10 The bridge function of production ecology in pest and disease management

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10.1 Introduction

There are several ways which pests or diseases affect physiological processes in plants and cause yield loss and damage. They may for example, reduce crop stands by elimination of plants, reduce inputs such as light, carbon dioxide and water, interfere with transportation of assimilates or nutrients and remove or consume previously produced structural material. These effects can be quantified in the laboratory under well defined conditions. The quantified relations at process level may be integrated in simulation models that are used to provide insight in yield loss at the field level. Eventually, these simulation models enable quantification of growth and yield reduction under various circumstances. This may help to define damage thresholds that depend on yield expectation and change in time. This chapter shows how such a process may take place.

10.2 Factors that define, limit and reduce crop growth

Crop growth, the accumulation of dry matter and its distribution among various crop organs, is determined by irradiation, temperature and the physiological, phenological, optical and geometrical characteristics of the crop, provided that water and nutrients are abundantly available and pests, diseases, weeds and any other factors that reduce crop growth are absent. Under these conditions, the growth of the crop is entirely governed by these characteristics and by the prevailing weather (mainly incoming radiation and temperature). Such a situation is, however, rare since the great majority of agricultural crops (> 99%) suffers from water and/or nutrient shortage and by pests, diseases and weeds.

The distinction in crop growth situations proposed by de Wit & Penning de Vries (1982) may be helpful to illustrate this. When water and nutrients are abundantly available, crop growth is fully determined by factors that define crop growth and by the prevailing weather. According to the calculations de Wit presented more than 20 years ago, crop growth may reach values between 150–350 kg dry matter per ha per day under Dutch conditions. The rule of thumb of 200 kg ha^{-1} day^{-1} is the simplest and in very many cases most adequate model of crop growth.

When water is limiting or nutrients are not abundantly available, other production situations are reached. Table 12 gives the four Production Situations, together with some characteristic yield levels. For computation of these values, a typical transpiration coefficient of 300 kg transpired water per kg dry matter

Table 12. The four Production Situations proposed by de Wit & Penning de Vries (1982).

Production Situation	Limiting factor	Growth rate × period	Total dry matter production in a growing season, under Dutch conditions (kg ha^{-1})
1	radiation (growth rate), temperature (length of growing period)	200 kg ha^{-1}d^{-1} × 100 d = 20000	
2	water, e.g. 300 mm available; transpiration coefficient 300 kg H$_2$O per kg dry matter	ca. 200 kg ha^{-1}d^{-1} × 50 d = 10000	
3	nitrogen, e.g. 50 kg N ha^{-1} available; lower limit 1 % N in total dry matter		5000
4	phosphorus, e.g. 1.5 kg P ha^{-1} available; lower limit 0.05 % P in total dry matter		3000

produced was used, in combination with minimum concentrations of nitrogen and phosphorus of 1 % and 0.05% on dry weight basis. The situations indicated in Table 12 seldom occur in this schematic form. Water may be so limiting that total dry matter production is lower than in Production Situation 4, so the indicated situations are merely guidelines. In practice many other sets of conditions may be encountered.

Crop growth is usually limited by various factors during part or all the growing season. On top of that, growth-reducing factors may be present. The consequences of pests and diseases may differ considerably in various Production Situations. For example, cereal aphids cause a yield loss of circa 300 kg grain ha^{-1} when yields are circa 5000 kg grain ha^{-1} and aphid density is 15 aphids tiller^{-1} at flowering, whereas the same aphid density results in a yield loss of circa 1000 kg grain ha^{-1} at a yield of 8000 kg grain ha^{-1}. The explanation for this phenomenon is given below. Other diseases do not cause such a superproportional effect but have a proportional or even subproportional effect on yield loss with increasing yield (Rabbinge, 1986).

In order to explain this, growth reduction and yield loss must be analysed in detail.

10.3 Crop condition and pests and diseases

Many studies in crop protection consider the effect of crop condition on various components of the population dynamics or dispersion of pests and diseases, but ignore yield losses.

Crop condition, often expressed in nitrogen content, affects various epidemiological parameters; for example, the latency period, infectious period and intrinsic rate of increase (number of daughter lesions per mother lesion per day) of powdery mildew on wheat. As a result, the upsurge of an epidemic may be accelerated in well fertilized wheat fields, whereas at low nitrogen contents, which usually result in very low yields, the disease hardly develops.

In many pests similar reactions to growth circumstances are found, e.g. yellow rust (stripe rust), leaf rust, cereal aphids in wheat, and spider mite, apple scab and mildew in apple. The presence of such a reaction to crop condition should be taken into account in decision-support systems for crop protection. For example, epidemiological parameters dependent on crop conditions were introduced in the EPIPRE system which was developed and implemented in cereal production in the Netherlands and other European countries in the 1980s. Thus the model calculations on population dynamics in EPIPRE are tailored to the specific characteristics of the individual field as expressed in expected yield.

The dispersion of pathogens may vary, depending on crop condition. A crop that is dense because water and nutrients are readily available has a geometrical structure that prevents an intensive diffusion of spores. Studies have been done to quantify the consequences of crop condition on pest and disease development. Their results are rarely used in pest and disease management. However, our quantitative understanding of these aspects of pest and disease development is very limited at present.

10.4 Yield loss and yield levels

Factors that reduce crop growth have always played a role in agriculture, but the way they are approached has changed considerably in the last 20 years. Technological advances have produced various preventive and curative measures to eliminate the effects of factors that reduce crop growth. The concept of economic injury level was introduced in the late 1950s. Until then, pest and disease control was carried out whenever symptoms were present or when farmers intuitively decided that it was necessary. Preventive control by breeding and by agronomical hygiene was promoted and generally accepted.

The emphasis on preventive measures was continued and in addition other control measures were developed, using fixed economic injury levels. These economic injury levels presume fixed relations between density of the pathogen and yield loss or damage. It is assumed that the production situation does not affect the level of damage, in other words that there is a fixed proportional relation between yield and damage (fixed percentage damage).

Whereas this assumption may hold for many leaf pathogens that affect crop growth only through reduction of leaf area it may be too simple when other processes are affected. The fact that damage caused by cereal aphids increases disproportionately with yield may illustrate this. Therefore, when in the early 1980s appropriate agronomical measures enabled yields (especially in well-endowed regions) to approach potential levels, it was necessary to introduce flexible economic injury levels for pests and diseases taking into account crop growth rate and yield level. It was possible to develop these flexible economic injury levels as more knowledge and understanding of the nature of crop growth reduction and damage became available. Thus, no fixed relations between disease/pest intensity and yield loss need to be used in pest and disease management. Pest and disease management can now be tailored to the specific circumstances of individual fields and can vary in time. Thus, pesticide use can be limited and efficiency of inputs per unit of output can increase considerably. Such an objective is attractive both from an agricultural point of view and for environmental reasons.

