# The simulation of photosynthetic systems

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## Abstract

A model is described to simulate the growth of a maize crop. After evaluating physiological data, programming aspects are discussed. The simulation language is CSMP.

The photosynthetic rate of the crop surface is calculated from the amount of light, the light distribution, photosynthetic function, leaf area, and temperature. The leaves grow at the expense of photosynthetic products. Growth rate is made dependent on the age of the tissue, the amount of reserve products, the availability of water and temperature. Respiration is the sum of growth respiration (calculated from the growth rate of the plant), and maintenance respiration; their relative contributions are discussed.

Results of simulation of field trials in different places agree reasonably well with reality.

## Introduction

In some previous publications (de Wit & Brouwer, 1968; Brouwer & de Wit, 1969) the purposes of an ELementary CROp growth Simulator (ELCROS) were discussed and attention was given to those aspects that govern the functional balance that exists between the growth of the shoot and the root. ELCROS is designed according to the general principles of biological model-building, discussed in the opening paper of this symposium.

It is assumed that a crop, or each plant of a crop, contains a pool of reserves. The PHotosynthetic Rate is the only source of reserves (carbohydrates), whereas the reserves are used for ReSPiration, Growth of Root Weight, Growth of Leaf Weight and Growth of STem weight. These rates of changes are presented by valve symbols in the relational diagram of fig. 1. Photosynthesis and respiration transfer material from the surroundings, but the growth rates transfer carbohydrates from the reserve pool to sthe structural Weight of the RooTs, LeaVes and STem, i.e. into organic material that cannot be classified as reserves. These levels or contents of integrals are presented within rectangles. The manner in which the root growth may depend on conditions is presented in the diagram. The Temperature of the Soil is obtained from observations or out of the meteorological chapters of the program and the Relative Growth Rate of the Roots is obtained from a graph which differs for different species. This is not a rate to update a level, but an auxilliary value necessary for further computations and as such presented in a circle. The Possible Growth rate of the Root

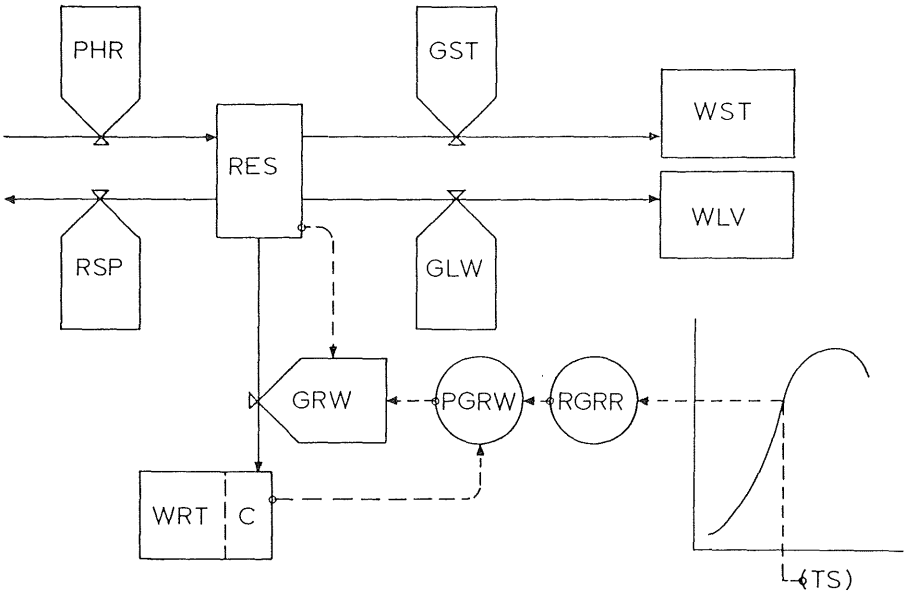

Fig. 1. The relational diagram of the central part of ELCROS.

Weight is now calculated by multiplying the relative growth rate by the Weight of the RooTs that are still so young that they are Capable of growth. This possible growth rate, again an auxilliary value, is only realized as an actual Growth rate of the Root Weight, when there are sufficient reserves. It is noted that in this way of presentation, the flow of organic material (kg $CH_2O$ $ha^{-1}$ $day^{-1}$) is presented by full drawn arrows and the flow of information by dotted lines. Taking into account the 24 hour rhythm of the weather, it may be supposed that rates which are calculated for a given moment do not change materially for a period of about an hour, so that the time in this simulation model may be advanced with time steps of this order.

Operating versions of ELCROS are available in the languages DYNAMO and CSMP 360. In subsequent sections CSMP-conventions are used to express relations.

A simulation programme of this type must be regarded, for the time being, more as a guide to research than as a final stage. Many ad hoc suppositions regarding the underlying physiological mechanisms have to be made and it is the purpose of this paper to accentuate these to provoke discussion. Special attention will be given here to some aspects governing the rate of photosynthesis, the rate of leaf growth and the rate of respiration. The interrelations between shoot and root growth have been treated elsewhere (Brouwer & de Wit, 1969), whereas meteorological aspects have to be discussed later.

## The photosynthetic rate

The calculation of the instantaneous photosynthetic rate in dependence of the light conditions, the canopy architecture, the amount of leaves and the photosynthetic properties of the leaves are being discussed in other papers of this symposium, so that it suffices here to make some general remarks.

The problem consists out of two parts. At first, the light distribution over the indivudual leaves of a crop has to be calculated and then the photosynthetic rate of the crop is obtained by addition of the photosynthetic rate of each leaf, calculated by means of its photosynthetis function.

The evaluation of the light distribution is a purely geometrical problem, which has been solved to a large extent, as is illustrated by fig. 2, in which the measured and calculated transmission and reflection rates inside a corn crop are presented, calculation being based on measurement of the reflection and transmission coefficients of individual leaves and the leaf distribution function. Although the architecture of the canopy may vary during the growth of a crop, the influence of this should not be over-emphasized. For instance, the leaves of grass varies from very erectophile for short swards in spring to very planophile for long swards in autumn. However, if it is supposed that the photosynthetic function is the same, this large difference in leaf distribution leads under Dutch conditions only to a difference in gross photosynthesis of 25–50 kg $CH_2O$ $ha^{-1}$ $day^{-1}$, on a total of about 375 kg $ha^{-1}$ $day^{-1}$ (de Wit, 1965).

The influence of the photosynthesis function of the individual leaves is more important because of its variability; if the photosynthetic efficiency of leaves of a crop remains the same at low intensity, but the maximum photosynthesis increases by 100 %, then the photosynthesis of the crop may increase by about 50 % (de Wit, 1965).

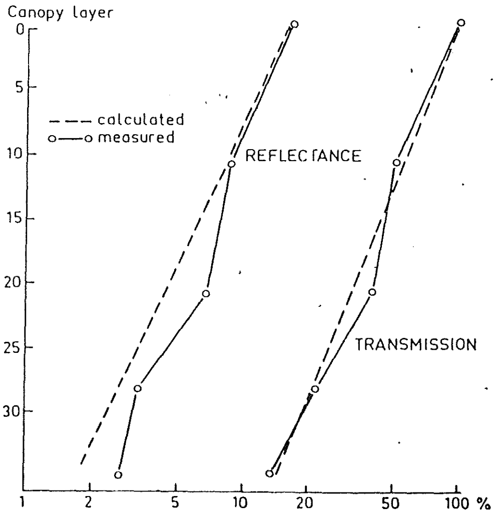

Fig. 2. Calculated and measured transmission and reflection in a corn crop with a leaf area index of 3.5; 1 canopy layer = 0.1 LAI (Idso & de Wit, 1970).

