

6.1 Pests, diseases and crop production

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6.1.1 Introduction

Knowledge of plant growth, insight into crop and soil management and appropriate agronomic measures have led in practice to production levels that sometimes equal the potential level. In Section 1.2, four different crop production levels are distinguished, depending on availability of growth requirements and abiotic conditions. At all production levels, pests and diseases may depress the attainable yield through different mechanisms. The nature and species of pests and diseases may differ at different yield levels.

In this chapter we deal with crops grown at Production level 1, thus in the case of ample plant nutrients and soil water all the time. To attain these optimal conditions capital investments and large amounts of fossil energy have to be used. Only a very small fraction of this is used for crop protection measures. However, the financial costs of using and applying pesticides are increasing and the environmental side effects of these compounds are becoming a problem. Therefore interest in crop protection systems with a reduced usage of pesticides is increasing, and crop protection is developing more and more into a science for planning and managing the crop pathogen system.

In most studies on pest and disease management, population dynamics of pest and disease organisms are emphasized, but the combination with the growing crop is virtually neglected. This makes it impossible to assess the damage properly, and limits the use of these models. To overcome this limitation, it is necessary to link them with crop growth models. The dynamic character of the interrelations between host and parasite requires a dynamic description of the substrate, i.e. the crop, and of the environment of a pathogenic organism.

Only a few combination models exist in which both crop growth and population dynamics of the pest or disease organisms 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 sub-processes. When too many phenomena observed at the system level are introduced into the model, its behaviour is 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 (Section 1.3).

In this section I give some of the basic relations in population dynamics (Subsection 6.1.2), and describe some attempts at their modelling (Subsection 6.1.3).

Then I present two types of combination models: first I discuss summary models (Subsection 6.1.4). These models are designed to produce a shortcut to the objectives of the comprehensive model, without losing the sensitivity of the full analysis (Section 1.3). Models of this type are used to simulate the effect of a pest or a disease on crop growth without further consideration of the nature of damage.

Crop-pathogen interactions are introduced in these models to compute the impact of the perturbations. The simulations 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. Secondly I discuss an example of a comprehensive model of crop growth and a disease (Subsection 6.1.5). This combination model is used to test hypotheses on the nature of the disease-crop interrelations. The summary model of crop growth (SUCROS, Section 3.1) suffices in cases where the effect of diseases or pests on crop growth is assessed, whereas the complicated BACROS model (de Wit et al., 1978) is used to test some hypotheses on the nature of the disease-crop interrelations. An extrapolation of use of models for crop protection in practice is discussed briefly in Subsection 6.1.6.

6.1.2 Population dynamics of pests or disease causing organisms

When a population grows without constraints, the well known exponential growth curve describes the number of organisms in time (Section 2.1). This curve transforms into a logistic curve when there is a limited supply of food, or when a growth-retarding compound is produced during the growth process. For example yeast growth is inhibited by alcohol, which is produced during bud formation, the multiplication process in yeast (de Wit & Goudriaan, 1978). Mathematically the growth process can be described by

$$dG/dt = RGR \cdot G \cdot (1.0 - RED) \quad (101)$$

in which RGR represents the relative growth rate, and RED expresses a reduction factor. RED may be described by the ratio between actual amount of organisms (yeast cells, G) and the maximum amount (GM):

$$RED = G/GM \quad (102)$$

The amount of yeast cells is found by the analytical solution of the rate equation

$$G = GM/(1.0 + K \cdot \exp(-RGR \cdot t)) \quad (103)$$

Exercise 65

- Compute K from an initial value of G and its maximum value. What process or ratio is described by this factor?
- Derive the rate equation (Equation 101) from the analytical formula (Equation 103) by differentiation.

The exponential growth equation is only valid in very few cases of population growth and during short periods. The logistic equation (Equation 103) is appropriate as a description of the growth of population numbers in simple organisms like yeasts.

To distinguish between development and size of organisms is in these cases not necessary. However as soon as more complicated organisms are considered, development and growth should be treated separately, as is the case with many pest and disease organisms. For example in fungi each spore is not immediately ready to produce new spores, but a whole phase of its life cycle has to be passed before sporulation may start (latent period). A young larva of a pest organism is not able to produce offspring but has to become adult before there is any new egg produced. An adult pest organism is only able to produce offspring during a short period, and the same holds for a sporulating lesion (infectious period). To account for this delay in population development van der Plank (1963) developed a rate equation with which the population growth of many disease organisms can be described:

$$dN_t/dt = R(N_{t-p} - N_{t-i-p}) (1 - N_t/N_m) \quad (104)$$

In which N_t is the number of visibly diseased sites at time t ; R is the number of lesions per sporulating lesion per day, or relative growth rate; p is the duration (d) of the latent period; i is the duration (d) of the infectious period; N_m is the maximum number of sites which can become infected.

