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Preface

The biennial meeting of the group took place at the Institute of Plant Protection and Plant Diseases, University of Hannover from 28 February to 1 March 1995. Fourthy participants from 10 European countries attended the meeting. Beside a core of 15-20 regular members as in former meetings a high number of younger scientists, mainly postgraduate students, presented their latest research results and contributed very much to constructive and encouraging discussions.

Apart from the paper sessions some time was spent on basic discussions dealing with the self-image and future orientation of the group. Although the economic importance of cereals has decreased in some areas of Europe further research activities in this important crop seem to be necessary and justified. Cereals still cover most of the cultivated area in Europe. Recent alterations in culture practices and plant protection strategies (e.g. extensive, low input farming, large set-aside areas within rotations), regional changes in the landscape structure but also new trends in climatic conditions may have important consequences for the dynamics, the pest status and the natural regulation of pests as well a strong impact on the cereal ecosystem in general. The cereal ecosystem offers a convenient and suitable "model" to study such induced changes in biotic and abiotic interactions in detail and to evaluate the consequences for sustainable integrated production systems; moreover different aspects of "applied nature conservation" in agro-ecosystems can be included. The following future research objectives of WG members were considered of major importance:

- Long-term monitoring and population dynamic studies of pests (aphids) and natural enemies
- Quantification (modelling) of predator/parasitoid efficacy and plant -pest- enemy interactions including multitrophic interactions (chemical ecology)
- Plant resistance (genetically based resistance and induced resistance)
- Interaction of plants, pests (e.g. aphids as vectors) and pathogens (e.g. BYDV)
- Effects of low input farming systems on cereal pests and natural regulation
- Pesticide-side effects, focused on seblethal effects and foraging behaviour, risk modelling
- Site specific mapping (GIS) of pests and natural enemy societies in relation to climatic conditions, vegetation and landscape, including population genetics and clonal diversity
- Temporal and spatial distribution pattern of pests and beneficials
- Effects of habitate structure (large vs small fields, field boundaries, ecotones) on biodiversity ("applied nature conservation") and pest-antagonist interactions.

H.M. Poehling

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CONTENTS

RESEARCH REPORTS

Development and reproductive potential of cereal aphids (Homoptera: Aphididae) on winter wheat cultivars

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Summary

The effect of different winter wheat cultivars on the biological performance (weight, developmental time, mean relative growth rate and fecundity) of *Rhopalosiphum padi* was investigated in the laboratory.
Aphids cultivated on wheat varieties 'Haven' and 'Orestis' kept the poorest food quality. They developed slowly, reached a reduced mean relative growth rate and the smallest fecundity. In contrary 'Xanthos' and 'Lambros' were found as cultivars with best food quality.
To test the degree of variation of performance between aphid races, different colour morphs of *Sitobion avenae* were cultivated on 'Orestis'. The brown coloured strains showed a reduced fitness compaired to those coloured green.

Introduction

Cereal crops were damaged seriously by aphids during the 1968-1978 period in Europe. (Carter et al., 1982, Vickerman & Wratten, 1979). Besides the use of insecticides host plant resistance could have a limiting effect on aphid population levels. The hypothesis is that even a slight level of plant resistance may extend the time period over which biotic and abiotic factors can operate and reduce the rate of aphid population increase to enable natural enemies to control their host population (Caillaud et al., 1994, Van Emden, 1990). Plant breeders are strongly interested in informations about characters which can easily indicate the level of resistance of plant varieties. The objectives of this study were to determine in a first set of experiments the effects of different winter wheat cultivars on the biological performance of *Rhopalosiphum padi*. Because aphid species exist in a multitude of races and genotypes in a second set of experiments colour morphs of *Sitobion avenae*, that are easy to distinguish were used to determine differences in the fitness of these strains cultivated on 'Orestis'.

Materials and Methods

Plant Culture and Experimental Design

Seedlings of different winter wheat cultivars 'Xanthos', 'Haven', 'Astron', 'Lambros' and 'Orestis' were potted individually in 8 cm pots. For all experiments, tests were initiated when plants were in the 2-3 leaf stage. The plants were placed in a constant clima cabinet at 20°C and 16:8 (L:D) h photoperiod with an RH of 60 ± 5%.

On each plant a single aphid larvae (< 24 h old) was allowed to feed. To protect the aphids and exclud the possibility of running away the plants were covered individually with a glass cylinder that was covered with a gauze.

All pots were scattered randomized below the lights.

Aphids

Aphids used for this study were collected from wheat at the field nearby Rostock, M/V. Whereas *Rhopalosiphum padi* is in culture since two years, the different colour morphs of *Sitobion avenae* for one year. Strains of both species were cultivated on nonvernalized winter wheat. *R. padi* (strain BS) used as control was cultivated at the BBA Braunschweig since 1988.

Parameters Evaluated

To find cultivars with lowest food quality *R. padi* was used. For later experiments the wheat variety 'Orestis' was used to estimate differences in performance between colour morphs of *S. avenae*.

To monitor biological performance, larval weight (in the first 24 h after birth), adult weight (in the first 24 h after reaching maturity) and developmental time (from birth to adult stage) were registered. Because weight is realized in time, mean relative growth rates (MRGR) were calculated for all individuals using the formula after Fisher(1920) and Radford (1967). To analyse fecundity, adult aphids were placed on their host plants after weighing and allowed to produce offsprings for the time equivalent to their developmental time.

Data Analysis

Data sets were considered to be independent and were analyzed separately using SPSS software.

Results and Discussion

The conditions for the development of the aphids differed significantly among cultivars. Using adult weight as character, the lowest performance was found on 'Astron' (Fig. 1). Size ie weight is unlikely to be a powerful indicator of aphid performance over a wide range of conditions. This is because weight is a consequence of the effects of host plant quality, temperature and birth weight (Dixon et al., 1982; Leather & Dixon, 1984). Apterous females of *R. padi* developed fastest on 'Lambros'. There were no significant differences in development time between the other cultivars (Fig. 2). MRGR's were highest on 'Xanthos' and 'Lambros'(Fig. 3). With exception of 'Astron', the number of *R. padi* nymphs produced in the time equivalent to developmental time was smaller on that cultivars which allowed also a small MRGR (Fig. 4). For aphids cultivated on 'Haven' and 'Lambros' the number of embryos were analysed (Fig. 5). There were no differences in the number of embryos with pigmented eye spots, but total number of embryos differed significantly (P< 0,05). Large embryo counts are only an indication of the initial rate of reproduction (Leather & Wellings, 1981) because ovulation continues after adult moult of *R. padi,* but only for the first 10 days of reproduction (Leather & Dixon, 1983). In comparision to alatae females, apterous *R. padi* developed faster and were havier in weight. It is therefore difficult to use winged cereal aphids for screening cultivars.

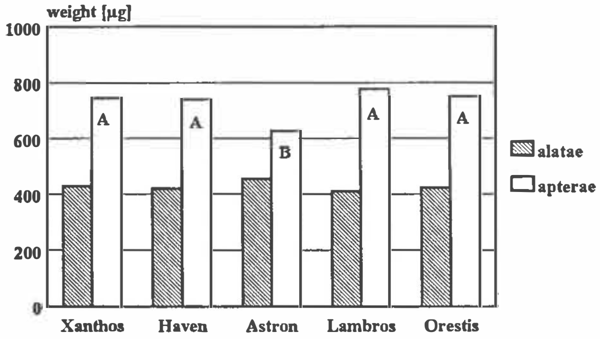

Fig. 1: Adult weight of *Rhopalosiphum padi* on different cultivars of winter wheat at 20°C.

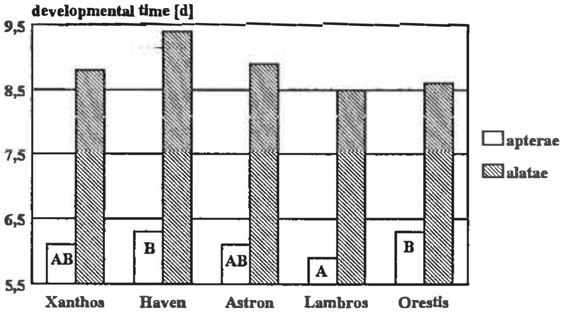

Fig. 2: Developmental time (D) of *Rhopalosiphum padi* on different cultivars of winter wheat at 20°C.

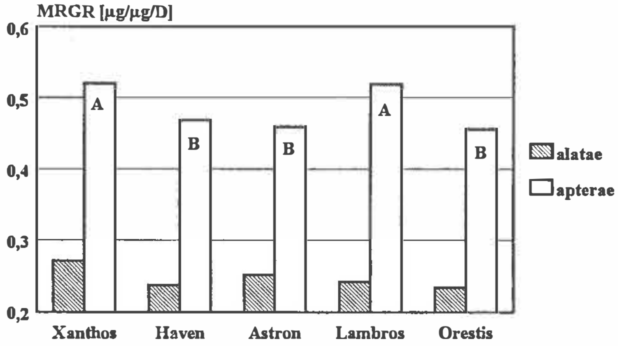

Fig. 3: Mean relative growth rate of *Rhopalosiphum padi* on different cultivars of winter wheat at 20°C.