It has been often observed, an example being given in fig. 3, that the photosynthetic rate of the leaves of a plant depends to a considerable extent on leaf age or leaf position along the stem. It is impossible to account for this at present, because the distribution of leaves of different ages throughout the canopy for the main plant species is not known. Moreover, neither the technique of measuring and characterization of this distribution, nor the programs to evaluate the influence of this distribution on crop photosynthesis have been developed.

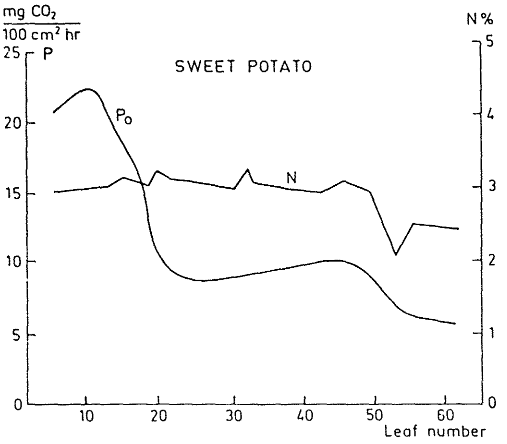

Fig. 3. Variation of the photosynthetic activity (P) and nitrogen content (N) at high light intensity and the contents of the main nutrients with leaf position, numbered from the top expanding leaf onwards (Tsuno & Fujise, 1963).

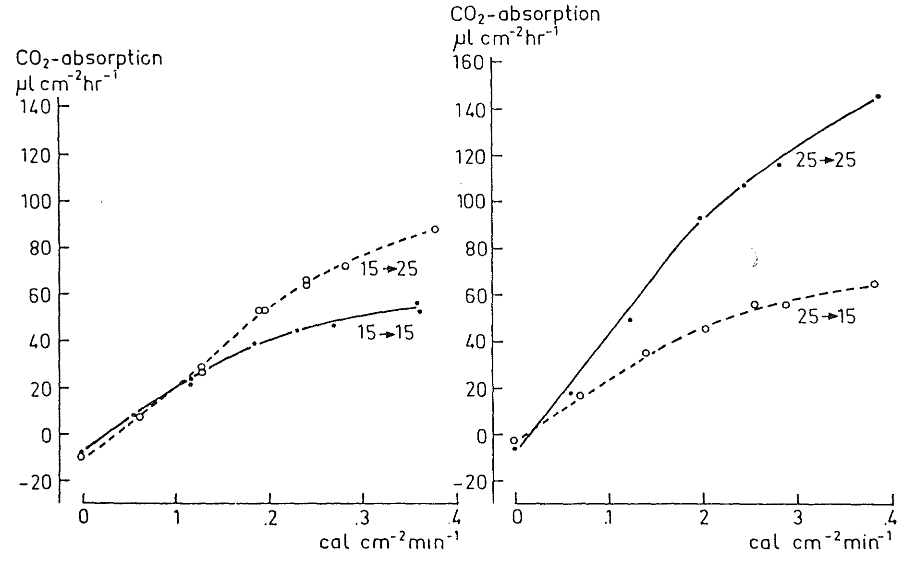

Fig. 4. The photosynthesis of corn plants per unit leaf surface at 15 and 25°C and after switching from 15 to 25 and 25 to 15 C (Brouwer, unpublished).

In ELCROS we neglect at present the effect of ageing and calculate the instantaneous photosynthetic rate (PHR in fig. 2), by means of the numerical method described by de Wit (1965), it being supposed that each leaf has a certain life-span, but that otherwise the photosynthesis function does not change with age.

As far as the influence of temperature on photosynthesis is concerned, the instantaneous effect of temperature is taken into account. However, it is neglected that the temperature regime during the formation of leaves has an effect on their rate of photosynthesis afterwards (fig. 4).

### Programming aspects

It takes of course an excessive and unnecessary amount of computing time, when for each hour of simulation the crop photosynthesis is numerically calculated from the basic data. Instead calculations are done once and summarized in a two-entry table with the Area of the LeaVes and the SINE of the height of the sun as entries. One table is used for clear skies and an other for overcast skies. The height of the sun at the hourly intervals is calculated from the latitude, the day of the year and the hour of the day according to the well-known astronomical formula (de Wit, 1965), the condition of the sky is obtained from the weather section of the simulation program and the area of the leaves from the leaf growth section in ELCROS. The crop photosynthesis data in table 1 are obtained by supposing that the leaf distribution function is slightly plagiophile (de Wit, 1965), the scattering coefficient is 0.2 and that the leaf photosynthesis rate equals (LI/(.356 + LI)) × 84.5 kg $CH_2O$ $ha^{-1}$ $hour^{-1}$ in which LI is the light intensity (visible) in cal $cm^{-2}$ $min^{-1}$. This function is supposed to hold for 23°C. Although it is no particular trouble to introduce separately calculated tables for other temperatures, no large errors are made by assuming that the instantaneous effect of temperature may be accounted for by a multiplication factor which amounts to 0., 0., .28, .54, .79, 1.03, 1.08, 1.08, .99 and .45 for temperatures from 0 to 45°C, with 5°C intervals.

As for temperatures, it is at present assumed in ELCROS that the temperature of the leaves equals the temperature of the air at standard height or the temperature of the air at 10 cm above a soil surface covered with turf-grass and that the temperature of the main root zone has an amplitude of .45 times the amplitude of the air and lags two hours.

The temperature of the growing point is, depending on its position with respect to the soil surface, supposed to be between the soil and the air temperature.

These are sweeping assumptions, which can only be improved upon by simulating simultanously the growth of the crop and the micro-climate; Denmead's paper in this symposium may clarify why this has not been attempted as yet.

## The growth of the leaves

The process of growth has many aspects. Increase in weight, increase in length and thickness and increase in area have been used frequently to follow the rate of growth

Table 1. Crop photosynthesis rates of corn in dependence of the area of the leaves (ha ha$^{-1}$) and the SINE of the sun for clear (C) and overcast (O) skies.

