

**Aphids and Thrips:
The Dynamics and Bio-Economics of Cereal Pests**

Hans Larsson

*Faculty of Landscape Planning, Horticulture and Agricultural Science
Department of Crop Science
Alnarp*

**Doctoral thesis
Swedish University of Agricultural Sciences
Alnarp 2005**



Figure 3. Characteristic gooseneck on triticale after *Limothrips denticornis* injury.

Abstract

Larsson, H. 2005. Aphids and thrips: *The dynamics and bio-economics of cereal pests*.
Doctoral dissertation.
ISBN: 91-576-6918-x
ISSN: 1652-6880

The thesis investigates aphids and thrips in cereals - their biology, occurrence, economic damage, migration and control by integrated pest management. Experiments were carried out in all types of cereals in southern Sweden during the period 1978-2003.

The main pest problem in these cereals is the aphid *Sitobion avenae*. It attacks wheat, the most valuable crop and the second in acreage. A crop loss model is presented based on average annual yield loss in field experiments in high yielding varieties. The most serious thrips pests are *Limothrips cerealium* and *L. denticornis*. Other thrips such as *Haplothrips aculeatus*, *Stenothrips graminum*, *Thrips angusticeps* and *Frankliniella tenuicornis* are minor pests not causing serious damage to cereals but occurring practically every year.

Yield loss and economic injury levels were estimated for *S. avenae*, *Rhopalosiphum padi*, *L. denticornis*, *L. cerealium* and *S. graminum*. Grain quality parameters such as protein content, germination rate and mycotoxin concentrations in crops attacked by aphids and thrips were generally not decreased in a way that affected the price of the product.

The compensation ability of cereals against aphids and thrips is considerable, probably because of the high number of tillers and the fact that the pests generally do not directly attack the grains.

Warning and forecasting are essential within integrated pest management, and knowledge about the effect of weather on different pests is important, particularly in southern Sweden where several pests are on the northern limit of their geographical range. Weather is particularly important for *L. cerealium* and *S. avenae*. Investigations on the spatio-temporal dynamics of thrips in cereal crops during a single year revealed that many thrips species interact with acreage of the different cereals grown. The strong flyers, *L. cerealium* and *L. denticornis*, are specialised on cereals and their two generations provide the best possibilities to utilise different crops in the landscape. Populations of grain aphids were kept around a certain number, probably by natural predators, with aphid years followed by low populations, the so-called density dependence. Protection of these natural enemies through reduced application of pesticides in cereals might make the production more sustainable.

Key words: *Sitobion avenae*, *Limothrips denticornis*, *Limothrips cerealium*, yield loss, economic injury levels, critical weather periods, insecticides, natural enemies, pathogens, population dynamics, bio-economics

Author's address: Hans Larsson, Department of Crop Science, SLU, P.O. Box 44, SE-23053 Alnarp, Sweden. E-mail : Hans.Larsson@vv.slu.se

Contents

Introduction	7
Objectives	7
Cereals	7
Insects and pests	7
Pests investigated	8
Aphids	8
Thrips	8
<i>Limothrips cerealium</i>	
<i>Limothrips denticornis</i>	
<i>Haplothrips aculeatus</i>	
<i>Stenothrips graminum</i>	
<i>Thrips angusticeps</i>	
<i>Frankliniella tenuicornis</i>	
<i>Anaphothrips obscurus</i>	
Yield loss assessment	10
Weather influences on insects	10
Natural enemies and diseases	11
Integrated control and integrated pest management	11
Forecasting and prognosis	12
What are dynamics?	13
What are bio-economics?	14
Materials and methods	15
Field experiments with pesticides	15
Assessments of pest numbers and injury	15
Outline of the thesis	17
Results and discussion, survey of Papers I to V	18
The yield loss relationship	18
Economic injury levels	19
Intraspecific competition and interaction between species	22
Quality of grains after infestation	23
Critical weather factors and pests	24
Density dependence	27
The farming system: influence of nitrogen, fungicides, varieties and crop rotation	27
Insecticides	28
Natural enemies and pathogens	29
Spatio-temporal dynamics and forecasting	30
Bio-economics	31
Conclusions and implementations for the future	32
References	33
Acknowledgements	42

Appendix

Papers I-V

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I Larsson, H. 2005. A crop loss model and economic thresholds for the grain aphid *Sitobion avenae* (F.) in winter wheat in southern Sweden. *Crop Protection* 24, 397-405

II Larsson, H. 2005. Economic damage by *Limothrips denticornis* in rye, triticale and winter barley. *J. Appl. Ent.* 129, (7), 386-392

III Larsson, H. 2005. Multiple regression models for weather influence on *Sitobion avenae* populations in winter wheat (submitted)

IV Larsson, H. 2005. Spatio-temporal dynamics of cereal thrips (manuscript)

V Larsson, H. 2005. Natural occurrence of the fungus *Verticillium lecanii* (Zimmerman) Viégas (*Lecanicillum* spp.) on thrips, *Limothrips denticornis* (L.), in rye and the use of the fungus in integrated control (submitted)

Paper I was reprinted with kind permission from Elsevier.

Paper II was reprinted with kind permission of Blackwell Publishing Ltd.

Introduction

Objectives

The studies presented in this thesis had the following specific objectives:

To investigate the yield loss caused by aphids and thrips in cereals

To study the biology and dynamics of cereal thrips

To present economic injury levels and economic thresholds for the different species

To investigate the influence of weather on population dynamics

To evaluate an integrated pest management approach for cereal pests

Cereals

The acreage of cereals varied between 1.5-1.7 M ha in Sweden in the period 1870 to 1980, but since 2000 it has declined to approx. 1.1-1.2 M ha (SCB, 2005). However the distribution has shifted between the different cereals, as wheat, rye, barley, oats and triticale have all had their great periods. Rye was grown on about 850 000 ha between 1870 and 1920, oats on around 1.5 M ha up to 1945, wheat reached its greatest acreage around 1940 with 700 000 ha and barley was grown on about 900 000 ha in 1980 (Morell, 2001; Flygare & Isacson, 2003). The highest acreage of triticale was 45 000 ha. Because of the great acreage cropped with cereals, policies chosen for cereal pest management are of high importance.

Cereals are annual plants and are thereby available for exploitation by pests for only a very short period, particularly spring-sown cereals. The rate at which the pest population increases depends on weather, plant quality, plant resistance and the activity of natural enemies (Dixon, 1989).

Insects and pests

In agronomy, an insect is classified as a pest if the damage it causes to a crop is sufficient to reduce the yield or the quality of the harvested product by an amount that is unacceptable to the farmer (Dent, 2000). Injury is the effect of pest activities on host physiology, which is usually deleterious, while damage is a measurable loss host yield quantity or quality (Pedigo, 1999). Cereals have been important in agriculture ever since Man started to cultivate crops. Simultaneously with crop development, a range of insects and pests belonging to different groups have developed and can attack the various crops. Aphids and thrips are among the most numerous of the attacking insects, although the aphids were not treated with insecticides until the late 1970s and thrips not until the late 1980s. Expected losses from different levels of pest attack were not investigated in detail until the 1980s. The direct effect of cereal aphids on cereal yields were investigated in USA in the early 1960s (Wood, 1965) but in Europe similar investigations were not carried out until 1968, after severe outbreaks of the grain aphid (Fletcher & Bardner, 1969; Kolbe, 1969).

Some authors suggest that the cereal aphid problem has increased because of changes in agricultural practices (Baranyovits, 1972).

Pests investigated

Aphids

Cereal aphids cause direct injury by feeding on plants, but they also transmit barley yellow dwarf virus (BYDV). In Sweden, three species of cereal aphids exist: *Sitobion avenae*, *Rhopalosiphum padi* and *Metopolophium dirhodum*. BYDV is mostly a problem in oats, with the virus transmitted by *R. padi*. In contrast to other parts of Europe, BYDV is not spread in Sweden by *S. avenae* migrating to winter wheat in autumn.

The different species of cereal aphids have life cycles of varying degrees of complexity, e.g. *S. avenae* uses grasses as a single host (autoecious) species. The overwintering eggs are laid on grasses and cereals and there is no migration to a separate winter host plant. In milder climates, the summer form can overwinter successfully on grasses or cereals but that is hardly the case in Sweden. *R. padi* and *M. dirhodum* are host-alternating (heteroecious) species (Carter *et al.*, 1980).

Thrips

Damage by thrips takes the form of white or silvery marks on leaves and ears caused by the cell contents being sucked out. Severe thrips feeding can result in withering of the shoot and shrivelling of the grain (Lewis, 1973). In Sweden, the abundance of thrips species in cereals was first studied by Johansson (1938). He worked with sweep-netting and in wheat he found *Limothrips cerealium*, *Limothrips denticornis*, *Haplothrips aculeatus*, *Thrips* (probably *angusticeps*), *Frankliniella tenuicornis* and *Anaphothrips obscurus*. In southern Sweden, all the above-mentioned types of thrips were found while in central Sweden *F. tenuicornis* dominated, with *H. aculeatus* in second place. *L. cerealium* was not found in central Sweden and *S. graminum* in oats was only found in Scania.

Studies on thrips in Finland were carried out during 1960-1969 by Köppä (1970). He investigated the biology and abundance of the most important species of thrips living on cereals in Finland (*L. denticornis*, *H. aculeatus*, *F. tenuicornis* and *A. obscurus*). In the Netherlands, the cereal thrips species were studied in detail by Franssen & Huisman (1958) and Franssen & Mantel (1963, 1965). Species damaging cereals in the Netherlands included *L. cerealium*, *L. denticornis*, *H. aculeatus*, *S. graminum* and *T. angusticeps*. In Germany, Holtmann (1963) investigated the biology of cereal thrips and found the same species as in the Netherlands. *F. tenuicornis* and *A. obscurus* were found only in small numbers. Later Lattauske & Wetzell (1985) investigated the abundance dynamics of cereal thrips with sweep netting and also systematic sampling of plants. They found *L. cerealium*, *L. denticornis* and *T. angusticeps* dominating in winter wheat, winter rye and winter and summer barley.

Below, the life cycles of the different thrips species found in southern Sweden are briefly described.

Limothrips cerealium

L. cerealium hibernates beneath the bark of trees, in houses, in hollow stems of herbaceous plants, etc. It lives in the ears of cereals. Rye is the most important host plant for the first generation and oats for the second. The most important factor regulating the population density is the winter weather. Winters with the coldest monthly temperature < -1 °C kill the insect (Lewis, 1973).

Limothrips denticornis

The females hibernate in grasses and mosses. It lives in the leaf sheaths of cereals. The first generation lives on winter cereals and when rye is infested, the first specimens of the new generation emerge from mid-June onwards. From infested wheat the new generation emerges a couple of weeks later. The second generation lives mainly on spring barley (Köppä, 1970).

Haplothrips aculeatus

H. aculeatus is the latest species to lay eggs and has only one generation. The adults hibernate in grasses and mosses. In winter cereals *H. aculeatus* has a preference for rye and in spring cereals it prefers spring wheat (Köppä, 1970).

Stenothrips graminum

S. graminum has only one generation. The larvae fall to the ground and develop to adults, which hibernate in the soil for one or two winters. After the soil temperature has risen to 13.5 °C at 30 cm depth, the adults begin to emerge from the ground. The adults prefer oats and the larvae feed in the panicles (Franssen & Mantel, 1965).

Thrips angusticeps

T. angusticeps has a brachypterous (wingless) and a macropterus (winged) generation. Brachypterous thrips hibernate once or twice in the soil as uncoloured mature insects. They infest sugarbeet, rape and all cereals except oats. Macropterous thrips have a pronounced preference for flax and to a lesser degree for barley, wheat, rye and peas. From these crops the larvae infest the soil with brachypterous thrips. In rainy and cool summers, the infestation with brachypterous thrips can be 90% lower than in dry and hot ones (Franssen & Huisman, 1958).

Frankliniella tenuicornis

F. tenuicornis is mainly found in rye. The first adults of the new generation appear at the end of May from grasses. The great majority of these migrate to spring cereals (Köppä, 1970).

Anaphothrips obscurus

A. obscurus is found in abundance on oats but the first generation is found on winter cereals and leys. Eggs are laid on the leaves (Köppä, 1970).