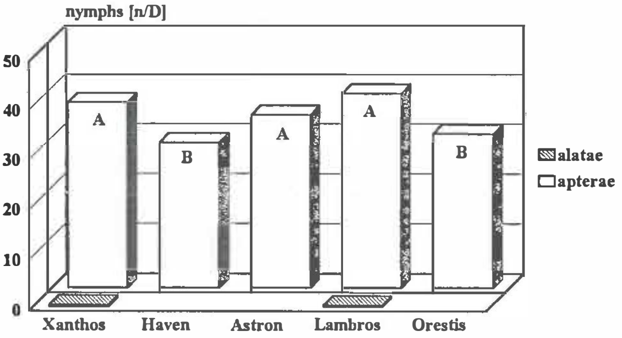

Fig. 4: Number of nymphs produced by *Rhopalosiphum padi* in the time equivalent to D on different cultivars of winter wheat at 20°C.

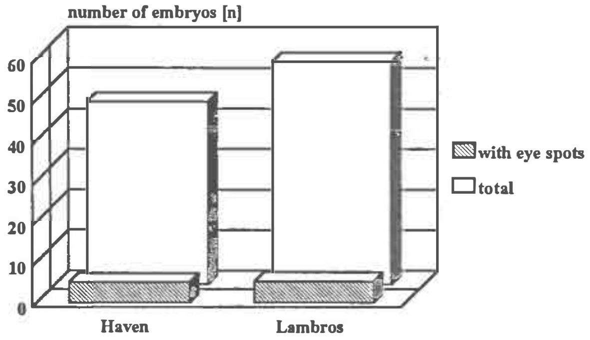

Fig. 5: Total number of embryos and number of embryos with pigmented eye spots of apterous *Rhopalosiphum padi* on cultivars of winter wheat at 20°C.

The colour morphs of *S. avenae* show strong differences in their performances. Brown coloured aphids of strains B4 and BP2 were lighter than green coloured aphids of strains GhBK, G3 and GehG14 (Fig. 6). The weight of brown aphids of *S. avenae* is comparable to those of *R. padi* (strain BS). Whereas brown *S. avenae* need a longer period of time to become adult than the green aphids, *R. padi* developed fastest (Fig. 7).

MRGR's differed significantly between both, the colour morphs and the species. The lowest performance of this character was reached by brown *S. avenae* (Fig. 8). The largest increase of weight per time was found for *R. padi* . These aphids produced also the most offsprings at the time given. With exception of strain G3 green coloured *S. avenae* had higher fecundity compared with brown morphs (Fig. 9). An examination of the 1992-1994 field collections showed that brown coloured morphs of *S. avenae* were predominant in high summer. However, it is possible that these have a better fitness at higher uv radiation.

It is important, therefore, that this variability in performance between different races of aphids is taken into consideration in resistance studies.

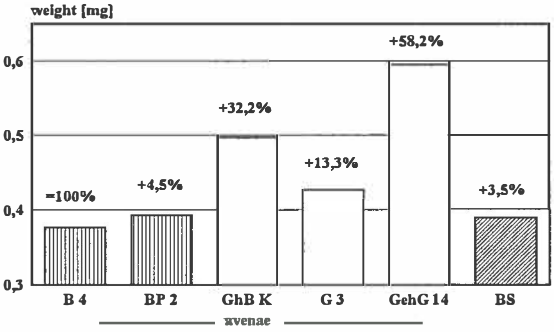

Fig. 6: Adult weight of *Rhopalosiphum padi* (origin: Braunschweig) and different strains of *Sitobion avenae* on winter wheat ('Orestis') at 20°C. (B4 - brown, BP2 - brown/pink, GhBK - green/light brown, G3 - green, GehG 14 - yellow/light brown)

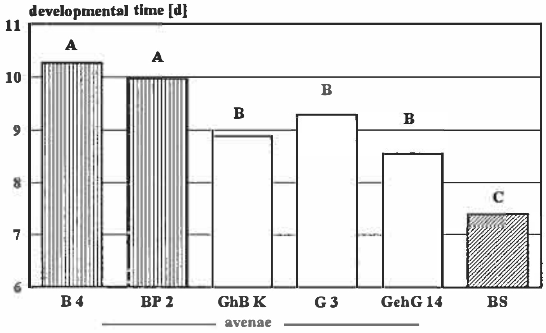

Fig. 7: Developmental time (D) of *Rhopalosiphum padi* (origin: Braunschweig) and different strains of *Sitobion avenae* on winter wheat ('Orestis') at 20°C.

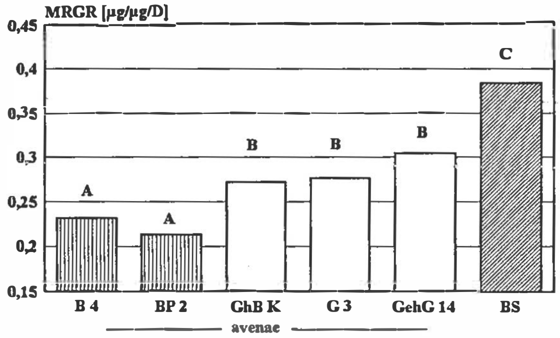

Fig. 8: Mean relative growth rate of *Rhopalosiphum padi* (origin: Braunschweig) and different strains of *Sitobion avenae* on winter wheat ('Orestis') at 20°C.

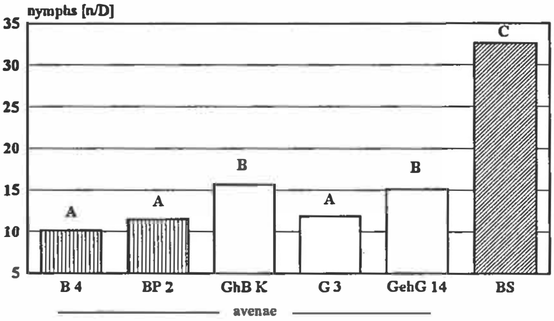

Fig. 9: Number of nymphs produced by *Rhopalosiphum padi* (origin: Braunschweig) and different strains of *Sitobion avenae* on winter wheat ('Orestis') at 20°C.

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FLUCTUATION IN ABUNDANCE OF CEREAL APHIDS IN HUNGARY, WITH SPECIAL REGARDS TO *DIURAPHIS NOXIA*

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ABSTRACT

The flight of cereal aphids was monitored by a Rothamsted type suction trap from 1990 until 1994. In 1993 the most abundant cereal aphid in the suction trap was *D. noxia* while in 1990 *Schizaphis graminum* (Rondani). In the other 3 years *Rhopalosiphum padi* (L.) was the most frequent, in this case in 1992 the summer peak was very high and the autumn peak was so low as to be negligible. However in 1991 and in 1994 the summer flight of *R. padi* was much weaker than the autumn one.

Diuraphis noxia (Kurdjumov) was first detected by a yellow pan trap in Central Hungary in 1989, in 1990 a Rothamsted type suction trap collected 31 individuals. *D. noxia* infestation was found in an autumn sown wheat field in October 1990. The *D. noxia* population that overwintered was holocyclic. Between 1990 and 1993 in natural conditions *D. noxia* proved to be pest once on a sparsely emerged spring barley field out of the 317 cereal fields examined. Apart from this it has been found once on cereals during spring in 1991 on the wheat field where it occurred in the autumn. It overwintered in egg stage and fundatrices were present in early April. *D. noxia* was most commonly found on early emerged volunteers.

D. noxia colonies were found on *Avena fatua* L., *Sorghum halepense* L. (Pers.), *Briza maxima* L.-Qu., *Bromus macrostachys* Desf., *Lagurus ovatus* L..

Progenies of fundatrices were used to artificially infest wheat plants on the beginnig of May. Infested plants were destructively sampled at weekly intervals from the end of May until beginning of July. In 1993 The *D. noxia* abundance was highest on 8 June while in 1994 on 21 June.

INTRODUCTION

Cereals are grown on roughly 1.5 million ha or about one third of the arable field area in Hungary. The first cereal aphid species reported in Hungary was *Schizaphis graminum* (Rondani) (Horváth, 1882). *Sitobion avenae* (Fabricius) was reported in 1897 by Horváth. In Hungary *Sitobion avenae* is considered to be the most frequent cereal aphid by Szalay-Marzsó (1970), Kuroli and Német (1987).

Diuraphis noxia (Kurdjumov) is indigenous in the Iranian Turkestanian mountain range and in the Mediterranean region, although no severe outbreaks have been reported from this region, (Mordvilko, 1929, Nevskii , 1929).It has been reported a pest of wheat and barley in southern Russia before 1900 (Grossheim, 1914). *D. noxia* has now spread from its original habitat and become a devastating pest in South Africa since 1978 (Walters et al., 1980) and in the United States since 1986 (Burton, 1989).

D. noxia was detected in Hungary in 1989 by Basky and Eastop (1991) it is a new record in Central Europe and in the Balkan region.

The present study gives an account of spatial distribution of *D. noxia* in Hungary, the structure of its populations and its hostplants. Information on the population changes of other cereal aphids is included.

MATERIAL AND METHODS

A Rothamsted type suction trap continuously collected the aphids from 1 April until 30 October. The trap was emptied daily and aphids were identified with the help of a stereo microscope. Between 1990 and 1992 a survey was carried out on the Great Hungarian Plain to determine the presence or absence of *D. noxia* on 317 cereal fields. At least a thousand plants were examined in each field. The survey was continued after harvest on stubble and on volunteer cereals.

