

4.3 Combination models, crop growth and pests and diseases

R. Rabbinge and L. Bastiaans

4.3.1 *Introduction*

Estimates of yield loss due to pests or diseases are essential in any supervised or integrated control system of pests and diseases (Chapter 1). They form the basis for an economic cost-benefit analysis of control measures and, therefore, help to develop rational crop protection systems. These yield losses may be expressed in mass of product or economic values. Here, both concepts will be used. Yield losses, whether mass of product or financial, are often only based on intelligent guesses made by agronomists or crop protection scientists. They are seldom based on a real knowledge of the nature or level of crop growth reduction due to the presence of pests or diseases. The increasing significance of pests and diseases as growth and production reducing factors (Smith et al., 1984), justifies more detailed analysis of the interaction between the host plant (crop) and its enemies. This may be done in a statistical analysis of the relation between disease severity or infection level and crop loss. Such analyses help to define injury levels under some field conditions and can be used in pest and disease management (Royle et al., 1988). However, they do not provide much insight into the nature of growth and yield reduction and cannot be extrapolated to other, not yet studied, field situations.

There are several ways in which pest or disease populations can affect different physiological processes in plants. They may, for example, reduce crop stands by eliminating the plants, they may reduce inputs such as light, CO₂ or water, they may affect rates of metabolic and growth processes directly or they may remove or consume previously produced material. Simulation models are useful for studying the quantitative consequences of the various effects.

Eventually, these simulation models will provide insight into the mechanism of growth and yield reduction and into the quantification of yield reduction under various conditions, as demonstrated in cereal aphids on winter wheat (Section 4.4).

4.3.2 *Statistical analysis and descriptive models*

In order to make competent decisions on the management of pests and diseases, it is essential to know how the different disease or pest epidemics will reduce yields. In most studies of pest and disease management, the concept of Economic Injury Level (EIL) is introduced as the value at which cost of control is in balance with the expected yield loss. However, because of time lags, control measures are often needed at some action threshold long before this economic

injury level is reached (Chapter 1). The EIL concept, when it was introduced by Stern (e.g. 1973), revolutionized the thinking of crop protection scientists. It presumes a fixed relation between disease or pest intensity and yield loss, irrespective of crop growth conditions. However, results differ greatly under various conditions, as illustrated for the fruit-tree red spider mite on apple, one of the most studied host plant-pest relations. Van de Vrie (1956) showed, for a well kept, well fertilized and intensively controlled 'Beauty of Boskoop' apple orchard in the Netherlands, that a spider mite density of maximally 40 mites leaf⁻¹ and 1080 mite days leaf⁻¹ caused a yield loss of 18% and a reduction in shoot growth of 30%. However, Avery & Briggs (1968a, b), in similar experiments in England with two-year-old 'Lord Lambourne' trees, found that a mite density of 70 mite days cm⁻² did not result in significant differences in apple yield ha⁻¹ or in shoot growth, dry weight of apples or number of buds. In a detailed study from 1965 to 1971 in various apple orchards in England, Light & Ludlam (1972) used different spraying treatments to determine immediate and delayed effects of mites. In their experiments, mite densities varied from 800 mite days leaf⁻¹ to 2000 mite days leaf⁻¹ and densities of up to 40 mites leaf⁻¹ were recorded. This experiment was statistically very well designed, and differences of 500 kg ha⁻¹ were significant. However, these showed up only when the number of mite days leaf⁻¹ exceeded 1350. In the following year, no significant differences in pomological characteristics could be detected.

At Hood River Valley, Oregon (U.S.A.) a four-year study, using individual ten-year-old 'Newton' and 'Golden Delicious' apple trees, was carried out by Zwich et al., (1976). The mite densities were observed at weekly intervals for various spider mite control treatments (timing and method of control). The trees were irrigated when necessary and nitrogen supply was abundant. Chemical control was in accordance with normal farming practices and pruning was done chemically. Maximum densities of 70 mites leaf⁻¹, and maximally 1400 mite days leaf⁻¹, were reached in these experiments. These high mite densities did not result in significant effects on yield or on other pomological characteristics. Only at the highest mite density was the chlorophyl content of the leaves significantly affected. Effects on fruit growth, shoot length, number of buds and trunk diameter were absent in the year following the heavy infestation. Apparently, the apple trees growing under 'optimal' conditions could tolerate high mite densities; up to 1900 mite days leaf⁻¹ or a maximum density of 70 mites leaf⁻¹. These results led Zwich et al. (1976) to fix the economic injury levels of fruit-tree red spider mites at 20-30 mites leaf⁻¹. This is approximately ten times the economic injury level which was proposed at the Technical Expert Meeting of the FAO in 1973.

It seems impossible to explain these conflicting experimental results. It indicates that the economic injury level depends on the conditions that prevail during the experiments, and thus a specific EIL based on field experiments alone is only possible when several experiments are done and statistically analysed. This is both time-consuming and painstaking. It would seem, therefore, attractive to

combine such field experiments with detailed physiological and biological studies on the nature and background of damage. Simulation studies may bridge the gap between both levels. However, crop physiological parameters are very loosely determined in all the experiments described, and neither the cropping history of the experimental orchards nor crop agronomy measures are given. Moreover, the data on spider mite densities are often incomplete, the age composition of the spider mite population is not determined, and accuracy of the population density is not given. Weather conditions during the experiments are also not recorded. This lack of information makes interpretation of the data virtually impossible.

Clearly, the above studies, which can be extended by many others, demonstrate that it is almost impossible to define generally applicable economic injury levels; the results are too conflicting.

Statistical methods are based on a description of the field situation but give no insight into the background of damage. Extrapolating the damage relations to other field situations is, therefore, hazardous, as the consequences of the interaction between pest and crop may vary considerably and could result in a different yield loss-pest density relation. For example, weather conditions may not only affect the epidemiological development of a disease but also the host-pathogen relation (Zadoks & Schein, 1979). Apart from when and where the pest is present, the crop growing conditions may considerably affect the reduction in yield. At high nitrogen contents in the leaves, epidemiological development of many diseases is promoted, because the latency period is shorter and the infectious period longer than under nitrogen-deficient conditions. The effect of the nitrogen conditions on the growth and yield reduction, per unit of disease or pest, is also important.

The effects of pests and diseases are, in general, more significant at higher yield levels. A healthy crop, essential for high yields, and the favourable micro-meteorological conditions in a dense crop, may promote the epidemiological development of many diseases and affect the yield loss-pest density relation. Increase in winter wheat yields in western Europe in the seventies, is largely due to better pest and disease control in crops that already had a high potential (Rabbinge, 1986). Cereal aphids cause progressive damage at increasing yield levels (Section 4.4). Other diseases cause proportional (mildew) or subproportional (Septoria) damage per unit of disease (Rabbinge, 1986). The existence of differential effects limits the use of generally applicable economic injury levels. When such differential effects are absent, well-designed and well-executed field experiments may lead to adequate economic injury levels. Experimentally determining flexible economic injury levels, however, would require a discouraging number of field experiments and, for this reason, the use of dynamic simulation models in combination with experiments would seem to be more appropriate.

4.3.3 *Dynamic explanatory models as a vehicle for development of EILs*

In most models of population dynamics for pest and disease organisms, the crop is considered as a constant substrate which imposes limitations only when all sites are becoming occupied.

However, the crop's condition may, for example, affect the length of the latency or infectious periods, and thus epidemiological development. Such effects are considered by extending the simple epidemiological models of Section 3.1. For instance, the nitrogen content of the leaves can be introduced, or several leaf layers with differing sensitivities to the disease can be distinguished. Leaf layers can be introduced using boxcar trains for the various leaf layers, and crop condition can be introduced as a forcing variable. The epidemiological model of mildew in winter wheat of Exercise 36 (Section 3.1) is used to introduce leaf layers with different nitrogen contents.

