

Crop growth models without hormones

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Summary

Dynamic simulation models of plant and crop growth are in general based on the state-variable approach. An important family of state variables is formed by tangible quantities like the weight of leaves and roots, the nitrogen content and the level of carbohydrate reserves. Together with exogenous variables like radiation and temperature, these state variables govern important growth processes.

However for the simulation of formation of organs and partitioning of assimilates, information seems also to be required on the current level of activities like CO₂ assimilation and the growth of various organs. How this information may be retained in auxiliary state variables is illustrated by considering the dynamic equilibrium between growth of roots and shoots and a few other examples.

These auxiliary state variables are not tangible quantities but mathematical artefacts of the simulation program. It is speculated that in real plants, similar information may be retained and transferred, for instance, by the hormonal system.

A hormonal system is a communication system. Such systems may be analysed either in terms of means (of the hardware used), or in terms of purpose (of the messages transferred). In dynamic models of crop growth, interest should be focused on the latter, whereas the existence of the hardware, the hormonal systems, may be taken for granted. Of course, these systems may be simulated for themselves, but there is no reason to do so in crop growth models.

Introduction

For the dynamic simulation of plant and crop growth, state-variable models have gained wide acceptance. The principle of this approach is introduced here by discussing the relational diagram of Fig. 1. This diagram concerns a model of a growing plant or crop, which is just detailed enough to consider the concept of the functional balance between shoots and roots.

In the models and their relational diagrams state, rate, driving and auxiliary variables are distinguished. State variables are tangible quantities and are in the di-

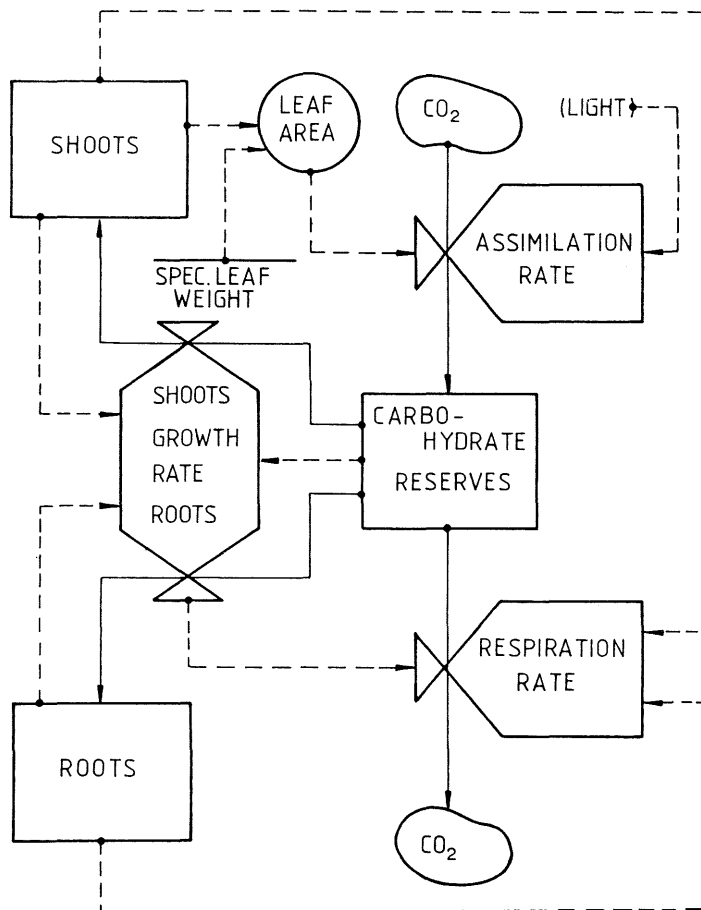


Fig. 1. A relational diagram of a crop growth model with a functional balance between roots and shoots. See the text for the explanation of the symbols.