In addition the survey included 12 grass, ten monocotyledon weed and 4 ornamental grass species. Thousand tillers were surveyed of each of the following species: *Agropyron pectinatum* (M. B.) P. B., *Phleum pratense* L., *Dactylis glomerata* L., *Poa pratensis* L., *Lolium perenne* L., *Agrostis alba* L., *Typhoides arundinacea* (L.), *Festuca rubra* L., *Festuca tenuifolia* Sibth., *Festuca arundinacea* Schreb., *Bromus pannonicus* Kumm et Sedtn., *Festuca pratensis* Hubs., *Echinochloa crus-galli* (L.), *Elymus repens* (L.) P. B: Neski. *Bromus mollis* L. *Hordeum murinum* L. *Setaria viridis* (L.) P. B., *Phragmites communis* Trin., *Cynodon dactylon* (L.) Pers., *Avena fatua* L., *Sorghum halepense* L. (Pers.), *Bromus macrostachys* Desf., *Briza maxima* L. -QU., *Lagurus ovatus* L., *Polypogon monspeliensis* (L.) Desf.

In 1993 wheat plants in 2-3 node stage were infested with the progenies of *D.noxia* fundatrices on 28 April. Two apteriform nymphs and 3 aptrae were placed into plastic vials with a piece of wheat leaf. The aphids were placed into the leaf sheathes with forceps and a fine brush.

Wheat plants at the early booting stage were infected the same way in 1994 (May 8th). One hundred plants were infested both years. The infested plants were destructively sampled from the last week of May until the first week of July. Ten samples were collected each time. These were placed individually in plastic bags for transport to the laboratory. There they were placed into Berlese funnels, illuminated above. A plastic vial containing 75 % alcohol at the bottom of the funnel served to collect aphids. The aphids were counted and separated into forms by the help of stereo-microscope.

RESULTS

In 1990 the Rothamsted type suction trap indicated a cereal aphid flight peak in the middle of June. *Schizaphis graminum* was the most abundant comprising 39 % of the cereal aphid catch, followed by *Sitobion avanae* 29 %, *Metopolophium dirhodum* (Walker) 18 % and *Rhopalosiphum padi* (L.) 13 %. In that year the summer flight was stronger in case of *R. padi* (Fig.1).

In 1991 the summer peak of cereal aphid flight fell in the last 10 days of June. The most abundant species was *R. padi* with a low summer and high autumn flight, this species comprised 68 % of the total cereal aphid catch. The second numerically most important was *D. noxia* 15 %, followed by *S. graminum* 12 % (Fig 2).

In 1992 the suction trap caught 1123 alata aphids and 10 % of the total catch was cereal aphid. The prevailing species was *R. padi* with a higher summer and a lower autumn peak (Fig. 3).

In 1993 the prevailing cereal aphid species in the suction trap was the *D. noxia*. Its flight was more intensive at the end of June and beginning of July (32625 and 17900 individuals respectively). In that year the number of other cereal aphids in the suction trap was much lower: *R. padi* was the second most numerous with a total catch of 809 individuals, followed by *S. avenae* and *S. graminum* (Fig. 4).

In 1994 *R. padi* was the prevailing cereal aphid species in the suction trap (69 %) with a considerable summer and even higher autumn flight peak The second most abundant cereal aphid species was *D. noxia* (22 %). The summer peak flight of *R. padi* was in the middle of June while that of *D. noxia* was in the beginning of July (Fig. 5).

FLIGHT OF CEREAL APHIDS IN THE SUCTION TRAP

SZOLNOK 1990

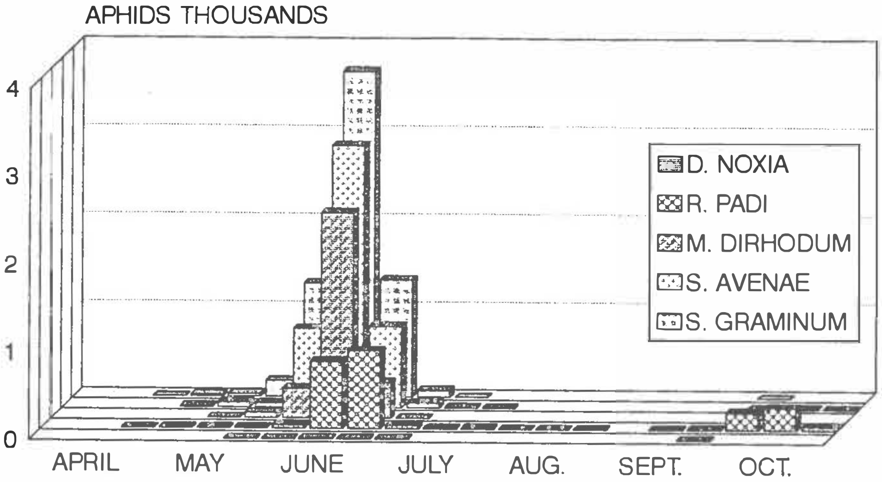


Fig. 1

FLIGHT OF CEREAL APHIDS IN THE SUCTION TRAP

SZOLNOK 1991

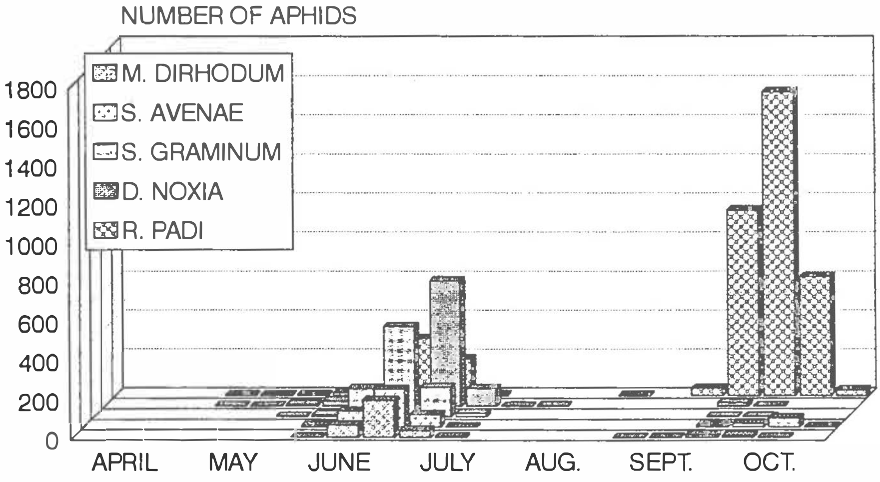


Fig. 2

FLIGHT OF CEREAL APHIDS IN THE SUCTION TRAP

SZOLNOK 1992

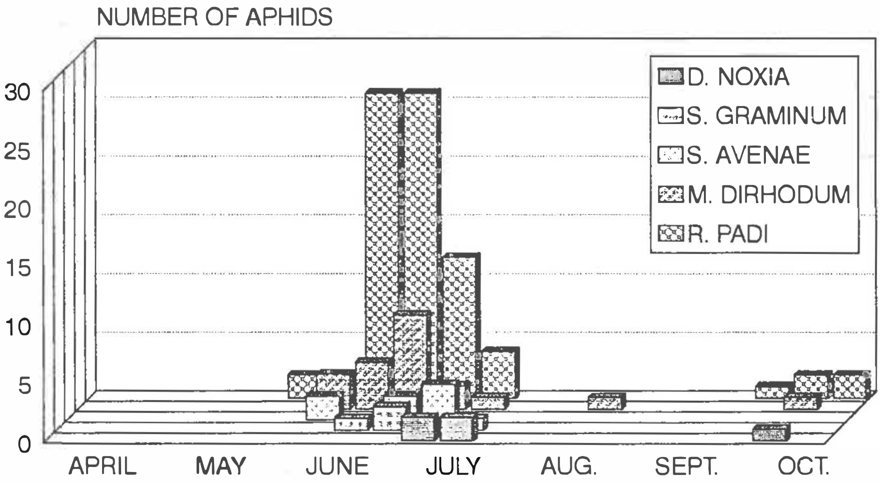


Fig. 3

FLIGHT OF CEREAL APHIDS IN THE SUCTION TRAP

SZOLNOK 1993

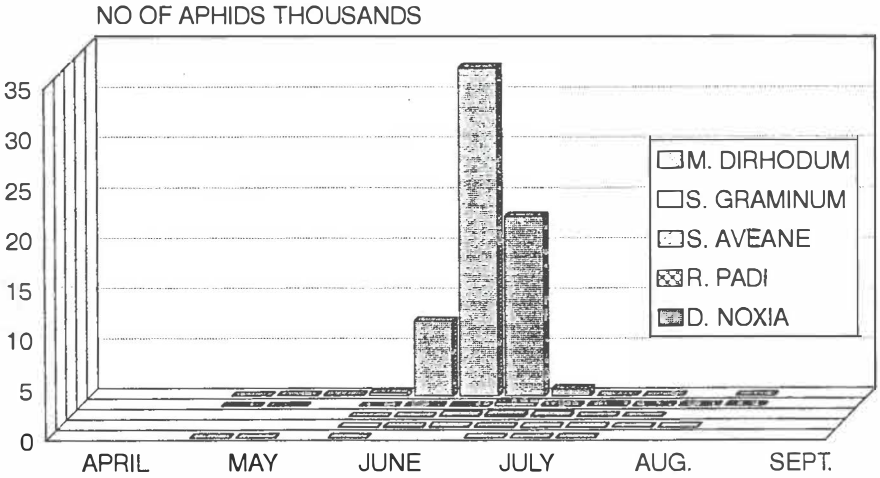
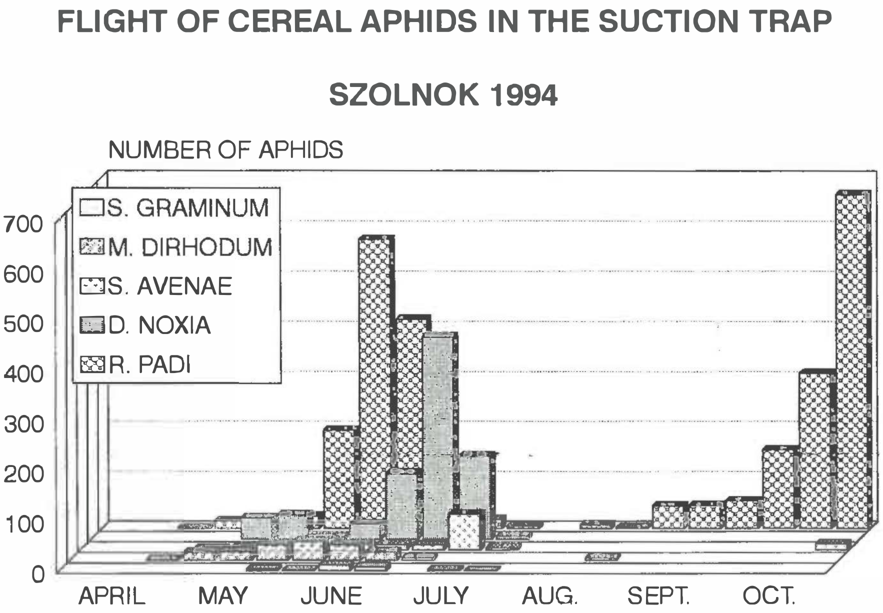