Exercise 66

- When does this formula transform in the logistic growth equation?
- What is the maximum number of sites on a field of 0.5 ha, when the minimum size of a lesion is 0.1 mm² and the crop has a LAI of 4?

It is difficult to solve Equation 104 analytically, so numerical methods have to be used. With the numerical integration of the van der Plank equation, dynamic simulation was introduced in botanical epidemiology (Zadoks, 1971; Waggoner et al., 1972). In pest population dynamics, numerical methods were used earlier, but extensive use of numerical simulation models started only recently (Fransz, 1974; Gutierrez et al., 1975; de Wit & Goudriaan, 1978; Rabbinge, 1976).

6.1.3 Simulation models of population dynamics

Models for pest or disease organisms are in fact a quantitative description of their life cycle. For example, take the life cycle of a fungus. The infection cycle starts when a spore reaches the plant and germinates. After a certain period (the incubation period) the infection becomes visible on the plant. (In the formula-

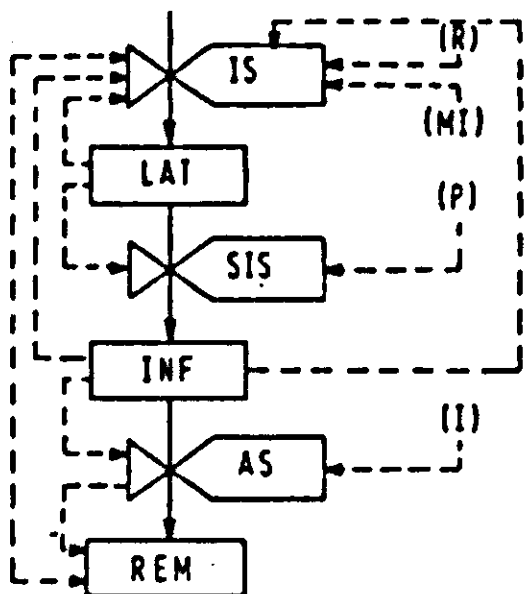


Figure 81. Relational diagram of a summary model of a fungus epidemic.

tion of Equation 104, incubation period and latent period are taken to be identical). The time between infection and time of sporulation by an infected lesion is called the latent period. In many plant fungi the latent period exceeds the incubation period. (In many human diseases the incubation period is larger than the latent period, so that a carrier of the disease is already infectious for other people before the symptoms of the disease are visible.) The newly formed spores are dispersed and may cause new infections on fresh leaf material. The time of sporulation is finite and is called infectious period. In Figure 81 a relational diagram of a fungus epidemic is given. Latent (LAT), infectious (INF) and removed (REM) lesions are distinguished and the rate of decrease and increase of each of these variables is indicated.

Exercise 67

When the incubation period q is not equal to the latent period p , what changes in the rate equation (Equation 104) are then necessary?

Exercise 68

Express the number of latent, infectious and removed lesions with the symbols used in Equation 104.

On basis of the simple relational diagram of Figure 81 a simulation model can be constructed that may answer questions concerning the relative importance of the parameters: relative rate of infection R , the length of the latent period P , the length of the infectious period I and the maximum number of lesions MI . Zadoks (1971) developed such a model and demonstrated the dominating role of the length of the latent period, as shown in Figure 82.