Yield loss assessment

Decisions in pest management are based on the economic threshold, which depends on the relationship between crop yield and pest infestation (Walker, 1983). In order to determine economic thresholds and relate pest attacks to differences in yield, different levels of pest attack must be obtained. Applications of pesticides at different concentrations and times in the same trial can be used to obtain different levels of attack. The other option to obtain variation in levels of attack is to use data covering results from several years. Variation in yield due to other factors, such as climate or soil differences, is often of high importance. Furthermore, complex attacks by a range of pests are often found and distinguishing the effects of individual pest species is difficult (Walker, 1983). Assessing crop losses due to pests is important in making decisions about pest management based on costs and benefits and in allocating resources to the most important pests. The crop consists of a group of plants and each individual plant is a plastic, dynamic system in which pests reduce the uptake of nutrients or water, reduce photosynthesis and interrupt transport within the plant to stores or reproductive parts. The plant can partly compensate for any loss by increased activity, changes in leaf area or shoot growth. Such compensation can be one of the reasons for the success of cereals as crops (Walker, 1983).

Decisions in plant protection on whether to apply pesticides or not require quantified data on the effect on crops and surroundings. Yield benefits are quantified and compared to the costs, both in terms of money but also the social and environmental benefits and costs, such as the effect of pests and pesticides on human and animal health, and on wildlife (Pedigo, 1999).

Weather influences on insects

Temperature markedly increases the proliferation rate of many cereal pests and temperature is often seen as the most important factor for pest population development (Acreman & Dixon, 1989; Wennergren & Landin, 1993). Adaptation to high temperatures has been observed within cereal aphids (Asin & Pons, 2001). For example, drought stress can increase the population development of *S. avenae* (Honek, 1991; Pons, Comas & Albajes, 1993; Pons & Tatchell, 1995), mainly through the effect of drought on host plant phenology and quality.

The optimum temperature for reproduction and development is 20 °C for pests such as *S. avenae* and *M. dirhodum*. Temperature changes affect not only the pest but also its host plant and natural enemies, *e.g.* low temperatures can reduce aphid population growth but simultaneously the low temperature reduces the number of natural enemies and the aphids can thereby reach similar densities in hot and cold years (Skirvin, Perry & Harrington, 1997). Rainfall and wind are also often reported as being of importance for pest densities (Pierre & Dedryv er, 1985).

Pest attacks fluctuate widely from year to year because of changes in the weather pattern and because of the activity of naturally occurring parasitoids and predators. Carabids, ladybirds, hoverflies, lace wings and earwigs are examples of effective predators of cereal aphids. The farmer can help beneficial organisms by using insecticides as sparingly as possible and *e.g.* by choosing specific aphicides such as pirimicarb (Oakley *et al.*, 1996).

Natural enemies and diseases

Natural enemies of a pest might be able to suppress the increase of that pest and thereby decrease the likelihood of the pest attaining damaging population levels. As a result of the close relationship between a pest and its natural enemies, outbreaks of *e.g.* cereal aphids have often been followed by swarms of hoverflies and ladybirds so abundant that they drive holidaymakers off beaches (Carter *et al.*, 1980).

The more diverse the arthropod fauna, the lower the likelihood of an aphid outbreak. The consumption of aphids by polyphagous predators early in the season can have a significant effect in reducing peak aphid abundance (Dixon, 1989).

Although the factors that affect the colonisation and population build-up of aphids are known, it has proven difficult to quantify their overall effect on aphid increase. The complexity of the system with the factors host quality, weather and natural enemies, the number of species and interactions is amazing (Dixon, 1989).

Many surveys have proven the importance and role of predators (generalist predators, syrphids, coccinellids, staphylinids) and parasitoids in controlling the populations of cereal pests such as aphids (Dean, 1974; Wetzel, Ghanim & Freier, 1981; Holmes, 1984; Elliott, Kieckhefer & Beck, 2000; Sigsgaard, 2002; Schmidt *et al.*, 2003; Legrand *et al.*, 2004). Funderburk, Stavisky & Olson (2000) showed that populations of *Orius* spp. (Heteroptera, Anthocoridae) are effective predators of thrips in field peppers. Several models have also been presented describing population dynamics of *e.g.* *S. avenae* and predators and parasitoids (Vorley & Wratten, 1985; Freier, Triltsch & Rossberg, 1996; Skirvin, Perry & Harrington, 1997; Plantegenest *et al.*, 2001).

However, the small size of thrips and their claustral habits make it difficult to directly investigate the reasons for changes in population size. Furthermore, agricultural crops provide new opportunities for quick colonisation and establishment of large populations of opportunistic thrips. That might be the reason for several authors concluding that natural enemies are of no importance for thrips density (Parrella & Lewis, 1997, Loomans & Greene, 1997). The latter findings have led to speculation about population attributes of thrips outstripping the capacities of natural enemies to suppress populations (Mound, 1997). However, demonstrations of the impact of various parasites and predators on thrips have now meant that density dependence is also accepted for thrips (Funderburk, 2002).

Pest diseases might be an interesting concept in pest management, especially for pests such as thrips because they live in enclosed areas on the plant, such as leaf sheaths and spikes. Entomopathogenic fungi can therefore be applied to control pests living in humid microclimates (Gillespie & Claydon, 1989). The natural occurrence of such fungi has been determined in *e.g.* Denmark (Nielsen *et al.*, 1996).

Integrated control and integrated pest management

Integrated pest management (IPM) is essentially a holistic approach to pest control that seeks to optimise the use of a combination of methods to manage a whole

spectrum of pests within a particular cropping system (Dent, 2000). This is possible by the integration of all available control mechanisms, such as cultural practices, host plant resistance and chemical control, together with the natural regulating factors of the environment.

When pollution of the environment through pesticides became well documented in the 1970s, the public interest in IPM increased. The pesticide residues found in groundwater generated serious concern as they indicated that not only the biological environment of flora and fauna, but also the physical environment was affected beyond acceptable levels. The change in attitudes included farmers asking for alternatives, Ministries of the Environment and agriculture moving to decrease the use of chemical pesticides and consumers demanding products with minimum chemical inputs (Lenteren, Minks & de Ponti, 1991).

Cereal production shows a general trend towards higher yields and an intensification of plant protection treatments. Modern varieties are grown with higher nitrogen inputs than older varieties and as a consequence more pesticides are used. Comparisons of high and low input production systems for wheat have shown that the economic net outcome of both systems is equal. However, an integrated use of pesticides must be based on the application of economic thresholds. Forecasting and prognosis of pest attacks are also helpful tools in achieving a more efficient use of insecticides (Bigler, Forrer & Fried, 1991).

Strategic, tactical and policy models are helpful tools in IPM and are distinguished primarily in terms of the geographical scale and time span over which they operate (Conway, 1984). Strategic models provide more general guidelines and principles that are applicable over a wide range of circumstances. They determine the relative reliance that should be placed on different control options in IPM, such as pesticides, biological control, cultural control or resistance. The main effect of strategic models is on the approaches and attitudes of the decision-makers who have to deal with pests or pathogens (Conway, 1984).

Tactical models aim to offer advice on the day-to-day management of a particular crop in a specific field. Typically they are used as an aid for farmers in decision-making about insect pest management, usually for advice on whether an insecticide should be applied to the crop. The model and output information have to be highly reliable. The data required to establish and verify the predictive relationship have to be based on laborious, detailed and lengthy field experiments. An example of a tactical model is EIPRE, which has been used for monitoring and forecasting of cereal aphids (Rabbinge & Carter, 1984).

National policy is determined primarily by decision-makers at national level and policy models are used to weigh the costs and benefits in pest and pathogen control. Scientists need to become involved in the decision-making and policy-making processes of major institutions and government organisations, *e.g.* by evaluating the long-term implications of persistent insecticide use or the use of high input agricultural techniques in developing countries (Conway, 1984).

Forecasting and prognosis

The abundance and distribution of pests varies greatly between years (Freier & Wetzel, 1984; Wikteliuss & Ekbohm, 1985). Forecasting is the best available strategy when the pests are of occasional importance (Watt, 1983). The ideal forecasting system is one that avoids time-consuming crop inspections, that is

based on remote monitoring or rapid observations and that makes accurate predictions early in the year. The most reliable aphid forecasting tool in England has been the number of aphids caught in local suction traps before the end of ear emergence (Entwistle & Dixon, 1986). Useful information about cereal aphids in both Europe and Sweden has been provided by suction trap surveys (Taylor, 1986; Sigvald, 1997). For *S. avenae* no significant correlation between autumn migration and the following spring migration has been found. In Scania, a significant correlation has been found between spring migration catches in the suction trap and the population found later in the field (Sigvald, 1997).

However, outbreaks often fail to develop despite large spring migrations. The simplest explanation for smaller outbreaks than expected is that large aphid populations present early in crops allow natural enemies to feed and increase numerically and these natural enemies subsequently prevent the aphids from increasing (Prew *et al.*, 1985). If a more rational system for control is to be developed, it has to be based on systematic long-term measurements that are not discontinued each time there is a decline in the level of infestation of a particular pest species (Taylor, 1977).

Population dynamics of cereal aphids and methods of predicting population trends have been investigated since the 1970s (Rautapää, 1976). Investigations often take into account natural enemies (Freier, Mattes & Wetzels, 1982; Entwistle & Dixon 1989).

Decision models with uncertainty analysis have been proposed (Rossing, Daamen & Jansen, 1994; Peterson & Hunt 2002). Validation of models that predict the peak density of grain aphids and the yield loss has been carried out by Carter *et al.* (1989a). The effectiveness of early spraying was overestimated because of overestimation of the persistence of insecticide effects.

In Denmark, a decision system for *S. avenae* has been developed based on several models (Hansen, 2003). The first part is a migration model based on the temperature in April and May and the rain in May, leading to information about when population growth will begin in the fields. A count of aphids has to be carried out in the field 7-10 days after the warning obtained from the migration model. The aphid count is used for the further calculations within the model. By using an economic threshold model, it can be calculated whether it will be necessary to spray the field.

What are dynamics?

Why do pests become extremely abundant one year and then apparently disappear a few years later? The reasons are twofold: Firstly, because of exogenous perturbations like fluctuations in weather and fluctuations in food; secondly, because of mechanisms that involve population density feedbacks like natural enemies. Population dynamics are the study of how and why population numbers change in time and space. Temporal population dynamics are most studied but spatio-temporal dynamics of populations are more complex. Mono-factorial (single-mechanism) explanations do not work in complex population dynamics because one mechanism causes the oscillations and another prevents the first from diverging (first and second order mechanisms). The first order mechanism is food quantity and the overwhelming majority of examples of second-order population

oscillations in nature are explained by the mechanism of specialist predation (including parasitoids), with a few additional cases involving other kinds of trophic interaction (food and parasites) (Turchin, 2003). Climate usually accounts for less than 30% of variance in insect population dynamics in natural ecosystems.

What are bio-economics?

The subject of bio-economic theory is the optimal management of renewable biological resources (Allen *et al.*, 1984). Initial bio-economic models in fisheries used the concept of maximum sustainable yield, which implies a stable equilibrium. However, natural populations often have non-equilibrium dynamics, such as limit cycles or chaos (Turchin & Taylor, 1997). Economic assessment of these transition processes requires incorporation of discount rates into the cost-benefit analysis. Bio-economic theory has been applied to pest management, but in most cases only short-term revenues have been considered (Stern, 1975; Pedigo, 1996).

Most optimisation models in pest management concentrate on maximising the difference between benefits and costs in the same year and *e.g.* side effects of large-scale pesticide treatments are ignored in cost-benefit analyses (Shoemaker & Onstad, 1983).

Apart from the fixed costs associated with crop production, there are variable costs associated with controlling pests. If pesticides disturb the ecological system, the application of pesticides can increase the need for future applications. The management problem is to specify the timing and application of pesticides while balancing the control cost and crop damage so as to maximise the current value of the net profit per hectare. The net income over a number of years is dependent on the planning horizon and should be optimised. Taking social aspects into consideration generally implies a lower discount rate and a longer planning horizon than for an individual farmer (Stenseth *et al.*, 2003). A bio-economic model incorporating basic ecological principles provides a valuable framework for pest management systems, which takes into account both ecology and economics. The ability to predict outbreaks of pest populations is therefore critical (Pedigo, 1999).

Materials and methods

Field experiments with pesticides

Aphids and thrips were investigated in cereal field experiments during the period 1978-2003. Approximately 350 trials were carried out in wheat, rye, barley, triticale and oats.