Fig. 4



FLIGHT OF CEREAL APHIDS IN THE SUCTION TRAP

SZOLNOK 1994

Fig. 5

Of the 317 fields surveyed, 41 fields sown with autumn cereals were inspected in the in autumn. A very low *D. noxia* infestation was found on 11 of those fields with 1-2 infested plant per m^2. The spring survey included 103 fields, and revealed the presence of *D. noxia* in two fields. *D noxia* fundatrices were found in April in one of the fields where it had been present the autumn. The level of the spring infestation was one -fifth of the autumn one. The other spring infestation was found in a sparsely emerged spring barley field where *D. noxia* reached pest status. In some cases the plants became dwarf, and in the rolled leaves there were large colonies of *D. noxia*. Practically 100 % of the plants were infected. Of the 173 stubbles examined, *D. noxia* was found in 37 cases where the volunteers emerged early, the infestation rate of the volunteers was never higher than 1-2 %.

Characteristic leaf curling, yellow stripes and *D. noxia* colonies were present on the ornamental grasses: *Briza maxima* and *Lagurus ovatus*. *Bromus macrostachys* was so severely damaged that 30 % of the plants died as a result of *D. noxia* infestation.

Small colonies were found on *Avena fatua* and *Sorghum halepense*, but without the characteristic symptoms of *D. noxia* feeding.

Yellow chlorotic spots typical of the feeding sites of *D. noxia* were present on *Typhoides arundinacea*, *Festuca rubra* and *Festuca arundinacea*, but not a single aphid was present on these grasses at the time of survey at the end of July.

Neither the symptoms of *D. noxia* feeding nor *D. noxia* individuals were found on the other examined grass and monocotyledon weed species.

On the artificially infested plants the *D. noxia* population gradually increased in 1993 until 8th July and than continuously decreased. The proportion of alatiform nymphs was the highest from 8 June and the tendency was the same in case of alatae as well (Fig 6).

D. noxia colonies were much less abundant in 1994 than in 1993 (Fig.7), there was a steady decline in the abundance in 7 July. The proportion of the alatae and alatiform nymphs was much lower than that of apterae and nymphs.

DISCUSSION

Based on the suction trap data from the examined 5 years *R. padi* was the most abundant cereal aphid in three years, *S.graminum* proved to be the most abundant once. Kuroli and Német (1987) also observed the annual changes in the abundance of cereal aphid species during their 8 years observation period.

In 1993 The suction trap caught an enormous number of *D. noxia*. In that year *D. noxia* individuals originated from the artificially infested wheat field which was less than one km distance from the suction trap. As the population declined on the wheat the number of *D. noxia* individuals increased in the suction trap. In 1994 the abundance of *D. noxia* was much lower on the artificially infested plants. Partly because the infestation happened later in a more advanced phenological stage (beginning of booting) and partly because the season was less dry than in the previous year.

Some predator activity might cause the sharp decline in the *D. noxia* population by 7 June in 1994. The survey of the 317 fields was carried out in the Great Hungarian plain which is the main wheat growing area of Hungary. The location did not have any effect on the presence or the absence of *D. noxia*. Apart from two cases during spring population decreased into undetectable level, but the Russian wheat aphid was always present on early emerged volunteers. *D. noxia* is able to overwinter in Hungary. The lack of infestation in spring may be due to the activity of *Coccinellids* which are searching for food already at that time when fundatrices hatch.

The pest status of *D.noxia* on *Bromus macrostachys*, *Briza maxima* and *Lagurus ovatus* ornamental grasses and the presence of *D. noxia* colonies on *Avena fatua* and *Sorghum halepense* weed species is new record (Halbert et al. 1990).

CHANGES IN THE NUMBERS OF DIFFERENT DIURAPHIS NOXIA MORPHS ON THE WHEAT PLANTS SZOLNOK, 1993

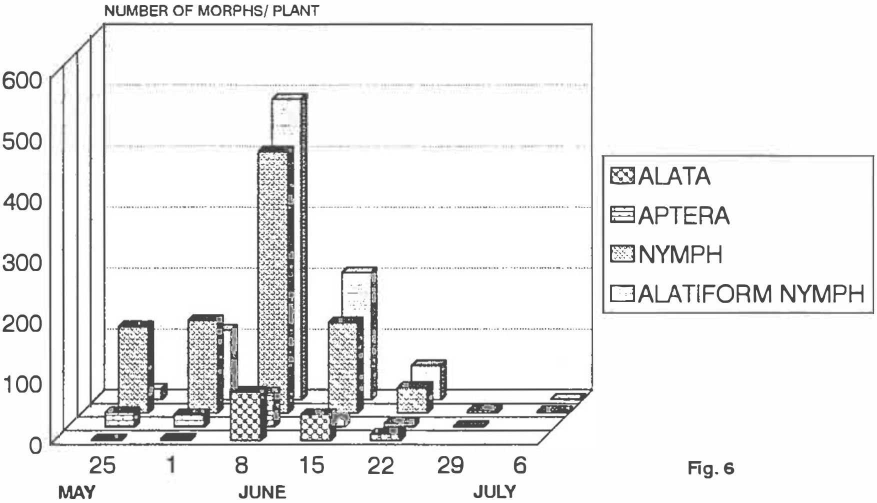


Fig. 6

CHANGES IN THE NUMBERS OF DIFFERENT DIURAPHIS NOXIA MORPHS ON THE WHEAT PLANTS SZOLNOK, 1994

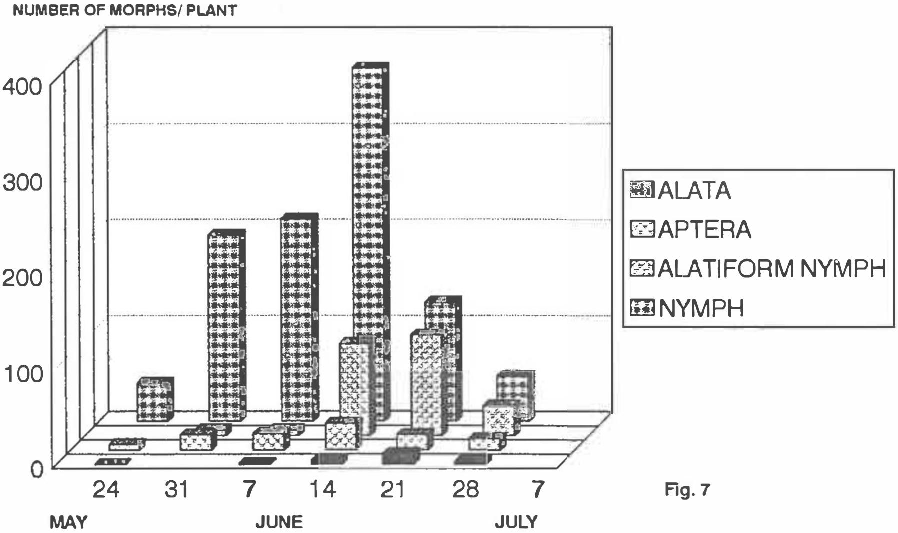


Fig. 7

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THE FUNCTIONAL RESPONSE OF THREE MAJOR PARASITOIDS OF *Sitobion avenae* : *Aphidius rhopalosiphi, A. ervi* AND *P. volucre* - HOW COULD DIFFERENT BEHAVIOURS CONDUCT TO SIMILAR RESULTS?

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INTRODUCTION

POWELL (1986) stated that integrated control of the cereal aphids could be achieved by improving the antagonist activities in the field. The problem is however to reach an equilibrium in such a system and to maintain the pest population fluctuations below the economic threshold.

The aphids - parasitoids systems are characterized by patchy host distribution, overlaping generations of the two partners and generations which are not synchronous between the host and the parasitoid. In such a system, the stability of the interaction increases when spatial refuges for the host or / and a invulnerable class of hosts or / and a "TYPE III" functional response of the parasitoid to its host exist (MURDOCH and STEWART-OATEN 1989). In the Nicholson - Bailey discrete-time model (HASSELL and MAY 1973), the aggregation by parasitoids towards patches with high aphid densities; observed by HAGVAR and HOFSVANG (1987); is found to have a stabilizing effect, which is not observed in continuous interactions (MURDOCH and STEWART-OATEN 1989).

