

4.4 Simulation of aphid damage in winter wheat; a case study

W.A.H. Rossing, J.J.R. Groot and H.J.W. van Roermund

4.4.1 Introduction

Winter wheat yields in the Netherlands increased from approximately 4000 kg dry matter ha⁻¹ in 1945 to 8000 kg ha⁻¹ in 1980 (Rabbinge, 1986). This yield increase was the result of improved cultural methods which reduced the significance of yield-limiting factors such as shortages of water and nitrogen, the introduction of short-straw varieties with a higher harvest index and a longer grain-filling period and, finally, the improved control of growth- and yield-reducing factors. The latter are relatively more significant at high yield levels, due to the positive effect of 'good crops' on the increase rate of pests and diseases – mainly as a result of higher nitrogen levels in attacked tissue (e.g. White, 1984). Moreover, in 'good crops' most yield-limiting factors have already been eliminated. This resulted in a tendency to use insurance spraying, i.e. spraying without first establishing the presence of pests or diseases. Overuse of crop protection agents, however, reduces the net profit for a grower, increases environmental side effects and can stimulate secondary pests and diseases by killing their natural enemies.

In the Netherlands, three aphid species occur in winter wheat: the grain aphid, *Sitobion avenae*, the rose grass aphid, *Metopolophium dirhodum*, and the bird cherry oat aphid, *Rhopalosiphum padi*. Usually, *Sitobion avenae* occurs in the highest numbers. Cereal aphids have been economically significant pests in winter wheat since the late sixties. Around that time, top dressings of nitrogen were introduced which prolonged the maturation period of the crop when cereal aphids cause the most damage. It was shown that a high nitrogen content of the crop accelerates aphid population growth by increasing fecundity and inhibiting wing formation (Vereijken, 1979).

Because of their uneconomical turnover of food, aphids take up large amounts of phloem sap. Vereijken (1979) showed that yield losses are not only caused by the feeding on assimilates, but that other factors exist which adversely affect the crop physiology. These are: (1) honeydew, excreted by the aphid, covers the stomata of the leaves and affects photosynthesis, and (2) toxins or growth regulators are injected with the saliva, and may influence the rate of leaf senescence. The latter is considered to be of little significance in the Dutch cereal aphid-winter wheat system.

Relations between aphid density and damage have been developed, based on regression analysis of field observations (Entwistle & Dixon, 1987). Rabbinge et al. (1983) hypothesized that the yield level of the control treatment should be considered when calculating the damage relation. However, conducting new field experiments at various yield levels, under various intensities of pest attack,

would not overcome the limitations of system's description at the system level (cf. Chapter 1). Here, a simulation approach, based on laboratory experiments, is presented which describes the effect of *S. avenae* on the physiology of the winter wheat crop. Thus, with knowledge of the process level, the effects on the system level (yield and yield reduction) are predicted. Although our knowledge on the exact nature of the interaction between pest and crop is incomplete, the simulation model contributes to our understanding of the relative significance of various damage components and will also help in further research.

4.4.2 *The life cycle of Sitobion avenae*

Host plant species of *S. avenae* belong to *Gramineae*. Overwintering takes place as viviparae or as eggs. Starting at the end of May, alatae (winged aphids) can be found in winter wheat, which is preferred to other cereals. The first instar nymphs are produced by parthenogenesis and develop through four nymphal instars before moulting into adults. Most of these nymphs develop into apterous (wingless) adults, whose reproductive rate is higher than that of alate adults. The aphid population usually starts to increase around anthesis (DC 60, Decimal Code for crop development stage, Zadoks et al., 1974), and the population density usually reaches a maximum at the late-milky ripe stage of wheat (DC 77). Ears are preferred to leaves as feeding sites.

The rate of population development depends on food quality, especially the nitrogen content of the crop, and also on temperature and the presence of predators and parasites. The reproductive rate is density-dependent. As a result of high aphid density and a decline in food quality, an increasing proportion of the nymphs born to the apterous adults after DC 73 develops into alate adults. These alatae leave the crop, causing a rapid decline in field populations which is enhanced by the effect of natural enemies.

Under short day conditions in autumn, *S. avenae* produces sexual offspring. First gynoparae and then mostly males. After mating, oviparae are produced, which lay winter eggs on the winter host (Carter et al., 1982).

Exercise 73

The time, needed for a fictitious aphid population to double in size, depends on the food quality (which is related to the crop development stage, coded with the decimal code for crop development) and on the temperature. On Day 0, the decimal code for crop development stage is 50 and the aphid density is 0.05 aphids ear⁻¹. The doubling time for the population (at 20°C) is during DC 50–DC 60: 4 days, DC 60–DC 70: 2.5 days, and for DC 70–DC 77: 6 days, respectively. An increase in temperature of 10 degrees causes the doubling time to reduce to 50% of its value at 20°C. Inversely, a decrease in temperature of 10 degrees results in values of the doubling time which are twice the reference.

The duration of different crop development periods (in days) also depends on temperature:

	DC 50–DC 60	DC 60–DC 70	DC 70–DC 77
10°C	11	10	35
20°C	7	7	27
30°C	4	5	19

- Calculate the aphid density at anthesis (DC 60), at the end of anthesis (DC 70) and at the late-milky ripe stage (DC 77) at a constant temperature of 20°C.
- Assume that a farmer will spray his crop if the aphid density exceeds the threshold of 15 aphids tiller⁻¹. After how many days will the threshold be passed at a temperature of 20°C?
- Write a CSMP program to simulate the population growth of *S. avenae*. Do not distinguish age classes. Assume a sinusoidal daily course of temperature between 12°C and 28°C.

4.4.3 Simulation of crop growth

When simulating the interaction between wheat growth and aphids, only the post-anthesis phase is considered. Growth, the increase in crop dry matter, is simulated as a function of radiation, ambient temperature and nitrogen availability in the soil. The model consists of sink-source relations, which describe the flow of carbohydrates and nitrogen. It is based on models by Groot (1987) for winter wheat and van Keulen & Seligman (1987) for spring wheat. The time step of integration is one day. A simplified relational diagram of the model is given in Figure 68.

Simulation starts at anthesis with measured weight and nitrogen content of the organs (roots, stems, leaves and ears), and the amount of water-soluble carbohydrates (reserves) in the stem as inputs. Generally, 10% to 15% of the stem weight consists of reserves at anthesis. To determine the strength of the only sink, the grains, the number of grains per unit area must be known.

The nitrogen source for grain growth consists of translocatable nitrogen present in biochemical structures which are easily decomposable into amino acids. Some of the nitrogen is permanently incorporated in cell material and this residual nitrogen is not available for translocation to the grains.

The carbohydrate source for grain growth consists of the daily gross photosynthesis and stem reserves (see Figure 68). Photosynthesis is calculated according to the procedure described in Section 4.1. The maximum rate of photosynthesis at light saturation, AMAX, decreases with increasing crop development as proteins are broken down to meet the nitrogen requirements of the sink. In the model, AMAX is proportional to the ratio of the translocatable nitrogen fraction (TNF) of an organ and the translocatable nitrogen fraction at anthesis (TNFA) (Vos, 1981):