Field experiments are costly and may take many years to complete. It is important that they are carried out in arable fields in order to study normal populations representative of normal practical conditions. The field plot experiments were designed to resemble actual farm fields. Aphids and thrips are quite sessile insects once they have established in the crop, so plots of 4 x 15 m² were considered sufficient to prevent interplot migration having an influence on the results. When pirimicarb was used, guard zones were established between the plots to protect neighbouring plots from the influence of pesticide drift.

Experimental field trials involve the use of properly randomised and replicated procedures, associated with adequately sized plots and the reduction of inter-plot effects. The experimental design used here was a completely randomised block design. The coefficient of variation for individual experiments was normally very low, indicating high quality of the experiments.

Insecticides were used to provide a range of infestation levels, or simply in order to get an attacked and/or unattacked level, and crop yields were measured. Different degrees of pest attack were obtained by applying pesticides at different concentrations, times or of different types in randomised blocks. The most effective insecticide for aphids was fenvalerate and for thrips cypermethrin. The assumption was that the pyrethroids neither stimulated the growth nor reduced the yield of the cereals. A risk might be that insects were repelled from the treated plots and increased the populations in untreated plots. This would result in higher populations in untreated plots than in the whole field, but it should not disturb the yield loss relationship.

Assessments of pest numbers and injury

Aphid and thrips densities were assessed in all field experiments. The different aphid species found in the plots were counted from early infestation until the population began to decline. For *L. denticornis*, samples of plants were collected and examined in the laboratory for the presence of eggs, larvae, prepupae, pupae and adults. For the injury, estimates were made both for the leaf sheath and the damage on the flag leaf.

The turpentine extraction method modified after Lewis (1960) was the first step in sampling and analysing an enormous amount of ears and panicles for thrips. About 60 extractors of 1.5 litre volume were used. Ten ears or panicles were placed in each extractor, turpentine was applied to the lid and the insects left the plants and fell down into the alcohol pot. The plants were left for two hours in the extractor. The method worked well for larvae and adults but not for thrips pupae. The migration of thrips was examined between fields with water traps and the flight

activities higher up in the air with suction traps. White water traps were placed just above the vegetation to detect flight activity of thrips (Lewis, 1959). A suction trap (12 m high) used for sampling the migration of aphids in Sweden is situated close to the studied area in Alnarp and was used also to study thrips migration (Sigvald & Gustafsson, 1993).

Most experiments in the present thesis were infested with both aphids and thrips and often with several species of each group. To evaluate the results from the field experiments it was necessary to analyse the yield loss relationship with multiple regression, always assuming that there was no loss without insects and that the insecticide in itself was not increasing or decreasing yield.

Outline of the thesis

Both aphids and thrips can be important pests in modern cereal crops. To successfully forecast and control the pests, knowledge of the dynamics caused by weather and biotic influences, such as parasitoids, predators and diseases of the pest, and of the damage thresholds for the pests is important. This thesis comprises investigations on density-independent weather influences, migration, biocontrol and economic thresholds for the pests in cereals.

In Paper I, a crop loss model and dynamic economic thresholds for different expected yield levels and different growth stages were proposed for the grain aphid *Sitobion avenae* in winter wheat.

In Paper II, the damage by *Limothrips denticornis* in rye, triticale and winter barley was investigated. The yield loss was estimated for *L. denticornis* alone and together with aphids and thrips in the ears.

In Paper III, the influence of weather on *Sitobion avenae* was modelled with multiple regression. Critical weather periods in the 14-month period preceding the population peak could explain a major part of the population fluctuations. The aphid population had periodic density-dependent dynamics, resulting in low populations after high population peaks.

In Paper IV, the migration of thrips species between cereal crops was investigated. Terrestrial and aerial populations of the dominating cereal thrips species *Limothrips cerealium*, *L. denticornis*, *Haplothrips aculeatus*, *Stenothrips graminum*, *Thrips angusticeps*, *Frankliniella tenuicornis* and *Anaphothrips obscurus* were studied simultaneously on winter and spring cereals.

In Paper V, the possibility of using the fungus *Verticillium lecanii* in integrated control of thrips and aphids was investigated. Low doses of insecticide and irrigation together with the fungus could limit the population of *Limothrips denticornis* and also of aphids.

Results and discussion, survey of Papers I to V

The yield loss relationship

The primary aim of a yield loss assessment is to determine the type of relationship that may exist between pest infestation and yield loss. In this thesis the yield loss relationship was investigated in Paper I (*S. avenae*) and Paper II (*L. denticornis*). The yield loss caused by *S. avenae* was 40 kg ha⁻¹ for each insect per tiller (Paper I) and was found to be the highest among the aphid species (Table 1). Among the thrips species, *L. denticornis* was found to give the highest yield loss (Table 1), with 21 kg ha⁻¹ for each insect per tiller.

The intensity of pest attack can be described as the product of three factors - the numbers of the pest present, their developmental stage and the duration of the pest attack (Dent, 2000). The experimental approach here was to obtain a relationship between infestation and yield with the help of insecticide field experiments. The response of the plant to damage falls into three main categories. The first type of response (susceptible response) is typical of insects that cause direct damage, where the yield declines in direct proportion to the number of insects present. The second response (tolerant response) is typical of insects feeding on the plant foliage where a certain level of damage can be tolerated before yield is affected. Above the threshold level of damage, yield declines rapidly with increasing insect density. In the third response (the over-compensatory response), the plant reacts to the presence of damage in such a way that yield is actually increased above that which would have been achieved in the absence of the pest. This response is usually limited to early infestations and low levels of damage, so that damage greater than that causing over-compensation reduces crop yield (Dent, 2000). The latter type of response is probably not present in cereals, even if the tolerance of wheat plants to aphids can be very high, as has been shown for wheat grown under optimal conditions in growth chambers (Moewes, Freier & Heimann, 1997). In Figure 1, the yield loss model for *S. avenae* in wheat is compared with a general yield loss model for pests that destroy and threaten the whole yield, *i.e.* pollen beetles (Nilsson, 1994). In field experiments, small yield increases are difficult to determine because the LSD 5% is about 200-300 kg ha⁻¹ (Papers I, II). Thus the loss that is measurable is larger than 200 kg ha⁻¹ and therefore it is impossible to show in a single trial whether the wheat can compensate for low pest densities. However, in the present study the yield loss at high densities of *S. avenae* increased slowly compared to the yield loss in the model for pollen beetles. A high infestation of pollen beetles in oilseed rape can reduce the yield by 80% (Nilsson, 1994) while a high infestation of *S. avenae* in wheat only reduces the yield by 10% (Paper I). The comparatively low yield loss caused by *S. avenae* at high densities is probably a result of intraspecific competition between the aphids, but might also be due to compensation by the wheat (Walker, 1983). The high number of tillers in cereals and the aggregation of aphids always make it possible for low infested tillers to compensate their attacked neighbours.

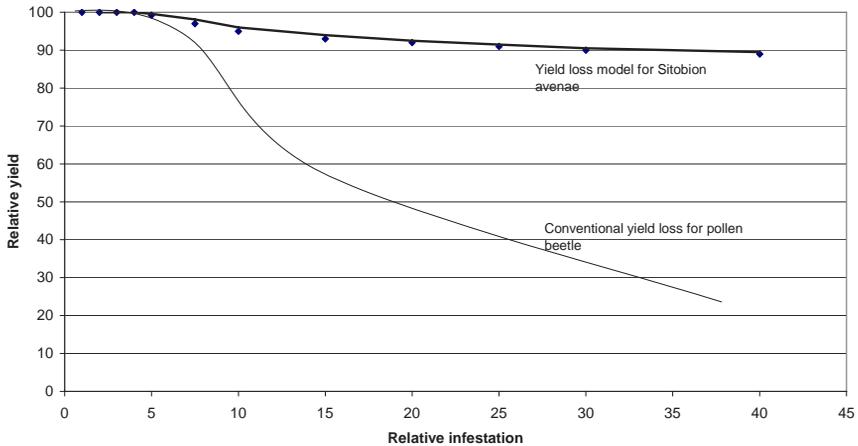


Figure 1. Yield loss relationship for *S. avenae* compared with a yield loss relationship for pollen beetle in oilseed rape. A high beetle infestation in oilseed rape can reduce the yield by 80% but a high aphid infestation in wheat only reduces the yield by 10%.

Economic injury levels

The economic injury level (EIL) is governed by five primary variables: cost of the management tactic (C), market value (V), injury units per pest (I), damage per injury unit (D) and proportional reduction of pest impact (K). The relationship of these variables to the EIL is (Pedigo 1999):

$$EIL = C / (V * I * D * K)$$

An environmental EIL focuses on environmental issues and incorporates environmentally sound actions. Activities to support greater environmental responsiveness in the EIL include accounting for environmental costs, reducing damage per injury by increasing plant tolerance and reducing pesticide application rates (Pedigo, 1996). The use of objective economic thresholds has an important impact on environmental quality, particularly in crops where it is the basis for IPM by decreasing the frequency of application (Pedigo, 1996). Higley & Wintersteen (1992) estimated the level of risk posed by different insecticides to environmental components such as surface waters and groundwater, aquatic organisms, birds and beneficial insects and to human health. Producers were then asked how much they would pay to avoid risks from insecticides and these environmental costs often doubled the EIL. An environmental charge of 200 SEK ha⁻¹ for insecticide applications would increase the EIL so much that treatments would only have to be applied during aphid years (Larsson, 1991b).

Preliminary economic thresholds for *S. avenae* and *R. padi* have been estimated since 1986 (Larsson, 1986), but were established more accurately in the present

work (for *S. avenae* in Paper I and for *R. padi* in Table 1). The economic thresholds determined here for *S. avenae* and *R. padi* were found to be 7 and 8 aphids per tiller, respectively (Paper I and Table I). An economic threshold for *L. denticornis* of 15 thrips per tiller was also established here (Paper II), as were economic thresholds for *L. cerealium* and *S. graminum* (Table 1). Other species such as *H. aculeatus*, *T. angusticeps*, *F. tenuicornis* and *A. obscurus* has not been proven to cause significant damage in cereals. However, thrips in the ears together with aphids can contribute to economic damage (Paper II).

The brachypterous generation of *T. angusticeps* is able to kill seedlings of flax, sugarbeet and barley (Franssen & Huisman, 1958), while *F. tenuicornis* (Köppä, 1970) and *A. obscurus* (Hewitt, 1914) have been reported to cause heavy damage in barley and oats, respectively. If sufficiently high population levels are reached, all thrips species are potential pests, but cereals can in most cases tolerate these three thrips species living on the foliage.

Table 1. Yield losses and economic injury levels estimated for the most important pests in cereals

Crop	Yield loss***, kg ha ⁻¹ for each insect per tiller	Confidence interval	Economic injury level***, insects per tiller
<i>Sitobion avenae</i>	Winter wheat	40	7
<i>Rhopalosiphum padi</i>	Barley, oats	35	8
<i>Limothrips denticornis</i>	Rye, triticale	21	15
* <i>Limothrips cerealium</i>	Winter wheat	8	3-14
** <i>Stenothrips graminum</i>	Oats	7	1-12
<i>Haplothrips</i> , <i>Thrips angusticeps</i> , <i>Frankliniella</i> , <i>Anaphothrips</i> .	Wheat, triticale	Not significant	

*12 experiments in wheat, multiple regression of mixed aphid and thrips populations

**16 experiments in oats, multiple regression of mixed aphid and thrips populations

*** yield losses and economic injury levels calculated as described in Papers I and II

M. dirhodum has been an increasing pest problem in wheat in Europe and is the subject of several studies (Cannon, 1986; Holt, Griffiths & Wratten, 1984; Howard & Dixon, 1992). Early maturation in winter barley provides some resistance to *M. dirhodum* (Howard & Dixon, 1995). In Sweden, very few years

have populations high enough for economic damage, but the results from years with high populations of *M. dirhodum* indicate that the damage can be comparable with the damage of *S. avenae*.

The most damaging species of aphids and thrips thus attack vital parts of the cereal plant, e.g. *S. avenae*, *L. cerealium* and *S. graminum* attack the ears and panicles and *L. denticornis* the leaf sheaths.

Extending the economic injury level concept to multiple species requires consideration of host plant responses to injury. A central requirement is that injuries caused by the different species produce a homogeneous physiological response in the plant, which is probably the case for aphids and thrips. The most appropriate approach for establishing common ground is to quantify injury per individual for each different species (Dosdall, 2004). The next step is to estimate the regression between injury and yield loss or between individual and yield loss as seen in Table 1. When insect densities are quite high, competition reduces injury rates per individual. This was found for both *S. avenae* (Figure 1) and *L. cerealium* and *S. graminum* (Figure 2). Multiple pest species commonly infest crops simultaneously but injury equivalence values do not normally exist for decision support. It is important to determine the abundance and species diversity of pests attacking the crop and of the natural enemies present.