The functional response of an antagonist is determined by the intensity of exploitation of its prey as a function of the resource density (SOLOMON 1949 *in* MOLS 1993). HOLLING (1959 *in* HASSELL *et al.* 1977) had described three types of such functional responses. TYPE I explains the density independant response, where the antagonist attacks always the same proportion of the prey available until it reaches its maximum capacity. In TYPE II relationship, the predator or parasitoid kills the prey at a decreasing proportion when the prey density increases. In this case it is an inverse density dependance response. Finally, in TYPE III response, the proportion of prey consumtions increases till an indermediate density and then begins to decrease. This sigmoid response may be due to changes in the foraging behaviour of the antagonist (MOLS 1993) or to changes in the rate of attack that increases with host density (HASSELL *et al.* 1977).

It has been found in the begining that invertebrate predators and parasitoids were associated with TYPE II response (HASSELL and ROGERS 1972, HASSELL and MAY 1973), however some sigmoid functional responses were also suspected (HASSELL *et al.* 1977). They have concluded from their studies that only the TYPE III functional response leads to a stable interaction, positive density dependance, till the host density reaches the inflexion point of the sigmoid curve (HASSELL *et al.* 1977). In these limits the parasitoid can control its host without numerical response of the adults (MOLS 1993).

In this context, I examined the fixed time functional response (WALDE and MURDOCH 1988) of *Aphidius rhopalosiphi* (De Stefani-Perez) *A. ervi* (Haliday) and *P. volucre* (Haliday) (Hymenoptera : Aphidiidae), three major parasitoids of the cereals aphids in Western Europe (JONES 1972, LATTEUR 1976) on *Sitobion avenae* (Fabricius) (Homoptera : Aphididae), one of their hosts. The main objective is to determine the parasitoid which gives more stable interaction and the lower density level.

During this experiment, after a conventional functional response experiment, I have splitted the behaviour of the female parasitoids by direct observations of the handling time, searching time, resting time and cleaning time, parameters that interfere in this kind of relation.

MATERIALS AND METHODS

Insect rearings, standardisation of the aphids and of the female parasitoids for the experiment

The green strain of *S. avenae* was collected on winter wheat *cv.* Estica near Louvain-la-Neuve in 1993. It is maintained on winter wheat *cv.* Camp Remy, at 20±1.5 °C, 60% r.h. and 16 hr. light. The cultures of *A. rhopalosiphi* and *A. ervi*, initiated with individuals collected from the same field, were maintained in the same conditions of their host. The strain of *P. volucre* was collected in 1994, from *S. avenae* mummies, at the same place.

Aphid parasitoids can parasitize all host instars but second and third instars are often preferred (SHIROTA *et al.* 1983). Therefore the female parasitoids were provided with larvae of 2nd and 3rd instars (48 to 96 hr old) of S. *avenae*.

Because the size of the female parasitoids will influence their bionomics (SHIROTA *et al.* 1983), the female parasitoids used for the experiment were reared only from 2nd and 3rd instar aphids. They were 6 to 26 hr old, fed with a honey solution, and maintained in contact with other females and males of conspecies.

Functional response comparison

This experiment was performed at a day/night temperature of 20°C/18°C, a photoperiod of 16:8 hr. and 60% r.h. The host densities tested were 2, 4, 6, 8, 10, 16, 32, 64 and 120 of 2^{nd} to 3^{rd} instars larvae. Each experimental arena was constituted by 10 '7 days old' wheat seedlings, *cv.* Camp Remy, covered by a plastic bottle of 1005 cm^3. The top of the bottle was closed with a 300 µm muslin. In each bottle, a female parasitoid was introduced and allowed to parasitise for 24 hrs. The aphids were maintained at 22°C until the formation of mummies. Both mummies and surviving aphids were counted. Five replications were realised at the densities of 2, 4, 6, 16, 32 and 120 aphids and ten replications were performed for the densities of 8, 10 and 64 aphids. Five check replications, without parasitoid female introduction, were performed in order to compare aphid mortality in the two conditions.

Estimation of real handling time and real searching time

These measures were taken in the same experimental set up during half an hour on five replicates for the densities of 8, 10, 64 and 120 aphids. During this period all pauses, cleaning times, searching times and handling times (time taken by a parasitoid from the moment it reaches a host to parasitize until leaving it to search again) were noted.

Data analysis

It is posiible to distinguish between TYPE II or a TYPE III fuctional response, indeed, in the first case, a' - the instantaneous attack rate (container^{-1} hour^{-1}) - and T_h - the handling time - are constant. These parameters are constant if there is a significant linear relationship between the proportion of hosts surviving (1/ln(x)) and the host density (1) (DRANSFIELD 1979, MACKAUER 1983), indicating a TYPE II response.

$$1 / \ln((N_0-N_{par})/N_0) = -T_h * N_0 - 1/a' \qquad (1)$$

where a' (container^{-1} hour^{-1}) = instantaneous attack rate

T_h (hour) = handling time

N_0 = initial density

N_{par} = number of host parasitized

In that case, T_h and a' were introduced in the equation of random search for host (2) (HASSELL *et al.*, 1977). Expected N_{par} was estimated for the different densities in that way and compared with the N_{par} of the experiment (SHU-SHENG 1985). In order to compare the three species, a 95% confidence interval on these parameters was calculated by the DUD - least square SAS procedure (SAS Institute, 1985).

$$N_{par}=N_0*(1-\exp(-a'*T_s/(1+a'*T_h*N_0))) \qquad (2)$$

When relation (1) is not significant two other steps have been followed. First, the original data have been fitted to HOLLING "TYPE III" (TENHUMBERG and POEHLING 1994) function (3). The "k" parameter gives information on the pest level when the equilibrum host - parasitoid is reached, and allows to compare this level between the three parasitoid species.

$$N_{par}=k*N_0^2/(N_0^2+d^2) \qquad (3)$$

where k = the maximum number of host parasitized

d = the amount of host when half of 'k' is reached

The second step was to test the heterogeneity of the parameters T_s and T_h, mesured in the laboratory in function of the host density. a', estimated from (4) (MOLS 1993), was also tested for heterogeneity in relation with host densities. These are in view to explain the origin of these TYPE III functional responses and to determine the rôle played by each parameters.

$$a' = \ln(N_0/(N_0-N_{par}))/T_s \qquad (4)$$

where T_s (hour) = the real searching time = total time - resting time - number of host encounter * T_h

RESULTS

Number of hosts recovered in controls, without parasitoid introduction, were not significantly different ($F(3,21) = 1.685$; $p = 0.174$) from the cumulated number of hosts and mummies found in the presence of parasitoids. The data were then report to their initial density.

$$N_{par(corr)} = (N_{par(obs)} / (N_{par(obs)} + N_{(surv)})) * N_0.$$

In a first step, handling time (T_h) and instantaneous attack rate (a') were estimated with (1). The relationships were not significantly linear for neither of the three species (Tab.1). Their functional response is thus not a "TYPE II" one (Fig.1), the parameters T_h and a' are not constant at all the densities.

Tab.1 Estimation of T_h and a'. Linearity of the relationships were tested.

Species	T_h day	a' container^{-1}day^{-1}	dl	F	p
A. rhopalosiphi	0.007	0.619	(1,45)	1.209	0.277 NS
A. ervi	0.007	0.510	(1,41)	0.885	0.352 NS
P. volucre	0.004	0.493	(1,39)	0.163	0.688 NS

The second step was then to fit the data with the HOLLING "TYPE III" equation. The results showed that the three parasitoid species couldn't be distinguished on their functional response basis (Tab.2 and Fig.1). The maximum number of host parasitized were between 39 and 46. The density necessary to reach half of this performance range between 27 and 35 hosts. At this point, the parasitism level reached its maximum value, about 73 %.

Tab.2. Parameters associated with the "TYPE III" functional response fiting, their 95% confident intervals and the level of fiting significance. "k" is the maximum number of host parasitized and, "d" is the amount of host when half of "k" is reached.

	k	lower	upper	d	lower	upper
A. rhopalosiphi	38.6	33.1	44.1	27.2	19.6	35.1
A. ervi	45.8	36.6	55.0	35.1	20.8	49.5
P. volucre	42.3	34.2	50.4	31.8	20.3	43.4

	df	F0.9995	Fobs
A. rhopalosiphi	(2,58)	8.7	212***
A. ervI	(2,60)	8.7	126***
P. volucre	(2,58)	8.7	147***

In order to determine the parameter variation which lead to TYPE III functional responses for the three species, variations of handling time, searching time and instantaneous attack rate with host densities were analysed (Tab.3).

The results indicates that the searching times of *A. rhopalosiphi* and of *A. ervi* stayed constant at the four investigated densities but changed significantly for *P. volucre*. This last species spent less time to search at higher densities.

Handling time of *A. rhopalosiphi* and *A. ervi* varied significantly with the host density. This was not observed for *P. volucre*. Handling time of *A. rhopalosiphi* was constant till the density of 64 aphids and then increased significantly. For *A. ervi,* this parameter decreased significantly until this same density.

Instantaneous attack rate of *A. rhopalosiphi* and *A. ervi* varied significantly with the host density, which is not the case of *P. volucre.* For *A. rhopalosiphi* and *A.ervi,* a' increased until the density of 8 aphids and then decreased, at a highly significantly rate (F(4,33) = 4.633**; p = 0.004) for *A. ervi* and at a no significant rate (F(4,30) = 1.488 NS; p = 0.231) for *A. rhopalosiphi.* Theoretically a' had to increase till the density "d".

