# ON DAMAGE, UNCERTAINTY AND RISK IN SUPERVISED CONTROL

## aphids and brown rust in winter wheat as an example

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# On Damage, Uncertainty and Risk in Supervised Control

## aphids and brown rust in winter wheat as an example

Proefschrift

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# Stellingen

1. De positieve relatie tussen opbrengstniveau van wintertarwe en schade door de graanluis wordt veroorzaakt door honingdauw.
   *Dit proefschrift*

2. De schadedrempel is een subjectieve maat.
   *Zadoks, J.C., 1985. On the conceptual basis of crop loss assessment: The threshold theory. A. Rev. Phytopathol. 23: 455-473*

3. Het wenteltrapalgoritme is een goede vervanger voor de traditionele benadering in onzekerheidsanalyse, waarbij gebruik wordt gemaakt van een lineair metamodel.
   *Jansen, M.J.W., Rossing, W.A.H. & Daamen, R.A., 1993. Monte Carlo estimation of uncertainty contributions from several independent multivariate sources. In: Proceedings Congress Predictability and nonlinear modelling in natural sciences and economics. 5-7 April 1993, Wageningen. In press*

4. "Nut" is nutteloos bij advisering van telers over taktische beslissingen in de gewasbescherming.
   *Schoemaker, P.J.H., 1982. The expected utility model: its variants, purposes, evidence and limitations. J. Econ. Liter. 20:529-563*

5. Informatie en pesticiden zijn substitueerbare produktiemiddelen.
   *Dit proefschrift*

6. Pannell's conclusie dat voor onkruiden onzekerheid leidt tot uitstellen van chemische bestrijding, is grotendeels het gevolg van een statische analyse, waarbij de populatiedynamica ten onrechte wordt verwaarloosd.
   *Pannell, D.J., 1990. Responses to risk in weed control decisions under expected profit maximization. J. Agric. Econ. 41:391-403*

7. De opheffing, rond 1991, van het waarschuwingssyteem voor graanziekten, EPIPRE, en het waarschuwingssysteem voor *Phytophthora infestans* in aardappel, valt niet te rijmen met de voorbeeldfunktie die beide systemen wordt toebedeeld in het Meerjarenplan Gewasbescherming.

8. Promovendi aan de Landbouwuniversiteit gaan minstens zes maal hun boekje te buiten.

9. De kwalitatieve karakterisering van cultivars in de Beschrijvende Rassenlijst voor Landbouwgewassen dient te worden vervangen door een kwantitatieve, gebaseerd op productie-ecologische grootheden.

10. Een verbod van de import van veenturf is een effektieve maatregel ter bescherming van natuur- en milieubelangen in binnen- en buitenland.

11. In de romp van de specialisatie Ecologische gewasbescherming (LU-studierichting Planteveredeling en gewasbescherming) wordt onvoldoende aandacht besteed aan produktie-ecologie.

12. Belangenbehartiging door de agrarische standsorganisaties dient niet alleen bedreven te worden in vergaderzaal en wandelgang, maar ook op *beeldbuis, markt en braderie.*

13. Dubbel-blinde of dubbel-ziende beoordeling van wetenschappelijke publicaties is te verkiezen boven de huidige half-ziende, waarbij één-oog al snel tot koning verwordt.

14. In 'het natuurlijk milieu voor wetenschap' is geen plaats voor een monocultuur van proefschriftkaften.

Walter A.H. Rossing
On damage, uncertainty and risk in supervised control
aphids and brown rust as an example
Wageningen, 25 oktober 1993

# Abstract

In supervised control of pests and diseases real-time information on pest and disease intensity and cost-benefit analysis of decision alternatives are used to support farmers' decisions on pesticide application. This thesis focuses on improving supervised control in the pathosystem aphids - brown rust - winter wheat. First, effects of the grain aphid, *Sitobion avenae,* on crop physiology are studied to arrive at simple relations between aphid density and damage. Second, the consequences of uncertainty about the costs of alternative strategies for optimal timing of chemical control of aphids and/or brown rust (*Puccinia recondita*) are evaluated.

Uptake of assimilates by *S. avenae* and reduction of the rate of net leaf photosynthesis by honeydew were quantified and introduced into a model which simulates growth and development of winter wheat from flowering till ripeness. Attainable yields from 4000 to 10000 kg ha$^{-1}$ and damage at the higher yield levels were simulated satisfactorily. Honeydew caused more damage than assimilate uptake at crop development stages until milky ripeness. Attainable yield, crop development stage, and timing and intensity of infestation were of major importance in explaining variation in damage. The results of the simulation model were summarized in regression models which predicted damage at given infestation levels as good as the best published empirical model.

Sources of uncertainty in a decision model for evaluating costs of chemical control strategies were quantified using field data. Assessment of the contribution of various sources of uncertainty to model output uncertainty showed white noise in the relative growth rates of both aphids and brown rust to be the major cause of uncertainty. Risk-neutral damage thresholds representing pest intensities at which expected costs of control just exceed expected costs of no control, were considerably lower than the deterministic damage thresholds based on average input values. At the risk-neutral damage thresholds only 30% of chemical applications was found to be cost-effective. To support pest control under uncertainty a framework is proposed in which alternative strategies are evaluated in terms of 'profitability' and 'risk', operational measures of the economic objectives 'return on investment' and 'insurance', respectively.

**Additional index words:** damage threshold, decision support, honeydew, *Metopolophium dirhodum,* photosynthesis, profitability, *Puccinia recondita,* respiration, *Rhopalosiphum padi,* risk analysis, *Sitobion avenae, Triticum aestivum,* uncertainty analysis, yield reduction

*Aan mijn ouders*
*Aan Erna*

# Voorwoord

De afronding van het proefschrift is een goede gelegenheid een woord van dank te richten aan al diegenen die mij stimuleerden en ondersteunden bij de totstandkoming ervan.

Mijn dank gaat in de eerste plaats naar mijn ouders. Zij wekten mijn belangstelling voor landbouw en milieu en gaven mij alle steun en ruimte deze verder te ontwikkelen. Het afscheid van mijn vader, twee jaar geleden, doet mij daarom ook nu bijzonder verdriet.

Mijn promotoren, prof. dr P. van Beek, prof. dr ir R. Rabbinge en prof. dr J.C. Zadoks, zijn de geestelijke vaders van het project "Verbetering van bestrijdingsmiddelgebruik in de tarweteelt" waarop ik in 1984 werd aangesteld. Als begeleidingscommissie waakten zij gedurende de eerste jaren over de grote lijnen in het projekt, daarbij veel ruimte latend voor mijn eigen inbreng. Vergaderingen van de begeleidingscommissie waren enerverende oefeningen in het slaan van bruggen tussen operationele analyse en produktie-ecologie. Daarnaast boden de vergaderingen mij een kijkje in de keuken van onderzoeksmanagement, een onvermijdelijk onderwerp als drie chefkoks aan één tafel zitten. Paul, de discussies over de aanpak van geleide bestrijding als beslisprobleem hebben me geholpen scherper zicht te krijgen op het onderwerp. Professor Zadoks, u wil ik bedanken voor de consciëntieuze wijze waarop u de manuscripten van commentaar voorzag en het vertrouwen dat u in mij stelde bij de aanstelling als toegevoegd onderzoeker bij de vakgroep Fytopathologie. Rudy, aan jou een speciaal woord van waardering als direkte begeleider gedurende het overgrote deel van het werk. Je enthousiasme en je vermogen resultaten in een groter kader te plaatsen werkten zeer motiverend. Het vertrouwen dat je in me stelde was een belangrijke stimulans bij het afronden van het werk. Daarnaast noem ik graag de mogelijkheden die je me bood kennis en vaardigheden te ontwikkelen op het brede terrein van onderwijs en onderzoek in de produktie-ecologie.

Bij het onderzoek naar schade door graanluizen zijn de inspanningen van Rob Groot, Herman van Roermund, Nicoline Roozen en Erna van de Wiel van grote waarde geweest. Als onderdeel van hun afstudeervakken deden zij experimenteel werk en legden de basis voor het simulatiemodel. Hennie de Ruiter leverde een essentiële bijdrage aan de organisatie en uitvoering van de veldproeven. Peter van Leeuwen (CABO-DLO) zorgde ervoor dat de fotosynthese metingen in Cel 9 op rolletjes liepen. Dank ook aan de CABO-DLO medewerkers in ruw lab en chemisch lab die zorgden voor een betrouwbare en vlotte verwerking van de gewasmonsters. Wim Mantel (IPO-DLO) en Seamus Ward ontsloten de set met veldwaarnemingen over populatiedynamica van en schade door graanluizen. Thanks are also due to Leena Mattila, IAESTE student at the department of TPE during the summer of

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Walter Rossing
Wageningen, 9 september 1993.

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## Chapter 1

# General introduction

# Supervised control of pests and diseases

Insects and plant pathogens reduce yields of crops. Worldwide, the extent of physical yield reduction, or damage, caused by these biotic growth reducing factors has been estimated to be 35% (Cramer, 1967). Variation in damage between locations and years is caused by differences in the nature and extent of pest or disease attack, and by differences in crop growth rates caused by the availability of resources (Rabbinge, 1986). Damage may lead to financial loss, depending on the price of the product (Zadoks, 1987). Regulation, rather than eradication, of pests and diseases has become the dominant paradigm in crop protection research (Zadoks and Schein, 1979). Regulation, or management, of pests and diseases aims at preventing unacceptable financial losses, utilizing knowledge of population dynamics and genetics, crop ecology, pest and disease control technologies, and economics of crop production. Different concepts of pest and disease management have evolved, differing in objectives of management, and the range of control technologies considered, including supervised control, integrated control and integrated farming.

Supervised pest and disease control is an approach which advocates the use of real-time information on pest and disease intensity and cost/benefit analysis of decision alternatives as a basis for rational decisions on pesticide application by farmers. Damage thresholds representing the intensity of the insect or plant pathogen populations at which the benefit of chemical control, the damage prevented, just exceeds its cost (Mumford and Norton, 1984; Zadoks, 1985), are used to summarize the results of the cost/benefit calculations. Farmers are given the information through advisory systems (Zadoks and Schein, 1979). Research supplies monitoring techniques and algorithms for calculating costs and benefits.

The concept of supervised pest and disease control has been developed alongside the concept of integrated pest and disease management. Integrated pest and disease management aims at utilizing all suitable techniques and methods in as compatible a manner as possible to maintain the insect and plant pathogen populations at levels below the damage threshold (*after* FAO, 1968). Thus, while in supervised control chemical control is optimized within the constraints imposed by other crop husbandry practices, in integrated pest and disease management these constraints constitute decision variables to be optimized along with decisions on chemical control. Both concepts focus on minimizing loss or maximizing yield in one field and in one growing season. For assessment of decisions over a multi-year period at the farm level, other objectives are relevant as well. This has led to the concept of integrated farming (Vereijken *et al.*, 1986).

Supervised pest and disease control, integrated pest and disease management as well as integrated farming represent responses to the negative economic and ecological side-effects arising from high nutrient inputs and prophylactic use of pesticides to control pests and diseases in several pathosystems in industrialized and developing countries (reviews by Perkins, 1980; Eveleens, 1983; Dekker, 1986; MJP-G, 1991). Prophylactic use of pesticides enhances pesticide resistance in target organisms, which causes control measures to fail. Destruction of beneficial natural enemies causes resurgence of pests and development of secondary pests. Negative side effects may extend beyond the limits of the agro-ecosystem since certain pesticides, especially insecticides, accumulate on their way through the food chain (review by Edwards, 1987), or contaminate natural resources such as drinking water and agricultural soils.

Many systems based on the concepts of supervised control or integrated pest and disease management have been developed. A recent state of the art report in a European perspective is given by Secher and Murali (1991). Due to various reasons, only few systems have been adopted in practice (Rabbinge, 1981; Norton, 1982). A system which has been adopted widely both in the Netherlands, the country of origin, and in other European countries, is EPIPRE (Zadoks, 1981, 1989a; Drenth *et al.*, 1989). EPIPRE is a computer-based system which generates field-specific recommendations on chemical control of five diseases and of three species of cereal aphids in winter wheat. Recommendations are based on calculations of costs and benefits of chemical control, using as inputs a farmer's observations of crop development stage, and disease and aphid incidence, i.e. presence on a predetermined number of tillers. The system utilizes mathematical models of population dynamics, including the effect of pesticides, and damage to calculate financial loss without and with immediate chemical control. Field experiments showed EPIPRE to result in financial returns which were, on average, equal to but more variable than returns of conventional procedures, as a result of lower pesticide input (Reinink, 1986). Positive effects which could not be expressed in financial value included increased notion and knowledge of damage thresholds among participants, and decreased exposure of farmers and environment to pesticides (Zadoks, 1984; Rossing *et al.*, 1985).

Initially, cost/benefit calculations in EPIPRE were based on purely empirical models, which were updated yearly using the latest information on prices of product and pesticides. In parallel, research was initiated aimed at heuristically upgrading the system (Drenth and Stol, 1990; Daamen, 1991b). In this thesis results of upgrading studies are reported. Attention is focussed on (1) increasing fundamental knowledge of the causes of damage in the winter wheat - grain aphid pathosystem to arrive at simple relations between pest intensity and damage, and (2) development of an approach to supervised control in which uncertainty about biological aspects of the system is taken into account.

## Problem definition and research objectives

### Quantification of damage by Sitobion avenae in winter wheat

*Sitobion avenae* F., the economically most important cereal aphid species in western Europe, affects growth of winter wheat in three ways: directly by removing assimilates, and indirectly by interfering with plant processes through honeydew deposited on green plant surfaces (Rabbinge *et al.*, 1981) and by the transmission of barley yellow dwarf virus. Virus transmission is economically important only when plants are infected in an early stage of development (Plumb *et al.*, 1990) and it is not considered here.

Early attempts to quantify the effect of aphids on yield of winter wheat have related damage to the intensity of infestation, expressed as aphid density at the peak of the infestation, or as the number of aphid-days, i.e. the integral of aphid density over time. Such approaches have resulted in descriptive regression models. In addition, plant development stage at the time of infestation, production level of the crop, host plant cultivar, and fungicide type (Dik, 1990) were reported to affect cereal aphid damage (reviews by Dixon (1987) and Wellings *et al.* (1989)). Due to the complex, multifactorial nature of damage purely experimental, descriptive approaches are likely to be insufficient to identify the variables which contribute most to variation in damage between years and locations. The difficulties of a purely descriptive approach can be overcome by adopting a crop ecological viewpoint (Rabbinge, 1986; Rabbinge *et al.*, 1989).

Crop ecology aims at understanding crop growth and production using knowledge of physiological processes and their interaction with the abiotic and biotic environment. Pests and diseases, but also weeds, air pollutants and extreme weather conditions reduce yield from the attainable to the actual yield level. The size of the yield reduction, i.e. damage, depends on (1) the growth rate of the healthy crop, (2) the plant growth processes affected by a growth reducing factor, i.e. the injury components, and (3) the timing and the intensity of growth reduction. The timing and the intensity of reduction of crop growth depend on the life cycle and the population dynamics of a particular insect or plant pathogen. Explanatory crop growth models represent valuable tools for integrating effects of growth reducing factors on crop growth, and give more insight into the consequences of different injury components for damage.

The first objective of this study is to quantitatively explain the effects of *S. avenae* on growth and production of winter wheat at different attainable production levels based on insight in the direct and the indirect effects on physiological processes.

## Consequences of uncertainty for supervised control

The costs associated with a decision on chemical control of pests and diseases are not known with certainty at the time the decision is made. The uncertainty is caused by lack of information on the actual state of the system and on the future course of the system. Uncertainty may be described as the occurrence of different states of nature, each with its own likelihood. Uncertainty about costs of a control decision can be quantified and expressed in statistical terms. In contrast, risk may be described as the occurrence of unfavourable outcomes, i.e. high costs, and represents the subjective interpretation of uncertainty. Several studies have shown farmers to have different perceptions of the uncertainty about costs associated with an infestation of a particular insect or plant pathogen, often not in accordance with reality (Tait, 1987). Therefore, information on such uncertainty is relevant for farmers' decision making.

In classical supervised control, which was developed by entomologists and phytopathologists, uncertainty about the financial consequences of alternative decisions is ignored (Zadoks, 1985). Agricultural economists have introduced the decision theoretic approach into pest management research in which uncertainty is taken into account. In this approach an *a priori* probability distribution of financial loss due to a pest or a disease is updated with information obtained by e.g. monitoring, use of a system model, or consultation of an expert, to arrive at *a posteriori* probability distributions for alternative decisions on control using Bayesian statistics. By combining these *a posteriori* probability distributions with a mathematical model of a farmer's attitude towards the various possible outcomes, customized damage thresholds are calculated (Carlson and Main, 1976; Mumford and Norton, 1984; Gold, 1989, Pannell, 1991). Tait (1987) put forward that such ready-made thresholds are useful only if they reflect an individual farmer's attitude towards uncertainty, and if the farmer carries out the recommendation without further assessment. Both conditions appear not to be met. Risk attitudes of individual farmers have been found to vary considerably between years, and farmers use information from various sources before taking a decision (Tait, 1987; Webster, 1987). Therefore, an alternative approach to supervised control is needed.

The second objective of this study is to develop a framework for supporting decisions on chemical control in which uncertainty and risk are taken into account, in a fashion compatible to the managerial objectives of a farmer.

## Approach and thesis outline

Figure 1.1 shows the various steps followed to address the two objectives of this study, together with references to relevant chapters. In Chapters 2, 3 and 4 the first objective of this study is addressed. A preliminary model was constructed which simulated growth and development of winter wheat from flowering to ripeness, into which a submodel of the direct and indirect effects of injury by *S. avenae* was incorporated. The crop model was based on an existing model of growth and development of winter wheat, while the submodel was constructed and parameterized using literature data. Uncertainty in the data describing the effect of honeydew on leaf photosynthesis was found to have major effects on simulated yield and damage. This led to experiments in which the effects of a substitute honeydew solution on leaf photosynthesis was measured at three moments after application onto flag leaves of field-grown wheat plants (Chapter 2). In addition, a field experiment is reported in Chapter 2 which was used to evaluate the updated preliminary model.

Model evaluation involved comparison of the simulation results of both the crop model and the combined crop-injury model to field data (Chapter 3). The evaluation was carried out both qualitatively and quantitatively. The combination model could only be tested at high attainable yields, whereas experimental data representing a range of attainable yields were available for comparison with simulation results of the crop model.

In Chapter 4 the combination model was used to assess the effect of the timing of the infestation and the attainable yield level on damage. The results of these simulation experiments were summarized in regression equations relating simulated damage per aphid-day to simulated attainable yield, for different periods of crop development. The agreement between predicted and measured damage was assessed for the simulation-based regression models and for a number of other published damage models, using independent experimental data. This provided an additional test of the performance of the simulation model.

In Chapters 5, 6 and 7 the second objective of this study is addressed. The development of a framework for supporting decisions on chemical control in which uncertainty and risk are taken into account is illustrated for two pathosystems represented in EPIPRE: cereal aphids (especially *S. avenae* and *Metopolophium dirhodum*) and brown rust (*Puccinia recondita*).

In Chapter 5 the relations are described which were used to predict the costs of different strategies on chemical control in a particular field. Together,

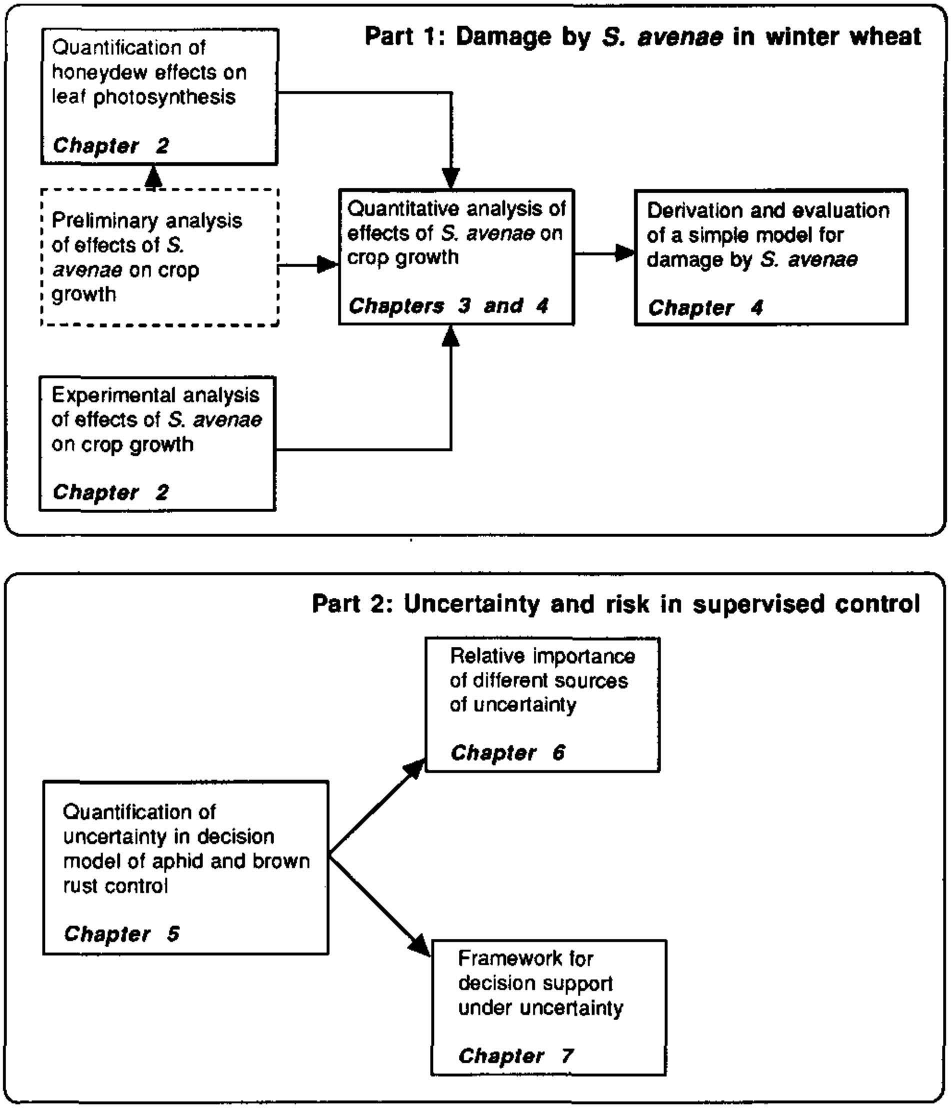


Figure 1.1. Outline of the thesis.

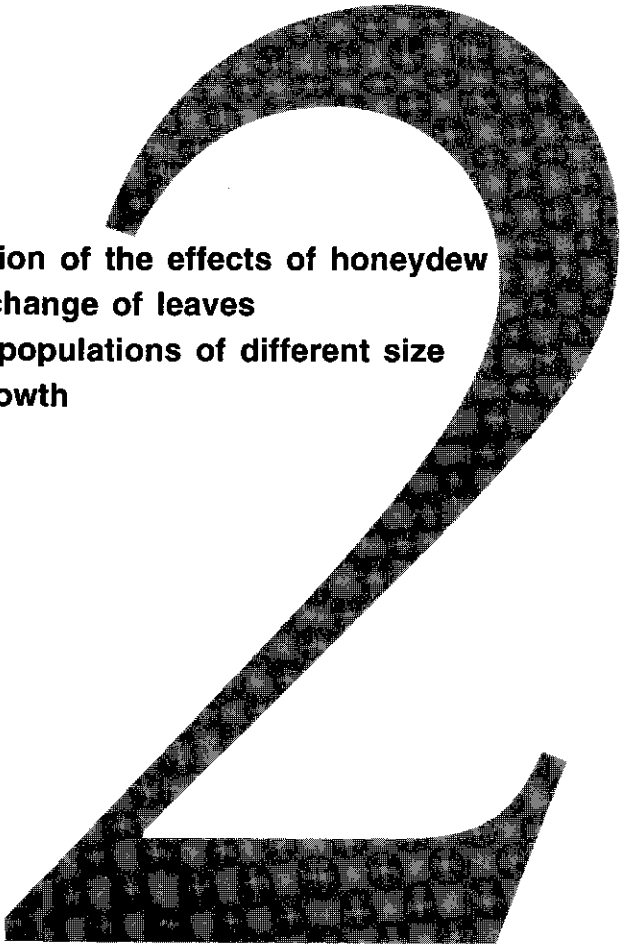
these relations constitute a decision model which represents a part of EPIPRE, updated with recent experimental data and extended (upgraded) with a statistical description of the various sources of uncertainty. The model pertains to an arbitrary commercial winter wheat field in the Netherlands.

The decision model described in Chapter 5 was used in two ways. First, the model was used to prioritize the sources of uncertainty with respect to their contribution to the uncertainty about model outcome. This led to a methodology for allocation of research resources (Chapter 6). Second, the model was used to demonstrate the consequences of alternative chemical control decisions in terms of their contribution to pest control objectives (Chapter 7).

Part 1

# Damage in winter wheat caused by the grain aphid *Sitobion avenae*

Chapter 2



## Quantification of the effects of honeydew on gas exchange of leaves and aphid populations of different size on crop growth

Rossing, W.A.H. & Wiel, L.A.J.M. van de, 1990.
Simulation of damage in winter wheat caused by the grain aphid *Sitobion avenae*. 1. Quantification of the effects of honeydew on gas exchange of leaves and aphid populations of different size on crop growth.
*Netherlands Journal of Plant Pathology* 96:343-364.

**Abstract** Damage in winter wheat caused by the grain aphid, *Sitobion avenae* F., was studied in the laboratory and at field level. Honeydew substitute solution was applied to flag leaves of winter wheat plants. One and fifteen days after application, the rates of net carbon dioxide assimilation and transpiration were measured. The rate of dark respiration was significantly higher one day after application of honeydew substitute as compared to the control. Other parameters describing the carbon dioxide - light response were not significantly affected. Fifteen days after honeydew substitute application, the two experimental years yielded different results. Under hot and dry conditions, the rate of dark respiration was higher while the rate of carbon dioxide assimilation at high irradiance, the mesophyll conductance and the leaf nitrogen content were lower than for the untreated control. In addition, chlorotic symptoms were visible. At moderate temperature and relative humidity, the initial light use efficiency was significantly lower fifteen days after treatment with honeydew substitute whereas other parameters were not significantly affected.

In field experiments at two locations natural aphid populations consisting of mainly *S. avenae* were treated weekly with an aphicide from crop development stages DC 71, 73, 75 and 77, respectively, to create infestations of different size and duration. In the unsprayed controls densities reached 15.8 and 44.4 aphids per tiller, amounting to 182 and 544 aphid-days, respectively. Crop samples were analyzed weekly, starting at flowering. At the smaller natural infestation, no significant effect on any yield component nor on yield was found at any treatment. The larger infestation caused a significant reduction of leaf area index, leaf weight, amount of water-soluble carbohydrates and grain weight on various sample dates when the infestation was not sprayed before DC 75. No effects were found on tiller and grain density nor on nitrogen content of plant parts at harvest.

## Introduction

Aphids infesting cereal crops constitute an irregularly occurring economic problem in western Europe (Watt, 1983). In the Netherlands, *Sitobion avenae* F. and *Metopolophium dirhodum* Wlk. are the most abundant species in winter wheat (*Triticum aestivum* (L.)), *Rhopalosiphum padi* L. occurring in lower densities (Carter *et al.*, 1982). Although both *S. avenae* and *M. dirhodum* can cause significant damage (Ankersmit and Carter, 1981; Holt *et al.*, 1984), *S. avenae* usually attains higher densities under Dutch conditions. Therefore, attention is focussed on *S. avenae* in this paper.

In supervised crop protection, analysis of costs and benefits of chemical control is carried out to establish the pest density at which pesticide use pays off (Zadoks, 1985; Drenth *et al.*, 1989; Zadoks, 1989a). Such analysis requires information on the population dynamics and the damage caused by the pest. The population dynamics of *S. avenae* has been studied extensively, considering both temporal (e.g. Carter *et al.*, 1982) and spatial aspects (e.g. Rabbinge and Mantel, 1981). This paper considers the effect of injury by the grain aphid *S. avenae* on the yield of winter wheat.

Studies on the effect of injury by *S. avenae* and *M. dirhodum* on wheat yield indicate that damage is a complex function of the distribution of aphids over the plant, the duration and the size of the aphid infestation, and factors which determine and limit crop growth (Wratten, 1975, 1978; Wratten and Redhead, 1976; Entwistle and Dixon, 1987; Wellings *et al.*, 1989). In an early report (van Roermund *et al.*, 1986a, b), we applied a systems approach making use of a simulation model. Essential processes of the *S. avenae* - winter wheat system were described and quantified in a simulation model, which was then used to predict the dynamics of the state of the system. The system consisted of a sufficiently large field of winter wheat growing at the prevailing weather conditions, the available amount of soil nitrogen and the aphid infestation present. Water limitation was not included. The processes distinguished were photosynthesis, uptake of nitrogen from the soil and distribution of carbohydrates and nitrogen over various plant parts. In the model, *S. avenae* affected both the availability of carbohydrates and nitrogen for the grains (Rabbinge and Coster, 1984) and the rate of carbon dioxide assimilation (Rabbinge *et al.*, 1981). Variables describing the state of the system were crop development stage and dry weight and nitrogen content of plant organs. Preliminary runs with the simulation model showed the effect of honeydew on photosynthesis to be a significant component of damage. The information available concerns mainly the effects of honeydew immediately after application to leaves (Rabbinge *et al.*, 1981). Data on the effects after a longer period of time are limited and also, data to evaluate the performance of the model are needed.

This paper reports results of experiments in which the short and medium term effects of honeydew on gas exchange of flag leaves of winter wheat were quantified. Secondly, the results of field experiments to establish the effect of *S. avenae* populations of various size and duration on crop growth and production are presented.

## Material and methods

References to crop development stage are in Decimal Code (DC) (Zadoks *et al.*, 1974). Weights are expressed in terms of dry matter.

### The effect of honeydew on gas exchange of leaves

In a series of gas exchange experiments, the effect of honeydew of *S. avenae* on parameters characterizing the carbon dioxide assimilation - light curve was established. To ensure a sufficiently large supply of honeydew, a substitute solution was prepared, reflecting the amino-acid and sugar composition of real honeydew. This composition was determined in a separate experiment carried out before the start of the gas exchange studies.

### *Chemical composition of honeydew*

To determine the chemical composition of honeydew excreted by *S. avenae* feeding on winter wheat, 20 healthy winter wheat plants (cv. Arminda, DC 61), grown on a clay soil (30-65% lutum) near Wageningen, the Netherlands, under optimal nutrient supply (approximately 200 kg (N) ha$^{-1}$), were potted and transferred to a greenhouse (average temperature 18 °C, 90% relative humidity). Apterous adult *S. avenae*, collected from a virus-free culture, were confined to the ears using perspex leaf cages (Vereijken, 1979). Each cage contained approximately 40 aphids. After three days, the cages were removed and rinsed with a small amount of warm demineralised water. The solution was filtered to remove exuvia and dirt and stored at -18 °C. Amino-acids were analyzed by high pressure liquid chromatography. Sugars were determined volumetrically according to the method of Schaffer and Somogyi (1933), adapted by Vertregt and Verhagen (1979). The method distinguishes between monosaccharides (glucose and fructose) and higher sugars: di- and oligosaccharides. Using an ultrasonic bath, a 25 (weight-) % honeydew substitute solution was prepared for use in the experiments, similar in amino-acid composition to real honeydew, using glucose and sucrose as sugars.

### *Plant material for the gas exchange experiments*

In March 1986, winter wheat plants, cv. Arminda (DC 12), grown outdoors were transferred to 26 cm diameter buckets (content 5 liter) filled with clay soil (22 % lutum) and supplied with an abundant fertilizer rate of phosphate and potassium. Five plants were potted in each bucket. The buckets were dug into the ground arranged in a rectangle, mimicking the natural crop structure. To prevent border effects a strip of one meter around the plot was sown to spring wheat. At development stages DC 14-15 and DC 23, nitrogen fertilizer was applied at a rate of 1 and 2 gram ammonium-nitrate per bucket, respectively. Water was supplied when necessary. One day prior to treatment the buckets were dug up and transferred to a roofed part of the experimental site to prevent rain from washing off the honeydew during the experiment. The plants were sprayed with triadimenol (Baytan, 0.5 g l$^{-1}$) during the second week of the experiment to control a beginning powdery mildew infection.

In 1987, winter wheat plants (cv. Urban) were not transferred to pots because of extremely wet field conditions in March. The plants remained at an experimental farm at Nagele, North East Polder and were subjected to normal farm practice until the start of the experiment in July. Total soil nitrogen amounted to 275 kg ha$^{-1}$. Weeds, mildew and aphids were controlled chemically.

*Experimental procedure and data analysis*

Both in 1986 and 1987 flag leaves of winter wheat plants were given one of the following treatments: no applications (control), application of water (water), single application of honeydew substitute (hd1) and twice an application of honeydew substitute, waiting half an hour between applications (hd2). The latter two treatments were aimed at creating honeydew substitute deposits of different size. Honeydew substitute was applied with a pipette and gently spread over the adaxial leaf surface of the flag leaves with the forefinger.

For the measurements, plants were moved to the laboratory. In 1987, plants were dug up carefully and individually transferred to 5 l buckets. The soil-moisture level was maintained at field capacity.

Rates of carbon dioxide assimilation, respiration and transpiration of flag leaves were measured, using laboratory equipment for routine measurements of photosynthesis comparable to the type described by Louwerse and Van Oorschot (1969). Relative humidity in the leaf chambers was approximately 50-60% and air temperature was 23 °C. Four or five flag leaves of main stems from at least two different buckets were included in each leaf chamber. Net carbon dioxide assimilation, transpiration, stomatal resistance and carbon dioxide concentration inside the substomatal cavity were calculated according to the procedure of Goudriaan and Van Laar (1978).

The measurements were carried out one and fifteen days after treatment. In addition, carbon dioxide assimilation of flag leaves treated twice with honeydew substitute was measured three days after treatment in 1987 (abbreviated as hd3d) to evaluate whether effects found one day after treatment persisted. In this way, short and medium-term effects of honeydew were quantified. Evaluation of long-term effects (after 4 to 5 weeks) are beyond the scope of this paper.

Two series of measurements were carried out. In the first, irradiance was varied from 0 J m$^{-2}$ s$^{-1}$ to approximately 300 J m$^{-2}$ s$^{-1}$ in 6 steps at a constant ambient carbon dioxide concentration of 632 mg m$^{-3}$ (345 ppm). The carbon dioxide assimilation - light response curve is described by a negative exponential function (Goudriaan, 1982):

$$P_n = (P_m + R_d)(1 - \exp(-\varepsilon I / (P_m + R_d))) - R_d \qquad (2.1)$$

where $P_n$ is the net carbon dioxide assimilation rate (μg ($CO_2$) $m^{-2}$ $s^{-1}$), $P_m$ the carbon dioxide assimilation rate at light saturation and an ambient carbon dioxide concentration of 632 mg $m^{-3}$ (μg ($CO_2$) $m^{-2}$ $s^{-1}$), $R_d$ dark respiration rate (μg ($CO_2$) $m^{-2}$ $s^{-1}$), $\varepsilon$ the initial light use efficiency (μg ($CO_2$) $J^{-1}$), and $I$ the amount of absorbed photosynthetically active radiation (PAR, J $m^{-2}$ $s^{-1}$). The parameters $P_m$, $R_d$ and $\varepsilon$ were determined for each leaf chamber, using a non-linear least squares regression procedure (SAS, 1985).

In the second series the ambient carbon dioxide concentration was increased to 900 ppm and decreased to 50 ppm in discrete steps, at maximum irradiance of *ca.* 300 J $m^{-2}$ $s^{-1}$. Carbon dioxide assimilation was related to internal $CO_2$ concentration to eliminate the variation in stomatal resistance, using a negative exponential function (Kropff, 1987):

$$P_n = P_{m,m} (1 - \exp(-g_m (C_i - \Gamma) / P_{m,m})) \qquad (2.2)$$

where $P_{m,m}$ is the carbon dioxide assimilation rate at carbon dioxide saturation (μg ($CO_2$) $m^{-2}$ $s^{-1}$), $C_i$ the internal carbon dioxide concentration (μg ($CO_2$) $m^{-3}$), $\Gamma$ the carbon dioxide compensation point (μg ($CO_2$) $m^{-3}$), and $g_m$ the mesophyll conductance (m $s^{-1}$). The parameters $P_{m,m}$, $\Gamma$ and $g_m$ were determined per leaf chamber, using a non-linear least squares regression procedure (SAS, 1985).

Differences in parameter values between treatments were evaluated in an analysis of variance. If differences at the 10% significance level were found, the Student-Newman-Keuls test was carried out to compare treatment means (Snedecor and Cochran, 1980).

After carbon dioxide assimilation measurements in 1986 MgO-powder was dusted onto the leaf area to mark the area covered with honeydew substitute. The result was photographed for estimation of the leaf area covered. As the outlines of the areas were blurred this method yielded only a rough estimate. Therefore, instead of measuring the area covered, the amount of honeydew applied was determined in a separate experiment, treating 10 flag leaves of winter wheat plants (DC 61) with honeydew substitute as described above. After one day, each leaf was washed with warm, demineralized water and the resulting solutions were pooled. The solution was filtered and freeze-dried and the dried material weighed. The same procedure was followed for 10 leaves treated with water. In 1987, the same procedure was applied to the leaves immediately after the carbon dioxide assimilation measurements. Also, the amount of nitrogen in the flag leaves used for photosynthesis measurements was determined.

In 1987, the diffuse reflection of photosynthetically active radiation was measured using a spectro-radiometer (LiCor Li-1800) to establish the additional reflection caused by honeydew.

## Quantification of damage in field experiments

### *Experimental layout*

In 1984, two experiments were carried out at the experimental farms "de Bouwing" and "de Eest", the Netherlands. Information on the experimental sites and on crop husbandry practices is given in Table 2.1. The experiments were set up according to a randomized block design, with 4 treatments and 6 replications. Plots were 8 m wide and 11 m long on "de Bouwing" and 8 m wide and 9 m long on "de Eest", respectively, yielding a net-plot of 4 m width and two adjacent buffer strips of 2 m width each. The latter received the same treatment as the net-plot.

Table 2.1. General information on the field experiments at the experimental farms "de Bouwing" and "de Eest".

| | de Bouwing | de Eest |
|---|---|---|
| Location | Randwijk, central river-clay | Nagele, sea-clay |
| Cultivar | Arminda | Arminda |
| Soil type | clay 35-55% | clay 33% |
| Previous crop | potatoes | sugar beets |
| Sowing date | 22 October 1983 | 4 November 1983 |
| Sowing rate | 138 kg ha$^{-1}$ | 148 kg ha$^{-1}$ |
| N-mineral (kg ha$^{-1}$) * | 60 | 80 |
| N fertilization (kg ha$^{-1}$) | 80+65 | 60+80+40 |
| Weed control | 22 Oct: 8 l ha$^{-1}$ Tok Ultra | 4 May: |
| Disease control | 15 May: 0.5 kg ha$^{-1}$ Bayleton+ | 8 l ha$^{-1}$ DM68 |
| | 2 kg ha$^{-1}$ maneb | 20 June: |
| | 15 June: 3 kg ha$^{-1}$ Corbeltop | 0.5 kg ha$^{-1}$ Bayleton |
| | 18 July : 2 kg ha$^{-1}$ Bayleton CF+ | +2 kg ha$^{-1}$ maneb |
| | 2 kg ha$^{-1}$ maneb | +1 kg ha$^{-1}$ Captafol |
| Plant density at flowering | 546 ± 59 (SEM) | 636 ± 56 (SEM) |
| Yield of treated control | 8754 ± 461 (SEM) | 8114 ± 559 (SEM) |

* amount of soil nitrogen available in February.

### *Treatments*

Chemical control of cereal aphids (Pirimor, 0.25 kg ha$^{-1}$) was carried out to create infestations of different size. The treatments consisted of:

A. weekly chemical control of aphids starting at DC 71;
B. weekly chemical control of aphids starting at DC 73;
C. weekly chemical control of aphids starting at DC 75;
D. weekly chemical control of aphids starting at DC 77;
E. *no chemical control of aphids;*

The treatments started at DC 71, approximately coinciding with aphid immigration. On "de Bouwing" the aphid population collapsed after DC 75. Therefore treatments C and D were omitted. On "de Eest" treatment B was not carried out due to technical problems.

### *Crop analysis and aphid sampling*

Samples of 50 ear-bearing tillers chosen at random from the buffer of each plot, were harvested at weekly intervals, from flowering (DC 60) until final harvest (DC 92). After assessment of the development stage, the tillers were divided into ear, leaf lamina and stem fractions. The stem fractions included ligules, auricules and leaf sheaths in addition to the true stem. Leaf laminae were further divided into living and dead tissue fractions. Living leaf area was measured using a leaf area meter (Licor Li-3100). Dry weights of the fractions were determined after drying at 105 °C for 15 h. The stem fractions were dried at 70 °C for 15 h to enable subsequent chemical analysis of water-soluble carbohydrates. After threshing and drying at 105 °C for 15 h, grain dry weight and 1000 kernel weight were determined. The nitrogen content of the fractions and the amount of soluble carbohydrates in the stem fraction were determined at 2 to 3 weekly intervals starting at flowering (day 179 at "de Eest" and day 172 at "de Bouwing"). Final grain yield was also determined by combine harvesting. The crop at "de Eest" was treated with glyphosate one week prior to harvest as the straw was still partly green, although the ears were ripe.

The size of the aphid population was monitored by recording the aphid incidence (i.e. presence on a tiller) in a sample of 100 tillers per plot. If incidence was lower than 10% or higher than 90% the absolute number of aphids on 100 tillers per plot was recorded. In this way, the coefficient of variation in the population estimates was less than *ca.* 10% (Ward *et al.*, 1985). Monitoring started at DC 40. The aphid-index (Rautapää, 1966) was calculated by integrating the aphid density over time, using linear interpolation to calculate aphid density between data points.

Differences between treatments were evaluated in an analysis of variance. If differences at the 5% significance level were found, treatments were ranked according to the Student-Newman-Keuls test.

## Results

### The effect of honeydew on gas exchange of leaves

*Chemical composition of honeydew*

The amino-acid and sugar composition of honeydew of *S. avenae* is shown in Table 2.2. Of the 13 amino-acids identified, threonine was present in the largest amount. Mono- and higher saccharides occurred in approximately equal amounts.

*Weather conditions during the gas exchange experiments*

The time courses of daily maximum and minimum temperatures in 1986 and 1987 and the amount of precipitation in 1987 are shown in Figure 2.1. Daily

Table 2.2. Chemical composition of honeydew of *Sitobion avenae*, feeding on ears of winter wheat, development stage DC 61. The weight-ratio of sugar and amino-acids is 46.

| Sugars | % | Amino-acids | % |
|---|---|---|---|
| glucose, fructose | 51.5 | alanine | 3.7 |
| higher saccharides | 48.5 | aspartic acid | 7.9 |
| | | glutamic acid | 6.3 |
| | | glycine | 2.3 |
| | | histidine | 9.8 |
| | | isoleucine | 4.5 |
| | | leucine | 7.3 |
| | | lysine | 2.5 |
| | | proline | 8.0 |
| | | phenylalanine | 6.3 |
| | | threonine | 26.3 |
| | | tyrosine | 7.3 |
| | | valine | 7.8 |
| | ----- | | ----- |
| | 100.0 | | 100.0 |

temperature was higher in 1986 with maximum values frequently exceeding 25 °C. During the second half of the experimental period in 1987, heavy thunderstorms occurred. In 1987, dew was recorded on the leaves, whereas in 1986 plants remained dry throughout the experimental period as a result of their sheltered position.

*Honeydew amount and leaf coverage*

In 1986, 6.4 g m$^{-2}$ honeydew substitute was recovered one day after single application compared to 10.9 g m$^{-2}$ after double application. The fraction of the leaf area covered amounted to 50-60% in both treatments. No measurements of the amount of honeydew substitute were carried out fifteen days after application.

In 1987, differences between the treatments were small. One day after treatment, the total amount recovered was 2.8 ± 0.7 (SEM) g m$^{-2}$ and 2.3 ± 0.6 (SEM) g m$^{-2}$ for single and double application, respectively. The fraction of leaf area covered varied from 10% to 20% in both treatments. After fifteen days, no differences with the water treated control were measured. Because of the

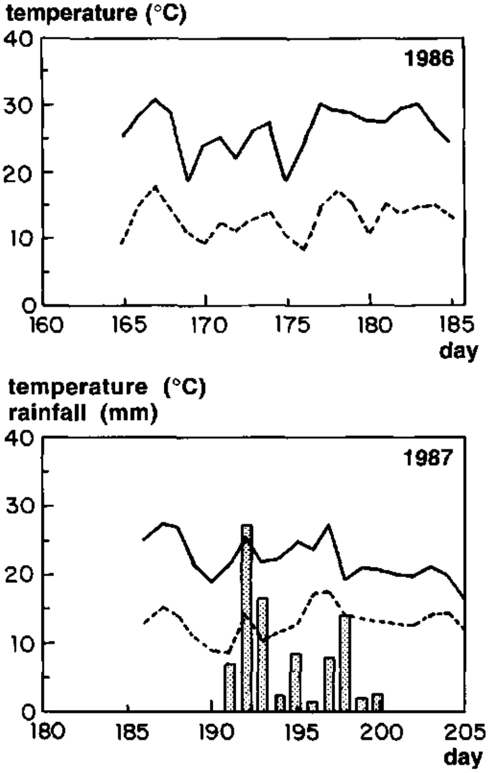


Figure 2.1. Daily maximum (——) and minimum (- - - -) temperatures (°C) during the experiments in 1986 and 1987, and precipitation (mm, ▨) in 1987. Precipitation was absent in 1986.

similarity in the amount of honeydew recovered, the results of the treatments hd1 and hd2 were lumped before analysis, indicated as hd. Three days after double application, the total amount of honeydew recovered was 2.2 ± 1.2 (SEM) g $m^{-2}$. Here too, the fraction of leaf area covered amounted to 10 to 20%.

*Effects of honeydew on carbon dioxide assimilation - light response*

The results of carbon dioxide assimilation measurements at various light intensities in 1986 and 1987 are shown in Figures 2.2, 2.3 and 2.4. For brevity, the results of the water treated control are not shown. These did not differ significantly from the untreated control.