For *L. denticornis* it was possible to show a correlation between the percentage of leaf sheath damaged and the thrips population in the leaf sheath (Paper II). The damage on the flag leaf was not always significant. The damage on the leaf sheath could explain the yield loss caused by *L. denticornis*. Severe infestation of a plant may result in a characteristic gooseneck shape, as shown in Figure 3 (Back of title page).

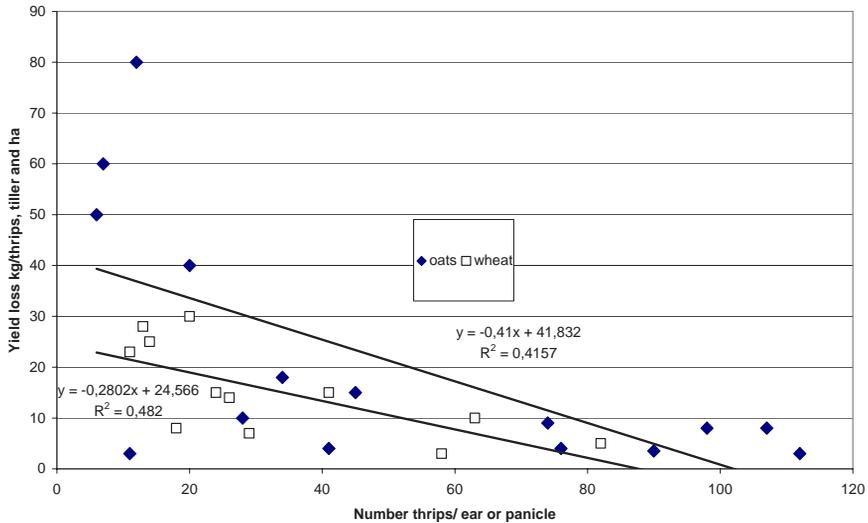


Figure 2. Yield loss in kg per thrips, tiller and ha at different thrips densities. Values for *L. cerealium* and *S. graminum* in wheat and oats, respectively. Injury per individual decreased with increasing populations. (The same experiments as in Table 1).

Monitoring aphid populations for decision-making on control treatments is time-consuming work and many authors have developed sampling plans based on the relationship between mean density and proportion of tillers with aphids (Rabbinge & Mantel, 1981; Ward *et al.*, 1986; Feng & Nowierski, 1992; Feng, Nowierski & Zeng, 1993; Hein *et al.*, 1995). In Sweden, an empirical relationship has also been used (Larsson, 1986). Changes in aerial populations have been studied with suction traps and the catches appear to be representative of the populations within a radius of 20-50 km around the trap as means over several days (Taylor, 1986). In good weather conditions they are also good estimates of the number of aphids and the time of infestation of the surrounding crops (Walters & Dewar, 1986).

Intraspecific competition and interaction between species

The cereal aphids are found in dense colonies at their preferred sites on the host plant. The aggregation in a single patch leads to intraspecific competition (Müller & Steiner, 1991; Chongrattanateekul, Foster & Araya, 1991; Chongrattanateekul *et al.*, 1991). The aggregation of insects in patches is probably a density-dependent population regulation factor and in aphids it induces dispersal, since crowding results in the proliferation of winged forms. The yield loss model presented in Paper I indicates important intraspecific competition at the higher population levels of *S. avenae*.

Simultaneous occurrence of several species of aphids and thrips on crops is a problem when investigating crop losses. In Papers I and II, multiple linear

regression was used to separate the effects of the different species from each other. This method does not consider the interaction between species and individuals. Three species of aphids are common in cereals, giving rise to potential interspecific competition. However, these three species are separated in both time and space. *R. padi* is very early and attacks the lower parts of the stems, *S. avenae* is intermediate and attacks the ears and *M. dirhodum* is the latest and attacks the upper leaves. High early infestations of *R. padi* were sometimes found to change the infestation pattern of *S. avenae*. Thrips species were also found to be separated in time and space (Paper IV). Figure 4 shows an overview of the temporal differences and population levels for the five thrips species found on rye. *T. angusticeps* and *F. tenuicornis* attack the foliage early in the season and at lower population levels per plant compared to *L. cerealium*, *L. denticornis* and *H. aculeatus*. *L. denticornis* attacks the leaf sheath around earing and the two species found in the ears, *L. cerealium* and *H. aculeatus*, are also separated in time.

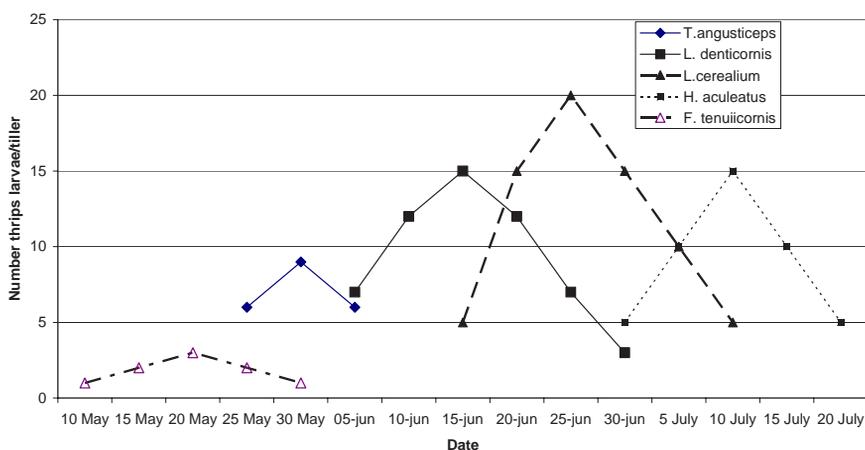


Figure 4. Temporal differences and population levels between larval populations of the 5 thrips species found on rye. *Thrips angusticeps* and *Frankliniella tenuicornis* are found on the leaves, *Limothrips denticornis* in the leaf sheaths and *Limothrips cerealium* and *Haplothrips aculeatus* in the ears.

Quality of grains after infestation

Yield losses can be expressed as reduced yield quantity or quality at harvest. If the quality is negatively influenced, the price of the total yield may be decreased. On average, only small effects on quality were detected after treatment with *S. avenae* in winter wheat when volume weight, thousand kernel weight and protein content were used as quality parameters (Paper I). Germination of grains from thrips-infected trials was investigated in the period 1983-1987. In total, 57 insecticide experiments with treated and untreated plots of rye, oats, wheat and barley were investigated. Thrips populations were mostly between 10-20 thrips per ear. No

significant differences were found for germination between infected (untreated) and uninfected (treated) plots. The untreated plots had lower germination (66%, compared to 87% in treated plots) only in one experiment in oats with thrips populations up to 128 thrips per panicle.

Thrips-attacked grain can be susceptible to fungal infection which may lower the quality (Bournier & Bernaux, 1971). From next year, new EU regulations will limit the level of mycotoxin concentrations in grain for consumption. Therefore, possible relationships between thrips population levels and increased mycotoxin levels are of significance. Grain from untreated and insecticide-treated plots from four experiments in oats and ten experiments in wheat with high populations of thrips have been analysed for content of trichothecenes, nivalenol, deoxynivalenol and HT-2 toxin (Pettersson & Agedal, 1993). Ergosterol, which is an indication of fungal invasion, was also analysed (Pettersson, 1992). Normal levels of ergosterol were found in all samples and the levels of trichothecenes were also low. All four experiments in oats contained deoxynivalenol but grain from the treated plots had levels as high as or higher than grain from the untreated plots.

Critical weather factors and pests

Overwintering can be critical if the species is on the edge of its natural range. Thus *L. cerealium* cannot stand winters with a mean monthly temperature below -1 °C. The species is thus limited to southern Sweden. Variation in winter temperature is one explanation for the wide population fluctuations determined between years (Figure 5). *L. cerealium* normally overwinters under bark and sometimes also goes into houses, causing trouble in automatic fire alarms (Anonymous, 2003a, b; Cuthbertson, 1989). It cannot survive the winter indoors but can probably survive outdoors on house facades. Temperatures in cities are higher than in the surrounding countryside and therefore the insect might survive winters colder than -1°C.

Multiple regression of the weather factors showed that day-degrees in September and average temperature in February explained 70% of the population variation for *L. cerealium*; Population= -113+ 0.7 (day-degrees in September) – 6.4 (February temp) ($R^2=0.71$). *L. denticornis* was significantly negatively correlated with the January-February temperatures, showing that it is a northern species that can have problems with wet winters. The combination of high temperatures and rainfall during summer was also shown to increase the infection of *V. lecanii* in *L. denticornis* (Paper V).

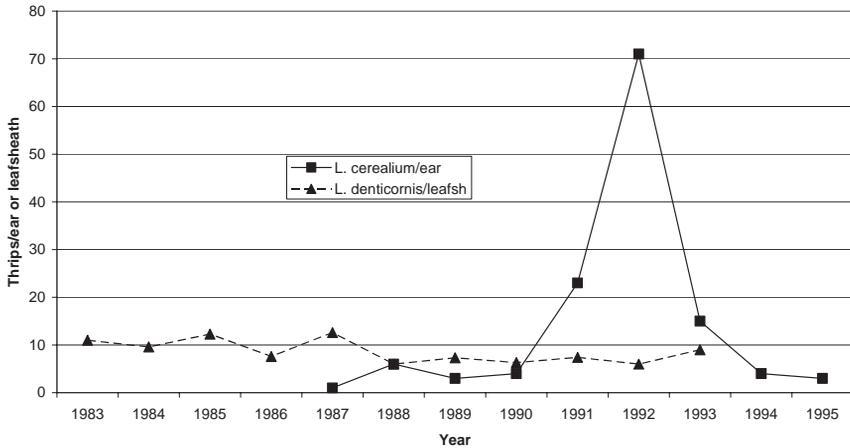


Figure 5. Average population of *Limothrips cerealium* in 4 experiments per year in winter wheat, 1987-1995 and average population of *L. denticornis* in rye and triticale, 1983-1993.

In the present thesis, the influence of weather on *S. avenae* populations was analysed (Paper III). Multiple regression made it possible to construct a model including the critical periods for the aphids. The most important weather factors were found to be rain during spring of the preceding year, temperature during July-October of the preceding year, temperature in January-March, days with no wind in March-May and minimum temperatures in May. For *M. dirhodum* and *R. padi*, the day-degree sum in May-June, the winter temperature and the autumn weather have been shown to be correlated with the summer population peak (Larsson & Wiik, 2003).

Turchin (2003) drew the empirical conclusion that neither monofactorial nor highly polyfactorial models work for calculation of population peaks. The best model for such a calculation seems instead to be oligofactorial. Climate usually accounts for less than 30% of variance in insect populations in natural habitats (Turchin, 2003). The weather in the model in Paper III explained 75% of the variation in population oscillations. One reason for the high degree of explanation could be that agricultural habitats are sparsely populated with natural enemies and the possibilities for the aphids to use the food resource without competition from other species are great. Price & Hunter (2005) presented a weather model for sawfly that accounted for 73% of population change. The more favourable the weather, the better the plant growth and productivity, which favours many kinds of insect herbivores according to the plant vigour hypothesis (Price, 1991). Natural enemies are likely to have a weak top-down impact on dynamics because plant quality is so important. Price & Hunter (2005) also found that the precipitation in October of the previous year influenced the population through the quality of the host plant. Another possible way to predict pest peak populations from weather might be to run several independent models, as is done in meteorology (Deutscher Wetterdienst, 2005), and if for example 9 model forecasts

of 10 indicate high populations next year, the probability of a pest outbreak is high.

A model predicting aphid peak population, including the aphid peak two years before and only two weather factors, is shown in Figure 6. The weather factors together with information about earlier aphid populations, *i.e.* delayed density dependence, give a high explanation of the aphid dynamics. Population = $7.2 + 3.8$ (temperature in February) + 0.07 (day-degrees in July of preceding year) - 1.2 (aphid peak two years before) ($R^2=0.90$).

The weather changed during the period studied here and since 1990 the early summer and the winter have been significantly warmer. The crops were also influenced by the weather and early heading occurring with warm Februaries and warm Mays. Crop yield is correlated with a warm autumn, rain and warm weather in May (Larsson & Wiik, 2003).