Tab.3. Effect of host density on T_s, T_h and a'. For the searching time, data are transformed with arcsin(sqr(Ts/Tt)). a' (container^{-1} hour^{-1}). D = decrease, I = increase, the numbers are host densities.

Param.	Species	Mean	F(df)	p	Var. with N_0
T_s	*A. rhopalosiphi*	6.171	0.696(3,17)	0.567NS	-
(hr)	*A. ervi*	4.749	0.260(3,19)	0.853NS	-
	P. volucre	7.298	4.194(3,16)	0.023*	D
T_h	*A. rhopalosiphi*	3.28	5.408(2,81)	0.006**	I (IF N_0 > 64)
(sec)	*A. ervi*	2.21	4.168(2,27)	0.026*	8->D->64->I->120
	P. volucre	15.88	1.053(2,7)	0.398NS	-
a'	*A. rhopalosiphi*	0.163	2.343(8,51)	0.032*	I->8->D->120
	A. ervi	0.207	3.399(8,53)	0.003**	I->8->D->120
	P. volucre	0.104	1.221(8,51)	0.306NS	-

DISCUSSIONS

It appears that *A.ervi, A. rhopalosiphi* and *P. volucre* exhibited a TYPE III functional reponse, same maximum potentiel number of hosts parasitized and the parameter "d" situated between the 27 and 35 densities. Therefore they will lead to a same equilibrum level close from three aphids by seedling in the experimentals conditions. However to extrapolate these results to the field conditions a variable time functional response or a multi - patch choice, in laboratory (WALDE and MURDOCH 1988) or in glasshouse, has to be performed, on winter wheat plants close to the flowering stage.

The functional response of *Aphidius uzbeckistanicus* complex was already estimated on its two main hosts *Metopolophium dirhodum* (Walker) (DRANSFIELD 1979) and *S. avenae* (SHIROTA *et al.* 1983) and on a non natural host aphid, *Hyalopteroides humulis* (Walker) (DRANSFIELD 1979). Our results supports the results of SHIROTA *et al.*. However, from DRANSFIELD point of view, *S. avenae* will be considered as a non optimal host by *A. rhopalosiphi.* Indeed DRANSFIELD (1979) showed a TYPE II response of this parasitoid on *M. dirhodum* but not on the non natural host aphid : *H. humulis*. The latter may arise from a necessity "to learn" to parasitize this non natural host. However, our TYPE III answers may, more likely, come from the greater spatial complexity of our system. The maximum number of host parasitized ranged between 34 and 60, in the first studies, and 30 and 40 in the second are in agreement with our results.

Different mechanisms are able to produce a density dependent response. For instance, the parameters a' and / or T_s can increase with an increase of N_0, or T_h can decrease with the host density, or the spatial distribution complexity of the hosts can increase (HASSELL *et al.* 1977, MOLS 1993, WALDE and MURDOCH 1988). In our case the spatial complexity, ten seedlings in a "one liter" volume bottle certainly play greater role, indeed, during the direct observations, we observed that females parasitoid prefer to walk up and down a lot of times on the same seedling, and to superparasitize the same hosts, than to change of seedling. An increasing complexity should therefore increase the searching time for a same number of fresh host encounters. Nevertheless this complexity probably does not act in the same way on the three parasitoid species. Indeed the two *Aphidius* spp. are able to change their instantaneous attack rate and their handling time while *P. volucre* changes its searching time, according to an increase in host density.

However, in this study, all these parameters do not vary as expected. The searching time of *P. volucre* decreases with the host density. This greater activity at lower densities may be due to a greater physiological pressure for "an urge for oviposition". And, as *Praon* spp. superparasitize their hosts less easely than *Aphidius* spp. (MACKAUER, 1990), this pressure is greater, at low densities, for the former than the later. The handling time, which is very short (ranged from 2 to 16 secondes), does not play a real limitation on the functional response shape. For *A. ervi* this T_h decreases with the H_0 and for *A. rhopalosiphi*, it increases at the higher density. This last increase may be due to a greater difficulty to reach its host when it is grouped in crowded patch. The instantaneous rate of attack of the two *Aphidius spp.* increase until the density of eight individuals then decrease. Theoretically this parameter should increase until the "d" density and then must stay constant.

In conclusion, these three parasitoid species reached similar TYPE III functional responses using different ways.

ACKNOWLEDGMENTS

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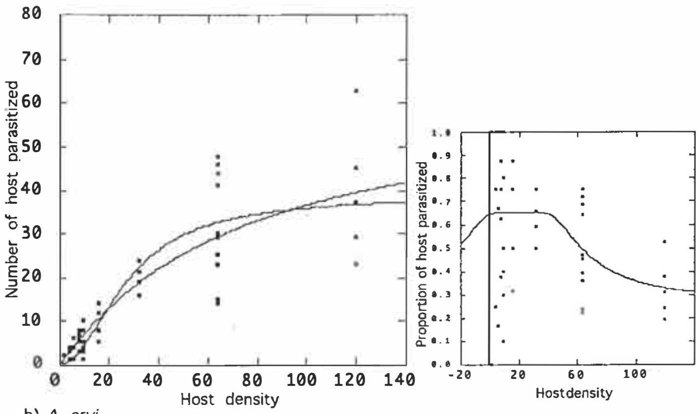
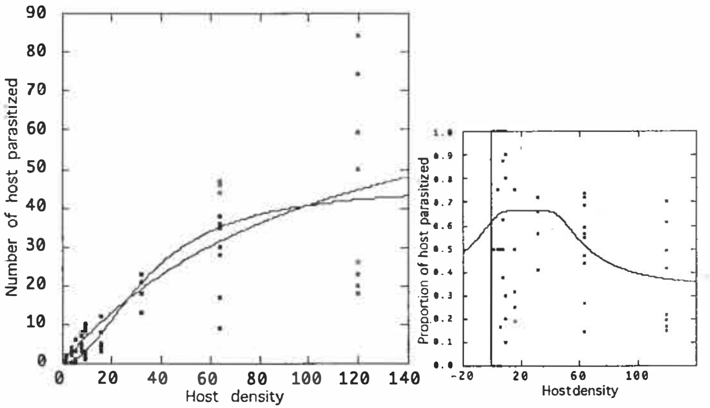
a) *A. rhopalosiphi*



b) *A. ervi*



c) *P.volucre*

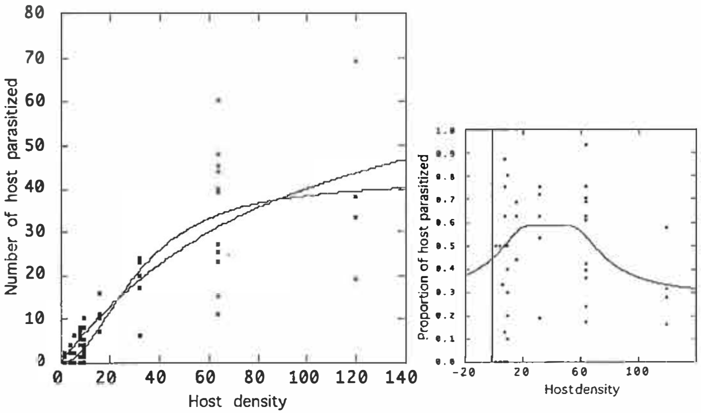


Fig.1. Numbers and proportions of host parasitized in function of the host density

A Model to Describe the Effect of Climate Change on Aphid and Coccinellid Population Dynamics

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Abstract

A model (Carter *et al.* 1982) describing the population dynamics of *Sitobion avenae* was modified and improved to include the population dynamics of the aphidophagous coccinellid, *Coccinella septempunctata.* The model has been run at three different temperature regimes to determine the effect of temperature upon the interaction between the aphid and the coccinellid. The model predicted that an increase in temperature leads to a greater number of aphids in the absence of the predator. However, the presence of the predators reduces the number of aphids predicted.

Introduction

The question of whether predators of aphids will be more or less effective, under predicted climate change scenarios, has important consequences for crop protection. To answer this question, a computer model was constructed for the cereal aphid *Sitobion avenae* and its major predator in Britain, the coccinellid *Coccinella septempunctata* (Carter *et al.* 1982).

Sitobion avenae is a major pest of cereal crops in Britain (Carter *et al.* 1980; Carter *et al.* 1982; Tatchell 1991; Vickerman and Wratten 1979). In general a rise in temperature increases the reproductive and development rates of both insects, and it is therefore important to discover how an increase in mean temperatures will alter their dynamics.

An existing model of *S. avenae* population dynamics (Carter *et al.* 1982) was modified to improve the equations describing aphid reproduction and development. A sub-model was then incorporated to describe the population dynamics of *C. septempuncta.* This paper describes the model, and a preliminary analysis of its output.

Description of the model

General description

The model is written in FORTRAN-77 in a VAX/VMS environment, and uses temperature as a driving variable, with an hourly time step. There are slight differences in the model according to which one of three temperature regimes is investigated: hot, moderate and cold. These temperature regimes were defined by examining the mean monthly temperatures between April and August for the years from 1966 to 1993, obtained from the Rothamsted meteorological data archives. An analysis of variance showed that there was siginificant between-year variation, and the years were ranked according to the difference between the mean temperature over the five months examined. They were then classified into three distinct groups, labelled hot, moderate and cold. A flow chart of the processes involved in the model is shown in Figure 1. The model is predominantly deterministic, but some stochastic processes are included where appropriate.

