A SIMULATION MODEL OF PLANT GROWTH WITH SPECIAL
ATTENTION TO ROOT GROWTH AND ITS CONSEQUENCES

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INTRODUCTION

MANY INTERNAL and external factors are involved in plant growth. The papers presented in this symposium demonstrate well enough how much work has already been done on various aspects of root growth and root activities. One is hardly able to detect a single aspect which has been overlooked. However, even when the effect of one of the factors studied is known in detail in a well defined situation at a well defined moment in the life cycle of the plant, it is difficult to predict the effect of such a factor throughout the whole life-cycle. A plant physiologist has to face the problem of integrating detailed knowledge into the whole of an intact developing system. The imagination of the scientist may often be stretched to the limit in providing a qualitative understanding of plant growth and thus the provision of a quantitative solution is an even greater problem (Fogg, 1963). In order to achieve success, the problems have to be attacked with more efficient methods than those used so far.

Models have been shown to be useful tools in the search for a better understanding of and communication in the various sciences, including biology (S.E.B. Symposium XIV, 1961). However, the model that has to integrate all the details of plant growth, will be as complicated as the plant itself. Because any model has limited objectives it is possible to discriminate between essential and less essential aspects. Plants growing at a high level of nitrogen will differ in various ways from plants growing at a lower level. For example, the indole acetic acid content of the former will be higher (Söding, 1952) but IAA application to the nitrogen-deficient plant will not result in an increased growth rate. The nitrogen content will also be different and applying nitrogen to the nitrogen-deficient

plant will result in growth promotion. Therefore, the nitrogen will be chosen as the causal factor rather than the IAA in spite of the fact that the effect of nitrogen on growth may be mediated by IAA. Hence, in the model, some aspects may be overlooked but the essential ones have to be used. Essentiality will always be a question of purpose and opinion and it is opinion that is really simulated. However, in the model to be presented below, any alternative possibilities can be introduced and tested as well.

EXPERIMENTS WITH PLANTS

A number of experimental results may illustrate how the present authors arrived at some of the basic assumptions incorporated in their model.
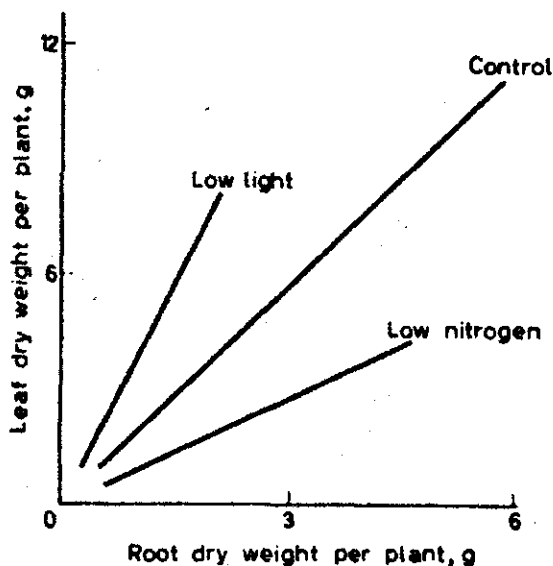

Figure 1. Diagram showing the relation between leaf dry weight and root dry weight of bean plants (Phaseolus vulgaris) growing in nutrient solution at a light intensity of 0·1 cal cm⁻² min⁻¹ (control) as compared with a reduction of either the light intensity or the nitrogen supply

In a constant environment bean seedlings were found to grow exponentially with a constant distribution pattern of the dry matter produced between the leaves and roots. When the light intensity was reduced, the overall growth rate decreased but root growth was

decreased more than leaf growth, resulting in a higher leaf to root ratio. A reduced supply of nitrogen also reduced the overall growth rate but in this case leaf growth was decreased more than root growth resulting in a lower leaf to root ratio (*Figure 1*).

This behaviour is easily explained by the assumption that leaves and roots are competing for carbohydrates and nitrogen and that the organ which will be most successful in obtaining its requirements is that which is nearest to the source. In fact, the growth of one organ depends on the translocation of essential substances produced by another organ and thus on the physiological activity of the latter.
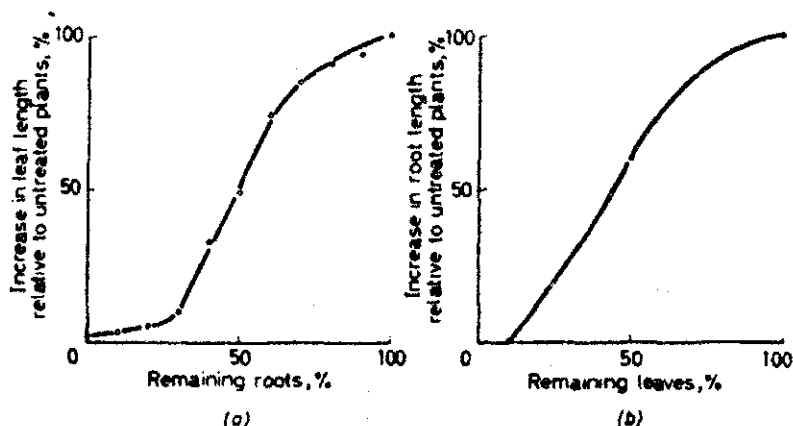
Figure 2. Influence of removing various portions of either the root system (a) or the assimilating surface (b) of bean plants (Phaseolus vulgaris) on the growth rate of leaves (a) and roots (b) respectively during the first 24 h after clipping