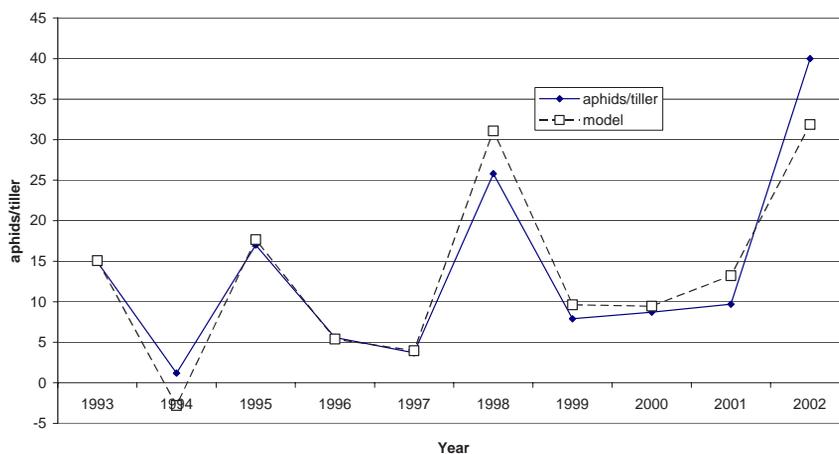


Figure 6. Average population of *S. avenae* in winter wheat 1993-2002 and a weather model including delayed density dependence, through aphid peak two years before, together with two weather variables, *i.e.* the day-degree factor for July of the preceding year and the temperature in February.

Normally, *S. avenae* move from their overwintering sites to winter wheat in the spring. However, early sowing and warm autumns might lead to egg laying also occurring in winter wheat in southern Sweden. An investigation in Scotland has shown that cooler weather leads to later arrival of *S. avenae* to the fields in the spring. A positive correlation was found between arrival date in the crop and the number of day-degrees above the developmental threshold of 5°C (Walters & Dewar 1986; Leather, 1994). In Sweden, a positive correlation has been found between the earliness of migration date (measured with catches in suction traps) and the summer peak (Sigvald, 1997).

Many pests react drastically on the weather in critical phases of their lifecycle. Examples are the larvae drop to the ground in July of *T. angusticeps* and *S.*

graminum for overwintering in the soil. A lot of rain dominating this period leads to a low number of overwintering larvae and thereby the population can be low for several years ahead. For example, *T. angusticeps*, measured as unwinged adults per 10 sugarbeet plants in May, decreased after the wet year 1987 followed by a wet July in 1988 to a very low level in 1989 (Larsson, 1990).

Density dependence

The possibility of analysing density dependence in long time series of aphid populations was evaluated in Paper III. The periodic dynamics in the population series were proven by autocorrelation tests (ACF). The autocorrelation test was found to be of the phase-forgetting kind, which suggests that oscillations in the population are driven by endogenous dynamics (Turchin & Taylor, 1997). The problem is to analyse the combined effect of density-dependent and density-independent factors. The analyses of the weather effects on the aphid population in Paper III gave an explanation of the whole population dynamics, including density-dependent effects. Models like that in Figure 6 combining both weather and information about former populations are more realistic. Several authors have also raised concerns about the validity of using time-series analysis to detect density dependence. One particular concern is the suggestion that exogenous driving variables, such as cyclic weather patterns, can lead to the spurious detection of density dependence in natural populations (Hunter & Price, 1998).

Density dependence in thrips populations has been questioned (Parrella & Lewis, 1997; Loomans & Greene, 1997; Mound, 1997) and there is a lack of examples from agricultural crops. The population curves in Figure 5 give no indication of density dependence for the two species of *Limothrips* studied.

The farming system: Influences of nitrogen, fungicides, varieties and crop rotation

In this thesis the aphid and thrips populations were studied during a very long period (Papers I-V) in which cultivars and fertilisation and plant protection practices changed. It is therefore important to have some information about changes that have taken place and that might have an impact on the aphid and thrips populations.

Most investigations (Hanisch, 1980; Prew *et al.*, 1982, 1985; Hasken & Poehling, 1995; Duffield *et al.*, 1997) show a positive relationship between amount of nitrogen applied and natural populations of *M. dirhodum* and *S. avenae*, although some investigations show diverging results (Zhou & Carter, 1991). Very dense stands of wheat can favour infection by fungi, thereby limiting aphid population growth (Duffield *et al.*, 1997). Swedish experiments showed an increase of aphids peaks in 18 of 24 trials in winter wheat with an increase of nitrogen application from 100 to 140 or 180 kg N ha⁻¹ (Andersson *et al.*, 1986). Fungicides had a certain effect on aphids and the yield increase with insecticide alone was greater than the yield difference between the combined treatment of fungicide and insecticide minus the yield for the fungicide treatment (Andersson *et al.*, 1986). In barley, an increase in aphids after both increased nitrogen and application of

fungicides has been recorded (Larsson & Wiik, 1992). Both nitrogen and fungicides keep the crop green longer, which gives aphids and thrips increased possibilities to feed in the crop.

Older investigations have shown that some fungicides can reduce longevity and reproduction of aphids but higher doses also favour the aphids (Sagenmüller, 1977). In later investigations (Zhou & Carter, 1991), no significant effects on the aphid population were found with fungicides. However, fungicides can influence population development indirectly through inhibiting the aphid-infecting fungi (Zimmerman, 1976) or killing natural enemies (Poehling, 1987).

Crop varieties change all the time and it is difficult to judge if they have any real effect on infestation of aphids or thrips. The late maturing variety Kosack ripened very late in some years of the present study and that could have influenced the aphids. In an investigation with new and old (before 1986) varieties of winter wheat and winter barley in Germany, old varieties of wheat had more aphids than new ones but old varieties of barley had less aphids than new varieties (Sengonca, Jösch & Kleinhenz, 1994).

The infestation of thrips varied more with the different species of cereals than different varieties of winter wheat, triticale and rye (Paper II).

Thrips species in the soil can be controlled by crop rotation. The brachypterous generation of *T. angusticeps* hibernates in the soil and susceptible crop like flax and brassicas can be protected completely from infestation by following a three-year rotation with red clover and oats before the susceptible crop (Franssen & Huisman, 1958). *S. graminum* also hibernates in the soil and to prevent infestation the most important step is to not to grow oats after oats and also to keep a distance to the last year's oat crop.

Insecticides

In this thesis, insecticides were used to control aphids and thrips (Papers I, II and V). In most papers about aphid and aphid damage from field experiments where insecticides have been used to create control plots in Europe, there is no information provided about the occurrence of thrips. However thrips are probably common in many cereal crops, as we found in Sweden, and this fact may be partly responsible for the large variation obtained by different workers about aphid damage.

Selective aphicides have always been the first choice for aphid control since pirimicarb came on the market (Baranyovits, 1972; Niehoff & Poehling, 1995; Oakley *et al.*, 1996). The use of pyrethroids against aphids (Carter *et al.* 1989b) and a generally reduced rate of insecticides have been proposed as a way to promote natural enemies (Wiles & Jepson, 1995; Longley *et al.*, 1997).

Insecticides used against pests always also risk killing predators and parasitoids. Parathion has been found to be the insecticide most toxic to predators (Basedow & Mielke, 1977), cypermethrin less toxic than parathion and pirimicarb the least toxic (Brown, Lawton & Shires, 1983). An extensive test of fenitrothion, pirimicarb and fenvalerate in large plots of winter wheat and barley in Alnarp, Sweden (Nilsson, 1985) showed that fenitrothion was the most toxic to polyphagous predators such as carabids and pirimicarb the least toxic. Fenvalerate was of intermediate toxicity but was very toxic to spiders.

Low doses of pyrethroids have been proposed to decrease the costs and increase the selectivity for natural enemies. The disadvantages of low doses can be more insurance applications and larger sprayed acreage. The risk for the need of new applications rises and also an increased risk for resistance (Larsson, 1991a). In Paper V, it was shown that low doses of cypermethrin increased the population of aphids and only combination with *V. lecanii* controlled the aphids. The application of insecticides in wheat with a wipe-on method has been promising, with rather good control of the aphids in the ears and with less dose used per hectare (Nilsson, 2000).

BYDV is transmitted by both *S. avenae* and *R. padi* in Sweden. However no infection occurs in the autumn as it does in other parts of Europe and no insecticides are needed in the autumn. In winter wheat, infections are also rare in summer and insecticide spraying at heading only had an effect on the aphids in one case in 1990 (Paper I, III).

Insecticides provide farmers with a relatively cheap and effective way of controlling aphids. In the absence of a forecasting system, the tendency is to apply insecticide routinely and prophylactically without regard to pest incidence. This leads to over-use of pesticides, threatens biological diversity and kills natural agents of biological control, yet the increase in yield only goes to increase existing large grain surpluses. While the individual user considers only the direct monetary costs of pesticides, the optimal strategist also adds the costs of future damage from resistance and suppression of natural enemies, as well as costs of environmental pollution (Regev, 1984).

Natural enemies and pathogens

Coccinellids and chrysopids can be important as predators on thrips but of special interest is the predatory thrips *Aeolothrips* spp. (Bournier, 1983). Predatory thrips species usually feed on small, soft-bodied insects including other thrips and aphid nymphs. In small fields at Alnarp, larvae or adults of *Aeolothrips* often were found on 10% of the ears. One adult can kill up to 10 thrips larvae per day (Bournier, 1983). Three other groups of organism, mites, parasitic nematodes and anthocorid bugs, are now recognised as useful natural enemies against pest thrips (Mound, 2005).

Pathogens on thrips and aphids are well known but have not been used for practical control outdoors in temperate climates. In this thesis (Paper V), it was shown that *Verticillium lecanii* (*Lecanicillium* spp.) is a common parasite of thrips. Experiments with *V. lecanii* in combination with irrigation and low doses of insecticides aimed at controlling thrips also proved to have effects aphids. Further field experiments with *V. lecanii* and *Beauveria bassiana* showed effects on field populations of both aphids and thrips (Hjorth, 1990). Investigations in Denmark (Nielsen, 1995) on *L. cerealium* showed natural occurrence of *V. lecanii* and *B. bassiana*. The percentage of the population of aphids and thrips attacked by *V. lecanii* and/or *B. bassiana* was less than 10%. Nielsen also found sporadic infections of *Neozygites parvispora* on *L. denticornis*.

V. lecanii can be produced on sterilised wheat kernels in high amounts and further experiments should be carried out in large plots, applying the infected kernels on the soil. The results from small plots can be difficult to interpret because the

fungus is probably easily spread between small plots. Irrigation alone should also be evaluated to encourage natural infection of pathogens in the field. In some areas of Sweden with sandy soils (Kristianstad), it is quite common to irrigate the cereal fields before the irrigation starts in potatoes.

The combined use of entomopathogenic fungi and nematodes against thrips in the field has also been tested with promising results (Jung, 2004). The entomopathogenic nematodes can also be used in colder climates and are not as sensitive to cold weather as *V. lecanii* (Paper V).

Spatio-temporal dynamics and forecasting

Migrating cereal thrips (mainly *L. cerealium* and *L. denticornis*) in July-August regularly become a nuisance to the public because large numbers of them land on exposed skin. This is traditionally linked with the occurrence of thunderstorms, so thrips are called thunderflies (Kirk, 2004).

Information on the spatio-temporal distribution of pests and their natural enemies on arable crops is essential for any IPM strategy. In this thesis migration of cereal thrips between crops was investigated (Paper IV). The migration pattern for *L. denticornis* is illustrated in Figure 7. Cereal and grass-feeding thrips predominate in mass flights in Europe because cereal crops provide uniform breeding sites over large areas and all ripen more or less simultaneously. Wild grasses are also common and widely distributed and insects breeding in temporary habitats must migrate to survive (Lewis, 1973). However, the migration pattern depends on the thrips species, the number of generations and the acreage and phenology of the different winter and spring cereals. For example, the flight period depends on the weather and therefore creates peaks when the females move to the next crop. Four different crops are involved, but of the winter cereals rye and triticale are preferred because of their earliness. Females move from rye to triticale and the new generation can choose winter wheat or barley but prefers barley. The second generation then leaves barley in the end of July and beginning of August (Paper IV).