Application of honeydew substitute resulted in a significant reduction of the rate of carbon dioxide assimilation at high irradiances fifteen days after double application under the hot and dry conditions of 1986 (Figure 2.2). Other-

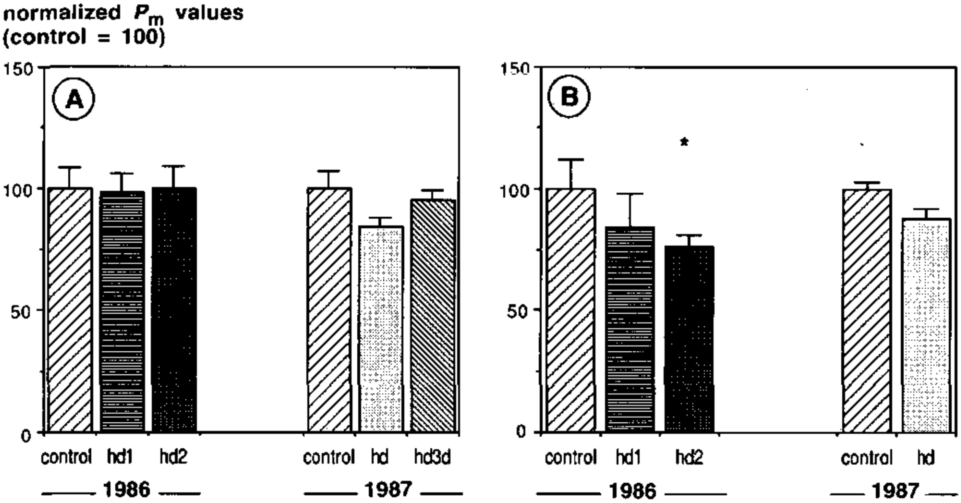


Figure 2.2. Normalized estimated parameter values of the rate of carbon dioxide assimilation at high irradiance ($P_m$) of flag leaves of winter wheat treated with honeydew substitute. A: one day (hd1, hd2, hd) and three days after treatment (hd3d); B: fifteen days after treatment. A description of the treatments is given in the text. Error bars represent the normalized standard error of the mean. An asterisk above a bar indicates a significant difference as compared to the water treated control ($p < 0.10$).
For the control treatment in 1986, values of $P_m$ were (mean ± SEM): $P_m$ = 1.50 ± 0.11 mg $CO_2$ $m^{-2}$ $s^{-1}$ after one day and $P_m$ = 1.23 ± 0.14 mg $CO_2$ $m^{-2}$ $s^{-1}$ after fifteen days. For the control treatment in 1987, values of $P_m$ were (mean ± SEM): $P_m$= 0.77 ± 0.06 mg $CO_2$ $m^{-2}$ $s^{-1}$ after one day and $P_m$ = 0.77 ± 0.03 mg $CO_2$ $m^{-2}$ $s^{-1}$ after fifteen days. The number of replications is indicated in Table 2.3.

wise changes in $P_m$ were minor after treatment.

The rate of dark respiration was increased significantly one day after treatment in both experimental years. Three days after application in 1987, however, values of $R_d$ were comparable to the control. Fifteen days after treatment, a significant increase in $R_d$ was measured in 1986 following double honeydew application (Figure 2.3).

The initial light use efficiency was significantly reduced in 1987 fifteen days after application (Figure 2.4). Other treatments with honeydew substitute did not have a clear effect.

The ratio of carbon dioxide assimilation and transpiration ($P/T$) and the ratio of internal and ambient carbon dioxide concentrations ($C_i/C_a$) were not affected by the honeydew treatments, except after double application in 1986 (Table 2.3). In the latter case, the ratio of assimilation and transpiration was reduced after both one and fifteen days, while the ratio of internal and ambient carbon dioxide concentration was increased one day after application.

Leaf nitrogen contents are shown in Table 2.4. In 1986, differences were small one day after treatment. After 15 days, a significant reduction of the

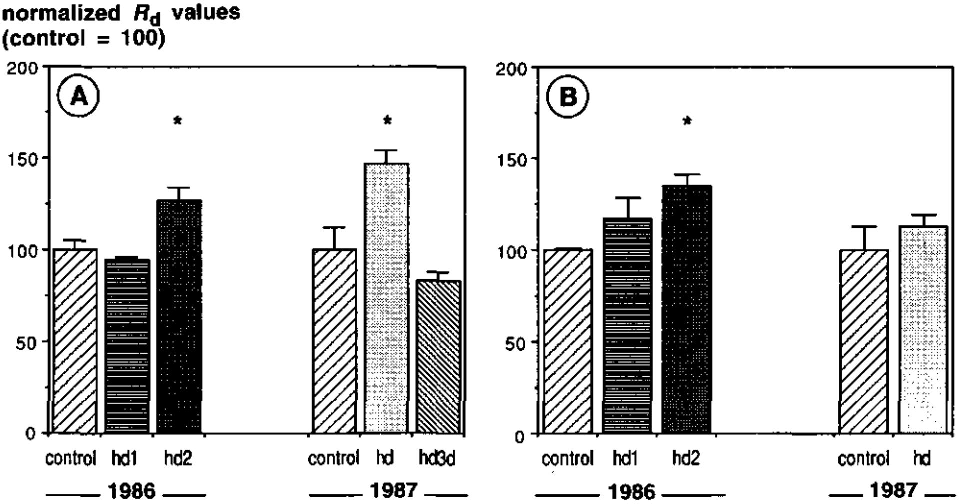


Figure 2.3. Normalized estimated parameter values of the rate of dark respiration ($R_d$) of flag leaves of winter wheat treated with honeydew substitute. A: one day (hd1, hd2, hd) and three days after treatment (hd3d); B: fifteen days after treatment. A description of the treatments is given in the text. Error bars represent the normalized standard error of the mean. An asterisk above a bar indicates a significant difference as compared to the untreated control ($p < 0.10$). For the control treatment in 1986, values of $R_d$ were (mean ± SEM): $R_d = 34 \pm 2$ μg $CO_2$ $m^{-2}$ $s^{-1}$ after one day and $R_d = 31 \pm 0.3$ μg $CO_2$ $m^{-2}$ $s^{-1}$ after fifteen days. For the control treatment in 1987, values of $R_d$ were (mean ± SEM): $R_d = 33 \pm 4$ μg $CO_2$ $m^{-2}$ $s^{-1}$ after one day and $R_d = 20 \pm 3$ μg $CO_2$ $m^{-2}$ $s^{-1}$ after fifteen days. The number of replications is indicated in Table 2.3.

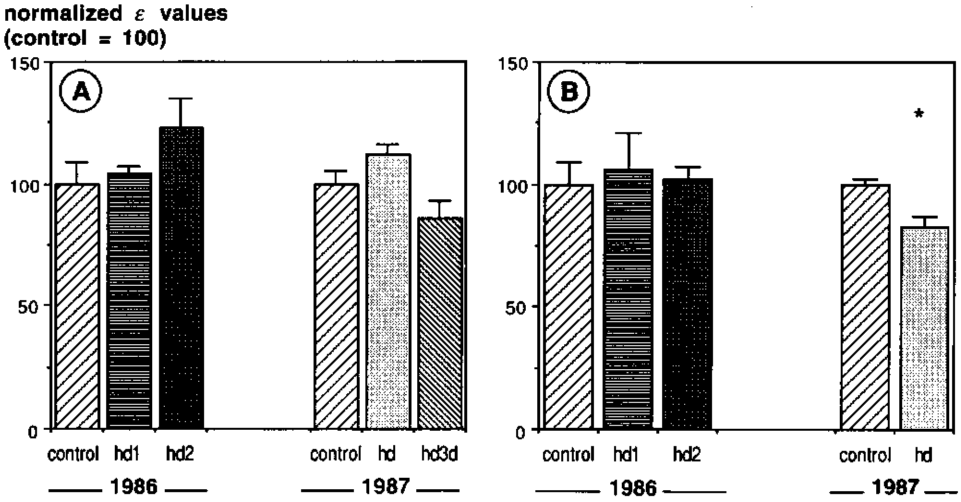


Figure 2.4. Normalized estimated parameter values of the initial light use efficiency (ε) of flag leaves of winter wheat treated with honeydew substitute. A: one day (hd1, hd2, hd) and three days after treatment (hd3d); B: fifteen days after treatment. A description of the treatments is given in the text. Error bars represent the normalized standard error of the mean. An asterisk above a bar indicates a significant difference as compared to the untreated control ($p < 0.10$). For the control treatment in 1986, the values of ε were (mean ± SEM): ε = 12±1.1 μg $CO_2$ $J^{-1}$ after one day and 13±1.1 μg $CO_2$ $J^{-1}$ after fifteen days. For the control treatment in 1987, values of ε were (mean ± SEM): ε = 12±0.6 μg $CO_2$ $J^{-1}$ after one day and 13±0.3 μg $CO_2$ $J^{-1}$ after fifteen days. The number of replications is indicated in Table 2.3.

nitrogen content was found in leaves treated with honeydew substitute as compared to the untreated control. In 1987, no differences in leaf nitrogen content were found after treatment.

### *Effects of honeydew on carbon dioxide assimilation - carbon dioxide response*

A significant (31%) decrease in mesophyll conductance occurred fifteen days after double application of honeydew in 1986. Otherwise, parameter values did not differ significantly from the untreated control.

### *Reflection of photosynthetically active radiation*

Average reflection of photosynthetically active radiation was not affected by treatment of leaves with honeydew substitute in 1987.

Table 2.3. Ratio of rates of photosynthesis and transpiration ($P/T$, g kg$^{-1}$) and internal and ambient $CO_2$ concentration ($C_i/C_a$) of flag leaves of winter wheat one, three and fifteen days after treatment with honeydew substitute. Light intensity was approximately 300 J m$^{-2}$ s$^{-1}$. A description of the treatments is given in the text. Different letters following treatments indicate significant differences (ANOVA followed by Student-Newman-Keuls test, $p < 0.10$).

| One and three days after treatment | | | | | | | |
|---|---|---|---|---|---|---|---|
| 1986 | | | | 1987 | | | |
| treatment | *n* | $P/T$ | $C_i/C_a$ | treatment | *n* | $P/T$ | $C_i/C_a$ |
| control | 4 | 1.40 a | 0.60 p | control | 4 | 1.11 a | 0.68 p |
| water | 2 | 1.39 a | 0.57 p | water | 2 | 1.16 a | 0.65 p |
| hd1 | 2 | 1.36 a | 0.56 p | hd | 8 | 1.13 a | 0.65 p |
| hd2 | 4 | 1.17 b | 0.70 q | | | | |
| | | | | hd3d | 2 | 1.09 a | 0.70 p |
| **Fifteen days after treatment** | | | | | | | |
| 1986 | | | | 1987 | | | |
| treatment | *n* | $P/T$ | $C_i/C_a$ | treatment | *n* | $P/T$ | $C_i/C_a$ |
| control | 2 | 1.37 a | 0.59 p | control | 4 | 0.93 a | 0.75 p |
| water | 2 | 1.35 a | 0.57 p | water | 2 | 1.09 a | 0.73 p |
| hd1 | 2 | 1.38 a | 0.56 p | hd | 8 | 0.92 a | 0.73 p |
| hd2 | 4 | 1.18 b | 0.62 p | | | | |

## Quantification of damage in field experiments

### *Aphid population dynamics*

In both experiments, the aphid population consisted mainly of *S. avenae*, the fraction *M. dirhodum* never exceeding 5%. *R. padi* was not found in the samples. Aphid density is shown in Figure 2.5. In the untreated (E-)plots peak densities were reached at DC 75, amounting to 15.8 and 44.4 aphids per tiller on "de Bouwing" and "de Eest", respectively. Chemical control resulted in aphid loads of 17.1 (A), 66.0 (B) and 182.2 (E) aphid-days at "de Bouwing" and 50.6 (A), 328.6 (C), 481.8 (D) and 544.3 (E) aphid-days at "de Eest".

Table 2.4. Nitrogen content (g (N) $kg^{-1}$ (dry matter)) of flag leaves of winter wheat one, three and fifteen days after treatment with honeydew substitute. A description of the treatments is given in the text. Different letters following treatments indicate significant differences (ANOVA followed by Student-Newman-Keuls test, $p < 0.10$).

| One and three days after treatment | | | | | |
|---|---|---|---|---|---|
| 1986 | | | 1987 | | |
| treatment | *n* | N-content | treatment | *n* | N-content |
| control | 4 | 44 a | control | 4 | 35 a |
| water | 2 | 46 a | water | 2 | 38 a |
| hd1 | 2 | 46 a | hd | 8 | 36 a |
| hd2 | 4 | 43 a | | | |
| | | | hd3d | 2 | 35 a |
| **Fifteen days after treatment** | | | | | |
| 1986 | | | 1987 | | |
| treatment | *n* | N-content | treatment | *n* | N-content |
| control | 2 | 42 a | control | 4 | 25 a |
| water | 2 | 44 ac | water | 2 | 28 a |
| hd1 | 2 | 38 bc | hd | 8 | 26 a |
| hd2 | 4 | 37 b | | | |

### *Crop growth analysis*

In neither experiment, the tiller density was affected by the aphid populations. This is expected as tiller density is determined before and during booting when no aphids were found. In the calculations constant tiller densities were used, 546 $m^{-2}$ for "de Bouwing" and 636 $m^{-2}$ for "de Eest", respectively. At "de Bouwing", treatment E significantly decreased leaf weight and leaf area index as compared to treatment A on two sample dates but no significant effects on grain yield were found (Table 2.5 and Figure 2.6a). Neither stem weight, amount of soluble carbohydrates nor nitrogen fractions of the organs were consistently reduced after aphid infestation. Green leaf area duration was reduced, although not significantly.

Table 2.5. Course of grain weight ($10^{-6}$ kg), leaf area index ($m^2$ $m^{-2}$), leaf weight (kg $ha^{-1}$) and green leaf area duration ($m^2$ $m^{-2}$ day) of winter wheat at three treatments on 'de Bouwing' in 1984. Treatments, not followed by the same letter are significantly different ($p < 0.05$). Treatment A: weekly chemical control of aphids from DC 71; treatment B: weekly chemical control of aphids from DC 73; treatment E: no chemical control of aphids.

| Date | Treatment | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | A | | | B | | | E | | |
| | grain weight | leaf area index | leaf weight | grain weight | leaf area index | leaf weight | grain weight | leaf area index | leaf weight |
| 20 June | | 4.7 | 1922 | | | | | | |
| 27 June | | 3.3 | 1398 | | | | | | |
| 3 July | | 3.4 | 1619 | | | | | | |
| 11 July | 12.3 a | 2.9 k | 1383 p | | | | 13.1 a | 2.7 k | 1256 p |
| 18 July | 18.2 a | 3.1 k | 1401 p | | | | 18.8 a | 3.2 k | 1365 p |
| 25 July | 20.4 a | 2.2 k | 1412 p | 19.9 a | 2.1 k | 1239 p | 20.3 a | 2.0 k | 1312 p |
| 31 July* | 20.3 a | 1.8 k | 1056 p | 18.6 a | 1.5 k | 892 pq | 20.4 a | 1.2 k | 746 q |
| 8 August | 38.3 a | 0.8 k | 422 p | 38.7 a | 0.5 k | 277 p | 40.0 a | 0.4 k | 217 p |
| 23 August | 39.5 a | 0.0 k | 0 p | 37.8 a | 0 k | 0 p | 40.0 a | 0.1 k | 5 p |
| Green leaf area duration | 163 e | | | 157 e | | | 151 e | | |

* significant block effect grain weight, leaf area index and leaf weight ($p$<0.05)

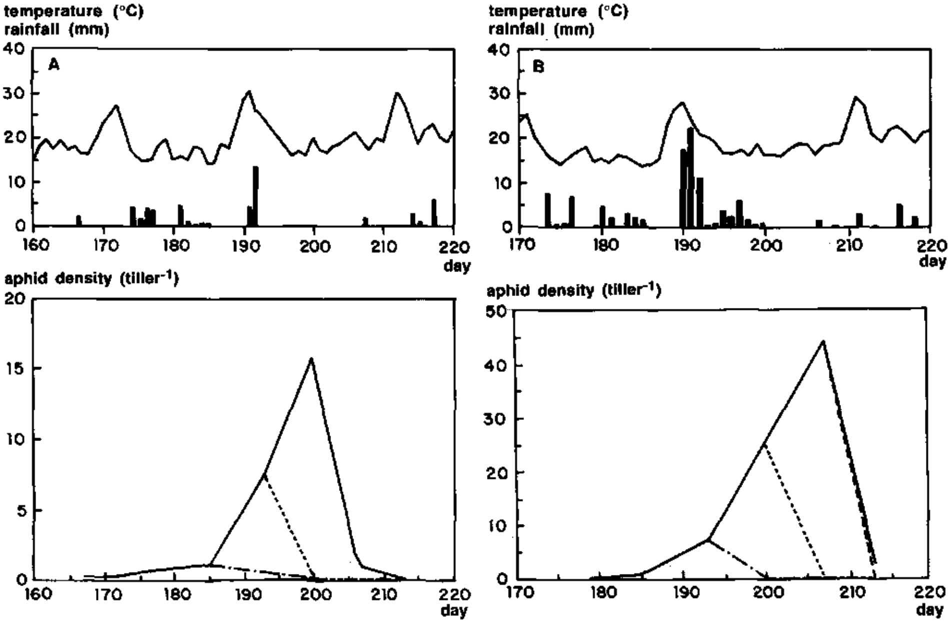


Figure 2.5. Aphid density (tiller$^{-1}$) at "de Bouwing" (a) and "de Eest" (b) during the field experiment in 1984. Treatments at "de Bouwing" are A (··········), B (- - - -) and E (——). Treatments at "de Eest" are A (··········), C (- - - -), D (— — —) and E (——). At the top of the graphs daily maximum temperature (°C, ——) and precipitation (mm, bars) during the experiment are indicated. A description of the treatments is given in the text.

At "de Eest", treatments C, D and E significantly reduced grain yield, grain weight, leaf weight and leaf area index on a number of sampling dates (Figure 2.6b and Table 2.6). Grain density (the number of grains per square meter) was not affected by the treatments. Green leaf area duration was reduced significantly by treatments C, D and E as compared to treatment A (Table 2.6). Nitrogen fractions of leaves and ears were reduced significantly in treatment E (29.7 and 21.2 g kg$^{-1}$, respectively) as compared to treatment A (31.1 and 20.7 g kg$^{-1}$, respectively) on 25 July (day 207). At the final harvest, the amount of soluble carbohydrate in treatment E (8.9 g kg$^{-1}$) was significantly lower as compared to treatment A (31.3 g kg$^{-1}$).

Table 2.6. Grain weight ($10^{-6}$ kg), leaf area index ($m^2$ $m^{-2}$), leaf weight (kg $ha^{-1}$) and green leaf area duration ($m^2$ $m^{-2}$ day) of winter wheat at four treatments on 'de Eest' in 1984. Treatments, not followed by the same letter are significantly different ($p < 0.05$). Treatment A: weekly chemical control of aphids from DC 71; treatment C: weekly chemical control of aphids from DC 75; treatment D: weekly chemical control of aphids from DC 77; treatment E: no chemical control of aphids.

| Date | Treatment | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | | | C | | | D | | | E | | |
| | grain weight | leaf area index | leaf weight | grain weight | leaf area index | leaf weight | grain weight | leaf area index | leaf weight | grain weight | leaf area index | leaf weight |
| 27 June | | 4.52 | 1930 | | | | | | | | | |
| 3 July | | 3.99 | 1823 | | | | | | | | | |
| 11 July | | 4.00 | 1823 | | | | | | | | | |
| 18 July | 11.59 a | 4.03 k | 1933 p | | | | | | | 10.81 a | 4.02 k | 1887 p |
| 25 July | 16.25 a | 3.79 k | 2162 p | | | | | | | 16.15 a | 3.17 l | 1946 p |
| 31 July | 20.73 a | 3.10 k | 1781 pq | 19.74 a | 3.25 k | 2014 p | | | | 20.03 a | 2.67 l | 1484 q |
| 8 August | 32.74 a | 2.61 k | 1304 p | 30.30 ab | 2.31 kl | 1147 pq | 29.21 b | 1.99 kl | 988 q | 29.30 c | 1.85 l | 922 q |
| 15 August* | 34.56 a | 1.53 k | 806 p | 33.68 a | 0.91 l | 481 q | 30.62 b | 0.73 l | 396 q | 30.53 b | 0.89 l | 464 q |
| 23 August | 35.61 a | 0.22 k | 121 p | 32.60 a | 0.08 l | 57 p | 32.25 a | 0.10 l | 61 p | 31.88 a | 0.04 l | 24 p |
| 31 August | 34.18 a | 0.03 k | 20 p | 33.77 a | 0.00 k | 0 p | 31.91 a | 0.00 k | 0 p | 31.82 a | 0.00 k | 0 p |
| Green leaf area duration | 179 e | | | 172 f | | | 168 f | | | 160 g | | |

* significant block effect grain weight, leaf area index and leaf weight ($p$<0.05)

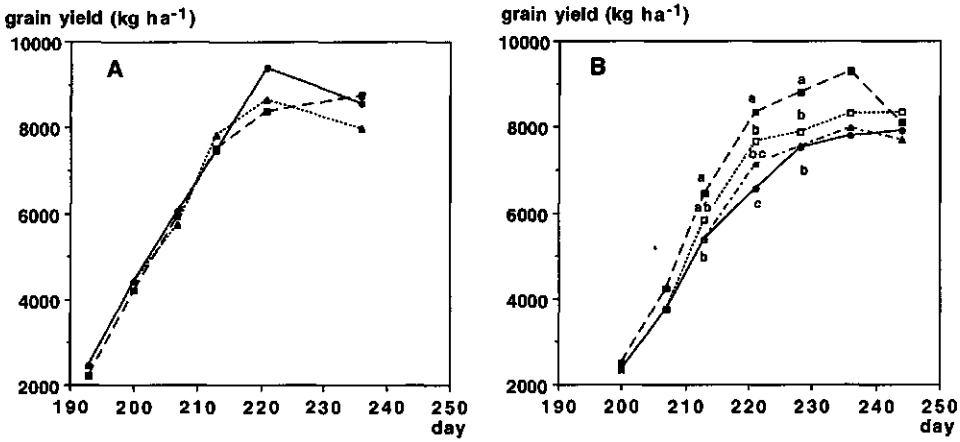


Figure 2.6. Grain yield (kg ha$^{-1}$) at "de Bouwing" (a) and "de Eest" (b). Treatments at "de Bouwing" are A (– –■– –), B (·····▲·····) and E (——●——). No significant differences between treatments were found. Treatments at "de Eest" are A (– –■– –), C (·····□·····), D (–·–▲–·–) and E (——●——). Similar or no letters for a treatment indicate no significant differences ($p < 0.05$). A description of the treatments is given in the text.

# Discussion

## The effect of honeydew on gas exchange of leaves

### *Data requirement*

In the simulation model constructed to predict damage by *S. avenae* in winter wheat, published information on effects of *S. avenae* on crop physiology was used for parameterization (van Roermund *et al.*, 1986a, b). Preliminary runs with the model revealed the need for additional information on the effect of honeydew on leaf carbon dioxide assimilation because simulated yield was sensitive to the parameter values used, whereas the parameter estimates were uncertain.

Early experiments concerning the effect of honeydew on carbon dioxide assimilation of wheat leaves considered effects both within five hours and one week after application (Rabbinge *et al.*, 1981). In these experiments, statistically significant reductions of the rate of carbon dioxide assimilation at high irradiance, the initial light use efficiency and the ratio of internal and ambient carbon dioxide concentrations were found immediately following application. These effects were attributed to impaired carbon dioxide exchange due to blocking of the stomata. The results of the carbon dioxide assimilation measurements one week after application were not conclusive due to lack of a control treatment.

### *Plant material*

In the present study, the condition of the plant material differed considerably between the two experimental years. Compared to 1986, the leaf nitrogen content of control plants was significantly lower in 1987, resulting in lower rates of carbon dioxide assimilation at high irradiance at a similar development stage. These differences were presumably caused by weather conditions before the experiment started. Average daily total global radiation during the four weeks preceding the experiments amounted to 1835 J $m^{-2}$ $d^{-1}$ in 1986 and 1577 J $m^{-2}$ $d^{-1}$ in 1987. Thus, the level of maximum photosynthesis in 1987 may reflect adaptation of the leaves to the conditions of lower light intensity. Moreover, successive periods of abundant precipitation and drought in 1987 may have adversely affected nitrogen uptake by the crop. The values of carbon dioxide assimilation in 1987 are comparable to those reported by Rabbinge *et al.* (1981).

### *Honeydew amount and leaf coverage*

The amount of sugars recovered from the leaves one day after application differed considerably between 1986 and 1987. Possible causes for the differences are differences in leaf wetness and mechanical effects of wind. In 1987, honeydew was applied to wet leaves, whereas in 1986 leaves were dry. In 1986, treated potted plants were placed on a roofed area at the experimental site, which reduced mutual cleaning of leaves in the wind.

Fifteen days after treatment in 1987, the amount of dry matter recovered from the leaf surface of treated leaves did not differ from the control. The decrease is attributed to the heavy rains between 13 and 20 July, and to consumption by phyllosphere fungi.

Fokkema *et al.* (1983) recovered 6.3 g $m^{-2}$ honeydew (as glucose) from leaves of glasshouse-grown wheat infested with more than one hundred aphids per ear. Unfortunately, the duration of the exposure of the plants to the population was not reported. Rabbinge and Coster (1984) measured honeydew production rates of *S. avenae* on winter wheat plants (DC 45-75). Using their data and the aphid infestation of treatment E at "de Eest" (which started in DC 71), we calculated the total amount of honeydew produced until DC 77 to be approximately 7 g $m^{-2}$ (leaf area index 3.4 $m^2$ $m^{-2}$). Under field conditions, the aphid population only occasionally exceeds densities of 30 aphids per ear and honeydew will be diluted by dew and rain. Thus, the amount of honeydew applied in 1986 represented a situation with a large aphid infestation, whereas the amount applied in 1987 was comparable to commonly occurring deposits.

### *Effects of honeydew on carbon dioxide assimilation - light response: one and three days after treatment*

One day after treatment with honeydew substitute, effects on the carbon dioxide assimilation - light response were similar in both experimental years. Values of the rate of dark respiration ($R_d$) were increased significantly compared to the control, in 1986 only at the larger amount applied. Neither carbon dioxide assimilation at high irradiance ($P_m$) nor the initial light use efficiency ($\varepsilon$) were significantly affected. Rabbinge *et al.* (1981) found a significant reduction of $P_m$ and $\varepsilon$ immediately after application of honeydew. No information was given on $R_d$. These authors attributed the reduction of $P_m$ and $\varepsilon$ to coverage of stomata, the size of the effect depending on the fraction of stomata covered. Apparently, the coverage of stomata affects carbon dioxide assimilation only for a short period of time. The fraction of stomata covered may decrease due to dew, crystallization of honeydew and removal of honeydew due to effects of stomatal movement. Scanning electron microscope photographs taken one day after honeydew application showed gaps around the stomata in the further intact honeydew film (personal communication R. Rabbinge, 1986, and own observations). Conclusions will be possible when the fraction of stomata covered by honeydew is estimated in combination with gas exchange parameters. New techniques for the former have recently been developed (Hurej and Van der Werf, 1993).

Increased values of $R_d$ one day after honeydew application have been tentatively ascribed to stimulation of phyllosphere saprophytic micro-organisms by Smedegaard-Petersen (1982) and Smedegaard-Petersen and Tolstrup (1985) who measured significant increases of $O_2$ consumption by leaves of barley, 12-24 hours after inoculation with saprophytic *Cladosporium* spp. and *Alternaria alternata.* The response of the plants subsequently declined until values comparable to the control were reached after five to seven days. In our experiments, three days after honeydew application no effects on dark respiration could be found. Thus, stimulation of the growth of the population micro-organisms by honeydew, if it occurred in our experiments, seemed limited to a few days. This agrees with results of Fokkema *et al.* (1983) who studied growth of populations of saprophytic fungi and bacteria on leaves of spring wheat *in vitro* after application of 4.5 g $m^{-2}$ 15% glucose solution. Populations increased exponentially until three days after application when the rate of increase decreased considerably even though the amount of glucose had only been consumed by 50% and still exceeded the amount of naturally occurring glucose.

### *Effects of honeydew on carbon dioxide assimilation - light response: fifteen days after treatment*

Fifteen days after treatment with honeydew substitute, the effects on the carbon dioxide assimilation - light response differed between the experimental years. The differences can be ascribed to differences in environmental conditions. In 1986, high temperature and low relative humidity caused crystallization of honeydew substitute and most likely reduced the growth of the phyllosphere mycoflora (Bashi and Fokkema, 1977). Therefore, the effects found were probably caused by honeydew *per se*, whereas the moderate temperatures and the occurrence of dew in 1987 were conducive to growth of saprophytic micro-organisms, which confounded the effects of honeydew.

In 1986, a complex of effects was found fifteen days after double application of honeydew substitute: an increase in $R_d$ and decreases in $P_m$, mesophyll conductance ($g_m$) and leaf nitrogen content. Macroscopically, chlorotic areas were visible, especially at sites which were covered by honeydew substitute. Similar symptoms were observed in field experiments under hot and dry conditions (Vereijken, 1979; own observation, July 1984). Injury by honeydew under such extreme environmental conditions may be caused by prolonged exposure of leaves to the high osmotic potential of the honeydew solution as was suggested by Vereijken (1979). Several authors have reported increases in $R_d$ as a general consequence of repair processes in injured plants (e.g. Kosuge and Kimpel, 1981). The decrease in $P_m$ after fifteen days appears to be the result of changes in biochemical processes in the leaf rather than coverage or malfunctioning of stomata as no changes in the ratio of internal and ambient carbon dioxide concentrations were found.

In 1987 fifteen days after application, differences in the amount of honeydew between treatments with water and honeydew substitute were absent. Honeydew was washed off by the heavy rains or was consumed by the phyllosphere mycoflora. Apart from a decrease in the initial light use efficiency, no significant effects were found after treatment. It is tempting to attribute the decrease of initial light use efficiency to absorption of photosynthetically active radiation by the phyllosphere mycoflora. However, as only reflection and not transmission of PAR was measured, no conclusion can be drawn. Rabbinge *et al.* (1981) found 6% reduction of absorption of photosynthetically active radiation by flag leaves of spring wheat, 48 days after treatment with honeydew at low relative humidity as compared to an untreated control. No information was given on the statistical significance of the effect.

The relation between relative humidity and the effect of honeydew on wheat leaves is also found in other reports. In a greenhouse experiment at relatively dry conditions (40-70% relative humidity), Rabbinge *et al.* (1981) observed that leaves treated with honeydew yellowed and died more quickly than controls. Under field conditions, Fokkema *et al.* (1979) found no evidence of accelerated senescence after spraying flag leaves of spring wheat with nutrients, consisting of 2% glucose, 0.5% yeast extract and 0.05 "Tween 80", a mixture of *Aurobasidium pullulans*, *Cladosporium* spp. and nutrients, and water respectively. The experiments took place in 1975 and 1977, years with moderate temperature and relative humidity.

The increases of the rate of transpiration relative to the rate of carbon dioxide assimilation, which were found both one and fifteen days after double application of honeydew substitute in 1986 (Table 2.3), may have been caused by leaf exudation (Ajayi and Dewar, 1983) due to the high osmotic potential of honeydew. In 1987, no effects on the *P/T* ratio were observed. These results support the surmised injurious effect of honeydew substitute under hot and dry conditions.

## Quantification of damage in field experiments

In the field experiment at "de Bouwing", the lack of significant effects is partly attributable to the lower aphid densities and the large variation in the data caused by the heterogeneity of the soil. An alternative explanation concerns the condition of the crop at the onset of the experiment. At flowering, a relatively large reserve of soluble carbohydrates was available, amounting to 18% of the total stem dry matter compared to 9% at "de Eest". Also, leaf area index at anthesis exceeded the value on "de Eest", contributing to a large amount of carbohydrates available for grain growth. This may have allowed more compensation of the effects of aphid infestation than at "de Eest". Quantitative evaluation of this hypothesis is possible by means of a simulation model of aphid damage.

Yield of grain dry matter decreased between the penultimate and final harvest in some treatments at both experimental locations. The maximum decrease was observed in treatment A at "de Eest" and amounted to 1176 ± 696 (SEM) kg $ha^{-1}$. Apart from sampling errors, the decrease may be due to respiratory loss, at "de Eest" aggravated by the presence of green plant parts after grain filling had ceased.

In the field experiment at "de Eest", grain yield was reduced by aphid infestation on the ears. Of the three yield components, tiller and grain density were not affected but grain weight was reduced significantly. Leaf area duration was reduced as a result of accelerated leaf death. The results confirm earlier reports by Wratten (1975, 1978), Lee *et al.* (1981a,b) and Rabbinge *et* *al.* (1981). Soluble carbohydrates seem to be exhausted more quickly in the presence of aphids (cf. Wratten and Redhead, 1976). Ear nitrogen content was increased and leaf nitrogen content was decreased at the time the aphid population peaked. At the final harvest, no differences in nitrogen content of plant parts were found.

Lee *et al.* (1981a) found early infestations of *S. avenae* on spring and winter wheat (DC 61 to DC 75) to be more damaging than late infestations (DC 75 to DC 91). The size of the largest infestation was almost four times as large as in the present experiments. Our results indicate that the crop remains susceptible until mid milky ripe (DC 75).

Differences in experimental design and variability in results are inherent to a purely experimental research approach and call for a large body of information before general conclusions on damage by *S. avenae* can be drawn (Entwistle and Dixon, 1987). Alternatively, empirical information on processes involved in the interaction between grain aphid and crop can be combined with crop-physiological knowledge in a simulation model. Then, conclusions on the effect of aphid injury on yield are of a causal rather than a statistical nature. Also, the simulation model can be used to evaluate the quantitative consequences for grain yield of uncertainty in the relation between injury by honeydew and weather conditions. The results of such analysis are presented in Chapter 3.

## Symbols used in Chapter 2

| | | |
|---|---|---|
| $C_a$ | external $CO_2$ concentration | (µg ($CO_2$) $m^{-3}$) |
| $C_i$ | internal $CO_2$ concentration | (µg ($CO_2$) $m^{-3}$) |
| $g_m$ | mesophyll conductance | (m $s^{-1}$) |
| $I$ | absorbed photosynthetically active radiation (PAR) | (J $m^{-2}$ $s^{-1}$) |
| $P$ | net $CO_2$ assimilation rate | (µg ($CO_2$) $m^{-2}$ $s^{-1}$) |
| $P_m$ | net $CO_2$ assimilation rate at light saturation and an ambient $CO_2$ concentration of 632 mg $m^{-3}$ | (µg ($CO_2$) $m^{-2}$ $s^{-1}$) |
| $P_{m,m}$ | net $CO_2$ assimilation rate at $CO_2$ saturation | (µg ($CO_2$) $m^{-2}$ $s^{-1}$) |
| $P_n$ | net $CO_2$ assimilation rate | (µg ($CO_2$) $m^{-2}$ $s^{-1}$) |
| $R_d$ | rate of dark respiration | (µg ($CO_2$) $m^{-2}$ $s^{-1}$) |
| $T$ | transpiration rate | (mg ($H_2O$) $m^{-2}$ $s^{-1}$) |
| $\Gamma$ | $CO_2$ compensation point | (µg ($CO_2$) $m^{-3}$) |
| $\varepsilon$ | initial light use efficiency | (µg ($CO_2$) $J^{-1}$) |

Part 1

# Damage in winter wheat caused by the grain aphid *Sitobion avenae*

Chapter 3

## Construction and evaluation of a simulation model

Rossing, W.A.H., 1991.
Simulation of damage in winter wheat caused by the grain aphid *Sitobion avenae*. 2. Construction and evaluation of a simulation model.
*Netherlands Journal of Plant Pathology* 97:25-54.

**Abstract** To evaluate the relative importance of various mechanisms of damage caused by grain aphid (*Sitobion avenae* F.) populations in winter wheat, a simulation model of crop growth and development is combined with a model of aphid injury. The model applies to the time interval from flowering to ripeness which constitutes the main period of grain aphid immigration and development in winter wheat in the Netherlands. The crop model describes crop growth and development as a function of the prevailing weather and the available amount of soil nitrogen, and consists of sink-source relations and distribution functions for carbohydrates and nitrogen. Injury by *S. avenae* affects crop growth both directly and indirectly. Direct effects on growth are due to aphid feeding. Indirect effects are caused by the aphid excretion product honeydew which affects leaf net carbon dioxide assimilation. Alternative hypotheses on the nature of the direct effects are formulated. Inputs to the model are average daily temperature, daily global radiation, the amount of mineral nitrogen in the soil and the density of the aphid population. Mmajor output is grain weight.

The accuracy of the model is assessed by visual and statistical comparison to field data. The accuracy of both crop and damage model is satisfactory except for the final part of the growing season. Then, insufficient information on processes involved in leaf death and termination of phloem transport to the grains results in overestimation of the rate of grain filling.

The consequences of the lack of detailed information on the relation between environmental factors and the effect of honeydew on leaf carbon dioxide assimilation are assessed in a sensitivity analysis.

## Introduction

Economic losses in winter wheat due to infestation by the grain aphid (*Sitobion avenae* F.) have been reported from most western European countries (Kolbe, 1969; George, 1974; Latteur, 1976; Dedryver, 1978; Vereijken, 1979; Reitzel and Jakobsen, 1980). Regression models for forecasting damage have been developed based on growth analysis of wheat crops infested with aphid populations of various sizes and during various periods of time (Wratten, 1978; Vereijken, 1979; Wetzel *et al.*, 1980; Lee *et al.*,1981; Rabbinge and Mantel, 1981; Watt *et al.*, 1984; Entwistle and Dixon, 1987). The accuracy of a number of these regression models is discussed by Entwistle and Dixon (1987). Rabbinge and Mantel (1981) and Rabbinge *et al.* (1983) hypothesized that the yield level of the uninfested crop should be considered in the analysis of aphid damage, as the effect of the aphids on crop physiologic processes is not constant nor linearly related to yield. Adaptation of the forecasting models to various attainable yield levels would require numerous additional experiments. Moreover, as the causes of damage are not taken into account, the range of situations in which a regression model can be used is restricted to the range used in its construction.

An alternative approach is to predict crop yield from knowledge of plant physiologic and crop ecologic processes and the way they are affected by *S. avenae*. The outlines of this eco-physiologic approach to crop-pest interaction have been described by Rabbinge and Rijsdijk (1981), Boote *et al.* (1983), Rabbinge (1986) and Rabbinge *et al.* (1989). Taking this approach, an aphid - winter wheat model is described and evaluated. The model simulates crop growth and development from anthesis to ripeness as function of the prevailing weather, available amount of soil nitrogen and the aphid infestation present. Water is assumed not to be limiting. The model is used to assess the contribution of various injury components of *S. avenae* to damage and to evaluate the consequences of the lack of detailed information on some processes in the aphid - winter wheat system for predicted yield.

## Materials and Methods

### Model for crop growth

An adapted version of the NWHEAT model (Groot, 1987) is used to simulate post-anthesis growth and development of winter wheat in the absence of aphids, as a function of prevailing temperature and radiation and the available amount of nitrogen in the soil.

The core of the model consists of relations which describe the supply and demand of carbohydrates and nitrogen, respectively. Carbohydrates produced by carbon dioxide assimilation are used for maintenance respiration and growth of the grains, the sinks in order of priority. Surplus of carbohydrates is stored temporarily in the stems, before relocation to the grains. The actual rate of carbohydrate transport from the sources to the sinks equals the demand ("sink-limited growth") or the supply ("source-limited growth"), whichever is the smallest. Nitrogen is taken up from the soil into the vegetative plant parts: leaves, stems and ear structures other than grains. In these vegetative plant parts nitrogen is incorporated in structural material ("residual nitrogen") and in proteins ("translocatable nitrogen"). The latter fraction is the source of nitrogen redistribution to the grains, the only sink. The actual rate of nitrogen transport from the source to the grains is calculated in analogy with the procedure for carbohydrates. In the model the carbohydrate and nitrogen balances interact as the rate of carbon dioxide assimilation at high light intensities is positively correlated with the weight fraction of translocatable nitrogen in the vegetative organs. Also, when the translocatable nitrogen fraction of a vegetative organ decreases below a critical level, the organ dies at a constant relative rate. The rate of crop development is described as a linear function of temperature. The threshold temperature for crop development is 9 °C. A detailed description of the model is given by Groot (1987).

The model is modified in three areas. Firstly, to accomodate calculation of light interception by the ears the distribution of light within the ear layer is calculated according to the procedure described by Goudriaan (1988), assuming the angle distribution of the ears to be uniform between 60 and 120 degrees relative to the horizontal. Secondly, the relative death rate of leaves is modified according to Van Keulen and Seligman (1987). The relative death rate depends on the actual content of translocatable nitrogen relative to a maximum content deduced from experiments with high nitrogen fertilizer input. In the model, the relative rate of leaf death increases linearly from zero, at relative nitrogen contents of 0.9 and higher, to 0.2 day$^{-1}$ at relative nitrogen contents of 0.4 and lower. Moreover, leaves are assumed to die at a relative rate of 0.03 day$^{-1}$ due to mutual shading which occurs if the leaf area index exceeds the value of 4 m$^{2}$ m$^{-2}$. Finally, shortage of carbohydrates occurring when the maintenance respiration of the crop exceeds gross carbon dioxide assimilation causes leaf death.

The final adaptation concerns the onset of grain set which is estimated to occur at 0.11 of the period of physiological time from anthesis to dead ripeness, approximately coinciding with DC 71 (Decimal Code for crop development, Zadoks *et al.*, 1974) using results of an extensive literature survey by Van Keulen and Seligman (1987).

Inputs to the model are shown in Table 3.1. Grain yield is the major output. The model is written in CSMP, Continuous System Modelling Program (IBM, 1975). Time interval of rectilinear integration is one day.

## Model for damage

*Sitobion avenae* affects growth of the winter wheat crop both directly and indirectly (Rabbinge and Mantel,1981; Rabbinge *et al.*, 1981; Wellings *et al.*, 1989). The direct effects on growth result from removal of carbohydrates and nitrogen by phloem sap feeding of aphids. Indirect effects come about through honeydew deposition onto photosynthetically active plant surfaces.

### Direct effects

#### *Concept*

In the model, uptake of phloem sap by feeding aphids is conceptually identical to the uptake of phloem sap by growing grains. Both aphids and grains are sinks characterized by a demand for carbohydrates and nitrogen. Information

Table 3.1. Inputs for the crop model.

| | |
|---|---|
| *Site variables* | Latitude |
| *Meteorological variables* | Maximum daily temperature* |
| | Minimum daily temperature* |
| | Total global radiation* |
| *Soil variables* | Available soil nitrogen from anthesis to harvest* |
| *Crop variables* | Dry weight of green leaves*, stems* and ears* at anthesis |
| | Nitrogen concentration of green leaves*, stems* and ears* at anthesis |
| | Soluble carbohydrates in stems at anthesis* |
| | Tiller density at anthesis* |
| | Grain density* |
| | Leaf area index of leaves* and ears* at anthesis |
| | Date of anthesis* |
| | Date of harvest |

* Variables used in input error analysis.

in the literature strongly suggests that aphids primarily exert a demand for nitrogen while carbohydrates are ingested concomitantly. Mittler (1958) assumed on the basis of his results with *Tuberolachnus salignus* (Gmelin) that an increase in N-content in the phloem sap enhances the growth rate of the aphid and diminishes the excretion rate. Hertel and Kunkel (1976) established a negative correlation between the concentration of amino acids in the artificial diet and the amount of carbohydrates excreted by *Myzus persicae* (Sulz.). Vereijken (1979) found a higher honeydew production of *S. avenae* on plants with a low nitrogen status than on plants well supplied with nitrogen. Jensen (1969) reported that barley plants infected with barley yellow dwarf virus (BYVD) had increased levels of soluble nitrogen while Ajayi and Dewar (1982) reported *Metopolophium dirhodum* (Wlk.) feeding on BYDV-infected plants to produce significantly less honeydew per day than on control plants. These data indicate that aphids adjust their feeding rate according to the availability of nitrogen at the feeding site, the sieve tubes of the phloem (Dixon,1975). Therefore, in the model the nitrogen demand of the aphids determines their rate of ingestion of phloem sap.

The partitioning of nitrogen in the phloem sap between aphids and grains can be described in different ways, the exact interaction between these sinks not being known. Here, four hypotheses concerning the partitioning are formulated and their consequences for damage are evaluated. Aphids may be

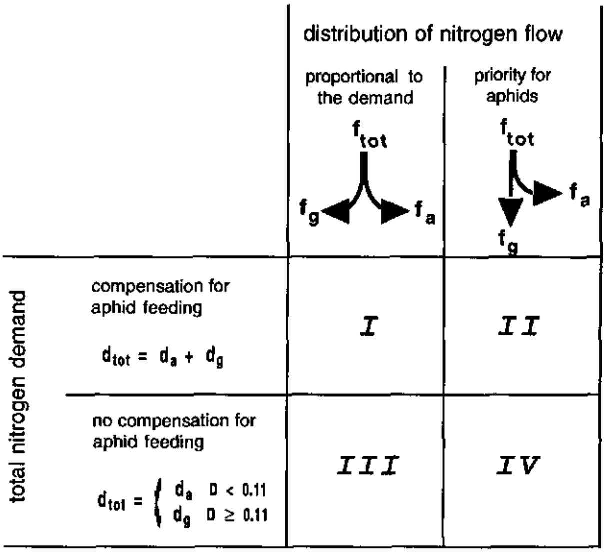


Figure 3.1. Illustration of hypotheses I to IV which describe the effect of aphids on the size of the sink for nitrogen in the plant ("total nitrogen demand") and the partitioning of phloem sap nitrogen between aphids and grains ("distribution of nitrogen flow"). The variables *f*, *d* and *D* indicate the actual flow to a sink, the demand of a sink and the development stage of the crop, respectively. The suffixes *tot*, *g* and *a* represent the total sink, the grain sink and the aphid sink, respectively (*cf.* Appendix to Chapter 3).

the first to utilize the flow of nitrogen due to their feeding position in the rachis at the base of the grains. After the demand of the aphids is met, the remainder of the phloem sap nitrogen is utilized by the grains, whose demand may thus not be fully met. Alternatively, aphids may be assumed to share the nitrogen flow with the grains in proportion to their sink strength (Figure 3.1). Aphid feeding may be compensated for by an increase in the flow of nitrogen from the source. Assuming full compensation, the net flow rate of nitrogen is determined by the sum of demands of aphids and grains. Alternatively, no compensation may occur. Summarizing, the four hypotheses concerning partitioning of phloem sap nitrogen are (Figure 3.1):

(I): compensation for aphid feeding by increased total demand, which is equal to the sum of demands of grains and aphids; the flow of nitrogen is distributed in proportion to the respective demands.