agram presented as rectangles. Here only the amount of shoots, of roots and of the carbohydrate reserves are considered. The rates of change of these state variables are given by rate variables, which are symbolized by valves that control the flows presented by the full drawn lines. It appears that the reserves increase by assimilation and decrease by respiration and by growth of roots and shoots. The dotted lines indicate which information is necessary to calculate the rate variables. It is readily seen that the respiration rate is supposed to depend on the amount of shoots and roots and on the rate of growth of these organs. These are the maintenance respiration and the growth respiration, respectively. The assimilation rate depends on the leaf area and the light. The latter varies independently of the crop: it is a forcing variable and therefore placed between parentheses. The leaf area is given within a circle because it is here an auxiliary variable calculated from other variables, in this

case from the amount of shoots and the specific leaf weight. This weight is symbolized by a bar because it is supposed to be a constant here. The growth rate is assumed to depend on the availability of the carbohydrate reserves and its distribution over root and shoot in one way or another on the amounts of these organs that are present.

Once these relations are quantified, the actual simulation procedure is simple. After calculating all rate variables, these are used to update the state variables according to the scheme: state variable at time $t + \Delta t$ is equal to state variable at time t plus its net rate of change at time t multiplied by the interval of integration Δt . The dreary work is repeated again and again by the computer.

During the last 15 years most progress has been made with the simulation of those aspects of growth that are directly related to transpiration, assimilation, respiration and nutrition. This is not surprising, because it concerns processes of mass transfer between plant and crop and its surroundings that are as such open to measurement and experimentation. This is far less the case for the processes that control the development of form and function. The simulation of organ formation and the partitioning of growth over these organs in dependence of plant development and environmental conditions, meets therefore with considerable problems. Some of these will be illustrated by discussing solutions used for the simulation of three processes: the dynamic equilibrium between root and shoot growth, tillering of grasses and seed formation, and senescence.

In a concluding paragraph is discussed why in crop growth models no attention is paid to the existence of the hormonal system as such.

The dynamic equilibrium between the growth of roots and shoots

The experiments by means of which Brouwer proved the existence of a dynamic equilibrium between the growth of roots and shoots were charmingly simple. First he showed that the shoot/root ratio of young plants growing under constant conditions hardly changes with time. To determine whether this should be attributed to a fixed distribution of carbohydrates over these two plants parts or to a dynamic equilibrium, Brouwer removed either part of the roots or part of the shoots. The equilibrium proved to be dynamic, because the original shoot/root ratio was restored in both cases by an increased relative growth of the organ that was partly removed and a decreased relative growth of the undisturbed organ.

Brouwer attributes this equilibrium to the fact that one organ provides growth essentials for the other. Restricted to water, the reasoning is then as follows. If part of the root system is removed, less water is taken up but transpiration continues. Therefore the water content of the plant decreases, which causes the stomata to close to such an extent that transpiration equals uptake again. The decreased water content, or increased water stress, makes also that the shoot grows less, so that carbohydrates may accumulate. Thus, more of them are transferred to the roots, which grow then relatively faster and gradually restore the original shoot/root ratio.

The relations that govern the translocation of carbohydrates are little known in the quantitative sense, so the simulation is short-circuited by introducing a parti-

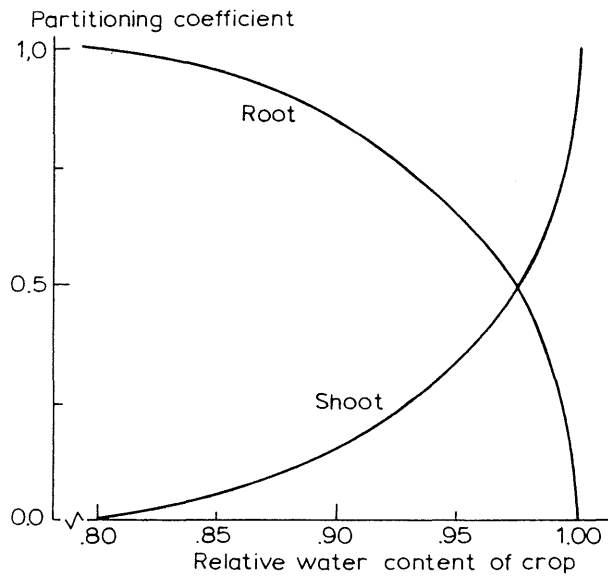


Fig. 2. The partitioning of growth over roots and shoots in dependence of the relative water content of the crop (de Wit et al., 1978).