Exercise 64

Introduce leaf layers into the model of Exercise 36. Each leaf layer has an LAI of 1.5, so at the beginning one leaf layer and on Day 180 (with the highest leaf mass) three leaf layers are distinguished. After Day 180, leaf dying due to ageing starts from the lowest leaf layer, via the middle and finally reaches the upper leaf layer. Run the model and study its results. Explain the differences with the results of Exercise 36.

The effect of leaf layers on the epidemic may be amplified or reduced when the condition of the leaf layer in terms of nitrogen content is introduced. This is the next step in model development. Crop condition in terms of nitrogen content is introduced as a forcing function that influences the latency and infectious periods. The nitrogen content in the various leaf layers is, for reasons of simplicity, kept constant during the growing season. In the middle leaf layer, layer 2, it is kept at 3.0% and in the first layer, the lower layer, a lower percentage is maintained whereas the third or upper leaf layer has a slightly higher nitrogen percentage. How the various nitrogen contents affect the lengths of the latency and infectious periods is given in Table 15.

Exercise 65

Introduce the nitrogen content of the various leaf layers in the model of Exercise 64 and compute the consequences of the changes in latency and infectious periods for the upsurge of the mildew epidemic. Explain the differences in the results between Exercises 64 and 65.

Table 15. Effect of nitrogen contents in leaves of winter wheat on latency period and infectious period of mildew *Erysiphe graminis* expressed as a multiplication factor.

Proportion nitrogen in leaves (%)	Latency period (multiplication factor)	Infectious period (multiplication factor)
2.0	1.5	0.8
2.5	1.2	0.9
3.0	1.0	1.0
3.5	0.8	1.2

The epidemiological model, although more realistic, is still not complete as it does not account for changes in nitrogen content during the growing season and neglects the effect of mildew on crop performance, which may ultimately result in shifts in the epidemiological parameters. This effect of the disease on crop performance is exemplified in the following paragraphs and in Section 4.4.

The effect of disease or pest on crop performance may vary considerably depending on the place and the method of interaction (Boote et al., 1983). In Table 16, some sites of coupling between crop and pests and diseases are indicated. Various rates may be affected. The rate of photosynthesis may be affected by a direct effect on the light use efficiency through light stealing, or on the assimilation rate at light saturation because of a physiological change. Such a direct effect is found as a result of, for example, mildew-diseased wheat. This disease decreases photosynthesis at light saturation and has no effect on light use efficiency (Rabbinge et al., 1985). Another disease, beet yellows virus (BYV) causes a decrease in both light use efficiency and photosynthesis at light saturation (van der Werf et al., 1989a). The cereal aphid, through its excretion product, honeydew, besides causing direct phloem consumption, also affects light use efficiency and photosynthesis. (Rabbinge et al., 1983).

Maintenance respiration and growth respiration may be affected by mites that drain assimilates from the parenchyma cells and promote suberization. Further growth rate may be affected directly through leaf mass or tissue consumption. Stand reducers may cause loss of plants, which may result in yield loss unless sufficient compensation, and the capability and time to realize this compensation, is available. Some pests and diseases may affect the turgor of cells, either directly or by disrupting the tissue in such a way that transpiration is promoted. Leaf senescence may be promoted and growth of root, stem or storage organ may be directly affected, caused by having to compete for assimilates. Various aspects of growth reduction may be distinguished (Table 16). These aspects are also present in the crop growth model SUCROS87. Therefore, some of the crop growth reducing factors of Table 16 will be discussed below in a way that the order of capturing and use of solar energy is followed as a line. The relational

Table 16. Various examples of crop growth-reducing factors, place and nature of effect.

Type of effect	Yield-loss determining aspects	Example
Stand reducers	<ul style="list-style-type: none"> – number of plants lost – distribution of lost plants – compensation ability of remaining plants 	damping-off fungi
Light stealers	<ul style="list-style-type: none"> – covered area – type of tissue – total or partial absorption 	yeasts
Assimilation rate reducers	<ul style="list-style-type: none"> – effect on AMAX and/or EFF – position of affected leaves 	powdery mildew beet yellows virus
Assimilation sappers	<ul style="list-style-type: none"> – rate of CH_2O consumption – harmful excretion products 	mites
Tissue consumers	<ul style="list-style-type: none"> – type of tissue – rate of consumption 	cereal leaf beetles

diagram of Figure 63 indicates where the effects of the various harmful organisms are focused.

Stand reducers, such as damping-off fungi, reduce plant biomass and the number of plants. Analysis is difficult as it requires similar approaches to those described in Section 4.2 on light or nutrient capturing by weeds. The distribution of the remaining plants in the field and their capacity to compensate should then be considered.

Light stealers Some leaf pathogens have a 'light stealing' effect on crops as they live in dead host tissue which absorbs photosynthetically active radiation, which is caused, for example, by perthotrophic and saprophytic fungi. Leaf coverage due to excretion products or light interception by leaves with necrotic lesions may interfere with photosynthesis. Coverage of leaves with mycelium may also affect light absorption.

Assimilation rate reducers Many pathogens and pests affect the CO_2 assimilation rate; they may affect the photosynthesis rate at light saturation or the light use efficiency. Mechanisms by which pathogens affect photosynthesis have been summarized by Buchanan et al. (1981). Viruses and some fungi may reduce the number of chloroplasts per unit leaf area or alter the chloroplast ultrastructure and components of the electron transport chain, thus decreasing photosynthesis.

