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## Disease and crop physiology: a modeller's point of view

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### Introduction

Disease and pest management requires a knowledge of both the crops and the disease or pest. The interrelationships between host and parasite have a dynamic character, that is, they change with time, which has to be recognized in a proper description of the substrate and the environment of a parasitic organism. In the past, most studies of disease and pest management have emphasized the population dynamics of the disease and pest organisms, but their association with the growing crop has been virtually neglected. Elaborate studies on the population dynamics of pests or disease-causing organisms may be used in predicting future pest and disease intensity, but the value of these studies is limited when a reliable assessment of damage is not available. Models may help to develop management strategies.

Among dynamic models, various types can be distinguished according to the objectives of the study. When explanation is the aim, the corresponding explanatory models based on a systems hierarchy try to predict and explain integrated behaviour from a more detailed knowledge of the underlying physiological and morphological processes (De Wit & Goudriaan, 1978; De Wit *et al.*, 1978). Much of the information presented in other chapters of this book illustrates studies of detailed plant physiological processes involved in crop-pathogen interrelations. To integrate this type of knowledge, and to determine the effects in terms of production ecology, a modelling approach of the explanatory type is needed. Of course, all knowledge of detailed processes becomes descriptive at the ultimate level of reduction, but one should nevertheless distinguish between descriptive and explanatory models. Descriptive models describe the behaviour of a system using only one level of integration. Descriptive models may be static or dynamic. In the latter case, the system and its behaviour may change in the course of time. Usually, descriptive models are static, as, for example, multivariate regression models, and their explanatory value is limited.

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Explanatory models predict the behaviour of a system at the level to be explained using system-synthesizing elements, or subprocesses, at the next lower level of integration. These elements may be static (for example, light distribution in a canopy based on geometric and physical characteristics of the canopy) or dynamic (for example, crop growth, known in detail from plant physiology). Some comprehensive simulation models of pests and diseases have already led to simplified econometric models which can help decisions about 'spraying or praying'. However, the practical value of these models is limited as their reliability is low. Multivariate regression models have given better results in crop loss assessment; their superiority is mainly owing to the tuning procedure involved in the development of such models. These models accommodate better to average field conditions since they include data about the variations in plant stand, nutrient and water supply, and the level of injury by the disease or pest at a certain population density, which all together determine the yield. Regression models perform best in predicting the mean performance of a population of fields, whereas dynamic models may give better results when applied to the individual field.

Only a few combination models exist in which both crop growth *and* population dynamics of the pest or disease organism are based on detailed analysis. Such combination models are often of a dualistic nature, containing on the one hand a great number of descriptive elements, and on the other a great deal of detailed knowledge of subprocesses. When too many phenomena observed at the system level are introduced into the model, its behaviour is often governed by the descriptive relationships. In those cases the explanatory value of the models is limited and the modelling effort becomes a sophisticated method of curve fitting. Comprehensive models with a satisfactory compromise between completeness of basic data, time needed for experimental and modelling effort, and reliable output, are rare indeed.

In this chapter we will discuss two types of combination models. First we will discuss summary models. These models are designed to produce a shortcut to the objectives of the comprehensive model, without losing the sensitivity of the full analysis. Models of this type are used to calculate the effect of a pest or a disease on crop growth without further consideration of the nature of damage. Changes in crop-pathogen interactions are introduced in these models to compute the impact of the perturbations. The calculations give some insight into the relative importance of the nature of crop-pathogen interrelations. A complete explanation cannot be given as too many basic relations are neglected. Second, we will discuss an example of a comprehensive model of crop growth and a disease. This combination model is used to test hypotheses on the nature of the disease-crop interrelations.

### Dynamic simulation of crop growth

During the last decade considerable attention has been paid to the development of procedures for the calculation of crop growth which are based on the process of photosynthesis. Some review articles summarize this effort (Waggoner, 1977; Loomis, Rabbinge & Ng, 1979; Penning de Vries, 1981). These calculations are usually based on the assumptions that photosynthetic activity is maximal and crop canopies are closed. The actual production of a crop is then found by accumulating this photosynthetic activity and multiplying this sum by the harvest index, the ratio of seed dry weight to total dry weight. Other methods, in which attention is paid not only to photosynthesis but also to respiration and the partitioning of assimilates between various plant organs, are scarce. Comprehensive models that incorporate all these aspects in sufficient detail are not yet available. The level of detail of some subprocesses depends mainly on the interest and knowledge of the model builder and his opinion on the relative importance of these subprocesses. A model with many details, simulating the assimilation, respiration and transpiration of crop surfaces (BACROS), has been developed by De Wit *et al.* (1978). However, the morphogenesis of the crop and the functioning of different organs are completely neglected in this otherwise comprehensive model; partitioning processes are only introduced as a functional balance between shoot and root that is independent of the relative water content of the canopy. This model is used later in an evaluation of the effects of stripe rust on crop productivity and in an effort to study the nature of stripe rust damage.