| ALV | SINE | | | | | | | | | | | Sky |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0. | .1 | .2 | .3 | .4 | .5 | .6 | .7 | .8 | .9 | 1. | |
| 0. | 0. | 0. | 0. | 0. | 0. | 0. | 0. | 0. | 0. | 0. | 0. | C |
| | 0. | 0. | 0. | 0. | 0. | 0. | 0. | 0. | 0. | 0. | 0. | O |
| 1. | 0. | 7.0 | 15.5 | 21.0 | 25.0 | 28.2 | 31.2 | 34.0 | 36.0 | 38.3 | 40.0 | C |
| | 0. | 1.7 | 3.2 | 5.5 | 7.2 | 8.5 | 10.7 | 12.5 | 14.0 | 15.6 | 16.8 | O |
| 2. | 0. | 9.0 | 20.0 | 28.2 | 35.0 | 41.5 | 47.2 | 52.1 | 56.2 | 60.4 | 63.7 | C |
| | 0. | 2.0 | 4.5 | 7.2 | 10.0 | 12.7 | 15.2 | 17.9 | 20.2 | 22.7 | 24.5 | O |
| 3. | 0. | 10.2 | 21.3 | 31.0 | 39.5 | 47.0 | 54.5 | 61.4 | 66.7 | 72.6 | 77.1 | C |
| | 0. | 2.4 | 5.2 | 8.5 | 11.5 | 14.5 | 17.5 | 20.5 | 23.0 | 26.1 | 28.2 | O |
| 4. | 0. | 10.5 | 22.0 | 32.0 | 42.0 | 50.0 | 58.5 | 65.9 | 72.5 | 79.1 | 84.4 | C |
| | 0. | 2.5 | 5.7 | 9.0 | 12.2 | 15.5 | 18.5 | 21.8 | 24.7 | 27.7 | 29.9 | O |
| 5. | 0. | 10.8 | 22.5 | 32.4 | 42.2 | 50.5 | 59.0 | 68.2 | 74.0 | 82.5 | 88.3 | C |
| | 0. | 2.5 | 5.8 | 9.2 | 12.4 | 15.8 | 18.8 | 22.3 | 25.4 | 28.5 | 30.7 | O |
| 6. | 0. | 11.1 | 22.9 | 32.7 | 42.3 | 51.0 | 59.5 | 69.3 | 75.5 | 84.3 | 90.4 | C |
| | 0. | 2.6 | 5.9 | 9.4 | 12.6 | 16.0 | 19.2 | 22.6 | 25.6 | 28.8 | 31.1 | O |
| 7. | 0. | 11.4 | 23.2 | 33.1 | 42.4 | 51.5 | 60.0 | 69.8 | 76.5 | 85.2 | 91.5 | C |
| | 0. | 2.6 | 6.0 | 9.5 | 12.7 | 16.1 | 19.3 | 22.7 | 25.7 | 29.0 | 31.3 | O |
| 8. | 0. | 11.5 | 23.5 | 33.3 | 42.5 | 51.9 | 60.4 | 70.1 | 77.0 | 85.7 | 92.0 | C |
| | 0. | 2.6 | 6.1 | 9.6 | 12.8 | 16.2 | 19.4 | 22.8 | 25.8 | 29.1 | 31.4 | O |
| 9. | 0. | 11.6 | 23.8 | 33.4 | 42.6 | 52.2 | 60.8 | 70.2 | 77.5 | 85.9 | 92.3 | C |
| | 0. | 2.7 | 6.1 | 9.6 | 12.9 | 16.2 | 19.5 | 22.9 | 25.9 | 29.1 | 31.5 | O |
| 10. | 0. | 11.7 | 24.0 | 33.5 | 42.7 | 52.7 | 61.2 | 70.3 | 78.0 | 86.0 | 92.5 | C |
| | 0. | 2.7 | 6.2 | 9.7 | 13.0 | 16.3 | 19.5 | 22.9 | 26.0 | 29.2 | 31.5 | O |

in time. It depends on the aim of the experiment which of these items will give the information required.

In ELCROS a number of aspects of growth have to be taken into account. At first it intends to describe the accumulation of dry matter into the structural tissues. This is the dry matter accumulated minus the directly available reserves which are kept in a separate pool for distribution to the growing organs. Secondly, the development of the leaf surface has to be known in order to get the basis for the photosynthetic activity. The primary growth item is therefore the flux of reserves into the structure of the growing plant parts. The rate of it depends on the amount of tissue capable of growth, the relative growth rate of the tissues, and the availability of growth essentials.

In seedlings all the tissue takes part in growth. Provided that growth essentials are optimally available this occurs depending on the temperature at the maximum rate, which is conveniently expressed as the relative growth rate on base of total Weight (RGR $= (dW/dt)/W$). In older plants, however, part of the tissue is mature and incapable of growth. In spite of this, single plants will grow exponentially when the supply of growth essentials increases linearly with the size of the plant.

In this case the mature material is always a constant (and small) fraction of the total. When however, deviations from the exponential growth occur, as is the case with mutual shading or changing water supply, this fraction varies and may comprise a large part of the total weight. When, as customarily done, the relative growth rate is expressed on base of total weight, variable values will be obtained, although the relative growth rate of the tissues capable of growth and in the presence of all growth essentials, is likely to remain constant.

The amount of tissue capable of growth may be estimated on basis of the pattern of leaf growth. It has been observed that at constant temperature the subsequent leaves of a corn plant (as in other plants; Went, 1957) are appearing at a constant rate and that only the last three visible leaves are increasing in size (fig. 5), (Brouwer, unpublished; Grobbelaar, 1962). From other experiments with bean plants it appeared that the leaves next in age which do not grow in the intact plant, resume growth when the youngest leaves are removed. This is such a generally accepted consequence of the removal of sinks (Humphreys, 1966) that it may be assumed to occur also during the vegetative growth of corn, although the exact proof is not possible since the removal of the complete youngest leaves is impossible without damaging the whole plant. The removal of the visible part only does not effect the meristem nor the growth, since both cell division and cell extension take place somewhere inside the sheaths of the older leaves (Milthorpe & Davidson, 1965).

A corn plant with 10 visible leaves numbered from 1 to 10 from oldest to youngest, is now considered as an example. Leaves number 10, 9 and 8 are growing at about the same rate (Grobbelaar, 1962) and are assumed to be fully capable of growth. The leaves 1 through 5 cannot be forced to grow at all even with complete damage of the shoot apex, apart from auxilliary buds in the axis of these leaves. These auxilliary meristems are contrary to the other Gramineae, of only little importance in corn. The leaves in between (7 and 6) are particially capable of growth resumption so that

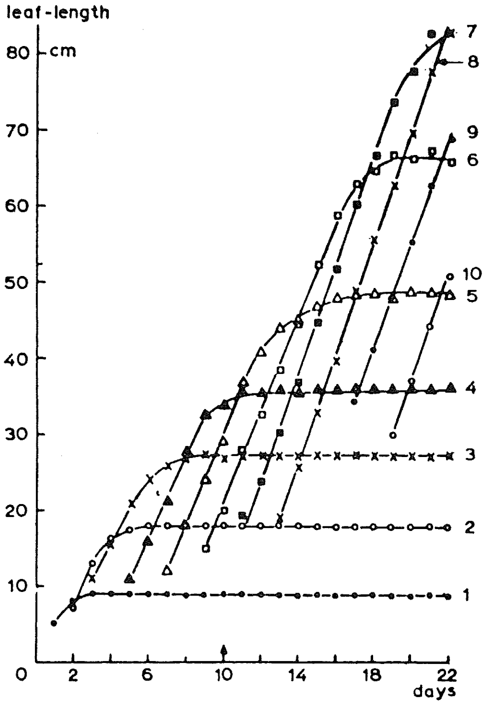

Fig. 5. The increase in length of successive leaves of the corn plant versus time. Only three leaves are growing at the same time and leaves are appearing at a constant rate (Grobbelaar, 1962).

a gradual decrease of the fraction of tissue fully capable of growth has to be introduced in ELCROS in dependence of age.

For a corn plant growing at a temperature of 20°C it may take 2.3 days between two leaf initions, so that according to the above assumptions the tissue which has been grown in the last 9.2 days (4 × 2.3) is still fully capable of growth. Within this period the plant weight increases at least tenfold which means that only 10% of the total weight is mature. Hence in a first estimate of the relative growth rate, no large errors are introduced when the total weight is used as a basis for calculation, provided that the plants have been growing exponentially with a constant supply of growth essentials per unit growth. As such the supply of the growing tissues with carbohydrates, water and minerals has to be considered. In the present version of ELCROS mineral supply is assumed to be optimal throughout for all plant parts. Although water is optimally available to the roots, local stresses may occur in the transpiring parts, due to the resistance in the plant. This is accounted for by comparing the amount and activity of the roots which are present to the amount and activity of the roots which should be present to maintain full turgidity of the leaves, taking into account the transpiration rate. The principles of estimating this relative amounts of roots have been discussed in a previous paper (Brouwer & de Wit, 1969).