Host species, variety and phenology are important determinants of spatial patterns of insect pests in agricultural systems. Agricultural systems are characterised by biological cycles which are usually synchronised in time and create attractive signals for phytophagous insect population developing outside the system (Nestel, Carvalho & Nemny-Lavy, 2004). The dynamic re-distribution of insects in space is an intrinsic characteristic of insect populations and its understanding is of relevance to IPM. Forecasting insect pests in space and time in heterogeneous landscapes requires updated knowledge of pest population levels and their position in the managed space and an estimate of their future population levels and the way the surrounding habitat may affect their levels (Nestel, Carvalho & Nemny-Lavy, 2004).

Host plant abundance is probably the most important factor for the thrips species specialised in cereals like *L. denticornis*. Many authors have discussed serious damage in rye in the early 1900s (Brummer, 1939; Jablonowski, 1927; Hukkinen, 1934, 1942). At that time rye was the dominant crop in northern Europe. In

Sweden, for example, there were about 3.8 Mha cultivated land of which 23% was rye, *i.e.* about 850 000 ha compared with about 30 000 ha now (Morell, 2001). That should have given *L. denticornis* great possibilities to reach very high damaging population levels.

In suction trap catches, *L. cerealium* and *L. denticornis* were found to be the dominating species (Paper IV) but all species from the cereals had their specific peaks. The migration of the overwintering *Limothrips* generation and the two new generations during summer could be detected and suction traps could be an instrument to follow the fluctuations of cereal thrips.

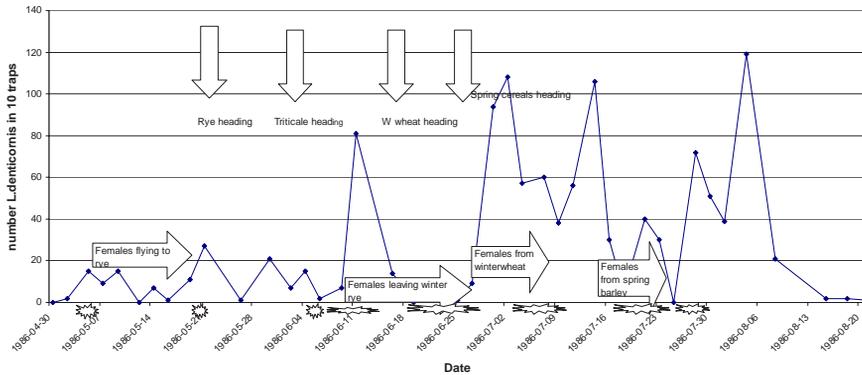


Figure 7. Catches of *Limothrips denticornis* in 10 water traps. Vertical arrows show time of heading of different cereals, horizontal arrows show the time when females are found in the sampling from the cereals. Suns show days with temperatures over 20 °C and with winds less than 5 m s⁻¹.

Bio-economics

The subject of bio-economic theory is the optimal management of renewable biological resources. Initial bio-economic models use the concept of maximum sustainable yield, which implies a stable equilibrium. Most optimisation models in pest management maximise the difference between benefits and costs in the same year. Current pesticide management calculates neither the environmental costs like effect on natural enemies nor the future costs of resurgence and resistant pests.

We need a better understanding of the trade-off between the costs and benefits of control. Ecologists tend to ignore economics, while economists typically have a simplistic understanding of ecology and pest control managers commonly underrate both (Stenseth *et al.*, 2003).

The policy could be to minimise insecticide use in cereals because we need insecticides in oilseed rape, potatoes and sugarbeet. A governmental tax on insecticides could finance applied research in entomology. The initial cost for applying insecticides is very low, especially if a low dose is chosen and applied together with a fungicide. Future costs could also arise from more applications in coming years because of resurgence of pests or insecticide-resistant aphids.

Conclusions and implementations for the future

Figure 8 summarises a proposal of how yield losses from pests could be minimised in an IPM system. Field monitoring and field trials are the basis for understanding the impact of pests on crops. A range of studies have been carried out and a large amount of information is available about cereal aphids. However, the biology and dynamics of cereal thrips are less well understood. Much more investigations are needed about aphids and thrips, both concerning density dependence aspects and relations to natural enemies and pathogens.

Field monitoring and trials, together with a more detailed knowledge about the biology and population dynamics, should make calculations of bio-economics of pests possible.

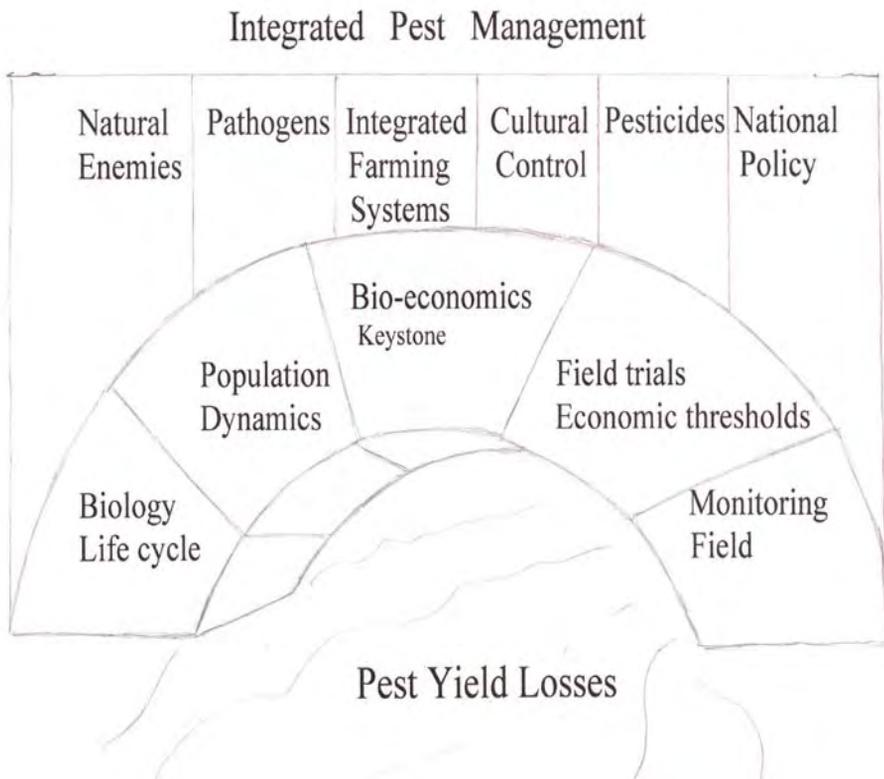


Figure 8. Integrated pest management as a bridge over pest losses, with bio-economics as the keystone. Modified after Pedigo (1996).

To study the effects of weather on pests, long-term reliable field studies of the populations are a necessity. In order to be able to investigate one pest in the field, knowledge is needed not only about that specific pest but also about other pests occurring in the field, in order to separate the effects of different species and to apply multiple economic thresholds. The farming system is continuously changing and so is the importance of the different pests. Other inputs, particularly fertilizers and fungicides, can also have a large impact on insects. The acreage occupied by different crops in the landscape has a great influence on the possibilities for pest outbreaks. Thus, continuous field monitoring and trials, together with a more detailed knowledge about the biology and population dynamics, should make calculations of bio-economics of pests increasingly possible.

To keep pests at low numbers, their natural enemies and pathogens are a prerequisite. Farming systems should be organised and control mechanisms such as irrigation used in a manner that protects the natural enemies and encourages pathogens. As a last resort, insecticides should be used but for more efficient use of insecticides, a national policy is needed.

References

- Acreman, S. J. & Dixon, A. F. G. 1989. The effects of temperature and host quality on the rate of increase of the grain aphid (*Sitobion avenae*) on wheat. *Annals of Applied Biology* 115, 3-9.
- Allen, P. G., Botsford, L. W., Schuur, A. M., & Johnston, W. E. 1984. *Bio-economics of aquaculture*. Amsterdam. Elsevier.
- Andersson, K., Larsson, H., Nilsson, I. & Wiik, L. 1986. Experiments with crop systems in winter wheat in Scania 1978-1985. *Weed and plant Protection Conferences 1986*. Växtskyddsrapporter Jordbruk 39, 211-233.
- Anonymous 2003a. Thunder flies bug big business: Shropshire firefighters are going into action against hordes of tiny terror insects which plague businesses and the fire service each year by accidentally triggering fire alarms during the mating season. *Fire*. August.
- Anonymous 2003b. Insekter orsakade åtta utryckningar på en vecka. *Helsingborgs dagblad*. 24 Juli 2003.
- Asin, L. & Pons, X. 2001. Effect of high temperature on the growth and reproduction of corn aphids and implications for their population dynamics on the northeastern Iberian peninsula. *Environmental Entomology* 30(6), 1127-1134.
- Basedow, T. & Mielke, H. 1977. Aspekte der Parathion-anwendung in Weizenfeldern. *Nachrichtenblatt Deutschen Pflanzenschutzdienst* 29, 65-69.
- Baranyovits, F. 1972. The increasing problem of aphids in agriculture and horticulture. *Outlook on agriculture* 7, 102-108.

- Bigler, F., Forrer, H. R. & Fried, P. M. 1991. Integrated crop protection and biological control in cereals in Western Europe. Biological control and integrated crop protection: towards environmentally safer agriculture. *Proceedings of an international conference organized by the IOBC/WPRS Veldhoven, Netherlands*, 8-13 Sept. 95-116.
- Bournier, A. 1983. *Les thrips. Biologie, Importance Agronomique*. INRA, Paris 128 pp.
- Bournier, A. & Bernaux, P. 1971. *Haplothrips tritici* et *Limothrips cerealium* agents de la moucheture des blés durs. *Ann. Zool. Econ. Anim.* 3, 247-259.
- Brown, K. C., Lawton, J. H. & Shires, S. W. 1983. Effects of insecticides on invertebrate predators and their cereal aphid prey: Laboratory experiments. *Environmental Entomology* 12, 1747-1750.
- Brunner, V. 1939. Beiträge zum Problem der durch Thysanopteren verursachten Schartigkeit des Roggens. *Acta Agraria Fennica* 11, 127-145.
- Cannon, R. J.C. 1986. Summer populations of the cereal aphid *M. dirhodum* on winter wheat: three contrasting years. *Journal of Applied Ecology* 23, 101-114.
- Carter, N., McLean, I. F. G., Watt, A. D. & Dixon, A. F. G. 1980. Cereal aphids: a case study and review. In Coaker, T H (Ed.) *Applied Biology* vol V, 271-348. London, Academic Press.
- Carter, N., Entwistle, J. C., Dixon, A. F. G. & Payne, J. M. 1989a. Validation of models that predict the peak density of grain aphids (*Sitobion avenae*) and yield loss in winter wheat. *Annals of Applied Biology* 115, 31-37.
- Carter, N., Powell, W., Wright, A. F. & Ashby, J. E. 1989b. Effectiveness of different insecticides applied at various growth stages to control aphids on winter wheat. *Crop Protection* 8, 271-276.
- Chongrattanameteekul, W., Foster, J. E. & Araya, J. E. 1991a. Biological interactions between the cereal aphids *R. padi* and *S. avenae* on wheat. *Journal of Applied Entomology* 111, 249-253.
- Chongrattanameteekul, W., Foster, J. E., Shukle, R. H. & Araya, J. E. 1991b. Feeding behaviour of *R. padi* and *S. avenae* on wheat as affected by conspecific and interspecific interactions. *Journal of Applied Entomology* 111, 361-364.
- Conway, G. R. 1984. *Pest and pathogen control. Strategic, tactical and policy models*. International Institute for Applied System analysis. The Pitman Press, Bath.UK.
- Cuthbertson, D. R. 1989. *Limothrips cerealium* – an alarming insect. *Entomologist* 108, 246-256.
- Dean, G. J. 1974. Effects of parasites and predators on the cereal aphids *Metopolophium dirhodum* and *Macrosiphum avenae*. *Bulletin of Entomological Research* 63, 411-422.
- Dent, D. 2000. *Insect pest management*. 2nd ed. CAB international. Wallingford, UK.
- Deutscher Wetterdienst 2005. The SRNWP-PEPS: a regional multi-model ensemble in Europe. www.dwd.de/en/Funde/Projekte/PEPS/SRNWP-PEPS_description.doc (accessed 20-Oct-2005).
- Dixon, A. F. G. 1989. Cereal aphids as an applied problem. In *Biology and population dynamics of invertebrate crop pests*. Ed Russell G E Intercepr. Andover, Hampshire.