A summary model of crop growth may suffice in cases where the effect of disease or pests on crop growth is assessed. A summary model which is very suitable for this purpose has been developed by Van Keulen (1976) as a simple method for calculating potential rice production. In this model the considerable explanatory detail in the environmental and photosynthesis modules, which are presented in BACROS, is replaced by shortcuts and simple formulae which suffice to describe the dynamic character of these processes. The plant growth sections in the summary model are, on the other hand, more elaborate. Various plant organs are considered, so that it is possible to couple pathogenic infection to different parts of the plant. Crop development, i.e. initiation, growth and development of individual organs, is introduced into the model in a descriptive way, thus it contrasts with the photosynthesis model, which is based on explanatory models of assimilation, respiration and transpiration of crop surfaces. A temperature-dependent development rate is accumulated and this integral, called development stage, initiates changes in respiration and partitioning of carbohydrates to new growth centres. Van Keulen's summary model of crop growth and development is described in the next paragraphs, explaining in more detail that

part involving photosynthate supply, which is extensively treated in De Wit *et al.* (1978).

### Basic structure of summary model of crop growth

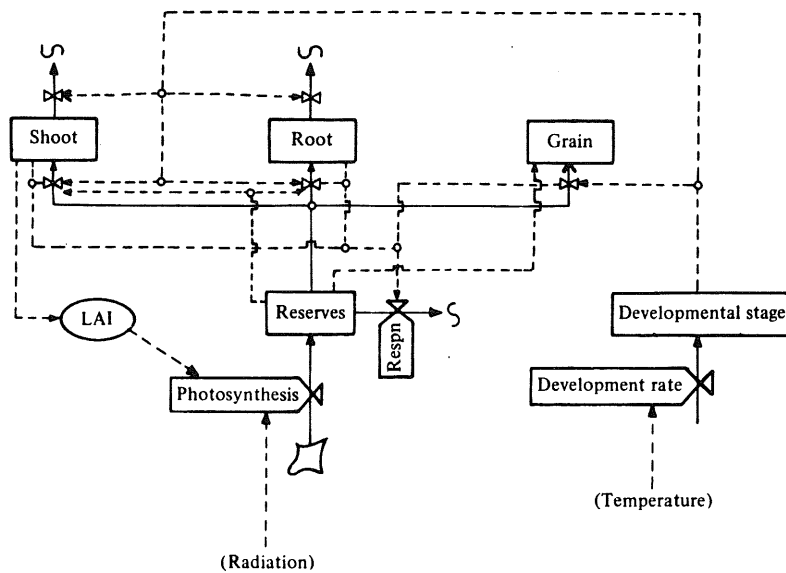
The basic structure of the summary model is presented in a relational diagram (Fig. 1). Shoot, root and grain (for example, of wheat) increase at a relative rate dependent on the developmental stage, which accounts for the partitioning of photosynthates. All plant organs grow from the assimilation stream, whose size depends on the incoming radiation and the leaf surface (leaf area index, LAI) participating in photosynthesis. Before partitioning of the carbohydrates to the plant organs, growth respiration (dependent upon growth rate) and maintenance respiration (dependent upon organ weight) are subtracted.

Ageing of plant organs is expressed as a relative rate of decrease of weight of these organs, which is governed by the developmental stage.

### Photosynthesis

In the summary model the basis for the calculations is the photosynthetic rate of the canopy under optimal growing conditions. De Wit's (1965)

Fig. 1. Relational diagram of a summary model of crop growth. Rectangles represent state variables; rate variables are given by valves. Flows of material are presented by solid lines and flows of information by broken lines. ~ expresses a sink and  $\sphericalangle$  expresses a source.



computation procedure, reformulated by Goudriaan & Van Laar (1978a), is used to find the photosynthetic rate of closed green crop surfaces. On the basis of the photosynthesis:light response curve of a single leaf in ambient air of normal temperature and carbon dioxide concentration, Goudriaan & Van Laar calculated a photosynthesis:light response curve for closed canopies without further knowledge of the geometric characteristics of the canopy. Only the total leaf mass needs to be known. Effects of chloroplast distribution, nitrogen content of the leaf blade, age of the leaf and environmental conditions such as carbon dioxide concentration and temperature are all expressed as changes in the efficiency with which the simple leaves use light, and these changes will result in changes in daily total gross photosynthesis. The distribution of radiation within the canopy can be determined from the radiation climate above the canopy, which is dependent on the position of the sun in the sky, the prevalent cloudiness and the way in which the incident radiation is absorbed by the leaves. With this method, Goudriaan & Van Laar calculated total daily gross photosynthesis as a function of the LAI and daily global radiation. Van Keulen (1976) used this method in his summary model to compute the daily gross photosynthesis of a canopy under the assumption that the actual rate of gross photosynthesis is proportional to the fraction of the total energy intercepted by the canopy.

The actual daily photosynthetic rate ( $BF$ ) for a closed canopy in the summary model is found by calculating the fraction of the sky that is overcast during a day and multiplying the daily gross photosynthetic rate for overcast skies ( $PO$ ) by this fraction, and then adding to this product the fraction of clear sky multiplied by the gross photosynthetic rate ( $PC$ ):

$$BF = (1 - F) \times PC + F \times PO.$$

The fraction overcast ( $F$ ) is calculated according to:

$$F = (DTRS - 0.2 \times HC) / (HC - 0.2 \times HC)$$

in which  $DTRS$  = actual daily total global incoming radiation in  $J m^{-2} s^{-1}$  and  $HC$  = incoming radiation when the sky is completely clear. The incoming radiation on overcast days equals 0.2 of the amount of radiation at clear days.  $PC$ ,  $PO$ ,  $DTRS$  and  $HC$  are introduced in the model as time- and location-dependent variables. Van Keulen (1976) calculates the gross photosynthetic rate of a crop ( $GFOT$ ) by multiplying the gross photosynthesis of a closed canopy with a factor that accounts for the extinction of radiation in the canopy. This multiplication factor presumes radiation intensity decreases exponentially in a canopy, the relative rate of decrease being dependent on the LAI. The factor has considerable effect when the  $LAI \leq 3$ , but becomes negligible with higher leaf areas.