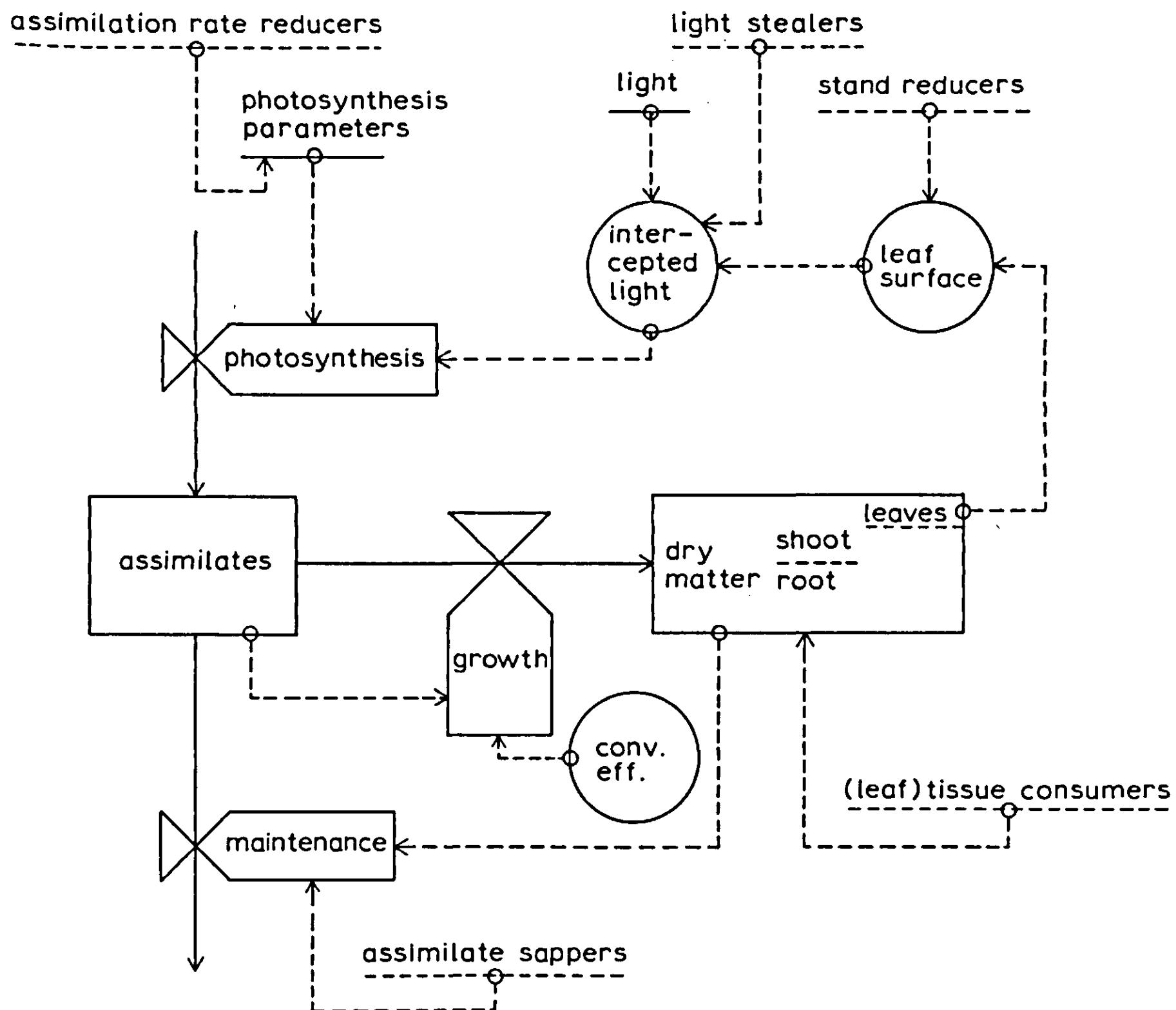


Figure 63. Relational diagram of the model SUCROS87 indicating where the effects of various harmful organisms are focused.

Bacteria may also cause structural damage to chloroplasts. Some pathogens and insects may accelerate leaf senescence. This may be due to changes in the nitrogen balance or to excretion products affecting the activity of leaves. All these effects have been shown to exist in detailed studies under well-defined conditions. However, their quantitative meaning in terms of crop growth and production is virtually unknown. Some diseases such as rusts and mildew may cause malfunctioning of the stomatal guard cells, resulting in greater resistance to CO_2 uptake by well-watered plants (Ayres, 1981). This effect on stomatal behaviour may result in a change of assimilation rate and thus water use efficiency.

Assimilate and tissue consumers The distinction made between the two is that tissue consumers remove crop tissues, and assimilate consumers feed on unconverted assimilates. Since each kg of assimilate produces less than 1 kg of tissue, the tissue consumers are more costly in terms of crop growth. However, second-

ary damage by assimilate consumers, for instance due to honeydew, may result in higher total levels of damage. These secondary effects are mainly caused by a considerable change in the physiological characteristics of the crop due to the pest organisms.

Turgor reducers, such as nematodes that feed on the roots, and root pathogens affect the water balance of the plant. They also affect the crop nutrient balance by disrupting phloem transport to the roots, reducing the energy supply for the active uptake of nutrients such as K, and by disrupting the passive flow of water and nutrients by the eventual decay of that tissue.

Evaluation of the various host plant-pest interactions can be done for the conditions of an optimally functioning crop, when water and nutrients are abundantly available, by introducing damage mechanisms into the model SUCROS87 (Section 4.1).

4.3.4 *SUCROS87 coupled with growth-reducing factors*

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 (*Lema cyanella*) may be attached to the model SUCROS87. Larvae of cereal leaf beetles consume leaf mass at a rate of about $250 \text{ cm}^2 \text{ d}^{-1}$ ($= 1.2 \text{ g dry matter d}^{-1}$). Only the larvae consume leaves. After growth and development they pupate, moult and develop into adults that may give rise to another generation. The rate of increase in the number of cereal leaf beetle larvae depends on the egg-laying rate of the adult females. After hatching, the larvae immediately start feeding. Their effect on crop growth is introduced into the model, using the parameters for wheat, by a decrease in the amount of leaves. This rate of decrease in leaf weight is assumed to be proportional to the number of larvae, lumping all development stages of the larvae together. Consumption of leaf mass by the adults is neglected, and the relation of ageing and reproduction rate on food quality are not considered. Population dynamics of the beetles are 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 only 50% of the next generation will produce eggs.

Exercise 66

Develop a simple model of *Lema cyanella* when environmental conditions are considered to be constant and the different development stages 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, and assume during development a constant relative dispersion of one.

The population model can be linked to the crop growth model by introducing a consumption rate of leaves that drains leaf mass. This rate depends on the number of beetle larvae and the daily consumption rate per larva. The leaf area index, LAI, is affected by this decrease in leaf mass due to beetle 'grazing'. There is also another consequence for the crop growth model, as the maintenance respiration is affected by the ratio of weight of green leaves divided by the total leaf weight, WL_{VG}/WL_V. This ratio (MNDVS) was introduced in SUCROS87 to express the change in maintenance respiration due to ageing or to a decrease in nitrogen content. Since the beetles reduce WL_{VG}, they indirectly affect simulated maintenance respiration. To avoid this, the factor expressing the reduced maintenance respiration, due to ageing or low nitrogen content, is transformed into a forcing function, based on the WL_{VG}/WL_V ratio, as determined in Section 4.1, in course of time: MNDVS = AFGEN(MNDVST, DVS).

Exercise 67

Link the model SUCROS87 to 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 on Day 195. The simulation should reproduce the results of Figure 64.

Tissue death and assimilate consumption Plant mites inject their stylets through the epidermis into the parenchyma cells and swallow the contents. The attacked cells may die and the surrounding cells often demonstrate phenomena such as suberization of cell walls, decreased photosynthetic activity and increased maintenance respiration. Plant mites are found in many agricultural and horticultural crops. They are especially prolific in glasshouse crops but, under suitable conditions, may also cause damage in arable crops such as potato. To illustrate this, the model SUCROS87 for potato is linked to a mite population. The model for the potato crop is changed in two places to introduce the effects of mites.

First, the maintenance respiration is increased by an amount considered to be proportional to the mite density. Although this may be true at relatively low densities, it overestimates the effects of the mites at high densities. Second, an effect of the mites on the photosynthetic activity is introduced. This effect is also mite-density-dependent, the basis of these effects is derived from measurements made by Tomczyk & van de Vrie (1982) and damage data of Sabelis (1981) on chrysanthemums and roses. Mite density is introduced by way of a forcing function, lumping all the different morphological stages together. A more realis-