10.5 Effects of pests and diseases on crop growth

Various pests or diseases may affect different basic processes that govern growth, as illustrated in Table 13 (an amended version of the diagram presented by Boote et al., 1983). They may, for example, reduce crop stands by elimination of plants, reduce inputs such as light, carbon dioxide and water, interfere with transportation of assimilates or nutrients and remove or consume previously produced material. Different crop growth components may be affected. The rate of biomass increase is affected by tissue consumers such as lepidopteran larvae or leaf beetles. Assimilation rate may be affected via a reduction of leaf area or light absorption or via effects on water and nutrient relations.

Leaf consumption and leaf senescence caused by leaf miners, spider mites, aphids, leaf pathogens or air pollutants affect leaf area and thus the assimilation rate. Weeds, other competing plants, perthotrophic and saprophytic fungi steal light and thereby affect absorbed light, thus reducing the assimilation rate. Aphids, root-feeding coleopterans and various bacteria affect the turgor of plants, by reducing the availability of water, hence causing stomatal closure and a decrease in assimilation rate.

Many aphids and other phloem sap feeders affect the ratio of various elements such as N, P and K. This influences assimilation rate because the functioning of chloroplasts or various steps in the photosynthesis process are affected.

The growth rate per organ may be affected by changes in partitioning coefficients caused by disrupted functional balances in the plant as a result of infestation by nematodes. The conversion of assimilates into structural crop components may be affected by selective consumption of assimilates, for example by aphids. Finally, the leaf area index may be affected by influences on the specific leaf area because the presence of viruses or other leaf pathogens induces suberization or extra parenchymal cell layers.

Table 13. The effects of pests and diseases on crop growth.

Crop growth component	Damage mechanism	Agent of damage
a. rate of biomass increase	tissue consumption	lepidopteran larvae, leaf beetles.
b. assimilation rate: effects via		
• leaf area	leaf consumption, senescence promotion	leaf miners, spider mites; aphids, many leaf pathogens, air pollutants;
• incident light	light stealing	weeds, competitors, perthotrophic and saprophytic fungi;
• water	turgor reduction	aphids, root-feeding coleopterans, bacteria;
• N/P/K	phloem sap uptake	aphids.
c. growth rate per organ:		
• assimilate partitioning	functional balance disruption	nematodes;
• assimilate conversion	assimilate consumption	aphids.
d. leaf area index	reduction of specific leaf area	viruses, various leaf pathogens.

Table 13 is not comprehensive, it merely illustrates how damage mechanisms induced by various pests and diseases affect different crop growth components. The consequences for crop growth may differ considerably, depending on the stage of crop development during which the disease is present, or on the conditions for crop growth, which are dictated by the factors that define and limit crop growth. The examples discussed below will illustrate this.

10.6 Beet yellows virus

Beet yellows virus was a major leaf disease in the 1950s in virtually all sugar beet growing areas. Since then the disease has declined in importance because of improved plant hygiene and agronomical measures and the reduced importance of fodder beet. Virus yellows can be caused by two different viruses: beet yellows virus (BYV), which belongs to the closterovirus group, and beet mild yellowing virus (BMYV), which belongs to the luteovirus group. The epidemiology of the disease has been studied since the early 1950s. Recently, van der Werf (1988)

showed that the rate of within-field spread of these viruses depends on crop growth stage at time of infection and environmental conditions. The complement to this epidemiological research is research on the relations between damage and crop growth and environmental conditions (van der Werf et al., in prep.).

BYV reduces crop growth through four components:

- reduced leaf area index
- reduced light absorption
- reduced photosynthesis (both light use efficiency and photosynthesis at light saturation are affected)
- increased respiration.

In Figure 61 it is shown how the leaf area index of an early infected sugar beet crop (5 June) is strongly reduced whereas the leaf area index of a late infected sugar beet crop (14 July) is scarcely affected. Leaf area index is reduced by virus infection because specific leaf weight increases as a result of the accumulation of sugars and starch and of changes in the morphological structure of the leaves. The later the infection the smaller the effect as leaves which have appeared before the plant contracts infection are not invaded by the virus via the phloem pathway.