Gross photosynthesis is now found from:

$$GFOT = BF \times (1 - \exp(-0.6 \times LAI)).$$

In the summary model the LAI is not introduced as a driving force, nor simulated, but simply computed from the weight of the above-ground material, assuming a fixed specific leaf weight of  $0.066 \text{ kg m}^{-2}$ , a figure which seems to be representative for small grains.

In the comprehensive model of crop growth, the photosynthetic rate is computed on the basis of light-use efficiency, the maximum assimilation rate of individual leaves and stomatal behaviour. Within this latter model,  $C_3$  and  $C_4$  plants are distinguished and allowance is made for a stomatal regulatory mechanism that maintains a more or less constant carbon dioxide concentration in the stomatal cavity (Goudriaan & Van Laar, 1978b).

#### *Respiration*

The energy trapped in the photosynthetic process is immediately used in various ways, so that only a changing fraction remains in newly fixed compounds. The remainder is liberated in respiratory processes which support two distinguishable areas of activity.

First, *growth processes*, i.e. the synthesis of structural plant material, such as proteins, fats and carbohydrates. A variable amount of photosynthetic material is used to produce new material, depending on the composition of the plant material being synthesized. In a detailed study of growth respiration, which represents a sophisticated way of bookkeeping for all the processes involved, Penning de Vries (1975) calculated the efficiency of conversion for different structural compounds: this he called the production value (see Table 1). The percentage of photosynthetic compounds used for the construction of new plant materials is in the order of 40% for a fat- and protein-rich crop like soybean, and approximately 25% for a carbohydrate-rich canopy like sugar beet. In the summary model, calculations are made for small grains and the fraction of photosynthetic material invested in constructing structural material is then 30% of the total amount. Thus, all factors are lumped together to find one conversion factor.

Table 1. *Efficiency of conversion of substrate (glucose) into plant constituents*

Compounds	Production value (g material $\text{g}^{-1}$ glucose)
Carbohydrates	0.826
Nitrogenous compounds	0.404
Organic acids	1.104
Lignin	0.465
Lipids	0.330

In the comprehensive model, the actual processes are simulated so that this lumping is not necessary. Penning de Vries showed that these conversion factors of photosynthetic material are virtually independent of temperature. Of course, this does not hold for the growth process itself.

Second, *maintenance processes* are the other sink for photosynthetic material. The structure of already existing cells must be maintained and this involves the turnover of protein and the sustaining of ionic gradients and membrane structures. Again the composition of the material determines the energy required, the main variable being the protein content. The complicated character of maintenance ensures that accurate quantitative estimates of these processes are rare. Although the size of maintenance respiration is low in comparison with growth respiration, its presence during the plant's entire life span means that its contribution to the total energy spent for respiration is comparable with that spent on growth processes (Penning de Vries, 1981). Maintenance respiration is directly affected by temperature and seems to have a  $Q_{10}$  value of 2 to 3.

Since maintenance of existing structures has a higher priority than synthesis of new structural material, the computations are done in such a way that growth respiration is calculated after the respiration needed for maintenance has been subtracted.

#### *Development*

As indicated in the relational diagram (Fig. 1), the developmental phase of the crop is used to govern relative partitioning rates and relative ageing rates. In most models of crop growth, development and morphogenesis are not considered. A major reason for this is that developmental processes are poorly understood; for example, explanation is virtually absent for processes such as the appearance of leaves, the transition between vegetative and reproductive phases, or the flowering and heading of plants. Still, the development of a crop greatly interferes with its growth, therefore development should be properly simulated in a realistic crop growth simulator. Development is affected by temperature and day length in most crops. These governing factors may be introduced to compute the rate at which the crop develops; this is usually done by defining crop development in terms of the temperature sum, i.e. the product of average temperature and time. A more flexible approach is used in this summary model in which development is mimicked by integrating a temperature and day-length-dependent development rate. The input relation of this rate should be determined from crop development experiments in which the average development period (for example, from germination until flowering) is determined at different temperatures. The development rate, integrated over different developmental stages, is one of the most critical variables in the model. It determines, for example, partitioning of assimilates and leaf duration.

### Partitioning

The distribution of the newly formed photosynthetic products is greatly affected by the development of the crop. Early in the growth of the crop carbohydrates can only be transported to roots and shoot, but after flowering there is a considerable shift in partitioning. This may of course be different in plants whose growth is non-determinate, such as beans.

The proportion of material going to the different organs has been studied by plant physiologists in great detail, especially for small grains (Lian & Tanaka, 1967, Spiertz, 1978). To estimate the size of the various carbohydrate flows, labelling with  $^{14}\text{C}$  is used. For rice it is estimated that 70% of stored carbohydrates are translocated to the grain, 30% being lost in respiration. Of the carbon fixed after flowering, 85% is accumulated in the grain, the remainder being used for the upkeep of other organs. Before flowering, only 10% of the photosynthetic products are stored in the stem, the other 90% being divided between root and shoot in the ratio of 1:3.