It has been shown that this type of interdependence can be characterized conveniently as a functional equilibrium (Brouwer, 1963). Disturbing this equilibrium by partial excision of the supply organ (*Figure 2(a)* root excision, *Figure 2(b)* defoliation) was found to result in a reduced growth rate of the dependent organ (Brouwer, 1963). As expected, a rapid restoration of the originally existing ratio occurred after excision (*Figure 3*) as a consequence of the reduction in growth rate of the dependent organ and a relatively increased growth rate of the supplying organ. Earlier Richardson (1953) had shown that defoliation effects were quite comparable with the effect of lowering photosynthesis either by a reduction of the light intensity or by withholding carbon dioxide (*Figure 4*).
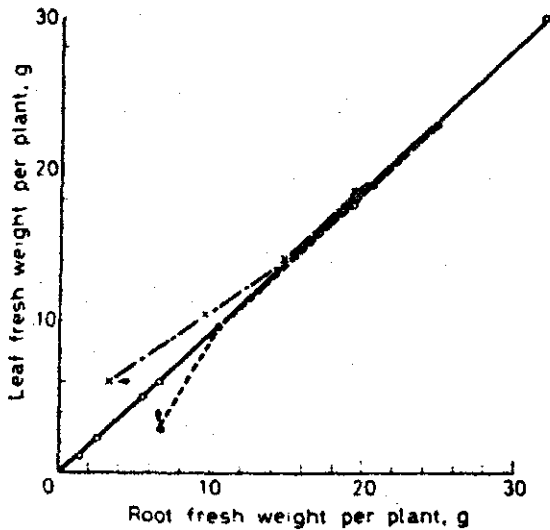
Figure 3. *Recovery of the original leaf to root ratio of bean plants* (Phaseolus vulgaris: circles) *after removal of 50 per cent of the leaves* (crosses) *or 50 per cent of the roots* (dots)
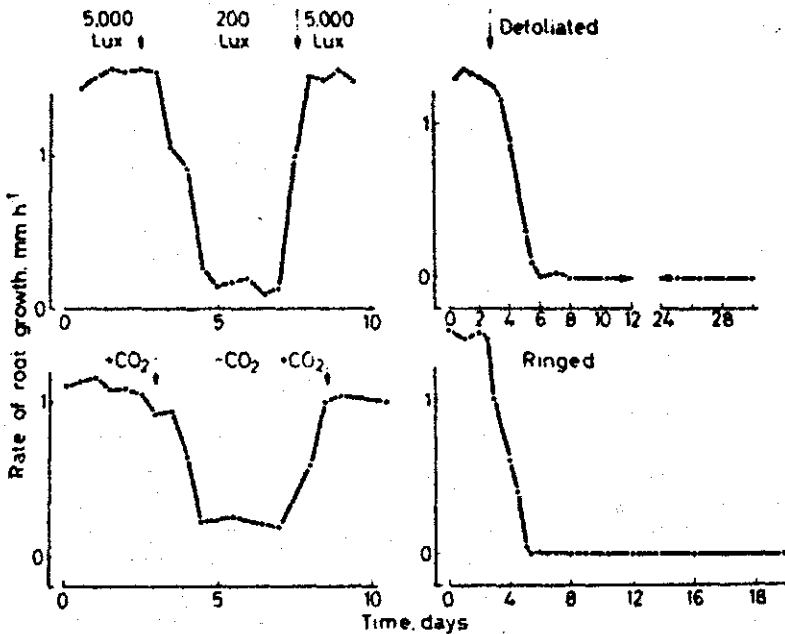

Figure 4. *Effect of various treatments, all resulting in a decrease of the carbohydrate flow to the roots, on root growth of Acer pseudoplatanus.* (From Richardson, 1953, by courtesy of North Holland Publishing Company.) 5,000 *and* 200 Lux *equal* 0·025 *and* 0·001 cal cm⁻² min⁻¹ *respectively*)