The leaves of the sugar beet already show a slight change in light absorption at relatively low infection levels and before clear symptoms are visible. Both reflection and transmission of radiation are affected. More light is reflected and
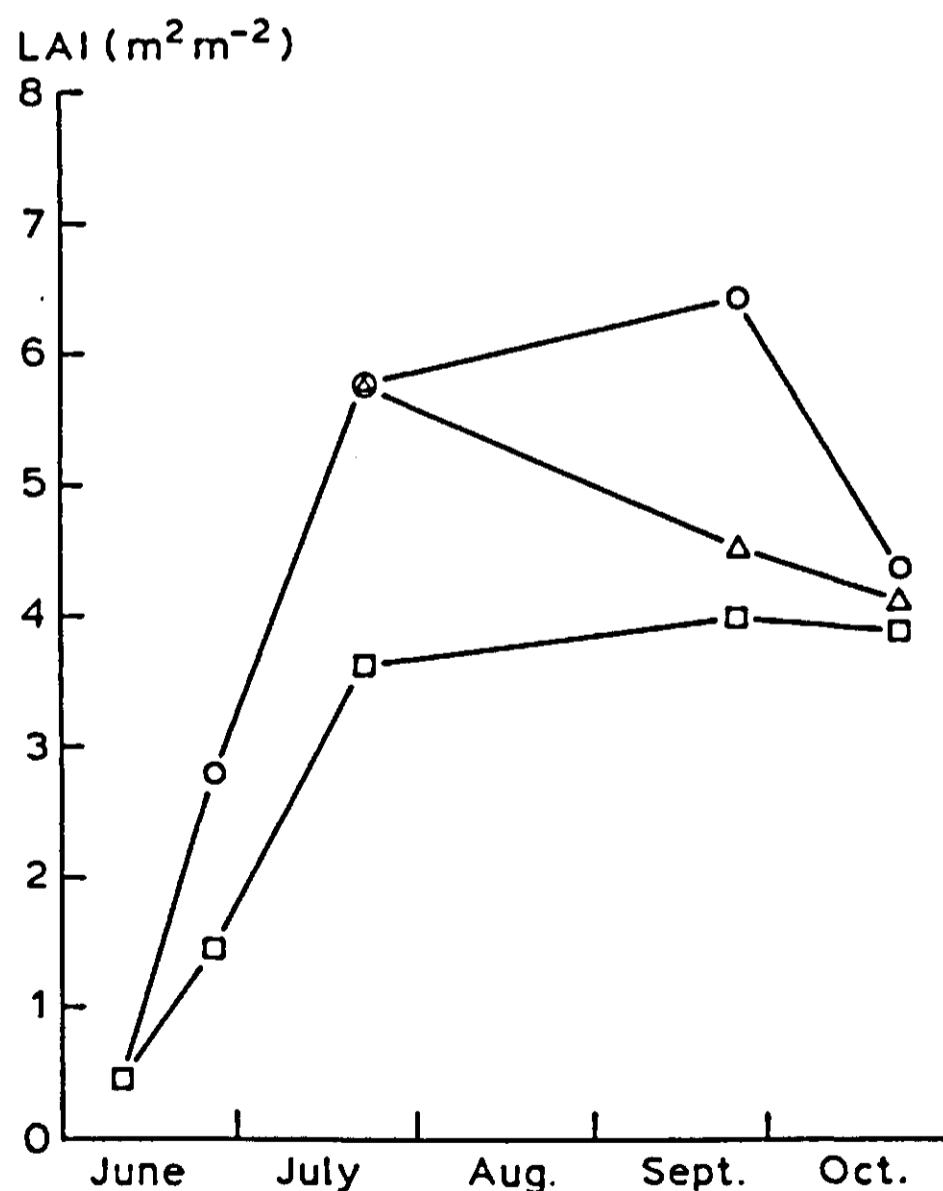
Figure 61. Leaf area index of healthy sugar beet (o) and beet infected with BYV on 5 June (□) or 14 July (△). Ten representative plants were examined on 11 and 27 June and 23 July, five on 18 September and seven on 24 October, respectively.
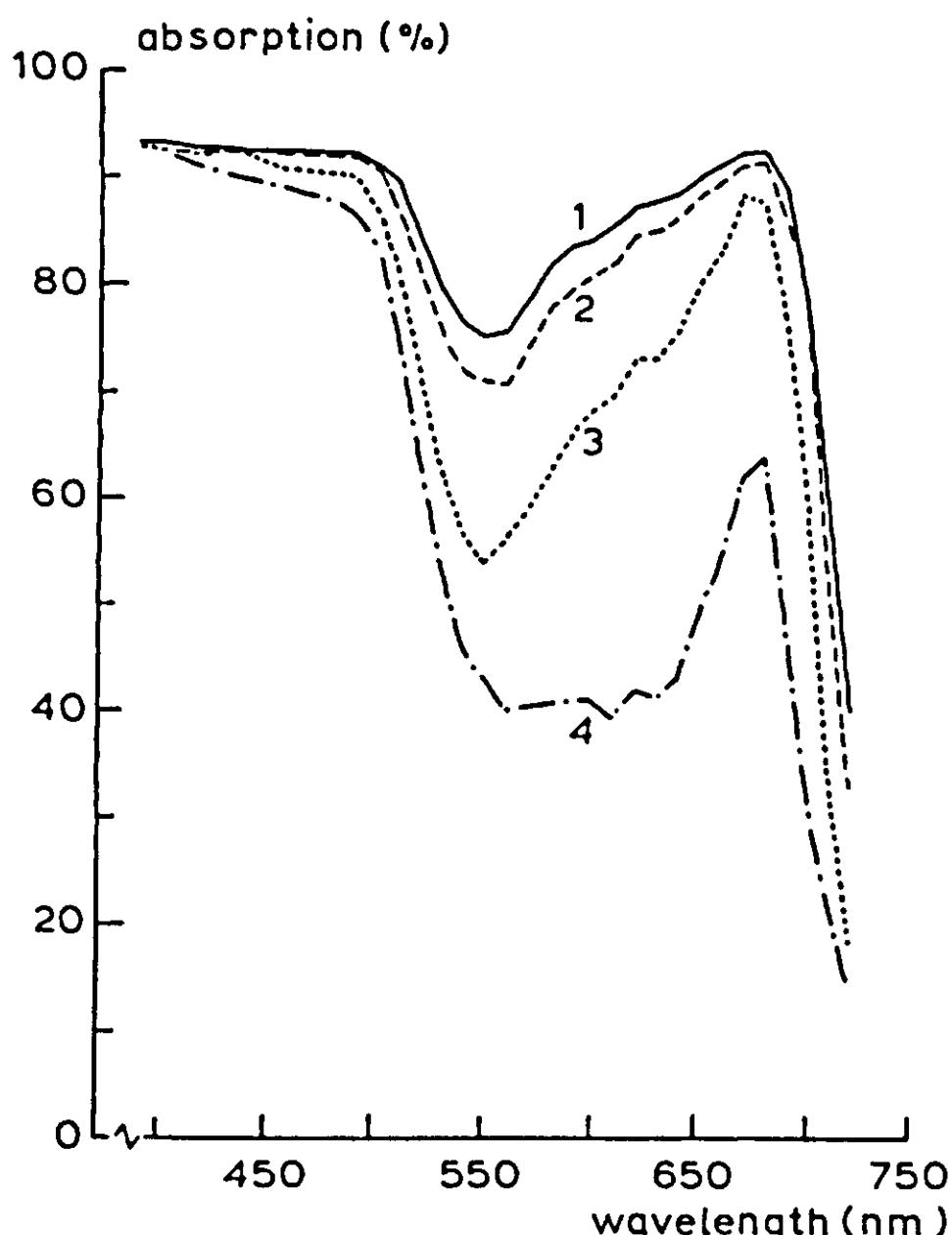
Figure 62. Absorption spectra of healthy (1) and BYV-infected green (2), greenish yellow (3) or bright yellow (4) beet leaves.

more light is transmitted, and as a result much less photosynthetically active radiation is absorbed (Figure 62). When symptoms are clear, as in infected bright yellow leaves, the effect is considerable.

The third component of crop growth reduction concerns a physiological change in the leaves. Photosynthesis initial light use efficiency and photosynthesis at light saturation are affected (Figure 63).

Light use efficiency is affected by the reduced light absorption indirectly, but also directly, probably through an effect on the photochemical process in the CO_2 assimilation.