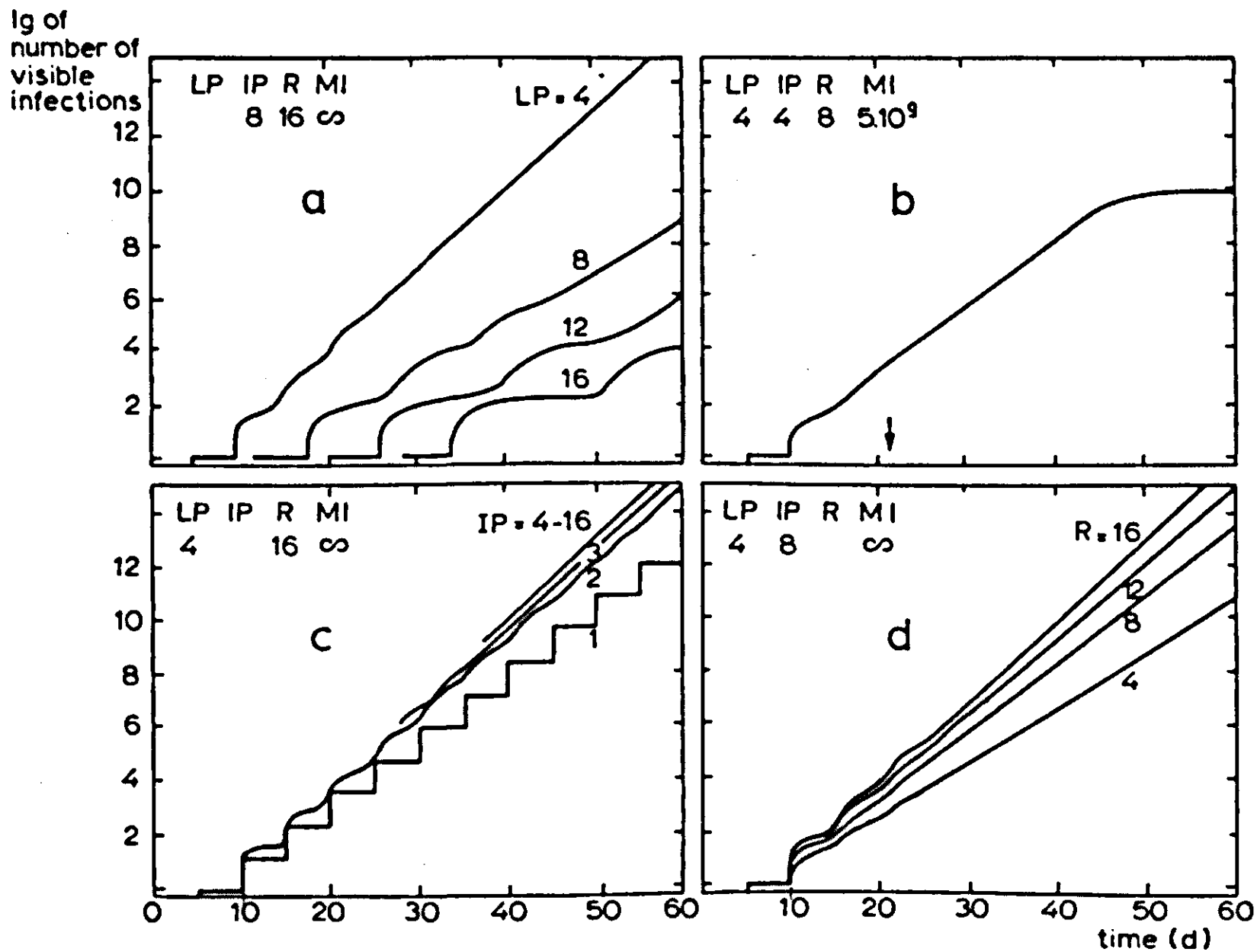


Figure 82. Simulated epidemics. a. The effect of various durations of the latent period (LP). b. The effect of a limited possible number of infections (MI). c. The effect of varying the duration of the infectious period (IP). d. The effect of varying daily multiplication factor (R). Vertical ordinate scale: lg of visible infections. (From: Zadoks, 1971).

Exercise 69

Try to explain the results of Figure 82 by reasoning.

More elaborate population models include other time delays and dispersion in time (Subsection 2.1.8) during development (de Wit & Goudriaan, 1978; Rabbinge, 1976). These models incorporate more or less complicated submodels of the processes and of their relation to climate, crop condition and natural enemies. Processes like lesion growth, spore dispersal and the geographical distribution of disease populations in crops have been studied in this way (Shrum, 1975); Waggoner, 1977; Kampmeijer & Zadoks, 1977; Rijdsijk, 1980). Elaborate models describing parasite and/or predator populations in relation to pest organisms have also been made (Gutierrez et al., 1975; Rabbinge, 1976; Sabelis, 1981). These models incorporate age distribution of the pest organism and dispersion during development. Moreover the complicated predator-prey relations are introduced.

6.1.4 Interactions between plant and disease or pest organisms

In most models of population dynamics the crop is considered as a constant substrate which imposes only limitations when all sites are becoming occupied. Most crop models on the other hand treat pest and/or disease causing organisms as unimportant biotic factors that do not affect the productivity. Combination models are seldom developed, as their architects have to speak two languages, namely that of the agronomist developing crop growth models and that of the plant pathologist developing epidemiological and population dynamical models.

To demonstrate the interactions for some pests and disease-causing organisms, simple pest and disease models, as demonstrated above, are connected to the simplified crop model, SUCROS (Section 3.1). In addition, one example of an interaction between a more elaborate crop model and disease model will be discussed in the next subsection.