Relative growth rates found in various experiments are given against temperature in fig. 6. The variation within the region of 15 to 30°C is considerable. This is due to

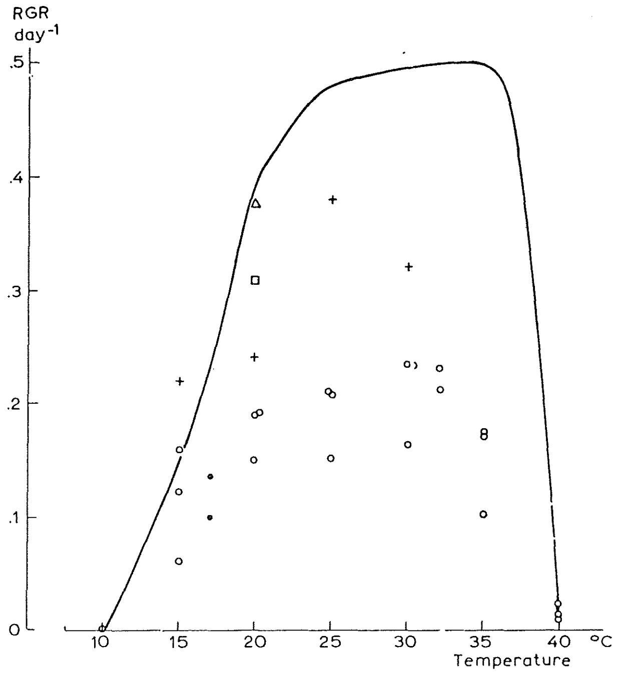

Fig. 6. Relative growth rates of corn tops and roots under various conditions (see text) and the estimated relation between the relative growth rate of young tissue, well supplied with carbohydrates and at full turgidity, in dependence of temperature.

various constraints on the growth. The open dots concern the relative growth of the roots of plants which were kept with their shoots at a temperature of 20°C. Fig. 7 shows that between 20 and 30°C the carbohydrate content was low, indicating a constraint on the growth due to lack of reserves. It is likely that the relative growth rate of whole plants, growing at various temperatures under comparable conditions were subjected to the same constraint, although here also water stress in the above ground parts of the plants may have interfered.

To overcome these constraints plants were transferred from a nutrient solution with nitrogen to one without nitrogen. As a consequence shoot growth was inhibited by N-shortage which resulted in an increased carbohydrate content and an enhanced growth rate of the roots (Brouwer et al., 1961). The relative growth rate of the roots calculated for a 5-day period after transference is plotted in fig. 6 as a square. Prolonged treatment without N results in plants with a relatively well-developed root system and a high carbohydrate content. The growth of the leaves is then checked by the N-supply. Supplying N in these conditions releases the check almost immediately so that during a transient period leaf growth proceeds uninhibited by carbohydrates, minerals and even water stress, the latter since the large water absorbing area as compared with the

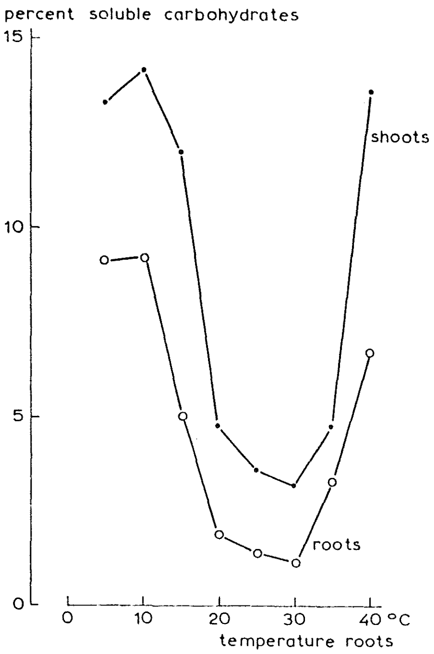

Fig. 7. The carbohydrate content of corn in dependence of the temperature of the roots at a shoot temperature of 20°C (Grobbelaar, 1962).

transpiring surface, decreases the resistance to transfer of water. The relative growth rate of the shoot calculated from such an experiment is plotted as a triangle in fig. 6 (Brouwer et al., 1961). It may be doubted whether they represent maximum values, since due to the previous check in growth, a relatively high percentage of older tissue was involved.

This is not the case with young seedlings which depend on the growth essentials in the seeds. The irrelative growth rates are entered into fig. 6 as crosses. There is still some doubt, however, whether all growth essentials were optimally available since Kny (1894) showed that removing either the roots or the shoot of seedlings resulted in a faster growth of the other, and Brown & Rickless (1949) observed relative growth rates of 2.45 day$^{-1}$ for cucumber root tops in vitro.

Hence, it is not even certain that the maximum relative growth rates found in these experiments are indeed the possible relative growth rates of young tissue not subjected to any constraints due to lack of reserves, water stress and minerals. Taking into account that corn is unable to grow at temperatures below 11°C, that there are no indications that under favourable conditions the optimum temperature for growth is below 35° and that it is not likely that the possible growth rates were actually reached the dependence of relative growth rate on temperature is for the time being entered in ELCROS as given by the full drawn line in figure 6. It has been shown that this curve is satisfactory by a comparison of growth rates in actual and simulated experiments. However, more attention has to be paid to experimental techniques enabling the determination of unconstrained growth rates.

## Programming aspects

To introduce the physiological considerations of the above section into a simulation program it is still necessary to make ad hoc assumptions regarding details of the operations. This is one of the aspects that makes programming worthwhile because it reveals more than anything else the weak aspects of our knowledge. As said in the introduction, the actual quantitative statements are made in the language CSMP, and explained during its use. It should be noted that the statements are not presented in computational order, because the language contains a sorting routine as explained in the opening paper of this symposium.

Since the capability of leaves to grow depend on their age, it is necessary to keep track of the age distribution of the leaf material in terms of the development stage at the moment of formation. It will be explained first in what manner this development stage is quantitatively characterized.

Silking of corn in the field occurs at practically the same time, irrespective of the density of planting, which indicates that the rate of leaf distribution is independent of the size of the individual plant. Since it has been observed also that the rate of leaf initiation at constant temperature and daylength is also independent of the number of leaves already formed, it is possible to introduce a development rate of corn which depends only on the external variables daylength and temperature. It being arbitrarily assumed that the DeVelopment Stage at emergence is zero and at the appearance of the male flower one, the DeVelopment Rate may be expressed in units of day$^{-1}$.