Photosynthesis at light saturation is probably affected via the carboxylation process. Again there is a very clear effect in bright yellow leaves and the effect is already considerable when only vein clearing is present. These effects, measured under field conditions by van der Werf (1988) confirm earlier observations by Hall & Loomis (1972a, b).

The effect of virus beet yellows on leaf respiration is also shown in Figure 63.

We incorporated the various components of damage measured at leaf level in a crop growth model to study the consequences at crop level. An amended version of the basic summary model of crop growth SUCROS87 was used (van der Werf, 1988; Spitters et al., 1989).

Each component was introduced on the basis of the relations described above.

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net CO_2 assimilation ($mg\ m^{-2} s^{-1}$)

absorbed PAR ($J\ m^{-2}\ s^{-1}$)
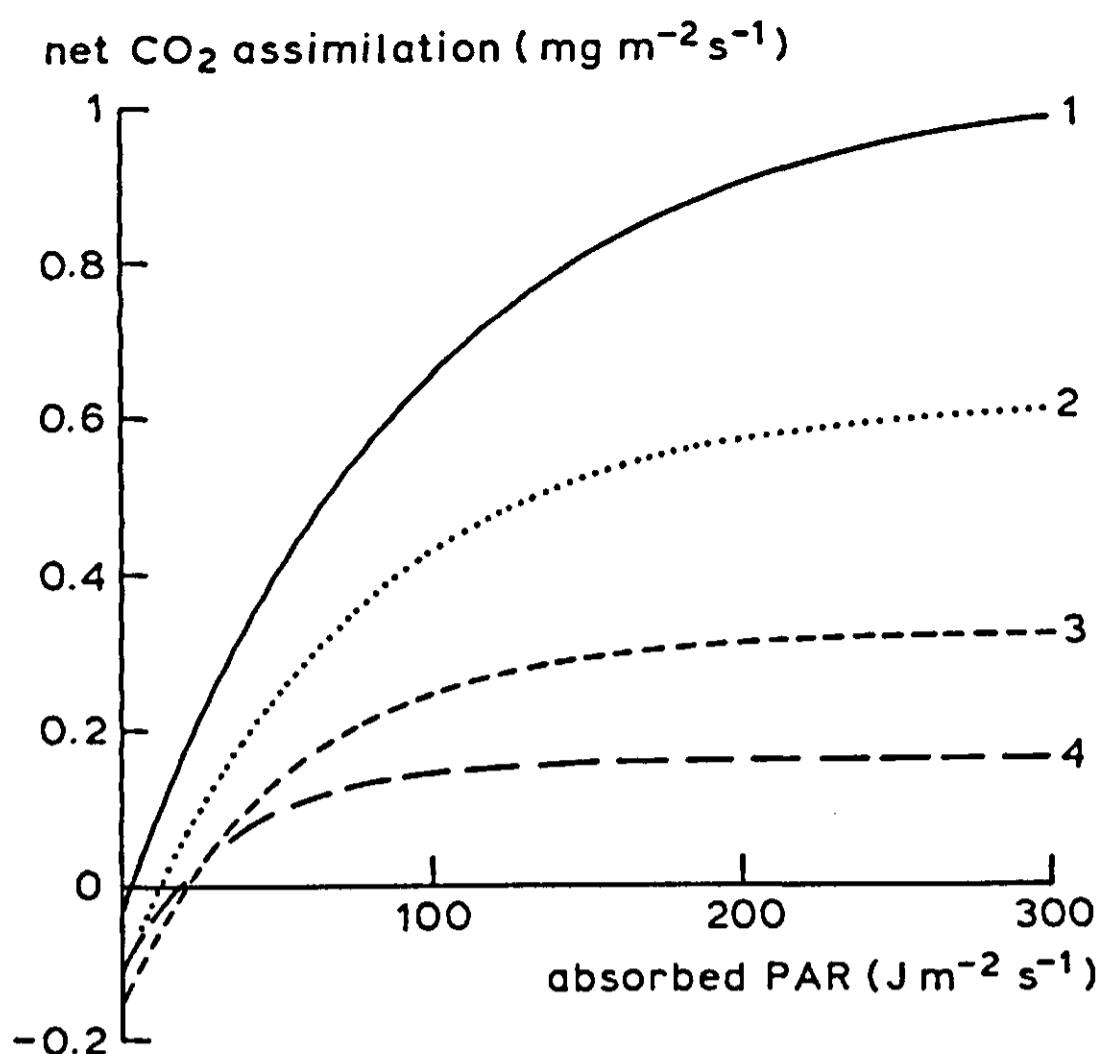
Figure 63. Characteristic photosynthesis–light response curves of healthy and BYV-infected beet leaves, fitted to experimental data. Numbers 1–4 represent healthy leaves, and infected leaves with vein-clearing, greenish yellow and bright yellow symptoms, respectively.

The course of the green and yellow leaf area index was introduced in the model through a forcing function derived from field observations. The outcome of the crop growth model was compared with the results of periodic crop growth analysis. Figure 64 shows the results of simulation runs using the environmental conditions as inputs, for two treatments and a disease-free control. Control and treatments are simulated satisfactorily. The various components of crop growth reduction measured at leaf level seem to be sufficient to explain the behaviour of an infected crop under field conditions. Results of the simulation model were then compared with yield loss, expressed as sugar yield, in various field experiments (Figure 65).

The simulated curve corresponds more or less with data from various field experiments. The absence of field-specific *LAI* data as forcing functions may partly explain the differences between measured and simulated data. It is very clear that infection date is most decisive for the explanation of yield reduction. The simulation model predicts that the relation between yield loss and infection date depends on the leaf area development of the crop. For a given infection date, early sown crops incur smaller yield loss than late crops.

Thus it is pointless to attempt to achieve late control of virus by spraying against aphids late in the season. Only an early control may prevent substantial damage. Tolerable densities of aphids in the course of time should also be ascertained by analysing the population dynamics and dispersal of aphids.