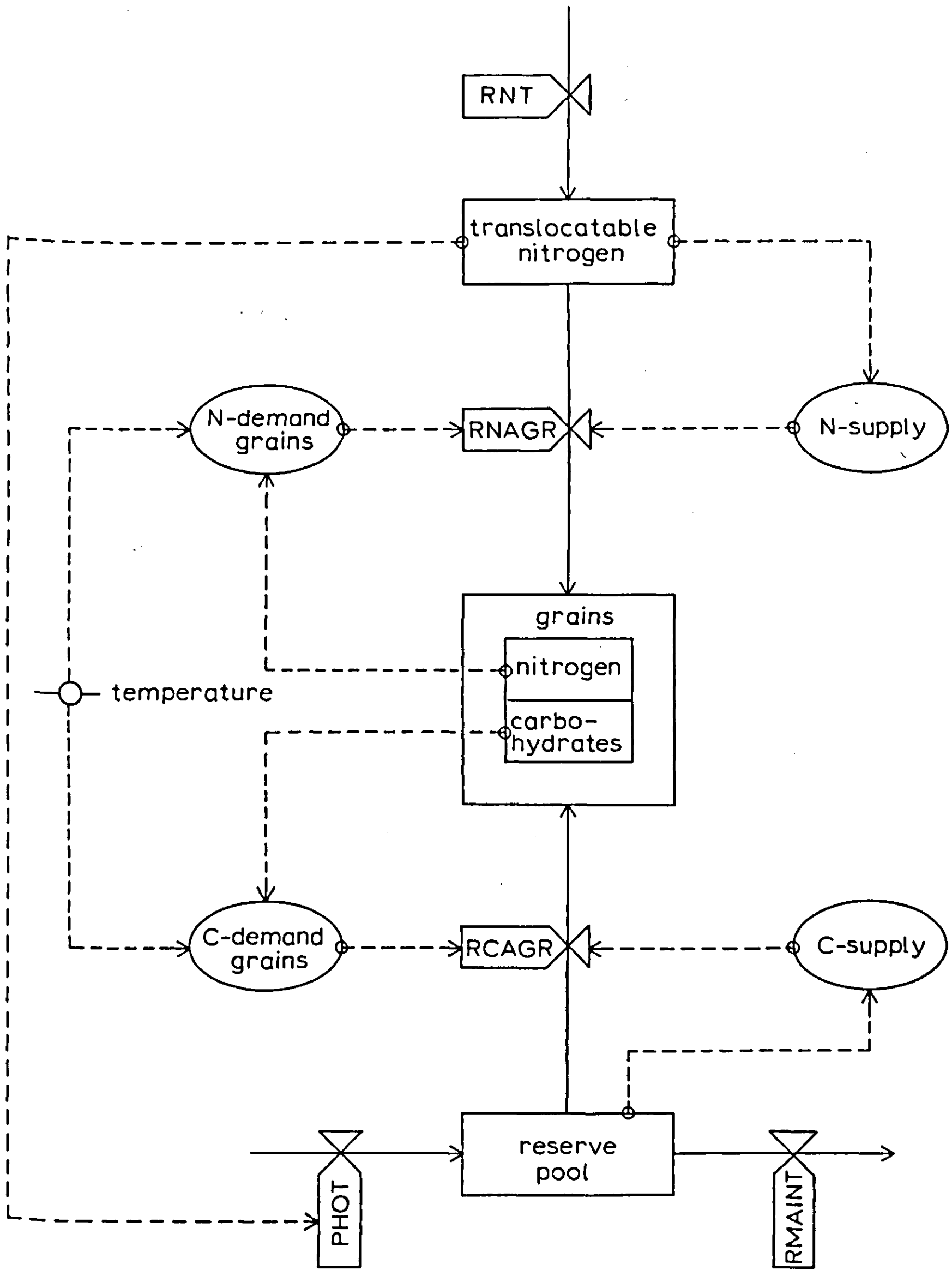


Figure 68. Simplified relational diagram of a crop growth model for winter wheat.

$$AMAX = AMAXA * TNF/TNFA$$

where AMAXA represents AMAX at anthesis. The initial light use efficiency, EFF, is independent of the nitrogen content of green plant material (e.g. van Keulen & Seligman, 1987).

Some of the assimilates are used for maintenance respiration. Maintenance respiration is calculated for each of the plant organs as a product of organ weight (WO) and maintenance respiration coefficient (MAINO, $\text{kg kg}^{-1} \text{d}^{-1}$) (see Section 4.1), with a correction for respiration activity. In active tissues, a continuous protein turnover occurs which requires energy. The respiration activity of an organ (RACT) is assumed to depend on the translocatable nitrogen fraction of an organ, relative to the translocatable nitrogen fraction at anthesis (Vos, 1981):

$$RACT = TNF/TNFA$$

$$TEFF = Q10^{*(TMPA - REFTMP)/10}$$

$$RMAINT = WO * MAINO * TEFF * RACT$$

TEFF represents the effect of temperature. Q10 is the multiplication at a 10 degree increase or decrease in the ambient temperature (TMPA), relative to the reference temperature (REFTMP).

After subtracting the maintenance requirements of all plant organs from the gross photosynthesis, the available assimilates (AVASS) are allocated to the reserves in the stem. The carbohydrates required for grain growth are supplied from this stem reserve pool. The rate at which carbohydrates are mobilized from the stem reserves (CSUPG) is determined by the time coefficient of the translocation process (TCTR). The time coefficient depends on the reserve level (RESL), which is defined as the amount of reserves (ARES) expressed as a fraction of the vegetative above-ground dry matter (WSTRAW):

$$ARES = INTGRL(ARESI, AVASS-RCAGR)$$

$$RESL = ARES /WSTRAW$$

$$TCTR = AFGEN(TCTR, RESL)$$

$$\text{FUNCTION TCTR} = 0., 50., 0.05, 8., 0.1, 2., 0.2, 1., 0.7, 1.$$

$$CSUPG = ARES / TCTR$$

The sink strength or demand of grains (CDEMG) is based on the potential growth rate of individual grains (PGRIG) which depends on the ambient air temperature (TMPA), according to Sofield et al. (1977a), and on the number of grains per hectare as measured in the field (NUMGR). As the potential growth rate of individual grains is measured in terms of dry weight, PGRGR is divided by the conversion efficiency of carbohydrates into grain dry weight (EFCGR), to obtain the demand of the grains in terms of carbohydrates:

$$PGRIG = AFGEN(PGRIGT, TMPA)$$

$$\text{PARAM NUMGR} = 2.46E8$$

$$PGRGR = PGRIG * NUMGR$$

$$CDEMG = PGRGR / EFCGR$$

The rate of carbohydrate accumulation in the grains (RCAGR) will equal the demand of the grains (CDEMG), unless the rate of carbohydrate supply (CSUPG) is limiting. When the carbohydrate supply exceeds the demand, the rate of carbohydrate accumulation in the grains is sink-limited, and the amount of stem reserves will increase. In CSMP, RCAGR is calculated by means of the FORTRAN function AMIN1 which selects the minimum of CDEMG and CSUPG:

$$RCAGR = AMIN1(CDEMG, CSUPG)$$

The rate of grain growth (GRGR) is calculated from the rate of carbohydrate accumulation by multiplying by the conversion efficiency EFCGR to account for the growth respiration of the grains. The weight of the grains (WGR) is obtained by integrating the grain growth rate:

$$GRGR = RCAGR * EFCGR$$

$$WGR = INTGRL(0., GRGR)$$

The nitrogen supply to the grains (NSUPG) depends on the size of the translocatable nitrogen pool and on the rate at which protein decay occurs. The amount of nitrogen available for translocation (ATN) is the difference between the current amount of nitrogen in the vegetative parts and the amount of residual nitrogen, i.e. the nitrogen incorporated in structural cell material. The rate of protein decomposition is characterized by a time coefficient (TCTN), usually of the order of 10 days (Penning de Vries, 1975). Higher temperatures accelerate the process. The temperature effect on protein decomposition has a Q_{10} value of 2, thus the already defined variable TEFF may be used:

$$NSUPG = ATN / TCTN * TEFF$$

$$PARAM TCTN = 10.$$

The nitrogen demand of the grains (NDEMG) is characterized by a potential rate of nitrogen accumulation in individual grains (PNARIG), defined as a function of ambient air temperature (TMPA), according to Sofield et al. (1977b):

$$PNARIG = AFGEN(PNARIT, TMPA)$$

$$NDEMG = PNARIG * NUMGR$$

When the nitrogen supply exceeds the demand, the rate of nitrogen accumulation is sink-limited. Hence, the rate of nitrogen accumulation in the grains will equal the demand of the grains, unless the supply is limiting:

$$RNAGR = AMIN1(NDEMG, NSUPG)$$

Finally, the amount of nitrogen in the grains (ANGR) is obtained by integrating the rate of nitrogen accumulation in the grains:

$$ANGR = INTGRL(0., RNAGR)$$

4.4.4 Simulation of aphid damage

To simulate aphid damage, aphid numbers as counted in the field are introduced into the model as a forcing function. Direct and indirect effects of *S. avenae* on winter wheat are distinguished. Direct effects result from uptake of carbohydrates and nitrogen. Indirect effects are due to honeydew excreted onto green plant surfaces.

Direct effects Conceptually, modelling the effect of aphids feeding on the crop is identical to modelling grain growth (Figure 69). Both aphids and grains are sinks for carbohydrates and nitrogen and the supply is partitioned among them.