Each of the subprocesses described above may be affected by a pathogenic organism. To illustrate the effect of different pest or disease organisms in terms of production ecology, different pathogenic organisms have been connected to the summary model of crop growth.

### Population dynamics of pests or disease-causing organisms

One of the most well known analytical formulae describing population growth rate is given by Van der Plank (1963):

$$\frac{dx}{dt} = R_c(x_{t-p} - x_{t-i-p})(1-x_t)$$

in which  $x$  = fraction of visibly diseased foliage;  $t$  = time;  $R_c$  = the corrected basic infection rate;  $p$  = latent period;  $i$  = infectious period. This formula transforms into the well-known formula for logistic growth when the latent period approaches zero and the infectious period reaches infinity:

$$\frac{dx}{dt} = r \times x_t(1-x_t)$$

where  $r$  = relative growth rate.

The occurrence of time-lags, such as latent periods, or finite multiplication periods, are normal in biology so that the logistic formula only holds in very exceptional cases, for example when yeast is grown under optimal conditions. However, it is difficult to solve the equation if terms are introduced to describe such time-lags. With numerical integration of the Van der Plank equation, dynamic simulation was introduced in botanical epidemiology (Zadoks 1971; Waggoner, Horsfall & Lukens, 1972). This new technique enabled the development



of more realistic simulation models. Fig. 2 shows the flow diagram of a simple simulation model integrating Van der Plank's formula.

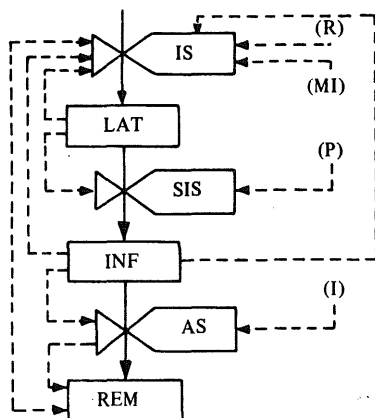
Infectious leaf area produces infective propagules, which can cause new infections leading to an increase of latent leaf area and a decrease of vacant leaf area. Thus, four conditions of leaf area are recognized

- (1) not-infected, or vacant;
- (2) infected but not-yet-infectious;
- (3) infected and infectious;
- (4) infected and no-longer-infectious.

The status of the non-vacant leaf area is indicated by rectangles, the vacant leaf area is absent in Fig. 2, as in Van der Plank's formula.

Time-lags between latent and infectious states, and between infectious and no-longer-infectious states, are governed by the latent period and infectious period respectively. The mathematical formulation for such processes is given by De Wit & Goudriaan (1978). The same model can be used for describing the population dynamics of pests. In that case the latent period is replaced by one or more developmental stages, and the infectious period is replaced by some adult developmental stage in the reproductive phase. Each of the rates is affected by environmental factors, so the model has to be modified appropriately. Models of this type give information on the total size of the population of pests or disease, and on the age distribution of populations.

Fig. 2. Relational diagram of a summary model of a fungus epidemic. IS = rate of infection; SIS = apparent infection rate; AS = rate of dying of infectious lesions; R = relative rate of infection; MI = potential number of lesions; LAT = latent; INF = infectious; REM = removed; P = latent period; I = infectious period.



More elaborate population models may add more or less complicated sub-models to the basic model in order to allow calculation of the subprocesses in relation to climate, crop condition and natural enemies. Processes like lesion growth, spore dispersal and the geographical distribution of the population in crops have been studied in this way (Shrum, 1975; Waggoner, 1977; Kampmeijer & Zadoks, 1977; Rijdsdijk, 1980). Elaborate studies describing parasite and/or predator population in relation to pest organisms have also been made (Gutierrez *et al.*, 1975; Rabbinge, 1976). Most models treat the crop as a qualitatively constant substrate for pests and disease-causing organisms. This limits the value of such models because opposite effects can be clearly demonstrated. Thus, resistance of barley to the leaf rust *Puccinia hordei* increased during crop development in both susceptible and more resistant barley cultivars, owing to an increase in latent periods and, thereby, a decrease in infection frequencies (Parlevliet, 1976). Last (1954) demonstrated the effect of differences in nitrogen fertilization on the growth of mildew on wheat. Rijdsdijk (1980) presented data concerning the effect of nitrogen fertilization on stripe rust of wheat in field experiments and in detailed studies under controlled conditions. A wealth of data is available to demonstrate the influence of pests or disease-causing organisms on the host, and covers aspects ranging from changing rates of photosynthesis and respiration, to changing root:shoot ratios (Martin & Hendrix, 1966), to crop losses.

Host plant and disease-causing, or pest, organisms show mutual interference. In most cases only one side of the coin is shown and this gives a limited view of the effect of a pest on its host plant or vice versa. For example, the condition of a wheat plant affects the latent period and infectious period of stripe rust, but on the other hand the stripe rust may promote loss of water and affect the functioning of the crop in such a way that less nitrogen will be available for the shoot, thereby decreasing the infectious period.

To demonstrate the interactions for some pests and disease-causing organisms simple pest and disease models have been connected to the simplified crop model described above. In addition, one example of an interaction between a more elaborate crop model and disease model will be discussed.