The simulation model was run several times for two infection dates, to evaluate
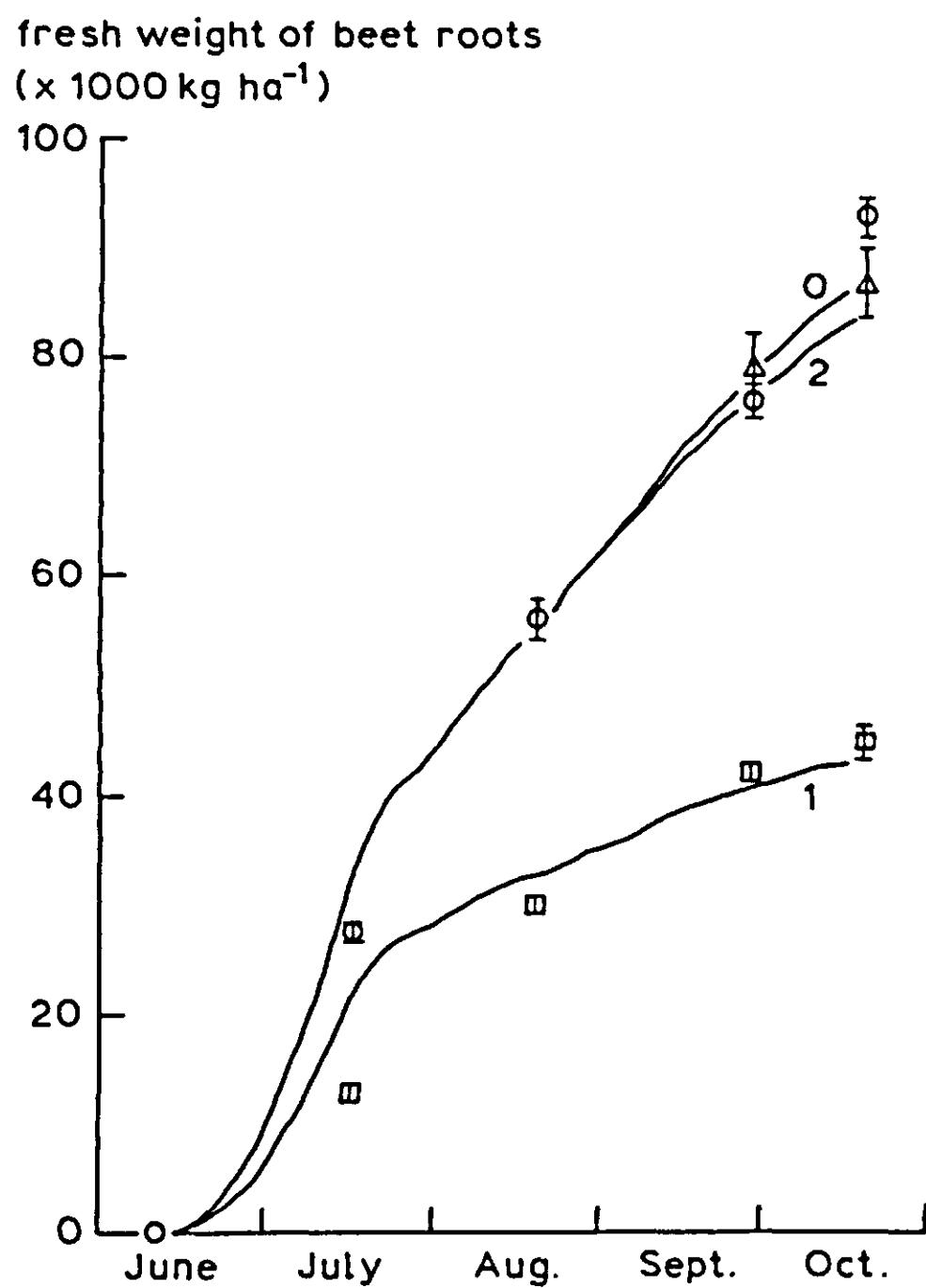
Figure 64. Experimental (symbols) and simulated (solid lines) growth patterns of sugar beet infected with BYV on 5 June (□ = line 1) or 14 July (△ = line 2), compared with that of healthy plants (o = line 0).
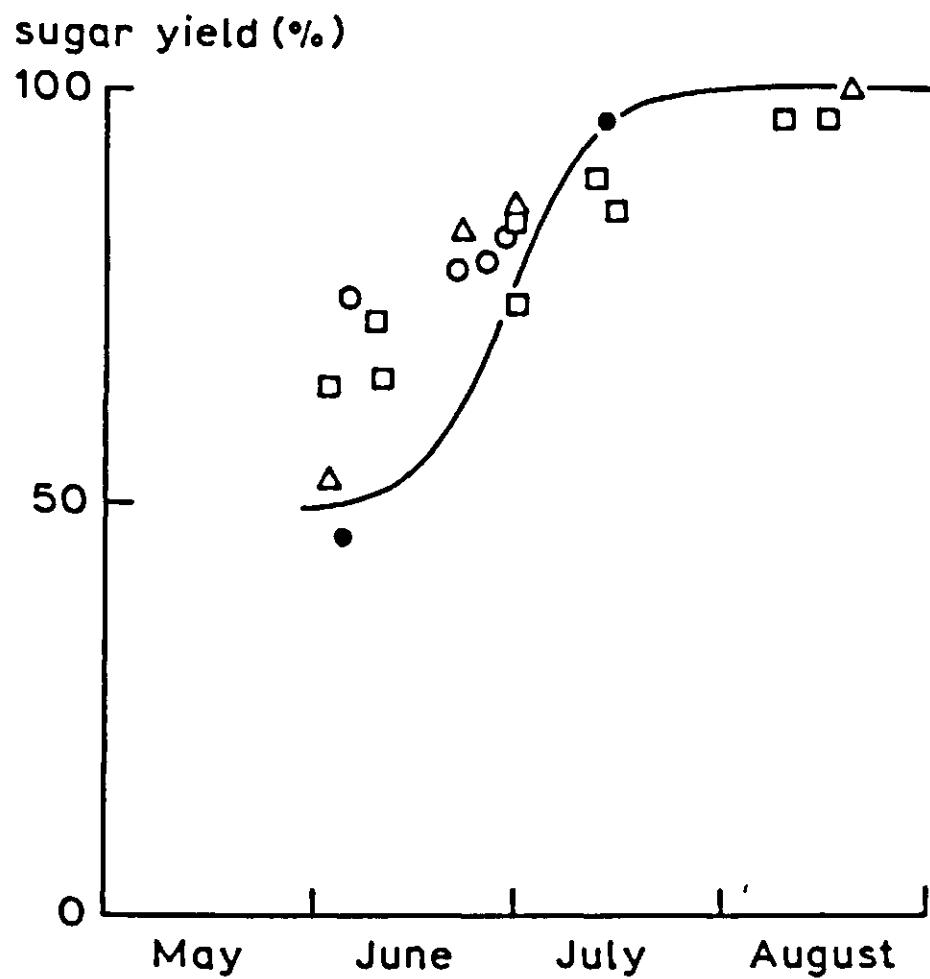
Figure 65. Simulated sugar yield (as % of control) as a function of infection date (———) in comparison with field experiments done by various authors: (□) Heijbroek, 1988; (△) Smith, 1986; (o) Russell, 1963; (●) van der Werf, 1988.