tioning coefficient for growth over root and shoot. In case water is the controlling factor, this coefficient is assumed to depend on the relative water content of the crop as illustrated in Fig. 2. This relative water content is in its turn a state variable out of another part of the model, which treats the balance between water uptake by the roots and transpiration by the shoots in well known physical terms. In this way the amounts of shoots and roots feed back on their growth rates. The form of the partitioning curve reflects the observations that with decreasing relative water content, the growth rate of the shoots decrease and of the roots increase rapidly at first, and slowly later on.

If the functional balance is simulated in this way, the time constant of recovery after removal of part of the roots is 2-3 days and after removal of part of the shoots proves to be somewhat longer. The shoot/root ratio decreases also with increasing evaporative demand and increases in the closed crop situation. This is all in accordance with experimental results (de Wit et al., 1978). More details may be simulated. For instance, it may be programmed that with increasing temperature more root surface is formed per unit weight. Then it is possible to maintain with the same root weight a higher relative water content, so that a higher shoot/root ratio results.

So far the partitioning of growth. As for the magnitude of the growth to be divided over roots and shoots, it is true by definition that the growth rate of an organ is equal to its weight times its relative growth rate. However, from the physiological standpoint, the relative growth rate of a crop, plant or organ which consists for the greater part out of tissue that is mature and unable to grow, is meaningless. In the early days of simulation attempts were made to by-pass the problem by keeping

track of the amount of meristematic tissue, and defining a relative growth rate for this material only (Brouwer & de Wit, 1968). However, the knowledge of the morphogenetic processes was too fragmentary to make this approach useful and this is probably still the case.

The problem was solved, at least for the time being, by assuming that there exists a direct relation between growth and carbohydrate reserves. To investigate this relation Penning de Vries et al. (1979) studied the effect of total soluble carbohydrates on the respiration rate, assuming that the first reflects the availability of reserves and the second the growth rate. Fig. 3 shows that up to reserve percentages of over 10 %, the respiration rate per unit weight increased about linearly with the concentration of total soluble carbohydrates. Accordingly, the growth rate of a crop or plant may be calculated by multiplying the total amount of reserves by a relative utilization rate of these.

To estimate this relative utilization rate it is noted that under many conditions plants are able to balance their reserves level reasonably well. If this is done around a daily average of for instance 5 % at an average daily net assimilation rate of $0.1 \text{ g g}^{-1} \text{ d}^{-1}$ the relative utilization rate has to be $(0.1/0.05) = 2 \text{ d}^{-1}$. If now the average net relative assimilation rate changes, growth is first adjusted by a corresponding change of the reserve level, but in due course the relative utilization rate of reserves is adapted in such a way that the original average reserve level is restored. Physio-