Mutilation of leaf mass

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 model of a wheat crop discussed in Section 3.1.

Larvae of cereal leaf beetles (*Lema cyanella*) consume leaf mass at a rate of about $250 \text{ cm}^2 \text{ d}^{-1}$ (= 1.5 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 is considered here as an autonomous process, thus it depends on the egg-laying rate of the adult beetles. After hatching, the larvae immediately start feeding. Their effect on crop growth is introduced into the model as a drain on the leaf weight. This rate of decrease of leaf 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 dependency of ageing and reproduction rate on food quality 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% develop into individuals which contribute to the next generation. Reproduction of the adult beetles is diminished when excessively high larval densities are reached; this depends on the ratio number of larvae/weight of leaves. The simulated effect of the growth of the population of beetles on grain growth is shown in Figure 83.

Exercise 70

Develop a simple population model of *Lema cyanella* when the environmental conditions are considered to be constant and the different development stages

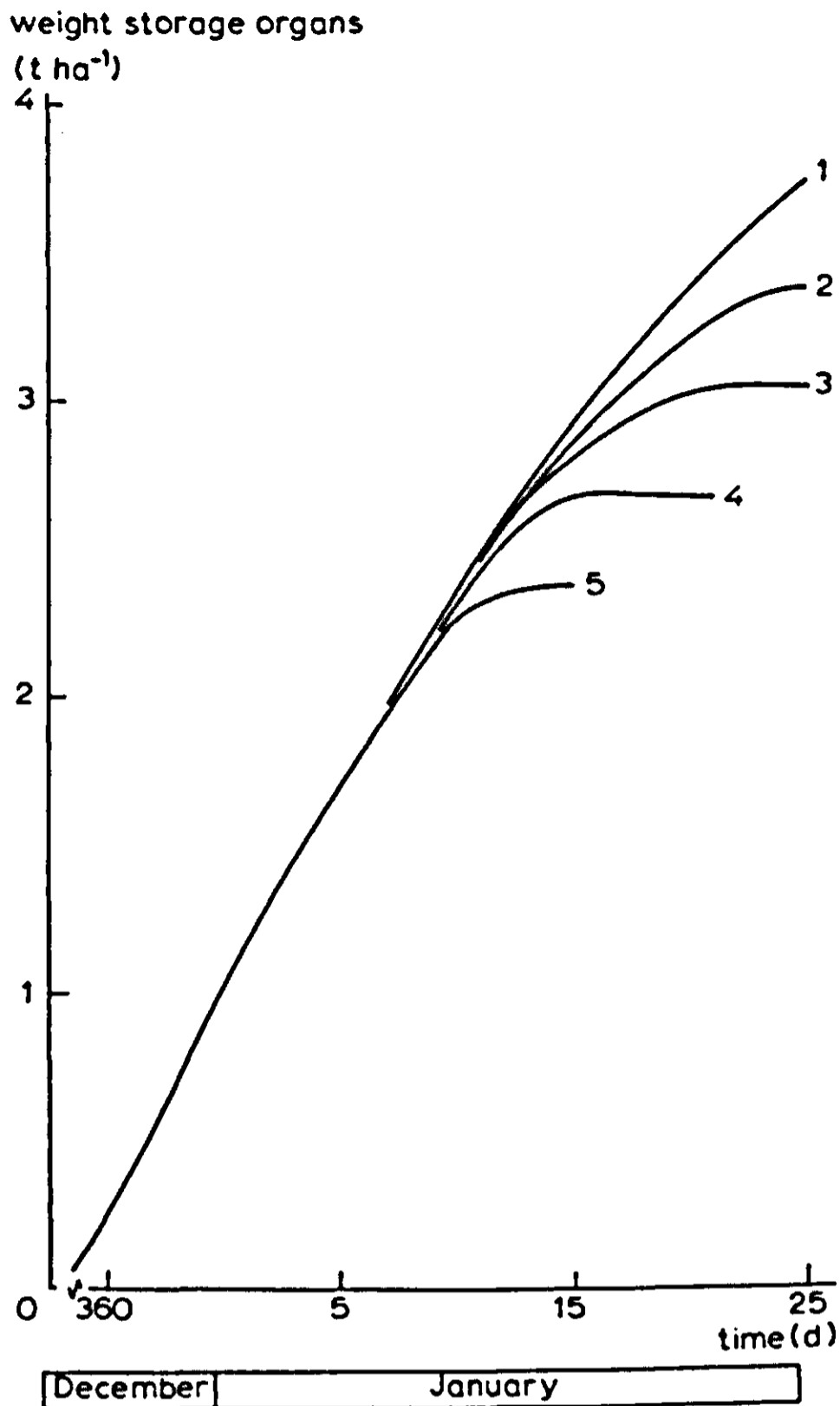


Figure 83. Simulated increase in weight of the storage organs for different levels of cereal leaf beetle attacks (1, no beetles; 2, 3, 4 and 5 starting with 50, 100, 200, 500 adult beetles, respectively at Day 350).