- Dosdall, L. M. 2004. Economic thresholds for multiple insect pest species in the same crop. *Government of Alberta. Agriculture, Food and Rural Development*. www1.agric.gov.ab.ca (accessed 20-Oct-2005).
- Duffield, S. J., Bryson, R. J., Young, J. E., Sylvester, B., Bradley, R. & Scott, R. K. 1997. The influence of nitrogen fertiliser on the population development of the cereal aphids *Sitobion avenae* and *Metopolophium dirhodum* on field grown winter wheat. *Annals of Applied Biology* 130, 13-26.
- Elliott, N. C., Kieckhefer, R.W. & Beck, D.A. 2000. Adult coccinellid activity and predation on aphids in spring cereals. *Biological Control* 17(3), 218-226.
- Entwistle, J. C. & Dixon, A. F. G. 1986 Short-term forecasting of peak population density of the grain aphid (*Sitobion avenae*) on wheat. *Annals of Applied Biology* 109, 215-222.
- Entwistle, J. C. & Dixon, A. F. G. 1989. The effect of augmenting grain aphid (*Sitobion avenae*) numbers in a field of winter wheat in spring on the aphids abundance in summer and its relevance to the forecasting of outbreaks. *Annals of Applied Biology* 114, 397-408.
- Feng, M. G. & Nowierski, R. M. 1992. Spatial distribution and sampling plans for four species of cereal aphids infesting spring wheat in southwestern Idaho. *Journal of Economic Entomology* 85(3), 830-837.
- Feng, M. G., Nowierski, R. M. & Zeng, Z. 1993. Binominal sampling plans for the English grain aphid *Sitobion avenae* based on an empirical relationship between mean density and proportion of tillers with different tally thresholds of aphids. *Bulletin of Entomological Research* 83, 187-196.
- Fletcher, K. E. & Bardner, R. 1969. Cereal aphids on wheat. *Report Rothamsted experimental Station Part 1*, 200-201.
- Flygare, I. A. & Isacson, M. 2003. *Jordbruket i välfärdssamhället 1945-2000. Det svenska jordbrukets historia*. Band 5. Natur och kultur/ LTs förlag.
- Franssen, C. J. H. & Huisman, P. 1958. De levenswijze en bestrijdingsmogelijkheid van de vroege akkertrips. *Versl. Landbouwk. Onderzoekingen* 64.10, Wageningen: 1-51.
- Franssen, C. J. H. & Mantel, W. P. 1963. Het voorspelen van schade door de kortvleugelige vroege akkertrips in het voorjaar. *Landbouwkundig tijdschr.* 75, 121-152.
- Franssen, C. J. H. & Mantel, W. P. 1965. Thrips in cereal crops (biology, economic importance and control). *Versl. Landb. Onderz. Rijkslandb. Proefstn.* 662, 97.
- Freier, B. & Wetzel, T. 1984. Abundanzdynamik von Schadinsekten im Winterweizen. *Zeitschrift für Angewandte Entomologie* 98, 483-494.
- Freier, B., Matthes, P. & Wetzel, T. 1982. Entscheidungshilfen zur Befallsvorhersage und zur gezielten Bekämpfung der Getreideblattlaus (*Macrosiphum avenae*) in Winterweizen. *Nachrichtenblatt für den Pflanzenschutz in der DDR.* 36(10), 193-196.
- Freier, B., Triltsch, H. & Rossberg D 1996. GTLAUS-A model of wheat-cereal aphid-predator interaction and its use in complex agroecological studies. *Journal of Plant Diseases and Protection* 103(5), 543-554.

- Funderburk, J. E. 2002. Ecology of thrips. Thrips and tospviruses: *Proceedings of the 7th International Symposium on Thysanoptera*. Eds. Marullo, R. & Mound, L. A. Canberra: Aust. Natl. Insect Collect.
- Funderburk, J. E., Stavisky, J. & Olson, S. 2000. Predation of *Frankliniella occidentalis* in field peppers by *Orius insidiosus*. *Environmental Entomology* 29, 376-382.
- Gillespie, A. T. & Claydon, N. 1989. The use of entomogenous fungi for pest control and the role of toxins in pathogenesis. *Pesticide Science* 27, 203-215.
- Hanisch, H. C. 1980. Untersuchungen zum Einfluss unterschiedlich hoher Stickstoffdüngung zu Weizen auf die Populationsentwicklung von Getreideblattläusen. *Journal of Plant Diseases and Protection*. 87(9), 546-556.
- Hansen, L. M. 2003. Kornbladlus i vinterhvede. *Danmarks Jordbrugsforskning. Forskningscenter Flakkebjerg*.
- Hasken, K. H. & Poehling, H. M. 1995. Effects of different intensities of fertilizers and pesticides on aphids and aphid predators in winter wheat. *Agriculture, Ecosystems and Environment* 52(1), 45-50.
- Hein, G. L., Elliott, N. C., Michels, G. J. & Kieckhefer, R. W. 1995. A general method for estimating cereal aphid populations in small- grain fields based on frequency of occurrence. *Canadian Entomologist* 127(1), 59-63.
- Hewitt, C. G. 1914. Sterility in oats caused by thrips. *Journal of Economic Entomology* 7, 211.
- Higley, L. G. & Wintersteen, W. K. 1992. A new approach to environmental risk assessment of pesticides as a basis for incorporating environmental costs into economic injury levels. *American Entomologist* 38, 34-39.
- Hjorth, A. 1990. Biological control with the entomogenous fungi *Beauveria bassiana* and *Verticillium lecanii*; Field studies for control of thrips in rye and oats. *Examensarbete 1990:6. Department of Plant and Forest Protection, Swedish University of Agricultural Sciences*. In Swedish. 55 pp.
- Holmes, P. R. 1984. A field study of the predators of the grain aphid *Sitobion avenae* in winter wheat in Britain. *Bulletin of Entomological Research* 74, 623-631.
- Holt, J., Griffiths, E. & Wratten, S. D. 1984. The influence of wheat growth stage on yield reductions caused by the rose-grain aphid, *Metopolophium dirhodum*. *Annals of Applied Biology* 105, 7-14.
- Holtmann, H. 1963. Untersuchungen zur Biologie der Getreide-Thysanopteren. Teil I. *Zeitschrift für Angewandte Entomologie* 51 (1), 1-41.
- Honek, A. 1991. Environment stress, plant quality and abundance of cereal aphids on winter wheat. *Journal of Applied Entomology* 112, 65-70.
- Howard, M. T. & Dixon, A. F. G. 1992. The effect of plant phenology on the induction of alatae and the development of populations of *Metopolophium dirhodum*, the rose-grain aphid on winter wheat. *Annals of Applied Biology* 120, 203-213.
- Howard, M. T. & Dixon, A. F. G. 1995. Factors determining the pest status of the rose-grain aphid *Metopolophium dirhodum* on winter barley in the United Kingdom. *Annals of Applied Biology* 127, 1-10.

- Hukkinen, Y. 1934. Über die Weissärgigkeit der Gramineen. *Acta Agralia Fennica*. 6, 139-158.
- Hukkinen, Y. 1942. Blick auf die Erforschung der Thysanopteren fauna Finnlands, besonders ihrer schädlichen Arten. *Annales entomologici Fennici*. 8, 25-45.
- Hunter, M. D. & Price, P. W. 1998. Cycles in insect populations: delayed density dependence or exogenous driving variables? *Ecological Entomology* 23 (2), 216.
- Jablonowski, J. 1927. Zur Klärung der Thripsschädenfrage. *Zeitschrift für angewandte Entomologie* 12, 451-512.
- Johansson, E. 1938. Studier rörande de på gräs och sädesslag levande tripsarnas biologi och skadegörelse. I. *Statens växtskyddsanstalt. Medd.* Nr 24, 1-65.
- Jung, K. 2004. Combined use of insect pathogenic fungi and nematodes against the onion thrips, *Thrips tabaci*, in the field. Management of plant diseases and arthropod pests by BCAs. *IOBC/wprs Bulletin*. 27(8), 141-143.
- Kirk, W. D. J. 2004. The link between cereal thrips and thunderstorms. *Acta Phytopathologica et Entomologica Hungarica* 39(1-3), 131-136.
- Kolbe, W. 1969. Studies on the occurrence of different aphid species as the cause of cereal yield and quality losses. *Pflanzenschutz Nachrichten Bayer* 22, 171-204.
- Köppä, P. 1970. Studies on the thrips species most commonly occurring on cereals in Finland. *Annales Agriculturae Fenniae* 9, 191-265.
- Larsson, H. 1986. Skadetrösklar för bladlöss i korn och höstvetete. *Weed and plant Protection Conferences 1986. Växtskyddsrapporter Jordbruk* 39, 211-233.
- Larsson, H. 1990. Behöver trips och betflugor bekämpas? *Betodlaren*, nr 2, 146-148.
- Larsson, H. 1991a. Bättre ekonomi med låga doser av pyretroider. *Regional växtskyddskonferens i Växjö*. Nr 38, 9:1-10.
- Larsson, H. 1991b. Ekonomisk betydelse av bladlöss i stråsäd vid förändrade priser. *32nd Swedish Crop Protection Conference 1991*. Uppsala 30-31 January. 187-196.
- Larsson, H. & Wiik, L. 1992. Odlingssystemförsök i stråsäd en sammanfattning. *33rd Swedish Crop Protection Conference 1992*. Uppsala 29-30 January. 191-201.
- Larsson, H. & Wiik, L. 2003. Väderleksfaktorerers inverkan på växtskadegörare - underlag för prognos- och varningsmodeller. *Slutrapport Jordbruksverket*. 24pp.
- Lattaushke, G. & Wetzell, T. 1985. Zum Artenspektrum und zur Abundanzdynamik von Getreide-Thysanopteren. *Arch. Phytopathol. Pflanzenschutz*, Berlin 21(5), 375-382.
- Leather, S.R. 1994. Overwintering in six arable aphid pests: a review with particular relevance to pest management. *Journal of Applied Entomology* 116, 217-233.
- Legrand, M. A., Colinet, H., Vernon, P. & Hance, T. 2004. Autumn, winter and spring dynamics of aphid *Sitobion avenae* and parasitoid *Aphidius rhopalosiphii* interactions. *Annals of Applied Biology* 145, 139-144.

- Lenteren, J. C., Minks, A. K. & de Ponti, O. M. B. 1991. Biological control and integrated crop protection: towards environmentally safer agriculture. *Proceedings of an international conference organized by the IOBC/WPRS Veldhoven, Netherlands*, 8-13 Sept. 7-9.
- Lewis, T. 1959. A comparison of water traps, cylindrical sticky traps and suction traps sampling thysanopteran populations at different levels. *Entomologica Experimentalis et Applicata* 2, 204-215.
- Lewis, T. 1960. A method for collecting Thysanoptera from Graminae. *Entomologist* 93, 27-28.
- Lewis, T. 1973. *Thrips, their biology, ecology and economic importance*. Academic Press London and New York.
- Longley, M., Jepson, P. C., Izquierdo, J. & Sotherton, N. 1997. Temporal and spatial changes in aphid and parasitoid populations following applications of deltamethrin in winter wheat. *Entomologica Experimentalis et Applicata* 83, 41-52.
- Loomans, A. J. M. & Greene, I. D. 1997. Interactions with hymenopterous parasites and parasitic nematodes. *Thrips as crop Pests* (ed. Lewis, T.) pp 355-397. CAB International, Wallingford, UK
- Moewes, M., Freier, B. & Heimann, J. 1997. Variation in yield loss per aphid day due to *Sitobion avenae* infestation in high yielding winter wheat. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz*. 104 (6), 569 -575
- Morell, M. 2001. *Jordbruket i industrisamhället 1870-1945. Det svenska jordbrukets historia*. Band 4. Natur och kultur/ LTs förlag.
- Mound, L. A. 1997. Biological diversity. *Thrips as crop Pests* (ed. Lewis, T.) pp107-216. CAB International, Wallingford, UK.
- Mound, L. A. 2005. Thysanoptera: Diversity and Interactions. *Annual Review of Entomology* 50, 247-269.
- Müller, F. P. & Steiner, H. 1991. Mutual influences between aphids and a joint host plant. *Beiträge Entomologie*. Berlin 41(1), 265-270.
- Nestel, D., Carvalho, J. & Nemny-Lavy, E. 2004. The spatial dimension in the ecology of insect pests and its relevance to pest management. In *Insect pest management*. Eds. Horowitz A R & Ishaaya I. Springer-Verlag Berlin Heidelberg New York.
- Niehoff, B. & Poehling, H. M. 1995. Population dynamics of aphids and syrphid larvae in winter wheat treated with different rates of pirimicarb. *Agriculture, Ecosystems and Environment* 52, 51-55.
- Nielsen, C. 1995. Populationsundersøgelse af trips i vinterhvede, med fokus på undersøgelse af insektpatogene svampe som mortalitetsfaktor. *Institut for Ökologi og Molekylær Biologi. KVL*. 122 pp.
- Nielsen, C., Madsen, T. U., Eilenberg, J. & Philipsen, H. 1996. Natural occurrence of entomopathogenic fungi on thrips in a Danish wheat field. *IOBC/WPRS Bulletin* 19, 166-171.