Since the equilibrium is governed by the activities of the organs involved, the leaf to root ratio will depend on those internal and external conditions which influence the activity of the supplying organ and/or the requirements of the dependent organ. Leaf growth decreased at root-medium temperatures above or below the optimal value (*Figure 5*). The effect was less severe when at the same time the requirements of the shoot were reduced as in this case by enhancing the air humidity. At constant conditions in the aerial environment, the shoot to root ratio increased with the higher activity per gramme of root weight (*Figure 6*).
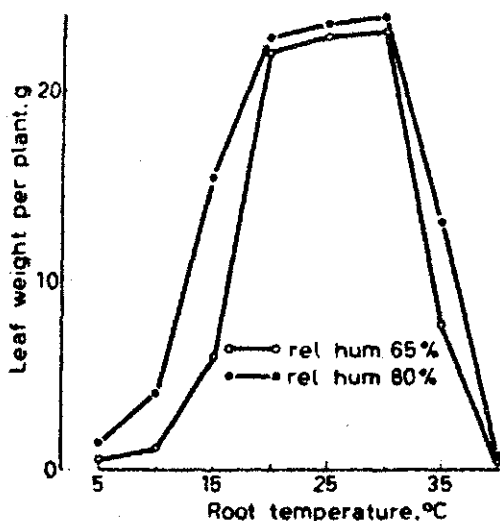

Figure 5. Influence of root temperature on leaf growth of bean plants (Phaseolus vulgaris) at two levels of air humidity and a constant air temperature of 20°C.

Although in this way a reasonable qualitative explanation can be given for the experimental data that are available, quantitatively considerable complications may occur. These are partly due to plant adaptations which influence their growth rates. When bean plants were transferred from a root temperature of 20°C to a root temperature of 35°C (aerial environment 20°C and 65 per cent relative humidity throughout), leaf growth was initially increased by the higher root temperature, but growth promotion was followed by a gradually increasing inhibition until, after 5-7 days, leaf growth

stopped completely (*Figure 7*). Root growth was immediately reduced by the high temperature. Initially, water permeability and activity of the roots, measured as exudation, was higher than at 20° C. The rate of exudation declined rapidly until it became zero after 7 days. This corresponded to the time at which suberization of the endodermal cells occurred and suggests that a causal relationship exists with the anatomical features found in the root (*Figure 7*). This points to the importance of considering growth and differentiation as separate phenomena, when plant growth is to be simulated.
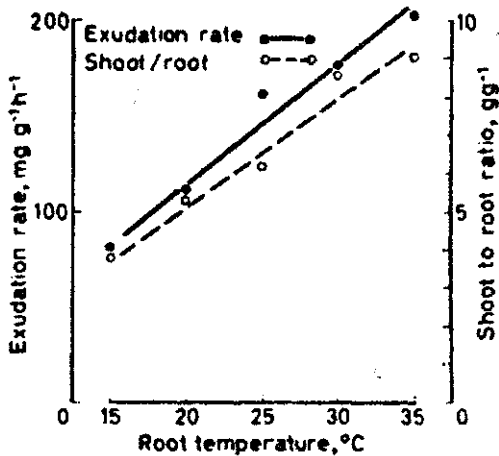

Figure 6. The influence of root temperature on the exudation rate and on the shoot to root ratio of tomato plants grown for 4 weeks on nutrient solutions maintained at temperatures from 15–35° C

The activity of a root will also be affected by its morphological characteristics as well as by its anatomical features. In maize plants, when the crown root initials were removed as they appeared, the seminal roots maintained growth for a longer period than in undisturbed plants (Brouwer and Locher, 1965). Since the subsequent crown root whorls of the intact plant consist of progressively thicker branches and the seminal roots of the treated plants continue to grow with finer branching, the average root surface and root length per gramme of root weight diverge. *Figure 8* shows the consequences of this phenomenon for the activity per gramme of root tissue in terms of shoot production (shoot to root ratio).
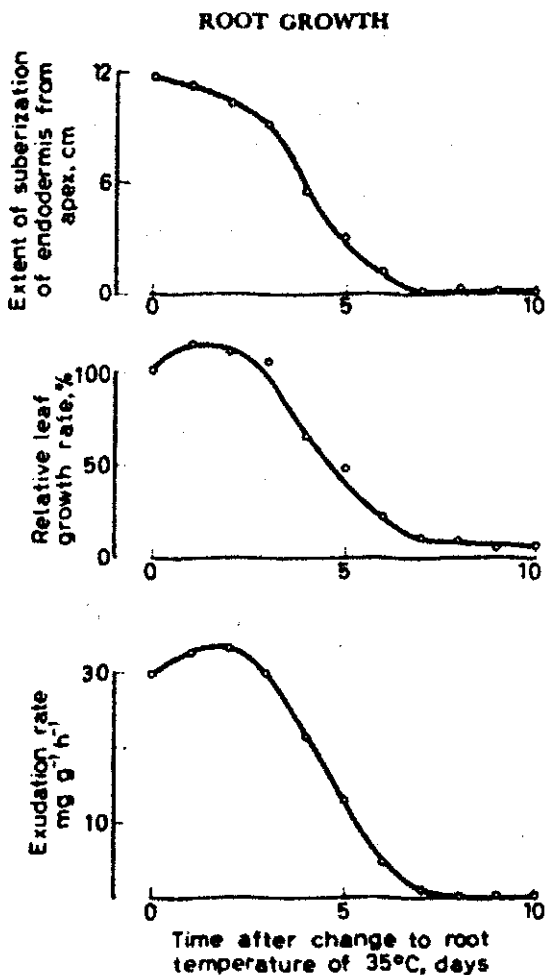
Figure 7. The time course of the changes in suberization of endodermis, leaf growth rate and exudation rate in bean plants after transfer from a root temperature of 20° C to a root temperature of 35° C. Air temperature 20° C throughout