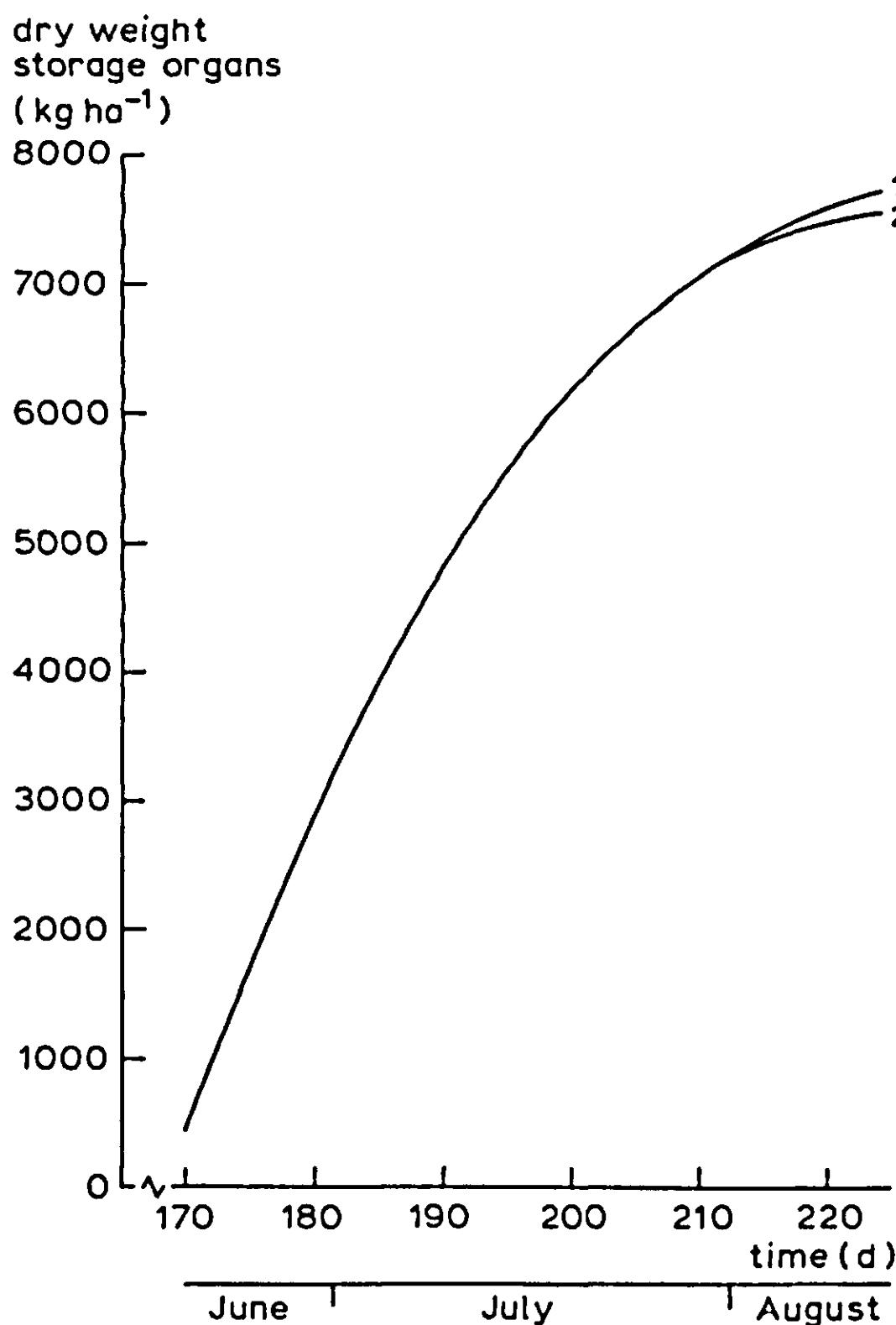


Figure 64. Simulated weight of grains (WSO, kg dry matter ha^{-1}) of a spring wheat crop for different levels of cereal leaf beetle attacks. 1: no beetles; 2: starting with 300 adult beetles on 14 July (Day 195).

tic population model, which may be combined with a comprehensive crop model, should consider the different morphological stages and the sensitivity of the development rate to temperature and food quality (Rabbinge, 1976).

Exercise 68

Introduce the effect of spider mites on maintenance respiration in the model SUCROS87 for potato. Give an imaginary population density curve in course of time, for a mite population that reaches a maximum on 29 July of 2 mites cm^{-2} , 6 mites cm^{-2} or 12 mites cm^{-2} , respectively. The first mites are found on 30 June, and the last ones have left by 18 August. Presume a linear increase and decrease in the mite population density. Each mite respires 50% of its body weight per day.

An adult mite has a weight of 50 μg . Your calculations should be the same as the results of Figure 65.

Computations using the model of Exercise 68 show that minor changes in the respiration rate, due to the presence of mites, have a major effect on the growth rate of the canopy; consequently, yield is considerably affected. The same is true for the effect on photosynthetic activity. This effect is introduced by a decrease in the assimilation rate at light saturation (Table 17). Computation using the model, which comprises both effects, shows that due to the combined effects of mites on respiration and photosynthesis at light saturation, yield is reduced by 16% when a maximum density of 12 mites cm^{-2} is reached (Table 18). The effect of the

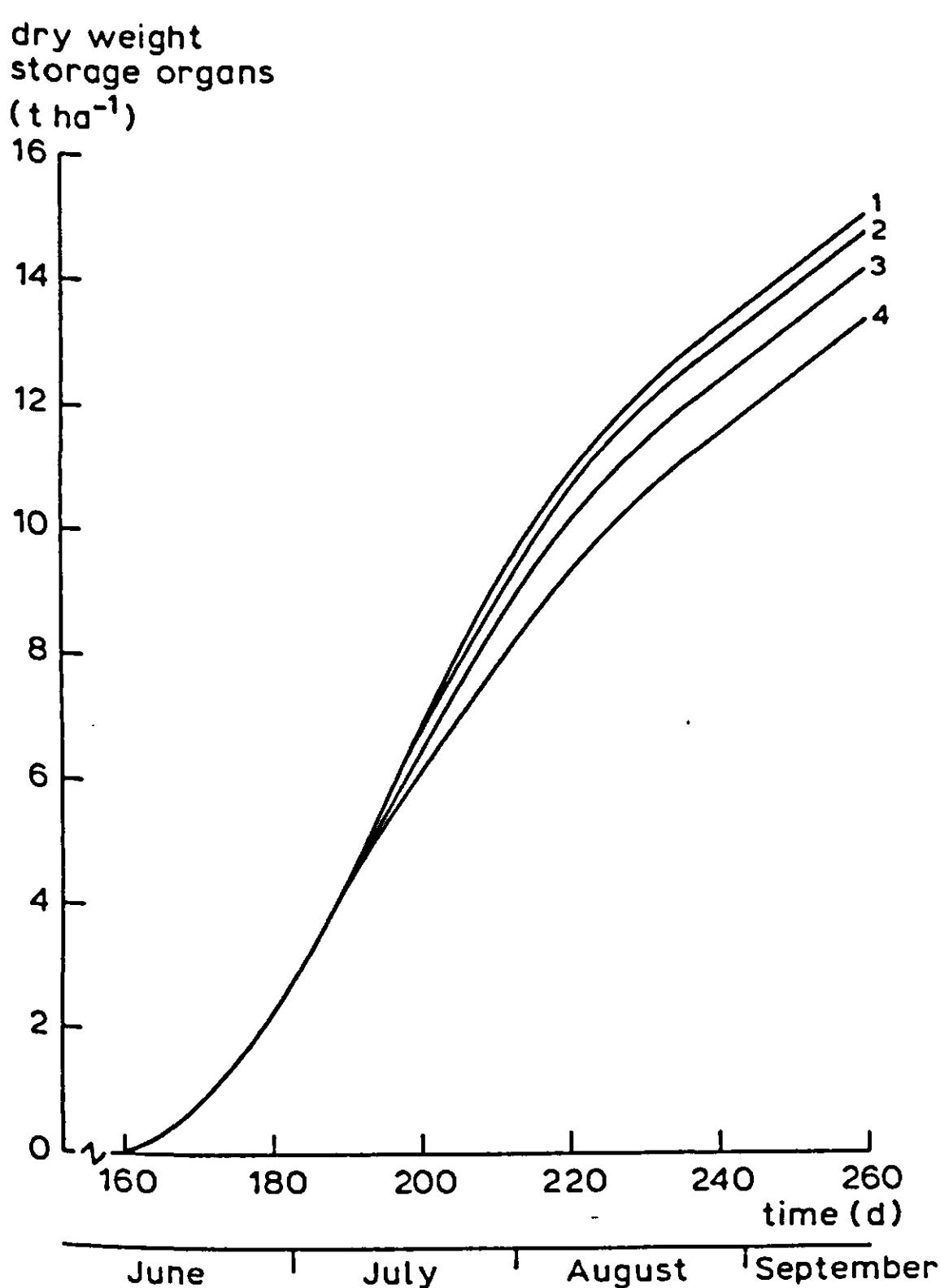


Figure 65. Simulated dry weight of storage organs (WSO, t ha^{-1}) of a potato crop in the presence of a mite population that affects maintenance respiration. A maximum mite density of 0, 2, 6 and 12 mites cm^{-2} leaf (curve 1–4, respectively) is reached on 29 July (Day 210).

Table 17. Decrease in photosynthesis at light saturation of potato leaves at various mite densities, expressed as a multiplication factor.