### **Interactions between plant and disease or pest organisms**

#### *Mutilation of leaf mass*

Many examples can be given of consumption of leaf mass by herbivores. However, the influence of leaf feeders seems limited unless their numbers become very high, or their consumption rate very large. For example, the effect of leaf hoppers on leaf mass is so high that sophisticated prediction and monitoring systems have been developed to prevent their disastrous effects. To demonstrate the effect of a leaf consumer on crop growth, a simplified simulator of

population growth of the cereal leaf beetle has been attached to the simple crop growth simulator discussed above and parameterized for winter wheat.

Larvae of cereal leaf beetles (*Lema cyanella*) consume leaf mass at a rate of about  $250 \text{ cm}^2 \text{ day}^{-1}$  ( $= 1.5 \text{ g dry matter}$ ). Only the larvae consume leaves. After growth and development they pupate and later moult into adults that may give rise to another generation. The rate of increase of the numbers of cereal leaf beetle larvae mainly depends on the immigration rate of the adult beetles which lay their eggs on the leaves. After hatching, the larvae immediately start feeding. Their effect on crop growth is introduced into the model as a drain on the shoot weight. This rate of decrease of shoot weight is assumed to be proportional to the number of larvae of the beetle, lumping all developmental phases of the larvae together. Consumption of leaf mass by the adults is neglected, and age and reproduction rate (dependent on food quality and development rate) are not considered. The beetle population is introduced in a very simple way by distinguishing four morphological stages: eggs, larvae, pupae and adults. The adult population is assumed to be 50% male, so that after egg-laying only 50% (females) will grow and contribute to the next generation. Reproduction of the adult beetles is diminished when excessively high larval densities are reached, this depending on the ratio of number of larvae: weight of shoot.

Some results of calculations with the model are presented in Fig. 3. It is shown that when the population density of the larvae reaches a level of  $15\,000 \text{ ha}^{-1}$ , or  $1.5 \text{ m}^{-2}$ , or  $0.004 \text{ tiller}^{-1}$  at flowering the effect on the yield loss will be less than 1%. It has also been shown that the time of introduction of the beetle is highly important. A late and heavy attack of the beetles scarcely affects the final crop yield, but an early and steady attack reaching a density of  $0.04 \text{ tiller}^{-1}$  may cause a severe decrease in yield (Fig. 3). In that case, 14% of the grain yield is lost and about 50% of the straw yield is not harvested.

#### *Leaf coverage*

To demonstrate the effect of a disease that covers the leaves with a thin layer and promotes leaf senescence, the powdery mildew *Erysiphe graminis* is coupled to the wheat simulator. The fungus is simulated with the Van der Plank equation (p. 208). Neither individual spores nor pustules are distinguished; instead, the sites are simulated, i.e. the leaf surface is represented in terms of potential sites, each site representing the minimum size of one lesion (a field of 1 ha, LAI = 4, contains about  $10^9$  sites).

The simple combination model used here only supplies information on the effect of the leaf-covering activity of mildew epidemics. This effect is introduced by multiplying the gross photosynthetic rate by the leaf area covered: total leaf area ratio. Some results of this model show that, when the assumption is made that the fungus is homogeneously distributed in the canopy, a considerable loss

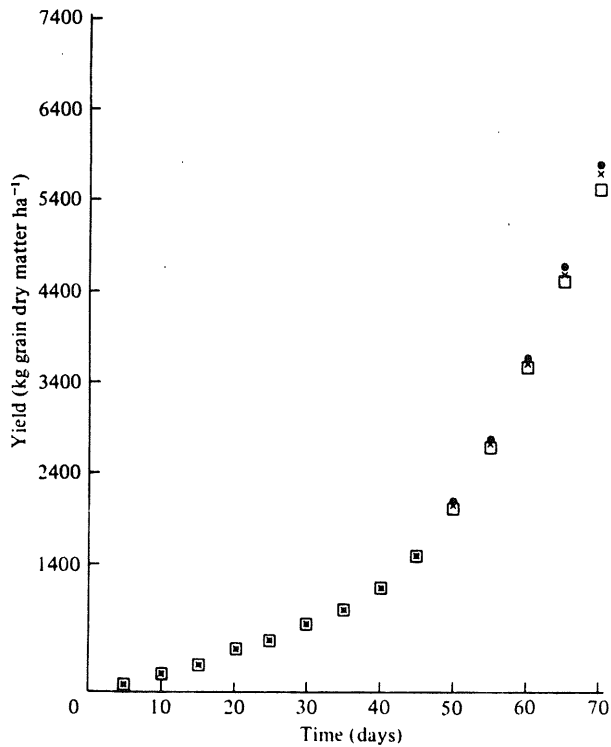
occurs (Fig. 4). However, in most cases the fungus grows from the bottom of the canopy towards the top, and is mainly located in the lower leaf layers. Losses are much lower if this location effect is introduced into the crop model. When the LAI  $\leq 3$ , effects are much greater than in crops with a higher LAI. In these crops with high leaf densities a large decrease or increase in respiration could affect the net assimilation rate, but in practice this seldom happens.

Extension of this model with the other effects caused by *E. graminis* is possible whenever more accurate knowledge of these effects on respiration rate or photosynthetic rate becomes available.