Overall temperatures also influence the branching pattern of maize roots. In a comparison of root systems grown at either 15 or 25° C it was found that the root surface per gramme of dry weight was 1,150 and 2,420 cm² respectively. Consequently, the roots of these pretreatments showed differences in activities when exposed to the same conditions, roots grown at 25° C being more efficient at all

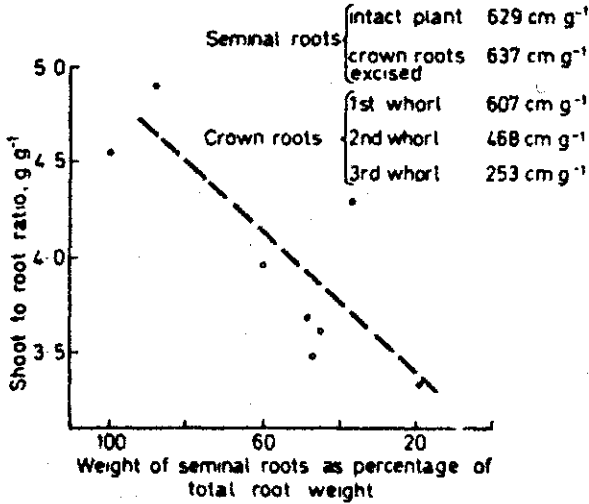| Seminal roots | intact plant | 629 cm g^{-1} |
	crown roots excised	637 cm g^{-1}
Crown roots	1st whorl	607 cm g^{-1}
	2nd whorl	468 cm g^{-1}
	3rd whorl	253 cm g^{-1}

Figure 8. *The relation between shoot to root ratios of maize plants and the percentage by weight of the seminal root system relative to the total root weight. This percentage was changed by removing part of the crown root initials at a very young stage*
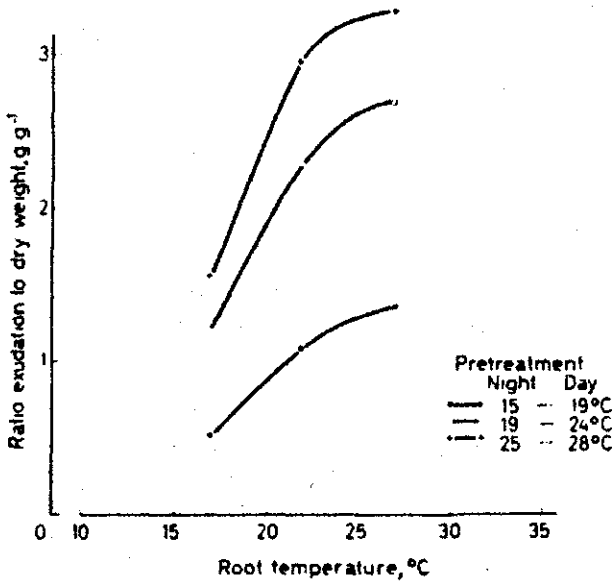

Figure 9. *The influence of root temperature on the exudation rate of decapitated maize roots grown at temperatures from 10-35 C*

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times (*Figure 9*). It is questionable whether the differences found are only due to the differences in morphological appearance. Certainly, various physiological properties might have changed also, but for the time being far too little is known for us to be able to use these changes in a simulation model. No clear insight has yet been gained of the morphogenetic effect of temperature. In the model, temperature is taken to act directly on differentiation, but it is hoped that in future it may also be possible to introduce these effects of temperature via physiological processes, for example, the production and breakdown of hormones or via sugar concentrations. As in the example of the removal of crown roots, the activity of the roots in terms of shoot growth is correlated here with the branching pattern, i.e., a higher shoot to root ratio corresponds to a finely branched root system.

From the evidence presented so far, it is concluded that maximum root activity enables the leaves to realize a growth rate that is limited only by the temperature of the growing leaf part. In relating root activity to root weight, both antomical and morphological features have to be kept in mind.

Any model that will really be helpful in understanding the physiology of growth and production must take into account the properties just mentioned and memorize and evaluate all the aspects of the history of the tissues involved. Since large memory, high-speed computers are available, it seems feasible to investigate their use in the simulation of crop growth.

THE ELEMENTARY CROP GROWTH SIMULATOR (ELCROS)

What is understood here by simulation will be illustrated at first by presenting the process of exponential growth according to a scheme and technique developed by Forrester (1962), to treat the dynamic (time-varying) behaviour of industrial organizations.