Mite density (mites cm^{-2})	Decrease in photosynthesis at light saturation (multiplication factor)
3	1
10	0.75
20	0.3

Table 18. Simulated effect of mites on dry weight yield of storage organs (WSO, kg ha^{-1}) of a potato crop (WSO control = 14950 kg ha^{-1}) at harvest (17 September; Day 260). It is assumed that the mites affect maintenance respiration (MAINT), and/or assimilation rate at light saturation (AMAX).

	Maximum mite density (mites cm^{-2} ; on 29 July (Day 210))					
	2 mites		6 mites		12 mites	
	WSO	reduction	WSO	reduction	WSO	reduction
MAINT	14665.	285.	14096.	854.	13242.	1708.
AMAX	14950.	0.	14816.	134.	14276.	674.
MAINT + AMAX	14665.	285.	13962.	988.	12569.	2381.

increase in maintenance respiration is relatively more important than the effect on photosynthesis at light saturation. Both effects seem to be additive. This is understandable because the places that are affected are independent of each other, and a positive feedback due to growth reduction of leaves is absent, because the mites are not introduced until Day 181 when leaf growth has already stopped. If the mites are introduced earlier, the two effects (on maintenance respiration rate and assimilation rate at light saturation) are no longer additive, as a positive feedback would be present due to reduced leaf growth and consequently leaf area and assimilation rate. At maximum mite densities of 2 or 6 mites cm^{-2} , yield reduction is almost negligible. The effect on maintenance respiration and photosynthetic activity only occurs when weather conditions are favourable for both crop and pest: high temperature, rapid crop development and limited radiation levels.

Further testing of this hypothesis may be done using this combination model. For example, effects of webbing, which appear sooner than injury symptoms (Sabelis et al., 1983), on light use efficiency and assimilation rate at light saturation, may be evaluated. However, the reliability of such model computations is

doubtful, as too many descriptive relations on the system level are needed, and too many estimates required. Therefore, comprehensive models are needed in this process of hypothesis testing to obtain insight into the consequences of the different effects that spider mites have on plant physiological parameters. This will require additional experiments at the process level, together with well-defined field experiments for model testing.

The ultimate aim of such studies is to develop damage relations, which can be used to control the acarine system under various conditions.

Leaf coverage To demonstrate the effect of organisms that cover the leaves with a thin layer, yeasts such as *Sporobolomyces* spp. (pink yeasts) and *Cryptococcus* spp. (white yeasts) or an organism like the saprophytic fungus *Cladosporum cladosporides* (black moulds), are coupled to the model SUCROS87 for wheat growth (Section 4.1). Yeasts and the saprophytic fungus occur on all surfaces where organic matter, sugars, proteins or other leaf exudates, needed for growth and respiration, are available. When cereal leaves produce exudates or are covered with the cereal aphid excretion product honeydew or with sugary exudates, numbers of up to 10^6 cells cm^{-2} are reached. The light stealing effect of yeasts is evaluated. The yeast epidemic is simulated using the logistic growth equation (Equation 37). A leaf area covered by yeast cells absorbs light before it is captured by the chloroplasts. It is assumed that a linear relation between absorption and the log value of yeast density in cells cm^{-2} exists. The absorption is introduced by multiplying daily photosynthetically active radiation (DPAR) by $(1 - \text{ABSORB})$, in which ABSORB expresses the light absorption by yeast cells.

Exercise 69

Construct a combination model for wheat growth with yeasts, and run it for different initial yeast densities at flowering (DVS = 1., Day 170) of 10, 100 and 10000 yeast cells cm^{-2} , respectively. The relative growth rate of the population $r = 0.8$, and a maximum of 10^6 yeast cells cm^{-2} is assumed. Repeat the calculations when the yeast population starts with an initial density of 10 cells cm^{-2} on Day 185 and Day 200, respectively.

At high yeast densities, light absorption is relatively less than at low yeast densities. This is due to the high number of yeast cell layers that cover a leaf at higher densities. The simulated reduction in grain yield is about 1000 kg ha^{-1} at an initial density of 10 yeast cells cm^{-2} on Day 170. The increase in yield loss at higher initial densities is small, as the maximum density of 10^6 cells cm^{-2} is reached in nearly all cases: the extra yield loss at an initial density of 10 000 cells cm^{-2} is only 500 kg ha^{-1} .

Light stealing may not be as high as assumed, and yeast cells may play an important role by suppressing perthotrophic fungi, such as *Septoria*, by competing for space and exudates (Rabbinge et al., 1984b). Thus, negative effects of yeasts and saprophytic fungi may be smaller than assumed, and positive effects such as competition may be larger, resulting in various net responses of growth and production under various conditions.

Assimilation rate reducer Beet yellows virus (BYV) can cause considerable yield reductions in sugar beet. In a field experiment in 1986, van der Werf et al. (1989a) demonstrated that plants infected on 5 June (8-leaf stage) with beet yellows virus (BYV; closterovirus group) produced only 45 t ha^{-1} of beet roots (fresh weight), whereas healthy plants produced 93 t ha^{-1} . Plants infected at the 28-leaf stage, on 14 July, produced 87 t ha^{-1} . Thus, timing of virus infection is crucial for yield reduction as both the rate of virus spread and the physiological parameters are affected (van der Werf et al., 1989a, b). The effect of virus infection on physiological parameters has been determined in detailed photosynthesis measurements, and in measurements of optical characteristics of infected leaves. Light reflection and transmission of photosynthetically active radiation are decreased in virus infected plants and, partly as a result of this, light use efficiency is considerably smaller (Table 19). Photosynthesis at light saturation (AMAX, Table 19) is also considerably decreased due to virus infection. Healthy or infected green leaves had similar rates of light-saturated photosynthesis; in leaves with vein clearing symptoms, AMAX had decreased by 30%, and in bright yellow leaves AMAX was four times smaller.

The effects of the virus on light use efficiency and photosynthesis at light saturation (Table 19), were introduced into the model SUCROS87. A possible effect of the position of the infected leaves is neglected. First, crop assimilation is calculated for healthy leaves, and then the same calculations are done for infested leaves with bright yellow symptoms. The weighted average for the actual crop assimilation is then found by multiplying the last computed assimilation rate by the fraction of diseased leaves (FRDIS), and the first computed assimilation rate

Table 19. Normalized values of the maximum assimilation rate at light saturation (AMAX, $\text{kg CO}_2 \text{ ha}^{-1} \text{ h}^{-1}$), light use efficiency (EFF, $\text{kg CO}_2 \text{ ha}^{-1} \text{ h}^{-1} \text{ W}^{-1} \text{ m}^2$) and dark respiration (RD, $\text{kg CO}_2 \text{ ha}^{-1} \text{ h}^{-1}$) for various categories of leaves on BYV infected plants.

Leaf category	AMAX	SD(\pm)	EFF	SD(\pm)	RD	SD(\pm)
healthy	100(37.)	2	100(0.40)	0.04	100(2.9)	0.7
vein clearing	72	2	89	0.04	138	1.1
greenish yellow	46	2	80	0.03	188	0.7
bright yellow	26	2	71	0.03	138	0.7

by $(1. - \text{FRDIS})$. Thus, first calculations of crop assimilation are done, and then the average is determined. This is necessary to prevent errors due to averaging which may occur when the relation between the affected photosynthetic parameters and crop assimilation is curvilinear, see also Sections 3.2 and 3.3.

For the first infection date (5 June), the proportion of yellowed leaves is given by:

$\text{FRDIS} = \text{AFGEN}(\text{FRDIST}, \text{DAY})$

FUNCTION $\text{FRDIST} = (0., 0.), (172., 0.), (182., 0.15), (192., 0.28), \dots$
 $(212., 0.47), (232., 0.54), (272., 0.63), (292., 0.63)$

and for the second infection date (14 July) by:

FUNCTION $\text{FRDIST} = (0., 0.), (242., 0.), (252., 0.05), (292., 0.12)$

Exercise 70

Introduce the effect of the virus on light use efficiency and photosynthesis at light saturation. Run the model for the two infection dates 5 June and 14 July, respectively.