Suction rates and honeydew production rates seem to be negatively related to the nitrogen content of the food source (Vereijken, 1979; Ajayi & Dewar, 1982). Concomitantly with nitrogen, carbohydrates in the phloem sap are taken up. Very little quantitative information is available on the relation between the rate of phloem sap uptake and the phloem sap nitrogen content. Coster (1983) and Rabbinge & Coster (1984) measured daily honeydew production rates of *S. avenae* on flag leaves and ears of winter wheat plants at various growth stages. The plants were supplied with sufficient water and fertilizer. The rate of phloem sap uptake was calculated by applying an energy budget approach (Llewellyn, 1988). Their results are listed in Table 27. Suction rates decrease as the crop matures. No data are available on the nitrogen content of phloem sap. Here, it is assumed to be 2% of the dry weight. Furthermore, the demand of the aphids is taken to be fully satisfied at the highest suction rate measured. Lower suction rates are attributed to mechanical and physiological changes associated with ripening of the crop. Thus, a potential suction rate SRAP of $8.92 \cdot 10^{-9}$ kg (N) mg^{-1} (aphid, fresh weight) day^{-1} is found. The nitrogen demand (NDEMA) is found by multiplying the potential suction rate by the average weight of one aphid (AWAP), the number of aphids per tiller (NUMAP) and the number of tillers per hectare (EARHA). Average aphid weight depends on the age distribution of the aphid population. As an approximation, the data of Mantel et al. (1982) are used, which represent average aphid weight at three crop development stages calculated from a large number of field observations.

$$\text{NDEMA} = \text{SRAP} * \text{AWAP} * \text{NUMAP} * \text{EARHA}$$

The demand for carbohydrates (CDEMA) is calculated from the demand for nitrogen, using the ratio of the rates of carbohydrates and nitrogen to the sinks calculated by the model one integration interval previously, to approximate the fraction of carbohydrates in the phloem sap.

Aphids and grains share the supply of nitrogen and carbohydrates. Several hypotheses can be formulated concerning the nature of the partitioning, as the true nature has not been established. Aphids may be the first to utilize the supply of phloem sap, the remainder going to the grains. Alternatively, the supply may be distributed over the sinks in proportion to the respective demands. The

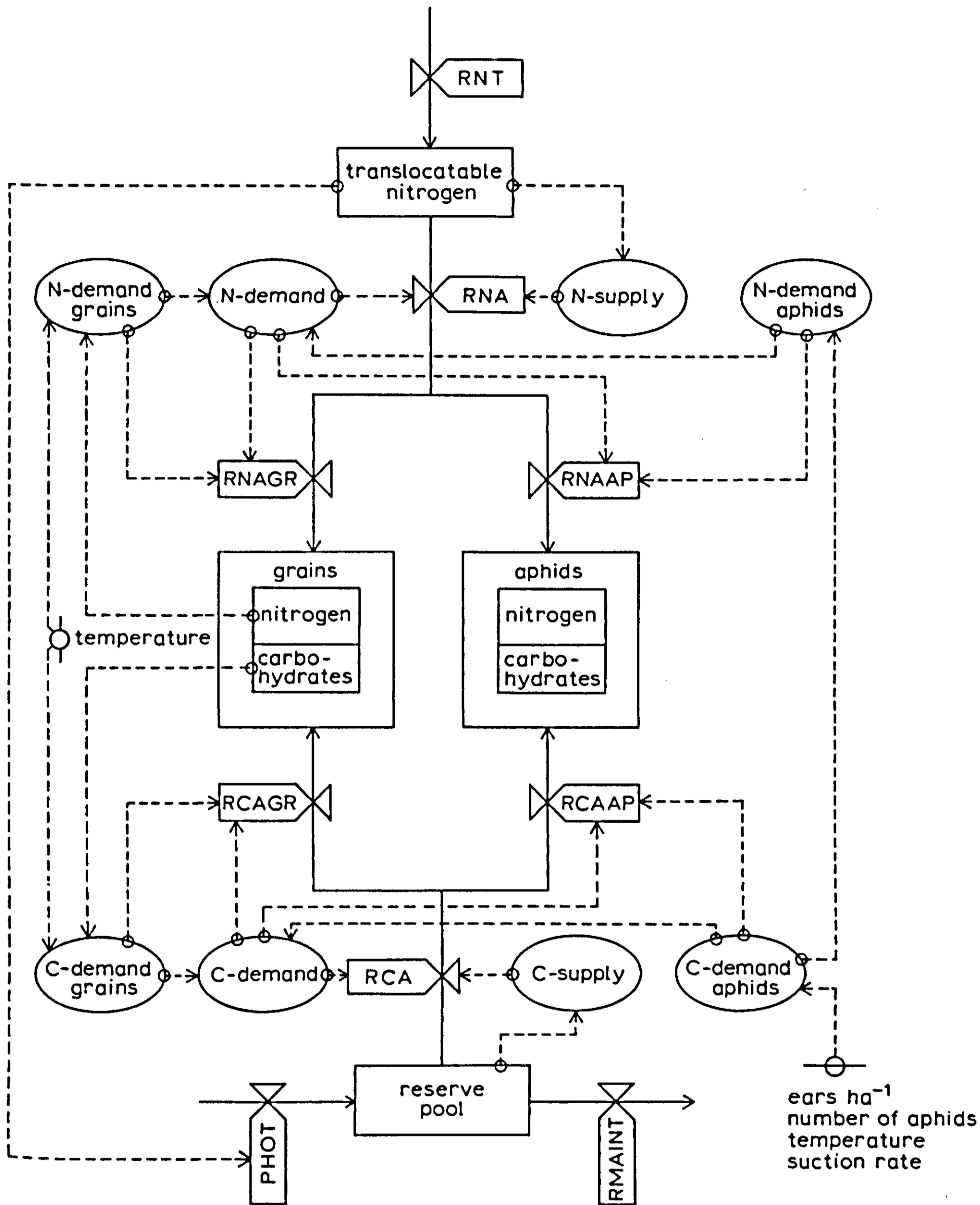


Figure 69. Simplified relational diagram of a model for direct aphid damage in winter wheat.

Table 27. Rate of honeydew production (mg (honeydew dry weight) mg^{-1} (aphid fresh weight) day^{-1}) and suction rate (mg (phloem sap dry weight) mg^{-1} (aphid fresh weight) day^{-1}) of *S. avenae* on spring wheat var. Bastion. Each figure is the average of 10 replicates. (Sources: Coster (1983) and Rabbinge & Coster (1984)).

Feeding position of aphids	Crop stage	Suction rate	Honeydew production rate	N content of flag leaves (f) or grains (gr) (g kg^{-1})
flag leaf	45	0.450	0.148	–
flag leaf	45	0.505	0.188	4.57 (f)
ear	65	0.446	0.180	–
ear	69	0.307	0.086	3.56 (gr)
ear	71	0.326	0.128	2.26 (gr)
ear	73	0.167	0.063	2.47 (gr)
ear	75	0.237	0.082	2.35 (gr)

incomplete fulfilment of grain demand may result in enhanced supply. Thus, total demand will consist of the sum of demands of grains and aphids. Here, two extreme situations are distinguished concerning the direct effect of *S. avenae* on the crop. In the following these are referred to as hypotheses I and II:

I. The total demand equals the sum of demands of grains and aphids; the supply is distributed in proportion to the respective demands.

II. When present, only the grains determine the total demand; the supply is first utilized by the aphids.

The simulation model is used to evaluate the quantitative consequences of these potential modes of interaction to damage.

Exercise 74

Write a CSMP program to simulate direct effect of aphids using hypothesis I.

Exercise 75

A winter wheat crop is infested with 30 *S. avenae* per tiller. Assume the ear density to be 635 m^{-2} . The N content of the phloem sap is 2%. Other data: NSUP = $15 \text{ kg ha}^{-1} \text{ d}^{-1}$, CSUP = $1000 \text{ kg ha}^{-1} \text{ d}^{-1}$, NDEMG = $2 \text{ kg ha}^{-1} \text{ d}^{-1}$ and CDEMG = $50 \text{ kg ha}^{-1} \text{ d}^{-1}$. Calculate numerically the reduction in the flow of carbohydrates to the grains due to *S. avenae*, assuming:

- a. hypothesis I to apply for the direct effects;
- b. hypothesis II to apply for the direct effects.

Indirect effects In experiments in which an artificial honeydew solution is applied to flag leaves of winter wheat, honeydew reduces the maximum rate of leaf photosynthesis, and increases the rate of maintenance respiration two weeks after application. One day after application, no effects are yet detectable (Ros-sing, in prep.). The effects are most pronounced under dry conditions, rain may remove honeydew before it affects the leaf. Here, only the effects found under dry conditions are used, neglecting environmental influences. The assumption is made that the effect increases linearly between one day and 14 days after deposition of the honeydew, and from then on remains constant. Moreover, the total effect is assumed not to exceed the maximum effect measured.