#### *Stripe rust (Puccinia striiformis) and winter wheat*

The examples of host plant-pathogen relations given above used a summary model of crop growth. This was possible since the objective was to show some of the effects in general terms. In most cases of pathogen-host plant rela-

Fig. 3. Simulated increase in weight of cereal grain. ● = beetles absent, × = beetle population at a maximum of 1 per 0.004 tillers, □ = beetle population 1 per 0.04 tillers at flowering, i.e. heavy attack.

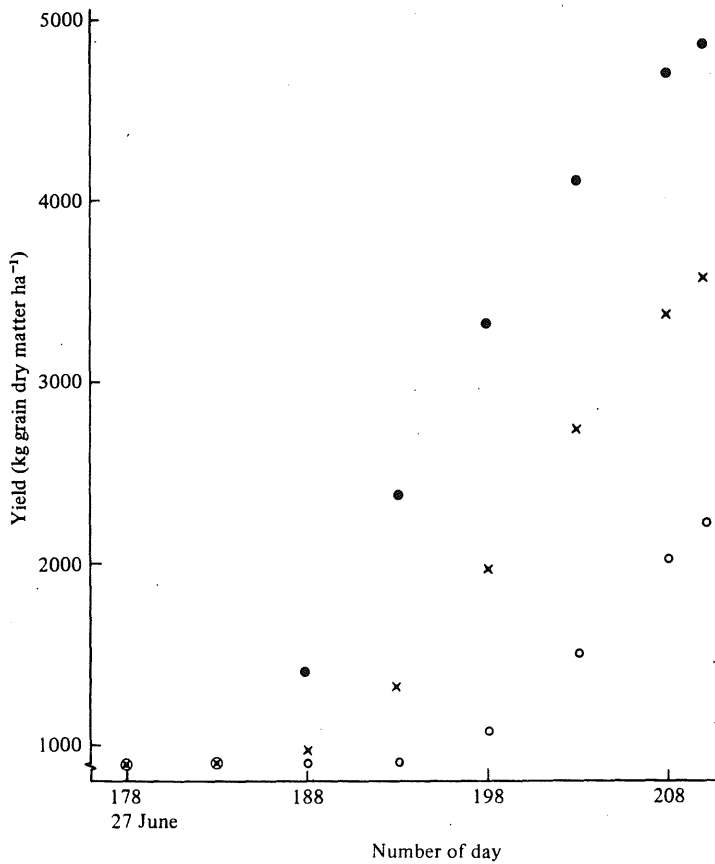


tions this is impossible as the interrelations are of a more complex nature. This is illustrated with stripe rust on winter wheat.

In an ecophysiological study of crop losses, exemplified in the infection of wheat by leaf rust, Van der Wal, Smeitink & Maan (1975) demonstrated that leaf rust infection increased the transpiration rate of spring wheat (also discussed by Ayres, this volume). Similar effects were shown for wheat with stripe rust (F. H. Rijdsdijk, unpublished data).

The increased transpiration rate may have been due to an increase in leaf conductance or a shift in shoot:root ratio, a combination of both, or a chain of effects. Simulation studies may help to test the hypothesis that the sporulating

Fig. 4. Simulated increase in weight of cereal grain. ● = control, disease absent; × = mildew epidemic reaches a maximum of 80% leaf coverage, mainly concentrated in the lower leaf layers; ○ = mildew epidemic reaches a maximum of 80% leaf coverage, homogeneously distributed in the canopy.



pustules of the fungus operate as holes in the leaf and to determine the consequences of such an effect. Summary models of crop growth with simplified relations for water balance and water use are insufficient to study this problem. An elaborate and detailed model of assimilation, transpiration and respiration of crop surfaces is needed to test the effect of stripe rust on crop behaviour.

De Wit's detailed simulation model (De Wit, 1978) is used to introduce this 'hole making' effect of rust. Within this model, transpiration is computed with a Penman-type formula in which leaf resistance is one of the most important variables. Leaf resistance can be found experimentally by measurements with a diffusion porometer (Stigter & Lammers, 1974). The dependence of stomatal resistance (the most important resistance for carbon dioxide and water diffusion) on environmental factors could be introduced into the model, but detailed analysis of stomatal resistance in relation to assimilation rate and transpiration rate have shown that a linear relation exists in many cases between stomatal conductivity and carbon dioxide assimilation rate (Goudriaan & Van Laar, 1978*b*). This indicates that stomata may regulate their aperture in such a way that a constant carbon dioxide concentration is maintained in the stomatal cavity (see also Raschke, 1975). Therefore, in the detailed crop simulator, this facultative regulation mechanism is introduced and the stomatal resistance (*SR*) is calculated from this equation:

$$SR = (68.4 \times (\text{CO}_{2\text{ext}} - \text{CO}_{2\text{int}}) - R_b \times 1.32 \times PHOT) / PHOT$$

where  $\text{CO}_{2\text{ext}}$  is the external carbon dioxide concentration;  $\text{CO}_{2\text{int}}$  is the regulated internal carbon dioxide concentration,  $R_b$  is the boundary layer resistance and *PHOT* is the actual photosynthetic rate, computed from a light response curve of carbon dioxide assimilation. The constants are necessary to transform the carbon dioxide diffusion resistance into a diffusion resistance for water.