The effect of infection date on growth and yield of sugar beet is given in Table 20. The simulation results demonstrate that a late infection, 14 July, does not do much harm; yield reduction is very limited. An early infection, 5 June, causes a considerable reduction in yield. This confirms field experiments of van der Werf et al., (1989a). However, the measured yield reduction is higher than the simulated yield reduction. This is probably due to the distribution of the virus yellowed leaves, which are mainly found in the upper leaf layers and thus their contribution to light interception is relatively high. Such an effect is not considered in the simulation; infested leaves are homogeneously distributed.

Another reason for the discrepancy between simulation and experimental results may be due to the fact that the increase in dark respiration due to the presence of a virus was neglected. The effect of reduced light use efficiency or reduced photosynthesis at light saturation may be different, because the sensitivity of crop photosynthesis to these parameters is not the same. Of course, the model may be totally inaccurate and, thus, the discrepancy between simulated and field results can be explained. However, this possibility should be considered only after studying the reasons for the discrepancy mentioned above.

Table 20. Simulated production of sugar beet infected by beet yellows virus on various infection dates. The virus affects the assimilation rate at light saturation (AMAX) and/or light use efficiency (EFF). (WSO = sugar beet, kg DM ha⁻¹; WSO control = 14575 kg ha⁻¹, harvest on 17 October, Day 290.)

Effect	Infection date 5 June		Infection date 14 July	
	WSO	WSO	WSO	WSO
	absolute	%	absolute	%
AMAX	10664	73.2	14377	98.6
EFF	12646	86.8	14479	99.3
AMAX + EFF	10014	68.7	14343	98.4

Exercise 71

Evaluate the effect of the virus on light use efficiency and on photosynthesis at light saturation. Repeat, therefore, the computations of Exercise 70, in case only one photosynthetic parameter is affected. Explain the differences.

The model computations clearly demonstrate the important contribution of both the reduction in photosynthesis at light saturation and the light use efficiency. The effect on light use efficiency and photosynthesis at light saturation is not additive. In absolute terms, the latter effect is more important, due to the strong effect of beet yellows virus (BYV) on photosynthesis at light saturation. However, a relative equal change in light use efficiency and photosynthesis at light saturation shows that the latter effect is relatively less important. Further analysis of the physiological background of the effects, and their consequences for growth and production of sugar beet, is needed to derive damage relations which can be used in crop protection management.

4.3.5 A detailed study of an assimilation rate reducer, mildew in winter wheat

The effect of mildew in wheat, *Erysiphe graminis*, on respiration and assimilation rates have been quantified (Table 21). Mildew clearly affects the assimilation rate at light saturation (Rabbinge et al., 1985). Even with a diseased crop for which the mildew is hardly visible, ca. 4% of the leaf area being covered, both the assimilation and the transpiration rates at light saturation are considerably reduced – by up to 50%. Light use efficiency and dark respiration are not significantly affected.

Tabel 21. Normalized values of the maximum assimilation rate at light saturation (AMAX, kg CO₂ ha⁻¹ h⁻¹), light use efficiency (EFF, kg CO₂ ha⁻¹ h⁻¹ W⁻¹ m) and dark respiration (RD, kg CO₂ ha⁻¹ h⁻¹). Mildew-diseased plants were grouped in classes of percentage of mildew-diseased leaf area (PMI). (Source: Rabbinge et al., 1985).

n ¹	PMI class	AMAX	SD (±)	EFF	SD (±)	RD	SD (±)
11	control	100.0 ² (45) ³	3.9	100.0 (.27)	0.02	100.0 (1.33)	0.21
11	0.1– 0.5	97.1	4.4	101.5	0.03	94.0	0.20
11	0.5– 1.0	86.5	4.1	100.4	0.03	99.2	0.29
9	1.0– 2.0	83.6	4.9	103.4	0.02	111.3	0.37
9	2.0– 3.0	66.8	4.1	94.0	0.03	109.8	0.25
10	3.0– 6.0	57.5	5.2	88.8	0.04	128.6	0.29
9	6.0–10.0	55.3	4.9	84.7	0.03	123.3	0.23
8	≥10.0	40.1	2.6	86.2	0.03	133.8	0.42

¹ Number of replicates.

² Age effects are eliminated.

³ Measured values for the control are given between brackets.

Exercise 72

Introduce the effect of mildew on photosynthesis at light saturation in the model SUCROS87 for growth of spring wheat. The intensity of the mildew disease expressed in severity is introduced using a forcing function:

$$\text{PMI} = \text{AFGEN}(\text{PMIT}, \text{DVS})$$

$$\text{FUNCTION PMIT} = (0., 0.),(0.79, 0.),(0.8, 0.5),(1.0, 7.5),(1.2, 5.), \dots \\ (1.5, 0.5),(2.5, 0.5)$$

Exercise 72 demonstrates how the consequences of detailed physiological observations can be evaluated under field conditions. The difference between the control (7773 kg grains ha⁻¹) and this visible mildew-diseased simulation amounts to 1182 kg grains ha⁻¹.

Evaluating the effects using a multi-layered crop growth model, demonstrated that even at low infection levels considerable reductions in crop growth rate may occur. It was also shown that this effect is more pronounced under a clear sky than when it is overcast (Table 22). The mildew in these simulations is distributed homogeneously over the leaf layers.

However, a homogeneous distribution of mildew will rarely be met in practice. The infection is more often initially located in the lower-leaf layers, and spreads

Table 22. Simulated daily gross assimilation of a wheat crop under an overcast and under a clear sky (DGAO and DGAC, kg CO₂ ha⁻¹ d⁻¹, respectively), at several crop development stages (DC). The mildew (PMI) was homogeneously distributed in the crop. For comparison, AMAX values (kg CO₂ ha⁻¹ h⁻¹) are presented. (Source: Rabbinge et al., 1985).

PMI	Day 143, DC 35, LAI ¹ = 2			Day 160, DC 50, LAI = 4			Day 173, DC 65, LAI = 4		
	DGAO	DGAC	AMAX	DGAO	DGAC	AMAX	DGAO	DGAC	AMAX
0.0	100 (156.) ²	100 (475.)	100 (45.)	100 (206.)	100 (644.)	100 (44.)	100 (207.)	100 (620.)	100 (39.)
0.5	99.2	96.1	91.5	99.3	96.3	91.3	99.1	95.6	90.3
1.0	98.5	92.9	85.0	98.7	93.2	84.7	98.4	91.9	82.9
2.0	97.3	87.8	75.8	97.7	88.4	75.4	97.0	86.1	72.5
4.0	95.6	81.2	65.2	96.2	82.1	64.5	95.0	78.5	60.3
8.0	93.5	74.3	55.4	94.3	75.4	54.5	92.3	70.4	49.2
16.0	91.4	68.4	48.0	92.5	69.8	47.1	89.5	63.6	40.8

¹ Leaf Area Index, in m² m⁻².

² Normalized values, control = 100. For control plants the values calculated by the model are presented in brackets.

from the bottom to the top of the canopy. This location effect was simulated assuming an overall value of the percentage of mildew-diseased crop as before, but with a mildew concentration in specific leaf layers of the canopy (Table 23). The effect on the gross assimilation rate was most marked when the mildew was either uniformly distributed over the canopy or concentrated in the upper-leaf layers. When the mildew was concentrated in the lower-leaf layers, the reduction was less, and the effect of mildew was substantial only when levels above 4% were reached.

Methods of assessing disease and determining the damage threshold should, therefore, take the location of visible mildew-diseased tissue into consideration. The consequences of this effect of mildew on crop growth and production at various locations and under various conditions, is computed using the extended wheat model of Section 4.4 and described by Daamen & Jorritsma (in prep.). Preliminary results of a study of these effects is given by Rabbinge & Rossing (1988).