(II): compensation for aphid feeding by increased total demand, which is equal to the sum of demands of grains and aphids; the flow of nitrogen is first utilized by the aphids.

(III): no compensation for aphid feeding: total demand is equal to the demand

of grains; the flow of nitrogen is distributed in proportion to the respective demands of grains and aphids.
(IV): no compensation for aphid feeding: total demand is equal to the demand of grains; the flow of nitrogen is first utilized by the aphids.
The rate of carbohydrate ingestion is assumed to be equal to the product of the weight ratio of carbohydrates and nitrogen in the phloem sap and the rate of nitrogen uptake.

*Quantification*

Coster (1983) in Rabbinge and Coster (1984) measured daily honeydew production rates of *S. avenae* on flag leaves and ears of spring wheat plants at various crop development stages. The plants were well supplied with water and nitrogen. The rate of phloem sap uptake was calculated by applying an energy budget approach (e.g. Llewellyn, 1988). The results are shown in Table 3.2. To calculate the nitrogen demand of the aphids from these data, the feeding rate must be related to the nitrogen content of the phloem sap at the time of uptake. The total nitrogen content of the flag leaves and ears, which was determined in the experiments of Coster, cannot be used for this purpose since in green tissue nitrogen is mainly present in proteins while in phloem sap nitrogen in predominantly found in amino-acids and amides. Here, the nitrogen content of the phloem sap in the experiments is estimated to be 2% of phloem sap dry weight, a figure representing the average nitrogen content of grains at the onset of grain filling. Furthermore, the assumption is made that the nitrogen demand of aphids feeding on ears was fully satisfied at the highest feeding rate measured by Coster (1983). Lower feeding rates are attributed to mechanical and physiological changes associated with ripening of the crop. Thus a value of $8.9 \times 10^{-9}$ kg (N) $\text{mg}^{-1}$ (aphid, fresh weight) $\text{day}^{-1}$ is obtained for the potential feeding rate ($p_a$). The nitrogen demand by the aphid population is described by

$$d_{N,a} = p_a \cdot w_a \cdot n_a \cdot n_t \tag{3.1}$$

where $d_{N,a}$ is potential rate of nitrogen accumulation in the aphids (kg (N) $\text{ha}^{-1}$ $\text{day}^{-1}$), $p_a$ potential feeding rate (kg (N) $\text{mg}^{-1}$ $\text{day}^{-1}$), $w_a$ average aphid fresh weight (mg), $n_a$ aphid density ($\text{tiller}^{-1}$), and $n_t$ tiller density ($\text{ha}^{-1}$). Average aphid fresh weight depends on the age composition of the population. When no detailed population census has been made, average aphid weight is calculated from total aphid density using crop development stage dependent conversion factors calculated by Mantel *et al.* (1982).

Concomitant with nitrogen, carbohydrates are taken up by the aphids. Analogous to the grains a potential rate of carbohydrate accumulation is defined

Table 3.2. Rate of phloem sap feeding ( mg (phloem sap dry weight) $mg^{-1}$ (aphid fresh weight) $day^{-1}$) and rate of honeydew production ( mg (honeydew 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. The weight fraction dry matter in phloem sap is 0.2. Data of Coster (1983) and Rabbinge and Coster (1984).

| Feeding position of aphids | Crop stage | Feeding rate | Honeydew production | N-content of flagleaves (f) or ears (e) (g $kg^{-1}$) |
|---|---|---|---|---|
| flag leaf | 45 | 0.45 | 0.15 | - |
| flag leaf | 45 | 0.51 | 0.19 | 45.7 (f) |
| ear | 65 | 0.45 | 0.18 | - |
| ear | 69 | 0.31 | 0.09 | 35.6 (e) |
| ear | 71 | 0.33 | 0.13 | 22.6 (e) |
| ear | 73 | 0.17 | 0.06 | 24.7 (e) |
| ear | 75 | 0.24 | 0.08 | 23.5 (e) |

for the aphids, which is a function of the potential rate of nitrogen uptake:

$$d_{C,a} = c_r \cdot d_{N,a} \tag{3.2}$$

where $d_{C,a}$ is potential rate of carbohydrate accumulation in the aphids (kg ($CH_2O$) $ha^{-1}$ $day^{-1}$) and $c_r$ the ratio of the amounts of carbohydrates and nitrogen in the phloem sap (kg ($CH_2O$) $kg^{-1}$(N) ). The dynamic function $c_r$ is calculated from the actual rates of carbohydrate and nitrogen flow to the sinks one integration interval earlier.

Total demands for nitrogen and carbohydrates are formulated for each of the hypotheses. After calculating the actual flows of nitrogen and carbohydrates according to the sink-source concept, the flows are distributed over the sinks, depending on the hypothesis on the nature of the aphid-grain competition for phloem sap. The actual relations are given in the Appendix to this Chapter.

## Indirect effects

### *Concept*

Honeydew produced by *S. avenae* feeding on ears is intercepted by ears, stems, leaves and ground. The interception of honeydew by the various plant parts is modelled in analogy with interception of light. Given the effect of honeydew on leaf carbon dioxide assimilation at every point in the crop profile, daily crop carbon dioxide assimilation can be calculated.

The experimental results of Chapter 2 suggest that the effect of honeydew on carbon dioxide assimilation of winter wheat leaves depends on environmental conditions: temperature, relative humidity, dew and rain. Part of the effect of honeydew is attributable to saprophytic micro-organisms in the phyllosphere. These saprophytes may increase the rate of dark respiration and decrease the initial light use efficiency at suitable environmental conditions. At present, information on the quantitative effect of environmental factors on the population dynamics of saprophytes and their interaction with leaf carbon dioxide assimilation is lacking.

In experiments under dry conditions which precluded growth of saprophytes, an effect of honeydew *per se* on leaf carbon dioxide assimilation was found (Chapter 2). This effect of honeydew consists of an increased rate of dark respiration and a reduction of the rate of carbon dioxide assimilation at light saturation, fifteen days after application of the honeydew. Here, these results are used to describe the effects of honeydew on carbon dioxide assimilation. The potential contribution of the saprophytic leaf mycoflora to damage is evaluated in the sensitivity analysis.

*Quantification*

According to data of Coster (1983) fourty percent of the ingested phloem sap is excreted as honeydew:

$$h = 0.40 \cdot f_{\mathrm{C,a}} \tag{3.3}$$

where $h$ represents the rate of honeydew excretion (kg ha$^{-1}$ day$^{-1}$) and $f_{\mathrm{C,a}}$ the actual flow of carbohydrates to the aphids (kg ha$^{-1}$ day$^{-1}$). According to Vereijken (1979), thirty percent of the daily honeydew production lands on the ears, the remainder being intercepted by leaves, stems and ground. Honeydew intercepted by the ears is distributed uniformly over the ear surface. Applying the concepts developed for light (Spitters, 1986) the rate of honeydew interception at depth L in the leaf and stem layer of the canopy, with $L$=0 at the top of the canopy, is:

$$h_{\mathrm{ls}}(L) = (1-e_{\mathrm{f}}) \cdot h \cdot k_{\mathrm{h}} \cdot \exp\left(-k_{\mathrm{h}} \cdot L\right) \tag{3.4}$$

where $h_{\mathrm{ls}}(L)$ is the rate of honeydew interception at depth $L$ in the leaf and stem layer (kg ha$^{-1}$ day$^{-1}$), $L$ the cumulative leaf area index calculated from the

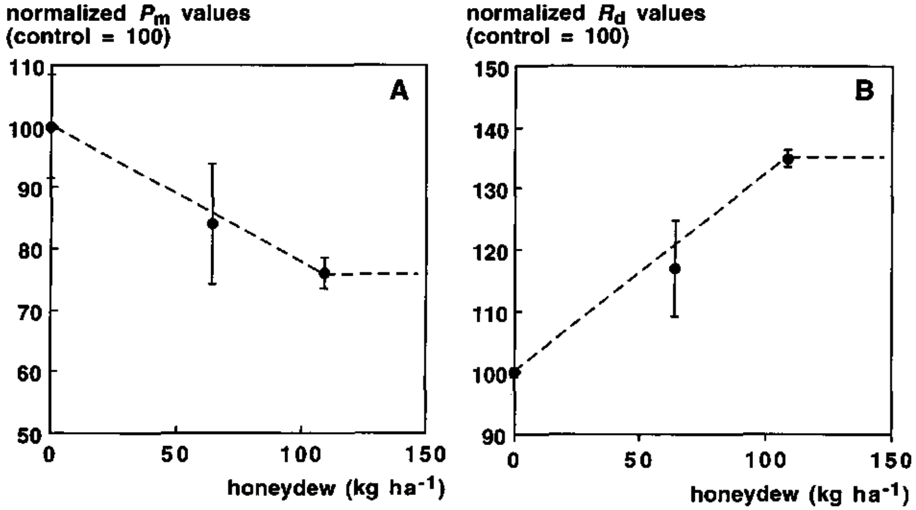


Figure 3.2. The effect of honeydew on carbon dioxide assimilation of flag leaves of winter wheat relative to the control, 15 days after deposition: (a) the effect on the rate of carbon dioxide assimilation at light saturation ($P_m$) and (b) the effect on the rate of dark respiration ($R_d$), based on the data of Chapter 2. Error bars represent standard error of the mean. The dotted lines are used in the simulation model.

top of the leaf and stem layer (ha ha$^{-1}$), $e_f$ the fraction of the total honeydew production intercepted by ears (-), and $k_h$ the extinction coefficient for honeydew (-). The value of $k_h$ was estimated at 0.8 equal to the value of the extinction coefficient for diffuse light interception by black leaves (i.e. no transmission or reflection) with a spherical leaf angle distribution (Goudriaan, 1988).

The increase in the rate of dark respiration and the decrease in the rate of carbon dioxide assimilation at light saturation are functions of the amount of honeydew deposited and the period of time elapsed since deposition. The size of the effects is approximately proportional to the amount of honeydew applied (Chapter 2) (Figure 3.2). In the model, no response is allowed above the maximum values measured. The effects are assumed to come about at a constant rate from the time of deposition. The increase in dark respiration is assumed to be caused by an increase in maintenance respiration only. The total effect of honeydew depositions ("droplets") of various sizes and ages is calculated by adding the effects of the individual droplets. Overlapping of droplets is assumed to be absent. The resultant fraction reduction of the rate of carbon dioxide assimilation at light saturation and the fraction increase in the rate of respiration are inputs for the carbon dioxide assimilation algorithm of the crop model.

## Results and discussion: Model evaluation

### Introduction

The process of model evaluation may be divided into verification and validation. Verification comprises the process of ensuring that a model behaves as the experimenter wants it to, and validation the testing for agreement in behavior between model and real system (Teng *et al.*, 1980). Verification also involves parameterization, the process in which parameters are adjusted to optimally represent the real system. Here, the data sets PAGV1 and EEST84 were used to adjust the rate of leaf carbon dioxide assimilation at light saturation and the onset of leaf death due to nitrogen shortage.

The most common method for model validation is probably visual inspection of similarity between model output and real system behavior. Though some authors argued that validation should largely be a subjective procedure (Anderson, 1974), other authors have stressed the importance of supplementing visual inspection with statistical procedures (Teng *et al.*, 1980; Ten Berge, 1990).

In this Chapter, two categories of error in model output are distinguished, (a) model parameterization and structure, and (b) model input. Model parameterization and structure are validated by visual comparison of model output with system behavior, and by sensitivity analysis. Criteria used for visual validation include similarity of the simulated and observed rates of change of selected variables, the coincidence in time of abrupt changes in simulated and observed variables, and the size of the discrepancy between simulated and observed results relative to the variation in the observations.Three variables are selected for visual validation: leaf weight, leaf nitrogen amount and grain yield. Leaf weight and leaf nitrogen amount determine to a large extent the size of the sources of carbohydrates and nitrogen, respectively, while grain yield is the variable of major interest. In the sensitivity analysis the effect of changes in model parameters ("fine sensitivity analysis") and in model structure ("coarse sensitivity analysis") on the value of output variables is examined (Carter and Rabbinge, 1980). The relative sensitivity $(\Delta z/z)/(\Delta y/y)$ is used as a measure of model sensitivity to changes in a parameter, where $z$ is the value of the relevant model output variable, $y$ the value of the parameter, and $\Delta z$ the change in $z$ caused by a change $\Delta y$ in $y$. The size of the perturbation $\Delta y$ is taken to be of the order of the variation of $y$ reported in the literature.

Up to this point, empirically determined model inputs, initial values of state variables and the time course of exogenous variables, are considered exact estimates. Due to spatial heterogeneity in the field they are in fact mean values of probabilistic variables. Hence, model output is probabilistic and, during validation, is to be compared with probabilistic observed system behavior. Ten Berge (1990) proposed a statistic to evaluate the variance of model output in relation to the variance of measured variables as a function of time, defined as

$$q(t) \equiv \frac{[z_o(t) - z_s(t)]}{\sqrt{\mathrm{var}[z_o(t)] + \mathrm{var}[z_s(t)]}} \tag{3.5}$$

where $z_o(t)$ and $z_s(t)$ represent the observed and the simulated quantities at time t, respectively, and var[$z_o(t)$] and var[$z_s(t)$] the respective error variances. The error variance of $z_s(t)$ is approximated as a function of the error variances of the input variables $x_i$ (i=1,..,$n$) by:

$$\mathrm{var}[\, z_s(t) \,] \approx \sum_{i=1}^{n} \left[ \frac{\Delta z_s}{\Delta x_i} \right]^2 \mathrm{var}(x_i) \tag{3.6}$$

where $\Delta z_s / \Delta x_i$ is the sensitivity of $z_s(t)$ to changes in $x_i$ and var($x_i$) the error variance of $x_i$ calculated as the sample variance divided by the number of units in the sample. The equation has been derived for uncorrelated inputs $x_i$ by Hahn and Shapiro (1967). In the present context the variable $z_s$ represents grain yield and $x_i$ the various model inputs. The sensitivity $\Delta z_s / \Delta x_i$ is assessed by running the model with the average plus and minus one standard error of the input, respectively, and calculating the average $\Delta z_s / \Delta x_i$ to account for non-symmetrical response. Interactions in $\Delta z_s / \Delta x_i$ of the various inputs are ignored, and the distribution of errors in $x_i$ is assumed to be normal. Under the null hypothesis of correctness of the model, the expectation of $q(t)$ is 0. In analogy with the related Student $t$-statistic, predictions are considered reasonable if the value of $q(t)$ ranges between -2 and +2.

## The crop model

### *Data for validation*

Six data sets from three locations and two years are available for validation of the crop model (Table 3.3). Four of these, EEST83, PAGV1, PAGV2, and PAGV3, originate from experiments designed to determine the optimum rate of fertilizer supply (Groot, 1987). Weeds, diseases and aphids were treated chemically on occurrence. The data sets are chosen to represent a range of grain yields which

Table 3.3. General information on the datasets used to evaluate the crop model and the 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 beets | sugar beets | sugar beets |
| 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 dat | 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 |

---

[*] H=herbicide, F=fungicide, I=insecticide.

[**] Insecticide treatment aimed at creating aphid infestations of different intensity.

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

were arrived at under conditions of nitrogen limitation only. Calculations using a crop model with a water balance showed that effects of water limitation after flowering were negligible in these experiments (personal communication J.J.R. Groot).

Two other data sets, BOUWING84 and EEST84, stem from the aphid-free control treatment of experiments designed to evaluate the damage model (Chapter 2). A slight aphid infestation in the control treatment could not be avoided due to immigration from neighbouring plots. In view of the rainfall frequency (Figure 2.5) and the soil type (Table 3.3), water limitation is assumed absent.

All data pertain to the cultivar Arminda. Weather data are collected at the weather station closest to the respective experimental site. All model validation runs are carried out with measured temperature, radiation and mineral soil nitrogen data. The crop development rate is introduced as it was observed to enable validation of yield and damage prediction without error in the prediction of crop development.

### *Visual validation*

Two simulation runs are made for each data set, the first with the leaf area index calculated as the product of the simulated weight of the leaves and constant specific leaf area, the second with the observed leaf area index as input. Results of the latter runs are used to identify errors in the simulation of the still poorly understood leaf area dynamics.

*Leaf weight and area dynamics.* The observed rate of leaf weight decrease is reproduced by the simulation model during the major part of the grain filling period for all data sets, except for EEST83 where it is overestimated (Figure 3.3). The observed increase in leaf weight for EEST84 which is probably attributable to a nitrogen fertilizer application of 40 kg (N) ha$^{-1}$ during flowering, is not reproduced by the model since in the model no growth of the leaves after flowering is assumed.

The onset of leaf death is simulated well for EEST84, EEST83, PAGV1 and PAGV2. For BOUWING84, the onset of leaf death is simulated too early, possibly due to an overestimation of initial leaf weight as in four subsequent samples leaf weight was constant but lower than in the initial sample. For PAGV3, the onset is simulated too late.

In the data sets, the specific leaf area decreases in the course of grain ripening by some 10 to 15% whereas in the model specific leaf area with constant value of 20 m$^2$ kg$^{-1}$ is assumed. As a result, the model tends to overestimate leaf area index towards the end of grain filling.

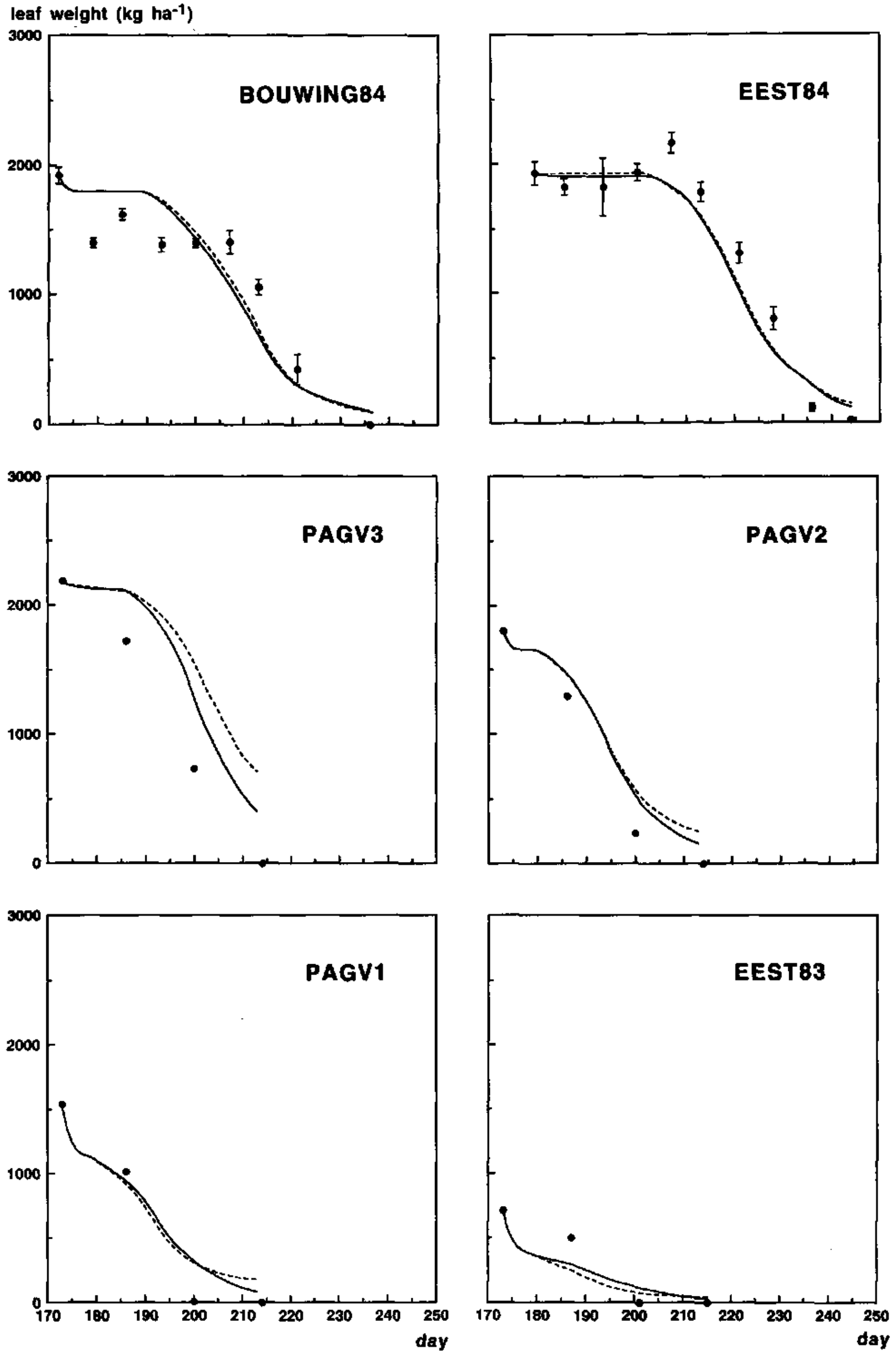


Figure 3.3. Observed (●) and simulated leaf weight for six data sets. In the model, leaf area index was calculated (- - - -) or introduced as observed (——). Vertical bars represent the standard error of the mean. A description of the data sets is given in Table 3.3.

*Leaf nitrogen dynamics.* The observed rate of decrease of the amount of nitrogen in the green leaves is reproduced by the simulation model (Figure 3.4). For EEST84, the model initially underestimates the amount of leaf nitrogen decrease, probably because of the late nitrogen fertilizer application. The nitrogen concentration of the leaves is simulated reasonably well at higher yield levels (not shown). At low yield levels (PAGV1, EEST83), leaf nitrogen concentration initially is overestimated due to underestimation of leaf weight.

*Grain yield.* The simulated and observed rates of increase of grain yield in the linear phase compare well for all data sets (Figure 3.5). Also, the onset of grain filling is predicted accurately. Slight discrepancies between simulated and observed grain yield in the linear growth phase for BOUWING84 are most likely due to an incorrect estimate of the date of flowering caused by the heterogeneous soil conditions at the experimental site.

Simulated and observed grain yields diverge towards the end of grain filling. Using observed values of leaf area index, final grain yield is underestimated for PAGV1, PAGV2, PAGV3 and EEST83. The relative error in grain yield is less than 11% for PAGV1, PAGV2 and PAGV3 and 19% for EEST83. In part these discrepancies are due to inconsistencies in the field data: grain yield is reported to increase during the last two weeks before harvest for PAGV1 and EEST83 while neither green leaves nor green stems were found. For EEST84 and BOUWING84, simulated grain yield is too high at the end of the growing season. This is caused by the absence of a predetermined cessation of grain filling in the model: grain filling continues until the source is exhausted. Using a large set of experimental data, van Keulen and Seligman (1987) calculated grain filling to cease at 0.72 of the physiological time between flowering and ripeness, on average, due to death of the sieve tubes in the stem and the rachis. Thus, the high leaf area index values for EEST84 and BOUWING84 at the end of the growing season have not contributed to yield as the grains were ripe before the straw. The consequence of a decrease in sink strength for simulated grain yield is evaluated in the sensitivity analysis.

### *Sensitivity analysis*

*Fine sensitivity analysis.* Fine sensitivity analysis is carried out for all model parameters using initial conditions of the data sets EEST84 and EEST83. Parameters with high relative sensitivity include the initial light use efficiency of leaves and the rate of carbon dioxide assimilation at light saturation which determine the size of the carbohydrate source and parameters determining the sizes of the nitrogen source and sink (Table 3.4). At the high crop nitrogen level

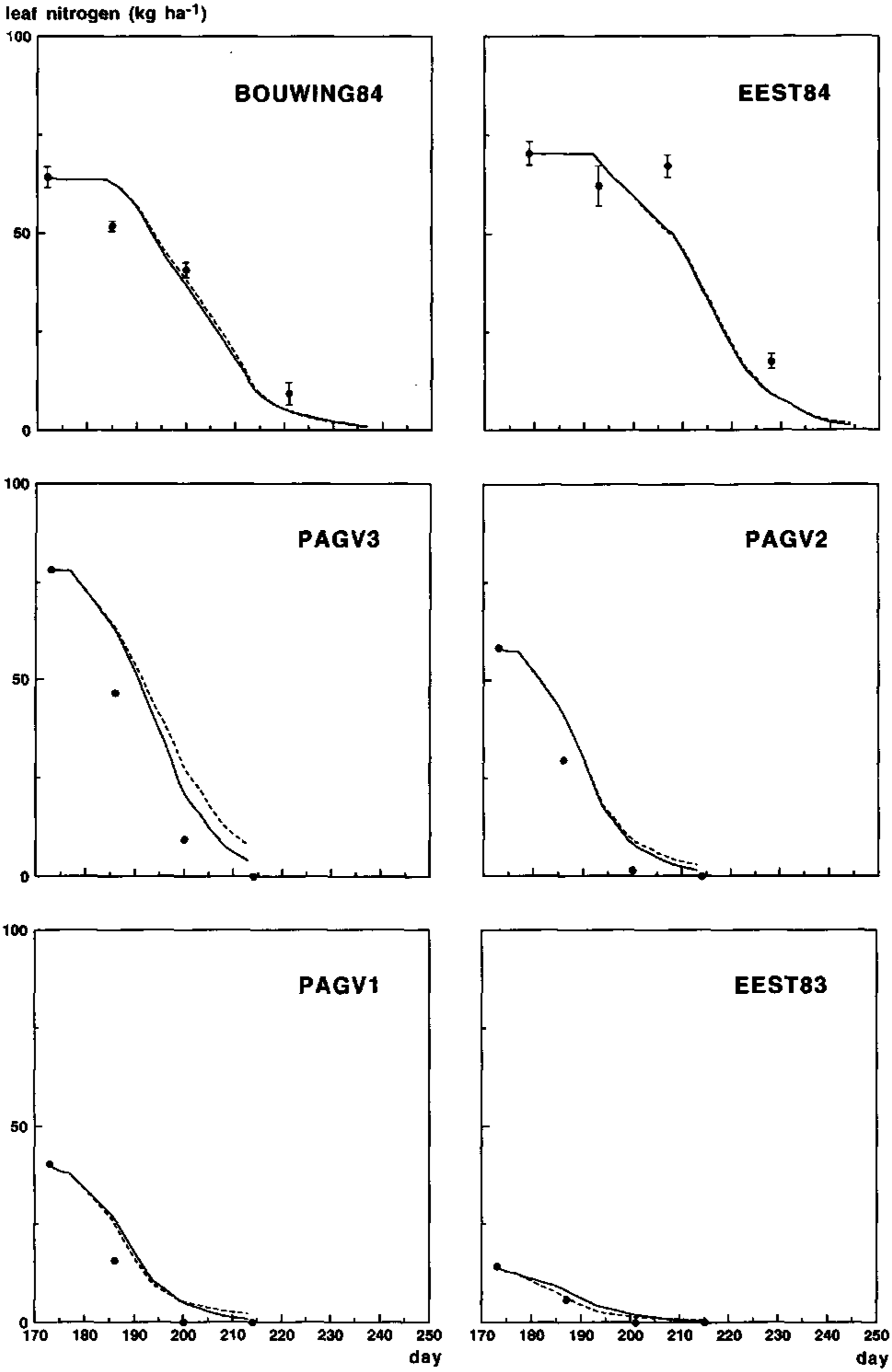


Figure 3.4. Observed (●) and simulated amount of leaf nitrogen for six data sets. In the model, leaf area index was calculated (- - - -) or introduced as observed (——). Vertical bars represent the standard error of the mean. A description of the data sets is given in Table 3.3.

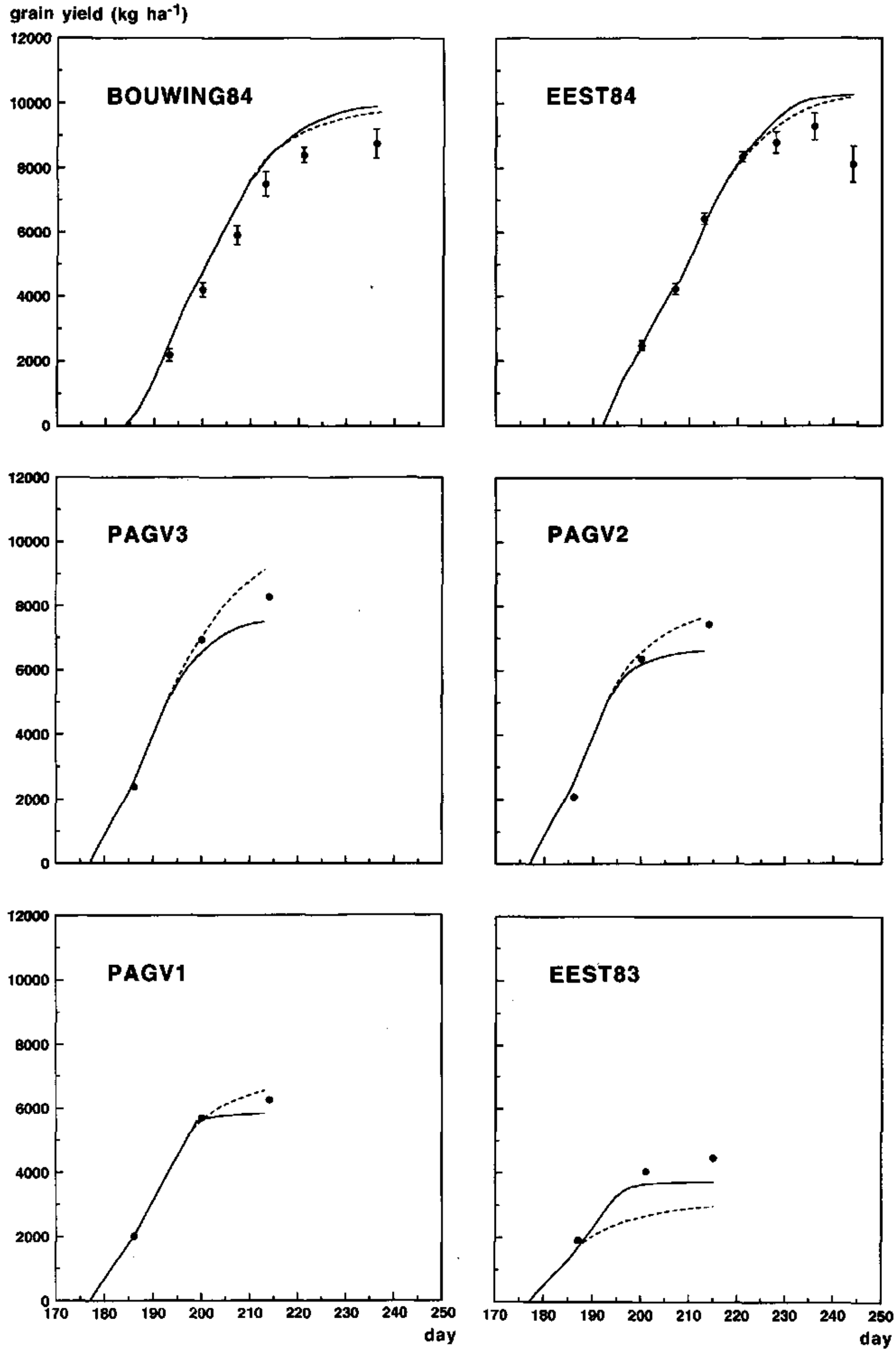


Figure 3.5. Observed (●) and simulated grain yield for six data sets. In the model, leaf area index was calculated (- - - -) or introduced as observed (——). Vertical bars represent the standard error of the mean. A description of the data sets is given in Table 3.3.

Table 3.4 Relative sensitivity of simulated end-of-season grain yield calculated with the crop model run with data of EEST84 and EEST83. In the runs the leaf area index is simulated. In the standard version of the model, simulated grain yield is 10187 kg ha$^{-1}$ for EEST84 and 2983 kg ha$^{-1}$ for EEST83. 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 CO2 assimilation | kg ha$^{-1}$ h$^{-1}$ | 35[a] | 35[a] | + 14 | + 14 | 0.33 | 0.43 |
| | | | | - 14 | - 14 | 0.39 | 0.50 |
| Initial efficiency of light use of leaves | kg ha$^{-1}$ h$^{-1}$ (J m$^{-2}$ s$^{-1}$)$^{-1}$ | 0.45[b] | 0.45[b] | + 11 | + 11 | 0.64 | 0.45 |
| | | | | - 11 | - 11 | 0.69 | 0.51 |
| Grain density | ha$^{-1}$ | 2.46 $10^{8}$ [c] | 1.41 $10^{8}$ [c] | + 8 | + 8 | -0.47 | -0.11 |
| | | | | - 8 | - 8 | -0.54 | -0.21 |
| Maximum rate of nitrogen uptake | kg ha$^{-1}$ d$^{-1}$ | 3[d] | 3[d] | + 100 | +100 | -0.07 | 0.29 |
| | | | | - 67 | - 67 | 0.19 | 0.22 |
| Time constant for nitrogen translocation | d$^{-1}$ | 8[d] | 8[d] | + 100 | +100 | 0.06 | 0.21 |
| | | | | - 50 | - 50 | 0.12 | 0.27 |
| Potential rate of nitrogen accumulation of grains | kg ha$^{-1}$ d$^{-1}$ | table[b] | table[b] | + 10 | + 10 | -0.47 | -0.12 |
| | | | | - 10 | - 10 | -0.55 | -0.21 |

[a] Basically from van Keulen and Seligman (1987), calibrated on datasets PAGV1 and EEST84.

[b] Van Keulen and Seligman (1987).

[c] Input.

[d] Groot (1987).

of EEST84, variations in grain density and potential rate of nitrogen accumulation of grains which determine the size of the nitrogen sink, have large effects on grain yield as these parameters affect the green area duration. For EEST83, nitrogen levels are so low that green area is dying at maximum rate from flowering. Therefore, changes in the maximum rate of nitrogen uptake and the time constant for nitrogen translocation which determine the size of the nitrogen source, have a larger effect on grain yield than changes in parameters determining the size of the nitrogen sink.

*Coarse sensitivity analysis.* By removing the ear layer from the calculation of carbon dioxide assimilation simulated grain yield of EEST84 increases by 1% due to higher light intensities in the leaf layer.

Cessation of grain filling at 0.72 of the time between flowering and ripeness causes considerable reduction of simulated grain yield except for EEST83 where most of the green area is already dead by this time due to nitrogen shortage (Table 3.5).

### *Analysis of errors in inputs*

The *q*-values for grain yield of EEST84 and BOUWING84 are shown in Table 3.6. Other data sets could not be evaluated due to lack of information on sampling error. Estimated errors in grain density, average daily temperature and flowering date cause major changes in output. Values of *q* increase

Table 3.5. Simulated grain yield (kg ha$^{-1}$) in the standard version of the crop model ("standard run") and simulated grain yield assuming grain filling to end at 0.72 of the time between flowering and ripeness ("sink limitation"). Leaf area index is simulated.

| Dataset | Simulated grain yield | | Observed grain yield |
|---|---|---|---|
| | standard run | sink limitation | |
| EEST84 | 10187 | 9653 | 9290/8114[1] |
| BOUWING84 | 9727 | 9186 | 8754 |
| PAGV3 | 9120 | 7673 | 8279 |
| PAGV2 | 7650 | 6938 | 7442 |
| PAGV1 | 6541 | 5952 | 6256 |
| EEST83 | 2983 | 2810 | 4496 |

[1] Penultimate and ultimate yield respectively (see footnote Table 3.3).

Table 3.6. Results of crop model input error analysis per sampling date (Julian day) for EEST84 and BOUWING84. SEM is standard error of the mean. For explanation of symbols see text.

EEST84

| day | $z_S$ | $\sqrt{(E(\text{var } z_S))}$ | $z_O$ | SEM($z_O$) | $q$ |
|---|---|---|---|---|---|
| 200 | 2442 | 280 | 2499 | 143 | -0.18 |
| 207 | 4344 | 373 | 4243 | 177 | 0.24 |
| 213 | 6178 | 512 | 6432 | 172 | -0.47 |
| 221 | 8262 | 167 | 8350 | 158 | -0.38 |
| 228 | 9276 | 289 | 8806 | 331 | 1.07 |
| 236 | 9918 | 421 | 9290 | 414 | 1.06 |
| 244 | 10187 | 491 | 8114 | 559 | 2.79 |

BOUWING84

| day | $z_S$ | $\sqrt{(E(\text{var } z_S))}$ | $z_O$ | SEM($z_O$) | $q$ |
|---|---|---|---|---|---|
| 193 | 2536 | 521 | 2202 | 197 | 0.60 |
| 200 | 4736 | 661 | 4213 | 224 | 0.75 |
| 207 | 6814 | 762 | 5913 | 293 | 1.10 |
| 213 | 8259 | 194 | 7504 | 380 | 1.77 |
| 221 | 9116 | 431 | 8385 | 239 | 1.48 |
| 237 | 9727 | 702 | 8754 | 461 | 1.16 |

towards the end of the growing season. Only the final $q$-value for EEST84 exceeds the limit of 2.

### *Discussion of the crop model*

The major output of the model, grain yield, is simulated reasonably well: both onset and rate of grain filling are predicted accurately until the onset of source-limited growth. During source-limited growth, the amount of photosynthetically active tissue determines the rate of grain filling and errors in the simulation of leaf area index become apparent. The evaluation points to a lack of understanding of the processes involved in leaf death, which becomes especially prominent at low crop nitrogen levels. In the model, leaf death rate is calculated by comparing the actual nitrogen concentration in the leaves to a maximum concentration found in experiments with high nitrogen fertilizer input.

At low nitrogen supply this may be incorrect as many processes adapt to the nitrogen history of the crop.

Compared to the penultimate harvest, grain yield decreases drastically at the final harvest for EEST84. This may constitute respiratory loss due to delayed harvesting, as the crop was still partly green at the scheduled harvest time and had to be killed with herbicide.

## The damage model

### *Data for validation*

The data sets EEST84 and BOUWING84 comprise crop growth analysis data of an experiment with aphid infestations of different size (Chapter 2). For validation of the damage model the data of the largest infestation are used. For EEST84, the aphid infestation caused a significant reduction of grain yield, leaf area index, leaf weight and amount of leaf nitrogen during the major part of the post-anthesis period. For BOUWING84, few significant effects were found due to the smaller aphid infestation and the heterogeneous soil conditions (river clay on sand). In the validation runs leaf area index is simulated.

Preliminary model runs showed that differences between hypotheses I and II or III and IV describing the direct effects of the grain aphid (Figure 3.1) are small as aphid load is low after onset of source-limited growth for both EEST84 and BOUWING84. Therefore, the validation focuses on hypotheses I and IV.

### *Visual validation*

*Leaf weight dynamics.* Both the onset and the rate of decrease of leaf weight in the infested crop of EEST84 are reproduced by the simulation model when the uptake of phloem sap by the aphids is compensated for by an increased flow rate (hypothesis I) which causes accelerated depletion of translocatable nitrogen in vegetative organs (Figure 3.6). For BOUWING84, the simulated onset of leaf death is too early and, initially, the rate of leaf death is overestimated, similar to the simulated results of the aphid-free control (*cf.* Figure 3.3). For both EEST84 and BOUWING84, the simulated reduction of leaf weight compared to the aphid-free control is less than the observed reduction indicating that factors contribute to leaf death which have not been taken into consideration in the model.

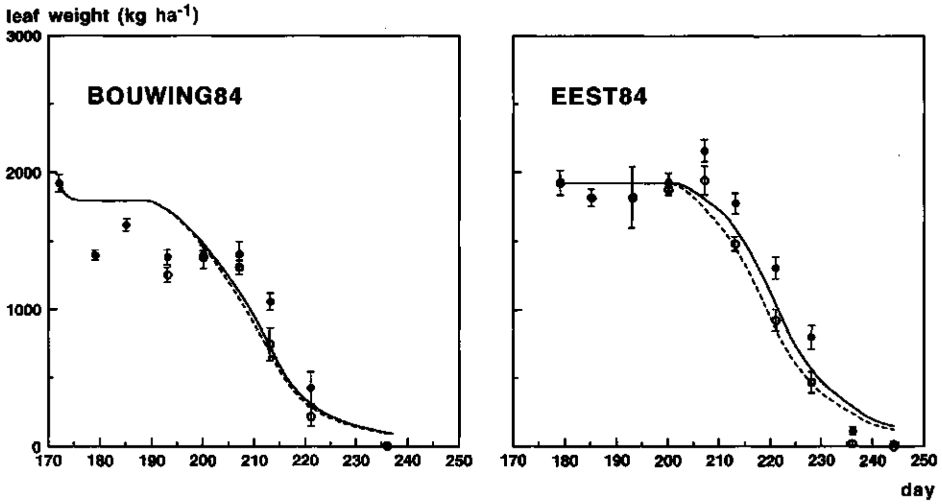


Figure 3.6. Observed and simulated leaf weight of EEST84 and BOUWING84 based on hypotheses I and IV to describe the direct effects of *Sitobion avenae*. Vertical bars represent standard errors of the mean. Observed grain yield of the control (●) and the most severely infested treatment (○). Simulated grain yield without aphids (——) and with an infestation as observed in the most severely infested treatment (- - - -) based on hypothesis I. Simulated results based on hypothesis IV are identical to simulated leaf weight without aphids. Leaf area index is simulated.

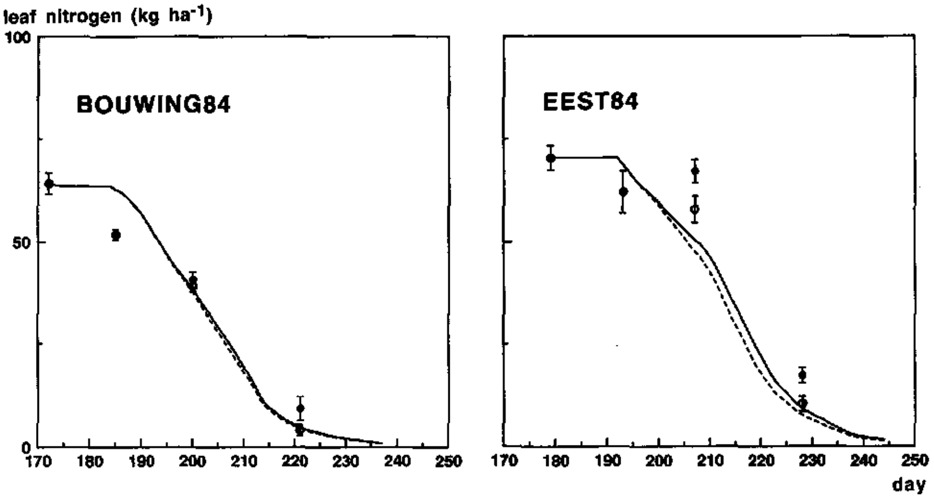


*Figure 3.7. Observed and simulated amount of leaf nitrogen of* EEST84 *and* BOUWING84 based on hypotheses I and IV to describe the direct effects of *Sitobion avenae*. Vertical bars represent standard errors of the mean. Observed grain yield of the control (●) and the most severely infested treatment (○). Simulated grain yield without aphids (——) and with an infestation as observed in the most severely infested treatment (- - - -) based on hypothesis I. Simulated results based on hypothesis IV are identical to simulated leaf nitrogen without aphids. Leaf area index is simulated.

*Amount of leaf nitrogen.* The onset but not the size of the observed reduction of leaf nitrogen by the aphid infestations is reproduced by the simulation model when compensation for aphid feeding by increased phloem sap flow rate is assumed (hypothesis I, Figure 3.7). For EEST84, the simulated onset of leaf nitrogen decrease is too early, similar to the results for the aphid-free control where it has been attributed to a late nitrogen fertilizer application.

*Grain yield.* For EEST84, the onset of aphid damage and the rate of grain yield increase during the linear phase are reproduced well by the damage model when compensation for aphid feeding by increased phloem sap flow rate is absent (hypothesis IV, Figure 3.8). Final grain yield is overestimated slightly. When compensation for aphid feeding by increased phloem sap flow rate is assumed (hypothesis I), damage becomes apparent when the process of grain filling changes from sink-limited to source-limited (day 212 for EEST84 and day 210 for BOUWING84). For BOUWING84, the simulation model predicts little damage during the major part of the growing season in agreement with the experimental data. Final damages simulated with hypotheses I and IV differ approximately 200 kg ha$^{-1}$ for EEST84 and 70 kg ha$^{-1}$ for BOUWING84.

### *Sensitivity analysis*

*Fine sensitivity analysis.* Fine sensitivity analysis is carried out with data of the aphid-infested plots of EEST84, using hypotheses I and IV to model the direct effects of aphids. Relative sensitivity is expressed in terms of grain yield and in terms of damage. The largest changes in output (Table 3.7) result from perturbation of the rate of phloem sap uptake as it determines the size of direct as well as indirect effects. Changes in the parameters describing the effect of honeydew on leaf carbon dioxide assimilation have a significantly smaller effect. The differences in relative sensitivities between hypotheses I and IV are small.

*Coarse sensitivity analysis.* In the coarse sensitivity analysis the contributions of the injury components aphid feeding, honeydew reducing the rate of carbon dioxide assimilation at light saturation, and honeydew increasing maintenance respiration to total damage are calculated. For this purpose, damage due to feeding only, and damage due to feeding and increased maintenance respiration are compared to total simulated damage. Secondly, the potential effect of rain and leaf saprophytes on grain yield is evaluated. The analysis is carried out with data of the aphid-infested plots of EEST84.