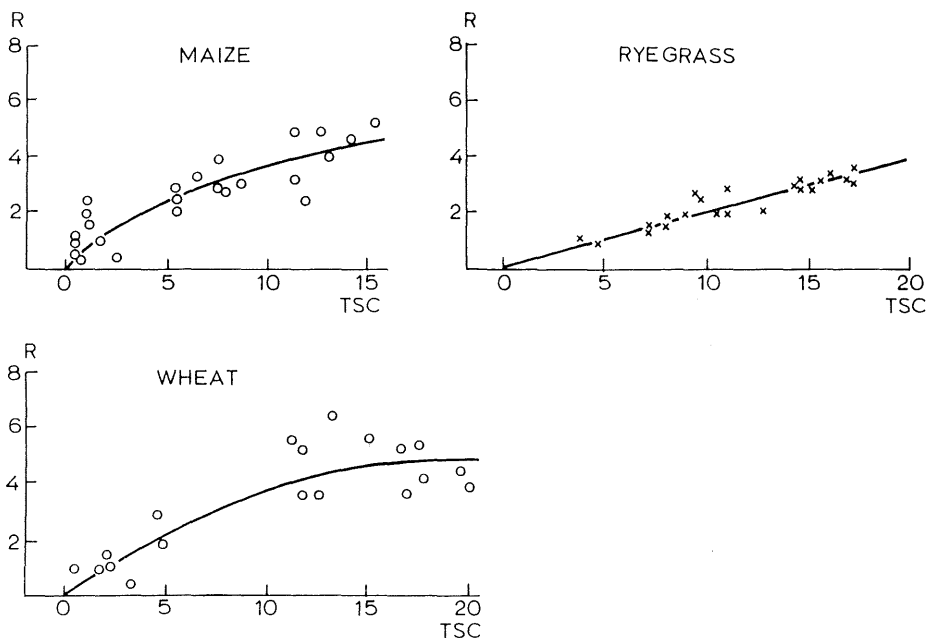


Fig. 3. Relations between respiration rate and total soluble carbohydrates (Penning de Vries et al., 1979). R = respiration rate of CO_2 per unit dry matter ($\text{mg g}^{-1} \text{ h}^{-1}$). TSC = total soluble carbohydrates as a percentage of total dry matter (%).

logically this implies that plants maintain the amount of meristematic tissue they need to cope with the current average assimilation level.

The simplest way to simulate this is illustrated in the relational diagram of Fig. 4. Here another state variable is introduced, which increases with the assimilation rate of the moment and decreases with a relative rate of decay. If this relative rate is set at 0.5 d^{-1} , then the value in this way conserved is the running two-day average ($1/0.5$) of the assimilation. The relative utilization rate of the reserves is now calculated as an auxiliary variable by dividing this running two-day average by the average reserve level that is supposed to be maintained. There is here a similarity with running a dynamic firm. For this, it does not suffice to consider only past performance by keeping track of the balance. To maintain control it is also needed to record the current level of activities and act upon it. This is done by recording rates of cash-

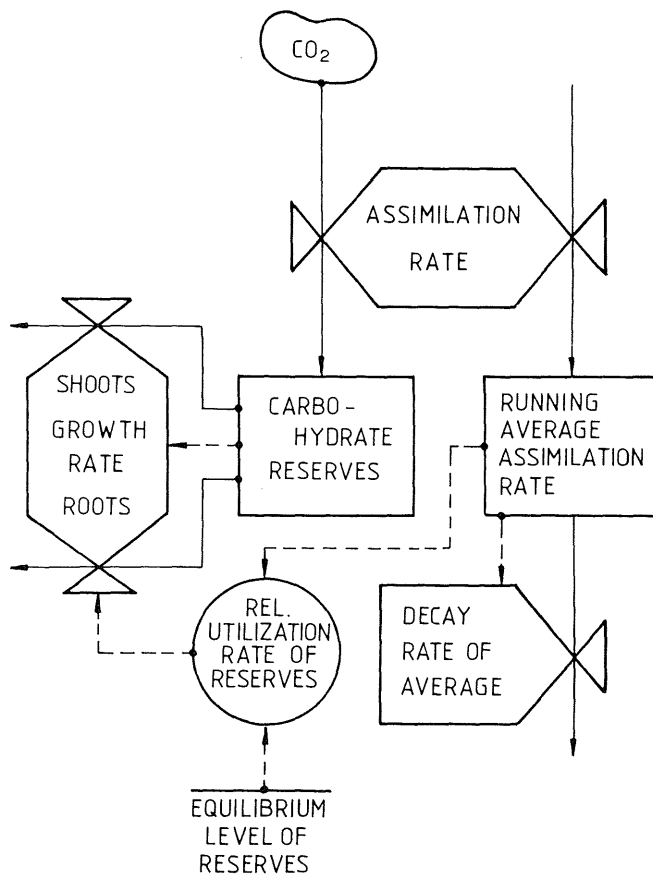


Fig. 4. A relational diagram for the adaptation of the relative utilization rate of reserves to the assimilation rate.

flow, incoming orders, outgoing goods and so on. The situation with crop growth models is similar. Here it does also not suffice to keep track of such tangible state variables as the amount of shoots, the amount of roots and the level of reserves. Besides that information is necessary on the current level of activities. This need is here met by the running average of assimilation, as an analogue of the cashflow in business systems. It is tacitly assumed by the modeller that the instrument to record its magnitude is available, be it as a hormonal level or otherwise, much like a manager who does not care about the technical aspects of the administration.