last 5, 10, 4, 20 days for the egg, larval, pupal and adult stages, respectively, and when there are initially 100 adult cereal leaf beetles that produce eggs at a rate of 3 per day. Assume that there is no influence of larval density on the rate of reproduction.

Exercise 71

Link the model of SUCROS and the simple population model and use this combination model to evaluate the effects of different cereal leaf beetle attacks. Assume that the adult cereal leaf beetles enter the crop at Day 350. The simulation should reproduce the results of Figure 83.

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 simple crop model, SUCROS (Section 3.1). The fungus is simulated with the van der Plank equation (Equation 104). Neither individual spores nor pustules are distinguished; instead, the sites are simulated, i.e. the leaf surface is expressed in terms of potential sites, each site representing the minimum size of one lesion. A field of 1 ha with LAI = 4 contains $4 \cdot 10^{11}$ sites.

Only the leaf covering effect of mildew epidemics is introduced in this example; no physiological damage that might occur is considered. This is done by multiplying the gross photosynthetic rate by the ratio between the leaf area not covered and the total leaf area. The simulated effect of a mildew attack on grain growth is shown in Figure 84.

Exercise 72

Construct this combination model and run it for different densities of the disease by setting the initial number of lesions to 10^9 , 10^{10} , $2 \cdot 10^{10}$, $5 \cdot 10^{10}$ ha⁻¹, the relative infection rate $R = 0.3$, the latent period equals 10 days and the infectious period 4 days. Use the DELAY function, explained in Table 2, Section 2.2, and take $N = 10$ (integer).

It is shown in Figure 84 that when the assumption is made that the fungus is homogeneously distributed in the canopy a considerable loss occurs. However in most cases the fungus grows from the bottom of the canopy towards the top, and it is mainly located in the lower leaf layers. Losses are much lower if this location effect is introduced into the crop model.

Exercise 73

Demonstrate these effects by adapting the combination model and running it for different initial fungus densities.

This combination model is still too simple to be realistic, because many other effects of *E. graminis* are not included. For example, the effect of *E. graminis* on respiration rate and photosynthetic rate are not quantified and introduced in the model. Moreover the use of assimilates by the fungus is not introduced in the model.