A relation between this DVR and temperature for a Dutch variety of corn and oats, determined under controlled conditions at 14 hours daylength is presented in fig. 8a. The Temperature of the Growing point being computed from data in the weather section the DeVelopment Rate on each moment may be obtained with:

```
DVR = AFGEN (DVRTB, TG)
FUNCTION DVRTB = (—5.,0.), (10.,0.), (15.,.011), (20.,.025), (25.,.039), . . .
                 (30.,.04), (35.,.04), (40.,.004), (60.,.004)
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The graph of fig. 8a for corn is here characterized by the pair of values of the FUNCTION DVRTB, the first number of each pair being the value of the independent variable TG and the second number being the DeVelopment Rate. The AFGEN function states that the value of the DeVelopment Rate is obtained by interpolation in DVRTB with TG as the independent variable. The DeVelopment Stage is now obtained by:

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DVS = INTGRL (0., DVR),
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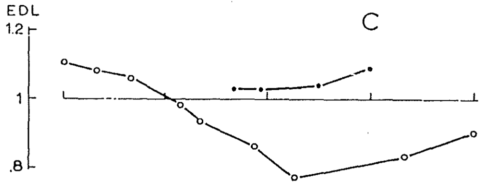
a CSMP function that indicates that the initial value of DVS (at emergence time) is zero, the rate of change is DVR and that DVS is obtained by integration.

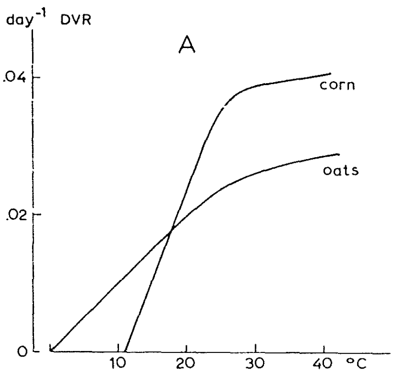
The actual number of days from emergence to flowering of corn and oats sown at successive intervals in the field is presented in fig. 8b. Fig. 8c presents the ratio of the actual and the computed vegetative period (EDL). As far as corn is concerned, the quotient is close to one indicating that corn under Dutch field conditions behaves as a day-neutral plant. However, in case of oats, the ratio is larger than one before the

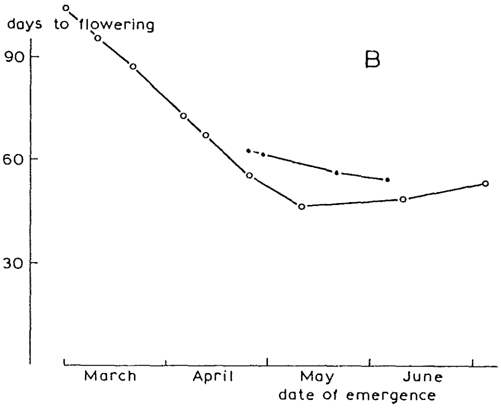
Fig. 8A. The relation between temperature and development rate of a corn and oat-variety at a daylength of 14 hours.

Fig. 8B. The relation between time of emergence and length of the period between emergence and flowering in the field in The Netherlands.

Fig. 8C. The ratio between actual and computed length of the vegetative period.







half of April and smaller than one thereafter. This shows that oats is a plant which is sensitive to the length of the day under Dutch conditions. A simulation of the influence of daylength has to be based on a thourough study of relevant literature, which has not been made by us.

To ensure now that the age distribution on the leaf material is saved in terms of the development stage at the time of formation a function is introduced which may be called a boxcartrain and which is schematically presented in fig. 9. The rate of growth is integrated in the first boxcar of the train and each time, the development stage is increased by a value .04, the content of the last boxcar is discarded and of the others

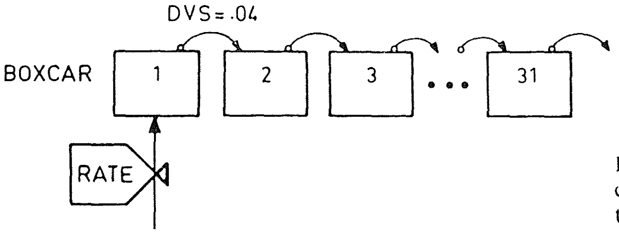


Fig. 9. A diagram of a boxcartrain to save the age distribution of grown material.

is moved to the car with the next highest number. Hence, just before a shift, the 1st, 2nd and 3rd and 31st contain the leaf material that is 0–0.04, 0.04–0.08, 0.08–0.12, ........, 1.2–1.24 units old, in terms of development stage. When the plant has reached the stage of 0.4, only the first 10 boxcars of the train contain material.

In ELCROS (CSMP-version), this operation for the Weight of the LeaVes may be referred to by:

WLVB = TRAIN (31, GLW, DVS,.04)

The symbol refers to the Weight of the LeaVes in the Boxcartrain, 31 denotes the number of boxcars in the train, GLW denotes the Growth of the Leaf Weight and the symbols DVS and 0.04 state that the shifting of the contents is performed each time that the DeVelopment Stage is advanced with 0.04 unit.

The total Weight of the LeaVes may now be obtained with the expression:

WLV = SUM1 (31, WLVB)

a function which indicates that the contents of the 31 boxcars in the train WLVB are summed.

Based on what has been said on the number of leaves that are capable of growth, it may be assumed that the contents of the 31 boxcars of the train WLVB have a capacity to grow which may be presented by the contents of the following Effect of MAturity table:

EMA (1–31) = 5 × 1.,.88, .67, .43, 23 × .02

This means that the content of the first 5 boxcars are fully capable of growth, the contents of the last 23 boxcars have retained only a rudimentary capacity to grow (reflecting dormant auxilliary buds), and the capacity to grow drops linearly from the 5th to the 9th boxcar. Hence, the Weight of the LeaVes that are Capable of growth may be obtained with:

WLVC = SUM2 (31, WLVB, EMA)

a function which means that WLVC is the sum of the 31 products of the content of each boxcar of the train WLVB and its EMA value.

To calculate the growth of the leaves, it is at first necessary to obtain the Relative Growth Rate of the Leaves from the Temperature of Air between the plants (which in its turn is computed in the weather section) by

RGRL = AFGEN (RGRTB, TA)

FUNCTION RGRTB = (—5.,), (10.,0.), (15.,.17), (20.,.25), (25.,.56), ...
(40.,.22), (45.,.08)

in which the RGRTB-function is similar to the curve in fig. 6.

The Possible Growth of the LeaVes, i.e. the growth when there are neither constraints by waterstress or carbohydrate shortage is now equal to:

PGLV = WLVC × RGRL

As far as the influence of the reserve percentage is concerned, it is assumed that at a Reserve PeRcentage of 0, growth is zero and at a reserve percentage of 4, growth is at its maximum rate; in other words, the Growth Constraint of the Leaves due to lack of Reserves is:

GCLR = LIMIT (0.,1., RPR/4.)

a function which sets GCLR equal to 0 or 1 when RPR is smaller than 0 or larger than 4, respectively and otherwise takes the value of RPR/4.

It follows from fig. 1 that the Reserve PeRcentage is equal to:

RPR = INTGRL (0., (PHR–RSP–GLW–GRW–GST)/TWT)

in which TWT is the Total WeighT of the plant or crop.

In a section which falls outside the scope of this article, the Growth Constraint due to Lack of Turgidity is calculated in a nearly similar way from the relative amount of roots. It is now assumed that either one of the other constraints work whichever is the lowest, so that the actual Growth rate of the Leaf Weight is:

GLW = PGLW × AMIN1 (GCLR, GCLT)