The carbon dioxide regulation mechanisms may be overruled by regulation through the leaf's water balance, i.e. if a marked water shortage occurs, the stomata will close. The holes due to rust pustules may cause a continuous closing of stomata and thus, decreased photosynthetic activity. In the model the diffusion resistance of the holes is introduced by using the calculations for a membrane with cylindrical pores (e.g. Penman & Schofield, 1951; Monteith, 1973). For such a porous membrane made up of  $n$  cylindrical pores, of length  $l$  and diameter  $d$ , per unit of surface, the resistance  $R_m$  is normally taken to be:

$$R_m = \frac{4l}{d^2 n D} + 2 \times \frac{1}{2dnD}$$

in which  $D$  is the diffusion coefficient of carbon dioxide, which depends on temperature. The first term of this formula is the diffusion resistance of the tubes

proper. The second term is the expression for the diffusional 'end effects' at both sides of the membrane. It represents the diffusion resistance of a semi-infinite half space, completely insulated at the free surface with the exception of  $n$  independent spots of given constant and uniform concentration. To compute the diffusion resistance for a canopy which contains a large number of these pores, the second part of the formula is used:  $R = 1/nDd$ .

The number of pores is calculated as follows: when the diameter  $d$  of a rust pore (= size of pustule) equals 1.6 mm, the potential number of pores per ha ( $n$ ), in a canopy with LAI = 5, equals  $5 \times 10^8 \text{ cm}^2/\pi \times (0.08)^2 = 2.5 \times 10^{10} \text{ sites ha}^{-1}$ . This means that when there is a 100% infection of the leaves, about 20% of the leaf area is replaced by pores, i.e.  $20\% = 0.5 \times 10^{10} \text{ sites ha}^{-1} = 50 \text{ sites cm}^{-2}$ , and the diffusion coefficient =  $0.2 \text{ cm}^2 \text{ s}^{-1}$ . Thus, the resistance of this canopy amounts to

$$R = \frac{1}{50 \times 0.2 \times 0.16} = 0.62 \text{ s cm}^{-1}$$

and the conductivity of the canopy is enlarged by  $0.016 \text{ m s}^{-1}$ ; a considerable increase, indicating that the transpiration rate may be affected considerably. To test this, the assumption is introduced in a computer simulation that the maximum infection level is reached. The results of such simulation show that when the other effects of leaf rust on assimilation, etc. are neglected, the total production of dry matter is not much lower, but that there is an enormous shift in shoot:root ratio, so that the shoot weight is about 10% lower than that without rust attack and the root weight is about 1.5 greater than that without rust attack (Figs. 5, 6 and 7). The transpiration rate of the canopy is considerably higher, on average about two times the normal transpiration rate.

These results illustrate the influence of the functional balance, i.e. internal regulatory mechanisms of the plant, since, owing to an increase in transpiration, the root system has to be extended to keep up the relative water content of the crop and this lowers the amount of assimilates available for the shoot.

Although these results seem quite logical, they are not in agreement with results obtained from field and container experiments by Van der Wal *et al.* (1975). This is probably because it was unreal and incorrect to assume that the decrease in assimilation rate of the canopy, and the increase in respiration due to the production of rust material, could be neglected. When one of these processes is introduced into the model, there is again a change in effects.

The decrease in assimilation rate due to the absence of photosynthetic activity in the pustules is introduced by multiplying the net assimilation rate by the percentage of the total leaf area attacked. As a result of this change in the model, the total amount of above-ground dry matter simulated with the model is about

25% less in infected than in non-infected control plants, i.e. a yield loss of about 2500 kg ha<sup>-1</sup>. Again the root weight is higher than in the control and this is probably owing to the functional balance, which causes an increase in root growth due to a higher transpiration rate. The decrease of assimilation rate caused by a loss in photosynthetically active leaf area resulted in the considerable decrease in crop growth found in these simulations.

Finally, the crop growth simulator is connected to a simulator of stripe rust epidemics, enabling latent, infectious and removed sites to be distinguished. The results of these calculations are also presented in Figs. 5, 6 and 7. A heavy attack of stripe rust causes a considerable decrease in shoot weight and a slight decrease in root weight, a result that confirms field observations. Still the model does not correspond completely with experimental results. Although the total loss in crop yield agrees rather well with the experimental outcome, the increase in root weight does not agree completely with some experimental results. This may be due to the incompleteness of the model, e.g. effects on maintenance respiration are neglected, or it may be caused by insufficient understanding of the way hormonal processes interfere with partitioning processes of carbohydrates. In spite of their imperfections, these simulations show how an effort is being made to gain a full understanding of the various processes which play a role in the crop-pathogen interrelations.

Fig. 5. Simulated increase in weight of shoot and ear with a comprehensive crop growth simulator. □ = unattacked crop; ○ = crop infected by a stripe rust epidemic, maximum leaf coverage of 20%; × = crop infected by a stripe rust epidemic, reaching maximum leaf coverage of 100%, i.e. 20% of leaf area replaced by holes, using a realistic simulator of the rust epidemics.