To evaluate the effect of honeydew on crop photosynthesis, the distribution of daily honeydew production over the canopy profile is calculated. The daily honeydew production (in $\text{kg ha}^{-1} \text{ ground day}^{-1}$) is derived from the actual phloem sap suction rate by multiplying by 0.404, a factor calculated from the data of Coster (1983) and Rabbinge & Coster (1984). On its way through the canopy, honeydew is intercepted by ears, leaves and stems, similar to light. The upper layer of the simulated crop consists solely of ears. According to Vereijken (1979), the ears intercept 30% of the honeydew produced. Beneath the ear-layer, the canopy is divided into layers of thickness DL ($\text{ha leaf ha}^{-1} \text{ ground}$). Of the produced honeydew, 70% will be intercepted by those layers or fall on the ground (HDLGHA, $\text{kg ha}^{-1} \text{ ground day}^{-1}$). Analogous to the light distribution inside a canopy, the amount of honeydew not intercepted, is assumed to decrease exponentially with the leaf area index, measured from the top of the canopy, LAI' (Figure 70). The extinction coefficient (k) for honeydew will be higher than the extinction coefficient for light, because no transmission or reflection of honeydew occurs. Here a value of 0.8 is used. The distribution is described by:

$$H_{\text{LAI}'} = H_0 \cdot e^{-k \cdot \text{LAI}'} \quad \text{and}$$

$$\text{HDLGHA} = \int_0^{\infty} H_0 \cdot e^{-k \cdot \text{LAI}'} d\text{LAI}' = H_0/k$$

The amount of honeydew intercepted in a leaf layer (Figure 70) is calculated:

$$\begin{aligned} \text{HDLAY}(z) &= \int_{(z-1) \cdot \text{DL}}^{z \cdot \text{DL}} H_0 \cdot e^{-k \cdot \text{LAI}'} d\text{LAI}' = -H_0/k \cdot e^{-k \cdot \text{LAI}'} \Big|_{(z-1) \cdot \text{DL}}^{z \cdot \text{DL}} \\ &= H_0/k \cdot (1 - e^{-k \cdot \text{DL}}) \cdot e^{-(z-1) \cdot k \cdot \text{DL}} \\ &= \text{HDLGHA} \cdot (1 - e^{-k \cdot \text{DL}}) \cdot e^{-(z-1) \cdot k \cdot \text{DL}} \end{aligned}$$

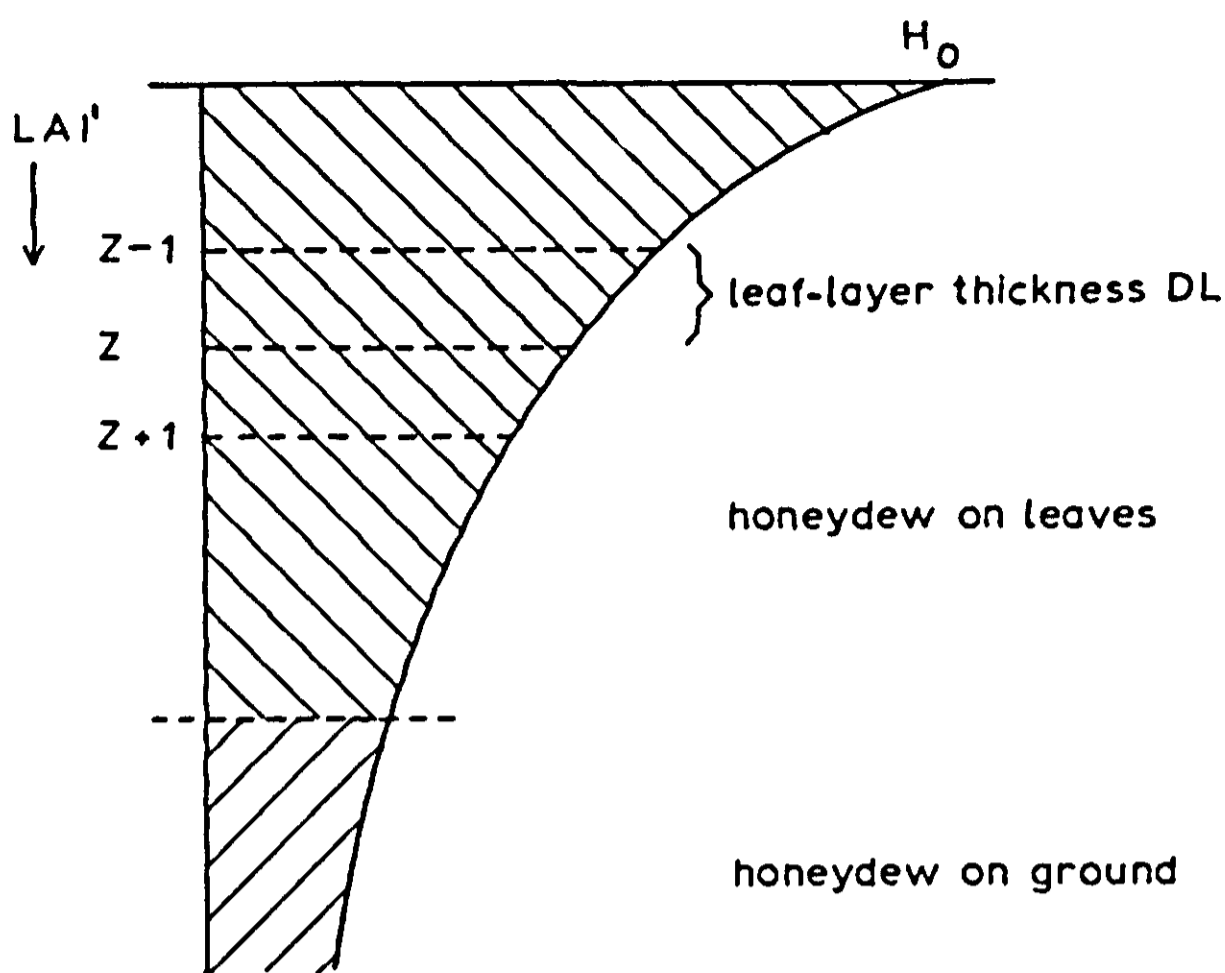


Figure 70. Interception of honeydew in the canopy as a function of the leaf area index (ha leaf ha^{-1} ground).

The total effect of honeydew at a certain depth is calculated by adding the effects of honeydew deposited at various times during grain growth. Thus, interference of honeydew deposited on subsequent days is assumed not to occur. The reduction of the maximum rate of photosynthesis and the increase in maintenance respiration is input for the photosynthesis algorithm of the crop model.

4.4.5 Simulation results

Data for evaluation Six data sets from three locations and two years are used to evaluate the crop model (PAGV1, PAGV2, PAGV3, EEST83, EEST84 and BOUWING84). The data sets represent a range of grain yields which were arrived at under conditions of nitrogen limitation only. Information on the experiments from which the data are derived is given in Table 28. The data sets collected in 1983 pertain to experiments in which the rate of fertilizer application was varied (Groot, 1987). The data sets of 1984 constitute the control treatment without aphids in experiments designed specifically to evaluate the damage model. Diseases, weeds and aphids were controlled on occurrence. Due to rapid

*) H = herbicide, F = fungicide, I = insecticide

**) insecticide treatment aimed at creating various aphid infestations

***) yield without and with aphids, respectively. The final yields for EEST84 were 8114 kg ha^{-1} and 7907 kg ha^{-1} due to delayed harvest. Here, the penultimate yields are shown.

Table 28. General information on the data sets used to evaluate the crop model and damage model.

	PAGV1	PAGV2	PAGV3
Location	Lelystad	Lelystad	Lelystad
Wheat variety	Arminda	Arminda	Arminda
Grain yield (kg ha ⁻¹)	6256	7442	8279
Soil type	Sandy loam	Sandy loam	Sandy loam
Percentage silt	23	23	23
Previous crop	sugar beet	sugar beet	sugar beet
Sowing date	25 Oct 1982	25 Oct 1982	25 Oct 1982
Flowering date	22 June 1983	22 June 1983	22 June 1983
Harvest date	2 August 1983	2 August 1983	2 August 1983
Row spacing (cm)	12.5	12.5	12.5
Sowing density (kg ha ⁻¹)	140	140	140
Total N (kg ha ⁻¹)	120	200	300
Growth regulator	yes	yes	yes
Protective chemicals*	H,F	H,F	H,F
Experimental design	Random block	Random block	Random block
Replicates	8	8	8
No. sampling dates	4	4	4
Sample size (tillers)	25	25	25
	EEST83	EEST84	BOUWING84
Location	Nagele	Nagele	Randwijk
Wheat variety	Arminda	Arminda	Arminda
Grain yield (kg ha ⁻¹)	4496	9290/7778***	8754/8549***
Soil type	Sandy clay	Sandy clay	Clay
Percentage silt	45	33	35-60
Previous crop	potatoes	sugar beet	potatoes
Sowing date	19 Oct 1982	4 Nov 1983	22 Oct 1983
Flowering date	22 June 1983	27 June 1984	20 June 1984
Harvest date	3 August 1983	31 August 1984	23 August 1984
Row spacing (cm)	15	15	24
Sowing density (kg ha ⁻¹)	148	148	138
Total N (kg ha ⁻¹)	94	250	250
Growth regulator	yes	no	no
Protective chemicals*	H,F,I	H,F,I**	H,F,I**
Experimental design	Random block	Random block	Random block
Replicates	8	6	6
No. sampling dates	4	10	9
Sample size (tillers)	25	50	50

increase of aphid numbers in 1984 a slight infestation in the control could not be avoided, affecting the two data sets. At regular time intervals, 0.5 m² of the crop was harvested and taken to the laboratory. There, the following analyses were carried out: dry weight of leaves, stems, ears and grains, nitrogen content of green leaves and dead leaves, amount of soluble carbohydrates in the stems and the green leaf area index.