This process is presented in *Figure 10*. The WeiGhT (WGT) of the plant is given in a square, which means that it is a level or a quantity which is maintained even when all growth is stopped. The unbroken arrow indicates that this weight increases by an inflow of dry matter. The Growth Rate (GR) is represented by the symbol for a valve. The dotted lines indicate that this growth rate in turn depends on the weight and a constant, the Relative Growth Rate (RGR). These dotted lines present a flow of information. The picture is a relational model presenting all the interrelations that

exist in a system which grows exponentially, but does not contain the quantitative aspects. Hence, it has to be completed with a mathematical model (*Figure 10(b)*) consisting of a set of equations. For this purpose two times J and K a short time interval DT apart (*Figure 10(c)*) are considered. The level equation shows that the WeiGhT (WGT) at time K (WGT.K) equals the WeiGhT at time J (WGT.J) plus the interval DT times the Growth Rate at the time J (GR.J). The rate equation shows how the Growth Rate at the next time K (GR.K) is equal to the WeiGhT at time K (WGT.K)
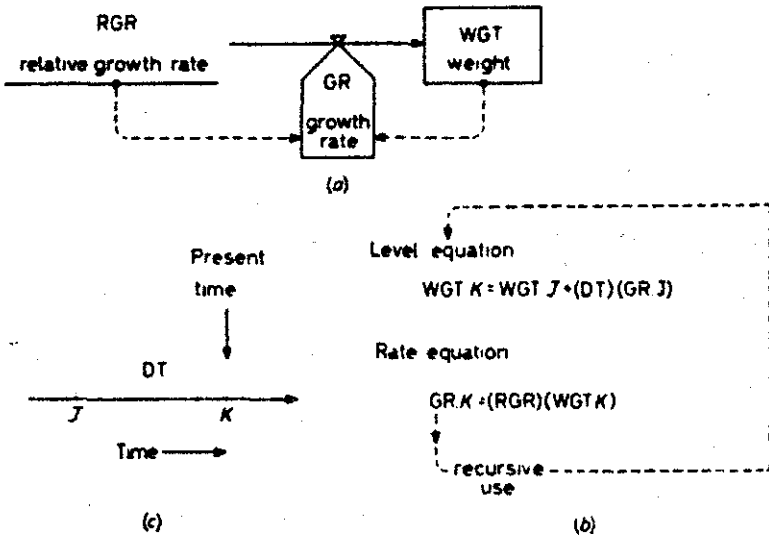

Figure 10. Simulation of exponential growth. (a) Relational model, (b) Mathematical model, (c) Time scale

times the Relative Growth Rate (RGR), a constant function of time in the case of exponential growth. Now time is advanced by one DT, so that the values that were associated with times K are now associated with time J. Then the level equation is used again, the new rate is calculated and time is again advanced one step and so on. A reasonable degree of accuracy can be obtained in this way by taking small enough time steps. It is obvious that this mathematical treatment incorporates the relational model presented in the diagram.

This approach can be used in describing elaborate systems, as in *Figure 11*, where a central part of the crop simulation programme which is being developed is presented.

A crop, or each plant of a crop, contains a pool of reserves. The PHotosynthesis Rate is the only source of reserves (carbohydrates), whereas these reserves are used for ReSPiration, Growth of Root Weight, Growth of Leaf Weight and Growth of the STem weight.

These rates are again represented by valve symbols. Photosynthesis and respiration transfers material to and from the surroundings, but growth as determined by the simulated growth rate causes transfer of carbohydrates from the reserve pool to the structural Weight of the RooTs, LeaVes and STem, i.e. into organic material
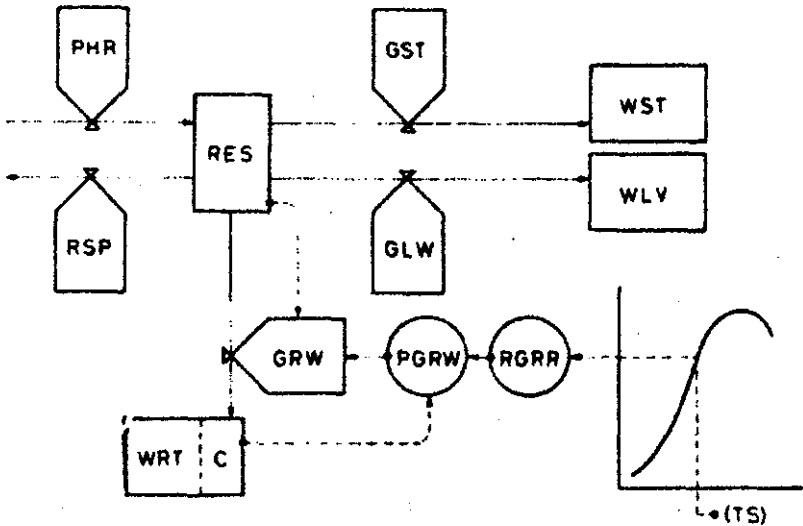
Figure 11. Relational model of the central part of ELCROS