This section will be concluded by making some remarks on the growth of the leaf area. A simple assumption is that the growth of the leaf area is proportional to the growth of the leaf weight so that the leaf area may be found from the leaf weight by division with a factor of about 750 kg leaf/ha leaf.

However, it is well known that the amount of leaf surface per unit leaf weight depends on conditions. At present, the influence of water and nutrient are not considered, because the main purpose of ELCROS is to simulate the growth of the crop under optimal conditions, as far as these factors are concerned. The supply of carbohydrates to the growing leaves has, apart from any other factor, a large influence on the morphology .For instance, if it takes 30 days from emergence to flowering and 15 leaves are formed within this period, there is only a two days supply of carbohydrates available for each leaf. If there are 100,000 plants on the field and the growth rate of the leaves is 200 kg ha$^{-1}$ day$^{-1}$, this amounts to about 4 grams of carbohydrates per leaf. If, however, the planting density is 2 times larger the supply per leaf is reduced to 2 grams and if the planting density is two times smaller it is increased to 8 grams. A leaf of 8 grams is not only longer and wider, but also thicker than a leaf of 2 grams, an effect which is accounted for in ELCROS by introducing a Weight Area Ratio of the Leaves (WARL) which is 500 kg/ha for an average growth rate of 1 gram per leaf per day or lower and 1000 for an average growth rate of 4 grams per leaf per day or higher.

This results indeed in plants with thin leaves when they are young or densely planted and in growth rooms, and thick leaves for widely planted corn in the field.

On basis of the above it is assumed that at any moment the Growth of the Leaf Area may be calculated with:

GLA = WARL × GLW

which in turn is integrated in a boxcartrain for the Area of the LeaVes:

ALVB = TRAIN (31, GLA, DVS,.04)

Although in this way the main factors that influence specific leaf weight are qualitatively introduced, the problem of morphology is a perfect example of an area where the physiological basis for the simulation program is still lacking.

## Respiration

### Physiology

It is often assumed without any good evidence that the respiration rate of a crop is, apart from the effect of temperature, proportional to the amount of leaves. This assumption leads to the well-known graph (fig. 10) in which the optimum Area of the LeaVes at which the net photosynthesis is at its maximum and the ceiling ALV, at which photosynthesis is fully counterbalanced by respiration, are visualized.

Simulation of this viewpoint leads to inconsistent results. If it is assumed that the respiration per unit plant material is low, it appears that yield levels which are observed in the field may be obtained, but then simulated respiration rates under controlled conditions are far too small. If it is assumed that the respiration per unit plant material is higher, simulated respiration rates under controlled conditions may be in the observed range, but then simulated ceiling yields in the field are far too small.

Now it has been shown conclusively by McCree & Troughton (fig. 11) that respiration rates of crops are not proportional to the weight of the vegetative material (or the area of the leaves), but much more related to the photosynthetic rate of the crop surface. In explanatory models serious attempts have to be made to incorporate physiological and biochemical knowledge of the growth processes to account for this. At this stage, we are only able to introduce a line of thought, which may be further evaluated at the section of this symposium which is devoted to crop respiration.

There is abundant evidence that in plants respiration is regulated to meet changing metabolic demands through an intimate coupling of respiration to phosphorylation which is visualized in the following way (Beevers, 1961). Many processes in the cell, like synthesis, growth and solute transfer need energy which is obtained from the conversion of ATP to ADP and Inorganic Phosphate. This ADP and IP are required in glycolysis and this process would be brought to a standstill if available ADP were converted into ATP. Strong evidence from this comes from experiments with un-

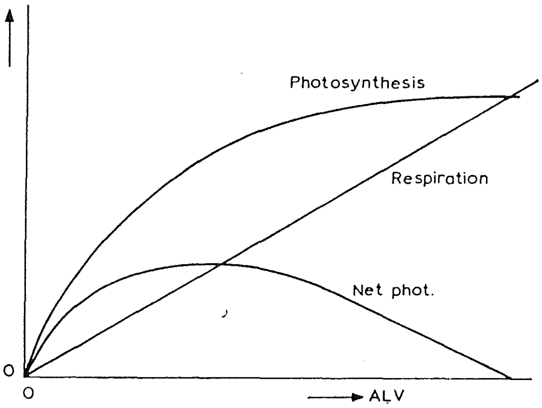


Fig. 10. The classical figure to illustrate the concepts of optimum and ceiling leaf area index on basis of the assumption that respiration is proportional with mass.

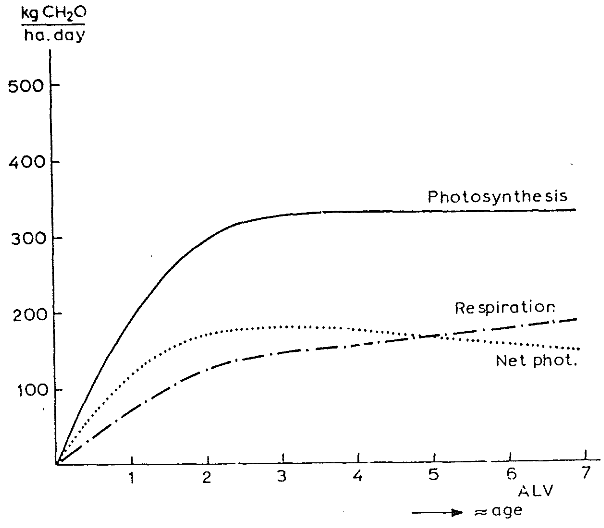


Fig. 11. Photosynthesis, respiration and net photosynthesis in relation to leaf area index, as measured with subterranean clover at 20°C (McCree, 1967).

coupling agents as DNP. These substances destroy the coupling between oxidation and phosphorylation of ADP. But ATP breakdown is unaffected and the result is an increased ADP-supply.

The drainage of respiratory intermediates and the consumption of ATP is great in actively growing tissue, so that the respiration rate in these is likely to be higher than in older tissue in which ATP turnover is lower, whereas the stimulation by DNP is likely to be smaller. This was indeed the case in carrot slices where actual respiration decreased from 100% of the uncoupled rate in young material to about 30% in older, whereas the rate of respiration in the uncoupled state (+ DNP) remained the same (Beevers, 1961). This indicates that the amount of enzymatic machinery did not change with age, and that respiration was here geared to the needs.

In his paper presented at this symposium, Beevers gives a somewhat more detailed analysis. He distinguishes a respiration associated with synthetic events (growth respiration), a respiration associated with protein turnover in older cells and with repair and maintainance of inherently unstable cell-structures (maintainance respiration) and hydrolyses of ATP in which there is no useful outcome to the plant ('idling' respiration).

In ELCROS, the growth respiration coefficient is expressed as the amount of weight that is lost during the synthesis of one weight unit structural material. This coefficient may be estimated in various ways.

At first it is observed that at 25°C, the relative growth rate of young tissue, well supplied with growth essentials, may amount to about 0.5 day$^{-1}$, whereas the relative respiration rate of such tissue is about 0.25 day$^{-1}$. If maintainance and idling respiration would be absent, this would indicate a growth respiration coefficient of about 0.5. This value is within the range reported for animal growth (Needham, 1964; Kleiber, 1961).