Aphid feeding constitutes the most important cause of damage for hypotheses I and II while the three components contribute equally to total damage

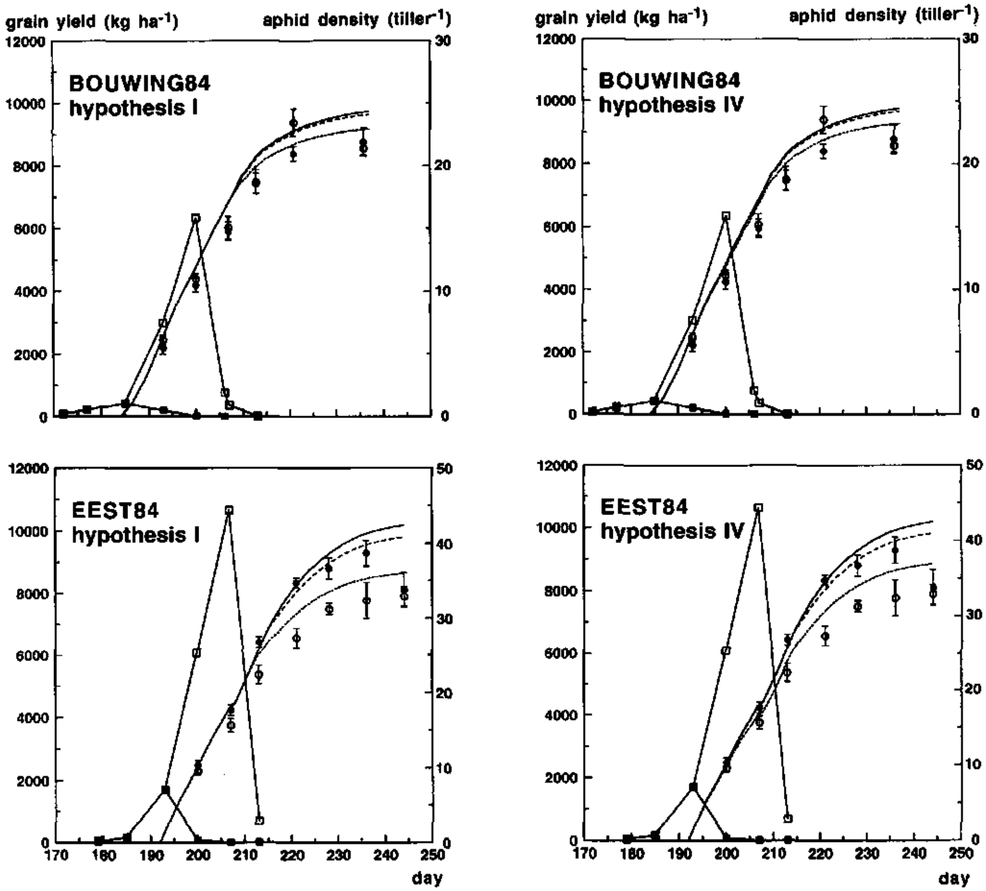


Figure 3.8. Observed and simulated grain yield of EEST84 and BOUWING84 based on hypotheses I and IV to describe the direct effects of *Sitobion avenae*. Vertical bars represent standard errors of the mean. Observed grain yield of the control (●) and the most severely infested treatment (o). Simulated grain yield without aphids (——), with an aphid infestation as observed in the control treatment (– – –) and in the most severely infested treatment (- - - -), respectively. The size of the aphid infestations is shown for the control (—■—) and the most severe infestation (—□—). Leaf area index is simulated.

when aphids do not affect the flow rate of phloem sap (hypotheses III and IV) (Table 3.8).

The dynamic contribution of each injury component to total simulated damage for EEST84 is represented in Figure 3.9. For hypothesis I, damage is apparent from the time simulated grain growth becomes source-limited (day 212), three days before the carbohydrate reserves are depleted in the run without aphids. Simulated damage due to each injury component increases with time. The increase of damage due to feeding after aphid density has become zero (day 221) is caused by enhanced depletion of translocatable nitrogen during feeding, later in the season resulting in lower carbon dioxide

Table 3.7 Relative sensitivity of end-of-season grain yield for a number of model parameters calculated with the damage model run with data of EEST84. In the runs leaf area index is simulated. Simulated grain yield in the absence of aphids is 10187 kg $ha^{-1}$. Simulated grain yield in the presence of aphids is 8655 kg $ha^{-1}$ and 8864 kg $ha^{-1}$ for hypotheses I and IV, respectively. Relative sensitivity is calculated as the ratio of percentage change in simulated grain yield or simulated damage and percentage change in parameter value.

| Parameter value | Unit | Reference value | Percentage change in parameter | Relative sensitivity | | | |
|---|---|---|---|---|---|---|---|
| | | | | hypothesis I | | hypothesis IV | |
| | | | | yield | damage | yield | damage |
| Phloem sap uptake rate | kg $mg^{-1}d^{-1}$ | $8.9 \times 10^{-9}$ [a] | +10 | -0.11 | 0.63 | -0.09 | 0.60 |
| | | | -10 | -0.12 | 0.68 | -0.09 | 0.63 |
| Extinction coefficient for honeydew | - | 0.8 [b] | -25 | -0.00 | 0.03 | -0.00 | 0.03 |
| Fraction of honeydew deposited on ears | - | 0.3 [c] | +33 | 0.00 | -0.03 | 0.00 | -0.02 |
| | | | -33 | 0.00 | -0.00 | 0.00 | -0.01 |
| Maximum relative reduction of $P_m$ | - | 0.24 [d] | +20 | -0.05 | 0.31 | -0.06 | 0.39 |
| | | | -20 | -0.05 | 0.30 | -0.06 | 0.38 |
| Maximum relative increase of $R_d$ | - | 0.35 [d] | +20 | -0.04 | 0.21 | -0.04 | 0.27 |
| | | | -20 | -0.04 | 0.20 | -0.04 | 0.27 |

[a] After Rabbinge and Coster (1984).

[b] This Chapter.

[c] Vereijken (1979).

[d] Chapter 2.

Table 3.8. Total damage and contribution of injury components for EEST84, simulated under different hypotheses on the partitioning of phloem sap between *S. avenae* and grains. The size of the aphid sink is calculated assuming demand for nitrogen. For explanation of the hypotheses see Figure 3.1.

| Hypothesis | Total damage kg ha$^{-1}$ | Injury components | | |
|---|---|---|---|---|
| | | feeding (%) | photos. reduction (%) | respiration increase (%) |
| I | 1532 | 51 | 28 | 21 |
| II | 1543 | 51 | 28 | 21 |
| III | 1251 | 35 | 37 | 28 |
| IV | 1323 | 37 | 36 | 27 |

*assimilation rates and increased death rates of non-grain organs. This* accounts for 37% of the total direct damage.

In the model based on hypothesis IV simulated damage is apparent from grain set onward since the demand of the grains is only partly met as a result of aphid feeding (Figure 3.9). Simulated damage due to feeding does not increase after departure of the aphids from the crop, as the rate of nitrogen depletion is not affected by feeding, contrary to the model based on hypothesis I.

So far, it has been assumed that, once present, honeydew remains on the plant. However, weather and saprophytic micro-organisms can reduce the amount of honeydew per unit area (Fokkema *et al.*, 1983). Quantitative relations are lacking. The effect of rain on damage due to honeydew is evaluated by assuming complete removal of honeydew and its effects after a daily precipitation intensity equal to or exceeding 5 mm, which occurred on days 190 to 193 and 197 for EEST84. The effect on simulated yield is an increase of less than 1% (42 kg ha$^{-1}$).

Saprophytic leaf fungi have been reported to affect the net rate of carbon dioxide assimilation of leaves in two ways. During a few days after honeydew deposition onto a leaf, stimulation of leaf micro-organisms causes an increase in the rate of dark respiration of the plant (Smedegaard-Petersen, 1982; Chapter 2). The effect is ascribed to plant defense reactions to penetration attempts by saprophytic fungi (Smedegaard-Petersen, 1982). In the longer term, saprophytic phyllosphere micro-organisms, especially the black molds, may increase to such densities that they intercept light, thus reducing the initial light use efficiency (Vereijken, 1979; Rabbinge *et al.*, 1981; Chapter 2). The

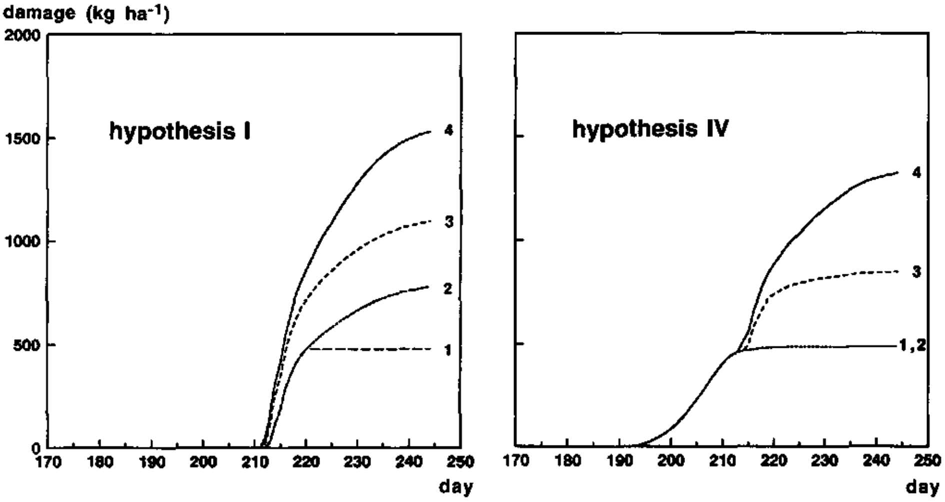


Figure 3.9. Simulated total damage (kg ha$^{-1}$) and injury components for EEST84, the most severe aphid infestation. Simulation runs are based on hypotheses I and IV to describe the direct effects of *S. avenae*.

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 carbon dioxide assimilation at light saturation.

quantitative consequences of these effects of leaf saprophytes on leaf carbon dioxide assimilation for grain yield can be evaluated with the simulation model.

The short-term effects of saprophytic micro-organisms on grain yield are evaluated by adapting the damage model to include an increase in the rate of maintenance respiration one day after honeydew deposition. Respiration increases in proportion to the rate of honeydew deposition with a maximum of 47% of the control after deposition of 2.6 g m$^{-2}$ day$^{-1}$ (data of Chapter 2; see also Smedegaard-Petersen, 1982), followed by a linear decline to normal values after 3, 5 or 7 days. These intervals represent the period of time for return to normal values reported in Chapter 2 for honeydew on winter wheat plants in the field and Smedegaard-Petersen (1982) working with barley plants inoculated with *Alternaria alternata* and *Cladosporium herbarum* in the laboratory. The results show that the additional reduction of simulated grain yield as compared to the standard version of the damage model varies from 130 kg ha$^{-1}$ to 275 kg ha$^{-1}$.

The longer-term effect of leaf saprophytes on grain yield is evaluated assuming damage to be the result of two injury components: aphid feeding and reduction of the initial light use efficiency. The reduction of the initial light use efficiency is proportional to the amount of honeydew deposited and increases linearly with time, starting at zero on the day of deposition. No response is allowed above the maximum reduction of 17% compared to the control, measured concomitant with a leaf coverage of 2.6 g (honeydew) m$^{-2}$ (Chapter 2). The results show that reduction of the initial light use efficiency decreases simulated yield by approximately 450 kg ha$^{-1}$.

*Analysis of errors in inputs.* In comparison with the crop model, aphid density is an additional source of input error. The results of the calculation of model error variances and *q*-values (Table 3.9) show that *q*-values remain within acceptable limits.

### *Discussion of the damage model*

*Parameterization.* The large effect of the rate of uptake of phloem sap on simulated yield and damage calls for accurate parameter estimates. In a review of honeydew production rates for various aphid-host combinations from which phloem sap uptake rates are calculated, Coster (1983) found his values for *S. avenae* on spring wheat cv. Bastion which are used in the present damage model, to be within the published range and very close to those found for the same aphid species on spring wheat cv. Opal by Rabbinge *et al.* (1981). Spiller and Llewellyn (1987) found considerably lower rates for honeydew production by *M. dirhodum* on seedlings of spring wheat (DC 10-11). The difference is possibly caused by a higher nitrogen content of the phloem sap of the seedlings (van Keulen and Seligman, 1987).

The submodel describing the distribution of honeydew over the canopy profile has not been compared to field data. However, fine sensitivity analysis showed that neither the value of the extinction coefficient for honeydew nor the partitioning of honeydew between ears and leaves is of major significance to yield and damage.

*Formulation of the effect of grain aphid feeding on crop growth processes.* The alternative hypotheses on the mode of interaction between aphids and grains do not result in major changes in simulated final grain yield of EEST84 (Table 3.8). However, the observed onset and the time-course of reduction of grain yield of EEST84 is simulated correctly only when aphids are assumed not to increase the size of the sinks for nitrogen and carbohydrates (hypotheses III and IV). Thus, compensation for aphid feeding by increased phloem sap flow to the grains (hypotheses I and II) is unlikely to be important. This conclusion is corroborated by results of Vereijken (1979) who found damage by *S. avenae* in two field experiments to agree with the damage expected from the efficiency of food utilization by the aphids. In the experiments, the crop was

Table 3.9. Results of input error analysis of the damage model per sampling date (Julian day) for EEST84 and BOUWING84 using hypothesis IV to describe the direct effects of *S. avenae*. SEM is standard error of the mean. For explanation of symbols see text.

EEST84

| day | $z_S$ | $\sqrt{(E(\mathrm{var}\ z_S))}$ | $z_O$ | SEM($z_O$) | $q$ |
|---|---|---|---|---|---|
| 200 | 2354 | 279 | 2324 | 138 | 0.10 |
| 207 | 4043 | 369 | 3758 | 212 | 0.67 |
| 213 | 5714 | 407 | 5378 | 296 | 0.67 |
| 221 | 7392 | 212 | 6571 | 325 | 2.00 |
| 228 | 8163 | 284 | 7515 | 179 | 1.93 |
| 236 | 8657 | 378 | 7778 | 575 | 1.28 |
| 244 | 8864 | 427 | 7907 | 309 | 1.81 |

BOUWING84

| day | $z_S$ | $\sqrt{(E(\mathrm{var}\ z_S))}$ | $z_O$ | SEM($z_O$) | $q$ |
|---|---|---|---|---|---|
| 193 | 2515 | 519 | 2447 | 144 | 0.11 |
| 200 | 4651 | 658 | 4428 | 155 | 0.33 |
| 207 | 6674 | 731 | 6032 | 354 | 0.79 |
| 213 | 7974 | 203 | 7455 | 320 | 1.42 |
| 221 | 8738 | 415 | 9383 | 441 | -1.07 |
| 237 | 9258 | 624 | 8549 | 199 | 1.08 |

treated with fungicide to preclude effects of leaf saprophytes. As a consequence, the accelerated leaf death observed in the aphid-infested plots of EEST84 must be due to other causes than aphid feeding. Both honeydew and saprophytic leaf fungi have been reported to decrease green leaf weight (Vereijken, 1979; Rabbinge *et al.*, 1981; Chapter 2) and leaf nitrogen amount (Chapter 2). These effects appear to depend on weather conditions, especially humidity and temperature but quantitative relations are lacking.

*Contribution of assimilate uptake by the grain aphid to damage.* Using hypotheses III and IV, the contribution of aphid feeding to total simulated damage is *ca.* 35% for EEST84 (Table 3.8). Vereijken (1979) and Rabbinge and Vereijken (1980) estimated the direct effect of cereal aphids to be 45-50%

of the total damage while Rabbinge *et al.* (1983) approximated it to be 16% at attainable yield levels over 6500 kg ha$^{-1}$.

*Contribution of short-term increase of dark respiration by leaf saprophytes to damage.* The sensitivity analysis showed that even for the relatively large infestation of EEST84, a short-term increase in the rate of dark respiration of leaves is not likely to contribute significantly to damage as has been suggested (Smedegaard-Petersen and Tolstrup, 1985 and references therein). Only at extremely high aphid densities, significant damage may occur. An example is found in experiments of Vereijken (1979) who created aphid infestations in winter wheat with peak densities of approximately 150 tiller$^{-1}$ (*S. avenae* only) by placing nylon gauze cages in the crop and introducing aphids. Due to the dry weather during these experiments honeydew crystallized rapidly, precluding long-term effects of saprophytic fungi. Fungicide sprays reduced damage by 50%, most likely by reducing the short-term effects. Under field conditions in the Netherlands, however, densities of uncontrolled cereal aphid populations seldom exceed 30 tiller$^{-1}$.

*Effect of weather conditions on the contribution of honeydew to damage.* Assuming suitable cool and humid weather conditions, simulated damage due to reduction of the initial light use efficiency by honeydew-stimulated leaf saprophytes is 450 kg ha$^{-1}$ for the aphid-infested plots of EEST84. With the standard version of the model, honeydew *per se* has been found to contribute *ca.* 760 kg ha$^{-1}$ to total damage. Thus, model calculations indicate that under hot and dry conditions grain aphid damage is larger as compared to cool and humid conditions, due to a larger contribution of honeydew to damage. Considering the size of the potential effect on yield and the uncertainty in the available information, the relation between weather conditions and the effect of honeydew on leaf carbon dioxide assimilation deserves more attention.

## Conclusion

The model described integrates knowledge of effects of *S. avenae* on growth processes of winter wheat from flowering to ripeness to explain the consequences of an aphid infestation for grain yield. Similar approaches have been adopted to analyze damage by other pests (e.g. brown plant hopper (*Nilaparvata lugens* (Stal)) in rice (Kenmore, 1980)), by diseases (e.g. powdery mildew (*Erysiphe graminis* D.C. ex Mérat) on winter wheat (Daamen and Jorritsma, 1990a,b)), by weeds (e.g. barnyard grass (*Echinochloa crus-galli* (L.) P.B. in maize (Spitters, 1989)), and abiotic causes (e.g. $SO_2$ in faba bean (Kropff, 1989)).

The development of the grain aphid - winter wheat model has served the purpose of organizing existing information and has enabled quantitative evaluation of alternative submodels in cases where little information on processes is available. Components of the grain aphid - winter wheat system which require more attention include the description of processes involved in leaf death at low crop nitrogen levels and the relation between weather variables and the longer term effects of honeydew on leaf carbon dioxide assimilation. Further validation of the model with data sets of different years and locations is desirable.

In spite of the gaps in knowledge identified, the accuracy of the damage model may be sufficient for use in supervised control advisory systems like EPIPRE (Drenth *et al.*, 1989). In practice only low aphid densities are tolerable due to the low costs of chemical control so that errors in the estimation of weather-dependent honeydew damage will remain below the level of detectability. An analysis of the accuracy of the damage model when used for the purpose of decision support is presented in Chapter 4.

# Appendix to Chapter 3

## Modelling partitioning of phloem sap between grains and aphids

The hypotheses I to IV are translated into terms of the crop model. The equations pertain to both nitrogen and carbohydrates. A total demand ($d_{tot}$) is defined. For the hypotheses I and II the total demand consists of the sum of the demands of grains and aphids:

$$d_{tot} = d_g + d_a \tag{A3.1}$$

where $d_{tot}$ represents the potential rate of carbohydrate or nitrogen accumulation in grains and aphids (kg ha$^{-1}$ day$^{-1}$), $d_g$ the potential rate of carbohydrate or nitrogen accumulation in the grains (kg ha$^{-1}$ day$^{-1}$), and $d_a$ the potential rate of carbohydrate or nitrogen accumulation in the aphids (kg ha$^{-1}$ day$^{-1}$).

For the hypotheses III and IV the total demand consists of the demand of the grains and, before grain set, the demand of the aphids.

$$d_{tot} = \begin{cases} d_a & D < 0.11 \\ d_g & D \geq 0.11 \end{cases} \tag{A3.2}$$

where $D$ represents crop development stage, with $D$=0 at flowering and $D$=1 at ripeness and d$D$/d$t$ a linear function of temperature.

The sink-source concept of the crop model is expressed as:

$$f_{tot} = \min\,(d_{tot}, s_{tot}) \tag{A3.3}$$

where $f_{tot}$ is the actual flow of nitrogen or carbohydrate to grains and aphids (kg ha$^{-1}$ day$^{-1}$), and $s_{tot}$ the potential rate of nitrogen or carbohydrate supply to grains and aphids (kg ha$^{-1}$ day$^{-1}$).

Partitioning of $f_{tot}$ over the sinks depends on the assumption on the nature of the interaction between aphids and grains. In the hypotheses I and III the partitioning is proportional to the demand:

$$f_a = d_a \,/\, d_{tot} \cdot f_{tot} \tag{A3.4}$$
$$f_g = d_g \,/\, d_{tot} \cdot f_{tot} \tag{A3.5}$$

where $f_a$ represents the actual flow of nitrogen or carbohydrate to the aphids (kg ha$^{-1}$ day$^{-1}$), and $f_g$ the actual flow of nitrogen or carbohydrate to the grains (kg ha$^{-1}$ day$^{-1}$). If priority is given to the aphids as in hypotheses II and IV, the model becomes:

$$f_a = \min\,(d_a\,,\, f_{tot}) \tag{A3.6}$$
$$f_g = \max\,(f_{tot} - d_a\,,\, 0). \tag{A3.7}$$

# Symbols used in Chapter 3

| | | |
|---|---|---|
| $c_r$ | ratio of carbohydrates and nitrogen in phloem sap | (kg ($CH_2O$) kg$^{-1}$(N)) |
| $d_{C,a}$ | potential rate of carbohydrate accumulation in aphids | (kg ($CH_2O$) ha$^{-1}$ day$^{-1}$) |
| $d_a$ | potential rate of carbohydrate or nitrogen accumulation in the aphids | (kg ha$^{-1}$ day$^{-1}$) |
| $d_g$ | potential rate of carbohydrate or nitrogen accumulation in the grains | (kg ha$^{-1}$ day$^{-1}$) |
| $d_{N,a}$ | potential rate of nitrogen accumulation in aphids | (kg (N) ha$^{-1}$ day$^{-1}$) |
| $d_{tot}$ | potential rate of carbohydrate or nitrogen accumulation in grains and aphids | (kg ha$^{-1}$ day$^{-1}$) |
| $D$ | crop development stage | (-) |
| $e_f$ | fraction of honeydew production intercepted by ears | (-) |
| $f_a$ | actual flow of nitrogen or carbohydrate to the aphids | (kg (N) ha$^{-1}$ day$^{-1}$) |
| $f_{C,a}$ | actual flow of carbohydrates to the aphids | (kg ($CH_2O$) ha$^{-1}$ day$^{-1}$) |
| $f_g$ | actual flow of nitrogen or carbohydrate to the grains | (kg ha$^{-1}$ day$^{-1}$) |
| $f_{tot}$ | actual flow of nitrogen or carbohydrate to grains and aphids | (kg ha$^{-1}$ day$^{-1}$) |
| $h$ | rate of honeydew excretion | (kg ha$^{-1}$ day$^{-1}$) |
| $h_{ls}(L)$ | rate of honeydew interception at depth $L$ in leaf and stem layer | (kg ha$^{-1}$ day$^{-1}$) |
| $L$ | cumulative leaf area index calculated from the top of the leaf and stem layer | (ha ha$^{-1}$) |
| $k_h$ | extinction coefficient for honeydew | (-) |
| $n_a$ | aphid density | (tiller$^{-1}$) |
| $n_t$ | tiller density | (ha$^{-1}$) |
| $p_a$ | potential feeding rate of aphids | (kg (N) mg$^{-1}$ day$^{-1}$) |
| $s_{tot}$ | potential rate of nitrogen or carbohydrate supply to grains and aphids | (kg ha$^{-1}$ day$^{-1}$) |
| $w_a$ | average aphid fresh weight | (mg) |
| $y$ | model parameter | (various) |
| $z$ | model output | (various) |
| $z_o(t)$ | observed quantity at time t | (various) |
| $z_s(t)$ | simulated quantity at time t | (various) |

## Part 1

# Damage in winter wheat caused by the grain aphid *Sitobion avenae*

## Chapter 4

# Calculation of damage at various attainable yield levels

Rossing, W.A.H., 1991.
Simulation of damage in winter wheat caused by the grain aphid *Sitobion avenae.* 3. Calculation of damage at various attainable yield levels.
*Netherlands Journal of Plant Pathology* 97:87-103.

**Abstract** A dynamic, process-based simulation model is used to evaluate the effect of injury by *Sitobion avenae* F. on yield of winter wheat at a range of attainable yield levels. The attainable yield is defined as the yield reached in the absence of pests and diseases, at the prevailing temperature and radiation and the available amount of soil nitrogen. Water limitation is not taken into account. Only the period from flowering to ripeness is considered. Aphid infestation intensity is expressed in aphid-days, the integral of aphid density (tiller$^{-1}$) over time (day). The calculations show that damage per aphid-day decreases from flowering to ripeness because damage caused by honeydew decreases with advancing crop development stage while damage caused by aphid feeding is about constant. Damage per aphid-day during a particular period of crop development increases in a nearly linear fashion with the attainable yield level. At attainable yield levels over approximately 9000 kg ha$^{-1}$ and until crop development stage early milky ripe (DC 73), however, damage per aphid-day increases at a higher rate with the attainable yield level as compared to lower yield levels. The crop-physiological causes are discussed.

Regression models are constructed that relate simulated aphid damage both during various periods of crop development and averaged over the entire post-anthesis phase, to the simulated attainable yield level. The accuracy of these simulation-based regression models and five published models of damage in winter wheat caused by *S. avenae* is evaluated using 21 data sets, obtained in experiments carried out between 1973 and 1984 in the Netherlands. Attention is focussed on two aspects of model accuracy: the agreement between predicted and measured damage and the size of the error in model predictions. In both aspects the simulation-based regression models are as good as the best published empirical models.

## Introduction

Cereal aphids have been an occasional pest in west European wheat cultivation only since the early seventies. Their increased economic importance has been attributed to changes in farm practice, especially high nitrogen fertilizer rates and fungicide inputs (Carter *et al.*, 1982). After evaluation of a large body of field experiments, Rabbinge *et al.* (1983) hypothesized that aphids cause relatively more damage at higher attainable yield levels, i.e. levels of yield in the absence of aphids and other crop growth reducing factors (Zadoks and Schein, 1979). Direct evidence for this hypothesis is difficult to obtain as this requires many experiments over a range of crop production situations.

In this Chapter, attention is focussed on *Sitobion avenae* F., the grain aphid, which constitutes the most abundant cereal aphid species in the Netherlands. In Chapter 3, a systems approach (de Wit and Goudriaan, 1978; Rabbinge *et al.*, 1989) was taken to quantify damage by *S. avenae* in winter wheat. A simulation model of growth and development of winter wheat from flowering to ripeness was combined with a model of injury by *S. avenae*. In these models, information on the processes involved (Groot, 1987; Van Keulen and Seligman, 1987; Chapter 2) was integrated to explain winter wheat yield, given the available amount of soil nitrogen, the prevailing weather and the observed aphid population. Water limitation was not taken into account. Evaluation of the crop growth model was carried out for attainable winter wheat yields ranging from 4000 kg ha$^{-1}$ to 9000 kg ha$^{-1}$. The injury model was evaluated at the higher yield levels only due to lack of data at other yield levels (Chapter 3).

In this Chapter, the winter wheat - *S. avenae* model is used to calculate the effect of a grain aphid infestation on grain yield at different attainable yield levels. Due to the explanatory nature of the model, differences in effects of aphid injury on yield can be attributed to their crop-physiological causes. Next, the results of the simulation study are summarized in regression models suitable for use in decision support systems like EPIPRE (Drenth *et al.*, 1989). Finally, the accuracy of these regression models is compared to the accuracy of a number of published models of damage by *S. avenae* in winter wheat, using a set of independent field data.

## Materials and methods

Weights in this Chapter are based on a grain moisture content of 16%. Crop development is expressed in Decimal Code (DC) (Zadoks *et al.*, 1974).

### Simulation of damage at various attainable yield levels

Grain yield in absence and presence of a *S. avenae* population is calculated using a computer model described in Chapter 3. With this model, growth and development of winter wheat during the post-anthesis phase, i.e. the period from flowering to ripeness, is simulated as a function of injury by *S. avenae*. Crop analysis data from nine experiments are used to initialize the winter wheat model at anthesis. The amount of soil nitrogen available from anthesis to ripeness is input for the model. In this way, nine different attainable yield levels are simulated using realistic initial crop conditions. All data have been collected in experiments designed to evaluate the effect of the rate of nitrogen fertilizer application on crop production. Six of the data sets used, BOUWING84, EEST83, EEST84, PAGV1, PAGV2 and PAGV3, have been described in Chapter 3. Three additional data sets, HELECINE1, HELECINE2 and HELECINE3, pertain to experiments carried out in north Belgium (Anon., 1984; Anon., 1985). General information on these experiments is given in

Table 4.1. General information on the data sets HELECINE1, HELECINE2 and HELECINE3 used to initialize the winter wheat crop model.

| | HELECINE1 | HELECINE2 | HELECINE3 |
|---|---|---|---|
| Location | Helecine (B) | Helecine (B) | Helecine (B) |
| Wheat variety | Corin | Corin | Corin |
| Grain yield (kg ha$^{-1}$) | 6151 | 5800 | 5077 |
| Previous crop | sugar beets | sugar beets | sugar beets |
| Sowing date | 10 Nov. 1984 | 10 Nov. 1983 | 10 Nov. 1983 |
| Flowering date | 7 June 1985 | 13 June 1984 | 13 June 1984 |
| Harvest date | 12 Aug. 1985 | 22 Aug. 1984 | 22 Aug. 1984 |
| Row spacing (cm) | 15 | 15 | 15 |
| Sowing density (kg ha$^{-1}$) | 160 | ? | ? |
| Total N (kg ha$^{-1}$) | 71 | 154 | 86 |
| Growth regulator | no | yes | yes |
| Protective chemicals[a] | H,F | H,F | H,F |

[a] H=herbicide, F=fungicide

Table 4.2. Time course of crop development and aphid population density used in the simulation model to calculate aphid damage at various attainable yield levels.

| Day of the year | Crop development stage | Aphid density (tiller$^{-1}$) | Aphid index (day tiller$^{-1}$) |
|---|---|---|---|
| 173 | 60 | 0.25 | 0 |
| 176 | 65 | 0.40 | 0.90 |
| 179 | 69 | 0.56 | 2.26 |
| 181 | 71 | 0.65 | 3.42 |
| 186 | 73 | 1.65 | 8.17 |
| 193 | 75 | 5.86 | 30.70 |
| 201 | 77 | 11.75 | 123.77 |
| 209 | 83 | 0.00 | 157.37 |
| 220 | 90 | 0.00 | 157.37 |

Table 4.1. Temperature and radiation data used as model input are 33 year daily averages of Wageningen, the Netherlands. The duration of crop development from flowering to ripeness is fixed on 47 days (Table 4.2). Running the crop growth simulation model with the various initial crop and soil conditions and the same set of values for temperature, radiation and crop development duration results in attainable grain yields ranging from 3000 kg ha$^{-1}$ to 10000 kg ha$^{-1}$.

The simulation model accounts for two components of aphid injury: aphid feeding on the phloem sap and reduction of net photosynthesis by honeydew. Aphid feeding is assumed to cause a decrease of the rate of carbohydrate and nitrogen accumulation in the grains equal to the rate of uptake of these components by the aphids. This assumption which has been referred to as hypothesis IV previously, appears the most appropriate for describing aphid feeding in view of experimental evidence (Chapter 3). Honeydew contributes to damage as it increases the rate of maintenance respiration and decreases the rate of carbon dioxide assimilation at light saturation. The change in these photosynthesis parameters is a linear function of the amount of daily intercepted honeydew and increases with time at a constant rate until a maximum is reached 15 days after honeydew interception. In the model, no response is allowed above the maximum values measured in experiments, i.e. 35% increase of the rate of maintenance respiration and 24% decrease of the rate of carbon dioxide assimilation at light saturation. A more detailed description of the model is given in Chapter 3.

The time course of aphid density introduced into the model is shown in Table 4.2. No distinction is made between various developmental classes. The aphids feed on the ears only. The simulation model is run repeatedly with the same weather data and initial conditions but with the aphid population density set to zero at subsequently earlier crop development stages. Thus, the average effect of aphids on grain yield can be calculated for different periods of crop development. In total, six periods of crop development are distinguished. The results are expressed per aphid-day by dividing damage incurred during a particular period of crop development by the concomitant integral of aphid density (tiller$^{-1}$) over time. This integral, the aphid-index, is a commonly used measure of infestation intensity (Rautapää, 1966).

## Construction of simulation-based regression models

The results of the simulation runs are summarized in regression models which relate simulated damage per aphid-day to simulated attainable yield, both averaged over the entire post-anthesis phase and for each of the six periods of crop development separately. Three types of regression models are fitted: a linear model, an exponential model and a logarithmic model. Choice of these models is suggested by visual inspection of the data. Least-squares estimates of the parameters of the regression models are calculated using a statistical software package (SAS, 1985).

## Accuracy of the simulation-based models in comparison with other models

The regression models with the best fit to the simulation results are hypothesized to give an, on average, accurate description of damage by *S. avenae* for the various periods of crop development. To test this hypothesis and to compare the accuracy of these simulation-based regression models to the accuracy of empirical regression models for *S. avenae* damage by Vereijken (1979), Rabbinge and Mantel (1981) and Entwistle and Dixon (1987), the predictions of each model are compared to damage measured in field experiments. An overview of the various models is given in Table 4.3. For evaluation of the models, data sets from 21 field experiments carried out in the Netherlands are available, 19 of which have been used previously by Rabbinge and Mantel (1981). The two additional data sets have been described in Chapter 2. Care is taken not to use the same data for model evaluation as have been used in the development of the models.

The experimental data used for evaluation of the models consist of aphid density (tiller$^{-1}$) sampled at approximately weekly intervals, all instars lumped, development stage of the crop and final yield of infested and uninfested plots. Aphid-days are calculated as the integral of aphid density over time, using linear interpolation to calculate aphid density between data points. Aphid-unit days are calculated according to the procedure described by Wratten *et al.* (1979). In this procedure, the densities of the age-cohorts L1-L3, L4 and adults are weighted to account for instar-related differences in feeding rate. Since in the available data sets instars are not distinguished, data of Mantel *et al.* (1982) are used to estimate the age distribution of the aphid population as a function of crop development stage. The factors used for conversion of aphid-days into aphid-unit days are shown in Table 4.4. The figures before DC 60 and after DC 77 are extrapolations. Between data points, the value of the multiplication factor is calculated by linear interpolation. A summary of the data sets is given in the Appendix to this Chapter. Where aphid density per ear is required as model input, 84% of the aphid population on a tiller is assumed to occur on the ear (Entwistle and Dixon, 1987).

Two aspects of model accuracy are evaluated. Firstly, the predictions of a regression model are compared to measured damage and statistically tested for systematic errors. This analysis assesses whether the model's representation of the real world system is demonstrably wrong. Penning de

Table 4.3. Models evaluated with respect to their accuracy in predicting grain aphid damage in winter wheat.

| No. | Source | Model | | Model type |
|---|---|---|---|---|
| 1. | Vereijken (1979) | yield loss (kg $ha^{-1}$) = 15.51 + 10.97 × (peak aphids $ear^{-1}$) | | single point |
| 2. | Rabbinge & Mantel (1981) | yield loss (kg $ha^{-1}$) = -79.9 + 17.2 × (peak aphids $tiller^{-1}$) | | single point |
| 3. | Rabbinge & Mantel (1981) | yield loss (kg $ha^{-1}$) = 66.7 + 24.3 × (peak aphids $ear^{-1}$) | | single point |
| 4. | Entwistle & Dixon (1987) | percent yield loss = 0.951 + 0.273 × (peak *S. avenae* $tiller^{-1}$) | | single point |
| 5. | Rossing (this Chapter) | yield loss (kg $ha^{-1}$) = [ -6.18 + 2.03 × $\log_{10}$ (attainable yield) ] × aphid-index | | single point |
| 6. | Entwistle & Dixon (1987) | | | multiple point |
| | | crop development period | percent damage per aphid-unit day | |
| | | < 53 | 0.075 | |
| | | 53 - 68.9 | 0.205 | |
| | | 69 - 70.9 | 0.075 | |
| | | 71 - 73 | 0.056 | |
| | | 73.1 - 76.9 | 0.037 | |
| | | ≥ 77 | 0.012 | |
| 7. | Rossing (this Chapter) | See Table 3.5 | | multiple point |

Table 4.4. Multiplication factors used for the conversion of aphid days into aphid-unit days calculated using data of Mantel *et al.* (1982) to estimate the age distribution of the aphid population. One aphid-unit is equivalent to one adult, one L4 or three L1-L3 (Wratten *et al.*, 1979).

| Crop development stage | Estimated fraction L1-L3 | Multiplication factor |
|---|---|---|
| < 60 | 0.74 | 0.51 |
| 60 | 0.74 | 0.51 |
| 70 | 0.80 | 0.47 |
| 77 | 0.60 | 0.60 |
| > 77 | 0.60 | 0.60 |

Vries (1977) referred to this aspect of accuracy as the truthfulness of a model. Secondly, the distributions of the prediction error, i.e. the difference between measured and predicted values, of the various models are evaluated using a statistical selection procedure. This aspect of accuracy may be called the usefulness of a model as in the context of decision making it is of more interest than the truthfulness.

The truthfulness of the regression models is evaluated by testing the prediction error for both systematic over- or underprediction and trend as a function of measured damage. Three statistical tests are used: an F-test in which both errors are evaluated simultaneously, and two non-parametric tests for detection of each error separately. In the F-test, the hypothesis is tested that the prediction error has expectation zero, whereas the alternative hypothesis allows for bias in the expected prediction error which is a linear function of measured damage. When the data sets are independent and representative for situations in which the model is to be used, the *f*-statistic is calculated as

$$f = \frac{(RSS_0 - RSS_1) / 2}{RSS_1 / (n-2)}, \qquad f \equiv F^2_{n-2}$$

where $RSS_0$ is the residual sum of squares under the null hypothesis, $RSS_1$ the residual sum of squares under the alternative hypothesis, and $n$ the number of observations. In addition, Wilcoxon's signed rank test is used to detect systematic over- or underprediction by evaluating the null hypothesis that the predicted damage and the measured damage originate from the same distribution. Spearman's rank correlation test is used to assess trend in the prediction error by evaluating the null hypothesis that there is no rank correlation between the prediction error and measured damage (Snedecor and Cochran, 1980).

The accuracy of the regression models is evaluated by means of a nonparametric selection procedure (Gibbons *et al.*, 1977). The procedure involves ordering the frequency distributions of the absolute value of the prediction error of the models on the basis of the value of a sample quantile. Here, the 50% quantile and the 75% quantile are used as ordering criteria. The 50% quantile represents the median accuracy of the model, while the 75% quantile in combination with the 50% quantile provides an indication of the variability in accuracy.

## Results and discussion

### Simulated damage at various yield levels

Simulated damage per aphid-day averaged over the post-anthesis phase is shown in Figure 4.1 for various simulated attainable yield levels. Average damage per aphid-day increases with the attainable yield level but levels off at high yield levels.

A more detailed analysis is presented in Figure 4.2 where simulated damage per aphid-day caused during various periods of crop development is shown as a function of simulated attainable yield level. Aphids present before mid-flowering (DC 65) cause the largest damage per aphid-day at all attainable yield levels. Simulated damage per aphid-day decreases with advancing crop development stage because damage caused by honeydew

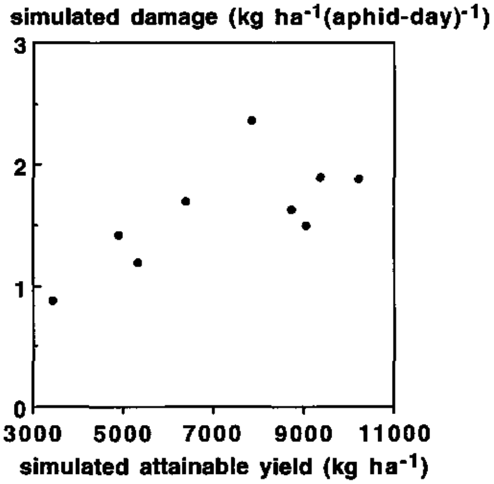


Figure 4.1. Simulated damage per aphid-day averaged over the post-anthesis phase at various attainable yield levels. The duration of the post-anthesis phase is fixed on 47 days.

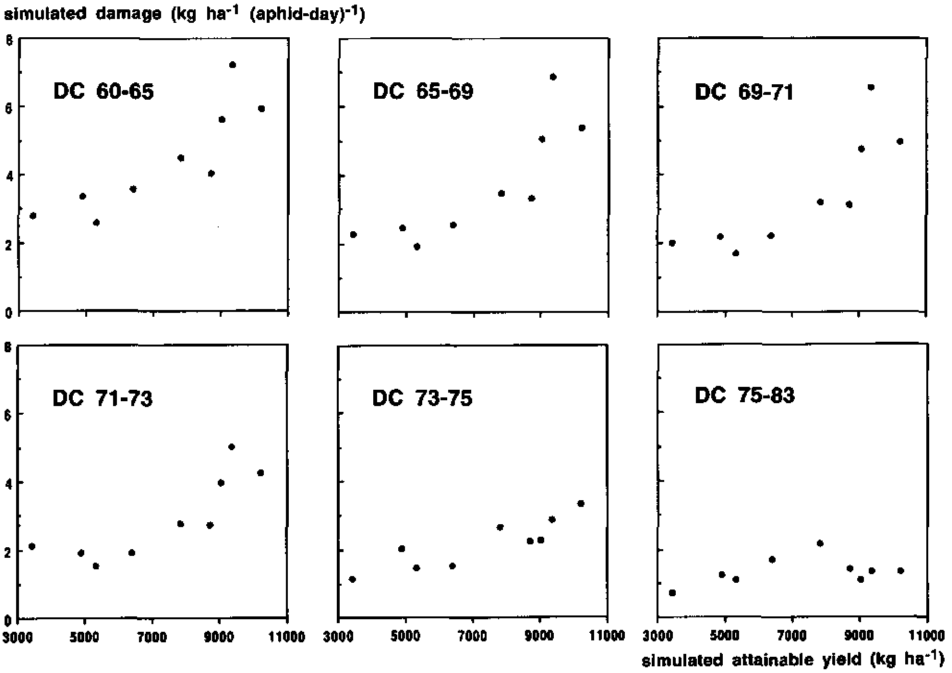
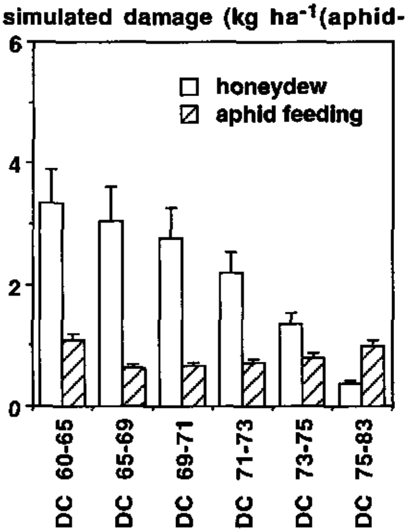


Figure 4.2. Simulated damage per aphid-day caused during six periods of crop development at various attainable yield levels.

decreases (Figure 4.3). Damage caused by aphid feeding remains approximately constant. Honeydew damage is larger at earlier crop development stages because the simulated effects of an intercepted amount of honeydew on net leaf photosynthesis accumulate with time.

Per period of crop development, simulated damage per aphid-day increases approximately linearly with the simulated attainable yield level except for the three highest yield levels where simulated damage exceeds the linear trend between DC 60 and DC 73 (Figure 4.2). The relatively large damage between DC 60 and DC 73 at attainable yield levels over 9000 kg ha$^{-1}$ is due to the large values of leaf area index in high-yielding crops. At large values of leaf area index the marginal contribution of green leaf area to yield is small due to mutual shading, whereas the damage resulting from the effect of honeydew on the rate of maintenance respiration (up to 35% increase) is fully proportional to leaf area index. The effect of honeydew on the maximum rate of carbon dioxide assimilation (up to 24% decrease) is proportional to leaf area index only at saturating light intensities. The dissimilar effects of additional green leaf area on yield and damage are illustrated in Figure 4.4 and Figure 4.5, respectively, where green area duration, the integral



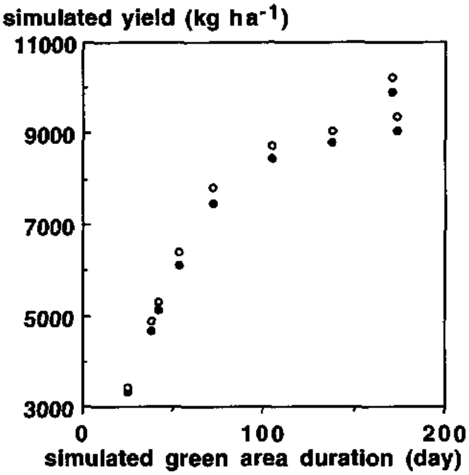


Figure 4.3. (left) Simulated damage by *S. avenae* due to honeydew and aphid feeding, respectively, during six periods of crop development, averaged over the nine attainable yield levels. The vertical bars represent standard errors.

*Figure 4.4. (right) Simulated yield and simulated green area duration in the absence (○) and presence (●) of an aphid infestation. The duration of the post-anthesis phase is fixed on 47 days.*

of leaf area index over time, is used to characterize the leaf area dynamics. The marginal contribution of green area duration to simulated yield decreases at high yield levels (Figure 4.4), whereas simulated aphid damage increases in proportion to green area duration between DC 60 and DC 73 (Figure 4.5). After DC 73 simulated damage is increasingly due to aphid feeding (Figure 4.3) because the time remaining until cessation of grain filling (approximately DC 83) is too short for accumulation of substantial honeydew damage. Since simulated damage by aphid feeding is largely independent of leaf area index, the correlation between simulated aphid damage and green area duration is lower after DC 73 as compared with earlier stages (Figure 4.5).

Variation in simulated response of the crop to the aphid population is due to differences in crop characteristics among the data sets used to initialize the model at flowering. The crop condition at flowering reflects the effect of variable factors like temperature, radiation and nitrogen and water availability up to flowering. For instance, the data sets EEST84, BOUWING84 and PAGV3 are similar with respect to nitrogen gift and simulated attainable yield. However, the simulated damage for EEST84 is greater than for the other two data sets due to the larger leaf area index and the smaller amount of reserves for EEST84 as compared to BOUWING84 and PAGV3.