that cannot be classified as reserves. The manner in which root growth may depend on conditions is presented in the diagram. The Temperature of the Soil is obtained from observations or from another part of the model 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 auxiliary value, necessary for further computations. Such an auxiliary is presented in a circle. The Possible Growth Rate of the Root Weight is now calculated by multiplying the relative growth rate by the Weight of the RooTs, which are still so young that they are Capable of growth. This amount is known by keeping track of growth from emergence. For instance, if it takes D days from emergence to flowering, it may be

observed that the roots which were formed during the last one tenth of a day (D) are still capable of growth. This possible growth rate, again an auxiliary, is only realized when there are sufficient reserves. The dependence of the growth rate on the reserves is again represented by a dotted line. The possible growth rate of the leaves is obtained in a similar way, but its realization depends not only on the presence of reserves, but also on the water stress in the leaves, in turn depending on the amount and activity of the roots and transpiration rate.

Many computational problems are avoided by using computer languages, specially written for the simulation of these types of open, recursive systems, which change status continuously with time, i.e. Digital Simulation Language (DSL-90) (Syn *et al.*, 1965), Continuous System Modelling Programme (CSMP) (IBM, 1967), DYNAmic MOdelling language (DYNAMO) (Pugh, 1963). These all have a routine that ranks the calculations in the proper order, so that elaborate programmes can be written in a problem-oriented fashion. All statements defining the initial values of the levels and the exogenous variables are executed first. Next the statements using variables and constants known up to then are calculated and finally the rates are computed. A built-in clock routine then takes care of the updating of the levels and the recursive use.

Updating has to take place so often that changes in the content of the levels at each cycle are small compared to the contents themselves. In crop growth simulation this is achieved by advancing time in steps of one-twentieth of a day.

In due course it is necessary to construct models taking all relevant limiting factors of crop growth into account, but the work load is at present restricted to considering models which enable us to simulate growth under conditions of optimal nutrient and water supply. Within this framework a further restriction is made by considering crop growth only from emergence to flowering. This period is of prime importance and of sufficient complexity to show the scope and limitations of simulation for the purposes of:

(*a*) extrapolating the knowledge gained under laboratory and controlled conditions to the field,

(*b*) studying the influence of climate and weather, density and time of sowing,

(*c*) analysing the effect of differences in varieties and species,

(*d*) evaluating the relative importance of the pertinent characteristics,

(*e*) planning research.

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The present ELementary CROp growth Simulator (ELCROS) contains various sections. In one, the daily course of the weather within the crop is generated on the basis of daily values of the minimum and maximum temperature, dew point, wind speed and radiation, taking into account the day of the year, hour of the day and latitude of the place. The course of transpiration is simulated, taking into account the leaf mass and stomatal resistance, as influenced by radiation intensity.

Another section simulates the effects of temperature and day length on the growth rate of the plants. The constraints imposed upon growth by translocation are introduced by different accessibilities of the reserves to the leaves, stems and roots.

Photosynthesis is introduced on the basis of an elaborate computer programme (de Wit, 1965) enabling a calculation of the crop photosynthesis as affected by the amount, optical properties and photosynthesis function of the individual leaves and the incoming radiation from sun and sky. The rate of respiration is calculated, taking into account the influence of temperature, reserve percentage, protein content of different plant parts and ageing. The growth section considers the influence of temperature, reserve status, age and age distribution of tissues and, as far as leaf and stem growth is concerned, the influence of water stress, resulting from a balance between transpiration and activity of the roots. Morphological changes are accounted for by considering the growth in weight as well as surface.

All sections are based on a qualified opinion regarding the physiological mechanisms involved as discussed previously for the root growth. At present, all parameters are adjusted to simulate the growth of maize, but the structure of the programme also enables simulation of other plant species in their vegetative stage.

SIMULATED EXPERIMENTS

The use of ELCROS is best illustrated by considering first some simulated experiments on the influence of defoliation and root pruning on subsequent growth and the influence of temperature on the growth of corn.

A clipping experiment was simulated by assuming that maize plants were allowed to grow undisturbed at a temperature of $20°C$, a humidity of 65 per cent and a light intensity of $0·14$ cal cm^{-2} min^{-1} for 9 days. On the ninth day, three treatments were given: in the first treatment, plants were allowed to continue growth undisturbed

for another 10 days; in the second treatment, half of the roots were pruned and in the third treatment half of the leaves were removed.