Tiller dynamics

Tiller formation in grass-swards is also supposed to be directly related to assimilation as illustrated in the relational diagram of Fig. 5. It is shown here that the equilibrium density of tillers is calculated in dependence of a running average of assimilation and the flux of assimilates that one tiller is able to monopolize. If the latter is 0.2 grams per day and the assimilation rate 300 kg per hectare per day, the equilibrium density is 1.5×10^6 tillers per hectare. This amount is an auxiliary variable, whereas the actual density of tillers is a state variable. The rate of formation of the tillers is now supposed to be equal to the difference between the equilibrium and the actual density of tillers, multiplied by a relative formation rate. If the actual density of tillers is lower than the equilibrium density, the rate of formation is positive and if it is higher this rate is negative. This implies induction of new tillers and dying of existing tillers, respectively. It is shown in the diagram that the same running average of assimilation controls the relative utilization rate of reserves, as explained earlier.

In the actual simulation program of Dayan et al. (1981) ten classes of tillers are distinguished to allow differentiation in size. In case of mowing, relatively more of the large tillers are supposed to be killed by removal of the growing point. The measured and simulated results of tillers agreed reasonably well for Rhodes grass. For both it appeared that lengthening of the cutting interval proved to result in a progressive decrease in the number of tillers capable of regrowth after cutting. Besides, simulated as well as measured data showed an alternation of high and low numbers of tillers capable of regrowth after consecutive cuttings at the higher cutting intervals. This reflected itself also in the yields, although there the alternation was larger in the simulated than in the actual situation.

Organ formation and senescence

The thousand-kernel weight of wheat and other grains is often remarkably constant in spite of large variations in growing conditions. Although the knowledge of the factors that govern kernel formation in small grains is still little developed, the foregoing approach may help to understand this phenomenon (van Keulen, 1982). For this purpose, the successive formation of vegetative tillers, tillers with ears, spikelets on the ears and seeds in the spikelets are considered. The simulation of the vegetative tillers is done in the same way as for grasses, whereas their rate of transfor-