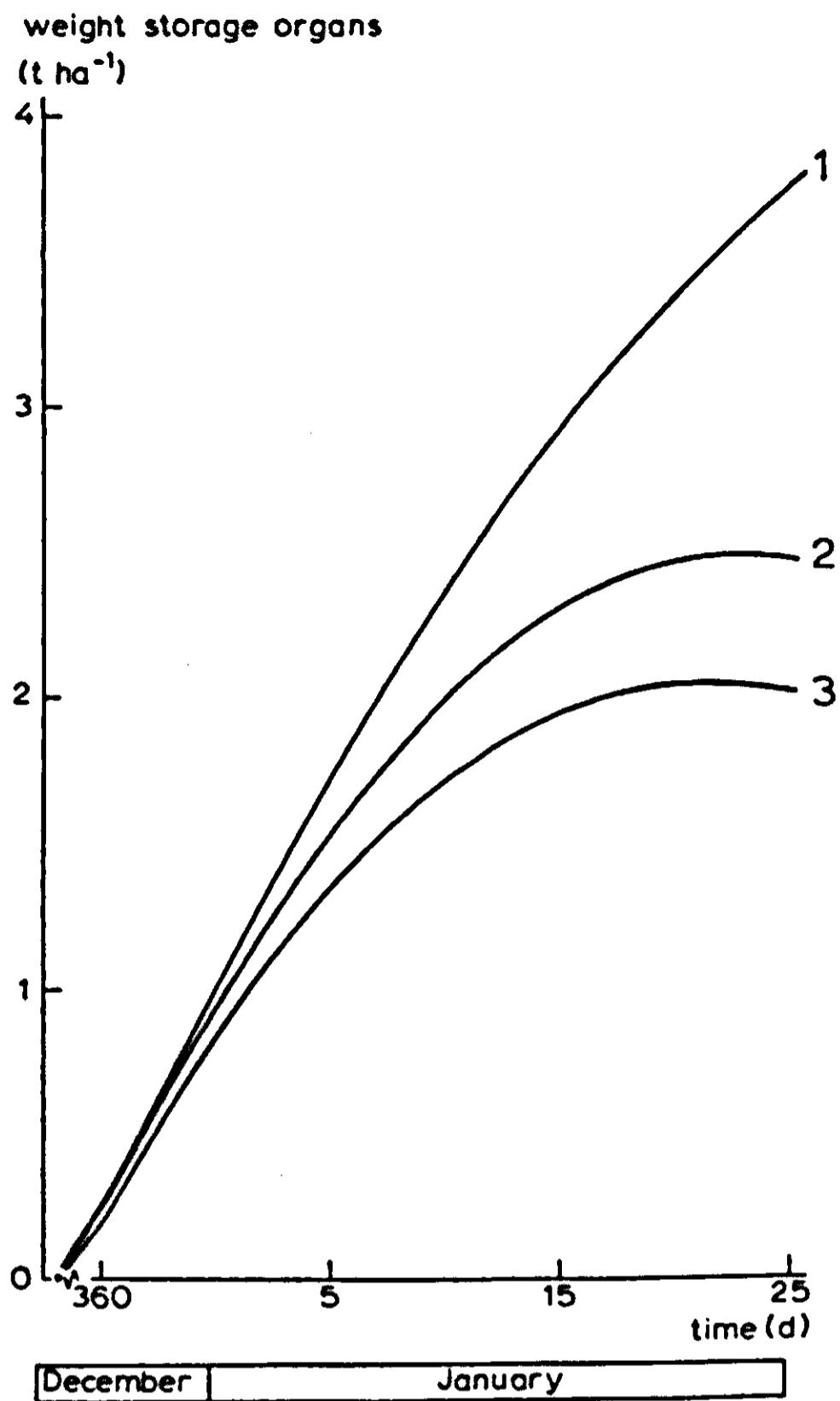


Figure 84. Simulated increase in weight of storage organs under influence of mildew (1: no disease, 2: mildew epidemic reaches a maximum of 67% leaf coverage mainly concentrated in the lower leaf layers, 3: mildew epidemic reaches a maximum of 67% leaf coverage, homogeneously distributed in the canopy).

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

In an ecophysiological study of crop losses, exemplified in the infection of wheat by leaf rust, van der Wal et al. (1975) demonstrated that leaf rust infection increased the transpiration rate of spring wheat. Similar effects were shown for wheat with stripe rust (F.H. Rijdsijk, unpublished data). The increased transpiration rate may have been due to an increase in leaf conductance or to a shift in shoot-root ratio, a combination of both, or other effects. Simulation studies may help to test the hypothesis that the sporulating pustules of the fungus are just little holes in the leaf cuticle and determine the consequences of such an effect. Summary models of crop growth with simplified relations for water balance and water use are insufficiently detailed 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.

The model BACROS is used to simulate this 'hole making' effect of stripe rust. Within this model, transpiration is computed with a Penman type formula, in which leaf resistance is one of the most important variables (Subsection 3.2.6). Leaf resistance decreases as a result of the many little holes, which leads to an increase in transpiration. Holes in the cuticle can be viewed as non regulating stomata, which in this case are assumed to permit only the diffusion of H₂O.

The diffusion resistance of the holes, parallel to that of the stomata, 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, length l and diameter d , per unit of surface, the resistance R_m , is normally taken to be:

$$R_m = 4 \cdot l / (d^2 n D) + 2 \cdot l / (2 n D d) \quad (105)$$

in which D is the diffusion coefficient for H₂O, 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 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 of a canopy that contains a large number of these pores, the first part of Equation 105 is small compared to the second one and can be neglected (Stigter & Lammers, 1974).

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 (n), in a canopy with LAI = 5, equals $5 \cdot 10^8 \text{ cm}^2 / (\pi \cdot (0.08)^2) = 2.5 \cdot 10^{10} \text{ ha}^{-1}$, or 250 cm^{-2} . When there is a 100% infection of the leaves, about 20% of the leaf area is replaced by pores (Rijsdijk, 1980). D equals $0.2 \text{ cm}^2 \text{ s}^{-1}$, so that the diffusion resistance of a surface with these holes amounts to:

$$R = 1 / (50 \cdot 0.2 \cdot 0.16) = 0.62 \text{ s cm}^{-1}$$

This corresponds with an increase of the conductivity of the canopy of 0.016 m s^{-1} , which indicates that a considerable increase in the transpiration rate is to be expected on basis of this hypothesis. To test this, the assumption was introduced in a computer simulation that a maximum leaf coverage of 20% exists continuously for 30 days. 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 a shift in shoot-root ratio; the shoot weight is about 10% lower and the root weight is about 20% greater than without rust attack (Figure 85). The transpiration rate of the canopy is on average about twice the normal transpiration rate. These results illustrate the influence of the functional balance (Subsection 3.3.6).