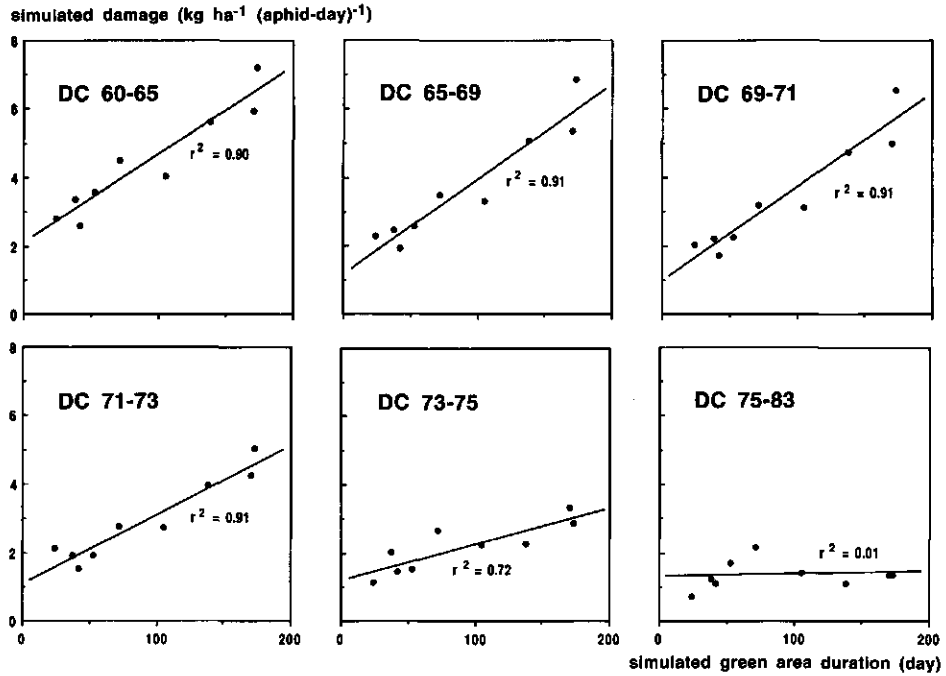


Figure 4.5. Simulated damage per aphid-day caused during six periods of crop development at various simulated green area duration. In the figures the coefficient of determination, $r^2$, is shown in combination with the line minimizing the residual sum of squares.

The duration of the post-anthesis phase affects damage because the development of the aphid population is significantly synchronized with crop development (Carter *et al.*, 1982) whereas the effects of aphid feeding and honeydew are functions of time. Consequently, a cool summer will result in a longer post-anthesis phase and more damage by a particular aphid infestation than a hot summer with a shorter post-anthesis phase. Whereas the model has been run with a post-anthesis phase of 47 days, the real post-anthesis phase in the crop data sets varies from 40 to 57 days. The quantitative consequences of a different duration of the post-anthesis phase depend upon the duration of the various periods of crop development in combination with the dynamics of the aphid population during these periods. Early during the post-anthesis phase the crop is more sensitive to aphids (*cf.* Figure 4.2) while aphid densities are usually low. Later, high densities may cause large damage in spite of the crop being less sensitive. In Figure 4.6, simulated average damage per aphid-day for a 57 day post-anthesis phase is compared to that for a 47 day post-anthesis phase, assuming the duration of all crop development periods to be increased with a factor 57/47. The aphid population is introduced as a function of crop development stage according to the data in Table 4.2,

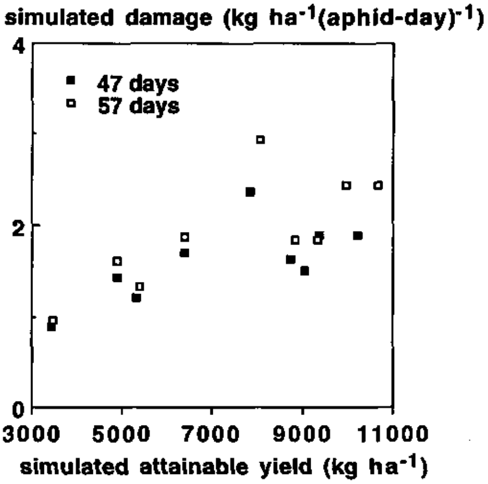


Figure 4.6. Simulated average damage per aphid-day (kg $ha^{-1}$ (aphid-day)$^{-1}$) at nine simulated attainable yield levels (kg $ha^{-1}$) and a post-anthesis phase of 47 (■) and 57 days (□), respectively.

resulting in an aphid load of 164 aphid-days for the 57 day post-anthesis phase. The protracted post-anthesis phase results in both higher simulated attainable yield (0-475 kg $ha^{-1}$) and higher simulated average damage (0.1-0.7 kg $ha^{-1}$ (aphid-day)$^{-1}$ ). Differences with the 47 day post-anthesis phase are most pronounced at higher yield levels. Total damage increases marginally (10 - 130 kg $ha^{-1}$).

## Construction of simulation-based regression models

Regression of simulated damage per aphid-day during different periods of crop development on simulated yield of an uninfested crop shows that, depending on the period of crop development, the best fit (highest $r^2$ and smallest residual error) is obtained five times with an exponential model and two times with a logarithmic model. Table 4.5 shows the best-fitting models.

## Accuracy of the simulation-based models in comparison with other models

The seven models for damage by *S. avenae* listed in Table 4.3 belong to two groups of prediction models: single point (models 1 to 5) and multiple point (models 6 and 7) (Zadoks and Schein, 1979). The single point models use a single characteristic of the aphid population curve to predict damage. In models 1 to 4 peak aphid density is used as the characteristic quantity, in model 5 cumulative aphid density (aphid-index). The multiple point models fractionate the aphid population curve and calculate the contribution of each fraction to

Table 4.5. Regression models best fitting the relation between simulated damage per aphid-day ($y$, in kg ha$^{-1}$ (aphid-day)$^{-1}$ ) and simulated attainable yield ($x$, in kg ha$^{-1}$). The statistic $r^2$ represents the fraction of the variation in $y$ accounted for by the model. The residual error has the same dimension as $y$.

| Crop development period | Model | $r^2$ | Residual error |
|---|---|---|---|
| 60-65 | $y = 1.47 \times 10^{6.28 \times 10^{-5}x}$ | 0.77 | 0.81 |
| 65-69 | $y = 0.85 \times 10^{8.28 \times 10^{-5}x}$ | 0.74 | 0.92 |
| 69-71 | $y = 0.71 \times 10^{8.77 \times 10^{-5}x}$ | 0.74 | 0.90 |
| 71-73 | $y = 0.75 \times 10^{7.70 \times 10^{-5}x}$ | 0.75 | 0.65 |
| 73-75 | $y = 0.77 \times 10^{5.91 \times 10^{-5}x}$ | 0.79 | 0.35 |
| 75-83 | $y = -3.27 + 1.20 \times \log_{10}(x)$ | 0.22 | 0.39 |
| 60-83 | $y = -6.18 + 2.03 \times \log_{10}(x)$ | 0.56 | 0.31 |

damage. In model 6 and 7 the fractions represent cumulative aphid density during various periods of crop development. In Figure 4.7 the relation between predicted damage and damage measured in field experiments is shown for each of the models using the data sets described in the Appendix to this Chapter.

Evaluation of the "truthfulness" of the seven models shows that all single point models based on peak aphid density (models 1 to 4) deviate significantly from measured values (F-test, $p<0.01$, Table 4.6). For these models, Spearman's rank correlation test indicates a significant trend in the prediction error while Wilcoxon's signed rank test points to significant bias in models 1 and 2 ($p<0.01$). For the single point model based on aphid index (model 5) a significant trend in the prediction error is found ($p<0.05$), while neither the F-test nor Wilcoxon's signed rank test detects significant deviations from reality. Neither of the models in which damage per aphid-day is a function of crop development stage (models 6 and 7) is rejected by any of the three statistical tests.

Entwistle and Dixon (1987) attribute the lack of correspondence between predictions based on peak aphid density and reality to differences in the distribution of aphids over the plant and to the importance of the duration as well as the size of the infestation. The results presented here do not support the first supposition as the distribution of aphids over the plant is not accounted for in models 6 and 7 while their predictions do not differ significantly from reality.

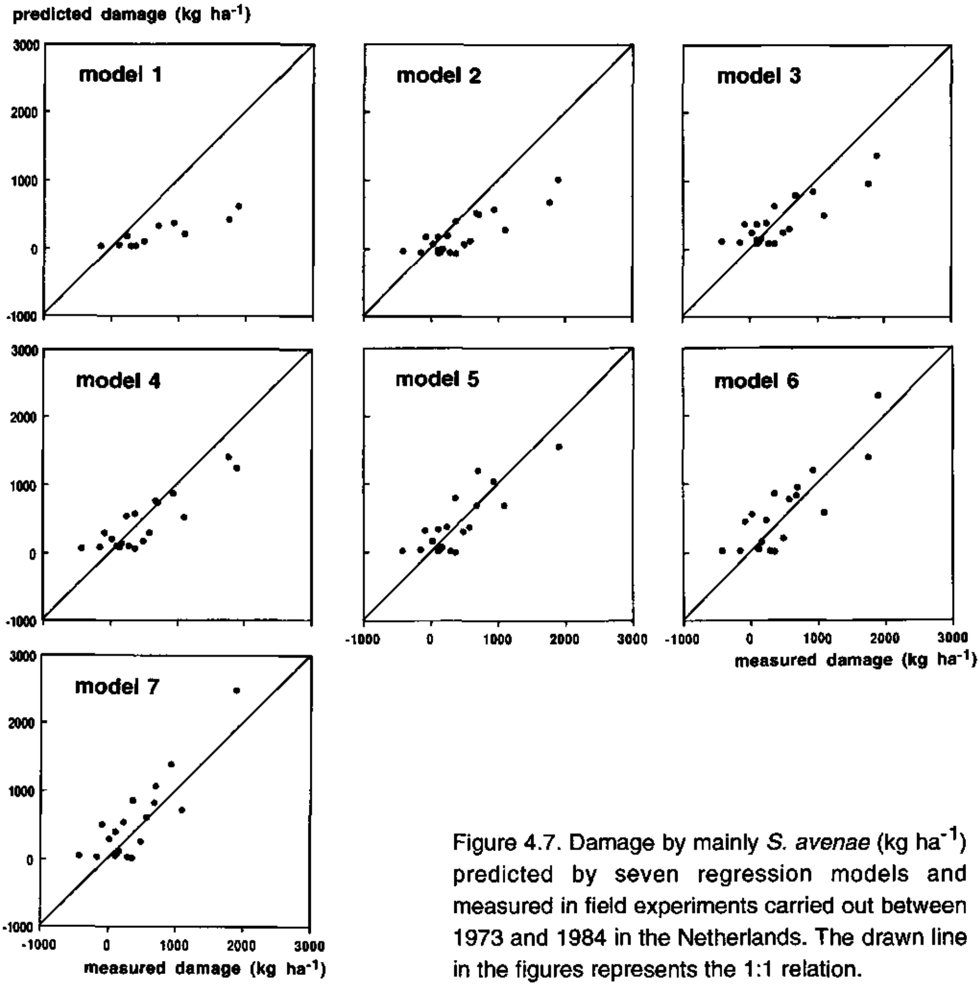


Figure 4.7. Damage by mainly *S. avenae* (kg ha$^{-1}$) predicted by seven regression models and measured in field experiments carried out between 1973 and 1984 in the Netherlands. The drawn line in the figures represents the 1:1 relation.

The presumed importance of the duration and the size of the population implies that aphid-index should be a more useful characteristic for predicting damage than peak aphid density. Indeed, the predictions of model 5 based on aphid-index are not significantly different from reality in two of the three statistical tests, contrary to the predictions of the models based on peak aphid density which are significantly biased. The analyses with the simulation model earlier in this paper have shown that in addition to the duration and the size of the aphid infestation, the shape of the infestation progress curve and the timing of the infestation are significant factors in determining damage. Taking these aspects of the infestation into account in the models 6 and 7 results in predictions which are not significantly different from reality.

Table 4.6. Statistical evaluation of the truthfulness of seven regression models for cereal aphid damage in winter wheat, using *n* datasets from the Netherlands. A description of the models is given in Table 4.3. The variables *f*, $Z_c$ and $r_s$ represent the statistics of the F-test, Wilcoxon's signed rank test and Spearman's rank correlation test, respectively.

| Model | *n* | *f* | $Z_c$ | $r_s$ |
|---|---|---|---|---|
| 1 | 11 | 234.30 ** | -2.67 ** | -.98 ** |
| 2 | 21 | 52.90 ** | -2.66 ** | -.67 ** |
| 3 | 21 | 17.09 ** | -0.26 | -.67 ** |
| 4 | 20 | 19.63 ** | -0.23 | -.74 ** |
| 5 | 20 | 2.88 | -0.52 | -.48 * |
| 6 | 20 | 1.51 | -1.16 | -.30 |
| 7 | 20 | 1.98 | -1.76 | -.07 |

* $p < 0.05$
** $p < 0.01$

The results of the analysis of "usefulness" of the regression models for predictive purposes differ from those of the analysis of the truthfulness of the models. Based on the median absolute value of the prediction error, model 5 is selected best (Table 4.7). Differences between the models are relatively small, the median absolute value of the prediction error of the majority of models differing less than 100 kg $ha^{-1}$ from the best. Confidence statements are not meaningful here in view of the relatively small and variable number of data sets used for model testing.

To illustrate the effect of the choice of a selection criterion on the selection result, the 75% quantile of the absolute value of the prediction error is also shown in Table 4.7. Based on the 75% quantile, model 3 is selected best. Thus, although the median absolute value of the prediction error of model 3 is larger than that of model 5, the probability of large prediction errors is smaller. The risk attitude of the decision maker determines which quantile of the frequency distribution is most appropriate as selection criterion.

Besides the absolute value of the prediction error, other measures can be used to express the accuracy of a model. These include, among others, the prediction error *per se* and the relative prediction error. Errors in the prediction of damage are of practical interest for supervised control only when they result in a wrong decision. Thus, when the predicted damage exceeds the cost of chemical control, a decision maker will be interested most in the error of overestimation by the model as this may result in a wrong decision (i.e. to spray). Similarly, when the predicted damage is smaller than the cost of

Table 4.7. Statistical evaluation of the usefulness of seven regression models for cereal aphid damage in winter wheat, using *n* datasets from the Netherlands. A description of the models is given in Table 4.3. The statistics shown are the median and the 75% quantile of the frequency distribution of the absolute value of the prediction error. Bold figures represent minimal values.

| Model | *n* | median ($kg\ ha^{-1}$) | 75% quantile ($kg\ ha^{-1}$) |
|---|---|---|---|
| 1 | 11 | 371 | 808 |
| 2 | 21 | 193 | 423 |
| 3 | 21 | 246 | **324** |
| 4 | 20 | 232 | 331 |
| 5 | 20 | **191** | 377 |
| 6 | 20 | 260 | 430 |
| 7 | 20 | 283 | 418 |

chemical control, only the error of underestimation is relevant. *A priori*, however, over- and underestimation are equally undesirable, rendering the absolute value of the prediction error a more appropriate criterion than the prediction error *per se*. In supervised control, predicted damage is compared to the cost of control and the prediction error then represents a better measure of uncertainty than the relative prediction error.

Although care is taken to select independent data sets for model evaluation, no information is available on the data used for calibration of the models 2 and 3. As the performance of these models is evaluated with 21 data sets, 8 of which have been used in their development (Rabbinge and Mantel, 1981), some overestimation of the accuracy of these models is likely.

Selection of the best model has been carried out assuming the data sets used for testing of the models to be representative for situations in which the models are to be used. In the context of supervised chemical control, the costs of the control operation determine to a large extent the range of damage which should be predicted with reasonable accuracy, low costs necessitating sufficiently accurate predictions of small damage only. The selection procedure should then be carried out using an appropriate subset of the 21 data sets available, omitting e.g. the sets where measured damage exceeds 1000 kg $ha^{-1}$.

## Conclusion

Calculation of aphid damage at low attainable yield levels is preliminary as proper validation of the winter wheat - *S. avenae* simulation model was not yet possible due to lack of detailed experiments with aphid infestations at low levels of nitrogen input.

Different simulated attainable yields have been obtained by initializing the crop growth model at flowering with data of field experiments carried out at different levels of nitrogen input. Conclusions on the effect of aphids may be different if variation in attainable yield is not caused by variation in nitrogen input but by variation in e.g. plant density due to wintering of the crop. Thus, attainable yield calculated in this study may differ from the concept of "expected yield" in the advisory system EPIPRE, which is the farmer's grain yield estimate at the onset of the growing season (Drenth *et al.*, 1989).

The calculations with the damage model for a range of crop-nitrogen conditions have shown that at crop development stages up to DC 73 aphid damage increases at an approximately constant rate with attainable yield level up to yield levels of *ca* 9000 kg $ha^{-1}$. At higher yield levels, the slope of the curve increases greatly. Aphid damage due to honeydew increases in proportion to leaf area index, whereas the contribution of additional leaf area index to crop yield decreases. As a consequence, damage per aphid-day is relatively large at high attainable yield levels as long as honeydew is the major cause of damage (up to DC 73). The second mechanism of damage, aphid feeding, is approximately independent of yield level and becomes the major cause of damage after DC 73 when unsprayed aphid populations generally reach their peak density.

The results of the simulation model are summarized by exponential and logarithmic relations between damage per aphid-day and yield of an uninfested crop. No biological meaning should be attached to the structure of the regression models. Their only purpose is to summarize the information derived from the simulation model.

Evaluation of the agreement between the predictions of seven regression models for aphid damage and real world data using 21 independent data sets has shown the models which account for the duration and the size of the infestation (models 5 to 7) to be superior to the models which use peak aphid density to characterize the infestation (models1 to 4) under both the F-test and Wilcoxon's signed rank test. The similarity in truthfulness of model 5 and models 6 and 7, respectively, indicates that the shape of the infestation progress curves and the timing of the infestations did not vary greatly between the data sets and was similar to the standard infestation used for constructing model 5 with the simulation model (Table 4.2).

Based on the median absolute value of the prediction error, model 5 has been selected the best. Although they are demonstrably biased, the single point models 3 and 4 may be more useful for decision making in supervised control systems than the multiple point models 6 and 7 due to the smaller median error in the predictions of the single point models.

Summarizing the output of the explanatory simulation model of the aphid - winter wheat system by means of regression analysis has yielded simple models which are as good as the best published empirical models in both truthfulness and usefulness. The advantage of the simulation approach in the development of these simple models over the strictly empirical approach followed for the other models is the explanatory nature of the simulation model which allows conclusions on the effect of grain aphid injury on winter wheat yield of a causal rather than a statistical nature.

# Appendix to Chapter 4

## Summary of data sets used for comparison of models for grain aphid (*Sitobion avenae*) damage

| Data set | Year | Location | Cultivar | Control yield[a] (kg ha$^{-1}$) | Infestation period (Decimal Code) | Peak aphid density (tiller$^{-1}$) | Infestation intensity |  | Damage (kg ha$^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  |  | (aphid-days) | (aphid-unit days) |  |
| 1.[b] | 1973 | Zennewijnen | Manella | 6550 | 37-85 | 1.22 | 29.8 | 16.3 | 130 |
| 2.[b] | 1973 | Lienden | Manella | 3580 | 37-85 | 2.41 | 29.9 | 15.6 | -420 |
| 3.[b] | 1974 | Colijnsplaat | Lely | 8170 | 37-73 | 0.77 | 13.8 | 6.8 | 100 |
| 4.[b] | 1974 | Westmaas | Caribo | 6700 | 37-75 | 3.92 | 50.1 | 25.3 | 160 |
| 5.[b] | 1975 | Colijnsplaat | Lely | 6150 | 41-79 | 8.37 | 125.9 | 64.4 | 20 |
| 6.[b] | 1975 | Herveld | Clement | 7360 | 45-79 | 11.28 | 243.0 | 126.2 | 570 |
| 7.[b] | 1976 | Colijnsplaat | Lely | 6830 | 60-87 | 27.45 | 500.8 | 279.8 | 360 |
| 8.[b] | 1976 | Westmaas | Anouska | 5990 | 60-87 | 14.28 | 219.7 | 119.8 | -90 |
| 9.[b] | 1976 | Wieringerwerf | Caribo | 7290 | 60-85 | 35.32 | 418.1 | 229.5 | 670 |
| 10.[b,c] | 1977 | Lienden | Caribo | 5250 | 60-83 | 14.92 | 241.5 | 130.2 | 100 |
| 11. | 1978 | Lienden | Caribo | 5250 | 60-87 | 8.69 | 226.7 | 127.5 | 490 |
| 12. | 1978 | Westmaas | Arminda | 8040 | 58-77 | 1.05 | 13.6 | 7.4 | 280 |
| 13. | 1978 | Borgercompagnie | Okapi | 8100 | 65-85 | 20.25 | 392.8 | 222.1 | 1090 |
| 14. | 1979 | Westmaas | Donata | 6730 | 37-79 | 64.03 | 1004.1 | 516.5 | 1890 |
| 15. | 1979 | Wieringerwerf | Okapi | 7770 | 41-79 | 37.91 | 608.6 | 326.5 | 930 |
| 16. | 1979 | Borgercompagnie | Okapi | 6430 | 65-85 | 1.50 | 20.3 | 11.5 | -160 |
| 17. | 1979 | Rolde | Okapi | 5910 | 50-85 | 3.00 | 45.7 | 26.3 | 100 |
| 18. | 1979 | Emmercompascuum | Okapi | 6160 | 56-83 | 0.50 | 5.4 | 3.1 | 360 |
| 19. | 1979 | Randwijk | Arminda | 7220 | 68-89 | 34.10 | 723.1 | 401.9 | 700 |
| 20.[d] | 1984 | Nagele | Arminda | 10776 | 60-79 | 44.35 | 544.4 | 295.7 | 1754 |
| 21. | 1984 | Randwijk | Arminda | 10155 | 55-82 | 15.83 | 194.7 | 106.6 | 238 |

[a] aphids treated with an insecticide on occurrance.

[b,c,d] data set not used for evaluation of damage models by Vereijken (1979), Entwistle & Dixon (1987) and Rossing (this Chapter), respectively.

## Part 2

# Uncertainty and risk in supervised control of aphids and brown rust in winter wheat

## Chapter 5

# Quantification of uncertainty in cost/benefit calculations

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Uncertainty analysis applied to supervised control of aphids and brown rust in winter wheat. 1. Quantification of uncertainty in cost-benefit calculations.
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**Abstract** Information on the uncertainty about predicted costs and benefits of chemical control is an indispensable, but usually ignored, aspect of decision support in crop protection. The consequences of ignoring uncertainty are illustrated using a model for evaluating financial loss associated with different strategies of chemical control of aphids (esp. *Sitobion avenae*) and/or brown rust (*Puccinia recondita*) in winter wheat in the Netherlands. Crop development, population dynamics and damage are simulated as a function of predicted average daily temperature and a time sequence of decisions on chemical control. The model is initialized with temperature sum and incidences of aphids and brown rust. Uncertainty about model output is computed from uncertainty about model parameters and inputs which are quantified using field data. The probability distribution of financial loss is estimated by stratified sampling from the input distributions followed by Monte Carlo simulation.

Compared to no control, chemical control of both aphids and brown rust may reduce the range of possible financial loss. Because the probability distributions of financial loss associated with no chemical control have long right tails, uncertainty leads to damage thresholds well below the deterministic thresholds, even when indifference to risk is assumed. In comparison, the damage thresholds currently used in the decision support system EPIPRE are risk-avoiding for aphids, and approximately risk-neutral for brown rust.

## Introduction

In the Netherlands, the use of fungicides and insecticides became common practice in winter wheat cultivation in the 1970s when effective fungicides were registered for use (Daamen, 1990). A computer-based advisory system, called EPIPRE, was developed to supply participating farmers with field-specific recommendations on chemical control of diseases and aphids (Zadoks *et al.*, 1984). The recommendations are based on cost/benefit analysis of pesticide application, using quantitative models to predict aphid and disease population growth and damage. Farmers' observations of aphid and disease incidence in their fields are used as initial conditions (Drenth *et al.*, 1989). Chemical control of pests and diseases based on an explicit evaluation of costs and benefits is known as supervised control (Chiarappa, 1974).

In EPIPRE, as in many other operational advisory systems (Gold, 1989), uncertainty about predicted costs and benefits of chemical control is not taken into account. In general, such simplification is allowed only when two conditions are met. First, when the relations in the model are linear. In that case, the average outcome of the model under uncertainty equals its outcome without uncertainty. Though this is rare in models of biological systems, optimal decisions may be relatively insensitive to non-linearity due to the inherent robustness of binary decision variables (Thornton *et al.*, 1984). Second, when the decision maker, the user of the model's output, is not interested in risk, i.e. the possibility of an unfavorable outcome of a decision. Acting upon average costs and benefits while ignoring other aspects of the probability distributions is rational only for decision makers which are neither risk-accepting nor risk-avoiding (Carlson, 1970; Sinn, 1983). In the Netherlands, the risk attitude of wheat farmers in relation to decisions on pesticide use has seldom received attention in research (Zadoks, 1989a). From other countries both risk-accepting and risk-avoiding attitudes have been reported (Carlson and Main, 1976; Tait, 1983; Thornton *et al.*, 1984). Thus, both conditions for *a priori* ignoring uncertainty and risk appear not to be satisfied.

This Chapter is the first of three in which we explore the uncertainty in a decision model which is used to evaluate options for chemical control of aphids (especially *Sitobion avenae*) and brown rust (*Puccinia recondita*) in winter wheat, and the consequences of uncertainty about model predictions for damage thresholds. The damage threshold (Zadoks, 1985) is defined as the level of pest attack at which the benefit of control just exceeds its cost (Mumford and Norton, 1984). The model computes costs of time series of decisions on chemical control for specific initial conditions, comprising current temperature sum and incidences of aphids and brown rust. Costs are calculated at field level. Time scale of the model is from ear emergence to dough ripeness, i.e. approximately from early June till late July. Spatial scale is a field of winter wheat in the Netherlands of 5 to 10 ha. The model represents an updated and upgraded version of part of the EPIPRE system. Aphids and brown rust are considered because they often occur simultaneously. Diseases other than brown rust are left out of the analysis in view of the exploratory nature of the study.

In this Chapter the uncertainty about components of the model and its consequences for model output are evaluated. In the next Chapter the relative contributions of the different sources of uncertainty are assessed. In Chapter 7 the concept of damage threshold is reviewed in relation to uncertainty.

## Description of the decision model

### General structure

The components of the decision model are shown in Figure 5.1. The core of the model is a set of mathematical relations which describe the dynamics of the biological subsystems crop development, population dynamics of aphids and brown rust, and their associated damage, as a function of chemical control. The parameters in the relations are estimated using empirical data.

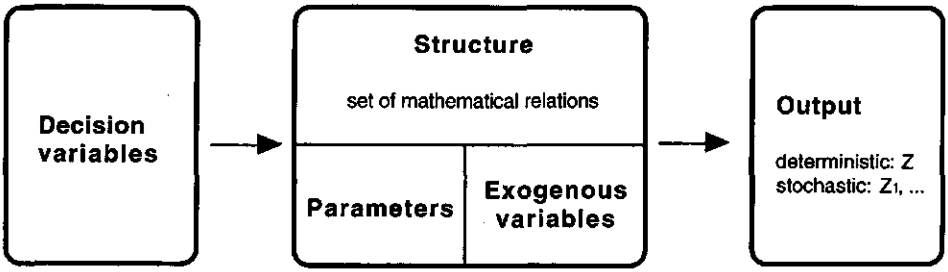


Figure 5.1. Schematic representation of the components of the decision model.

Exogenous variables which are input to the model comprise the temperature sum calculated from the time when crop development stage equalled pseudostem elongation (DC 30, decimal code of crop development, Zadoks *et al.*, 1974), the future average daily temperature, and the initial aphid and brown rust incidences. The decision variables describe the nature of the intervention in the system: no chemical control or chemical control of aphids and/or brown rust. A control strategy is defined as a series of consecutive decisions on chemical control in the course of the planning horizon, i.e. the time span until crop development stage dough ripeness (DC 83). Output variable of major interest is financial loss. Financial loss is defined as the financial equivalent of yield reduction due to aphids and/or brown rust, plus the eventual costs of chemical control. Output is stochastic when uncertainty about the various components of the decision model is taken into account.

## Sources of uncertainty about model output

Uncertainty about the predicted financial loss originates from three different sources: (1) uncertainty about the structure of the mathematical relations caused by limited understanding of the system under consideration and by simplification of complex processes, (2) uncertainty about model parameters due to variation in the data used to estimate the parameters, and (3) uncertainty about exogenous variables which are input to the model.

ad (1). In this Chapter, uncertainty about model structure is not taken into account. The structure of the various relations is presumed truthful as well as useful (Penning de Vries, 1977).

ad (2). The parameter values in the decision model are estimated from data collected in experimental and commercial wheat fields. Variation in these data is caused by variation between fields and variation within a field (Figure 5.2). Variation between fields can be attributed to factors such as year, soil type

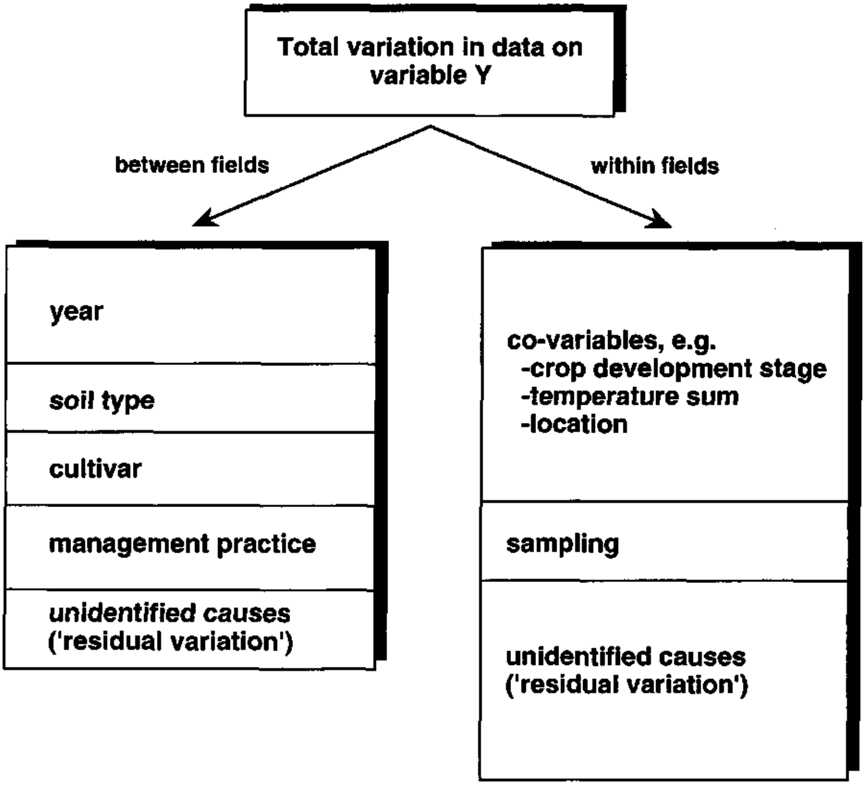


Figure 5.2. Illustration of allocation of variation in empirical data of an imaginary variable Y to different sources. The surface area of a rectangle represents the contribution of the respective source to total variation. The contribution is determined by analysis of variance, regression or other variance reducing techniques.

and cultivar by variance-reducing techniques such as regression. Within-field variation is caused by limited sample size in combination with spatial heterogeneity due to biological, soil and microweather characteristics. Within-field variation can be reduced by accounting for co-variables and correcting for variation due to sampling. The residual variation is commonly attributed to sampling, and can be ignored for prediction of financial loss. However, when information is available to rule out sampling as a major cause of residual variation, the variation must be regarded an inherent part of model uncertainty, caused by the simplified representation of complex ecological processes. For prediction of financial loss the random deviations of the empirical data from the fitted regression model are described as mutually independent, identically distributed normal variates, or shortly, white noise (Feller, 1971).

ad (3). Uncertainty about the various exogenous variables has different causes. Uncertainty about future average daily temperature is caused by the inherently stochastic nature of temperature. This type of variation can be described by stochastic weather generators (e.g. Geng *et al.*, 1985) or by sufficient historic data. Uncertainty about the initial temperature sum and uncertainty about the initial incidences of aphids and brown rust are caused by limited sample size and can be quantified with statistical methods.

Inaccuracy of data due to errors in scoring samples or due to systematic errors during data collection is disregarded.

## Decision variables

The decision variables concern decisions on chemical control of aphids and/or brown rust at the onset of each of $N$ decision periods. A decision period is defined as the time between two subsequent decisions. One of four decisions can be implemented in decision period $i$ : no treatment ($d_i$=1), treatment of aphids ($d_i$ =2), treatment of brown rust ($d_i$ =3), and treatment of both aphids and brown rust ($d_i$ =4), where $i$=1,...,$N$. Three aspects of a decision are considered: the nominal costs $C(d_i)$, the fraction of the target population killed on the day a decision is implemented, the direct pesticidal effect $K_X(d_i)$ (X=A for aphids, X=B for brown rust), and the period of time during which growth of the target population is arrested due to the control decision, the effective period $P_X(d_i)$. Whether population growth on day $t$ is zero, is expressed by the binary function $R_X$. $R_X$ assumes the value one if residual pesticidal effect is present, i.e. $0 \leq t - t_a \leq P_X(d_i)$, where $t_a$ is the day *decision* $d_i$ *is implemented and* $t$ *is the current day.* $R_X$ *is zero otherwise.* The costs associated with a decision, $C$, consist of costs of pesticide, labour, machinery, and wheel damage. The following simplifying assumptions are made: (1) decision periods are of fixed length; (2) application of pesticides is carried out on the first day of a decision period; (3) pirimicarb is used against aphids, triadimefon, fenpropimorph or propiconazole are used to control brown rust and (4) prices of wheat and pesticides are fixed. Estimates of $K_X$ and $P_X$ and their variation are based on information in the literature.

## Future average daily temperature

Average daily temperature is calculated as the mean of daily (i.e. 24-hourly) maximum and minimum temperatures. The variation in future average daily temperature is described by a sample of 36 years of daily maximum and minimum temperatures measured at the meteorological station of the Wageningen Agricultural University. This sample is considered to represent the variation in temperature in an arbitrary field of winter wheat for which predictions are made. The various yearly temperature sequences are assumed to occur with equal probability. Correlation between years is disregarded.

## Crop development

Development of winter wheat from DC 30 is a function of temperature. At DC 30, vernalization has been completed and effects of photoperiod (*see* Van Keulen and Seligman, 1987) will be negligible. Data of Carter *et al.* (1982) are used to regress crop development stage $D$ on temperature sum $T$. Crop development stage was monitored at least weekly in three winter wheat fields around Norwich, England in 1977, starting on the day 50% of the tillers in a field reached DC 30. No information on sample size or cultivars was given. Temperature sum was calculated as the integral over time of the average of daily minimum and maximum temperatures, with a development threshold of 6°C, starting on the day of the first sample. Temperature data were obtained from a nearby meteorological station. Since temperature was not measured in a field, within-field variation of temperature can not be accounted for. The temperature sum at the start of the planning horizon, $T_0$, is input for the model. Variation in $T_0$ is assumed negligibly small.

## Population growth of aphids and brown rust

Similar models are used to describe the population growth of aphids and brown rust. Population density on day $t$ in decision period $j$ is approximated by

$$X = \left( \prod_{i=1}^{j} (1 - K_X(d_i)) \right) X_0 \exp \left( \sum_{\tau = 1}^{t} (1 - R_X)\ r_X \right) \tag{5.1}$$

where $X$ represents the aphid density ($A$, tiller$^{-1}$) or the brown rust sorus density ($B$, leaf$^{-1}$) on day $t$, $X_0$ the initial aphid or brown rust density, and $r_X$ represents the relative growth rate of the aphid population ($r_A$, day$^{-1}$) or the brown rust population ($r_B$, day$^{-1}$) when no pesticide is applied.

Unpublished data (R. Rabbinge and W.P. Mantel) are used to estimate the relative growth rate of unsprayed aphid populations. The data comprise weekly estimates of aphid density (mainly *S. avenae*) and crop development stage. Sample size varied between 40 and 600 tillers per field. The coefficient of variation of aphid density was at most 20%. The data were collected in observational studies in fourteen commercial and experimental fields during seven years, on eight cultivars of winter wheat in the Netherlands.

Data of Daamen (1991a) are used to estimate the relative growth rate of unsprayed populations of brown rust sori. The data comprise estimates of crop development stage and number of brown rust sori on fully expanded leaves, based on fortnightly samples of green leaves from 80 culms. The data were collected in eight field experiments with six cultivars between 1983 and 1986 in the Netherlands.

Assuming the population density to change exponentially between consecutive sampling dates $\Delta t$ days apart, the relative growth rate of the population is calculated as:

$$r_X = \frac{\ln(X(t+\Delta t)) - \ln(X(t))}{\Delta t} \qquad (5.2)$$

Analysis of variance using multiple regression analysis with dummy variables (Chatterjee and Price, 1974) is performed to evaluate the effect of the factors year, cultivar and crop development stage on $r_X$. Variation in observed crop development stage is assumed negligible.

## Incidence-density relations of aphids and brown rust

The model is initialized with a sample estimate of current population intensity in a particular field. In EPIPRE, the sample is taken according to a protocol in which the incidence $I_A$, the fraction of tillers infested with aphids, is determined in a random sample of 100 tillers, while the incidence $I_B$, the fraction of green leaves containing one or more brown rust sori, is determined in a random sample of 40 tillers. These incidence estimates are subject to binomial sampling error.

The incidences are converted into initial densities, $X_0$, using an empirical incidence-density relation (Nachman, 1981) for both aphids and brown rust:

$$\ln(X_0) = \alpha_{1,X} + \alpha_{2,X} \ln\left(\ln\left(\frac{1}{1-I_X}\right)\right) \qquad (5.3)$$

Data of Rabbinge *et al.* (1980) are used to estimate the parameters of Equation 5.3 for aphids while parameter estimates for brown rust are given by Daamen (1991a). The data for aphids comprise weekly incidence and density estimates, both determined in the same random sample of 40 to 600 tillers per field. Sample size was adjusted to ensure the coefficient of variation to be less than 0.2. The data stem from observational studies in commercial and experimental winter wheat fields with various cultivars. In the data no distinction was made between fields.

The data for brown rust comprise fortnightly incidence and density estimates, both determined at the same random sample of green leaves from

80 tillers. The data stem from experiments carried out over three different seasons, with four different cultivars. Analysis of variance was used to evaluate the effect of year, cultivar, crop development stage, and field on the relation.

Data collection for both aphids and brown rust was carried out by experienced observers and incidence and density are assumed to be measured without observer bias. The samples are representative for the field they originate from.

### Damage due to aphids

The rate at which cereal aphids cause damage depends on the development stage of the crop and the attainable yield, i.e. the yield in absence of pests and diseases (Chapter 4). Because of lack of field data, a simulation model of post-anthesis growth of winter wheat into which effects of aphids were incorporated (Chapter 3) was used to calculate the rate of daily damage accumulation per aphid as a function of crop development stage. Damage during various periods of crop development was calculated by repeatedly running the model with aphid population density set to zero at subsequently earlier crop development stages. Initial crop conditions from different field experiments gave estimates of aphid damage at different attainable yield levels. A full account of the procedure is given in Chapter 4. To account for the variation in initial conditions in the field experiments, the model was run with the mean and the mean plus and minus 10%, respectively, of all initial conditions. The variation in damage estimates thus obtained is postulated to represent the variation between fields. The relation between the rate of daily damage accumulation per aphid and crop development stage is calculated for three classes of attainable yield using linear regression:

$$\frac{1}{A} \cdot \frac{\Delta S_A}{\Delta t} = \alpha_3 + \alpha_4 D \qquad (5.4)$$

in which $\Delta t$ equals one day, and $S_A$ is total aphid damage (kg ha$^{-1}$).

As no restrictions have been imposed on population density $A$, unrealistically large damage may result at large densities. Therefore, an upper limit for total aphid damage $S_A^{max}$ (kg ha$^{-1}$) is defined. Data of Rabbinge and Mantel (*see* Appendix to Chapter 4) are used to estimate $S_A^{max}$ and its variation.

### Damage due to brown rust

Daamen (1991a) showed that end-of-season damage by brown rust is related to brown rust stress, defined as the integral of brown rust density over time (sorus-days). Therefore, the rate of damage accumulation is a function of brown rust density. In the range of brown rust intensities of practical interest (0-2500 sorus-days) this function may be simplified to

$$\frac{1}{B}\cdot\frac{\Delta S_B}{\Delta t}=\begin{cases}\alpha_5\,Y_{att} & D\leq 83\\ 0 & D>83\end{cases} \tag{5.5}$$

in which $\Delta t$ equals one day, $S_B$ is total damage by brown rust (kg ha$^{-1}$), and $Y_{att}$ the attainable yield (kg ha$^{-1}$). After crop development stage DC 83 brown rust epidemics cause no more damage. To avoid unrealistically large damage at high brown rust intensities, an upper limit for total brown rust damage $S_B^{max}$ (kg ha$^{-1}$) is defined:

$$S_B^{max}=\alpha_6\,Y_{att} \tag{5.6}$$

An estimate of $\alpha_6$ is given by Daamen (1991a), based on field experiments in three years, with four cultivars.

## Financial loss

Financial loss in an arbitrary field, $L$, is calculated by combining the equations describing damage, and taking the price of winter wheat $w$ (Dfl kg$^{-1}$) and the cost $C$ associated with decision $d_i$ in period $i$ into account.

$$L=\underbrace{w\sum_{i=1}^{N}S_i}_{\substack{\text{loss due to}\\ \text{aphids and}\\ \text{brown rust}}}+\underbrace{\sum_{i=1}^{N}[C(d_i)]}_{\substack{\text{cost of control}\\ \text{strategy}}} \tag{5.7}$$

in which

$$S_i=\sum_{\tau=b(i)}^{l(i)}\left(\frac{\Delta S_A}{\Delta t}\cdot A+\frac{\Delta S_B}{\Delta t}\cdot B\right) \tag{5.8}$$

where $S_i$ is damage by aphids and brown rust during decision period $i$ (kg ha$^{-1}$), $b$(i) the first day of decision period $i$ and $l$(i) the last day of decision period $i$.

The probability distribution of financial loss can be described analytically in terms of the parameters of the probability distributions of the various sources of uncertainty if these latter are sufficiently simple, and if correlations between the variates are known. Alternatively, a Monte Carlo approach can be adopted in which realizations of the simultaneous output distribution of financial loss are generated by simple random sampling from the multivariate input distribution (*see* Hertz and Thomas, 1983). Monte Carlo analysis is the more flexible approach as it is independent of the structure of the model and its uncertainty, whereas the analytic approach requires rigorous assumptions on the probability distribution of the sources of uncertainty. A disadvantage of simple random sampling is the large computational effort required for a representative sample of the input space. Latin hypercube sampling (McKay *et al.*, 1979) has been put forward as an equally flexible but more efficient alternative for simple random sampling in Monte Carlo analysis. The increase in efficiency is achieved by stratified sampling ($M$ strata) from the probability distribution of each input and combining the samples of an input with those of other inputs in a random fashion. In this way, a representative picture of the input space is obtained using a relatively small sample.The latin hypercube sampling procedure can be applied to independent inputs with arbitrary probability density functions and to dependent, normally distributed inputs. The procedure results in unbiased estimates of any function of the inputs (Iman and Conover, 1980; Stein, 1987). For arbitrarily distributed, dependent variates approximations have been proposed by Iman and Conover (1982). In this Chapter, latin hypercube sampling is used to estimate the probability distribution of financial loss.

## Results

### Quantification of uncertainty about components of the decision model

*Decision variables*

Data on the direct aphicidal effect of pirimicarb vary between 0.36 and 0.99, depending on the concentration of active ingredient and the habitat of the target organism (Table 5.1). The effective aphicidal period of pirimicarb is small at 25 g a.i. $ha^{-1}$ and varies between 7 and 17 days at higher concentrations (Table 5.1).

Daamen (1991a) concluded that the fungicide triadimefon arrested growth of the brown rust population during approximately three weeks while direct fungicidal effects were negligible. Brown *et al.* (1986) report similar effects for triadimefon and propiconazole used against yellow rust (*P. striiformis*) on relatively susceptible cultivars (Table 5.2).

In the decision model the uncertainty about the fraction of the population killed as a result of a control decision is described by a beta distribution. This distribution is defined on the interval (0,1), and is characterized by two param-

Table 5.1. Direct aphicidal effect (-) and effective period (day) of pirimicarb under field conditions.

| Species | Dosage (kg a.i. $ha^{-1}$) | Direct [a] effect | Effective [a] period | Reference |
|---|---|---|---|---|
| *Metopolophium dirhodum* | 0.025 | 0.36 | < 5 | Poehling (1987) |
| | 0.050 | 0.86 | ~ 5 | *ibid.* |
| | 0.150 | 0.92 | ~ 5 | *ibid.* |
| *Sitobion avenae* | 0.025 | 0.94 | < 5 | *ibid.* |
| | 0.050 | 0.99 | 11 | *ibid.* |
| | 0.150 | 0.99 | 11 | *ibid.* |
| *Sitobion avenae* | [b] | 0.93(0.22) [c] | ~ 7 | Entwistle and Dixon (1987) |
| *Myzus persicae* | 0.140 | 0.70-0.88 | > 7 | Dewar *et al.* (1988) |

[a] The direct effect is the fraction of the population killed one day after application compared to an untreated control. The effective period is the time interval after application during which the growth rate of the population is negative or approximately zero.

[b] Pirimicarb, demeton-S-methyl and dimethoate at rates conventional for the UK

[c] SEM

Table 5.2. Effective period (day) of fungicides used against wheat rusts (*Puccinia* spp.).

| Species | Active ingredient | Effective period | Reference |
|---|---|---|---|
| *P. recondita* | triadimefon | 21 | Daamen (1991a) |
| *P. striiformis* | propiconazole / triadimefon | 21-25[a] | Brown *et al.* (1986) |
| *P. striiformis* | propiconazole / triadimefon | 30-55[b] | Brown *et al.* (1986) |

[a] On relatively susceptible cultivars.

[b] On relatively resistant cultivars.

eters, based on mean and variance of $\hat{K}_X$.

$$\hat{K}_X(d_i) = \varepsilon_{K_X}, \qquad \varepsilon_{K_X} \simeq \mathrm{Beta}\left(a_{X,d_i}, b_{X,d_i}\right) \tag{5.9}$$

Throughout the analysis a circumflex indicates a prediction while an overbar represents a mean. Uncertainty about the effective period $P_X$ is described by a *normal distribution:*

$$\hat{P}_X(d_i) = \bar{P}_X(d_i) + \varepsilon_{P_X}, \qquad \varepsilon_{P_X} \simeq N\left(0, \sigma^2_{P_X(d_i)}\right);\ \hat{P}_X(d_i) \geq 0 \tag{5.10}$$

Estimates of $a_{X,d_i}$, $b_{X,d_i}$, $\bar{P}_X(d_i)$ and $\sigma^2_{P_X(d_i)}$ for various $d_i$ are given in Table 5.3. The costs of control are assumed fixed (Table 5.4).