Table 14. Simulated contribution to total yield loss of four components of damage by BYV, inoculated in two stages of crop growth (ε is the initial light use efficiency, A_m is the photosynthesis at light saturation).

Damage component	Early infection*		Late infection**	
	% yield	added % loss	% yield	added % loss
no disease	100		100	
		7.1		1.5
1 (reduced leaf area index)	92.9		98.5	
		5.2		1.5
1 + 2 (reduced light absorption)	88.0		98.2	
		36.4		1.7
1 + 2 + 3 (reduced photosynthesis, ε and A_m)	56.0		96.6	
		11.7		0.5
1 + 2 + 3 + 4 (increased respiration)	49.4		96.1	
measured	48.2 ± 2.5		93.4 ± 5.1	

* Early infection: 5 June, 7 leaves, LAI = 0.1; ** Late infection: 17 June, 21 leaves, LAI = 5.1

, the various damage components (Table 14). This demonstrated that most of the yield reduction can be attributed.to the effect of the virus on light use efficiency and photosynthesis at light saturation. The other components have much less impact. There is no clear difference in relative importance of the damage components between infection dates.

The relative effect of beet yellows virus changes considerably in the course of time and this is apparently the result of a decrease in all damage mechanisms.

10.7   Cereal aphids in winter wheat

Another well studied example of yield reduction concerns cereal aphids. Since the early 1970s cereal aphids have increased considerably in economic importance and are now a yearly target of chemical control in many Western European countries. Their increase in pest status is most probably related to the increase in wheat yields. In a simulation study the effects of *Sitobion avenae*, the most abundant species in the Netherlands, were studied. To do this the various effects of the aphids were incorporated in a crop growth simulator (Rossing & van de Wiel, 1990; Rossing, 1990a, b), so that the effects observed by various authors (Wratten, 1978; Vereijken, 1979; Rabbinge & Mantel, 1981; Watt et al., 1984;

Entwistle & Dixon, 1987) could be reduced to a common denominator.

Winter wheat is affected directly or indirectly by the presence of cereal aphids. Direct effects result from the aphids' uptake of carbohydrates and amino-nitrogen by feeding, and the active substances they inject via their saliva. Active substances have not been observed in the saliva of summer populations of cereal aphids and are not considered here. Indirect effects are produced by virus transmission, honeydew excretion and changes in the phyllosphere microflora which may influence crop physiology. In this study only the effects of honeydew excretion onto leaf surfaces were considered. Both the direct and indirect effects of cereal aphids have been quantified in detailed studies. Rates of phloem sap uptake have been measured in energy budget studies (Vereijken, 1979; Rabbinge & Coster, 1984). The indirect effects studied are the effects of honeydew on photosynthesis of leaves of wheat. Rabbinge et al. (1981) observed that both the maximum rate of photosynthesis and light use efficiency fell immediately after the application of honeydew to wheat leaves. Rossing & van de Wiel (1990) found no significant effects after one day, but after 15 days they measured both a reduction of photosynthesis at light saturation and an increase in respiration. The processes resulting in what appears to be accelerated senescence remain to be identified.

In a modelling approach by Rossing (1990a), S. avenae is assumed to share the phloem sap supply with the grains. The aphids may be the first to obtain their share because of their feeding site, thus outcompeting the grains. Alternatively, the aphids and the grains share the supply with the grains in proportion to their respective demands. On the supply side the rate of phloem sap transport may or may not be increased because less phloem sap reaches the grains. An increase will result in enhanced depletion of reserves of assimilates and nitrogen in the leaves and thus accelerated senescence. Rossing (1990a) formulated four hypotheses concerning the partitioning of phloem sap between aphids and grains. Two of these will be discussed here:
–Hypothesis I
Aphid–grain competition: the phloem sap supply is partitioned in proportion to the respective demands of aphids and grains. There is demand-supply feedback, i.e. the total demand equals the sum of demands of grains and aphids.
–Hypothesis II
Aphid dominance: the phloem sap supply is first utilized by the aphids. There is no demand-supply feedback, i.e. the total demand equals the demand of grains.

Direct and indirect effects were introduced in a version of the SUCROS87 crop growth simulator modified to account for the nitrogen balance in the crop. The results of the model were compared with data collected in a field experiment. Aphid density in course of time was introduced in the model as measured in the field. Simulation runs were done for the two hypotheses mentioned above.