The results of these simulated treatments are given in *Figure 12* as the relation between shoot (leaf) and root weight on successive days. The undisturbed plants, which were widely spaced, grew with an almost constant shoot to root ratio and finished with a leaf weight of 0.9 kg ha^{-1}. The plants whose roots were subjected to
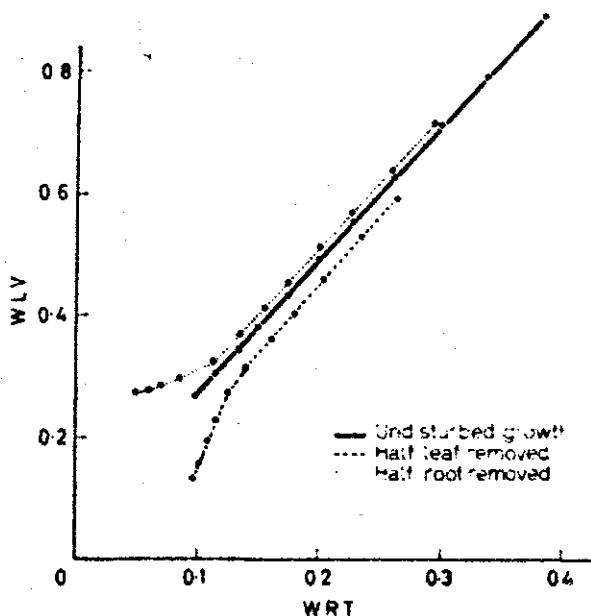
Figure 12. Simulated influence of defoliation and root pruning on the increase in weight of root (WRT) and shoots (WLV). The points represent the root and shoot weight on the ten successive days after clipping

pruning took about 5 days to regain a root to shoot ratio almost equal to the initial ratio, but they grew more slowly during this process. This was achieved as follows. The plants after pruning were unable to maintain the turgidity of the leaves at the same level as before. Because of this, the growth rate of the leaves was decreased, more reserves were accumulated at a level where they were available to the roots and root growth was thus enhanced. The reduction in leaf growth and the enhancement of root growth was maintained until the original shoot to root ratio was recovered and turgidity was

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then maintained again at the level of untreated plants. Full recovery was impossible because thicker leaves were formed during the period of lower turgidity.

Where defoliation occurred, the turgidity of the remaining leaves was enhanced so that their growth rate was increased. Hence, less reserves were available to the roots so that growth of these organs was reduced. The re-establishment of the original shoot to root ratio
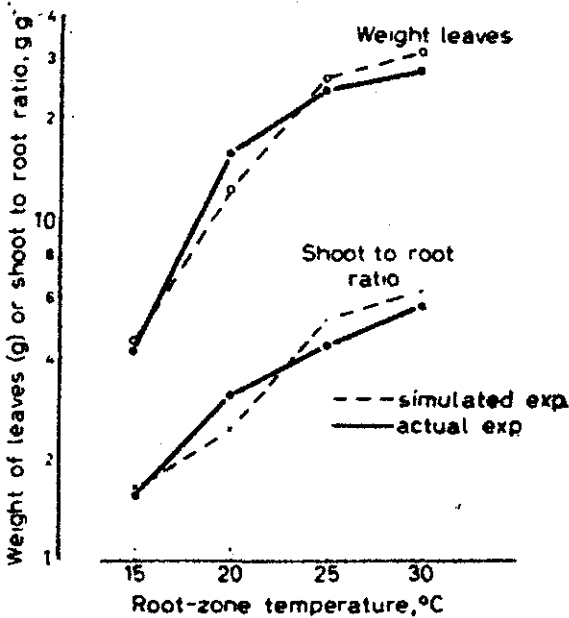

Figure 13. Influence of the root zone temperature on the weight of leaves and shoot to root ratio of actual and simulated corn plants, harvested 20 days after emergence

then took longer, because part of the photosynthetic apparatus had been removed, and the amount of leaf in the equilibrium situation was equal to about twice the amount of root. For the same reasons, the yield depression caused by defoliation was considerably greater than that by root pruning.

The similarity between the outcome of such simulated experiments and actual experiments, as for instance the experiment in *Figure 4*, shows that the interpretation incorporated into ELCROS accounts for the observations.

The results of actual and simulated experiments in which the root zone temperatures were varied are presented on a semilogarithmic graph in *Figure 13*. The increase in growth and the increase in shoot to root ratio with increasing root zone temperature results from the influence of this temperature on the morphology (i.e. surface to weight ratio of the roots) and their activity, introduced into ELCROS on the basis of exudation experiments discussed above. The higher the root zone temperature, the fewer roots are needed to maintain the turgidity of the leaves. Consequently more reserves are used to form new leaves which intercept more light at the wide planting density and thus contribute to the growth.