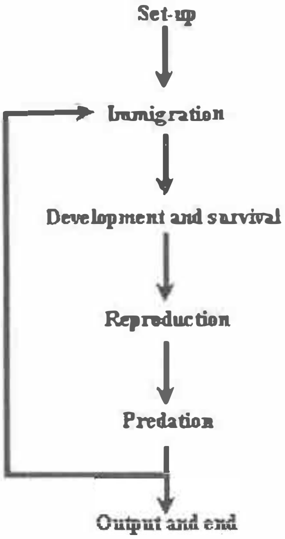

Figure 1: Simplified flow chart of model.

Set-up
The model begins by initialising the arrays and variables used. The aphid immigration patterns are then simulated to mimic data obtained from a Rothamsted Insect Survey suction trap between 1966 and 1993 (Woiwod and Harrington 1994). All dates in the model are recorded as Julian days. The start day, A_s, of aphid immigration is obtained by sampling randomly from a normal distribution derived from the suction trap data with a different mean, μ, and standard deviation, σ_1 , for each temperature regime (Table 1). The end day, A_e, of immigration is calculated from the equation shown below.

$$A_e = a + b\,A_s + e$$

where e represents a normal random variable with zero mean and standard deviation, σ_2

(Table 1). The distributions and equations for the moderate and cold regime were similar and it was decided to combine the two datasets, producing a single distribution and equations which was used for both moderate and cold regimes.

Regime	μ	σ_1	a	b	σ_2
Hot	135.44	10.53	10.8	1.08	11.9
Moderate	142.13	12.66	57.0	0.840	11.4
Cold	142.13	12.66	57.0	0.840	11.4

Table 1: Parameters of the start and end day of aphid immigration.

To simulate appropriate data for each day of immigration, the number of aphids caught in a Rothamsted Insect Survey suction trap is generated from a negative binomial distribution with mean, θ, and standard deviation, ψ (Table 2).

Coccinellid immigration is assumed to occur in two waves. The first wave simulates the immigration of those coccinellids that overwintered, moving into a field from their hibernation sites. The start date of the first wave, C_{s1} , and the end date, C_{e1} , are obtained from:

$C_{s1} = C_{p1} - 14$; $C_{e1} = C_{p1} + 14$

where C_{p1} is sampled randomly from a normal distribution, derived from the data of Zhou *et al.* (1994) with mean 140, and standard deviation 20. Data of Zhou *et al.* (1994) indicated that the average weekly coccinellid catch was 1. 0, and that the proportion of the daily catch that was zero was 0. 80. The number of coccinellids assumed to enter the field each day, *W*, is sampled randomly from a uniform distribution in the range -6 to 1. 5; any negative value of *W* being truncated to zero. The resulting values of *W* agree closely with Zhou's data.

Regime	θ	ψ
Hot	1.22	0.487
Moderate	1.55	0.241
Cold	0.583	0.293

Table 2: Parameters used to calculate the suction trap count.

The second wave simulates the immigration of coccinellids that have developed from eggs laid by the first wave, whilst moving from field to field, on their way to hibernation sites. The start date of the second wave, C_{s2} , and the end date, C_{e2} , are obtained from:

$C_{s2} = C_{p2} - 14$; $C_{e2} = C_{p2} + 14$

where C_{p2} is sampled randomly from a normal distribution, derived from the data of Zhou *et al.* (1994), with mean 180, and standard deviation 20. The maximum daily number of coccinellids in the second wave of immigration can be about five times larger than the maximum daily number in the first wave (Honek 1989). If the factor by which the maximum number in the second wave is larger than the first is denoted as P, then P is sampled from a normal distribution with mean 5, and standard deviation 5. The phenological data of Zhou *et al.* (1994) indicated that the daily number of coccinellids in the second wave of immigration followed approximately a normal curve in time. Therefore, the number of coccinellids assumed to enter the field between C_{s2} and C_{e2} are approximately distributed as a normal about C_{p2} in time, with standard deviation of unity, and with the number on each day taken to be a proportion, given by the area under the normal curve, of the maximum number that occurs on day C_{p2}.

Having set up the routines to control immigration, the model then sets up the values of mean daily temperature, t, in degrees Celsius, from an equation based on a double-Fourier curve (Kocabas *et al.* 1992). The equations of the curves for each temperature regime are shown below.

Cold regime : $t = 5.709 - 1.639A - 9.83B + 1.202C - 1.173D + e_t$;

Moderate regime: $t = 11.44 - 3.448A - 2.26B - 0.045C + 0.973D + e_t$;

Hot regime: $t = 5.709 - 1.998A - 13.14B + 1.195C - 2.371D + e_t$;

where: $A = \text{Sin}((2\pi k)/365)$; $B = \text{Cos}((2\pi k)/365)$; $C = \text{Sin}((4\pi k)/365)$; $D = \text{Cos}((4\pi k)/365)$; k is the Julian date; and where e_t represents a normal random variable with zero mean and standard deviation ϕ_1 (Table 3). Having calculated each mean daily temperature, the maximum within-day deviations from this value, that is the daily maximum, D_{max}, and minimum, D_{min}, temperatures, are then simulated assuming the deviations are symmetric about t. These were obtained from:

$$D_{max} = t + 0.5d \quad ; \quad D_{min} = t - 0.5d$$

where d represents the difference between maximum and minimum temperatures, and d is sampled randomly from a lognormal distribution with mean υ, and standard deviation ϕ_2 (Table 3).

Regime	ϕ_1	υ	ϕ_2
Hot	2.63	1.94	0.701
Moderate	2.40	1.88	0.647
Cold	2.19	1.90	0.557

Table 3: Parameters for determining daily maximum and minimum temperatures.

The equations used to describe the main processes within the model will be presented elsewhere, so only a brief description of the model is given below.

Immigration

In the next stage of the model, the model's internal clock is begun and the process begins with coccinellid and aphid immigration. The number of aphids immigrating into the field is calculated from the suction trap counts, simulated as described above. Coccinellid immigration is assumed to occur only when the density of aphids exceeds 10 aphids per m^2 (Adams 1984). The number of coccinellids assumed to enter the field, once this condition is met, is taken from the values calculated as described above.

Development and survival

After the first aphid immigrants have arrived, the model then calculates the development and survival of the aphids. Aphid nymphs are assumed to accumulate development in hourly increments towards a given total. Upon reaching this total they move into the next instar. The development rate for the hour is assumed to be related to temperature according to a sigmoid curve, derived from the data of Dean (1974). Similarly adult aphids are assumed to accumulate hour-degrees (H°) towards a total; having achieved this total they are assumed to die.

Coccinellid development is treated in a similar way to aphid development. The development of eggs, nymphs and pupae is accumulated hourly, at a rate calculated from a sigmoid curve fitted to the data of Hodek (1973). Adults that overwintered accumulate H° then die; those that developed from eggs are assumed to emigrate after 40 hours (Honek 1990, Zaslavsky and Semyanov 1986), and leave the simulated field.

Hourly survival of the aphids is calculated from the total proportion of aphids assumed to survive to the end of an instar, adjusted for the proportion of the instar completed during the hourly time step. This adjustment is needed because the length of the aphid instar is dependent upon temperature. Coccinellid survival is calculated similarly.

Reproduction

Aphid reproduction is dependent upon temperature, and the reproductive rate (number of nymphs produced per female per H°) is assumed to be linearly related to temperature, increasing from zero at 0°C to a maximum at 20°C (Dean 1974). Above the maximum, the reproductive rate decreases linearly to zero at 30°C. The reproductive rate of the apterae is assumed to be greater than that of the alatae (Wratten 1975), and the reproductive rate is assumed to be 1. 6 times greater than normal when the crop growth stage (Zadoks *et al.* 1974) is between 59 and 73 (Watt 1979).

The number of nymphs produced is then calculated by multiplying the reproductive rate by the number of aphids and the number of H° in each time step.

Coccinellid reproduction is dependent upon both temperature and aphid consumption (Ghanim *et al.* 1984; Dixon *pers. comm.*). The reproductive rate of coccinellids (eggs/female/H°) is linearly related to temperature increasing from zero at 0°C to a maximum at 20°C before decreasing again to zero at 40°C (Sethi and Atwal 1964). The reproductive rate of the coccinellids is also assumed to be linearly related to aphid consumption in the range 10mg/day to 20. 94mg/day (Dixon *pers. comm.*); these values represent the minimum and maximum daily food consumption of coccinellids.

The number of coccinellid eggs produced is calculated by multiplying the above reproductive rate by the number of H° in the time step, the number of female coccinellids and the proportion of those that are active. It is assumed that only active coccinellids will reproduce, and that coccinellid reproduction cannot occur unless a threshold aphid density of 0. 1 aphids/tiller (Adams 1984; Honek 1978, 1980) is reached; this prevents females from reproducing unless there are enough aphids to allow maturation of their ovaries.

Predation

To simulate predation, the model first converts the number of aphids per tiller to the biomass per m^2 by multiplying by the assumed number of tillers per m^2 and the average weight of an aphid (Adams 1984, Vereijken 1979). The ratio of alatae to apterae and the ratio of aphid instars eaten by each coccinellid instar are then calculated, assuming that first instar coccinellids eat only first instar aphids; second instar coccinellids eat first and second instar aphids; third instar coccinellids eat first to third instar aphids; and fourth and adult coccinellids eat all aphid instars and adult aphids (Adams 1984). Next the searching rate of the coccinellids, related to temperature, is calculated from a sigmoid curve. A similar curve is used to calculate the handling rate of the coccinellids. The proportion of active coccinellids is calculated from a surface which describes the relationship between activity, temperature and satiation.