*Crop development*

After visual assessment of the data, a negative exponential relation forced through $T$=0, $D$=30 with an asymptote at crop ripeness (DC 92) was selected to describe the data. Written in linear form, the relation is:

$$\ln\left(1 - \frac{D - 30}{D^{max} - 30}\right) = \alpha_7\, T \tag{5.11}$$

where $D^{max}$ equals 92, the maximum crop development stage. Due to lack of distinction between fields in the data, some overestimation of the within-field variation is expected. However, in view of the good fit ($r^2 = 0.98$) this error is negligible. Since variation due to sampling is negligible for both $T$ and $D$, the variation in crop development stage remaining after accounting for the relation with temperature sum represents inherent system randomness which is described as white noise. In the decision model, $\alpha_7$ is predicted as

Table 5.3 Probability distributions and parameters describing the direct effects $K_A(d_i)$ and $K_B(d_i)$ (-) and effective periods $P_A(d_i)$ and $P_B(d_i)$ (day) following control decision $d_i$ in the decision model.

| $d_i$ [a] | $K_A(d_i)$ | | $P_A(d_i)$ | | $K_B(d_i)$ | | $P_B(d_i)$ | |
|---|---|---|---|---|---|---|---|---|
| | distribution | parameters | distribution | parameters | distribution | parameters | distribution | parameters |
| 1 | beta [b] | 0, 1 [c] | normal [d] | 0, 0 [c] | beta [b] | 0, 1 [c] | normal [d] | 0, 0 [c] |
| 2 | beta | 2.93, 0.52 | normal | 12, 0.20 | beta | 0, 1 [c] | normal | 0, 0 [c] |
| 3 | beta | 0, 1 [c] | normal | 0, 0 [c] | beta | 0, 1 [c] | normal | 18, 0.20 |
| 4 | beta | 2.93, 0.52 | normal | 12, 0.20 | beta | 0, 1 [c] | normal | 18, 0.20 |

[a] $d_i$=1: no chemical control; $d_i$=2: aphicide application; $d_i$=3: fungicide application; $d_i$=4: mixed aphicide and fungicide application.

[b] Parameters of the beta distributions represent $a_{X,\,d_i}$ and $b_{X,\,d_i}$, respectively.

[c] Dummy values: fraction of population killed equals zero.

[d] Parameters of the normal distributions represent mean and coefficient of variation, respectively.

Table 5.4. Costs (Dfl ha$^{-1}$) associated with chemical control of aphids and/or brown rust in winter wheat (based on Drenth & Stol, 1990).

| Control target | Labour & machinery[1] | Wheeling damage[2] | Aphicide[3] | Fungicide[4] | Total |
|---|---|---|---|---|---|
| aphids | 40 | 45 | 30 | - | 115 |
| brown rust | 40 | 45 | - | 70 | 155 |
| aphids and brown rust | 40 | 45 | 30 | 70 | 185 |

[1] Contract labour.

[2] No fixed wheeltracks, spray after mid May, sprayswath width 11m.

[3] Based on Pirimor.

[4] Based on Bayfidan, Corbel or Tilt.

$$\hat{\alpha}_7 = \bar{\alpha}_7 + \varepsilon_{\alpha_7}, \qquad \varepsilon_{\alpha_7} \simeq N(0,\sigma^2_{\alpha_7}) \qquad (5.12)$$

Least squares estimates of $\bar{\alpha}_7$ and $\sigma_{\alpha_7}$ are -0.0031 and 0.000065, respectively ($n$=44). In addition to the uncertainty about $\alpha_7$, white noise has to be accounted for in the prediction of crop development stage:

$$\ln\left(1 - \frac{D-30}{D^{\max}-30}\right) = \hat{\alpha}_7\, T + \varepsilon_{W,D}, \qquad \varepsilon_{W,D} \simeq N(0,\sigma^2_{e,D}) \qquad (5.13)$$

in which $\sigma^2_{e,D}$ is the residual variance ($\hat{\sigma}^2_{e,D}$ =0.012). The data and the fitted relation are shown in Figure 5.3a. Extrapolation is required to arrive in DC 83, the end of the planning horizon. The parameter $\alpha_7$ is predicted at the start of each Monte Carlo run. Realizations of $\varepsilon_{W,D}$ are calculated each time crop development stage is predicted.

*Population growth of aphids and brown rust*

Preliminary analysis of the cereal aphid data showed a significant effect of crop development stage, both as a linear and as a quadratic term, on the relative growth rate $r_A$. Since an increase of the relative growth rate with crop development stage is biologically improbable (e.g. Carter *et al.*, 1982), a monotone function was preferred. Therefore, the relative growth rate was modelled as a function of crop development stage according to

$$r_A = \alpha_8 + \alpha_{10}\, e^{\alpha_9 (D-68)} \qquad (5.14)$$

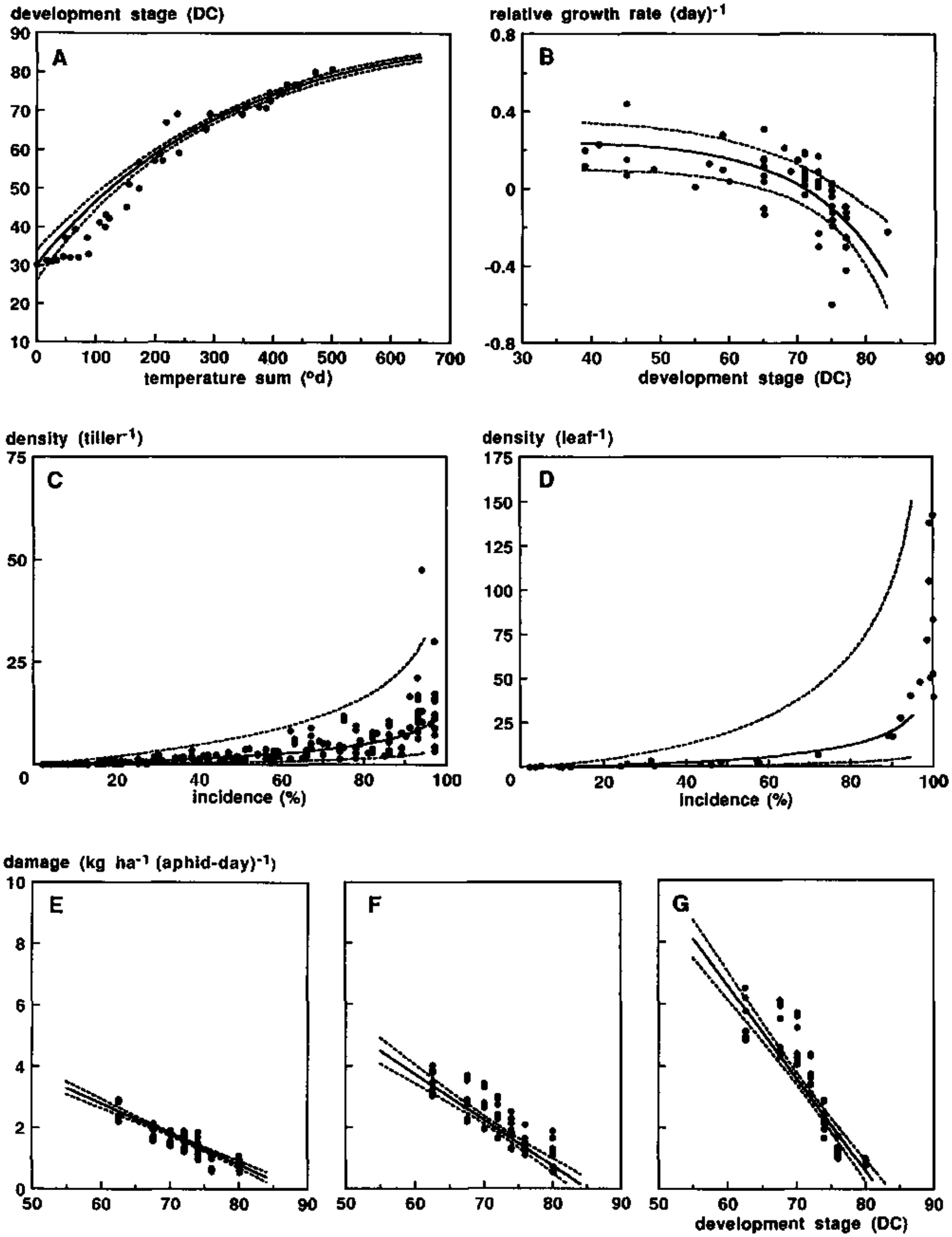


Figure 5.3. Overview of the mathematical relations in the decision model and the 95% confidence interval due to parameter uncertainty. Uncertainty due to sampling and white noise is not shown. A: Equation 5.11; B: Equation 5.14; C: Equation 5.3, aphids; D: Equation 5.3, brown rust; E: Equation 5.4, 3500-6000 kg ha$^{-1}$; F: Equation 5.4, 6000-9000 kg ha$^{-1}$; G: Equation 5.4, 9000-10000 kg ha$^{-1}$.

in which 68 is an offset, approximately equal to the mean value of $D$ in the data. The parameters $\alpha_9$ and $\alpha_{10}$ which determine the shape of the curve, were found to be independent of year and cultivar ($p > 0.1$). The parameter $\alpha_8$ which describes the level of the curve, however, differed significantly ($F_{13,43} = 2.71$, $n = 59$, $p < 0.01$) between year-field combinations. Fitted parameter values are shown in Table 5.5.

The contribution of sampling error to the residual variation in the relative growth rate was assessed using a Taylor expansion to estimate the sampling variance of $r_A$. The relation between mean and variance of a density estimate was calculated from the coefficient of variation. Sampling variance constitutes at most approximately 10% (0.0016) of the residual variance ($\sigma^2_{e,r_A}$, 0.018). Thus, variation due to sampling is negligible and the residual variation is modelled as a white noise process.

In the decision model, a prediction of the mean daily relative growth rate of aphids is made using Equation 5.14 and predicting $\alpha_8$, $\alpha_9$ and $\alpha_{10}$ according to

$$\begin{pmatrix}\hat{\alpha}_8\\ \hat{\alpha}_9\\ \hat{\alpha}_{10}\end{pmatrix} = \begin{pmatrix}\bar{\alpha}_8\\ \bar{\alpha}_9\\ \bar{\alpha}_{10}\end{pmatrix} + \varepsilon_{\alpha r_A}, \qquad \varepsilon_{\alpha r_A} \simeq N_3(0, \Sigma_1) \tag{5.15}$$

in which $\Sigma_1$ is the covariance matrix of $\alpha_8$, $\alpha_9$ and $\alpha_{10}$. Random deviation from the level $\hat{\alpha}_8$ in an arbitrary field results in a field-specific estimate $\hat{\alpha}_{8,f}$:

$$\hat{\alpha}_{8,f} = \hat{\alpha}_8 + \varepsilon_{\alpha_{8,f}}, \qquad \varepsilon_{\alpha_{8,f}} \simeq N\left(0, \sigma^2_{\alpha_{8,f}}\right) \tag{5.16}$$

White noise in the growth rate of the aphid population is accounted for by pre-

Table 5.5. Maximum likelihood estimates of $\alpha_8$, $\alpha_9$ and $\alpha_{10}$ in Equation 5.14, describing the relation between the relative growth rate of the cereal aphid population and crop development stage. Maximum likelihood estimates of the between-field standard deviation $\sigma_{\alpha_{8,f}}$ and the within-field standard deviation $\sigma_{e,r_A}$ are 0.053 and 0.133, respectively. The fraction of the variation explained, $r^2$, is 0.32 and the number of data points, $n$, is 59.

| Parameter | Estimate | Covariance matrix | | |
|---|---|---|---|---|
| $\alpha_8$ | 0.25 | 0.004913 | | |
| $\alpha_9$ | 0.087 | -0.001565 | 0.000749 | |
| $\alpha_{10}$ | -0.19 | -0.004924 | 0.001923 | 0.005657 |

dicting $r_A$ according to

$$\hat{r}_A = \hat{\alpha}_{8,f} + \hat{\alpha}_{10}\, e^{\hat{\alpha}_9 (D_t - 68)} + \varepsilon_{W,r_A}, \qquad \varepsilon_{W,r_A} \simeq N(0, \sigma^2_{e,r_A}) \qquad (5.17)$$

Maximum likelihood estimates of $\overline{\alpha}_8$, $\overline{\alpha}_9$, $\overline{\alpha}_{10}$ $\Sigma_1$, $\sigma^2_{\alpha_{8,f}}$ and $\sigma^2_{e,r_A}$ are given in Table 5.5. The fitted relation is shown in Figure 5.3b. The parameters $\alpha_{8,f}$, $\alpha_9$ and $\alpha_{10}$ are predicted at the start of each Monte Carlo run. Realizations of $\varepsilon_{W,r_A}$ are calculated once every 7 days, commensurate with the time scale of white noise in the data.

Analysis of variance of the brown rust data indicated no significant effects of year, cultivar, crop development stage or location on the relative growth rate $r_B$. The relative growth rates in subsequent intervals of 14 days appeared to vary independently. The contribution of sampling to the variation in the relative growth rate was assessed using the empirical relation between mean density and variance given by Daamen (1991a). As for aphids, sampling variance was approximately 10% of the residual variance of the relative growth rate of brown rust. For prediction of the population growth rate the residual variance must be taken into account as white noise.

In the decision model, a prediction of the mean daily relative growth rate is made according to

$$\hat{r}_B = \bar{r}_B + \varepsilon_{W,r_B}, \qquad \varepsilon_{W,r_B} \simeq N(0, \sigma^2_{e,r_B}) \qquad (5.18)$$

Estimates of $\bar{r}_B$ and $\sigma^2_{e,r_B}$ are 0.163 and 0.0066, respectively ($n$=25). The variance of $\bar{r}_B$ (0.00026) is negligible in comparison with $\sigma^2_{e,r_B}$, and is disregarded. In the model, realizations of $\varepsilon_{W,r_B}$ are calculated at intervals of 14 days, commensurate with the time scale of white noise in the data.

### *Incidence-density relations of aphids and brown rust*

Daamen (1991a) found no significant effect of year, cultivar, crop development stage or location on the incidence-severity relation for brown rust. Although for aphids no information on co-variables was available, it is assumed that these have no effect on the relation. This assumption is supported by results of Ward *et al.* (1986) who found no effect of co-variables based on one year's data on *S. avenae* from Sussex, England. Because both incidence and density were assessed accurately, the imperfect fit of Equation 5.3 is due to white noise.

In the decision model, a prediction of cereal aphid and brown rust density at given incidence is made using Equation 5.3 and predicting $\hat{\alpha}_{1,X}$ and $\hat{\alpha}_{2,X}$ according to:

$$\begin{pmatrix} \hat{\alpha}_{1,X} \\ \hat{\alpha}_{2,X} \end{pmatrix} = \begin{pmatrix} \bar{\alpha}_{1,X} \\ \bar{\alpha}_{2,X} \end{pmatrix} + \varepsilon_{\alpha_{1,2,X}}, \qquad \varepsilon_{\alpha_{1,2,X}} \simeq N_2\left(0,\Sigma_X\right) \tag{5.19}$$

in which $\Sigma_X$ is the covariance matrix of $\alpha_{1,X}$ and $\alpha_{2,X}$. In addition to the uncertainty about the parameter estimates, white noise has to be accounted for in the predicted density:

$$\widehat{\ln ( X_0 )} = \hat{\alpha}_{1,X} + \hat{\alpha}_{2,X} \ln\left(\ln\left(\frac{1}{1-\hat{I}_X}\right)\right) + \varepsilon_{W,X}, \quad \varepsilon_{W,X} \simeq N(0,\sigma^2_{e,x}) \tag{5.20}$$

in which $\sigma^2_{e,x}$ is the residual variance for aphids and brown rust. Finally, uncertainty exists about $I_X$ due to the farmer's sample estimate $I_{o,X}$:

$$\widehat{I_X} = \varepsilon_{I_X}, \qquad \varepsilon_{I_X} \simeq \text{Binomial}\left(I_{o,X}, n_X\right) \tag{5.21}$$

where $n_X$ represents the number of units in a sample. Least squares estimates of $\bar{\alpha}_{1,X}$, $\bar{\alpha}_{2,X}$ , $\Sigma_X$ and $\sigma^2_{e,x}$ are given in Table 5.6 for aphids and brown rust. The fitted relations are shown in Figure 5.3c-d. Predictions of ln $(X_0)$ need be made at the onset of each Monte Carlo run, only. Since $n_X$ is approximately 100, the binomial error distribution of Equation 5.21 is approximated by a normal distribution with mean $I_{o,X}$ and variance $I_{o,X}\left(1 - I_{o,X}\right) / n_X$, truncated at zero.

*Damage due to aphids*

In the decision model, damage per aphid-day at given crop development stage is predicted using Equation 5.4 and predicting $\hat{\alpha}_3$ and $\hat{\alpha}_4$ according to:

Table 5.6. Least squares estimates of $\alpha_{1,A}$ and $\alpha_{2,A}$ concerning aphids and $\alpha_{1,B}$ and $\alpha_{2,B}$ concerning brown rust in Equation 5.3, describing the relation between density and incidence. Additional statistics for cereal aphids: $r^2$= 0.87, residual error $\hat{\sigma}_{e,A}$=0.524, $n$=226. Additional statistics for leaf rust: $r^2$= 0.91, residual error $\hat{\sigma}_{e,B}$=0.79, $n$=31. Estimated covariances are cov($\alpha_{1,A}$, $\alpha_{2,A}$)= 0.000484 and cov($\alpha_{1,B}$, $\alpha_{2,B}$)= -0.000314.

| Parameter | Estimate | Standard error |
|---|---|---|
| $\alpha_{1,A}$ | 1.11 | 0.039 |
| $\alpha_{2,A}$ | 1.05 | 0.027 |
| $\alpha_{1,B}$ | 1.84 | 0.14 |
| $\alpha_{2,B}$ | 1.39 | 0.08 |

$$\begin{pmatrix} \hat{\alpha}_3 \\ \hat{\alpha}_4 \end{pmatrix} = \begin{pmatrix} \bar{\alpha}_3 \\ \bar{\alpha}_4 \end{pmatrix} + \varepsilon_{\alpha_{3,4}}, \qquad \varepsilon_{\alpha_{3,4}} \simeq N_2(0,\Sigma_2) \tag{5.22}$$

in which $\Sigma_2$ is the covariance matrix of $\alpha_3$ and $\alpha_4$. Least squares estimates of $\alpha_3$ and $\alpha_4$ and their variances are shown in Table 5.7 for three classes of attainable yield. The fitted relations are shown in Figure 5.3e-g. In the decision model, extrapolation to DC 55 and DC 83, respectively, is required. A curvilinear model might have resulted in a better fit for the class with highest attainable yields (Figure 5.3g). In view of the simulation origin of the data a common approach was preferred.

Maximum aphid damage is predicted according to

$$\hat{S}_A^{\max} = \bar{S}_A^{\max} + \varepsilon_{S_A^{\max}}, \qquad \varepsilon_{S_A^{\max}} \simeq N(0,\sigma^2_{S_A^{\max}}) \tag{5.23}$$

Based on the available data, $\bar{S}_A^{\max}$ is estimated to be 1890 kg ha$^{-1}$. The standard error $\sigma_{S_A^{\max}}$ is taken to be 200 kg ha$^{-1}$, approximately 10% of the estimated mean. The parameters $\alpha_3$, $\alpha_4$ and $S_A^{\max}$ are predicted at the start of each Monte Carlo run.

### *Damage due to brown rust*

In the decision model, damage per sorus-day is predicted using Equation 5.5 in which

$$\hat{\alpha}_5 = \bar{\alpha}_5 + \varepsilon_{\alpha_5}, \qquad \varepsilon_{\alpha_5} \simeq N(0,\sigma^2_{\alpha_5}) \tag{5.24}$$

Table 5.7. Least squares estimates of $\alpha_3$ and $\alpha_4$ in Equation 5.4, describing the relation between aphid damage and crop development stage for three classes of attainable yield. Additional statistics for yield class 3500-6000 kg ha$^{-1}$: $r^2$= 0.82, residual error $\hat{\sigma}_e$=0.25, $n$=62. Estimated covariance is cov($\alpha_3$, $\alpha_4$)= -0.00262. For yield class 6000-9000 kg ha$^{-1}$: $r^2$= 0.72, residual error $\hat{\sigma}_e$ =0.49, $n$=62, cov($\alpha_3$, $\alpha_4$)= -0.00992. For yield class 9000-10000 kg ha$^{-1}$: $r^2$= 0.82, residual error $\hat{\sigma}_e$ =0.74, $n$=62, cov($\alpha_3$, $\alpha_4$)= -0.0223.

| Yield class | Parameter | Estimate | Standard error |
|---|---|---|---|
| 3500-6000 | $\alpha_3$ | 8.81 | 0.435 |
| | $\alpha_4$ | -0.10 | 0.006 |
| 6000-9000 | $\alpha_3$ | 12.75 | 0.845 |
| | $\alpha_4$ | -0.15 | 0.012 |
| 9000-10000 | $\alpha_3$ | 24.60 | 1.269 |
| | $\alpha_4$ | -0.30 | 0.018 |

Estimates of $\overline{\alpha}_5$ and $\sigma_{\alpha_5}$ are 0.00014 kg kg$^{-1}$ and 0.000036 kg kg$^{-1}$, respectively ($n$=3; Daamen, 1991a). Maximum brown rust damage is calculated using Equation 5.6 where

$$\widehat{\alpha}_6 = \varepsilon_{\alpha_6}, \qquad \varepsilon_{\alpha_6} \simeq \text{Beta}\,(a_{\alpha_6}, b_{\alpha_6}) \tag{5.25}$$

The beta distribution conveniently describes the fraction $\alpha_6$, characterized by mean $\overline{\alpha}_6$ and variance $\sigma^2_{\alpha_6}$. The parameters $a_{\alpha_6}$ and $b_{\alpha_6}$ are estimated to be 25.86 and 60.25, based on $\overline{\alpha}_6$=0.30 kg kg$^{-1}$ ($n$=3; Daamen, 1991a) and $\sigma_{\alpha_6}$=0.05 kg kg$^{-1}$. The latter estimate is based on the experience that in the Netherlands brown rust rarely causes yield reductions higher than 40%. The parameters $\alpha_5$ and $\alpha_6$ are predicted at the start of each Monte Carlo run.

### Calculation of the probability distribution of model output

For a given initial state of the system described by temperature sum ($T_0$) and observed incidences of aphids ($I_{o,A}$) and brown rust ($I_{o,B}$), and for a particular decision strategy $\{d_1,...,d_N\}$, $M$ Monte Carlo runs are made. During a run the dynamics of the state of the system are calculated by discrete simulation with time steps of one day. A run ends at crop development stage DC 83 as from then on no more loss occurs. Thus, each run represents the realization of a crop-pest and crop-disease interaction during a growing season in an arbitrary field. In total, $M$ of these cases, i.e. year-field combinations, are simulated. At the start of each Monte Carlo run a stratified sample is drawn from the appropriate probability distributions of daily maximum and minimum temperatures, incidence sample estimates and each of the parameters, respectively. A stratum of daily maximum and minimum temperatures is equated with a temperature series of one year. Since 36 years of temperature data are available, a year's data are used more than once when $M$ exceeds 36. In the course of a Monte Carlo run, realizations of the sources of white noise $\varepsilon_{W,D}$ (Equation 5.13), $\varepsilon_{W,r_A}$ (Equation 5.17) and $\varepsilon_{W,r_B}$ (Equation 5.18) are drawn from their probability distributions at time intervals commensurate with the data. The algorithm is programmed in FORTRAN-77 using IMSL routines (IMSL, 1987) and runs on a VAX-8700 mainframe.

A suitable value of $M$ represents a compromise between the precision of the estimated probability distribution and the computational effort (Stein, 1987). Preliminary runs with $M$=300 and $M$=500 were compared to a "reference", consisting of a simple random sample with $M$=3000. Both for $M$=300 and $M$=500 differences in means and variances with $M$=3000 were small. However, latin hypercube sampling with $M$=500 was found to produce probability density distributions with tails rather similar to the reference on visual inspection. As this sample size was technically feasible, $M$=500 was selected.

## Estimated cumulative probability density functions of financial loss

To illustrate the output of the decision model, estimated cumulative probability density functions of financial loss are shown in Figure 5.4 for three strategies of control of aphids and brown rust. Some statistics are listed in Table 5.8. Compared to no chemical control in any decision period (NS) or chemical control at the start of the fourth decision period only (S4), chemical control at the start of the first decision period only (S1) decreases the frequency of occurrence of large financial losses for both aphids and brown rust. The least financial loss that may be incurred is approximately zero when no chemical control is carried out, whereas it approximately equals the costs of the control operation (*see* Table 5.4) when a chemical is applied. As a result, the probability density function of financial loss associated with immediate chemical control (S1) is narrower than the probability density function associated with no chemical control (NS) or postponed control (S4).

The initial conditions in the example have been chosen such that the mean financial losses of no chemical control and immediate chemical control

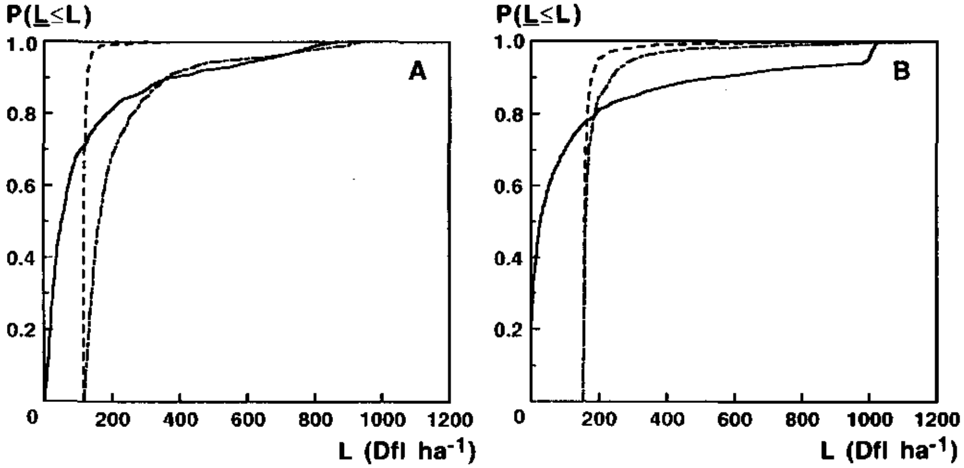


Figure 5.4. Estimated cumulative probability density curves of financial loss for three different tactics of control of aphids (A) and brown rust (B). Attainable yield is 8000 kg ha$^{-1}$. Initial conditions during calculations were: $I_{o,A}$ = 0.25; $I_{o,B}$ = 0.02; $T_0$ = 225 °d on day of the year 169. As a result $D_0$ = 61 (sd=4). Tactics comprise no chemical control in any decision period (NS) (——), spray at the start of the first decision period only (S1) (- - -), and spray at the start of the fourth decision period only (S4) (-·-·-·-).

Table 5.8. Statistics describing financial loss for three different strategies of control of aphids and brown rust. Initial conditions are given in the caption of Figure 5.4. Tactics comprise no chemical control in any decision period (NS), spray on the first day of the first decision period only (S1), and spray on the first day of the fourth decision period only (S4). In the last column financial loss calculated with the deterministic model version is shown.

Aphids

| Strategy | mean | sd | skewness | kurtosis | $P_{0.90}$ | range | deterministic loss |
|---|---|---|---|---|---|---|---|
| NS | 115 | 183 | 2.6 | 6.0 | 317 | 864 | 27 |
| S1 | 121 | 23 | 8.8 | 81.2 | 125 | 225 | 117 |
| S4 | 205 | 150 | 3.3 | 11.4 | 319 | 824 | 141 |

Brown rust

| Strategy | mean | sd | skewness | kurtosis | $P_{0.90}$ | range | deterministic loss |
|---|---|---|---|---|---|---|---|
| NS | 127 | 245 | 2.6 | 5.7 | 417 | 1021 | 29 |
| S1 | 165 | 35 | 9.0 | 100.1 | 174 | 497 | 157 |
| S4 | 191 | 104 | 6.2 | 45.8 | 237 | 1010 | 162 |

are approximately equal, for both aphids and brown rust (Table 5.8). Thus, these initial conditions represent a damage threshold, i.e. conditions at which chemical control should be carried out. The probability density functions of no chemical control and immediate chemical control intersect at one point, which represents the fraction of cases in which the former strategy results in smaller financial loss than the latter. Figure 5.4 shows that at this damage threshold no chemical control would result in smaller financial loss than immediate chemical control in approximately 75% of the cases evaluated, for both aphids and brown rust.

In the deterministic decision model, parameters and inputs are set to their average values and white noise is assumed absent. Deterministic financial losses associated with no chemical control (NS) or postponed chemical control (S4) are considerably smaller than stochastic results (Table 5.8). For immediate chemical control (S1) results of the stochastic and deterministic models are similar, reflecting the smaller degree of uncertainty about financial loss.

## Damage thresholds

Damage thresholds for aphids and brown rust have been calculated separately for a range of crop development stages using the deterministic and the stochastic version of the decision model (Figure 5.5). Lower damage threshold values imply that chemical control should be carried out at lower pest and disease incidences which is usually equivalent to earlier in time. The damage thresholds calculated with the deterministic version exceed those calculated with the stochastic version both for aphids and for brown rust. Thus, uncertainty causes chemical control to become economical at lower pest and disease incidences, which may lead to higher pesticide use.

Also shown in Figure 5.5 are the damage thresholds for aphids and brown rust according to EPIPRE (Drenth and Stol, 1990). For aphids, the EPIPRE thresholds are lower than the stochastic thresholds from flowering onward. For brown rust the EPIPRE thresholds are slightly higher than the deterministic thresholds from DC 55 until shortly before the end of flowering (DC 69), when the two measures coincide.

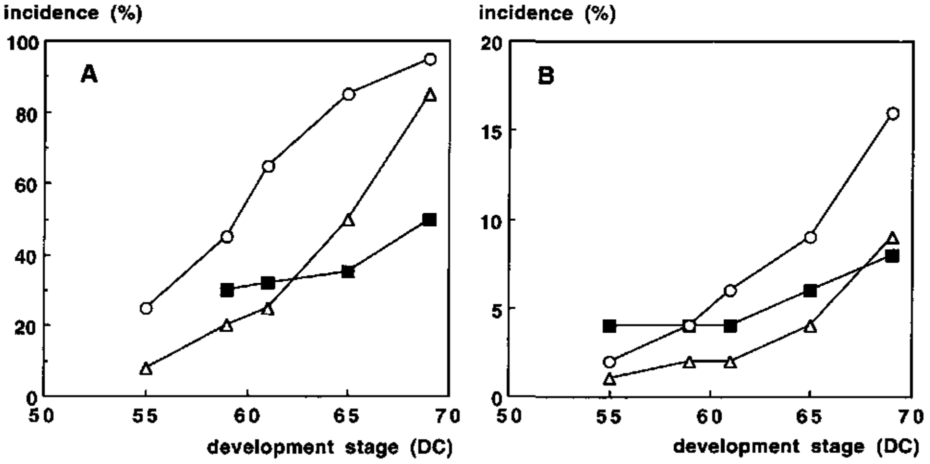


Figure 5.5. Damage thresholds for aphids (A) and brown rust (B) according to EPIPRE (—■—), the deterministic version of the decision model (—○—) and the stochastic version run with $M$=500 (—△—). EPIPRE damage thresholds were calculated assuming four green leaves per plant at all crop development stages. Attainable yield is 8000 kg ha$^{-1}$. The decision evaluation model was initialized with the following combinations of temperature sum (°day) and day of the year: DC55 : 165, 161; DC 59: 200, 164; DC 61: 225, 166; DC 65: 265, 169; DC 69: 320, 172. Crop development stages for the thresholds of the stochastic model represent means of 500 runs.

## Discussion

No formal validation of the decision model has been attempted. Nevertheless, the foundation of the model in EPIPRE, which has been evaluated extensively (Reinink, 1986; Drenth and Stol, 1990), and the availability of a relatively large set of field data for updating and upgrading (*sensu* Rabbinge, 1988) convey trust in the relevance of the model for practical supervised control of the multiple pathosystem winter wheat - aphids - brown rust. Updating has involved revision of all mathematical relations, partly because new information has become available (Daamen, 1991a; Chapter 4), and, more importantly, because previously interest has never been in analyzing the uncertainty. Upgrading concerned the introduction of daily temperatures and the relation between temperature sum and crop development stage. The data used to quantify the latter relation were collected during one year in the UK. Although this data base is rather narrow, the predictions of the model are similar to the relation between time and crop development stage used in EPIPRE (Drenth and Stol, 1990) which represents a long-term average for the Netherlands.

Compared to immediate chemical control the expected financial loss of no chemical control shows the larger deviation from the deterministic value. This is caused by the larger range of possible outcomes in combination with the long right tails of the probability distribution (Figure 5.4 and Table 5.8). It explains why the damage thresholds calculated with the deterministic version of the model exceed those calculated with the stochastic version at all crop development stages evaluated for both aphids and brown rust (Figure 5.5). The size of the difference between the deterministic and the stochastic thresholds reflects "the price of uncertainty", the degree to which uncertainty contributes to earlier spraying at current prices of wheat and agro-chemicals. The size of the difference increases with advancing crop development stage for brown rust. For aphids the difference decreases at later crop development stages because a maximum population density is reached (and $r_A$ equals zero, Figure 5.3b) before the end of the planning horizon. In conclusion, taking uncertainty about predicted costs and benefits of chemical control into account appears necessary, even without reference to the risk-attitude of the decision maker.

The stochastic damage thresholds represent those pest and disease incidences at which a risk-neutral decision maker, who is interested in average costs and benefits only, would just apply a chemical. Compared to the risk-neutral stochastic damage thresholds the EPIPRE thresholds for aphids are risk-neutral to risk-avoiding, i.e. equal to or lower than the stochastic damage thresholds, while those for brown rust are slightly risk-seeking to risk-neutral, i.e. higher than or equal to the stochastic damage thresholds. Entwistle and

Dixon (1987) also pointed out that the EPIPRE thresholds for aphids apparently implicitly assume a farmer to behave in a risk-averse manner. An alternative to giving a recommendation in which risk is implicitly accounted for (*see* Mann and Wratten, 1988), is to present information on the risk associated with different decision alternatives. Such explicit presentation of the consequences of uncertainty, advocated by Tait (1987), is addressed in Chapter 7.

Uncertainty about model structure is beyond the scope of this study. During development of the model, mathematical relations which best described the data (highest $r^2$ and smallest residual variance) have been preferred over alternative formulations. In two cases, alternatives have been rejected on different grounds. The first structural alternative is due to Entwistle and Dixon (1987), who proposed a multiple regression equation to describe aphid damage as a function of aphid density and population growth rate. The model is currently not used due to incomplete information on its uncertainty. However, when complete, it should be preferred over the current relation, since the latter is based on simulated data presumably representing the variation in the field. The second structural alternative concerns the stochastic model for the relative growth rate of aphids. During data analysis a model of similar structure as Equation 5.14 but with the residual variance increasing with crop development stage was found to describe the data as good as Equation 5.17. After fitting the model, the between-field variation in the parameters $\alpha_8$, $\alpha_9$ and $\alpha_{10}$ appeared insignificant. Ecologically, however, the variation in the relative growth rate is unlikely to increase with crop development stage because cereal aphid populations consistently reach peak densities around DC 75-77 and subsequently collapse. Variation between fields, on the other hand, is ecologically highly plausible due to factors like micro-weather and natural enemies which may vary between fields (Entwistle and Dixon, 1986, 1987). For these reasons the more complex stochastic model has been preferred in the decision model.

In a theoretical study on parameter uncertainty Kremer (1983) raised the question whether parameters should be treated as constant but poorly known or as inherently stochastic and varying in time. Using a simple model of algal competition he demonstrated that the two concepts may yield greatly different results. Although Kremer's results depended strongly on the simple nature of his model which contained few feedbacks, the issue has received attention from other authors (e.g. Beck, 1987). Reports on application of the two concepts in realistic ecological models appear rare, however. In this study, variation in the data which is not accounted for by regression is attributed to sampling of the dependent variable, resulting in the concept of a parameter being constant but poorly known. In the five cases where the contribution of sampling to residual variation could be quantified (Equations 5.3, both for aphids and brown rust, 5.13, 5.17 and 5.18) it has been found to be insignificant. In those cases, the residual variation is described as a part of the system, causing the parameters to vary in time. Such white noise is to be expected as not all factors influencing the dependent variable have been included in the regression equation and many of them may vary in time. To the best of our knowledge this study is the first report of actual quantification of white noise in an ecological study using empirical data to estimate the size and the frequency of variation in parameters.

The degree to which the various sources of uncertainty in the decision model contribute to the uncertainty about financial loss is analyzed in Chapter 6.

# Symbols used in Chapter 5

## State variables

| Symbol | Definition | Initial value |
|---|---|---|
| $A$ | Aphid density | $A_0$ tiller$^{-1}$ |
| $B$ | Brown rust density | $B_0$ leaf$^{-1}$ |
| $D$ | Crop development stage | $D_0$ - |
| $S_A$ | Aphid damage | 0 kg ha$^{-1}$ |
| $S_B$ | Brown rust damage | 0 kg ha$^{-1}$ |
| $S_i$ | Damage in decision period $i$ | 0 kg ha$^{-1}$ |
| $T$ | Temperature sum since DC 30 | $T_0$ °C day |
| $L$ | Financial loss | 0 Dfl ha$^{-1}$ |

## Other variables and parameters

| Symbol | Definition | Unit |
|---|---|---|
| $a_{A,d_i}, b_{A,d_i}$ | Parameters describing the variation in $K_A$ | -,- |
| $a_{B,d_i}, b_{B,d_i}$ | Parameters describing the variation in $K_B$ | -,- |
| $a_{\alpha_6}$, $b_{\alpha_6}$ | Parameters describing the variation in parameter $\alpha_6$ | -,- |
| $b(i)$ | First day of decision period $i$ | - |
| $C$ | Costs associated with a control decision | Dfl ha$^{-1}$ |
| $d_i$ | Control decision in decision period $i$ | - |
| $D^{max}$ | Maximum crop development stage | - |
| $I_A$ | Aphid incidence | - |
| $I_{o,A}$ | Observed aphid incidence | - |
| $I_B$ | Brown rust incidence | - |
| $I_{o,B}$ | Observed brown rust incidence | - |
| $K_A(d_i)$ | Fraction of aphid population killed due to control decision $d_i$ | - |
| $K_B(d_i)$ | Fraction of brown rust population killed due to control decision $d_i$ | - |
| $l(i)$ | Last day of decision period $i$ | - |
| $M$ | Number of Monte Carlo simulation runs | - |
| $n_A$ | Sample size for estimating $I_A$ | - |
| $n_B$ | Sample size for estimating $I_B$ | - |
| $N$ | Number of decision periods | - |
| $P_A$ | Duration of growth arresting effect on the aphid population | |

| | | |
|---|---|---|
| | following control decision $d_i$ | day |
| $P_B$ | Duration of growth arresting effect on the brown rust population following control decision $d_i$ | day |
| $r_A$ | Relative growth rate of the aphid population | day$^{-1}$ |
| $R_A$ | Presence or absence of aphicidal effect | - |
| $r_B$ | Relative growth rate of the brown rust population | day$^{-1}$ |
| $R_B$ | Presence or absence of fungicidal effect | - |
| $S_A^{max}$ | Maximum aphid damage | kg ha$^{-1}$ |
| $S_B^{max}$ | Maximum brown rust damage | kg ha$^{-1}$ |
| $t$ | Current day | - |
| $t_a$ | Day on which control decision $d_i$ is made | - |
| $w$ | Price of wheat | Dfl kg$^{-1}$ |
| $Y_{att}$ | Attainable yield | kg ha$^{-1}$ |
| $\alpha_{1,A}, \alpha_{2,A}$ | Parameters of incidence - density relation, aphids | -, - |
| $\alpha_{1,B}, \alpha_{2,B}$ | Parameters of incidence - density relation, brown rust | -, - |
| $\alpha_3$ , $\alpha_4$ | Parameters of damage per aphid-day - crop development stage relation | kg kg$^{-1}$ (aphid-day)$^{-1}$,<br>kg kg$^{-1}$ (aphid-day)$^{-1}$ |
| $\alpha_5$ | Damage per sorus-day per unit attainable yield | kg kg$^{-1}$ (sorus-day)$^{-1}$ |
| $\alpha_6$ | Maximum brown rust damage per unit attainable yield | kg kg$^{-1}$ |
| $\alpha_7$ | Parameter of crop development stage - temperature sum relation | (°C day)$^{-1}$ |
| $\alpha_8$, $\alpha_9$, $\alpha_{10}$ | Parameters of relative aphid growth rate - crop development stage relation | day$^{-1}$, day$^{-1}$, - |
| $\alpha_{8,f}$ | Field specific version of parameter $\alpha_8$ | day$^{-1}$ |
| $\varepsilon_{I_A}$ | Uncertainty in sample estimate $I_A$ | - |
| $\varepsilon_{I_B}$ | Uncertainty in sample estimate $I_B$ | - |
| $\varepsilon_{K_X}$ | Parameter uncertainty in $K_X(d_i)$ | - |
| $\varepsilon_{P_X}$ | Parameter uncertainty in $P_X(d_i)$ | day |
| $\varepsilon_{S_A^{max}}$ | Parameter uncertainty in $S_A^{max}$ | kg ha$^{-1}$ |
| $\varepsilon_{W,A}$ | White noise in incidence - density relation aphids | - |
| $\varepsilon_{W,B}$ | White noise in incidence - density relation brown rust | - |
| $\varepsilon_{W,D}$ | White noise in crop development stage - temperature sum relation | - |
| $\varepsilon_{W,r_A}$ | White noise in relation between relative aphid growth rate - crop development stage | day$^{-1}$ |
| $\varepsilon_{W,r_B}$ | White noise in relative brown rust growth rate | day$^{-1}$ |
| $\varepsilon_{\alpha_i}$ | Parameter uncertainty in $\alpha_i$ | variable |
| $\varepsilon_{\alpha_{r_A}}$ | Uncertainty in the parameters describing $r_A$ | day$^{-1}$, day$^{-1}$, - |
| $\sigma^2_{e,i}$ | Residual variance of i | variable |
| $\sigma^2_i$ | Variance of $i$ | variable |
| $\Sigma_i$ | Covariance matrix labelled as $i$ | variable |

Part 2

# Uncertainty and risk in supervised control of aphids and brown rust in winter wheat

6

Chapter 6

## Relative i[illegible]nce of different componen[illegible] uncertainty

Rossing, W.A.H., Daamen, R.A. & Jansen, M.J.W., 1993.
Uncertainty analysis applied to supervised control of aphids and brown rust in winter wheat. 2. Relative importance of different components of uncertainty.
Accepted by *Agricultural Systems*.

**Abstract** The components of an existing model for supervised control of aphids (especially *Sitobion avenae*) and brown rust (*Puccinia recondita*) in winter wheat contain uncertainty. Their contribution to uncertainty about model output is assessed. The model simulates financial loss associated with a time sequence of decisions on chemical control as a function of crop development, population growth, and damage. Four sources of uncertainty were quantified: model parameters, incidence sample estimates, future average daily temperature, and white noise. Uncertainty about the first two sources is controllable because it decreases when more information is collected. Uncertainty about the last two sources is uncontrollable, given the structure of the model.

Uncertainty about model output, characterized by its variance, is calculated by repeatedly drawing realizations of the various sources of uncertainty, and calculating financial loss after each draw. By processing new realizations of these sources one by one, the contribution of each source to total variance can be assessed using an adapted Monte Carlo procedure.

For most relevant initial conditions and decision strategies the sources of uncontrollable uncertainty cause more than half of the uncertainty about model output. White noise in the relative growth rates of aphids and brown rust is the most important source of uncertainty. Resources for improvement of the model are most effectively allocated to studies of the population dynamics of aphids and brown rust.

## Introduction

Predictions of costs and benefits of chemical control of pests and diseases at the field level are an essential element of supervised control (Zadoks, 1985). Such predictions can be made using dynamic models which relate pest or disease intensity to financial loss. Usually, uncertainty about the values of parameters and model inputs is ignored and calculations are carried out with average values. In principle, however, uncertainty must be taken into account when relations in the model are non-linear, when the contribution of different sources of uncertainty to output uncertainty of the model is of interest, or when risk has to be assessed.

A decision model for evaluating costs associated with different strategies of chemical control of aphids (especially *Sitobion avenae*) and brown rust (*Puccinia recondita*) in a field of winter wheat was presented in Chapter 5. It represents an upgraded version of part of the EPIPRE advisory system (Zadoks *et al.*, 1984; Drenth *et al.*, 1989). The model predicts financial loss associated with a particular time series of decisions on chemical control for given initial values of temperature sum and incidences of aphids and brown rust. Aphids and brown rust were considered because they often occur simultaneously. Diseases other than brown rust were omitted in view of the exploratory nature of the study. The effect of uncertainty about model parameters and model inputs on damage thresholds, i.e. densities at which chemical control is just economical for a farmer, was assessed. It was shown that ignoring uncertainty about model parameters and inputs results in damage thresholds which exceed the thresholds calculated under uncertainty, assuming risk-neutrality. Farmers deciding on chemical control based on the deterministic damage thresholds will spray their crops too late, and may incur economically unacceptable financial losses. Thus, as a consequence of non-linear relations in the model, uncertainty must be taken into account when calculating expected costs associated with different strategies of chemical control of aphids and brown rust.

In this Chapter, the contribution of uncertainty about parameters and inputs of the decision model to uncertainty about predicted financial loss is assessed. The major causes of model output uncertainty are identified for a number of relevant initial conditions and control strategies. Research prioritization is discussed in relation to the possibilities for reducing model output uncertainty.