EXTRAPOLATION

Although the overall agreement between simulated and actual experiments is reasonable, there are still deviations in the details.
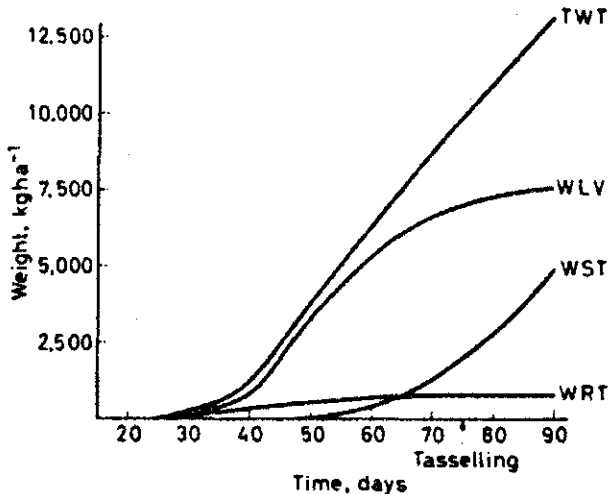
Figure 14.   Simulated growth of corn (Total weight, TWT; Weight of leaves, WLV; Weight of shoot WST; Weight of root, WRT) sown at a density of 10 plants per m² and emerging in Ames (Iowa), 18 May in 1963

These illustrate the degree of inadequacy in our knowledge of the physiological details of plant growth. An indication of the parts of the programme needing further research can be gained by changing the basic physiological data in ELCROS.

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The simulated growth of a field of maize, planted at a rate of 10 plants m^{-2} and emerging on 18 May in Ames on a soil with optimal water and nutrient supply, is presented in *Figures 14* and *15*. *Figure 14* shows the increase in weight of the leaves (sheaths + laminae), stems, roots and total weight. After 80 days, at the time of emergence of the female flower, the estimated weight was 1.25×10^4 kg ha^{-1}, which is in reasonable agreement with experimental results in that area reported by Shibles (personal communication). There was no sign of flattening of the curve at the end of the period of growth, which is in good agreement with observations and the proportion of stem was of the right order (Hanway, 1966). The simulated root
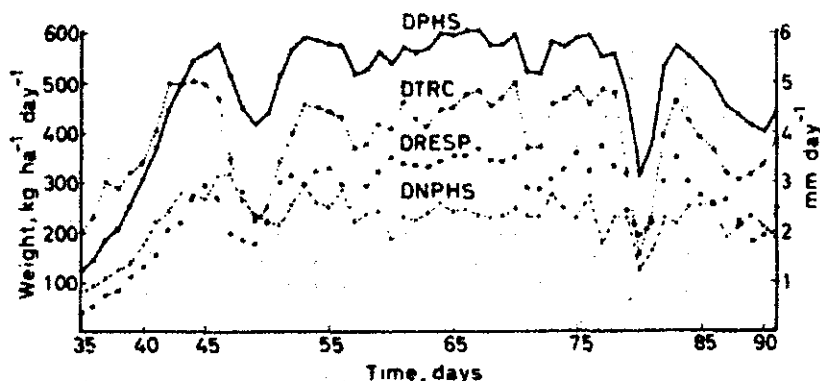

Figure 15. Simulated photosynthesis (DPHS), respiration (DRESP), net photosynthesis (DNPHS) and transpiration rates (DTRC) from the 35th day after emergence onwards of corn in Ames in 1963

weight seems low, but it has to be realized that optimum soil conditions, comparable to those in an aerated nutrient solution have been assumed. *Figure 15* shows the daily values of gross photosynthesis, respiration, net photosynthesis and transpiration. The leaf area on the fiftieth day was already 6.4 ha ha^{-1}, so that the crop surface was closed and photosynthesis and transpiration only fluctuated by variations in radiation and other weather factors. Respiration follows photosynthesis and was not proportional to the amount of plant material on the field. This is a combined effect of ageing and reserve percentage on the respiration rate and is in good agreement with the observations of McCree and Troughton (1966) under controlled conditions. The existence of a ceiling yield, at which the

respiration is equal to photosynthesis and the crop does not increase any more in yield (Davidson and Philip, 1958), is not corroborated.

Although the simulated and actual growth rates are in reasonable agreement, it should be realized that too little is known as yet about the influence of external and internal conditions on photosynthesis and respiration for an accurate prediction of the growth rates. Extrapolation to field conditions leads in general to corn plants with a leaf area index of 15 at a leaf weight of 10^4 kg ha^{-1}. However, such thin leaves are only obtained in actual field experiments at dense plantings (Crösmann, 1967, Williams, Loomis and Lepley, 1965). The cause of this discrepancy may be related to the large variation of the growth rate per stem with density of planting.

CONCLUSIONS

Experimenting with ELCROS has shown the importance of experimental techniques in which more attention is paid to variation in the behaviour of plants and crop surfaces and in which the effects of sudden environmental changes on the plants are followed with time.

ELCROS is used in interpolating and extrapolating knowledge from the textbook and from experimental results under controlled conditions to the field. The lack of agreement between the simulated and actual experiments is sometimes disappointing, but indicates more than anything else the areas in which our knowledge is lacking. Hence ELCROS is used as an efficient tool in planning research in the plant and crop sciences. Finally it is considered that simulation programmes of this kind may be effectively used in teaching crop husbandry.

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