Table 23. Location effect of the mildew disease on daily gross assimilation under an overcast sky (DGAO) and under a clear sky (DGAC) for crops with $LAI^1 = 2$ (DC 35) and $LAI = 4$ (DC 50). Starting from the top, leaf layers ($LAI = 1$ per layer) are numbered I to IV. The percentage of mildew covered leaf area (PMI) and AMAX ($kg CO_2 ha^{-1} h^{-1}$) of the diseased layers are represented by PMIL and AMAXL, respectively.

Infected leaf layers	PMI = 4				PMI = 8			
	PMIL	AMAXL ²	DGAO ²	DGAC ²	PMIL	AMAXL ²	DGAO ²	DGAC ²
LAI = 2, DC 35:								
none	0	100	100	100	0	100	100	100
I	8	55	95	82	16	48	93	78
II	8	55	99	92	16	48	98	90
all	4	65	96	81	8	55	93	74
LAI = 4, DC 50:								
none	0	100	100	100	0	100	100	100
I	16	47	95	83	32	42	94	81
I+II	8	55	95	80	16	47	93	75
IV	16	47	100	98	32	42	100	98
IV+III	8	55	100	96	16	47	100	95
IV+III+II	5.3	60	99	91	10.7	51	98	88
all	4	65	96	82	8	55	95	75

¹ Leaf Area Index, in $m^2 m^{-2}$.

² Normalized values; disease-free = 100.

The results of the combination model are compared with field experiments of Daamen (1988). In these experiments, the mildew epidemic was followed and the growth and production of wheat was measured. The experiments were done at the experimental farm 'Vredepeel', situated on loamy sand (which is sensitive to dry conditions), in the south-east of the Netherlands. The grain yields attained in the control measurements were $6500 \text{ kg dry matter ha}^{-1}$, whereas the potential was $9-12 \text{ t ha}^{-1}$. Water shortage caused a low growth rate during part of the growing season. In the simulation, the yields were higher than 6500 kg ha^{-1} but, taking into account the water shortage during the growing season (see also Section 4.2), when a water balance was introduced, simulated and measured values corresponded. The mildew expressed as an integrated value of the percentage of mildew-covered leaf area was also introduced into the model and it is shown that the experimental and simulated relative yields at various mildew-diseased levels of the crop correspond rather well (Figure 66).

The preliminary combination model of the growing crop and the disease has been used to evaluate the consequences of an integrated percentage of mildew

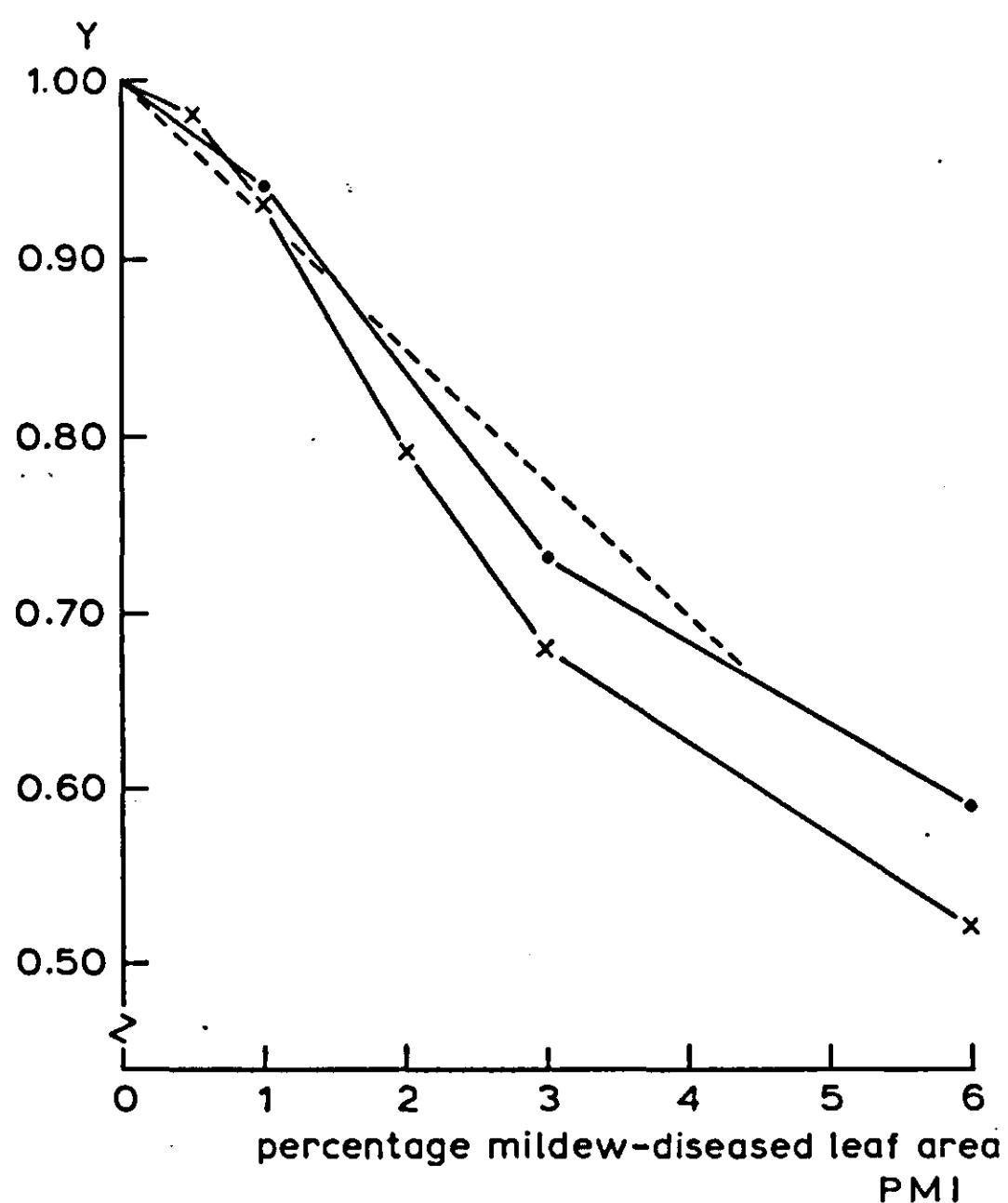


Figure 66. Relative grain yield (Y) at various percentages of mildew-diseased leaf area (PMI), during crop growth from DC 30 until milky ripe. Simulation using SUCROS87 (x), simulation using SUCROS87 combined with a primitive water balance (●) (Section 4.2), and damage function derived from field experiments (----).

severity of 3% during the growing season on crops growing in various production situations, which are dictated by a limited supply of water (Section 1.2). These results (Table 24; Schans, 1984, Internal Report Theoretical Production Ecology) show that yield reduction is proportional to yield, indicating that economic injury levels should be inversely proportional to yield.

A detailed analysis on the physiological background of the considerable effect that mildew has on CO_2 assimilation and transpiration, was done by measuring both rates at various external CO_2 concentrations, at the same time. Assimilation rate at light saturation and transpiration were both affected to the same extent. The assimilation rate/transpiration rate ratio (A/T) was, therefore, not significantly affected by the mildew disease (Table 25). The simultaneous reduction in assimilation and transpiration rates may have been caused by two different mechanisms: one based on a direct effect on carboxylation, and the second based on a direct effect on stomatal behaviour. This is illustrated in Figure 67. Curve A represents the response of assimilation rate (P) to the internal CO_2 concentration (CI). Line B is the CO_2 supply function, describing the diffusion of CO_2 from the atmosphere (with concentration CA) to the intercellular spaces (with concentration CI). The initial slope made by curve A with the abscissa (ε) represents the CO_2 use efficiency; i.e. the inverse of the carboxylation resistance. If there was a direct effect on carboxylation (mechanism 1) then the CO_2 flow from the stomatal cavities to the carboxylation sites would decrease. Because of the feedback loop between internal CO_2 concentration, assimilation rate and stomatal conductivity, the stomata would close (Goudriaan & van Laar, 1978; Farquhar & Sharkey, 1982). Consequently, the gas exchange rates would be reduced. If the second mechanism, a direct effect on stomatal behaviour, was taking place, then the ratio of CI/CA would be affected, although the consequences for photosynthesis might be similar to those of mechanism 1.