## Materials and methods

### Description of the decision model

The decision model described in Chapter 5 simulates financial loss due to attack by aphids and brown rust from ear emergence (DC 55 (Zadoks *et al.*, 1974)) to dough ripeness (DC 83), i.e. approximately from early June till late July, in a commercial field of winter wheat in the Netherlands of, say, 5 to 10 ha. Financial loss is defined as the costs of yield reduction caused by aphids and/or brown rust plus the costs of eventual control. Costs are calculated at field level. The model is used to estimate the probability distributions of financial loss associated with different strategies of chemical control. A strategy is defined as a series of decisions on chemical control made on the first day of consecutive decision periods of one week. The decisions which can be taken at the start of each week are either chemical control of aphids and/or brown rust or no chemical control. The series of decisions is fixed at the start of the simulation. The model comprises relations which describe the dynamics of crop development, population growth, and damage by aphids and brown rust as a function of the strategy on chemical control. The model inputs include the temperature sum accumulated since the day the crop attained development stage pseudo-stem elongation (DC 30), the future average daily temperature, and the initial values of aphid and brown rust incidences determined by the farmer.

Uncertainty about the values of input variables and of model parameters was quantified using empirical data (Chapter 5). Parameters were estimated by regression, the variance-covariance matrix of the estimates providing a measure of parameter uncertainty. Residual variation was ascribed to measurement effects and was disregarded for prediction. In some of the regression analyses, however, residual variances greatly exceeded the variances attributable to measurement effects. Apparently, the *y*-variable varied in an unpredictable manner, due to causes not accounted for in the regression model. In these cases the residual variation constitutes a source of uncertainty which must be taken into account for prediction of a new situation. The random deviations of the empirical data from the fitted regression model were described as mutually independent, identically distributed, normal variates. This source of variation is referred to as white noise. The input variable "initial temperature sum" was assumed to be known with negligible variation. Initial values of aphid and brown rust incidences were subject to observational error. The variation in future average daily temperature was described by 36 years of daily maximum and minimum temperatures measured at the meteorological station of the Wageningen Agricultural University from 1954 to 1990. Thus, analysis of the available information resulted in four categories of uncertainty: estimates of the initial state, model parameters, white noise, and future average daily temperature. In each category one or more components can be distinguished (Table 6.1). These components represent the smallest independent sources of uncertainty in the model. Uncertainty about the interactions between these model components was assumed to be absent.

## Relative importance of component uncertainty for model output uncertainty

Uncertainty about model components (Table 6.1) causes the outcome of the model, financial loss, to be uncertain. Here, the uncertainty about model outcome is characterized by its variance. Model output variance attributable to uncertainty about model component $x_i$ can be assessed in two ways. First, by calculating the decrease in expected model output variance resulting from removal of the uncertainty about $x_i$, and, second, by calculating the expected model output variance remaining after removal of the uncertainty about all components except $x_i$. The first approach is relevant for model parameters and estimates of the initial state where, theoretically, uncertainty is controllable. In these categories uncertainty declines when more empirical data are collected. The second approach is appropriate for the categories white noise and future average daily temperature where uncertainty is uncontrollable.

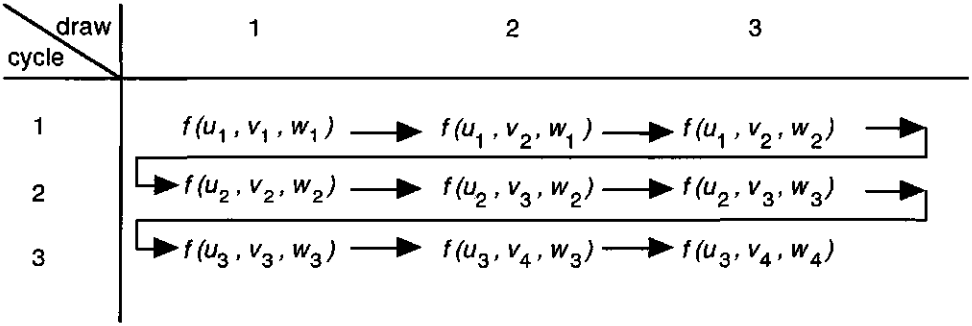
Table 6.1. Summary of sources of uncertainty in the decision model and their probability distributions. Details are given in Chapter 5.

| Category | Component | Distribution |
|---|---|---|
| Estimates of initial state | • incidence | binomial |
| | • temperature sum | -[a] |
| Parameters | various | (multivariate) normal, beta |
| Gaussian white noise | • relative growth rate | normal |
| | • incidence - density transformation | normal |
| | • temperature sum - crop development stage transformation | normal |
| Future average daily temperature | - | historic data (36 years ) |

[a] Temperature sum is assumed to be known with negligible uncertainty.

Jansen *et al.* (1993) developed an adapted Monte Carlo method to efficiently assess the contribution of uncertainty about a model component to model output variance. The method is illustrated in Figure 6.1. The procedure starts with a simple random sample of the $Q$, *i.c.* three, independent components of uncertainty in a model and calculation of model output, which is indicated in Figure 6.1 as $f(u_1, v_1, w_1)$. Processing one component at a time, new realizations of the components are drawn by simple random sampling from the appropriate probability distributions. After each draw model output is calculated and stored. After $Q$ draws, the values of all components have been changed once compared to their initial values, resulting in $f(u_2, v_2, w_2)$ in Figure 6.1, and the first cycle is completed. In total $M$ cycles are made. Since the components are changed one by one, the difference in model output between consecutive draws is solely due to variation in one component. The change in model output after ($Q$ -1) draws is due to variation in all components, except one.

The expected output variance of the full model is estimated as the variance of a column in Figure 6.1, each column representing a random sample of the model output distribution. The contribution of a source of controllable variation to model output uncertainty is calculated as the decrease in expected output variance resulting from removal of the uncertainty about one model component. For example, the expected model output variance



| cycle \ draw | 1 | 2 | 3 |
|---|---|---|---|
| 1 | $f(u_1, v_1, w_1)$ | $f(u_1, v_2, w_1)$ | $f(u_1, v_2, w_2)$ |
| 2 | $f(u_2, v_2, w_2)$ | $f(u_2, v_3, w_2)$ | $f(u_2, v_3, w_3)$ |
| 3 | $f(u_3, v_3, w_3)$ | $f(u_3, v_4, w_3)$ | $f(u_3, v_4, w_4)$ |

Figure 6.1. Illustration of the adapted Monte Carlo method for a model $f(\cdot)$ with three sources of uncertainty, $u$, $v$, and $w$. Consecutively drawn random values of, for example, $u$ are denoted by $u_1$, $u_2$, etcetera. The sample consists of three cycles. After Jansen *et al.* (1993).

remaining after removal of the controllable uncertainty about $u$ is estimated as the variance of the differences between columns 1 and 3 in Figure 6.1. The contribution of a source of uncontrollable variation to model uncertainty is assessed by the expected model output variance remaining after removal of the uncertainty about all other sources of uncertainty. For example, the contribution of the source of uncontrollable uncertainty $v$ to model uncertainty is estimated as the variance of the differences between columns 1 and 2 in Figure 6.1. The variance estimates are used to obtain a ranking of the relative importance of the various components of controllable and uncontrollable uncertainty, respectively.

The estimates of expected model output variance are unbiased and asymptotically normally distributed. Since their (co-) variances can be estimated, the difference between expected model output variances resulting from uncertainty in two components can be tested for deviation from zero.

Note, that after removal of uncertainty in, for example, component $u$ the expected model output variance represents the main effect of $u$, whereas the expected model output variance after removal of uncertainty in all components except $u$ constitutes the main effect of $u$ plus the interaction of $u$ with the other components of uncertainty. Thus, the two variance estimates do not necessarily add up to the full model's output variance.

The decision model and the Monte Carlo procedure are programmed in FORTRAN-77. The analysis of model output was programmed in C (Jansen *et al.*, 1993). Preliminary analyses showed that between 2,000 and 32,000 cycles were needed to arrive at sufficiently precise estimates of expected model output variance, i.e. with a coefficient of variation of approximately 0.10, or smaller. The greatest number of iterations was needed for decision strategies which resulted in highly skewed frequency distributions of financial loss.

In the analysis, a distinction is made between white noise and future temperature on the one hand, and model parameters and estimates of the initial state on the other. Uncertainty about white noise and future temperature can not be reduced without changing the structure of the model, and represents uncontrollable variation. Thus, the uncertainty about financial loss caused by these sources represents a lower bound for model uncertainty. In contrast, uncertainty about model parameters and estimates of the initial state decreases as more information is collected, and represents controllable variation. Therefore, the decrease of uncertainty about model outcome resulting from removing the uncertainty about these sources is the maximum improvement achievable within the framework of the model structure.

## Results

In Chapter 5 risk-neutral damage thresholds for aphids and brown rust were calculated for temperature sums which correspond with average crop development stages "50% of the ear visible" (DC 55), "onset of flowering" (DC 61), and "flowering completed" (DC 69). These temperature sums and incidences of aphids and brown rust are used as initial states in the calculation of the relative importance of the various categories and components of uncertainty. Three strategies of chemical control are evaluated for both aphids and brown rust: no chemical control at any time (NS), control at the start of the first decision period only (S1), and control at the start of the second decision period only (S2). Throughout the analysis attainable yield is 8000 kg ha$^{-1}$.

Expected variance of financial loss, the model output of interest, is greatest when no chemical control is carried out for both aphids and brown rust (Table 6.2). Immediate chemical control results in the smallest expected variance while chemical control at the start of the second decision period results in an intermediate variance estimate. These results correspond to the graphical and numerical results in the previous Chapter (Figure 5.4 and Table 5.8), which showed that chemical control reduces the range of possible financial losses.

In most cases the categories of uncontrollable variation, white noise and future average daily temperature, cause more than 50% of the uncertainty about financial loss (Table 6.2). More detailed analysis shows that white noise in the relative growth rates of aphids and brown rust usually contributes significantly more to model output variance than other white noise components or future temperature. This is illustrated for an initial temperature sum of 225 °d

Table 6.2. Expected variance of financial loss (Dfl$^2$ ha$^{-2}$) caused by different sources of uncertainty for combinations of three initial states and *three decision strategies (NS, S1 and S2). $T_0$ represents the initial temperature sum (°day), $I_{o,A}$ the estimated initial aphid incidence (-), and $I_{o,B}$* the estimated initial brown rust incidence (-). Attainable yield is 8000 kg ha$^{-1}$.

| Aphids | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Sources of uncertainty | Initial state | | | | | | | | |
| | $T_0$ =165; $I_{o,A}$ = 0.08 | | | $T_0$ =225; $I_{o,A}$ = 0.30 | | | $T_0$ =320; $I_{o,A}$ = 0.85 | | |
| | Strategy | | | Strategy | | | Strategy | | |
| | NS | S1 | S2 | NS | S1 | S2 | NS | S1 | S2 |
| All | 45800 | 715 | 1370 | 41100 | 587 | 2120 | 24100 | 758 | 5680 |
| White noise and future temperature | 32600 | 443 | 1030 | 30300 | 342 | 1700 | 17800 | 314 | 4780 |
| Model parameters and estimate of initial state | 13200 | 272 | 340 | 10800 | 245 | 420 | 6300 | 444 | 900 |

Table 6.2 Continued.

| Brown rust | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Sources of uncertainty | Initial state | | | | | | | | |
| | $T_0$ =165; $I_{o,B}$ = 0.01 | | | $T_0$ =225; $I_{o,B}$ = 0.02 | | | $T_0$ =320; $I_{o,B}$ = 0.08 | | |
| | Strategy | | | Strategy | | | Strategy | | |
| | NS | S1 | S2 | NS | S1 | S2 | NS | S1 | S2 |
| All | 76800 | 4030 | 4170 | 60800 | 1750 | 1850 | 60400 | 959 | 1730 |
| White noise and future temperature | 66000 | 3940 | 4030 | 53700 | 1820 | 1760 | 53700 | 1020 | 1560 |
| Model parameters and estimate of initial state | 10800 | 90 | 140 | 7100 | 0 | 90 | 6700 | 0 | 170 |

(equivalent with average crop development stage DC 61), and initial aphid and brown rust incidences of 30% and 2%, respectively (Table 6.3).

The consequences of removing the uncertainty about the sources of controllable uncertainty are illustrated for the same initial state (Table 6.4). For aphids, perfect knowledge of the parameters describing the relative population growth rate results in the greatest decrease of expected model output variance for the strategies NS and S2. For brown rust, the initial incidence estimate is the most important source of controllable uncertainty when fungicide is applied immediately (S1). However, the decreases of model output variance expected when the various components of controllable uncertainty were fully known, are small.

## Discussion

The contribution of uncontrollable variation to uncertainty about financial loss was generally more important than the contribution of controllable variation. Among the components of uncontrollable variation, white noise in the relative growth rates of aphids and brown rust appeared more important than other sources of white noise, or future temperature. The minor importance of uncertainty about future average daily temperature is not surprising as in the decision model only temperature integrated over time is considered. Such integration results in "smoothing" of day-to-day temperature fluctuations.

The results of the analysis indicate that, given the structure of the model, efforts to further refine estimates of parameters and initial incidences are not expected to greatly reduce output uncertainty (Table 6.2). Apparently the research effort put into the development and maintenance of EPIPRE (Zadoks, 1984; Drenth *et al.*, 1989; Daamen, 1991b) has yielded sufficiently precise parameter estimates. The uncertainty about financial loss due to the sample estimate of initial brown rust incidence is commensurate with the uncertainty due to the parameter estimates (Table 6.4). Thus, the sample size for brown rust recommended in EPIPRE appears adequate. For aphids, however, the uncertainty about financial loss due to the sample estimate of initial incidence is substantially smaller than the uncertainty due to the relative growth rate estimate, the largest source of variation (Table 6.4). Therefore, the recommended sample size for aphids may be decreased without greatly increasing the uncertainty in model predictions.

As white noise in the relative growth rates of aphids and brown rust was of major importance, a significant improvement of the decision model will involve a review of the concepts of population growth. More detailed models, such as the one by Entwistle and Dixon (1986) which takes into account the

Table 6.3. Expected variance of financial loss (Dfl$^2$ ha$^{-2}$) caused by white noise and future average daily temperature for three decision strategies (NS, S1 and S2) at initial state $T_0$ =225 °day (temperature sum), $I_{o,A}$ = 0.30 (initial aphid incidence) and $I_{o,B}$ = 0.02 (initial brown rust incidence). Attainable yield is 8000 kg ha$^{-1}$. Different letters following estimates indicate significant differences within strategies ($p < 0.05$).

Aphids

| Source of uncertainty | Strategy | | |
|---|---|---|---|
| | NS | S1 | S2 |
| White noise and future temperature | 30300 | 342 | 1700 |
| White noise in relative growth rate | 23600 a | 198 a | 1260 a |
| White noise in temperature sum - crop development stage relation | 697 c | 45 c | 54 d |
| White noise in incidence-density transformation | 5250 b | 76 b | 595 b |
| Future average daily temperature | 4830 b | 137 a | 157 c |

Brown rust

| Source of uncertainty | Strategy | | |
|---|---|---|---|
| | NS | S1 | S2 |
| White noise and future temperature | 53700 | 1820 | 1760 |
| White noise in relative growth rate | 41400 a | 1300 a | 1330 a |
| White noise in temperature sum - crop development stage relation | 3640 c | 304 d | 256 c |
| White noise in incidence-density transformation | 13500 b | 507 c | 749 b |
| Future average daily temperature | 18500 b | 974 b | 898 b |

Table 6.4. Expected reduction of variance of financial loss (Dfl$^2$ ha$^{-2}$) when uncertainty about model parameters and the estimated initial state is removed, for three decision strategies (NS, S1 and S2) at initial state $T_0$ =225 °day (temperature sum); $I_{o,A}$ = 0.30 (initial aphid incidence) and $I_{o,B}$ = 0.02 (initial brown rust incidence). Attainable yield is 8000 kg ha$^{-1}$. Different letters following estimates indicate significant differences within strategies ($p < 0.05$).

Aphids

| Source of uncertainty removed | Strategy | | |
|---|---|---|---|
| | NS | S1 | S2 |
| Model parameters and estimate of initial state | 10800 | 245 | 420 |
| Model parameters: | | | |
| Incidence-density transformation | 300 b | 0 a | 0 b |
| Damage relation | 300 b | 0 a | 0 b |
| Maximum damage | 0 b | 0 a | 80 b |
| Temperature sum - crop development stage relation | 1000 b | 0 a | 0 b |
| Relative growth rate | 4900 a | 91 a | 300 a |
| Direct aphicidal effect | 0 b | 27 a | 230 b |
| Effective aphicidal period | 0 b | 0 a | 130 b |
| Estimate of initial state | 0 b | 0 a | 140 b |

Brown rust

| Source of uncertainty removed | Strategy | | |
|---|---|---|---|
| | NS | S1 | S2 |
| Model parameters and estimate of initial state | 7100 | 0 | 170 |
| Model parameters: | | | |
| Incidence-density transformation | 2300 a | 30 b | 0 a |
| Damage relation | 900 a | 0 b | 30 a |
| Maximum damage | 500 a | 0 b | 50 a |
| Temperature sum - crop development stage relation | 0 b | 0 b | 80 a |
| Relative growth rate[1] | - | - | - |
| Direct fungicidal effect[2] | - | - | - |
| Effective fungicidal period | 0 b | 190 b | 80 a |
| Estimate of initial state | 800 ab | 420 a | 90a |

---

[1] Uncertainty about the mean relative growth rate is disregarded (*see* Chapter 5).

[2] Direct fungicidal effect absent.

field-to-field variation in aphid population growth rate, may be needed to reduce the effect of white noise in the decision model.

The coefficient of variation of the estimates of model output variance varied greatly with decision strategy. At $M$=2000 cycles the coefficient of variation of the variance estimates was 5-10% for NS while for S1 and S2 values of 25 to 40% occurred, which necessitated 32000 cycles to attain the desired precision. Since the computational effort grows quadratically with required precision, computer speed becomes a limiting factor to attain more precise estimates. The reason for the large variance of the estimates for the strategies S1 and S2 is the skewness of the distributions of financial loss (Table 5.8).

The structure of the decision model and the various estimates have been assumed valid. As the decision model constitutes an upgraded version of analogous modules in the EPIPRE advisory system which was tested extensively (Reinink, 1986; Drenth *et al.*, 1989), this seems a valid assumption.

The uncertainty analysis has identified the sources of uncertainty of major importance for uncertainty in predicted financial loss associated with a particular decision strategy. The results may be used to set research priorities, and to support pest and disease management. In combination with estimates of the likely gains in knowledge on model components resulting from different research efforts, the results can be used to allocate resources for efficiently reducing uncertainty about model output. When used for decision support in a farm management context, some degree of uncertainty in the model has to be accepted. The consequences of this uncertainty for decision making in supervised control of aphids and brown rust are addressed in the next Chapter.

## Part 2

# Uncertainty and risk in supervised control of aphids and brown rust in winter wheat

7

## Chapter 7

# A framework to s[illegible]rt decisions on chemical contr[illegible]der uncertainty

Rossing, W.A.H., Daamen, R.A. & Hendrix, E.M.T., 1993.
*A framework to support decisions on chemical pest control under uncertainty, applied to supervised control of aphids and brown rust in winter wheat.*
*Crop Protection,* in press.

**Abstract** An approach is presented for supporting decision making on chemical pest control in an uncertain environment. Timing of chemical control is considered a decision problem, which is analyzed in terms of objectives, strategies, selection criteria, and a model of the system dynamics. *Return on expenditure* and *insurance* are considered to be two generally applicable objectives in pest control. These objectives are made operational by defining the *profitability* of strategy *A* compared to strategy *B* as the probability that *A* results in lower costs than *B*, and the *risk* associated with a strategy as the 0.90 quantile of the probability distribution of costs associated with that strategy, respectively. We propose to express the performance of relevant strategies in terms of profitability and risk. Risk-neutral damage thresholds where expected costs of no chemical control at any time just exceed those of immediate application of a pesticide, constitute a yardstick for assessing a strategy's performance.

The approach is illustrated using a deterministic model of the pathosystem aphid - brown rust - winter wheat. Uncertainty is modelled as random inputs. No control and immediate pesticide application represent the only relevant strategies, since postponing chemical control decreases profitability and increases risk. The decline in risk due to pesticide application is larger for brown rust than for aphids. At risk-neutral damage thresholds the probability of positive returns on pesticide application amounts to only 30%. The causes of this bias to chemical control in recommendations for risk-neutral decision makers are discussed. Current recommendations for both aphids and brown rust appear to presume that farmers become more risk-averse as crop development advances.

## Introduction

Correct timing of the application of pesticides is essential to avoid unacceptable crop losses and to minimize negative effects on the environment. In principle, the best timing of chemical control can be calculated in advance when the future course of the pest population density, the associated damage, the effectiveness of control, the financial revenue of crop yield and the costs of chemical control are known. The economically optimal decision minimizes costs resulting from pest damage and control. In practice, however, a decision on pesticide application is made under uncertainty as a result of lack of knowledge of the dynamics of the biological processes involved, the actual field situation, and future weather. Then, the attitude of the decision maker towards the various possible outcomes of a decision determines which decision is considered best. Thus, uncertainty causes subjective elements to enter the decision process.

Broadly, three different approaches to support decisions on pesticide application were developed during the last decades (Mumford and Norton, 1984): the damage threshold concept and the marginal analysis concept which are both based on a deterministic approach, and the decision theory concept which is based on a probabilistic approach. Along different lines of thought, reflected in mathematical models, these concepts arrive at criteria for the optimal timing of chemical pest control. Application of these selection criteria results in a recommendation to a farmer, and as such the concepts are prescriptive. Uncertainty is taken into account only in the decision theory concept. In the other two concepts calculations are based on averages. The deterministic and the prescriptive characteristics of these concepts both represent serious shortcomings.

In a deterministic model uncertainty in various parts of the model is ignored. The model outcome is calculated using average values of model inputs and parameters. This result may differ considerably from the averaged model outcome obtained after taking into account the uncertainty in parts of the model. In Chapter 5 we showed that taking uncertainty in model parameters and inputs into account results in damage thresholds for control of aphids and brown rust in winter wheat which are considerably lower than those calculated by the deterministic model. The damage threshold (Zadoks, 1985) is defined as the level of pest attack at which the benefit of control just exceeds its cost (Mumford and Norton, 1984). Thus, ignoring uncertainty may lead to wrong recommendations. When acting according to the deterministic thresholds, farmers will spray their crops too late, and, on average, will incur avoidable loss.

Farmers choose between alternative decisions by considering not only expected outcome, but also the risk associated with each decision, i.e. the possible occurrence of unfavorable outcomes (Roumasset, 1979; Hendrix, 1989). Farmers' attitudes to risk associated with pest problems differ between individuals and, for one individual, change with time (Norton, 1976; Zadoks, 1985; Tait, 1987; Webster, 1987). With respect to pest control decisions farmers have been found to show attitudes ranging from risk-averse to risk-accepting (Zadoks, 1989a; Thornton *et al.*, 1984; Tait, 1983; Mumford, 1981; Webster, 1977; Carlson, 1970), indicating that farmers use information on the likelihood of various possible outcomes of a decision to arrive at a subjectively best alternative. This constitutes another argument for taking a probabilistic, rather than a deterministic approach to support decisions on pest control.

In information systems developed to advise farmers on chemical control decisions a farmer's risk attitude has been accounted for in, largely, two ways. If the decision support approach is deterministic, the recommendation is adjusted so that it is "on the safe side", i.e. biased toward chemical control (e.g. Cammel and Way, 1977; Daamen, 1981; Mann and Wratten, 1989). The degree of adjustment appears to depend mainly on the preference of the researchers or the extension workers. Alternatively, if the decision support approach is probabilistic, the risk attitude of a farmer is described as a subjective utility function which is used to calculate custom-made recommendations (e.g. Carlson, 1970; Webster, 1977; Lazarus and Swanson, 1983; Gold and Sutton, 1986; Thornton *et al.*, 1984). As pointed out by Tait (1987) and Webster (1987) these prescriptive approaches ignore the danger of further bias when a farmer superimposes his risk attitude upon the recommendation. Thus, a consultative rather than a prescriptive approach to decision support is called for.

The purpose of this Chapter is to present a framework to support decisions on chemical pest control in an environment of uncertainty. The framework provides information to assess the consequences of alternative pest control decisions with regard to the objectives of control. The objectives of pest control are defined in terms of return on expenditure and insurance. The degree to which these objectives are met is calculated for different pest control strategies using a simulation model of the pathosystem dynamics. The framework will be illustrated with chemical control in the multiple pathosystem aphids and brown rust in winter wheat, the dynamics of which were investigated in Chapters 5 and 6.

## A framework to support decisions on chemical control under uncertainty

As in any decision problem, four constituents can be distinguished in decisions on chemical control: objectives, strategies, system model, and selection criteria (Figure 7.1). Objectives reflect the decision maker's management goals, while strategies represent the means available to achieve the objectives. Here, a strategy is equivalent to a series of decisions on chemical control made in consecutive decision periods of fixed or variable length. Together, the decision periods constitute the planning horizon. Only the first decision of a strategy is implemented each time a decision has to be made, i.e. the problem is solved with rolling planning horizon. The system model predicts the outcome of the system as a function of the strategies. In decision support systems, a system model is usually a mathematical model of crop and pest growth and development and their interactions, based on empirical research. In addition to strategies, the system model requires inputs: the initial state of the system, weather forecasts, and parameters. The system model can supply information on various aspects of the system. However, the objectives determine which model outputs represent relevant characteristics of the performance of a strategy. Per strategy more than one characteristic may be considered. Usually costs associated with a strategy are a major performance characteristic. These costs comprise the financial equivalent of yield reduction caused by pests, plus the costs of eventual chemical pest control. Finally, selection criteria are applied

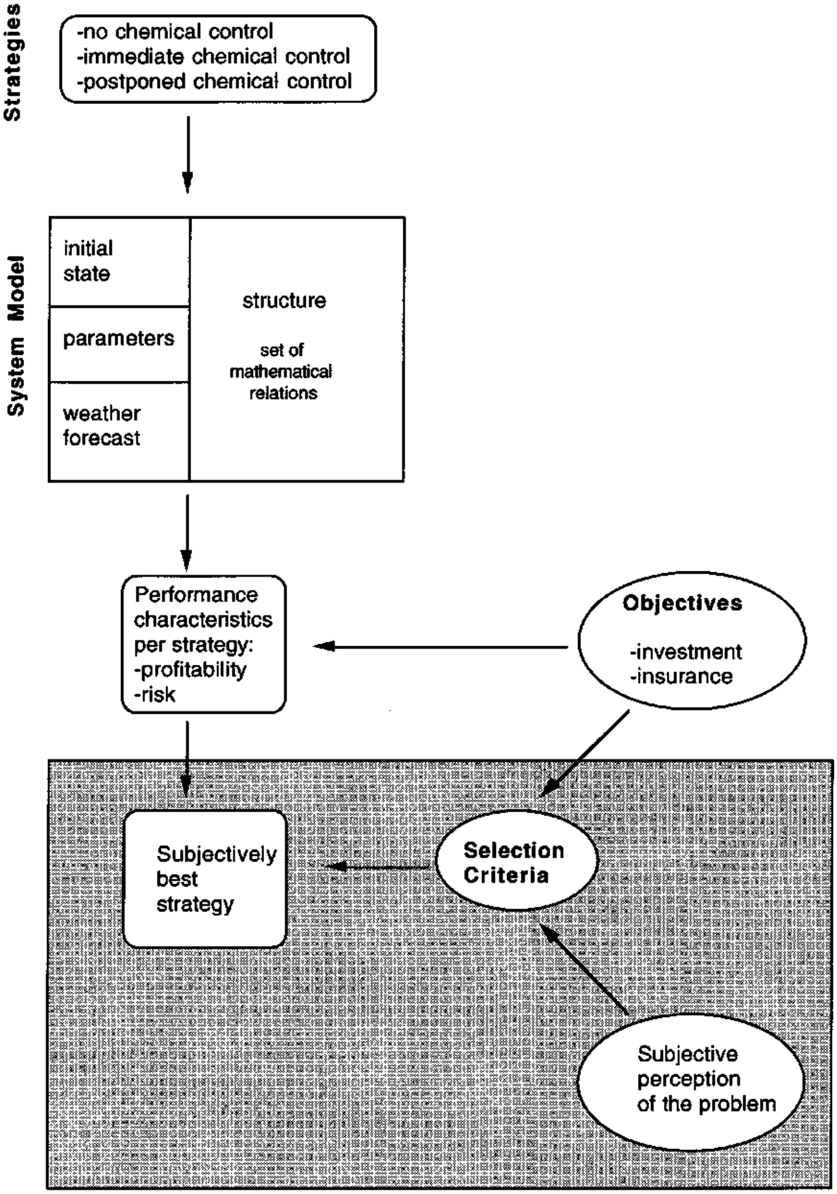


Figure 7.1. Schematic representation of a decision problem. Subjective aspects of the decision problem are shaded, and are not considered within the decision support framework.

which relate the performance of the various strategies to both the objectives of the decision maker as well as the decision maker's subjective perception of the problem. The selection criteria constitute the means of choosing the subjectively best strategy.

Usually, the costs associated with a strategy are not known with certainty at the time a decision has to be made. Uncertainty about costs is caused by uncertainty about the current state of the system, about the values of the parameters in the system model, and about exogenous factors, such as future temperature. Using empirical data in combination with statistical techniques, uncertainty about the system can be quantified in the system model, and the frequency distribution of costs associated with a strategy can be calculated.

Two components can be distinguished in objectives of pest control under uncertainty (Norton and Mumford, 1983): investment and insurance. When concern is primarily about positive returns on expenditure, the *investment* component of pest control is stressed, whereas when concern is predominantly about avoiding excessive costs, the *insurance* component of pest control is emphasized. In this Chapter, profitability and risk are proposed as operational interpretations of these general objectives of pest control. To assess the degree to which the investment component is met, the *profitability* of one strategy compared to another is calculated. In this study, the profitability of strategy *A* compared to strategy *B* is defined as the probability, expressed as percentage, that strategy *A* results in lower costs than strategy *B*. This requires evaluation of the frequency distribution of the difference between the costs associated with the two strategies. To assess the degree to which the insurance component is met, the *risk* of a strategy is calculated. Here, the risk of a strategy is defined as the value of costs which is surpassed with an arbitrarily chosen probability of at most 10%, or, the 0.90 quantile. Quantification of risk requires evaluation of the frequency distribution of costs associated with a particular strategy.

The priority given to investment or insurance appears to vary between farmers, and, for one farmer, between years. Thus, the actual choice of the optimal pest control strategy is based on selection criteria in which subjective weights are attached to profitability and risk. Application of subjective selection criteria is outside the scope of this consultative framework, with one exception: the selection criterion associated with risk-neutral behaviour. Risk-neutral decision makers prefer the strategy with the largest expected return (Anderson, 1977), or, in the case of crop protection, the smallest expected costs. Extremely large costs and extremely low costs are valued similarly. The selection criterion associated with risk-neutrality provides a reference, or "yardstick", to interpret the levels of profitability and risk, and is included in the decision support framework.

The framework will be illustrated using the multiple pathosystem of aphids and brown rust in winter wheat as an example.

Chapter 7

# An example: supervised control of aphids and brown rust in winter wheat

## Description of the system

The multiple pathosystem to be managed comprises an insect pest, aphids, and a fungal disease, brown rust, in a winter wheat field in the Netherlands of 5 to 10 ha. Aphids (especially *Sitobion avenae*, but also *Metopolophium dirhodum* and to a lesser extent *Rhopalosiphum padi*), and brown rust (*Puccinia recondita*) are frequently occurring growth reducing factors in winter wheat in the Netherlands. Averaged over 1974 to 1986, 80 and 50% of the commercial Dutch wheat fields were infested by aphids and infected by brown rust, respectively.

The aphids leave their winter hosts and migrate to the crops during early June, coinciding with crop development stages ear emergence (DC 55, Zadoks *et al.*, 1974) to early flowering (DC 61). Growing in an approximately exponential fashion the population goes through two or more generations on wheat before it collapses. The peak density often coincides with the mid milky ripe stage (DC 75) (Carter *et al.*, 1982). Damage can be as high as 2000 kg $ha^{-1}$ (Chapter 4). Good selective pesticides are available for aphid control.

Spores of brown rust may infect wheat plants. Fruiting bodies (sori) develop in infected tissue and produce new spores which are dispersed by wind. Infection of winter wheat may occur after emergence in autumn. Growth and reproduction of brown rust are favoured by temperatures between 15 °C and 20 °C, combined with periods of leaf wetness. In the Netherlands these conditions are often met in summer. As a result, brown rust epidemics frequently coincide with aphid outbreaks in June and July. Brown rust sori die when wheat leaves die, causing the population increase to stop around dough ripeness (DC 83). Brown rust can cause yield reductions up to 50% (Daamen, 1991a). The fungicides currently registered delay the growth of the population for 2-3 weeks without killing brown rust sori.

## The decision support framework

The consequences of different strategies on chemical control of aphids and/or brown rust are evaluated in terms of profitability and risk, using the system model developed in Chapter 5. This model simulates crop development, and aphid and brown rust population growth and damage in a winter wheat field in the Netherlands, with time steps of one day. System behaviour is described from ear emergence (DC 55) to dough ripeness (DC 83), i.e. approximately early June till late July. Exogenous variables comprise the current state of the system, the predicted average daily temperature, and the chemical control strategy. The current state of the system is described by the temperature sum accumulated since the day the crop attained the stage of pseudo-stem elongation (DC 30), and the initial aphid and brown rust incidences. A strategy comprises a series of decisions on chemical control of aphids and/or brown rust during consecutive decision periods of one week. Decisions are made on the first day of each period. Costs associated with a particular strategy, a major model outcome, comprise the cost of aphid and brown rust damage plus the cost of eventual chemical control. Costs of control of different combinations of target species are described in Chapter 5, Table 5.4. Return on grain yield is 0.40 Dfl $kg^{-1}$.

The structure of the model is based on part of EPIPRE, a computer-based advisory system for aphid and disease control in winter wheat (Drenth *et al.*, 1989; Zadoks, 1989a; Daamen, 1991b). Since this system has been tested extensively (Reinink, 1986; Drenth *et al.*, 1989), the system model is assumed valid.

During construction of the model special attention was given to quantification of uncertainty in various components of the model (Chapter 5). A summary of these components and their uncertainty was given in Chapter 6, Table 6.1.

The system model is used to calculate profitability and risk of relevant strategies at different initial states of the system. Each time a decision is to be made, three strategies can be pursued: no control at all (NS), chemical control at the start of the first decision period (S1), or chemical control at the start of one or more later decision periods. Preliminary analysis showed that postponing chemical control causes profitability to decline and risk to increase, compared to immediate chemical control. Thus, whatever the subjective selection criteria, a rational decision maker (*sensu* Tait, 1987) who aims at maximizing profitability and minimizing risk, will never decide to carry out chemical control at a predetermined point in time in the future. A farmer will decide to spray either immediately, or not at all. Postponing chemical control is therefore not a relevant strategy. The decision problem reduces to deciding whether at a given initial state of the system no control results in an acceptable combination of profitability and risk. If this is not the case, immediate chemical control is the better decision alternative. This decision process is repeated each time a decision is to be made (rolling planning horizon).

The consequences of relevant strategies on chemical control in single pathosystems of either aphids or brown rust, and in the multiple pathosystems of both aphids and brown rust are explored in terms of profitability and risk. Profitability and risk are represented graphically in nomograms in which two independent variables, initial aphid or brown rust incidence and initial temperature sum since crop development stage pseudo-stem elongation, describe the initial state of the system. The line representing the damage thresholds for risk-neutral decisions is included as a reference. Decision makers who accept initial states of the system above this line and do not decide to spray, are considered risk-accepting. Those deciding to spray immediately at initial states below the risk-neutral line are considered risk-averse.

### Implementation

The frequency distribution of costs associated with a strategy is calculated in a Monte Carlo approach in which *M* realizations of costs are generated by stratified sampling from the multivariate input distribution. Details are given in Chapter 5. By storing the sample from the input distribution the frequency distribution of costs of different strategies can be calculated under identical conditions. The profitability of strategy *A* over strategy *B* is assessed by tallying the fraction of the *M* cases in which strategy *A* results in smaller costs than strategy *B*. The risks associated with strategies *A* and *B* are estimated as the 0.90 quantiles of their respective frequency distributions of costs.

The number of Monte Carlo simulations *M* represents a compromise between the precision of the estimated probability distribution of costs and the computational effort. Here, $M$=500 is used which was found to produce estimates of the probability density function similar to a procedure with simple random sampling and 3000 Monte Carlo runs (Chapter 5).

For each nomogram profitability and risk is calculated for a grid consisting of a combination of 18 different initial incidences of aphids or brown rust, and 10 different values of initial temperature sum. Contour plots with iso-profitability lines and iso-risk lines are constructed by smoothing the grid points using a smoothing matrix to average the nearest neighbours (Golden Software, 1989).

At each initial temperature sum evaluated, the stochastic damage threshold is estimated as the smallest initial incidence at which the expected costs of immediate chemical control are smaller than the expected costs of no control.

## Results and discussion

### Profitability and risk: Illustration of the approach

The information needed for the construction of the nomograms is illustrated in Figure 7.2 for a single initial state of the system. First, the frequency distribution

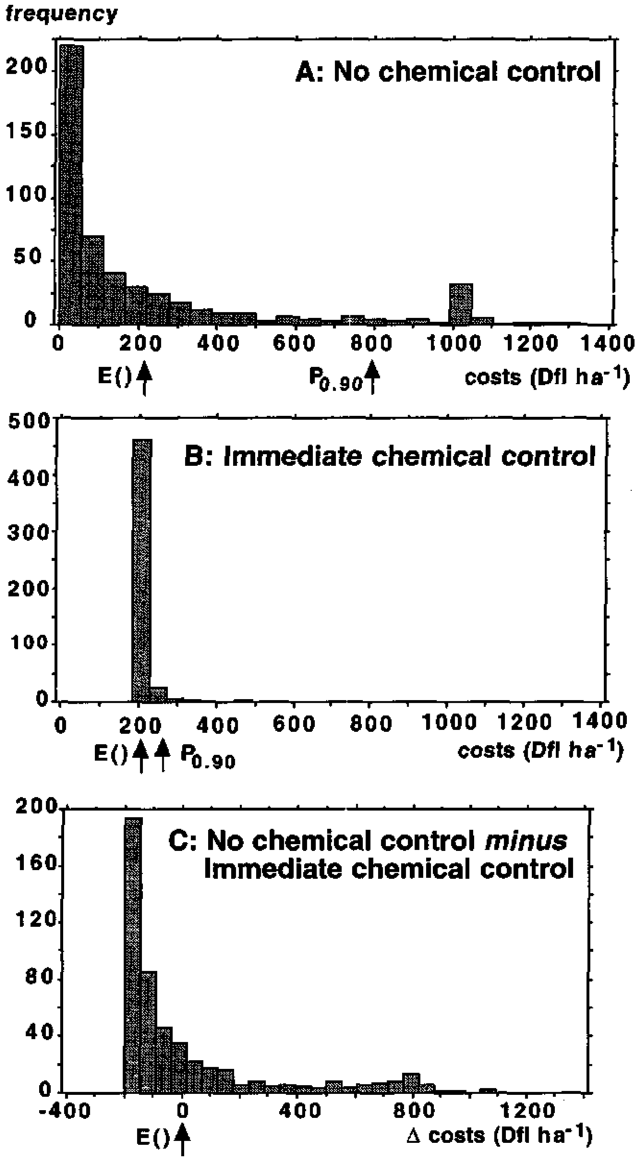


Figure 7.2. Frequency distributions of costs associated with no chemical control (A), immediate chemical control of aphids and brown rust jointly (B), and of the difference in costs between no and immediate chemical control (C) in 500 Monte Carlo runs. Initial state of the system: temperature sum 200 °days, equivalent with DC 58±4 (se), aphid incidence 5%, brown rust incidence 2%. Sample unit for aphids is 100 tillers, for brown rust top four green leaves on 40 tillers. Arrows indicate the 0.90- quantile ($P_{0.90}$) or the expected value ( E() ) of costs (see text for explanation).

of costs resulting from no control at any time (NS) is calculated by Monte Carlo simulation (Figure 7.2a). Next, using the same sample from the input distribution the frequency distribution of costs of immediate chemical control (S1) is calculated, in this example of aphids and brown rust jointly (Figure 7.2b). Risk associated with each strategy is estimated as the 0.90 quantile of the respective frequency distribution. For NS the risk in this example amounts to 796 Dfl ha$^{-1}$, while for S1 the risk is 215 Dfl ha$^{-1}$.The profitability of NS compared to S1 is calculated from the frequency distribution of the difference between costs associated with NS and S1 (Figure 7.2c). Differences in costs are calculated per Monte Carlo run. In this example, the expected value of the difference is approximately 0 Dfl ha$^{-1}$. Thus, the initial state chosen is equivalent to a risk-neutral damage threshold.

Characteristically for decision problems on chemical control, the frequency distribution of the difference between costs associated with NS and S1 has a long right tail (Figure 7.2c), caused by the occasional occurrence of extremely large costs when no control is carried out (Figure 7.2a). This skewed distribution implies that when the expected costs of NS just equal those of S1, i.e. the situation in which a risk-neutral decision maker would just decide to spray immediately, the probability that spraying will be more costly than not spraying is larger than 50%. In this example, the profitability of no control compared to chemical control is approximately 70%. Thus, a risk-neutral decision maker will apply a chemical even before there is a 50/50 chance of positive net return on his investment.

## Profitability and risk: The single pathosystems

The nomograms in Figure 7.3 and Figure 7.4 show the consequences of the strategies NS and the only relevant alternative, S1, in terms of profitability and risk, when aphids and brown rust are considered separately. The profitability of NS compared to S1 decreases as initial incidences of aphids or brown rust increase, and increases with advancing crop development (Figure 7.3a, Figure 7.4a). In contrast, risk increases with increasing initial incidences, and decreases with advancing crop development, both for NS and S1, irrespective of the pest organism involved (Figure 7.3b-c for aphids, and Figure 7.4b-c for brown rust). S1 causes risk to decline compared to NS (Figure 7.3b-c and Figure 7.4b-c). The risk after fungicide application is higher than after aphicide application due to, among others, the fungistatic nature of the fungicides, whereas the aphicide kills part of the population and temporarily arrests the population increase.

Risk-neutral damage thresholds for aphids coincide with a profitability of NS compared to S1 of 70 to 80% (Figure 7.3a), and a risk of 300 to 400 Dfl ha$^{-1}$ when no spray would be carried out (Figure 7.3b). As a result of spraying,

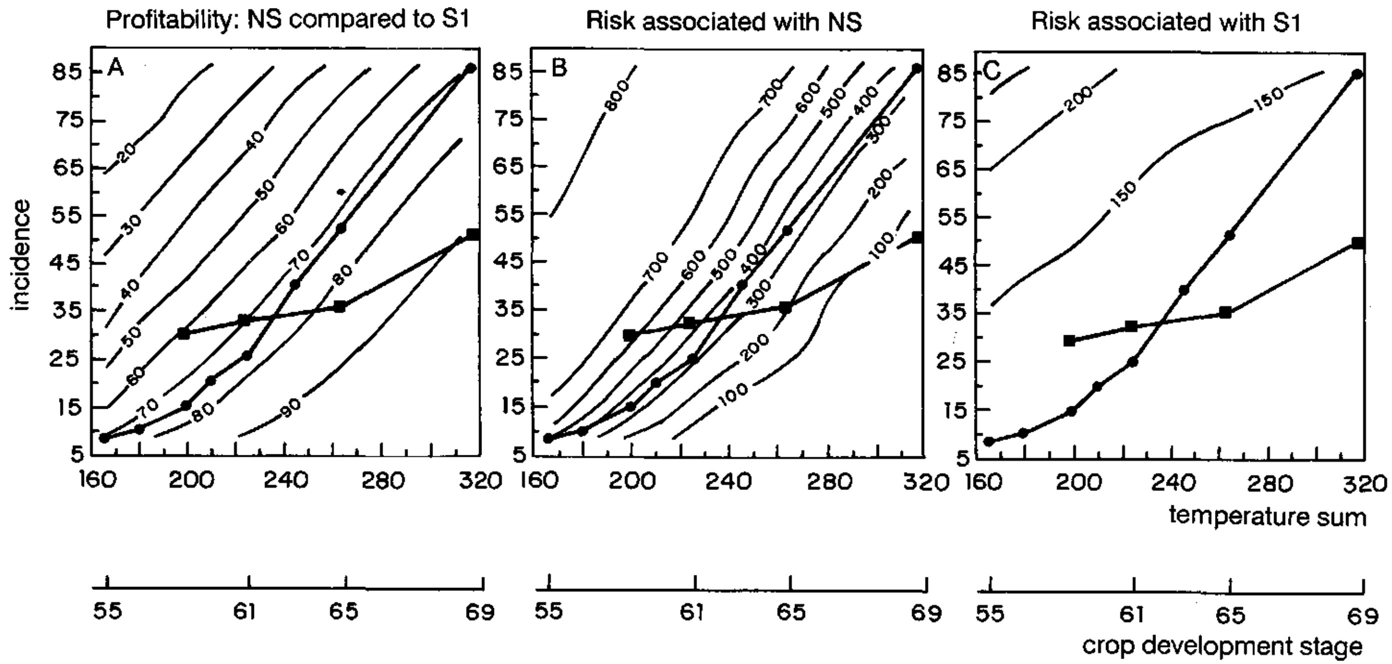


Figure 7.3. Contour plots of the *profitability* of no chemical control compared to immediate chemical control of aphids (A), and the *risk* associated with no chemical control (B) and immediate chemical control of the pest (C), at different initial temperature sums (°day) or equivalent crop development stages (DC), and aphid incidences (%). Sample unit is 100 tillers. Brown rust is absent. Profitability (%) and risk (Dfl ha$^{-1}$) is indicated in the contour lines. Also indicated are the risk-neutral damage thresholds (—●—) and the damage thresholds used in EPIPRE (—■—).