To evaluate the damage model, data of two experiments carried out in 1984 are available (EEST84 and BOUWING84). In these experiments, various aphid infestations were created by chemical control of a natural aphid infestation at various crop development stages (van Roermund et al., 1986). Here, the data of the plots which received no aphicide treatment are used. At the time of the intermediate crop harvests, aphid density was also established. Statistical analysis of the experimental results showed that grain yield, leaf area index, leaf weight and amount of leaf nitrogen, decreased significantly in EEST84 on a number of harvest dates due to the aphid infestation. For BOUWING84 few significant effects were found. Climatic data were collected from nearby weather stations.

All model runs are carried out with measured temperature, irradiation and soil nitrogen data. The development rate of the crop is fitted to the observed rate.

Evaluation of the crop model Here, both crop and damage models are evaluated by visual inspection of the time course of actual and simulated values of a number of variables. In the context of gaining better understanding of the winter wheat – *S. avenae* system, this approach seems justifiable. The use of quantitative methods is advocated if model results are to be used in a management environment (Teng et al., 1980). The output variables examined are grain yield, weight of the green leaves, amount of reserves, amount of leaf nitrogen and leaf nitrogen content.

For each data set two simulation runs were made, one with simulated leaf area index, the other with the leaf area index as observed in the field. In this way, errors in the simulation of leaf area dynamics, which are still poorly understood, can be identified.

Simulated and observed rates of increase in grain yield compare well in the initial linear phase for all data sets (Figure 71). Also, the onset of grain-filling is simulated satisfactorily, except for BOUWING84 where it is predicted too early. High soil heterogeneity in combination with a warm spell around flowering may have obscured accurate estimation of the date of flowering.

Simulated and actual grain yields compare less well towards the end of the growing season. For PAGV1, PAGV2, PAGV3 and EEST83 underestimation occurs due to overestimation of leaf death. This is especially prominent at low nitrogen fertilizer amounts applied in PAGV1 and EEST83, indicating that the description of leaf death limits the applicability of the model to yield levels above 6000 kg ha⁻¹. Some inconsistencies show up in the data: at low fertilizer rates, grain yield is found to increase for two weeks after the leaf area was estimated to be zero.

For EEST84 and BOUWING84 the grain yield is overestimated. This is partly due to the presence of a light aphid infestation, but more importantly to the presence of photosynthetically active tissue (both simulated and observed) until shortly before harvest. Van Keulen & Seligman (1987) calculate the end of the linear growth of individual grains to occur at 0.72 of the total time between flowering and ripeness. For a crop the end of linear growth is more gradual, due to differences in the onset of grain-filling between grains. Their approach is, therefore, not used in the present model. Nevertheless, the results for EEST84 and BOUWING84 show that decrease in the sink strength at the end of the growing season needs to be considered to avoid overestimating the period of grain-filling.

A more extensive evaluation of the crop model will be given elsewhere (Ros-sing, in prep.). It is concluded that the output variable of most interest, grain yield, is simulated acceptably, but that errors in predicting leaf death limit the applicability of the model to yield levels above 6000 kg ha^{-1} .

Sensitivity analysis of the crop model Sensitivity analysis consists of examining the effect of uncertainty in model parameters (fine sensitivity analysis) and model structure (coarse sensitivity analysis) on the value of output variables. As a measure of model sensitivity, the relative sensitivity $(\Delta z/z)/(\Delta y/y)$ is defined, where z is the value of the relevant model output variable, y the value of the parameter and Δz the change in z caused by a change Δy in y . The size of the perturbation Δy should not exceed the variation of y reported in the literature.

Fine sensitivity analysis is carried out using data sets EEST84 and EEST83. The results of most interest are listed in Table 29. Sink strength for carbohydrates depends on the density of grains and the potential growth rate of an individual grain. An increase in the value of these parameters causes a decrease in grain yield for EEST84, whereas yield increases for EEST83. Two mechanisms working in opposing directions are involved. Due to a higher potential growth rate, the reserves are utilized more quickly resulting in lower maintenance respiration. On the other hand, the reserves are depleted sooner, causing enhanced leaf senescence. For the poorer crop EEST83, the first mechanism is dominant, for the richer crop the second.

Changes in the value of parameters describing leaf photosynthesis have a more significant effect on grain weight than changes in those of ear photosynthesis. The latter apparently contributes less to grain yield.

The amount of nitrogen in the crop is limiting to grain yield, in both data sets. For EEST84, the amount of nitrogen in the soil only becomes limiting after severe reduction of the parameter value (see Table 29).

In the coarse sensitivity analysis, ears are excluded from the photosynthesis model. Runs are made with data of EEST84. Due to higher light absorption by leaves and stems, yield increased by 2%. If ears are assumed to be photosynthetically inactive and only shade the lower plant parts, final grain yield is reduced by 15%.

