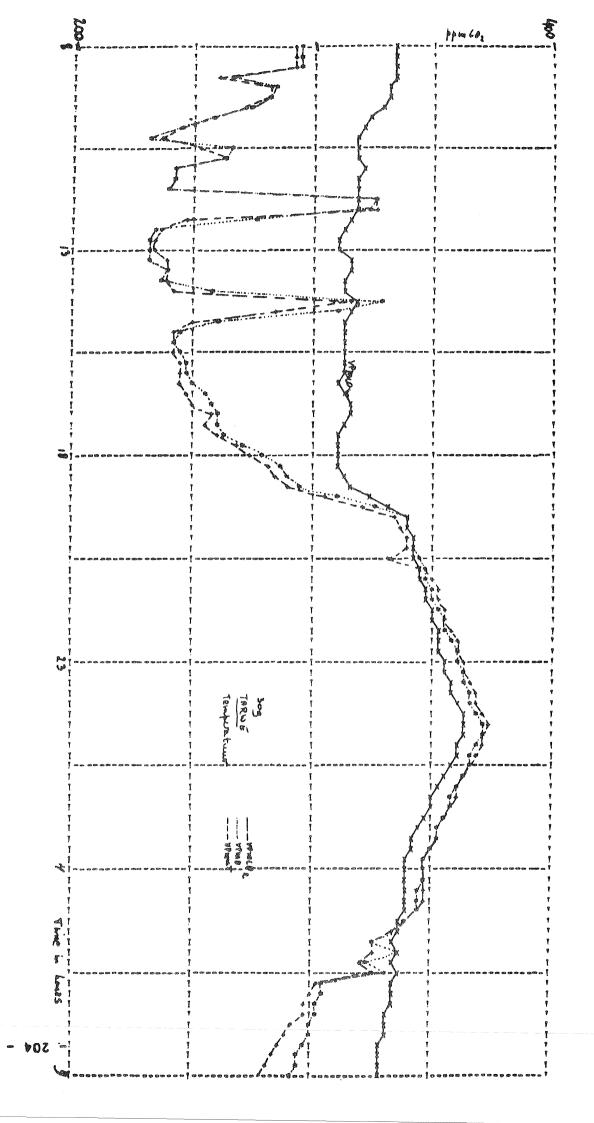
### Fig. 7

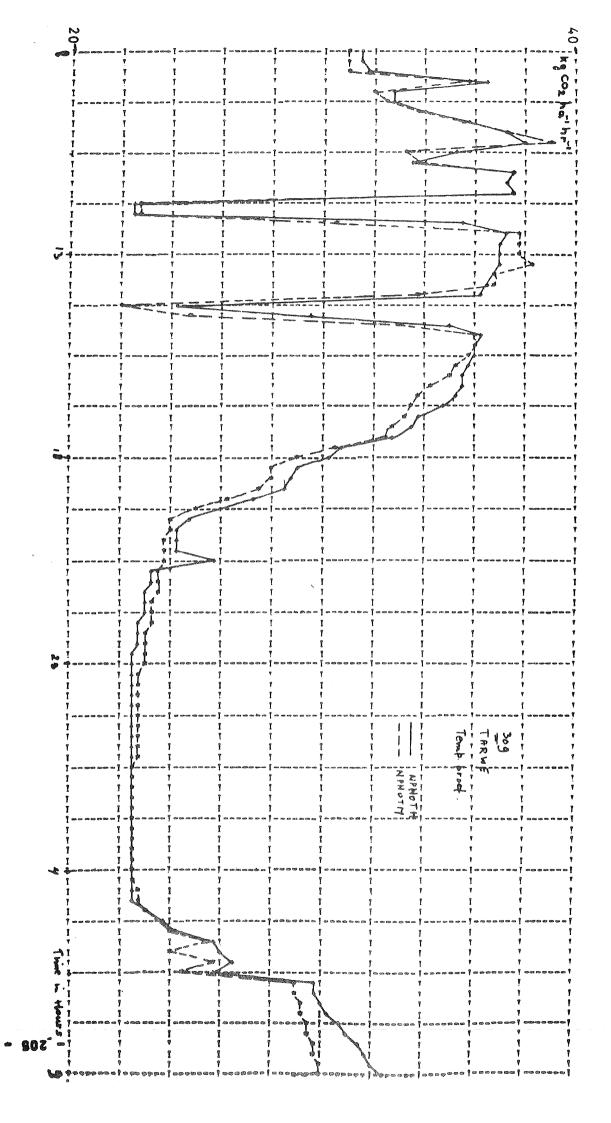
Effect of the light saturation value of photosynthesis (AMAX) of the individual leaf on the simulated net photosynthesis rate of Orca wheat on June 20.

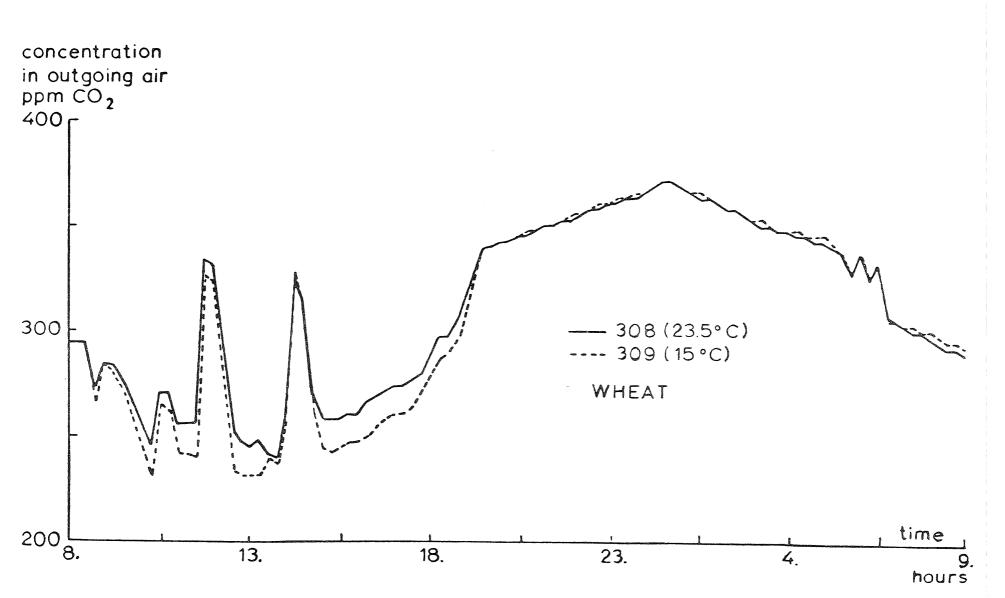


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