The stomatal regulation mechanism was studied by Rabbinge et al. (1985). In this study, the CO_2 response of assimilation rate was measured and the carboxylation resistance calculated from the relation between internal CO_2 concentration (CI) and net assimilation rate at an irradiance of 320 W m^{-2} . In Table 26, the CI/CA ratio is given for mildew-diseased and control plants, with an irradiance of 320 W m^{-2} . Mildew had no significant effect on the ratio so that stomatal resistance was not directly affected, although the presence of mechanism 2 may have been masked by the strong effects of mechanism 1. Nevertheless, it can be concluded that mildew does not influence the stomatal regulation mechanism. As a result, the water use efficiency, expressed as the assimilation/transpiration ratio, is rarely influenced by mildew. Whatever the exact nature of this effect may be, it was necessary to quantify both the effect and its consequences. Further analysis of how mildew affects crop behaviour can be done using a detailed model of assimilation and transpiration (BACROS, de Wit et al., 1978) as illustrated by Rabbinge (1982) for a different disease, stripe rust *Puccinia striiformis* in winter wheat.

Table 24. Simulated yield loss due to a mildew load on winter wheat of 3% leaf coverage (PMI = 3) during the growing season starting at DC 30, at various expected yields in kg grains ha^{-1} . (Source: Schans, 1984. Internal Report, Department of Theoretical Production Ecology).

Yield expected (kg ha^{-1})	Yield loss (kg ha^{-1})
6000	1800
8000	2400
10000	3000

Table 25. The ratio of assimilation (A) and transpiration rates (T) at an irradiance of 320 W m^{-2} and an ambient CO_2 concentration of 340 ppm for control and mildew-diseased plants at DC 50. (Source: Rabbinge et al., 1985).

n ¹	PMI class	A/T	SD \pm
23	control	10.6	0.95
11	0.1– 0.5	10.4	1.07
11	0.5– 1.0	9.3	0.67
9	1.0– 2.0	9.2	0.65
9	2.0– 3.0	9.4	0.80
10	3.0– 6.0	9.3	0.81
9	6.0–10.0	9.6	0.74
8	≥ 10.0	8.9	0.53

¹ Number of replicates.

4.3.6 Discussion

The combination models described above show how simulation at each stage of research, can help to provide insight into the quantitative interpretation of changes caused by the presence of pests or diseases in various plant physiological processes. This insight may help to derive damage relations which could be used in practice (Section 4.4). The comprehensive models integrate knowledge and ideas from the various disciplines but thorough testing of the models is still essential.

Thus, experiments still need to be done which will help to define input relations and which will test the simulation results. The explaining level of the disciplines delivers the input relations which are determined under well-defined conditions, and the explanatory level of the field situation produces the data needed for

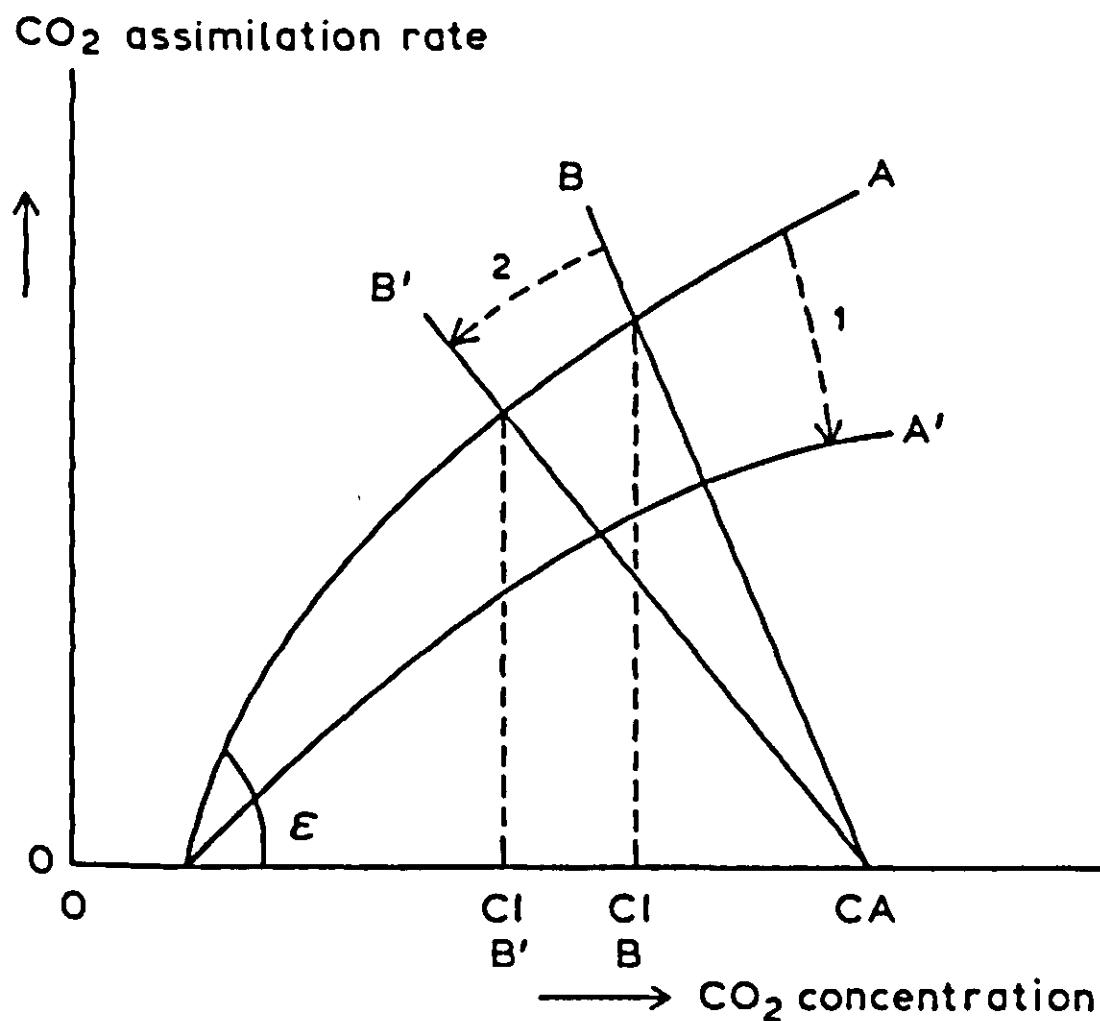


Figure 67. CO_2 assimilation rate at various internal CO_2 concentrations (CI, curve A); and the CO_2 supply function at various internal CO_2 concentrations (line B). Effects of mildew are indicated for two hypothetical mechanisms: (1) Reduced efficiency in CO_2 absorption (ε): curve A is transformed into curve A'. (2) Increased stomatal resistance: line B is transformed into line B'.

Table 26. The ratio (CI/CA) of the internal CO_2 concentration (CI) to the ambient CO_2 concentration (CA), for control and mildew-diseased plants at development stages DC 32 and DC 55. (Source: Rabbinge et al., 1985).

Plants	n ¹	$\text{CA} = 340 \text{ mg m}^{-3}$		$\text{CA} = 600 \text{ mg m}^{-3}$		$\text{CA} = 1000 \text{ mg m}^{-3}$	
		CI/CA	SD	CI/CA	SD	CI/CA	SD
DC 32: control	2	0.77	0.007	0.77	0.007	0.79	0.028
mildew-diseased	6	0.73	0.049	0.74	0.023	0.78	0.033
DC 55: control	2	0.74	0.014	0.73	0.021	0.71	0.049
mildew-diseased	5	0.73	0.021	0.72	0.029	0.70	0.016

¹ Number of replicates.

testing the models (Rabbinge, 1986). This heuristic way of working is very important, both to biology itself and in its agricultural application.