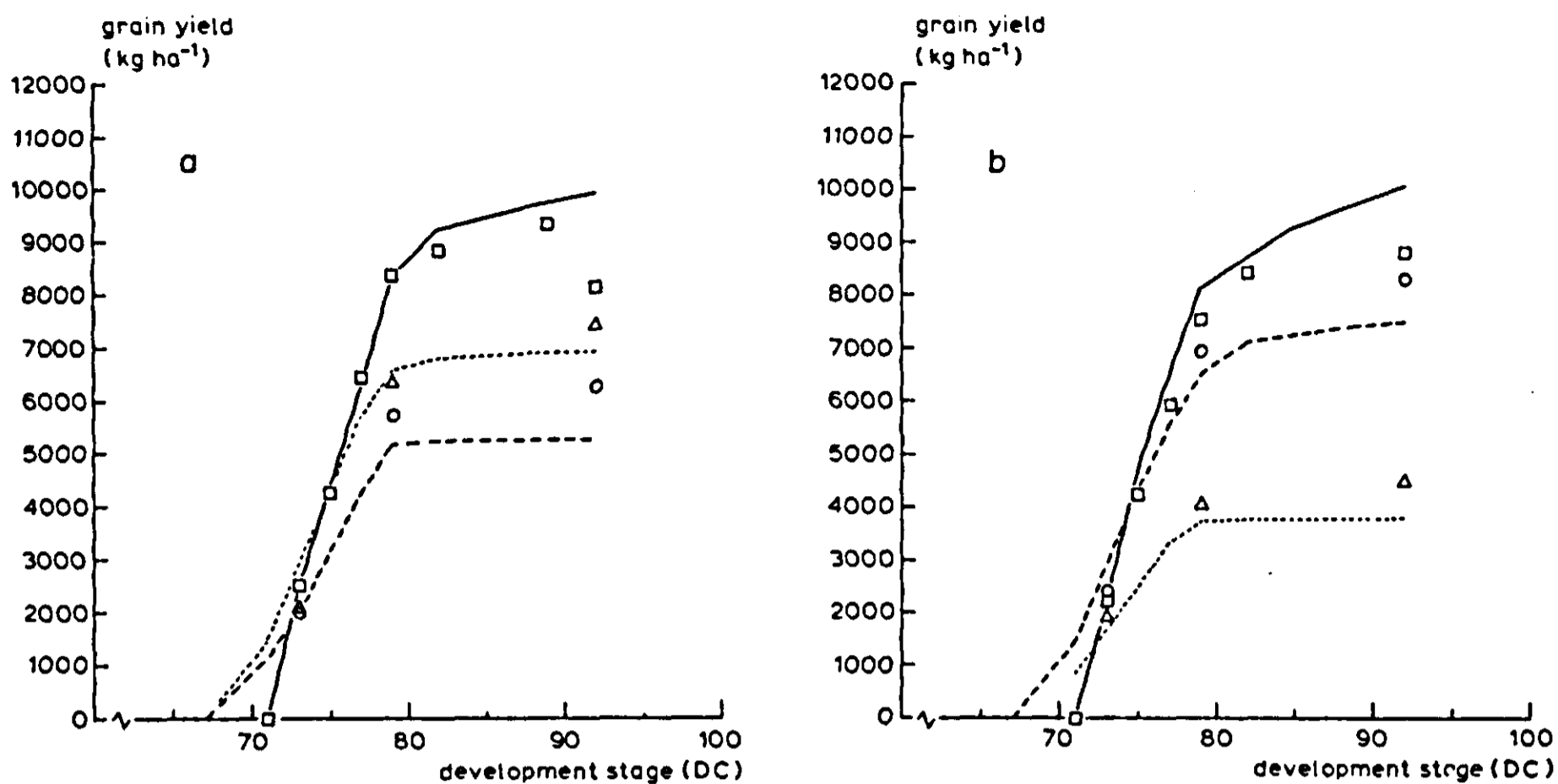


Figure 71. Evaluation of the crop model: simulated and observed grain yields of six data sets. Leaf area index is introduced as forcing function. a) EEST84 (—) simulated, (□) observed; PAGV1 (--) simulated, (○) observed; PAGV2 (---) simulated, (△) observed. b) BOUWING84 (—) simulated, (□) observed; PAGV3 (--) simulated, (○) observed; EEST83 (---) simulated, (△) observed.

Evaluation of the damage model Two data sets are available for evaluation. Here, only results of model runs for EEST84 are presented, where the effects of aphids are most pronounced. In Figure 72, actual grain yield for the high and low infestation plots of EEST84 is compared with simulation results using the two hypotheses on aphid phloem sap uptake (Subsection 4.4.4). For both hypotheses, grain yield is overestimated at the end of the growing season. This can be partly attributed to the causes identified in the evaluation of the crop model. However, the assumed maximum for the reduction of photosynthesis parameters also needs to be considered as this affects grain yield especially at the end of the season.

When modelling the uptake of phloem sap, assuming an increased demand due to aphid presence (hypothesis I), aphid damage becomes apparent when the process of grain-filling changes from sink-limited to source-limited, i.e. after the reserves have been depleted. If aphids are assumed not to increase total sink strength for carbohydrates and nitrogen (hypothesis II), grain yield is reduced from the onset of the aphid infestation. This agrees with field observations.

Although hypothesis II explains the early reduction of grain yield, the observed reduction of reserves, leaf nitrogen and leaf area index is only simulated using hypothesis I, as in that case aphids interfere with the supply.

Simulating grain yield of the control plots shows that the low aphid infestation certainly had some effect on grain yield.

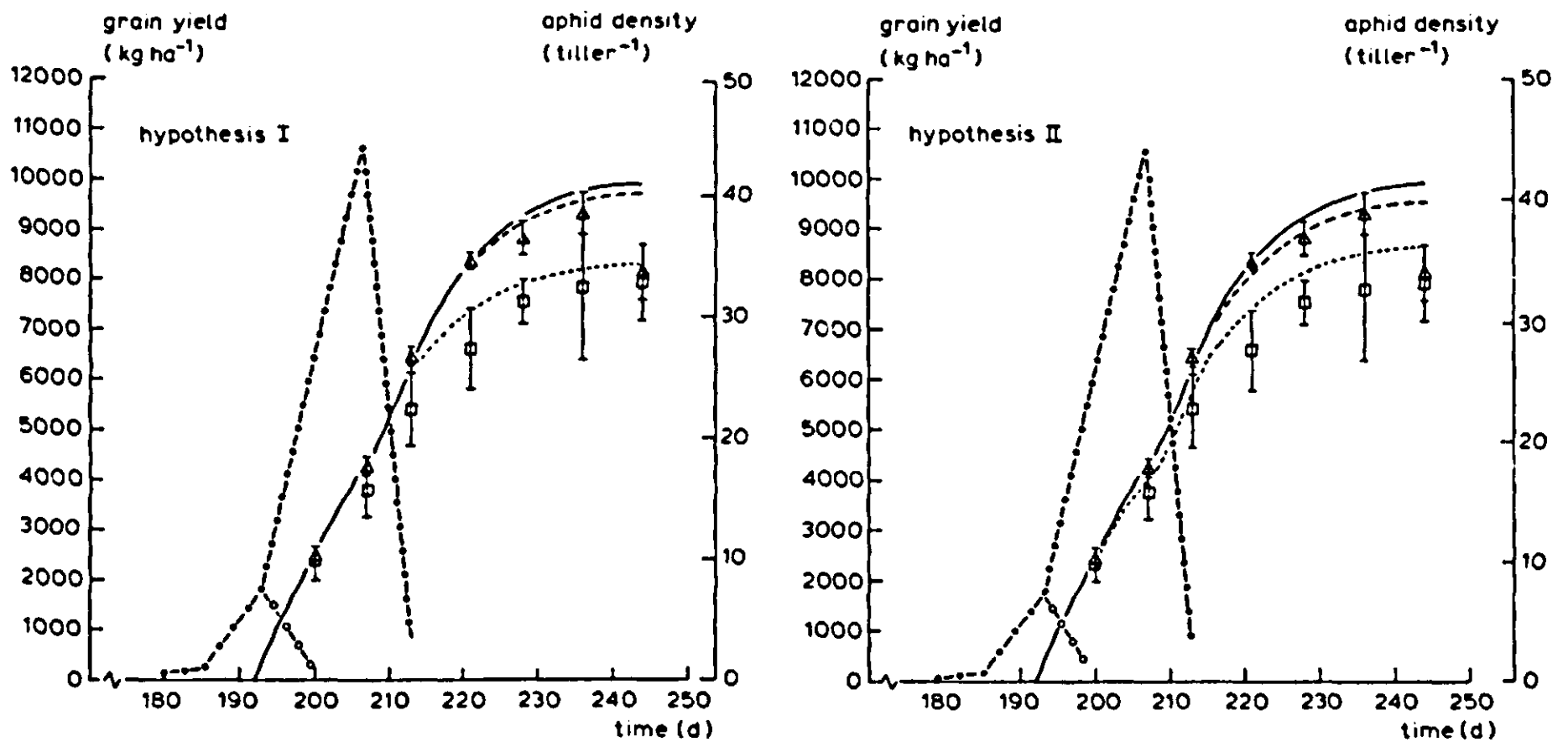


Figure 72. Evaluation of the damage model: simulated and observed grain yields of EEST84, using two alternative hypotheses on the direct effects of *Sitobion avenae* (see also text). Vertical bars represent standard errors of the mean. Simulated grain yield without aphids (—), aphid infestation as in control treatment (---) and high aphid infestation (---). The size of the aphid infestations is shown for the control (-o-o-) and the high infestation (-●-●-).

Sensitivity analysis of the damage model Fine sensitivity analysis is carried out with data of EEST84 using both hypotheses (Table 30a). Relative sensitivity is expressed in terms of grain yield as well as damage.

The greatest effects result from variations in the average aphid weight and the rate of phloem sap uptake. This is not surprising as both influence the direct and the indirect effects. Changes in the parameters describing the effect of honeydew have a relatively small effect.

As part of the coarse sensitivity analysis, the contribution of each of the damage components to total damage is evaluated. The results for EEST84 are listed in Table 30b. Uptake of phloem sap constitutes an important cause of damage. Hypothesis I results in higher damage and a higher contribution of aphid suction than hypothesis II.

Similar analysis at various yield levels using the data sets PAGV1, PAGV2, PAGV3 and EEST83 and an aphid infestation comparable to that of EEST84 shows that, using hypothesis II, the feeding component is more important at lower yield levels. Photosynthesis then compensates less for assimilate loss than at higher yield levels. Using hypothesis I, the contribution of phloem sap uptake is approximately equal at all yield levels.

The contribution of each damage component to total damage in course of time is represented in Figure 73 for EEST84. Under hypothesis I, effects show up from the time grain growth becomes source-limited (Day 213), three days before

Table 29. Relative sensitivity of end-of-season grain yield calculated with the crop model run with data of EEST84 and EEST83. In the runs, the leaf area index was simulated. Reference grain weight is 9898 kg ha⁻¹ for EEST84 and 2864 kg ha⁻¹ for EEST83, respectively. Relative sensitivity is calculated as the ratio of percentage change in grain weight and percentage change in parameter.