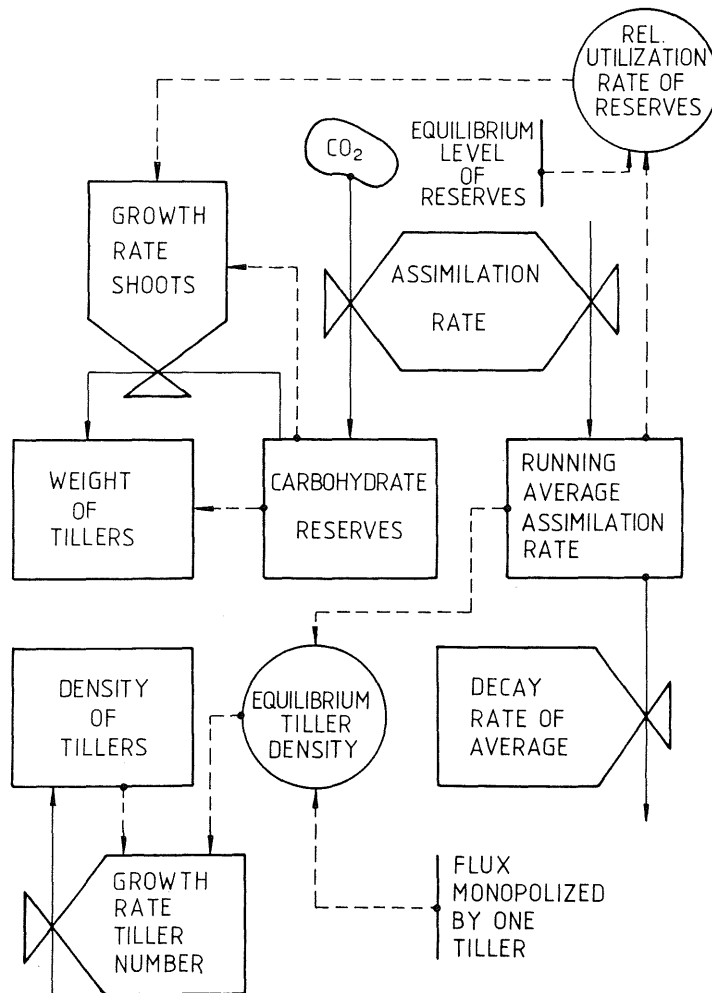


Fig. 5. A relational diagram for the growth and the adjustment of the number of tillers in a grass-sward.

mation into reproductive tillers is assumed to be dependent on the current flux of assimilates per tiller during ear formation. If a bright period is followed by an overcast period, the number of vegetative tillers is large, but since the assimilation per tiller during ear formation is low, only a small part develops into reproductive tillers. However, if a dull period is followed by a bright period, the number of vegetative tillers is small but their supply with assimilates is high, so practically all of them develop into reproductive tillers. These compensatory reactions are supposed to continue by simulating that the rate of spikelet formation depends on the running average rate of assimilation per ear, and the number of seeds per spikelet on this running average per spikelet.

In this way it is achieved that the crop continuously adapts itself to the prevailing conditions and that the number of kernels is adjusted to the supply of assimilates during anthesis. In many climates the season proceeds in such a way, that there is a good correlation between assimilation in this period and in the post-anthesis phase. Then the crop forms about the amount of kernels it needs, so that the thousand-kernel weight ends up around the normal value. If there is a cool overcast period or a dry spell at the end of the vegetative stage, followed by a bright period with sufficient water, the number of kernels may be too low. They then reach their normal individual weight before full senescence of the leaves and photosynthetic capacity is wasted at the end of the growing season. However, if a bright period is followed by a dull period, it is the other way around, so that the weight of the individual kernels remains below normal.

Under many conditions plant nutrients, and especially nitrogen, are limiting for growth. Much of the nitrogen needed for seed formation is then withdrawn from the vegetative plant parts. Too many seeds and a high rate of nitrogen transfer lead to early exhaustion of nitrogen in the vegetative parts, untimely death of leaves and a low thousand-kernel weight. However, the limited supply of nitrogen manifests itself already during ear formation and anthesis in a lower rate of assimilation, so that here again the number of seeds that is initiated is adjusted more or less accordingly.

Senescence and death of leaves is in practice very often governed by this so-called process of self-destruction (Sinclair & de Wit, 1975): the uptake of nitrogen, minerals and carbohydrates out of the vegetative mass by the seeds, leading to exhaustion and death of leaves. Such a process of exhaustion is probably common in all species, but particularly illustrative in species with many seeds (a high harvest index) and a high protein content, such as leguminous crops and cereals. The duration of the reproductive period in small grains can often be quantified quite well with such balance considerations (Spiertz, 1982). That hormones are involved in assimilate redistribution and senescence is without doubt (see e.g. Thimann, 1981), but in the self-destruction concept they are only intermediate steps. One must also conclude, however, that the cause-and-effect discussion about hormones, senescence and redistribution has not yet subsided (Nooden, 1981; Sheehy, 1983).

Hormones

The necessity of communication between plant plant parts needs no argumentation here. We should recognize, however, that though hormones are biochemical signals par excellence, they are by no means the only signals operative in plants. Water potential and turgor, for instance, are signals that communicate levels of water stress fast throughout the plant, and may cause leaf rolling, stomatal actions and cessation of extension growth. A nice example is also the folding of leaves of *Mimosa pudica* after touching one of them. In a model, such relations are represented by dotted lines (Fig. 1), indicating flows of information. Another non-hormonal form of communication is provided by the critically low concentrations of plant nutrients, which inform the cell directly about its maximum rate of growth. The amounts of key enzymes and the levels of their activities show often a response to past activ-

ities. Nitrate reductase activity in root systems, for instance, needs some hours of induction after a period in a nitrate-free medium; also RuDPCase activity needs some time (hours) to reach its maximum after a night of darkness (McDermitt, pers. comm.). Regulation of the rate of activation and de-activation of such enzymes gives the plant control over the period during which the information about the level of past activities is retained.