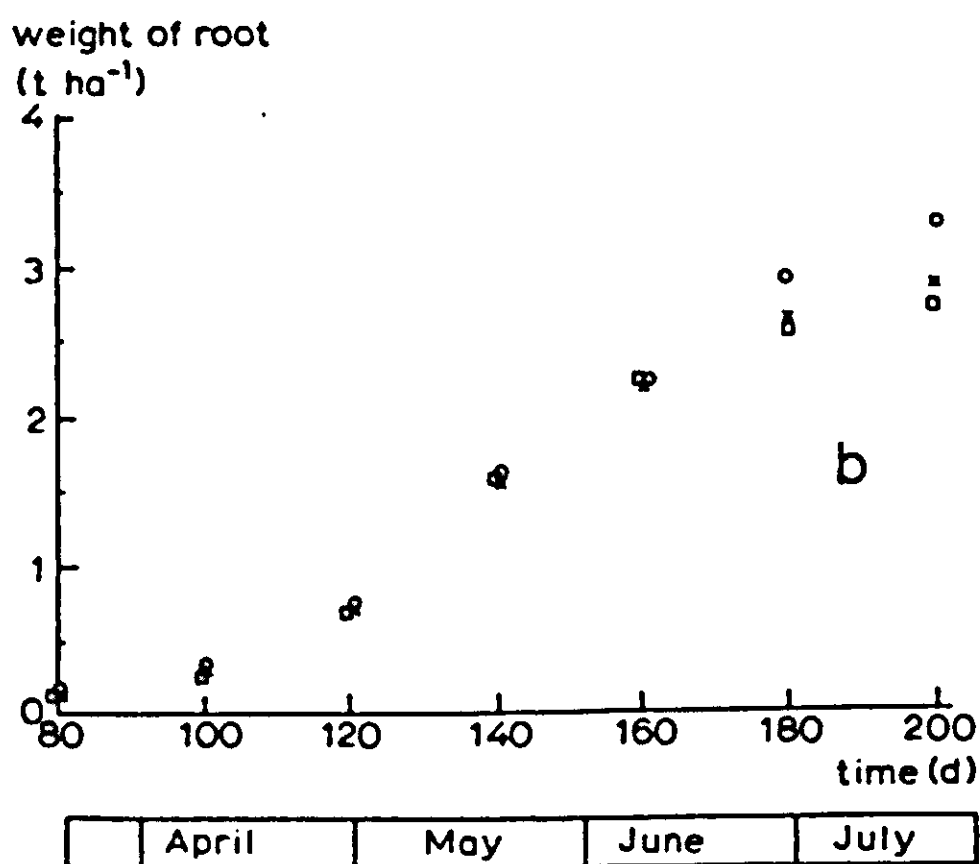
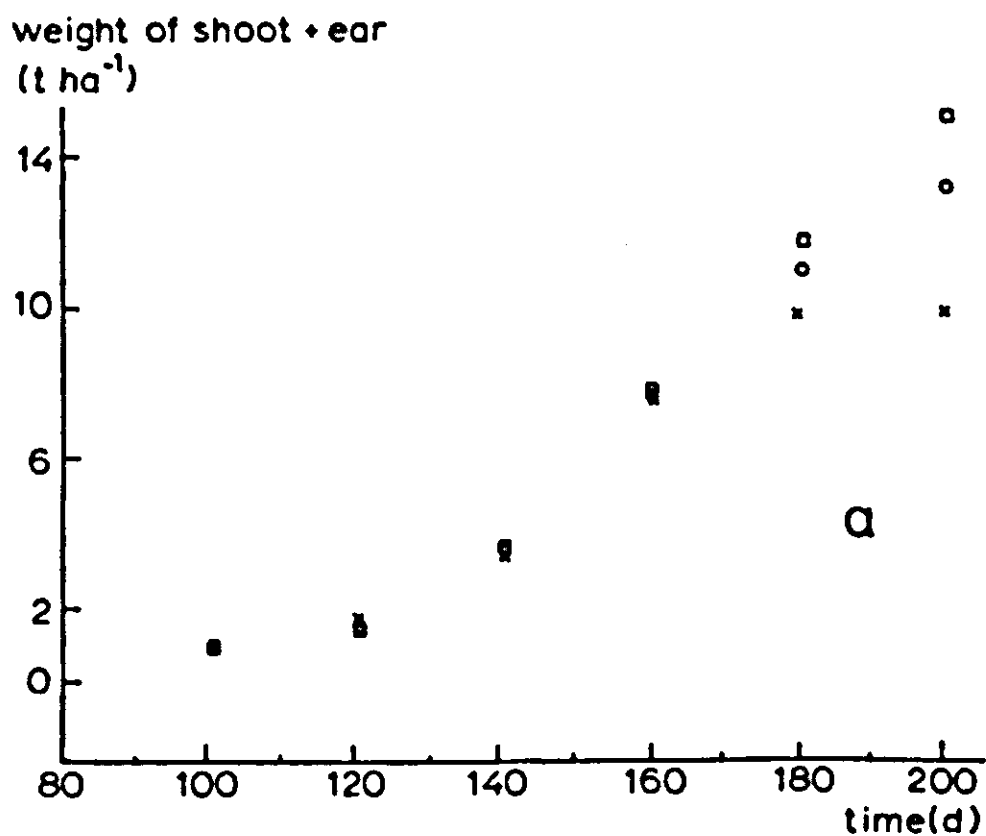