Parameter	Unit	Reference value		% change in parameter		Relative sensitivity	
		EEST84	EEST83	EEST84	EEST83	EEST84	EEST83
Maximum rate of leaf CO ₂ assimilation	kg ha ⁻¹ h ⁻¹	35 ^a	35 ^a	+ 14	+ 14	0.33	0.43
Maximum rate of ear CO ₂ assimilation	kg ha ⁻¹ h ⁻¹	25 ^b	25 ^b	+ 20	+ 20	0.15	0.11
Initial efficiency of light use of leaves	kg ha ⁻¹ h ⁻¹ • (J m ⁻² s ⁻¹) ⁻¹	0.45 ^c	0.45 ^c	+ 11	+ 11	0.64	0.45
Initial efficiency of light use of ears	kg ha ⁻¹ h ⁻¹ • (J m ⁻² s ⁻¹) ⁻¹	0.40 ^b	0.40 ^b	+ 13	+ 13	0.12	0.08
Size of an ear	cm ²	10 ^b	10 ^b	+150	+ 50	0.00	0.13
Grain density	ha ⁻¹	2.46 10 ^{8d}	1.41 10 ^{8d}	+ 8	+ 8	-0.47	-0.11
Potential rate of carbohydrate accumulation of grains	kg ha ⁻¹ d ⁻¹	table ^e	table ^e	+ 10	+ 10	0.01	0.00
Amount of nitrogen in the soil	kg ha ⁻¹	50 ^d	table ^d	+ 60	+ 20	0.07	0.00
Maximum rate of nitrogen uptake	kg ha ⁻¹ d ⁻¹	3 ^e	3 ^e	+100	+100	-0.07	0.29
Time coefficient for nitrogen translocation	d	8 ^e	8 ^e	- 67	- 67	0.19	0.22
Potential rate of nitrogen accumulation of grains	kg ha ⁻¹ d ⁻¹	table ^e	table ^e	+ 10	+ 10	-0.47	-0.12
Residual nitrogen fraction of leaves	kg ha ⁻¹ • (kg DM ha ⁻¹) ⁻¹	table ^e	table ^e	- 10	- 10	-0.55	-0.21
Onset of leaf death due to nitrogen shortage	-	0.4-0.9 ^a	0.4-0.9 ^a	as measured in the experiment	0.6-0.8	- 24 ^f	14 ^f

^a basically from van Keulen & Seligman (1987), calibrated on data sets PAGV1 and PAGV3

^b Groot (unpublished data)

^c van Keulen & Seligman (1987)

^d input

^e Groot (1987)

^f Absolute change in output (kg grain dry matter ha⁻¹).

Table 30a. Fine sensitivity analysis of the damage model. Relative sensitivity of end-of-season grain yield calculated with the damage model run with data of EEST84. In the runs the leaf area index was simulated. Reference grain weight is 9898 kg ha^{-1} without aphids, 8389 kg ha^{-1} with aphid damage according to hypothesis I and 8636 kg ha^{-1} according to hypothesis II. Relative sensitivity is calculated as the ratio of percentage change in grain weight and percentage change in parameter value.

Parameter	Unit	Reference value	% change in parameter	Relative sensitivity			
				Hypothesis I		Hypothesis II	
				Yield	Damage	Yield	Damage
Average apterous aphid weight	mg	table ¹	+10	0.63	-0.09	0.60	
Extinction coefficient for honeydew	-	0.8	-25	0.03	0.00	0.03	
Fraction of honeydew deposited on ears	-	0.3	+33	-0.03	0.00	-0.02	
Suction rate	$\text{kg mg}^{-1} \text{ d}^{-1}$	$8.92 \cdot 10^{-9}$	-33	-0.00	0.00	-0.01	
% reduction of AMAX after 15 days	-	24	+10	0.63	-0.09	0.60	
% increase in rate of dark respiration after 15 days	-	35	-10	0.68	-0.09	0.63	
			+20	0.31	-0.06	0.39	
			-20	0.30	-0.06	0.38	
			+20	0.21	-0.04	0.27	
			-20	0.20	-0.04	0.27	

¹ Function of the development stage of the crop.

Table 30b. Coarse sensitivity analysis of the damage model. Contribution of damage components to total damage in percentage of total damage, calculated under both hypotheses on partitioning of phloem sap between grain and aphids. For explanation of the hypotheses see text.

Hypothesis	Total damage (kg ha ⁻¹)	Damage components		
		Feeding (%)	Photosynthesis reduction (%)	Respiration increase (%)
I	1532	51	28	21
II	1323	37	36	27

reserves are depleted in the run without aphids. Damage due to all components increases with time. Damage due to uptake of phloem sap continues to increase after the departure of the aphids (Day 221), as enhanced nitrogen translocation, due to feeding, results in lower photosynthesis and increased rates of leaf death later in the simulation. This accounts for 37% of the total direct damage.

As under hypothesis II the demand of the grains is only partly met as a consequence of aphid feeding, damage occurs from grain set onwards. Damage due to reduction of net photosynthesis starts after grain-filling becomes dependent upon photosynthesis. With the departure of the aphids from the system, damage due to the uptake of phloem sap does not increase, as the rate of nitrogen translocation is assumed to be unaffected, in contrast to hypothesis I.

The effect of rain is evaluated by assuming complete removal of honeydew and its effects after daily precipitation of at least 5 mm, which occurred on Days 190 to 193 for EEST84. The effect on yield is less than 1%.

In experiments (Rossing, in prep.), an increase in the rate of dark respiration up to 56% is found one day after a honeydew application of 64 kg ha⁻¹ onto flag leaves. The efficiency of light use was decreased by 26% in one instance, two weeks after a honeydew application of 109 kg ha⁻¹. These effects were introduced in the model, combined with the reduction of the maximum rate of photosynthesis already described. The consequence for grain yield is an 8% (691 kg ha⁻¹) decrease, due to increased dark respiration and 3% (300 kg ha⁻¹), due to decrease in light use efficiency.

In a preliminary version of the model, van Roermund et al. (1986) modelled the aphid sink using a demand for carbohydrates and the nature of the competition according to hypothesis I. This is repeated here for EEST84, also using hypothesis II. The results are similar to the model runs where aphids exerted a demand for nitrogen.