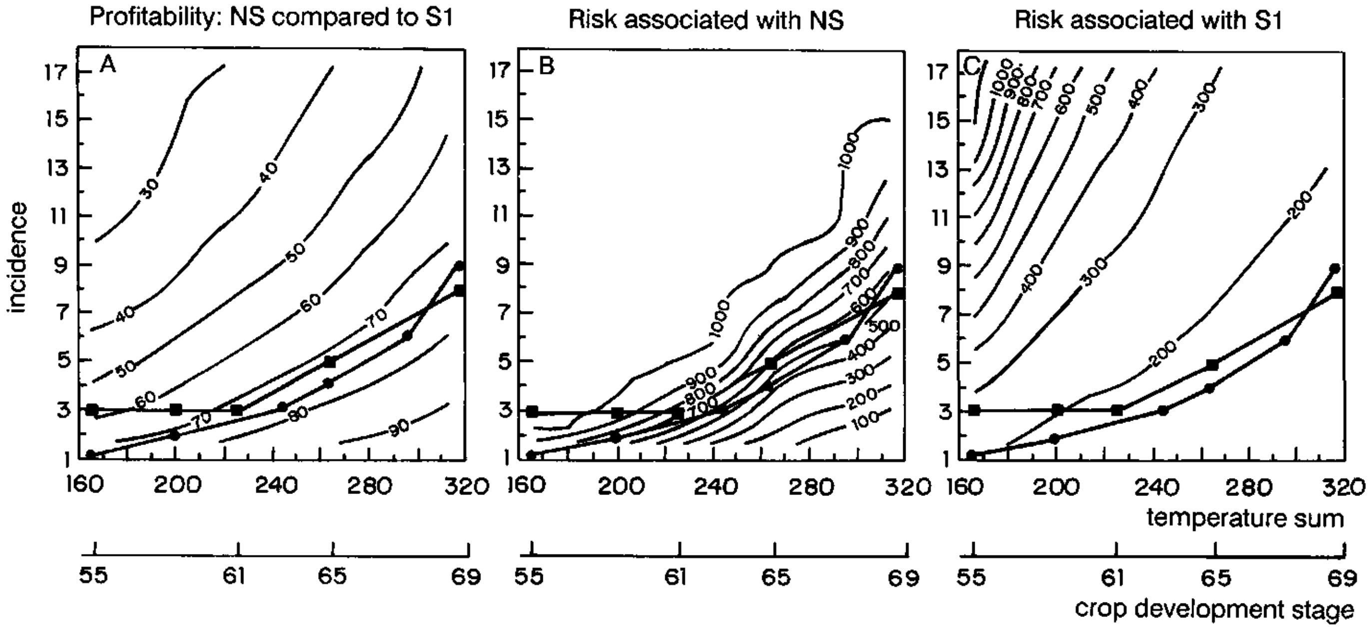


Figure 7.4. Contour plots of the *profitability* of no chemical control compared to immediate chemical control of brown rust (A), and the *risk* associated with no chemical control (B) and immediate chemical control of the disease (C), at different initial temperature sums (°day) or equivalent crop development stages (DC), and brown rust incidences (%). Sample unit is top four green leaves on 40 tillers. Aphids are absent. Profitability (%) and risk (Dfl $ha^{-1}$) is indicated in the contour lines. Also indicated are the risk-neutral damage thresholds (—●—) and the damage thresholds used in EPIPRE (—■—).

risk decreases to 100 to 150 Dfl ha$^{-1}$ (Figure 7.3c). At risk-neutral damage thresholds for brown rust, profitability of NS compared to S1 is similarly 70 to 80% (Figure 7.4a). Risk amounts to 400 to 700 Dfl ha$^{-1}$ when no spray would be carried out (Figure 7.4b). As a result of fungicide application risk decreases to 100 to 200 Dfl ha$^{-1}$ (Figure 7.4c).

At current control practices, represented by the EPIPRE damage thresholds (Drenth and Stol, 1990) in Figure 7.3 and Figure 7.4, S1 is just preferred over NS at levels of profitability of NS compared to S1 which increase with advancing crop development stage from 60% to 90% for aphids (Figure 7.3a), and from 60% to 75% for brown rust (Figure 7.4a). Concomitantly, the levels of risk associated with NS decrease from 600 Dfl ha$^{-1}$ to 100 Dfl ha$^{-1}$ for aphids (Figure 7.3b), and from approximately 1000 Dfl ha$^{-1}$ to 500 Dfl ha$^{-1}$ for brown rust (Figure 7.4b). Apparently in the EPIPRE recommendations, the emphasis put on profitability and investment during the early stages of crop development shifts to risk and insurance as crop development advances.

## Profitability and risk: The multiple pathosystem

Chemical control may concern aphids and brown rust jointly. As an illustration, the profitability of no control compared to immediate control of both pests is shown in Figure 7.5a for an initial aphid infestation of 25%. In all cases the risk-neutral damage thresholds coincide with a profitability of NS compared to S1 of approximately 70%. This level of profitability appears to represent a rather stable value in this system, both for the single pathosystems and for the multiple pathosystem. At the risk-neutral damage thresholds, risk varies between 600 and 800 Dfl ha$^{-1}$ when no spray would be carried out (Figure 7.5b). Immediate application of the aphicide-fungicide mixture reduces risk to 200 to 300 Dfl ha$^{-1}$ (Figure 7.5c).

## Restrictions on strategies: Consequences of postponement of chemical control

The implicit assumption in evaluating immediate chemical control as the only relevant alternative strategy to no control is that chemical control is feasible. However, weather or labour availability may preclude execution of the decision to spray immediately. These sources of uncertainty have not been included in the system model. When immediate chemical control was decided upon, but is not feasible, postponement of chemical control by one decision period is the best alternative strategy. Should postponement have unacceptable consequences, then the likelihood of having to postpone should

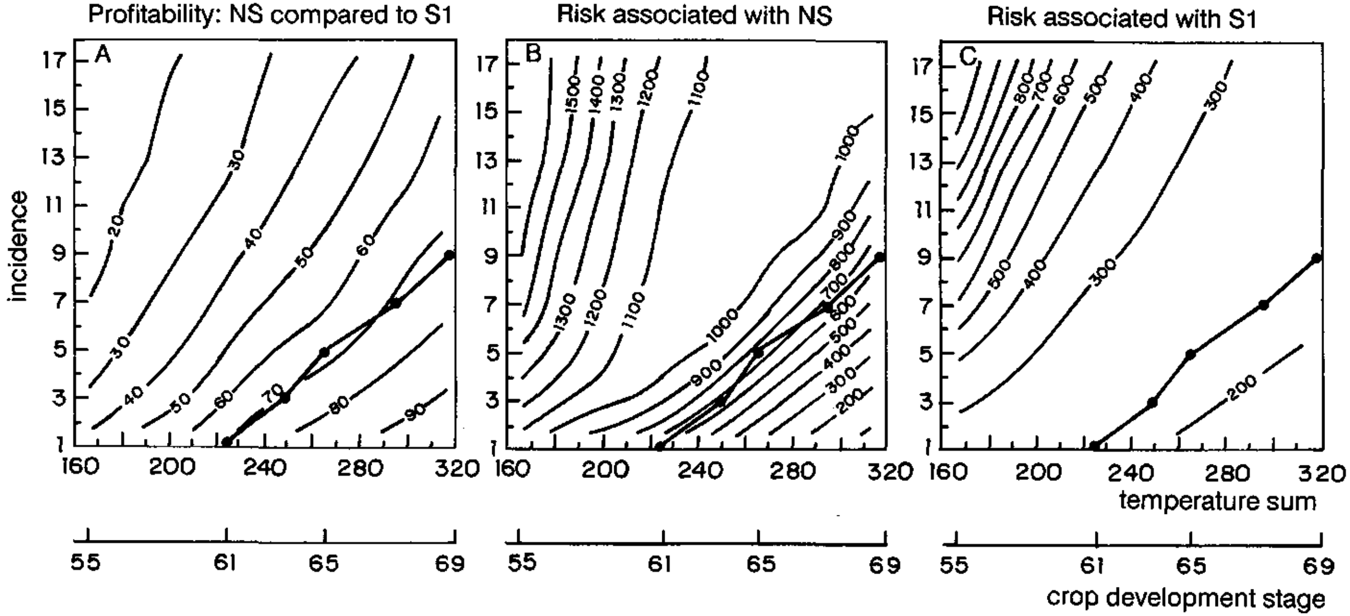


Figure 7.5. Contour plots of the *profitability* of no chemical control compared to immediate chemical control of aphids and brown rust jointly (A), and the *risk* associated with no chemical control (B) and immediate chemical control of both growth reducing factors (C), at different initial temperature sums (°day) or equivalent crop development stages (DC), and brown rust incidences (%), and 25% aphid incidence. Sample unit for aphids is 100 tillers, for brown rust top four top four green leaves on 40 tillers. Profitability (%) and risk (Dfl ha$^{-1}$) is indicated in the contour lines. Also indicated are the risk-neutral damage thresholds (—●—).

be taken into account earlier during the decision process. The system model is used to assess the consequences of postponement in terms of risk and profitability compared to immediate chemical control.

The consequences of postponing chemical control by one week (S2) are evaluated for aphids and brown rust separately. As expected for the second-best strategy the profitability of S2 compared to S1 is low, 3 to 5% for aphids and 30 to 50% for brown rust. The differences in profitability between aphid and brown rust control are caused by the differences in the population dynamics and in the effects of the pesticides.

More interesting in a decision support context is the change in risk. For aphids, risk increases by between 100 and 450 Dfl $ha^{-1}$ after postponing chemical control by one week as compared to immediate chemical control. Near the risk-neutral damage thresholds, however, the increase does not exceed 100 Dfl $ha^{-1}$. For brown rust, postponing chemical control causes risk to increase by 100 Dfl $ha^{-1}$ at most, compared to immediate chemical control.

## General discussion

The decision support framework is based on two premises. First, explicit information on the uncertainty about the outcome of different strategies is assumed relevant to support decisions on chemical control. Second, while decision problems on chemical pest control contain objective as well as subjective elements, only the objective elements should be dealt with in a decision support framework. The premises have led to the exploration of consequences of alternative pest control strategies in terms of objectives which have general economic applicability: return on expenditure and insurance. These objectives have been made operational by defining the profitability of strategy *A* compared to strategy *B*, and the risks of the strategies, respectively. Optimization has been used to calculate risk-neutral damage thresholds, which have served as "yardstick" to interpret the nomograms. Optimization aimed at identifying a single best strategy for a decision maker is not attempted within the decision support framework. Instead of making implicit assumptions about his risk attitude by applying a selection criterion, i.e. taking a prescriptive approach, a consultative approach is adopted in which selection of the subjectively optimal decision is explicitly left to the farmer.

Many pest control decision support systems described in the literature appear to concentrate on optimization. The farmer is presented with recommendations which may even be tailored to his risk attitude (*see* Gold, 1989). Such recommendations are useful only if they reflect an individual farmer's risk perception, and if the farmer carries out the recommendations without further weighing them. Both conditions are not met. The risk attitude of farmers was found to vary considerably between years, and farmers use information from different sources to arrive at a decision (Tait, 1987). Thus, exploration of the consequences of alternatives in terms of generally applicable objectives rather than finding the best decision, seems appropriate to support pest control decision making.

In the aphid - brown rust - winter wheat system, risk-neutral damage thresholds consistently coincide with a profitability of no control compared to immediate chemical control of approximately 70%. Thus, rather counter-intuitively, a risk-neutral decision maker will start spraying when the probability of positive return on expenditure is only 30%. Although the probability value may differ between pathosystems depending upon the uncertainty in the system and the structure of the system model, this result is likely to apply also for other pathosystems, since it hinges on the predicted occurrence of "disasters" when no control is carried out. Uncertainty about costs associated with no control may be decreased in two ways. First, by increasing the knowledge of system dynamics. Earlier uncertainty analysis of the aphid-brown rust-winter wheat system showed that especially better forecasts of the population dynamics of aphids and brown rust are needed (Chapter 6; Daamen and Rabbinge, 1991). Second, use of tolerant varieties and other appropriate crop husbandry practices can avoid large costs without chemical control (Wijnands and Vereijken, 1988; Rabbinge and Zadoks, 1989). Smaller uncertainty about costs associated with no control will lead to higher damage thresholds and less pesticide use.

For aphids the recommendations of EPIPRE have been shown to be slightly risk-accepting at early crop development stages, and strongly risk-averse at the end of the planning period (Figure 7.3). For brown rust the initial slight risk-acceptance changes into risk-neutrality (Figure 7.4). These recommendations reflect expert opinions on uncertainty in the system and on farmers' attitudes towards uncertainty. Government regulations in the Netherlands prohibit application of systemic fungicides at less than 6 weeks before harvest. Thus, at crop development stage DC 69, approximately equivalent to 320 °day, the final decision on control of diseases is made. This may constitute the cause of the increased emphasis on the risk component in the EPIPRE recommendations for brown rust. Although aphids may be sprayed until two weeks before harvest, aphicide is relatively cheap, and farmers tend to tank-mix it with fungicides. Thus, the strong emphasis on the risk component in the EPIPRE aphid recommendations may well reflect an adaptation of the advisory system to correspond with farmers' standard operating procedures.

The number of relevant strategies in the aphid-brown rust-winter wheat system was found to be limited to two: no control at any time, and chemical control at the start of the first decision period only. Because other strategies always resulted in lower profitability and higher risk, it seemed reasonable to exclude these *a priori*. In general, possibilities for reducing the number of strategies depend on the structure of the system model. For example, when the population dynamics of a pest follow a bimodal pattern due to immigration waves (Holt *et al.*, 1987), postponing chemical control to a later point in time is expected to be a relevant strategy. The same may hold for multiple pathosystems when a number of pests infest the crop in sequence.

If sources of uncertainty which are not accounted for in the system model can preclude immediate application of a chemical, the framework can be used to assess the consequences of postponement of the intended control operation in terms of profitability and risk. The disadvantage of such analysis is the increased amount of information which has to be assessed by the decision maker. The number of relevant strategies can be kept to a minimum by including all relevant sources of uncertainty in the system model, when needed using user-specified probabilities, as for the availability of labour during a particular decision period.

In this Chapter profitability and risk of strategies have been summarized in nomograms. For extension purposes other presentation formats may be more appropriate or convenient. When the number of relevant strategies increases above two, the number of nomograms representing profitability and risk soon becomes unwieldy. The computer provides a tool to read from databases, and to present profitability and risk only for the selected initial states of the system, in combination with the risk-neutral damage threshold as a reference. Crop management systems, such as CERA (Meijer and Kamp, 1991) for winter wheat in the Netherlands, can provide a suitable environment for transfer of information, with which a farmer can make his own assessment of the need to apply a pesticide.

## Chapter 8

# General and summarizing discussion

In the preceding Chapters two building blocks for supporting decisions on chemical control of cereal aphids and brown rust in winter wheat were described. In Chapters 2 to 4 a damage relation for the most abundant cereal aphid species was developed, while in Chapters 5 to 7 a framework to support decisions on chemical control of aphids and brown rust in winter wheat under uncertainty was presented. In this Chapter the results are summarized and discussed in relation to the objectives of the study and to information in the literature.

## Scales of decision problems in crop protection

A decision problem involves the selection of decisions which optimally meet the objectives of the decision maker within the prevailing biological and socio-economical constraints. Decision problems may be classified according to their temporal and spatial scales as operational, tactical, strategic or policy-oriented (after Conway, 1984). Policy-oriented decision problems typically concern decisions at the regional, national, or supra-national level, aimed at long-term developments comprising, e.g., five years or more. Examples of policy-oriented decision problems which concern crop protection include the choice of the allowable active ingredients and the acceptable volume of pesticides in the Dutch Multi-Year Term Plan on Crop Protection (MJP-G, 1991), and the hectareage requirement of agriculture in Europe under various objectives with respect to productivity and environment (WRR, 1992).

Strategic, tactical and operational decision problems may apply to similar spatial scales but they have different time scales. At the field level, which is the spatial scale under consideration in this thesis, strategic decisions typically pertain to more than one growing season, while tactical decisions involve decisions within one growing season. Examples of strategic crop protection decisions on the field scale include the choice of cropping sequence and the choice of the market segment, e.g. ecological or conventional produce, bulk or quality (Zadoks, 1989b; Vereijken, 1989). Tactical decisions comprise, for example, the timing of chemical or mechanical control and the type of equipment to be used. Operational decisions pertain to a time scale of one day and are decisions on how to best implement decisions made at the tactical level.

Decisions made at the larger spatial and temporal scales represent constraints for decisions at the smaller scales. The relevance of studying supervised control at the tactical level is derived from a farmer's strategic decision to use pesticides to protect his crop from unacceptable loss, and from the consent to use pesticides at the policy level. However, the approaches presented may be used for supporting decisions in any crop protection practice, whether biological, mechanical, or chemical.

## Mechanisms of damage by *S. avenae* in winter wheat

Experimental work at the process level and in the field (Chapter 2) in combination with a model of post-anthesis growth and development of winter wheat in which injury by *S. avenae* was accounted for (Chapter 3) showed damage to be largely explained by two damage mechanisms. The first *mechanism, assimilate consumption, constitutes the major cause of damage* when population density is high and crop development is advanced. The decline of the net rate of leaf photosynthesis due to honeydew contamination, the second damage mechanism, constitutes the major cause of damage when honeydew is deposited relatively early during crop development, i.e. around flowering, in sufficiently large quantities. As deposited honeydew persists on leaves, damage increases with time. The time dependence of honeydew damage causes *crop development stage to be an important component of a* simple relation between infestation intensity and damage. Further analysis of the system with the simulation model (Chapter 4) showed that, between early flowering (DC 60) and early milky ripe (DC 73), damage per aphid per day increases with attainable yield as a result of a larger fraction of honeydew being intercepted by leaf area. Thus, in addition to crop development stage, attainable yield is considered an important variable in a simple damage relation.

The simulation model of post-anthesis growth and development of winter wheat, into which the two damage mechanisms of the grain aphid were incorporated, represents a complex hypothesis which was tested in two ways. A detailed test of the model involved comparison of simulated and measured values of a number of state variables (Chapter 3). This test requires a large amount of input data and was carried out for one year and two locations, for the high attainable yield levels only. Further evaluation of the model at this level of detail is therefore desirable. A second, cruder, test of the model involved comparison of predicted total damage with measured damage caused by natural infestations of *S. avenae* in a large number of field experiments (Chapter 4). To minimize the input requirements of the model, the simulation results were summarized by regression, using crop development stage and attainable yield as independent variables. The performance of this simple simulation-based damage model was found to be as good as the best empirical model, thus corroborating the hypothesis on grain aphid damage.

## Damage and attainable yield

The simulation model enables analysis of the relation between damage per aphid per day and attainable yield. Between DC 60 and DC 73 damage per aphid per day increases approximately linearly with attainable yield. At attainable yields exceeding 9000 kg ha$^{-1}$ damage per aphid per day exceeds this trend, resulting in a superproportional damage relation *sensu* Rabbinge (1986). After DC 73 damage per aphid per day is proportional to attainable yield over the whole range of attainable yields evaluated. Therefore, whether total damage caused by a grain aphid infestation shows a superproportional or a proportional relation to attainable yield depends on the timing, the size and the duration of the infestation. This may explain why the superproportional damage relation postulated by Rabbinge *et al.* (1983) was not found in field experiments carried out in the UK (Entwistle and Dixon, 1987) or in the dataset described in Chapter 4 (Rossing, unpublished results).

## Honeydew damage and abiotic conditions

Although current understanding of the effect of *S. avenae* on growth and yield of winter wheat appears sufficient for application in a decision support system (Chapter 6), the role of abiotic conditions in the effect of honeydew on leaf photosynthesis is unresolved. Under hot and dry conditions fifteen days after honeydew substitute application, honeydew contamination was found to increase the rate of dark respiration, and decrease the maximum rate of carbon dioxide assimilation at high irradiance, the mesophyll conductance and the leaf nitrogen content. These physiological symptoms, as well as the chlorotic appearance of the leaves, resembled accelerated senescence. Under cool and humid conditions only the initial light use efficiency was decreased fifteen days after treatment with honeydew substitute (Chapter 2). Understanding of the causes of these differences in effect of honeydew on leaf physiology is especially needed to assess the biological control potential of phyllosphere saprophytes which remove honeydew and compete with pathogens under field conditions (Dik, 1990). Their activity, and therewith their potential as biological control agents, depends on abiotic conditions, especially temperature and vapour pressure deficit (Bashi and Fokkema, 1977; Dik, 1990: Chapter 6). Assessment of the costs and benefits of enhancement of naturally occurring populations of phyllosphere saprophytes, therefore, requires more information on both the population dynamics of these organisms and the dynamics of the honeydew substrate as well as the consequences for leaf photosynthesis, in relation to abiotic conditions.

## Damage thresholds and uncertainty

One of the reasons to analyze the effect of uncertainty about model components on model output is that the expected value of the output of the stochastic model differs from the output of the deterministic model because of non-linearity in model relations. Both for aphids and brown rust in winter wheat, uncertainty was found to result in lower risk-neutral damage thresholds, i.e. pest or disease incidences at which the expected costs of control just equal the expected benefits (Chapter 5). Such lack of "certainty equivalent" was also found in studies of uncertainty in other pathosystems (review by Pannell, 1991). Depending on the structure of the model, i.e. convex or concave, both decreases and increases in risk-neutral damage thresholds may occur, as compared to the deterministic damage thresholds.

The risk-neutral stochastic damage thresholds coincided with a profitability of no chemical control compared to immediate control of 70%. In other words, although immediate chemical control on average will result in lower costs than no chemical control, the probability that immediate chemical control will result in lower costs in a specific case is only 0.30. This low profitability of chemical control is caused by the occasional occurrence of extremely high costs if no chemical control is carried out. Such extremely high costs in the absence of chemical control can be avoided by increasing the knowledge of system behaviour, and by adopting uncertainty-reducing strategic crop management techniques, such as resistant cultivars (review by Dixon, 1987 for aphids; Bonthuis and Ebskamp, 1992), tailoring nitrogen fertilizer rate to the demand of the crop (Kowalski and Visser, 1983; Daamen *et al.*, 1989; Vereijken, 1989) or stimulation of natural enemy activity in the case of aphids (review by Dixon, 1987). Knowledge of system behaviour can be increased using both fundamental information generated by research, and forecasting information, e.g. short-term weather forecasts. Preliminary analysis showed information on the dominant temperature pattern during the first week of the forecasting period (i.e. cool, average and hot) to increase the risk-neutral damage thresholds for aphids and brown rust due to reduction of uncertainty on costs associated with no chemical control (Rossing, unpublished results). Thus, technology and information may replace pesticides as means for keeping the uncertainty about costs at a sufficiently low level.

## Research prioritization and uncertainty

As a result of the large amount of ecological data available on the aphids - brown rust - winter wheat system, a detailed estimation of key relations in this system and their uncertainties could be made. In the literature on uncertainty and risk such comprehensive analyses of pathosystems are rare. Often, only the initial pest density and the efficacy of the pesticide have been considered as sources of uncertainty (Pannell, 1991). Since the effect of interaction between sources of uncertainty in the model is neglected in partial uncertainty analyses, the results should be interpreted with caution. In the literature, quantification of uncertainty is commonly based on *guesstimates* rather than on statistical analysis of empirical observations on the spatial scale of interest. To be useful for supporting decisions on a field scale under uncertainty, field data should be used to quantify uncertainty about parameter estimates and white noise. Uncertainty about future temperature or other weather variables also may be quantified statistically in "weather generators". Alternatively, historic weather data may be used, if available. In some instances, a purely theoretical approach to uncertainty is possible without reference to field data, as was shown for the incidence sample estimates, where uncertainty was described by a binomial distribution (Chapter 5).

The description of the various sources of uncertainty in the decision model allowed estimation of the uncertainty about the major model output: costs associated with a chemical control strategy (Chapter 5). A logical next step concerned the ranking of the various components of uncertainty according to their contribution to model output (Chapter 6). The relative importance of the various components was assessed using a novel approach which was developed in a parallel study by Jansen *et al.* (1993). This approach overcomes drawbacks of conventional methods of uncertainty analysis (reviewed by Downing *et al.*, 1985; Beck, 1987; Janssen *et al.*, 1990), at the expense of more computations. The results of the uncertainty analysis indicate that new concepts for describing population growth are needed most, rather than new experiments to determine parameters more accurately.

From the various methods used throughout the thesis a research approach to decision support in crop protection emerges in which uncertainty analysis constitutes a necessary, although generally neglected element. The first step is to adopt a system analytical viewpoint, and identify state variables in the pathosystem which are hypothesized to be of major importance in explaining variation in damage and costs. Other hypotheses concern the relations between the state variables, and the influence of the environment on these relations. Explanatory simulation models represent useful instruments to synthesize quantitative descriptions of such crop ecological and population dynamical processes in a system and to test the hypotheses by comparing model behaviour with field data. Following validation of the simulation models key variables are identified and used to develop "summary models" in which variation in field data is described by regression analysis. The summary models should be fitted to field data to obtain proper estimates of the uncertainty about the relations describing system behaviour (Spitters, 1990). Results of simulation models are less suitable for this purpose, because the variation generated by simulation models depends on the structure of the model which is designed to represent average system behaviour and does not necessarily reflect variation within a field. The summary models are collated in a decision model which provides a basis for decision support. Uncertainty analysis and other tools from the field of operations research are used to assess the necessity of further research in relation to the objectives of the study, and to evaluate the riskiness of various relevant management strategies (*see* also Rabbinge and Rossing, 1987; Rossing 1988).

## Damage thresholds and risk

The dominant paradigm for risk analysis in agricultural economics has been maximization of expected utility (Anderson, 1977; Gold, 1989; Pannell, 1991). The decision maker's perception of risk is described by a mathematical function which relates the various possible outcomes of a decision to utility, a dimensionless quantity which expresses the preference of an individual decision maker to each outcome. Rational decision makers are assumed to prefer the decision which maximizes their expected utility, and decision support is aimed at providing a farmer with this tailor-made, optimal decision.

An alternative approach to risk in agricultural economics concerns the distinction of sets of decision alternatives which meet certain stochastic dominance criteria (e.g. Moffitt *et al.*, 1983). Similar to utility, stochastic dominance criteria presumably represent an individual decision maker's perception of risk concerning a crop protection decision.

Entomologists and phytopathologists have dealt with uncertainty by using stochastic dynamic programming (for instance, Shoemaker and Onstad, 1983) or simulation to minimize expected costs or maximize expected profit. These optimality criteria imply that decision makers are risk-neutral.

In operational supervised control systems damage thresholds commonly appear to be calculated with deterministic models, and are adjusted downward to account for uncertainty and presumed risk aversion of the farmer clientele (Daamen, 1981; Plant, 1986; Mann and Wratten, 1989).

These approaches to support tactical decision making developed by both agricultural economists and agricultural ecologists are *prescriptive*, i.e. they expect a farmer to follow up on the recommendation as this was made to fit his or her personal risk perception. In accordance with this perspective, uncertainty and risk are commonly used as synonyms. As pointed out by Tait (1987) and Webster (1987) unconditional implementation of recommendations by farmers is highly unlikely. Instead, farmers appear to collect information from different sources which is weighed using subjective factors to arrive at a decision. Therefore, Tait (1987) advocates the use of decision support systems by which a farmer is presented with relevant objective information to arrive at a decision. The framework in Chapter 7, which has been termed *consultative* as opposed to prescriptive, has been developed on the basis of such considerations. It presents information on two presumably relevant aspects of *uncertainty about the monetary consequences of a decision*, while leaving the choice of the optimal decision to the farmer.

Description of a farmer's risk perception is useful, and utility, stochastic dominance or other approaches may provide suitable measures of risk perception when farmers constitute part of the system to be managed. Such decision problems occur at spatial scales above the field or even farm level, and are policy-oriented or strategic. An example of such a decision problem is given by Smidts (1990). He analyzed risk perceptions of Dutch potato farmers with respect to marketing of ware potatoes in terms of relative utility. The results may be used by wholesale companies to develop portfolios of selling-options, to accommodate farmers in different categories of risk perception. Utility was not used as the selection criterion, as it would be in tactical decision support, but as a variable which describes a component of the system.

## Perspective

The study reported in this thesis has resulted in increased understanding of the relative importance of the various mechanisms of damage by *S. avenae* and a framework for supporting decisions on chemical control of aphids and brown rust. Although the results pertain to aphids and brown rust in winter wheat, the approach can be applied to both other pathosystems and other means of tactical crop protection, such as biological or mechanical control. Systems analysis and explanatory simulation models have already proven their usefulness for understanding damage by growth reducing factors (*see* overview in Chapter 3). The approaches described in this thesis for supporting decision making under uncertainty and for targeting research are novel. They seem especially promising for application to decision support in biological control where uncertainty about the outcome of a control strategy is particularly important.

The studies on damage by *S. avenae* and on uncertainty in the decision model for aphid and brown rust control both aimed at improving decision making by wheat growers. To achieve this goal a number of aspects deserve further attention. To reinforce understanding of the damage relation of *S. avenae* further testing of the explanatory simulation model at different locations is to be carried out. The necessity of refining the relation between abiotic conditions and the effects of honeydew on leaf photosynthesis should be determined in relation to manipulation of phyllosphere saprophytes as biological control agents.

The relevance of the concepts "profitability" and "risk" (Chapter 7) for decision support should be evaluated. Further analysis should also clarify whether additional sources of uncertainty need to be distinguished, such as availability of labour or accessibility of a field for a spraying operation. The existing organizational infrastructure for evaluating crop management systems with the aid of user-panels (Meijer and Kamp, 1991) provides a framework for such analysis. The analysis in Chapter 7 showed that, on average, pesticide use per unit area can be decreased by decreasing the uncertainty about the no control decision alternative. Information on the contribution of various strategic and tactical choices to uncertainty about yield loss is urgently needed. For this purpose, evaluation of the effect of cultivar choice, timing and rate of fertilizer application, and use of short-term weather forecasts on uncertainty about yield loss should be carried out. By synthesizing the information in consultative decision support systems the scope for substituting pesticides by strategic and tactical crop husbandry decisions can be shown to both farmers and policy makers.

# Samenvatting

Bij geleide bestrijding van ziekten en plagen in landbouwgewassen wordt een afweging gemaakt van de kosten en de baten van toepassing van een pesticide, ter ondersteuning van beslissingen over chemische bestrijding door telers. Hiertoe wordt informatie over de actuele aantasting gecombineerd met kennis over het toekomstig verloop van de aantasting en de daarmee gepaard gaande schade bij verschillende strategieën van bestrijding. Informatie over de actuele aantasting wordt verzameld door telers. Kennis over populatieverloop en schade is afkomstig van onderzoek. Sinds 1978 is het adviessysteem EPIPRE operationeel ten behoeve van geleide bestrijding van ziekten en bladluizen in wintertarwe. Het systeem wordt jaarlijks aangepast aan vigerende prijzen en toegelaten effectieve bestrijdingsmiddelen. Daarnaast wordt onderzoek verricht ten behoeve van meer fundamentele verbetering van het systeem. In dat kader wordt in dit proefschrift aandacht besteed aan (1) de kwantitatieve achtergronden van schade door de doorgaans meest abundante soort bladluizen, *Sitobion avenae*, en (2) ondersteuning van beslissingen tegen de achtergrond van onzekerheid en risico.

De graanluis, *S. avenae,* veroorzaakt direkte schade door onttrekking van assimilaten en indirekte schade door verlaging van de netto-fotosynthese van bladeren waarop honingdauw terecht is gekomen. Daarnaast kan schade optreden na overdracht van het gerstevergelingsvirus. Dit laatste schademechanisme speelt geen rol bij de hier beschouwde aantastingen vanaf de bloei. Het direkte en het indirekte effect van de graanluis werd gekwantificeerd aan de hand van literatuurgegevens en geïntroduceerd in een gewasgroeimodel. Dit model simuleert groei en ontwikkeling van wintertarwe vanaf bloei op basis van kwantitatieve beschrijving van de lichtverdeling in het gewas, bladfotosynthese, respiratie en verdeling van droge stof en stikstof, als funktie van temperatuur, straling en de beschikbare hoeveelheid stikstof in de bodem. Analyse van de uitkomsten van het model wees uit dat onzekerheid over de omvang van de indirekte effecten een groot effect had op de gesimuleerde schade. Dit gaf aanleiding tot experimenten waarin het effect van een substituut-honingdauw oplossing op de fotosynthese van vlagbladeren werd gemeten op één, drie en vijftien dagen na opbrenging (Hoofdstuk 2). Eén dag na behandeling was de respiratie verhoogd, terwijl na drie dagen geen effecten meer waar te nemen waren. Vijftien dagen na behandeling leken de effecten af te hangen van de temperatuur en de vochtigheid tijdens de proef. Onder warme en droge omstandigheden werd een verhoging van de respiratie waargenomen, gecombineerd met een verlaging van de fotosynthese bij lichtverzadiging, de geleidbaarheid van het mesofyl en het stikstofgehalte van het blad. Deze effecten werden toegeschreven aan honingdauw. Bij gematigde temperaturen en hoge luchtvochtigheid werd een verlaging van de initiële efficiëntie van lichtbenutting gemeten. Deze resultaten werden toegeschreven aan een combinatie van honingdauw en door honingdauw gestimuleerde saprofytische bladschimmels. In het simulatiemodel werd de beschrijving van de indirekte schade door de graanluis geparametriseerd op basis van de resultaten voor honingdauw onder droge en warme omstandigheden.

Het model werd getoetst door vergelijking van gesimuleerde en gemeten waarden van relevante toestandsvariabelen (Hoofdstuk 3). Voor toetsing van het gewasgroeimodel werd gebruik gemaakt van gegevens van proeven met verschillende niveaus van stikstofbemesting, resulterend in bereikbare opbrengsten tussen 4 en 9 ton graan (droge stof) per hectare. Gesimuleerde en gemeten waarden voor drooggewichten van blad en korrels en hoeveelheid bladstikstof vertoonden een acceptabele mate van overeenstemming gedurende het grootste deel van de periode na bloei. Aan het einde van het groeiseizoen trad over- of onderschatting van het korrelgewicht op, met name veroorzaakt door onvolledig begrip van processen van bladafsterving. Voor toetsing van het gewas-beschadigingsmodel werd een veldproef uitgevoerd bij hoge stikstofbemesting waarin bladluisaantastingen van verschillende intensiteit werden gecreëerd (Hoofdstuk 2). De gesimuleerde waarden voor drooggewichten van blad en korrels en de hoeveelheid bladstikstof waren goed in overeenstemming met de gemeten waarden als werd aangenomen dat opname van assimilaten door de bladluizen geen effect heeft op de snelheid van aanvoer van assimilaten en volledig ten koste gaat van de korrelvulling. Alternatieve beschrijving van de indirekte schade op basis van de gemeten effecten bij vochtige en koele omstandigheden leidde tot geringe veranderingen in de gesimuleerde resultaten. Toetsing van het gewas-beschadigingsmodel bij lage niveaus van stikstofbemesting is wenselijk. Daarnaast behoeft de beschrijving van de afsterving van blad bij lage stikstofgehalten en de relatie tussen weersvariabelen en (middel)lange-termijn effecten van honingdauw op bladfotosynthese nadere aandacht.

Uit de gevoeligheidsanalyse bleek dat schade, uitgedrukt in kg per hectare per bladluis per halm per dag, sterk afhing van het stadium van gewasontwikkeling en van de bereikbare opbrengst. Deze relaties zijn te verklaren uit het relatieve aandeel van direkte en indirekte schade in de totale schade (Hoofdstuk 4). Omdat het effect op bladfotosynthese toeneemt met de tijd, neemt schade door honingdauw af naarmate de honingdauw later op het blad wordt opgebracht. Na stadium "midden melkrijp (DC75) leidt onttrekking van assimilaten tot méér schade, uitgedrukt in kg per hectare per bladluis per halm per dag, dan verlaging van de bladfotosynthese door honingdauw. Schade door honingdauw neemt toe met het niveau van stikstofbemestig daar hoge bemestingsniveaus samengaan met een groter honingdauw onderscheppend bladapparaat.

De resultaten van het simulatiemodel werden samengevat in regressiemodellen. Uitgaande van een gestandaardiseerde aantasting door *S. avenae* zowel over het hele groeiseizoen ('single point model') als per periode van gewasontwikkeling ('multiple point model'), werd de gesimuleerde schade, uitgedrukt in kg per hectare per bladluis per halm per dag, gerelateerd aan de haalbare opbrengst. De mate waarin deze op simulatie gebaseerde regressiemodellen in staat zijn schade te voorspellen bij gegeven aantasting werd beoordeeld door vergelijking van voorspellingen met gegevens van 21 veldproeven uitgevoerd in Nederland tussen 1973 en 1984. Zowel wat betreft systematische afwijking als wat betreft de absolute afwijking van de metingen bleken de op simulatie gebaseerde regressiemodellen vergelijkbaar met de beste van vier gepubliceerde schaderelaties. Hierbij vertoonde het multiple point model minder systematische afwijking dan het single point model. De absolute afwijking van het single point model was echter, zowel wat betreft mediaan als wat betreft 75% percentiel, kleiner.

In het tweede deel van het proefschrift (hoofdstukken 5, 6 en 7) wordt aandacht besteed aan onzekerheid over de kosten en baten van chemische bestrijding en de gevolgen hiervan voor geleide bestrijding van bladluizen en bruine roest in wintertarwe. Volgens het concept van geleide bestrijding is chemische bestrijding noodzakelijk wanneer de geprojecteerde schade juist de kosten van bestrijding plus de geprojecteerde restschade te boven gaat. De intensiteit van de beschadiger waarbij dit het geval is, de schadedrempel, wordt berekend met een mathematisch model. Onzekerheid in onderdelen van het model veroorzaakt onzekerheid over de schadedrempel.

In het algemeen is het van belang onzekerheid over onderdelen van het model in berekeningen te betrekken als de relaties in het model niet-lineair zijn, als de bijdrage van verschillende bronnen van onzekerheid aan de onzekerheid in de modeluitkomst onderwerp van studie is, en als een schatting van risico gevraagd wordt. Deze aspekten komen, toegespitst op het pathosysteem bladluizen - bruine roest - wintertarwe, aan bod in, respectievelijk, de hoofdstukken 5, 6, en 7. Het model waarmee de kosten van verschillende strategieën van chemische bestrijding werden berekend, was een geactualiseerde versie van onderdelen van EPIPRE. De kosten van een bestrijdingsstrategie werden berekend met submodellen van gewasontwikkeling, populatiedynamica van de schadeverwekkers en schade. De initiële temperatuursom, de initiële incidenties bladluizen en bruine roest, en de toekomstige gemiddelde etmaaltemperatuur werden in het model ingevoerd. De berekeningen hadden betrekking op één veld, en op de periode vanaf in de aar komen van het gewas.

In hoofdstuk 5 worden de veranderingen in de berekende schadedrempels beschreven die het gevolg zijn van onzekerheid over onderdelen van het model. Deze onzekerheid werd gekwantificeerd in statistische termen waarbij vier categorieën van onzekerheid werden onderscheiden: parameters, al dan niet als onderdeel van funktionele relaties tussen variabelen, schattingen van de initiële toestand van het systeem, toekomstige minimale en maximale etmaaltemperatuur, en witte ruis. Witte ruis werd verondersteld op te treden als variatie in metingen noch aan bemonstering, noch aan andere co-variabelen kon worden toegeschreven. Witte ruis werd gemodelleerd als een stochastisch proces, met onderling onafhankelijke, identiek normaal verdeelde afwijkingen van de geschatte waarde van de afhankelijke variabele. De tijdschaal van het proces werd bepaald door de tijdschaal in de metingen. Door herhaalde, willekeurige trekkingen uit de kansverdelingen van de verschillende bronnen van variatie en berekening van de kosten ten gevolge van schade en bestrijding (Monte Carlo simulatie), werd de kansverdeling van de kosten behorend bij een bestrijdingsstrategie geschat. De stochastische schadedrempel werd berekend als de incidentie waarbij de *verwachte* toekomstige schade juist groter was dan de *verwachte* kosten van bestrijding plus de restschade. Deze schadedrempel vertegenwoordigt de incidentie van de schadeverwekker waarbij een risico-neutrale beslisser juist zou gaan spuiten.

Uit de berekeningen bleek dat de stochastische schadedrempel lager lag dan de deterministische schadedrempel, welke berekend was op basis van gemiddelde waarden voor de bronnen van onzekerheid. Dit was het gevolg van de lange rechter staart van de kansverdelingen van kosten als geen chemische bestrijding werd uitgevoerd. Bij chemische bestrijding aan het begin van de planningshorizon was de kansverdeling van kosten daarentegen zeer smal. De schadedrempels die gebruikt worden in EPIPRE bleken risico-mijdend gedrag van een teler bij de bestrijding van bladluizen te veronderstellen en, bij benadering, risico-neutraal gedrag bij de bestrijding van bruine roest.

In hoofdstuk 6 wordt de bijdrage van de diverse bronnen van onzekerheid aan de onzekerheid over de modeluitkomst berekend met een aangepaste Monte Carlo procedure. Onzekerheid over de modeluitkomst werd gekarakteriseerd door de variantie van de kosten en werd berekend door

Monte Carlo simulatie. Door herhaalde berekening van de variantie van de modeluitkomst waarbij steeds de realisaties van slechts één bron van onzekerheid werden gewijzigd, kon de bijdrage van iedere bron aan de modelonzekerheid op twee manieren worden bepaald. Ten eerste, door te veronderstellen dat de bron de enige oorzaak van onzekerheid is. Deze benadering is relevant voor bronnen van oncontroleerbare variatie, zoals toekomstige etmaaltemperatuur en witte ruis. Ten tweede, door te veronderstellen dat de bron de enige is waarvan de onzekerheid verdwenen is. Deze benadering is toepasbaar op bronnen van controleerbare variatie. Voorbeelden van dit type variatie zijn parameters en schattingen van de initiële toestand van het systeem.

Voor de meest relevante bestrijdingsstrategieën en initiële toestanden van het systeem werd de onzekerheid over de modeluitkomst voor meer dan de helft veroorzaakt door bronnen van oncontroleerbare variatie. Witte ruis in de relatieve groeisnelheid van zowel bladluizen als bruine roest bleek de belangrijkste bron van variatie. Aanzienlijke vermindering van de onzekerheid over de modeluitkomst vereist derhalve vervanging van de geaggregeerde parameter relatieve groeisnelheid door alternatieve modellen voor de populatiedynamica van de beschadigers.

In hoofdstuk 7 worden de gevolgen van onzekerheid over de kosten van chemische bestrijding voor ziekte- en plaag-management bestudeerd aan de hand van twee uitgangspunten. Ten eerste, informatie over de onzekerheid met betrekking tot de kosten van een bestrijdingsstrategie is relevant voor ondersteuning van beslissingen over chemische bestrijding. Ten tweede, beslissingen over chemische bestrijding worden genomen op basis van subjektieve interpretatie van objektief vast te stellen onzekerheid over de gevolgen van een beslissing, maar slechts de objektieve elementen horen thuis in een adviessysteem. Op grond van deze uitgangspunten werd een kader voor beslissingsondersteuning geschetst waarin bestrijdingsstrategieën werden geëvalueerd in termen van doelstellingen die algemene economische geldigheid hebben: investering en verzekering. Deze doelstellingen werden geoperationaliseerd als het *rendement* van strategie *A* ten opzichte van strategie *B*, gedefinieerd als de kans (in procenten) dat *A* tot lagere kosten leidt dan *B*, en het *risico* van elk van de strategieën, gedefinieerd als het niveau van kosten waar de ware kosten met een kans van 90% onder liggen. Uit analyse van het onderhavige pathosysteem bleek dat alleen géén chemische bestrijding en onmiddellijke chemische bestrijding relevante bestrijdingsstrategieën waren. Voor een groot aantal combinaties van initiële temperatuur en initiële incidenties bladluizen en bruine roest werd vervolgens het rendement van géén bestrijding ten opzichte van onmiddellijk bestrijden uitgerekend, alsmede het risico van beide strategieën, en weergegeven in nomogrammen. De stochastische schadedrempel werd gebruikt als 'meetlat' zodat rendement en risico van een beslissing konden worden afgezet tegen de optimale beslissing vanuit risico-neutraal perspectief. Bij de stochastische schadedrempel bleek het rendement van chemische bestrijding ten opzichte van geen bestrijding bij verschillende stadia van gewasontwikkeling steeds ongeveer 30% te bedragen, zowel voor bladluizen, voor bruine roest, als voor gecombineerde aantasting. Met andere woorden, hoewel onmiddellijke chemische bestrijding gemiddeld leidde tot lagere kosten dan geen bestrijding, was de kans dat chemische bestrijding in een specifiek geval tot lagere kosten zou leiden slechts 0.30. Dit lage rendement van chemische bestrijding bij de stochastische schadedrempel was het gevolg van het met lage kans optreden van extreem hoge kosten bij achterwege laten van bestrijding, terwijl onmiddelijke chemische bestrijding resulteerde in zeer geringe variatie in kosten.

Tenslotte worden in hoofdstuk 8 de resultaten van de studie samengevat en besproken, en wordt ingegaan op het nut van de ontwikkelde benaderingen voor kwantificering van schade, onzekerheid en risico in andere pathosystemen en bij andere methoden van bestrijding van ziekten en plagen.

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# Curriculum vitae

Walter Adelbert Henricus Rossing werd geboren op 28 oktober 1957 te Voorburg. In 1976 behaalde hij het Gymnasium-β diploma aan de R.K. Scholengemeenschap Canisiuscollege - Mater Dei te Nijmegen, en begon een studie Planteziektenkunde aan de Landbouwuniversiteit Wageningen. Hij studeerde in 1984 *cum laude* af op een vakkenpakket bestaande uit Entomologie, Fytopathologie, Optimaliseringtechnieken en Theoretische Teeltkunde. Van 1984 tot 1986 werkte hij als wetenschappelijk assistent bij de vakgroep Theoretische Produktie-ecologie aan het onderwerp "Verbetering van het bestrijdingsmiddelgebruik in wintertarwe". In deze periode werd de basis gelegd voor dit proefschrift. Na een tijdelijke aanstelling als toegevoegd docent bij de vakgroep Fytopathologie waar hij verantwoordelijk was voor de informatisering van de vakgroep, is hij sinds 1988 werkzaam als universitair docent bij de vakgroep Theoretische Produktie-ecologie. In dat kader verzorgt hij onderwijselementen waarin systeemanalyse en simulatie gebruikt worden ter vergroting van kennis over aard en omvang van schade door groeikortende faktoren in gewassen. Onderzoeksprojekten hebben betrekking op mechanismen van schade door stengelboorders en bladziekten in rijst in het kader van het projekt Simulation and Systems Analysis for Rice Production (SARP) in zuid-oost Azië, en op het modelmatig ontwerpen van economisch en ecologisch duurzame produktiesystemen in de bloembollenteelt.