An intellectually more satisfying way, but at this stage still speculative, is to calculate this coefficient on basis of biochemical pathways of synthesis. If it is assumed that all photosynthesis products are channeled through the stage of glucose and that N is supplied as $NO_3^-$, it is calculated that for the formation of 1 g proteins, fats, polymers of sugars and the uptake of 1 g of minerals about 2.35, 2.94, 1.15 and 0.1 g glucose, respectively, is needed. Hence, for 1 g tissue consisting of 25% protein, 6% fat, 59% polymer of sugars and 10% of minerals about 1.452 g of glucose is necessary, so that the growth respiration coefficient is about 0.45. This value is in reasonable agreement with the growth respiration coefficient of 0.33 reported by McCree in his lecture at this symposium, assuming that his gross photosynthesis is either used for growth or respiration. Since there is no indication that biochemical pathways depend on temperature, it is assumed that the growth respiration coefficient is independent of temperature.

At this stage it is difficult to separate maintainance and idling respiration (cf. Semikhatova, this symposium). Tentatively, it is assumed that both are a fraction of the uncoupled respiration rate, hence proportional to the amount of enzymatic machinery. According to Price (1960), this uncoupled respiration rate (i.e. in presence of substrate, oxygen and uncouplers) amounts to 200–300 $\mu$l $O_2$ per hour per mg protein-N at 25°C. This corresponds to a relative uncoupled respiration rate of 0.28 kg $CH_2O$ (kg dry matter)$^{-1}$ day$^{-1}$ for tissue with 4 percent protein -N. With Price, a $Q_{10}$ of 2.2 is assumed over rather a wide temperature range for the uncoupled respiration rate.

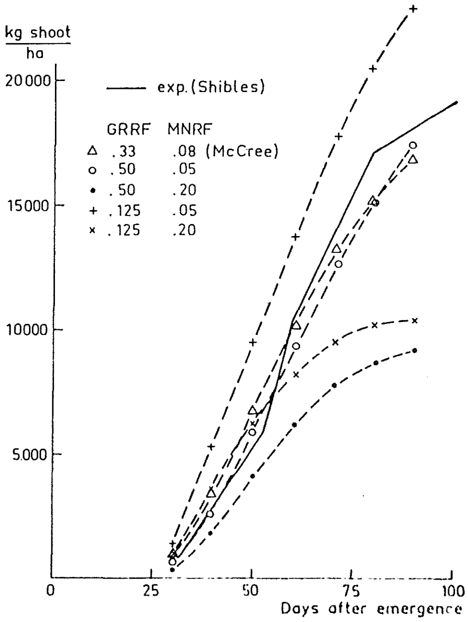


Fig. 12. Actual and simulated growth of corn in Ames (Iowa) in 1963 (data of Shibles, pers. com.).

Now there are observations that the respiration rate of mature leaves (Prinz zur Lippe, 1956; Ludwig, Saeki & Evans, 1965; James, 1953), expressed as a fraction of the uncoupled respiration rate, is about 0.25. However, according to McCree's data (this symposium) this fraction is about 0.08 (supposing a protein-N content of 4% in his clover).

It is obvious that the concept of a maintainance respiration coefficient is still not well formulated, and that estimates vary about threefold from 0.08 to 0.25.

To obtain some idea of acceptable order of magnitudes, growth curves of corn have been simulated with a range of growth and maintainance respiration coefficients for Ames in the year 1963 and compared with actual observations of R.M. Shibles (personal communication). The results are presented in fig. 12. Inspection of the curves show that with a maintainance respiration coefficient of 0.25 ceiling yields are at least a factor 2 too low. Perhaps not so surprisingly, it appears that the values of McCree for the growth and maintainance respiration factor (GRRF and MNRF) give a curve in the right order of magnitude, and it is on this type of evidence that McCree's factors are at present incorporated in ELCROS.

### Programming aspects

The programming of the respiration rate of a crop is now straightforward.

The ReSPiration rate Associated With the Growth of the organs is supposed to be:

RSPAWG = GRRF × (GLW + GRW + GST)

in which the GRowth Respiration Factor is set at 0.33 and GLW, GRW and GST are the growth rates of the leaf weight, the root weight and the stem weight.

Assuming that the relation between the uncoupled relative respiration rate of an organ with 1% organic N in dependence of temperature is given gy:

FUNCTION URRTB = (—5.,.0061), (0.,.0093), (5.,.014), (10.,.021), (15.,.031)
(20.,.047), (25.,.0.70), (30.,.104) (35.,.15), (50.,.14)

the first value between brackets being the temperature, the Uncoupled Relative Respiration in the Air and the Soil is obtained with:

URRA = AFGEN (URRTB, TA)
URRS = AFGEN (URRTA, TS)

TA and TS being the air and soil temperature.

On basis of observations it is assumed that in well fertilized corn plants the Nitrogen content of the LeaVes, the RooTs and the STem decrease for successive boxcars of their train (see previous section) according to:

NLV (1–31) = 10 × 4, 5 × 3.9, 3 × 3.8, 2 × 3.7, 3.6, 3.5, 3.4, 3.3, 3.2, 3.1, 2.9, 2.8, 2.7, 2.6
NST (1–31) = as for leaves
NRT (1–31) = one percent lower than for leaves.

Thus, the uncoupled respiration rate of the whole crop (see again previous section for the meaning of the used statements) is:

URRC = URRA × (SUM2 (31, WLVB, NLV) + SUM 2 (31, WSTB, NST)) +
+ URRS × (SUM 2 (31, WRTB, NRT)

The respiration associated with maintainance is then:

$$\mathrm{RSPAWM} = \mathrm{MNRF} \times \mathrm{URRC}$$

in which the MaiNtainance Respiration Factor is assumed to be equal to 0.08.[1]

## Results

To give an impression of the operation of ELCROS some simulated results will be discussed and to some extent compared with the results of actual experiments.

As has been said, ELCROS updates every hour, i.e. every hour all rates of changes are calculated and integrated with a time step of an hour. Hence to advance one day in time, all calculations are performed 24 times.

The growth of corn simulated this way for a period of 24 hours, during its 19th day after emergence is presented in fig. 13.

At midnight the reserve percentage is decreasing which is accompagnied by decreased growth rates. At the onset of light, the reserve percentage increases again, followed by increased growth rates first of the leaves, then of the roots. At the beginning

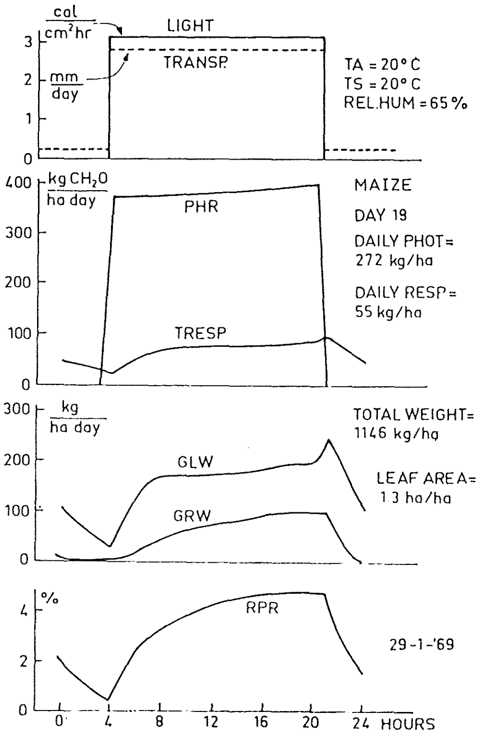


Fig. 13. The simulated photosynthesis, respiration, transpiration, growth of leaves and roots and the reserve percentage of corn under controlled conditions during a 24 hour period.

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[1] The simulated results of figs. 13, 14, 15 and 16 are obtained by using former estimates of 0.2 and 0.125 for GRRF and MNRF, respectively.

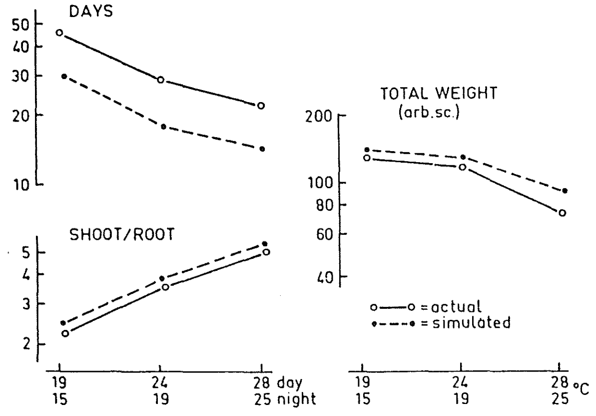

Fig. 14. Simulated and actual growth of corn up to the 11th leaf stage (DVS = .6).

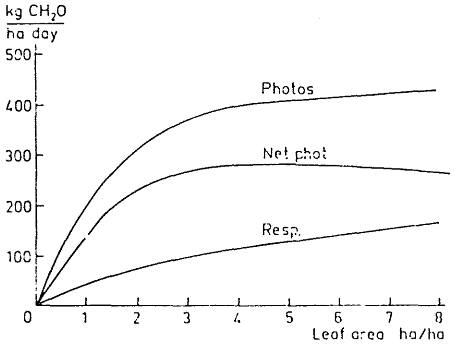

Fig. 15. Simulated photosynthesis, respiration and net photosynthesis of corn in relation to leaf area index at a temperature of 20 C.