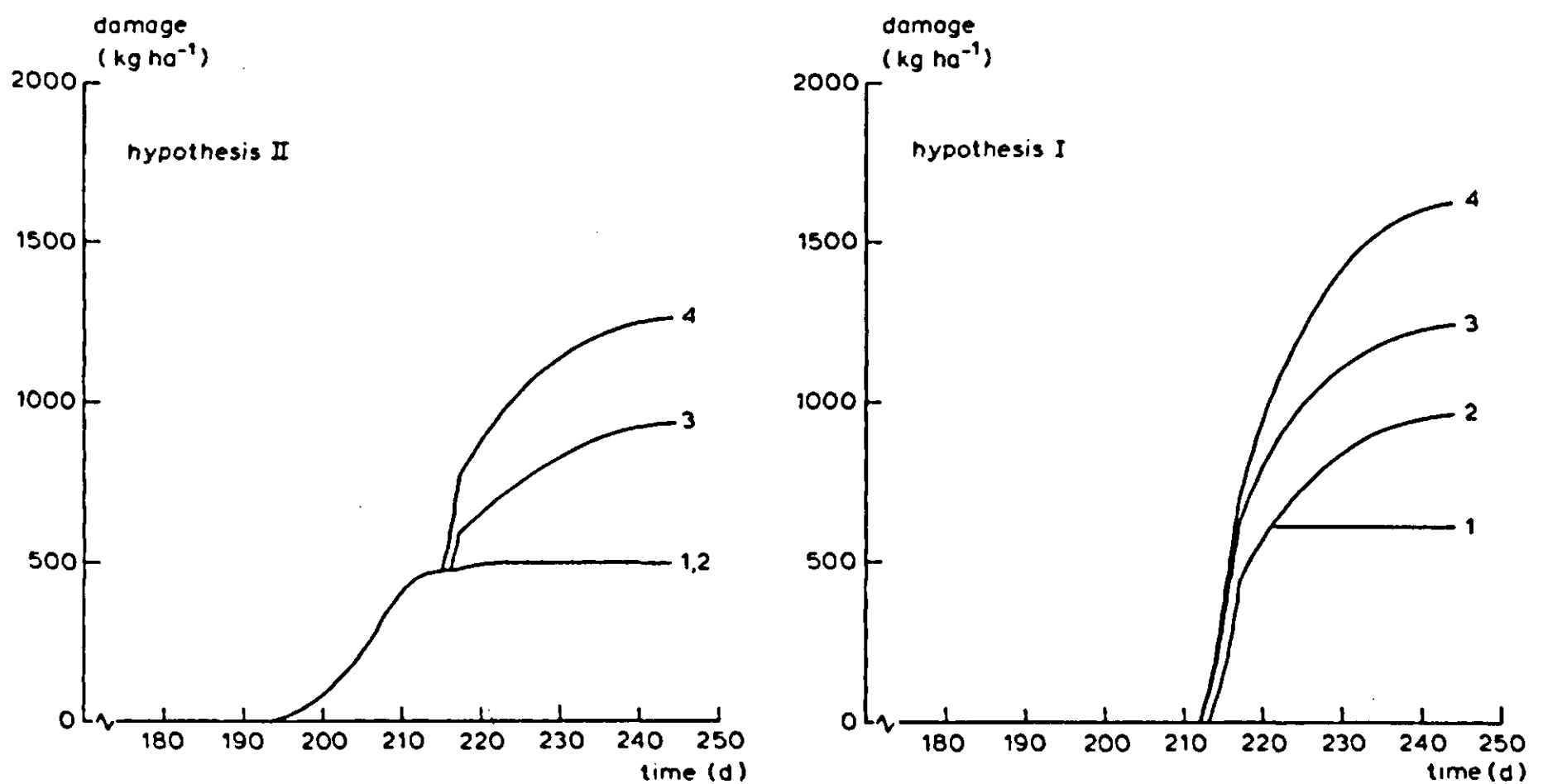


Figure 73. Simulated total damage (grain yield reduction, kg ha^{-1}) and damage components using two alternative hypotheses on the direct effects of *Sitobion avenae*. Data of EEST84, the highest aphid infestation. 1: carbohydrate uptake. 2: carbohydrate and nitrogen uptake. 3: carbohydrate and nitrogen uptake + increased maintenance respiration. 4: carbohydrate and nitrogen uptake + increased maintenance respiration + decreased maximum photosynthesis.

Exercise 76

- Explain the signs of the relative sensitivities in Table 30a.
- Recalculate the absolute damage (in kg ha^{-1}) as it was simulated with the model after the parameter values were changed.

Conclusions Quantitative information available on winter wheat – *S. avenae* interaction, is integrated in a simulation model of growth of winter wheat. As the information on the effect of *S. avenae* on the sink-source relations is incomplete, the model is used to evaluate the quantitative consequences of alternative hypotheses describing the direct effects. Most effects observed in field experiments can be explained by the hypotheses, but each one only provides a partial explanation. The maximum difference between the hypotheses in simulated final yield is 360 kg ha^{-1} .

4.4.6 Application to management

As indicated above, quantitative model evaluation is desirable before results can be used in a management environment. Although the evaluation presented here is only qualitative, the model is used to contribute to the calculation of dynamic economic thresholds as an example of model application. For this purpose, aphid populations of equal relative growth rate, and timing of the peak density as for EEST84, are introduced in the damage model as explained in the previous Subsection. Total damage per aphid per day for the various yield levels is shown in Figure 74. In Table 31 damage per aphid per day is calculated for various periods of crop development. At the higher yield levels, early infestations cause the greater damage as the effects of carbohydrate and nitrogen uptake persist for the rest of the season. At low yield levels, this pattern is obscured by the low values involved and the increasing significance of feeding damage with increasing crop age, as such crops lack compensation by photosynthesis due to their low leaf area indices.

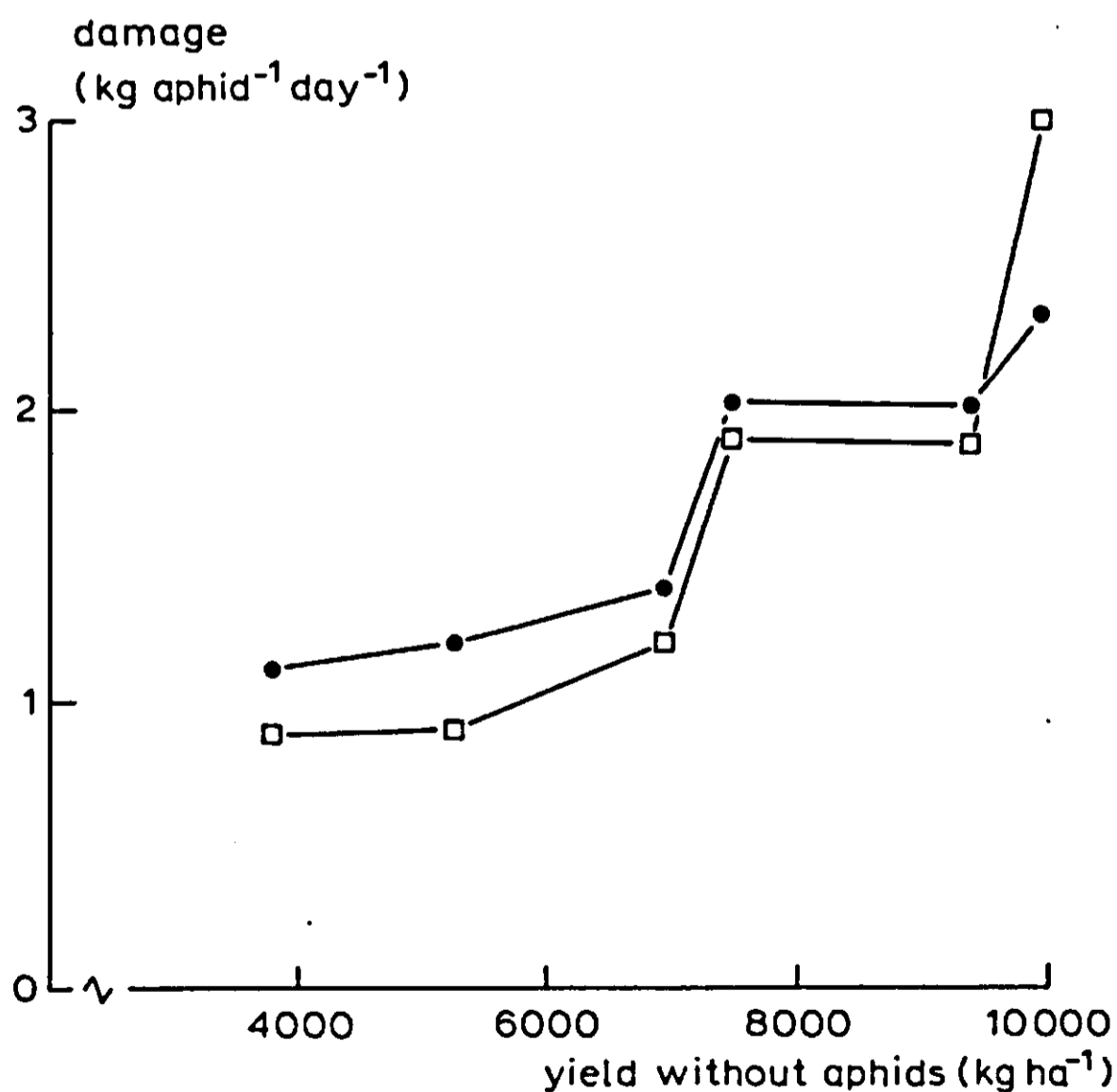


Figure 74. Damage per aphid per day at various yield levels, calculated with the damage model using alternative hypotheses to describe the direct effects of *Sitobion avenae*: hypothesis I (—□—) and hypothesis II (—●—)

Table 31. Simulated damage (kg aphid⁻¹ day⁻¹) for various crop growth stage periods, calculated under hypotheses I and II on aphid-crop interaction.

Data set	Hypothesis	Crop growth stages (Decimal Code)					
		60-65	65-69	69-71	71-73	73-75	75-79
EEST83	I	0.53	0.90	0.65	0.50	1.07	1.17
	II	0.53	1.16	1.14	1.14	1.03	1.22
PAGV1	I	0.57	0.72	0.55	0.54	0.90	1.48
	II	0.57	1.16	1.10	1.08	1.15	1.48
PAGV2	I	1.60	1.41	1.14	1.00	1.19	1.28
	II	1.60	2.19	1.63	1.41	1.23	1.28
PAGV3	I	2.66	3.59	2.60	2.05	1.77	1.12
	II	2.66	3.11	2.60	2.19	1.81	1.43
BOUWING84	I	8.46	5.32	3.73	3.64	1.73	1.08
	II	8.46	5.32	3.88	3.74	1.86	1.25
EEST84	I	11.26	6.72	4.72	4.61	2.79	1.78
	II	11.26	6.72	4.57	3.94	1.91	1.29