The aphid population reached a peak density of approximately 45 tiller^{-1} (Figure 66). The control was not completely free of aphids and a peak density of
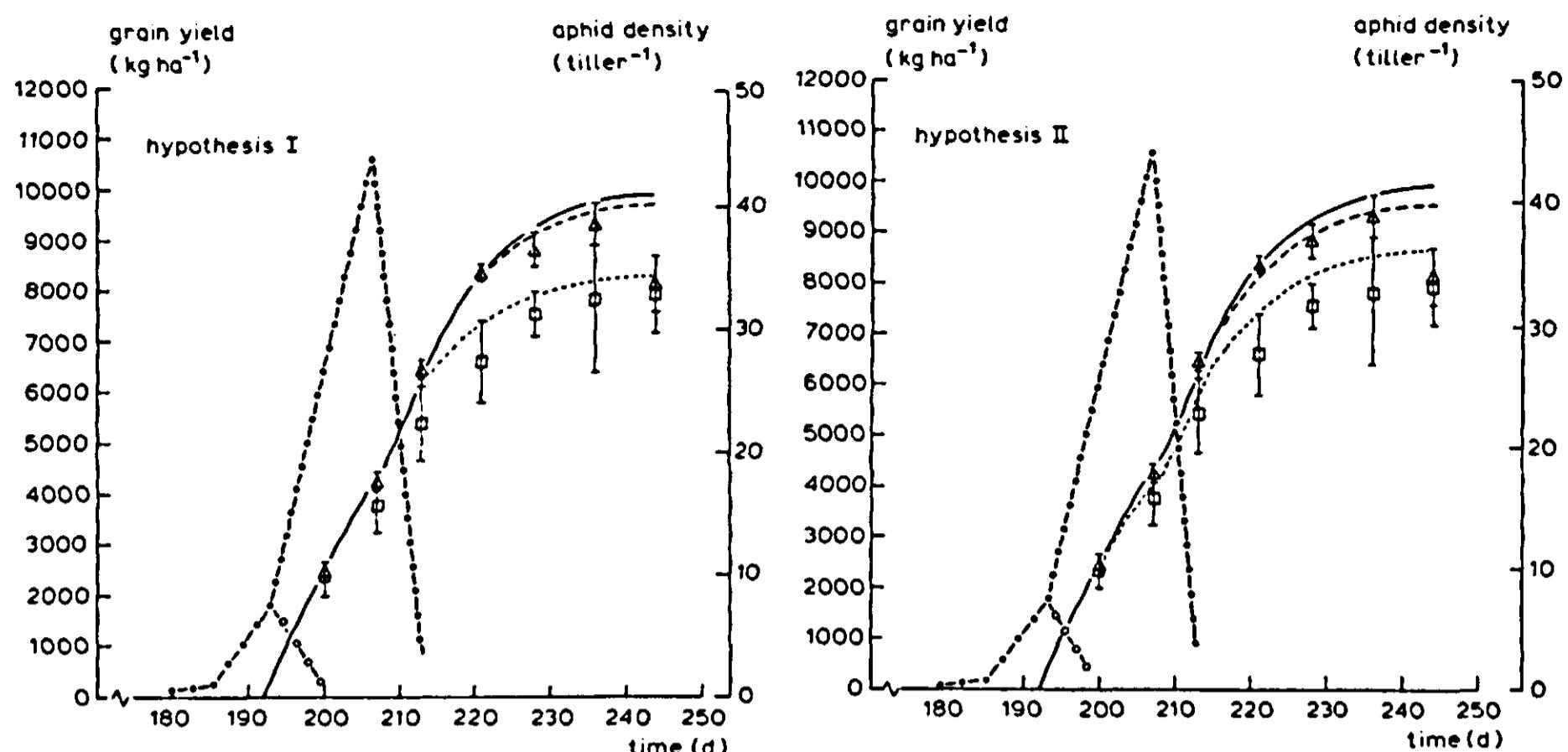
Figure 66. Actual and simulated grain yield of data set EEST84 at two aphid infestations using two hypotheses (I and II) on direct damage by *S. avenae*. Vertical bars represent standard errors of the mean. Grain yield without aphids (simulated: ———), aphid infestation as in control treatment (simulated: – – –; measured: △) and high aphid infestation (simulated: ···; measured: ☐). The size of the aphid infestations is shown for the control (-o-o-) and the high infestation (-●-●-).

about 5 aphids tiller^{-1} was reached. In the control, simulated and observed grain yield agree well during the first part of grain filling. Later, the model overestimates yield, because leaf senescence is underestimated. In the aphid treatment the two hypotheses result in a different time course of damage, but no major difference in final damage. In the model based on Hypothesis I damage occurs only when grain filling is source-limited. In the field experiment, however reduction of yield was measurable from the onset of grain filling when grain-growth is sink-limited. This pattern is reproduced correctly by Hypothesis II. However, the latter hypothesis does not account for the observed depletion of reserve carbohydrates nor the accelerated leaf senescence, as Rossing (1990a) showed in a detailed analysis. These phenomena are accounted for by Hypothesis I.

The contribution of various damage components to total damage is shown in Figure 67. As mentioned above, the time course of damage is different for the two hypotheses. Moreover, with Hypothesis I damage resulting from uptake of nitrogen in the phloem sap continues to increase after the aphids have left the crop (Day 221). Aphids accelerate depletion of the nitrogen pool and thus leaf senescence. For the conditions used in the simulation, direct effects account for approximately 50 % of the total damage.

The model was used to evaluate the damage caused by an aphid population under various crop growth conditions (Rossing, 1990b). For this purpose the model was initialized with crop data from a number of field experiments in which nitrogen input was varied. Temperature and radiation data were 33-year averages

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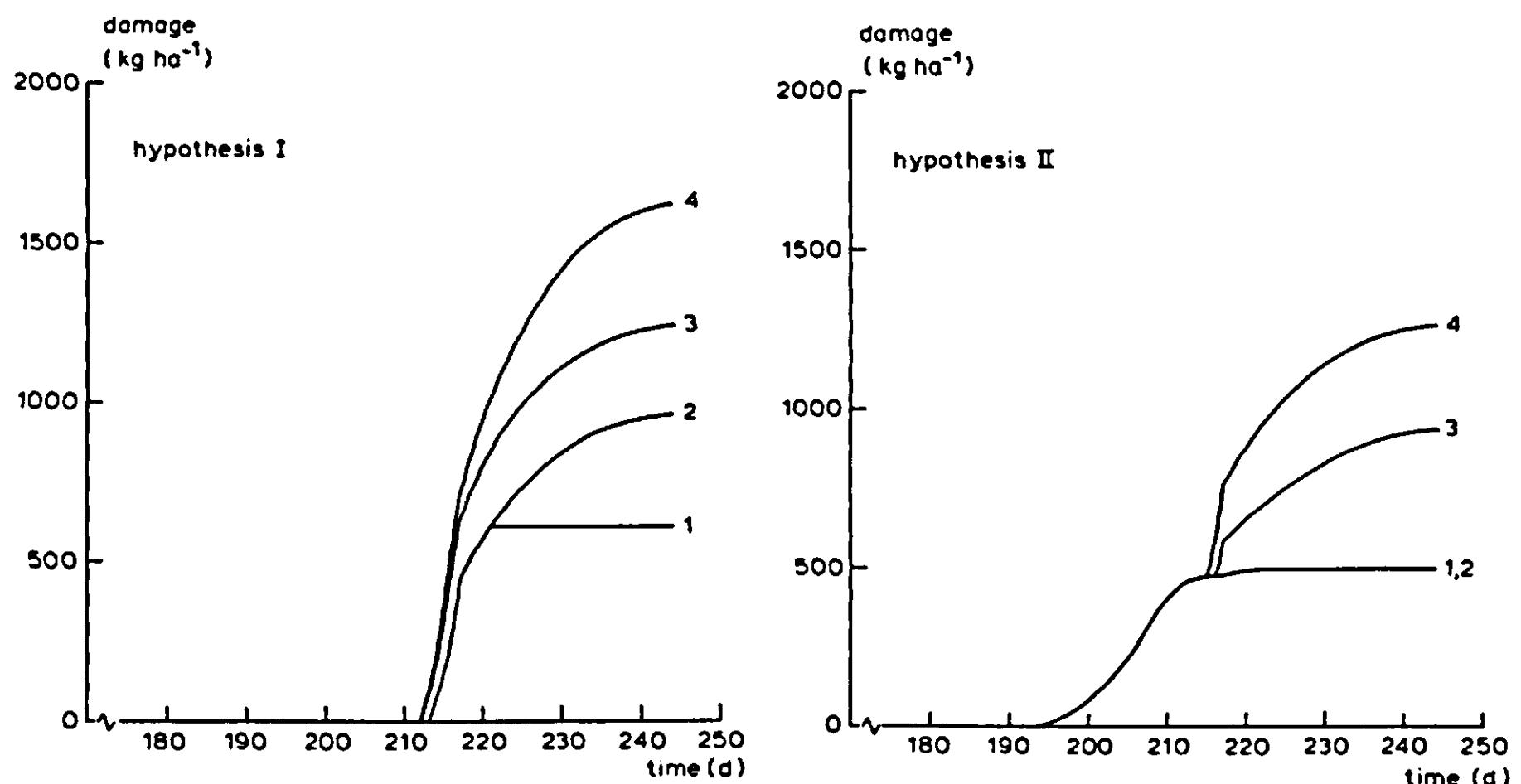
Figure 67. Simulated total damage (grain yield reduction, kg ha^{-1}) and damage components using two alternative hypotheses on the direct effects of *Sitobion avenae*. Data from EEST84, the high aphid infestation. 1: carbohydrate uptake. 2: carbohydrate and nitrogen uptake. 3: carbohydrate and nitrogen uptake + increased maintenance respiration. 4: carbohydrate and nitrogen uptake + increased maintenance respiration + decreased photosynthesis at light saturation.