- Nilsson, A. T. S. 1985. Insekticideffekter på arthropodfaunan i två skånska stråsådesfält. *Examensarbete 1985:3. Department of Plant and Forest Protection, Swedish University of Agricultural Sciences.* 85 pp.
- Nilsson, C. 1994. Pollen beetles (*Meligethes spp*) in oil seed rape crops (*Brassica napus* L.): Biological interactions and crop losses. *Swedish University of Agricultural Sciences. Department of Plant Protection Sciences. Faculty of Agriculture. Avhandlingar* 1. 39 pp.
- Nilsson, C. 2000. Miljövänlig bekämpning av bladlöss i ärt och höstvete. *Meddelande från södra jordbruksförsöksdistriktet. Rapport från växtodlings-och växtskyddsagar i Växjö.* Nr 51. 18:1-3.
- Oakley, J. N., Walters, K. F. A., Ellis, S. A., Green, D. B., Watling, M. & Young, J. E. B. 1996. Development of selective aphicide treatments for integrated control of summer aphids in winter wheat. *Annals of Applied Biology* 128, 423-436.
- Parrella, M. P. & Lewis, T. 1997. Integrated pest management in field crops. *Thrips as crop Pests* (ed. Lewis, T.) pp 595-614. CAB International, Wallingford, UK.
- Pedigo, L. P. 1996. Economic thresholds and economic injury levels. *University of Minnesota.* <http://ipmworld.umn.edu/chapters/pedigo.htm> (accessed 15-Sept-2005).
- Pedigo, L. P. 1999. *Entomology and pest management*, 3rd ed. Prentice- Hall, New Jersey.
- Peterson, R. K. D. & Hunt, T. E. 2002. The probabilistic economic injury level: Incorporating uncertainty into pest management decision-making. *Journal of Economic Entomology* 96(3), 536-542.
- Pettersson, H. 1992. Trichothecene analysis in Swedish cereals 1987-1990. *Third European Fusarium Seminar, IHAR Radzików*, 37-41.
- Pettersson, H. & Agnedal, M. 1993. Determination of ergosterol in cereals and relation to mould and mycotoxin concentrations. *Nordiska mykotoxinmötet 1993.*
- Pierre, J. S. & Dedryvér, C. A. 1985. Un model de prevision des pullulations du puceron *Sitobion avenae* sur blé d'hiver. *Phytoma.* Juin 1985.
- Plantegenest, M., Pierre, J. S., Dedryvér, C. A. & Kindlmann, P. 2001. Assessment of the relative impact of different natural enemies on population dynamics of the grain aphid *Sitobion avenae* in the field. *Ecological Entomology* 26(4), 404-410.
- Poehling, H. M. 1987. Nützlinge schonen-aber wie? Am Beispiel Getreidelaus. *Pflanzenschutz-Praxis* 2, 14-19.
- Pons, X. & Tatchell, G. M. 1995. Drought stress and cereal aphid performance. *Annals of Applied Biology* 126, 19-31.
- Pons, X., Comas, J. & Albajes, R. 1993. Overwintering of cereal aphids on durum wheat in a Mediterranean climate. *Environmental Entomology* 22 (2), 381-387.
- Prew, R. D., Church, B. M., Dewar, A. M., Lacey, J., Penny, A., Plumb, R. T., Thorne, G. N., Todd, A. D. & Williams, T. D. 1982. Effects of eight factors on the growth and nutrient uptake of winter wheat and on the incidence of pests and diseases. *Journal of Agricultural Sciences, Cambridge.* 100, 363-382.

- Prew, R. D., Church, B. M., Dewar, A. M., Lacey, J., Magan, N., Penny, A., Plumb, R. T., Thorne, G. N., Todd, A. D. & Williams, T. D. 1985. Some factors limiting the growth and yield of winter wheat and their variation in two seasons. *Journal of Agricultural Sciences*, Cambridge. 104, 135-162.
- Price, P.W. 1991. The plant vigour hypothesis and herbivore attack. *Oikos*. 62, 244-251.
- Price, P.W. & Hunter, M.D. 2005. Long-term population dynamics of a sawfly show strong bottom-up effects. *Journal of Animal Ecology* 74, 917-925.
- Rabbinge, R. & Mantel, W. P. 1981. Monitoring for cereal aphids in winter wheat. *Netherlands Journal of Plant Pathology* 87, 25-29.
- Rabbinge, R. & Carter, N. 1984. Monitoring and forecasting of cereal aphids in the Netherlands: A subsystem of EPIPARE. In *Pest and Pathogen Control*. Ed. Conway, G. R. The Pitman Press, Bath, UK.
- Rautapää, J. 1976. Population dynamics of cereal aphids and methods of predicting population trends. *Annales Agriculturae Fenniae* 15, 272-293.
- Regev, U. 1984. An economic analysis of man's addiction to pesticides. In *Pest and Pathogen Control*. Ed. Conway, G. R. The Pitman Press, Bath, UK.
- Rossing, W. A. H., Daamen, R. A. & Jansen, M. J. W. 1994. Uncertainty analysis applied to supervised control of aphids and brown rust in winter wheat. Part 1. Quantification of uncertainty in cost-benefit calculations. *Agricultural Systems* 44(4), 419-448.
- Sagenmüller, A. 1977. Wirkungen systemischer Fungizide auf die Getreideblattläuse *Sitobion avenae* and *Metopolophium dirhodum*. *Zeitschrift für Angewandte Entomologie* 82, 293-300.
- SCB 2005. Statistiska centralbyrån www.scb.se.
- Schmidt, M. H., Lauer, A., Purtauf, T., Thies, C., Schaefer, M. & Tschamtkke, T. 2003. Relative importance of predators and parasitoids for cereal aphid control. *Proceedings of the Royal Society of Biological Sciences*. Series B270(1527), 1905-1909.
- Sengonca, C., Jösch, H. & Kleinhenz, B. 1994. Einfluss verschiedener Wintergerste- und Winterweizensorten auf die Besiedlung und Populationsentwicklung von Getreideblattläusen. *Gesunde Pflanzen*, 46(1), 3-7.
- Shoemaker, C. A. & Onstad, D. W. 1983. Optimization analysis of the integration of biological, cultural and chemical control of alfalfa weevil (Coleoptera: Curculionidae). *Environmental Entomology* 12, 286-295.
- Sigsgaard, L. 2002. A survey of aphids and aphid parasitoids in cereal fields in Denmark and the parasitoids role in biological control. *Journal of Applied Entomology* 126, 101-107.
- Sigvald, R. 1997. Långtidsprognoser för viktiga bladlusarter i stråsäd, ärt, potatis med hjälp av sugfällor. *Slutrapport Jordbruksverket*. 4 pp.
- Sigvald, R. & Gustafsson, G. 1993. Forecasting and warning systems for pests and diseases in Sweden. *SP-report, Danish Institute of Plant and Soil Science*, 7, 23-31.

- Skirvin, D. J., Perry, J. N. & Harrington, R. 1997. A model describing the population dynamics of *Sitobion avenae* and *Coccinella septempunctata*. *Ecological Modelling* 96, 29-39.
- Stenseth, N. C., Leirs, H., Skonhott, A., Davis, S. A., Pech, R. P., Andreassen, H. P., Singleton, G. R., Lima, M., Machangu, R. M, Makundi, R. H. Zhang, Z., Brown, P.B., Shi, D., & Wan, X. 2003. Mice and rats: the dynamics and bio-economics of agricultural rodent pests. *Frontiers in Ecology and the Environment* 1(7), 1-12.
- Stern, V. M. 1975. The bio-economics of pest control. *Iowa State Journal of Research*, 49, 467-472.
- Taylor, L. R. 1977. Aphid forecasting and the Rothamsted Insect survey. *Journal of Royal Agricultural Society* England. 138, 75-97.
- Taylor, L. R. 1986. Synoptic dynamics, migration and the Rothamsted Insect Survey. *Journal of Animal Ecology* 55, 1-38.
- Turchin, P. 2003. *Complex population dynamics: A theoretical/empirical syntheses*. Princeton University Press, Princeton and Oxford.
- Turchin, P. & Taylor, A. D. 1997. Complex dynamics in ecological time series. *Ecology* 73, No 1, 289-305.
- Walker, P. T. 1983. Crop losses; the need to quantify the effects of pests, diseases and weeds on agricultural production. *Agricultural Ecosystems and Environment* 9, 119-158.
- Walters, K. F. A. & Dewar, A. M. 1986. Overwintering strategy and the timing of the spring migration of the cereal aphids *Sitobion avenae* and *Sitobion fragariae*. *Journal of Applied Ecology* 23, 905-915.
- Ward, S. A, Chambers, R. J., Sunderland, K. & Dixon, A. F. G. 1986. Cereal aphid populations and the relation between mean density and spatial variance. *Netherlands Journal of Plant Pathology* 92, 127-132.
- Watt, A. D. 1983. The influence of forecasting on cereal aphid control strategies. *Crop Protection* 2(4), 417-429.
- Wennergren, U. & Landin, J. 1993. Population growth and structure in a variable environment. I. Aphids and temperature variation. *Oecologica* 93, 394-405.
- Wetzel, T., Ghanim, A. & Freier, B. 1981. Zur Bedeutung von Prädatoren und Parasiten für die Überwachung und Bekämpfung von Blattläusen in Getreidebeständen. *Nachrichtenblatt für den Pflanzenschutz in der DDR*. 35(12), 239-244.
- Wikteliuss, S. & Ekbohm, B. S. 1985. Aphids in spring sown cereals in central Sweden. Abundance and distribution 1980-1983. *Zeitschrift für Angewandte Entomologie* 100, 8-16.
- Wiles, J. A. & Jepson, P. C. 1995. Dosage reduction to improve the selectivity of deltamethrin between aphids and coccinellids in cereals. *Entomologica Experimentalis et Applicata* 76(1), 83-96.
- Wood, E.A. 1965. Effect of foliage infestation of the English grain aphid on yield of Triumph wheat. *Journal of Economic Entomology* 58, 778-779.

- Vorley, W. T. & Wratten, S. D. 1985. A simulation model of the role of parasitoids in the population development of *Sitobion avenae* on cereals. *Journal of Applied Ecology* 22, 813-823.
- Zhou, X. & Carter, N. 1991. The effects of nitrogen and fungicide on cereal aphid population development and the consequences for the aphid- yield relationship in winter wheat. *Annals of Applied Biology* 119(3), 433-441.
- Zimmerman, G. 1976. Über die Wirkung systemischer Fungizide auf Aphiden befallende Entomophthoraceen (Zygomycetes) in vitro. *Zeitschrift für Pflanzenkrankheiten Pflanzenpathologie Pflanzenschutz*. 83, 261-269.

Acknowledgements

First, I want to thank my supervisors Eva Johansson and Christer Nilsson for critical discussions and helpful instructions for making this thesis possible.

I also thank Olof Hellgren for interesting discussions and for valuable help with computer problems.

I specially thank Bertil Christensson and Fatih Mohammad for technical assistance with the field experiments during many years.

I also thank all present and former colleagues in the previous Plant Protection Department.

I thank Roland Sigvald, Department of Ecology and Crop Production Science, Uppsala for permitting me to analyse the thrips in the catches from the suction trap in Alnarp.

I thank Hans Pettersson, Department of Animal Nutrition and Management, Uppsala for help with the analysis of mycotoxins in the grain.

The English language in my manuscripts was corrected by Mary McAfee, many thanks for excellent work.

Financial support was received from the Swedish Board of Agriculture, the Swedish University of Agricultural Sciences and Swedish Farmers' Foundation for Agricultural Research. All are gratefully acknowledged.

Finally I dedicate this thesis to my family, my wife Eva and my sons Tobias, Jakob and Niklas.