Without any doubt, however, hormones play also a very important role in the communication systems of the plant. There are, for instance, many arguments to attribute a role to hormones in the maintenance of the dynamic equilibrium between roots and shoots. Roots are after all the main organ for the synthesis of gibberilic acids and cytokinines, which are translocated upward with the water in the xylem to the transpiring organs, whereas the phloem stream contains for instance indolic, gibberilic and abscisic acid, which are translocated downwards to the roots with the carbohydrates. It is also well known that the production of cytokinines depends on the rate of growth of the roots, whereas the abscisic acid concentration in the leaves increases with increasing water stress and causes the stomata to close, and there is little reason to doubt that hormones mediate the effect of water stress on growth.

In spite of this intimate linkage, hormones do not appear in the crop growth models that are being developed. To understand this, it should be realized that the purpose of the hormonal system is communication. Like any other communication system, this system may be analysed from the engineer's point of view in terms of the hardware or from the user's point of view in terms of the messages that are transferred. Much of the research on hormones is biochemical and therefore devoted to the hardware. How impressive the results may be, they are not very useful to the modeller, because he is especially interested in the messages and tends to take the existence of the hardware for granted. Only when the hardware does not function properly he may become alarmed. In this way the crop growth modeller does not differ much from the user of the telex or better the Citizen Band Radio, taking into account the amount of noise he has to cope with.

Handbooks on plant growth regulation show that much research has been devoted to unveil the content of the messages of hormones. However, it generally is difficult to interpret results in a way helpful to modellers. External application of plant tissue yields dose-response curves, but it is difficult to assess the effective concentration within the plant. A build-up of the concentration by natural causes avoids this problem, but is relatively slow, and, as each of the many hormones affects many functions in the plant, it is difficult to disentangle the responses of individual processes to individual hormones. Much more needs to be known about how fast hormones are produced and de-activated or degraded, about their rate of translocation, about the individual dose-response curves and about the interactions of hormones, before modelling can be pursued with a fair minimum of speculation.

Though there is little direct evidence to prove it, it seems that levels of important hormones build up or decline with rates such that equilibrium levels can be reached within hours or days. This period corresponds roughly with the shortest time interval in which the modeller of crop growth is interested, and at least with the shortest time interval over which he can verify experimentally the performance of his crop

model. The chain of events that links induction of water stress to reduction of leaf growth can then be characterized very well as a direct relation without considering hormones as intermediates. The use of the functional-balance concept in crop growth models provides a clear example of this. This speed of hormonal-balance processes is a major reason that hormones are not essential in crop growth models. Slow hormonal processes, such as those that control photoperiodism and morphological development, are exceptions to this, and the fact that their dynamic simulation has little advanced beyond a descriptive stage may be a reflection of the insufficiency of knowledge about their hormonal aspects.

If one is interested in modelling plant performance at a time scale in which hormonal levels have not yet reached equilibrium, it seems worthwhile to consider seriously the fate of hormones. In a model to simulate growth of plants with 10-minute intervals, for instance, it is essential to recognize that the rate of growth does not respond directly to a change in water stress (Penning de Vries et al., 1979), but with a delay of several hours. This delay may be ascribed and simulated as a build-up of hormones. The chain of events of stress induction to growth-rate reduction must then be treated as a process with intermediate steps.

This conclusion is another way of saying that in any dynamic simulation model not more than two or three hierarchical levels should be simulated (de Wit, 1970). A crop model, generally, should not simulate relatively fast processes such as those of hormone balances. But a model to study growth of individual plant organs may have to do so.

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