for Wageningen, the Netherlands. An exponentially growing aphid population was introduced, with a peak density of 17 aphids tiller^{-1} at development stage DC 77 (Decimal Code, Zadoks et al., 1974). In Figure 68, the results of runs with the crop model and the damage model are combined in three graphs representing three development periods after flowering. The results show that at low and moderate yields aphid damage increases approximately linearly with yield of the control. At high yields damage exceeds the linear trend. High yields are attained only when green leaf area duration is large, resulting in more damage by honeydew. Later during the development of the crop the effects of honeydew are dominated by the direct effects, because honeydew effects take some time to develop.

10.8 Concluding remarks

The examples discussed above demonstrate how crop growth models may be used to bridge the gap between detailed laboratory experiments and the interpretation of field data. Thus, simulation studies help to elucidate the quantitative meaning of various components of crop growth reduction. This insight is used in further simulation experiments to derive economic injury levels that are flexible, dynamic and specific and depend on the production situation, taking into account the availability of water and nutrients. These economic injury levels are also dynamic because they may change in the course of time. An early infection or late
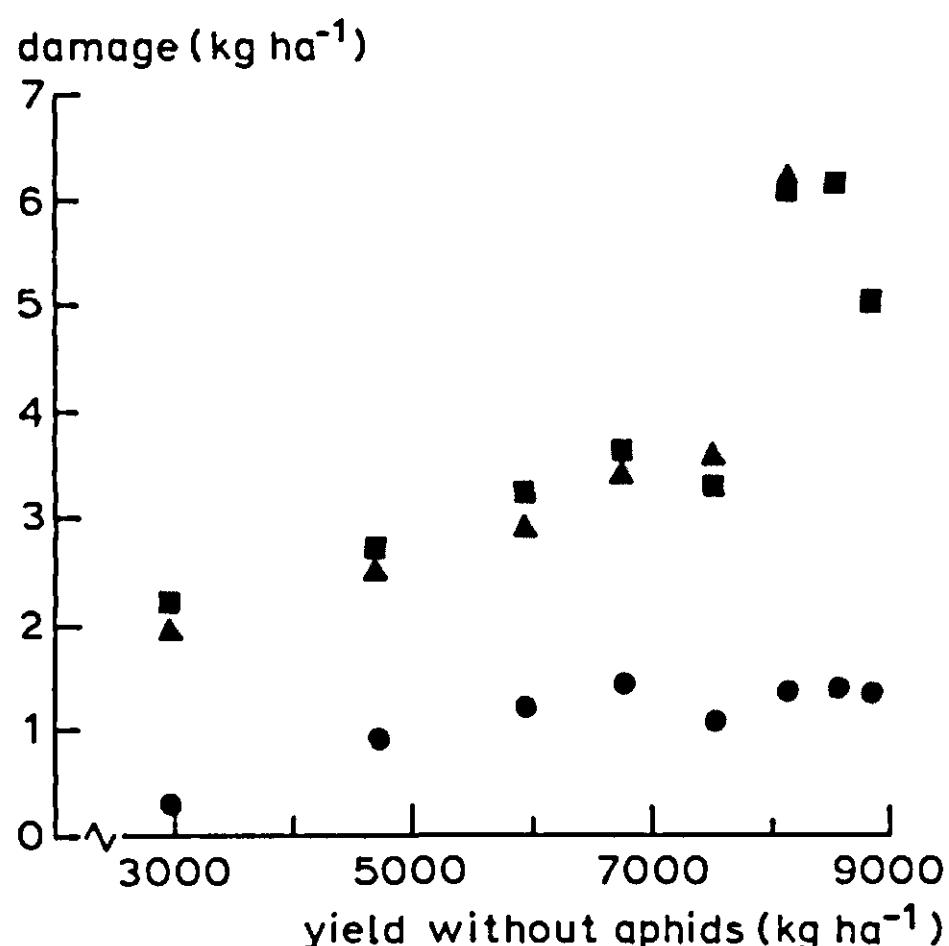
Figure 68. Simulated damage (kg ha^{-1} (aphid-day)$^{-1}$) for three periods of crop development (■ DC60-69; ▲ DC69-73; ● DC73-83), calculated with Hypothesis I on aphid–crop interaction.

infection may have considerably different consequences, depending on crop development stage. Finally, the economic injury levels may be tailored to the specific circumstances of individual fields.

The comprehensive simulation models used in this study are not adequate for pest and disease management. They help increase our understanding and may be used to derive economic injury levels that may be implemented in computerized pest and disease management systems. This clearly demonstrates the bridge function of production ecology.

10.9 References

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