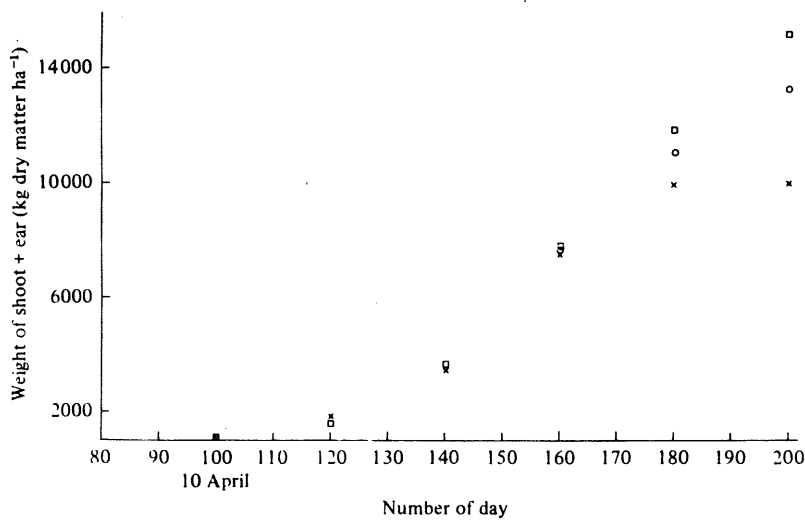




Fig. 6. Simulated increase in weight of root with a comprehensive crop growth simulator.  $\square$  = unattacked crop;  $\circ$  = crop infected by a stripe rust epidemic, maximum leaf coverage of 20%;  $\times$  = crop infected by a stripe rust epidemic, reaching maximum leaf coverage of 100%, i.e. 20% of leaf area replaced by holes, using a realistic simulator of the rust epidemics.

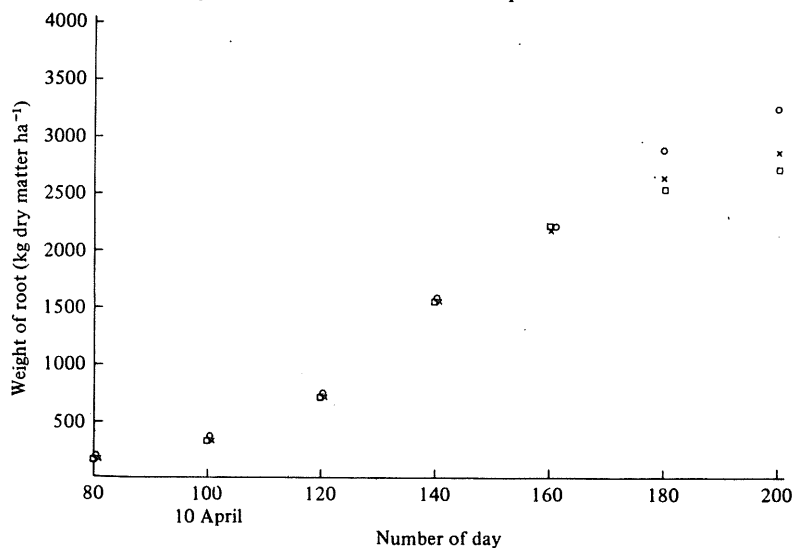
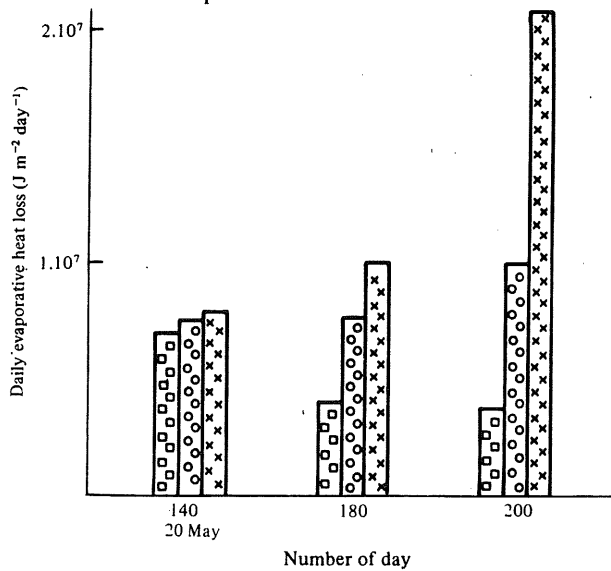


Fig. 7. Simulated daily evaporative heat loss in  $\text{J m}^{-2}$ .  $\square$  = unattacked crop;  $\circ$  = crop infected by a stripe rust epidemic, maximum leaf coverage of 20%;  $\times$  = crop infected by a stripe rust epidemic, reaching maximum leaf coverage of 100%, i.e. 20% of leaf area replaced by holes, using a realistic simulator of the rust epidemics.



### Discussion

Simple examples of host plant-pathogen models have been discussed.

To design these models, well-known phenomena had to be formulated in quantitative terms. The quantification of processes compels the model builder to make his assumptions and hypotheses explicit. He can then find out what effects are of minor importance, and what effects are of major importance. Subprocesses which seriously affect the behaviour of the crop-pathogen system have to be studied in more detail than subprocesses which only cause small deviations from an optimal growth of the crop. In this way, model building may help to formulate research priorities.

Another important aspect of model building is the capacity of models to test hypotheses. A model reflects its architect's opinion on the way processes operate in the real world. By a continuous procedure of model building and testing, successive hypotheses can be rejected or accepted. In doing this the model operates as a communication tool between the generalist, who is urged by the model to study some processes in more detail, and the reductionist, who is able to recognize from the model the meaning of the subprocess studied by him within the total behaviour of the system. In this way models help to bridge the gap between scientists working in the laboratory on plant physiological processes and their colleagues in the field trying to understand the behaviour of crops under conditions of stress.

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