Figure 85. Simulated increase in weight of shoot and ear (a), and weight of root (b) with a comprehensive crop growth simulator. □ = unattacked crop; o = crop infected by a stripe-rust epidemic, maximum leaf coverage of 20%, during a period of 30 days; x = crop infected by strip-rust epidemic, reaching maximum leaf coverage of 100%, i.e. 20% of leaf area replaced by holes, using a realistic simulator of the rust epidemics.

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 unrealistic 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. As a next step in hypothesis testing, the decrease of the CO₂ assimilation rate due to absence of photosynthetic activity in the pustules was introduced by multiplying the net CO₂ assimilation rate by the fraction of the total leaf area attacked. As a result, the total amount of above-ground dry matter simulated with the model was

about 25% less in infected than in non-infected control plants, i.e. a yield loss of about 2500 kg ha⁻¹. Again the root weight is higher than in the control. Such figures are 'in the ball park'.

Finally, the crop growth model BACROS was linked to a simulation model of stripe rust epidemics, enabling latent, infectious and removed sites to be distinguished. The results of these calculations (Figure 85) show that a heavy attack of stripe rust causes a considerable decrease in shoot weight and a slight decrease in root weight, a result that is confirmed by 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 relative 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 of carbohydrates. However, in spite of their imperfections, these examples show how an effort is being made to gain a full understanding of various processes that play a role in the crop-pathogen interrelations.

6.1.6 Using a disease crop production model in practice

The latter combination model is used as a research tool that leads to understanding of the effects of a pest or disease organism on its host plant. This insight may lead to better measures. The detailed population dynamic, crop and combination models themselves are seldom used for actual decision-making in crop protection. Their role is to test hypotheses, to gain insight and to pinpoint the most decisive variables for the rate of development of pests and diseases. They are used to compute the range of acceptable disease or pest levels according to the weather and the condition and developmental stage of the plants. These calculations have been made for different diseases and pests in winter wheat and this has resulted in simplified summary models and/or decision rules, which are used to determine whether control measures are needed. In the Netherlands these results are used in a supervised control system called EPIPARE (EPIdeemics PREvention) (Rijsdijk et al., 1981). EPIPARE is developed for wheat farmers. It works on a field by field basis and gives specific recommendations for every individual wheat field included. This was done in 1979-1980 by a team of research workers for 1000 fields and based on field information. This information is stored in a data bank and includes data on location, sowing time, cultivar, a few simple physical and chemical soil characteristics, herbicide application and nitrogen (N) fertilization. The information per field is updated whenever additional information is supplied by the farmer on the research team.

This information is used to run the simplified combination or the decision rules models to obtain recommendations that are then sent immediately to the farmers. This EPIPARE supervised control system is now operational in several

European countries and has lead to an improved economic plant protection system with reduced pesticide use and with optimal economic results. This optimal yield may be different from maximum yield as cost-benefit analyses are the basis for the advice.

At present this supervised control system of pests and diseases in winter wheat does not supply information and advice on supervised weed control or N and P fertilization. Reliable simulation models on N in soils and crops (Sections 5.1-5.3) are gradually becoming available, which may be used in future to advise on timing and amount of N added to winter wheat. The same holds for weed control. In this way an integrated crop protection system may be developed in which costs are reduced and economic yields are optimized.