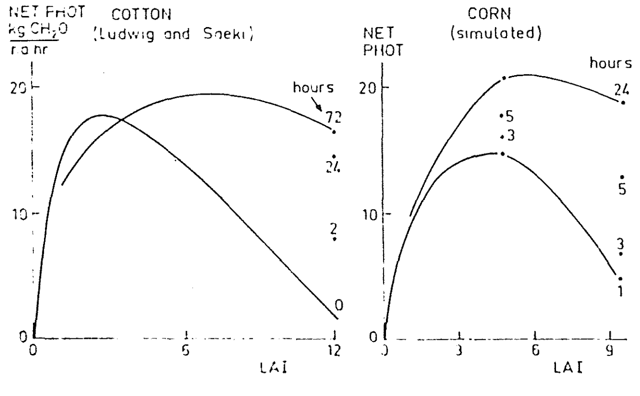

Fig. 16. The net photosynthesis of cotton (actual experiment) and corn (simulated experiment) at various times after increasing the leaf area index by placing single grown plants close together.

of the dark period, there is a rather sudden increase in growth rate of the leaves; this is a result of the decrease in transpiration, accompagnied by an increase of turgidity. The growth rate drops again soon due to the decrease of the reserve level.

The respiration is coupled to the growth rate and lags therefore behind the photosynthetic rate. The small increase in photosynthesis and transpiration during the day reflects the increase in leaf surface, the area of leaves being slightly above 1 ha $ha^{-1}$. The relative growth rate during the day is 0.16 and 0.10 $day^{-1}$ for the shoot and the root. Obviously the shoot/root ratio is increasing already somewhat because of the increase in mutual shading. The relative growth rates are comparable with actual corn under these conditions (fig. 6), reflecting that the net photosynthesis rather than the capacity to grow governs the rate of growth. Fig. 14, in which some actual and simulated data of corn growth are compared, indicates that the influence of temperature on growth and development rate is also simulated reasonably well, although the development rate of the plants used in the experiment deviated from the development rate – based on other experiments – introduced in ELCROS.

The simulated relation between the area of the leaves in ha $ha^{-1}$ (leaf area index) and the daily photosynthesis, respiration and net photosynthesis under controlled conditions is presented in fig. 15. These results are very similar to those with actual plants (fig. 11). This similarity is brought about by the assumption that respiration is partly coupled with the growth rate. A similar behaviour is obtained when it is assumed that respiration depends on the reserve level, and not directly coupled to growth. Both possibilities may be distinguished, perhaps, by studying the behaviour of plants during short periods of waterstresses, which are accompagnied by decreased growth rates and increased reserve levels. This has not been done as yet.

A similarity with fig. 11 can never been obtained by simulation if it is assumed that respiration is mainly controlled by the amounts of plant material.

Fig. 16 concerns an actual and simulated experiment in which plants grown at a wide spacing were suddenly crowded up to densities with a leaf area index of about 10. The actual experiment reveals that the net photosynthesis at high densities is zero directly after the crowding but that within a day a situation is obtained in which net photosynthesis does not depend any more on the leaf area index within the dense range. It was shown that this was due to a decrease in respiration during this 24 hour period. The simulated experiment reveals the same behaviour. Further analyses of the simulated data showed that mutual shading due to crowding reduced the photosynthesis per unit leaf area, which resulted in a decreased reserve percentage, which was in its turn accompagnied by a decreasing growth rate and a decreasing respiration rate. Because the speed of adjustment in the actual and simulated experiment is about the same, it seems likely that in actual plants a similar mechanism is operating as in the simulated plants.

The actual and simulated growth rates of corn in California, Iowa and The Netherlands are presented in fig. 17. The simulated curves were obtained by introducing the latitude, emergence date and the weather data for the places and years concerned. None of the other parameters were adjusted to obtain better agreement. Closed crop surfaces are reached at yields of 1500 kg $ha^{-1}$ and the slope of the curves thereafter

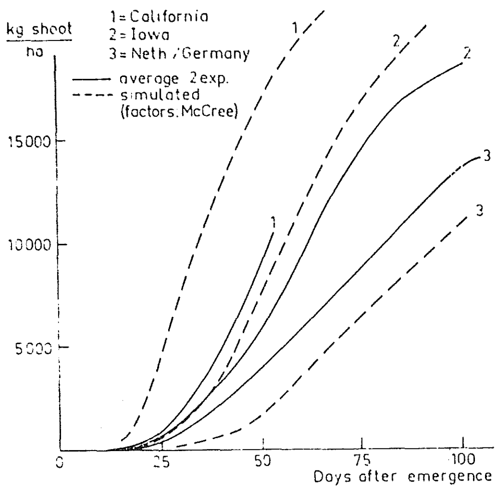

Fig. 17. Actual and simulated growth of corn under field conditions in California, in Iowa and in The Netherlands. Data from Williams and Loomis (1965), Shibles (pers.com.), and unpublished.

s termed the crop growth rate. At each of the three places, the actual and simulated crop growth rate is about the same, although the differences between places are considerable. This shows that the present version of ELCROS gives reasonable predictions, as far as this aspect is concerned.

However, the simulated crop in California is much earlier at its grand period of growth than the actual crop in California, whereas the reverse is the case in The Netherlands. Now the average temperature in California during the early stages of growth was about 25 C and in The Netherlands about 10 degrees lower. Taking the large effect of temperature on the relative growth rate and the photosynthetic rate into account the simulated difference between California and The Netherlands is understandable. As far as the actual experiments are concerned it is, however, not clear at all why the periods from emergence until the 1500 kg ha$^{-1}$ are so much the same in both places.

Taking into account the large effect of relatively small temperature changes within the range of 15 to 25 degrees on growth of corn, it does not seem improbable that the large discrepancy in early growth between actual and simulated experiments are due to systematic differences between the actual micro-climate and the simulated micro-climate. To study this possibility, the influence of changes of the daily amplitude of temperature and of the average daily temperature on the early growth of corn was simulated for Dutch conditions. The results are presented in fig. 18. It appears that differences between actual and simulated results as given in fig. 17 may be due to errors in average temperature of about only one degree. On the other hand it appears that relatively large errors in temperature amplitude do not affect the outcome very much.

Hence, the predictability of early corn growth depends to a large extent on the predictability of the average temperature around the surface of the soil.

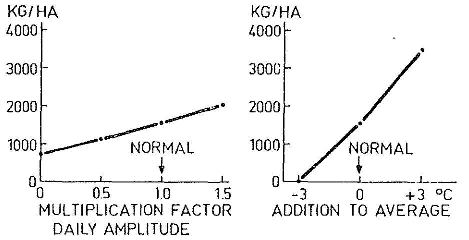

Fig. 18. Simulated influence of daily amplitude and average air and soil temperature on the total weight of corn in 1938 in The Netherlands at the time that under normal conditions a weight of 1500 kg/ha is reached (emergence: 160th day; weight of the leaves at emergence: 3 kg/ha).

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