The values derived from these equations are then used in a temperature-mediated functional response equation (Mack *et al.* 1981, Mack and Smilowitz 1982) to calculate the biomass of aphids eaten by each coccinellid instar.

The proportion of aphids killed, in each instar, is calculated and the numbers updated appropriately.

Finally the model updates the crop growth stage before either repeating the proceses above (Figure 1) for the next time step or ending if the crop growth stage exceeds 86.3, when the crop is deemd to be unsuitable for aphids (Carter *et al.* 1982).

Output

The model was run 100 times for each regime, both with and without coccinellids. Examples of the output for each regime are shown in Figure 2. The graphs show that the presence of coccinellids causes a reduction in the predicted number of aphids in all three regimes. The presence of coccinellids also causes the predicted maximum number of aphids to occur earlier.

The graphs also show that the maximum number of aphids, in the absence of coccinellids, increases and occurs earlier as the regime is changed from cold through moderate to hot.

The graphs also show that changing the regime does not seem to affect the maximum number of coccinellids. However, as the regime moves from cold through moderate to hot, the day on which the coccinellid peak occurs becomes earlier.

Runs of the model were also performed with temperatures within the regimes increased by 1°C or 2°C, in an attempt to predict the possible effects of climate change on the population dynamics of the two species; these results will be discussed elsewhere.

Discussion

The prediction that the presence of coccinellids causes a decrease in the number of aphids and the date of maximum numbers of aphids is to be expected due to the reduction of the prey numbers, especially of the reproducing adult aphids, so less nymphs are produced leading to an earlier peak in the numbers of aphids.

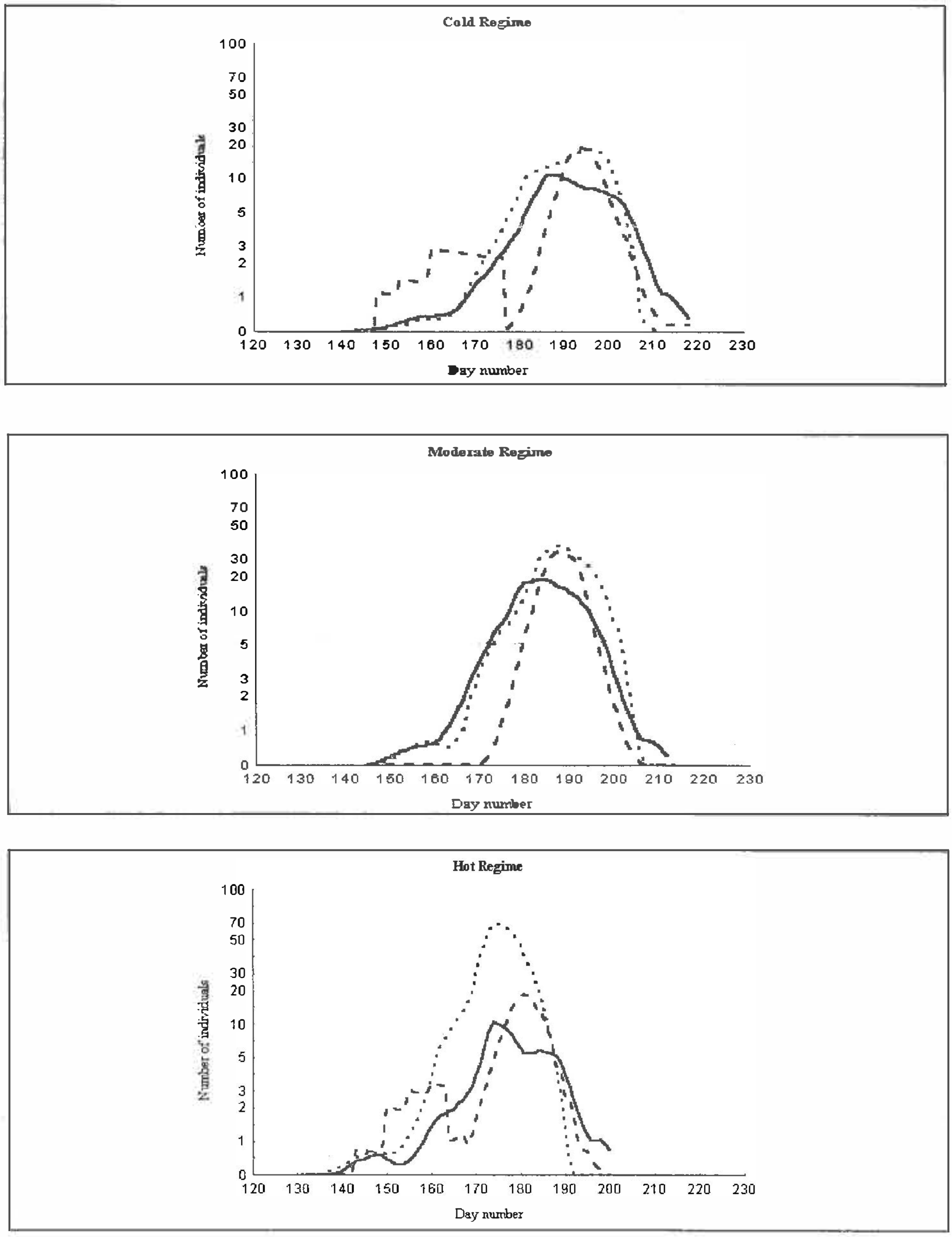

Figure 2: Graph showing representative output of model for the three regimes [——— , Aphids per tiller in presence of coccinellids; – – – –, Coccinellids per m^2; · · · ·, Aphids per tiller in the absence of coccinellids.

The predictions also appear to suggest that an increase in temperature results in greater numbers of aphids, which peak earlier. This appears to be due to its effect on the developmental and reproductive processes of the aphids. Further work is required to determine the precise effect of temperature on the numbers of aphids and the timing of the maximum aphid abundance, and also on the predator-prey relationship between the aphids and the coccinellids. It should then be possible to predict whether aphid outbreaks will be more or less likely, with increased global temperatures.

A model has been produced that describes accurately aphid and coccinellid biology, and the aphid and coccinellid populations dynamics in the field. The equations used in the model are biologically meaningful and were all derived from data available in the literature. In some cases the data are scarce, and the equations may need to be refined in the light of future work. A sensitivity analysis was performed on the parameters for the coccinellid model, and fieldwork was undertaken in an attempt to validate the model. The results of the sensitivity analysis and validation are still being examined, and will be reported in detail elsewhere.

The reasoning behind the use of a simulation model rather than a more analytical approach, lies in the nature of the problem. In order to investigate the effects of climate change on aphids and coccinellids, we need to understand how temperature affects the biology of the two species. Since the interactions between temperature and the various components of aphid and coccinellid biology are complex, this is most easily done through the use of a multi-parameter, mechanistic simulation model. Indeed, the majority of models describing aphid and coccinellid biology use a simulation approach (Barlow and Dixon 1980; Gilbert and Hughes 1971; Gutierrez *et al.* 1984; Mack and Smilowitz 1982; Frazer and Gilbert 1976).

The work described in this paper is similar in approach to the work of Frazer and Gilbert (1976), Mack and Smilowitz (1982), and Barlow and Dixon (1980) but differs in treating the components of aphid and coccinellid biology as non-linear functions of temperature, rather than linear measures as implied by the use of physiological time, such as H° or day-degrees.

Throughout the production of the proposed model, attention has been focused on the fact that it is not a means to an end, but is regarded as a tool to be used to enhance and further the understanding of the complex relationships between temperature and the biology of the two species modelled. Other approaches have been used, such as the simple Bombosch model (Chambers 1988), but this style of approach does not allow for the effect of temperature on either aphids or coccinellids. Gilbert and Gutierrez (1973) cautioned against the uncritical use of simulation models: " A simulation has no intrinsic value. It is useful only when it exposes our ignorance, or answers biological questions." The model proposed here is intended to answer the question of whether aphid outbreaks will be more likely under a climate change scenario, and since construction of the model has highlighted the lack of data concerning the basic biology and ecology of *C. septempunctata*, it fits both of these criteria. For simulation models to be useful in the field of crop protection, more attention should be focused on linking modelling activities with studies of the basic biology and ecology of beneficial insects.

Acknowledgements

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Investigations on the predatory effect of coccinellids in winter wheat fields and problems of situation-related evaluation

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Abstract

We investigated the usefulness of coccinellids in a complex research project of several years duration. During the first two years, quantitative data was gathered in winter wheat fields at two different sites (North Fläming in Brandenburg and Magdeburger Börde in Saxony-Anhalt) as well as in cages and climate chambers. The GTLAUS model for simulation of interaction between winter wheat, cereal aphids, and coccinellids was implemented and validated. In the end, we tested a new concept for establishing control thresholds for cereal aphids that includes predators. Some very interesting results have already been obtained.

Ladybirds (Coccinellidae) and hover flies (Syrphidae) are the primary predators of cereal aphids. *Coccinella septempunctata* L. and *Propylaea quatuordecimpunctata* (L.) predominate in winter wheat, but their population density varies greatly. Their numerical response was extremely difficult to predict, in part, due to compensatory effects from surrounding aphid-infested areas. Hunger did not appear to play a decisive role in density feedback. The effects of coccinellids on the retrogradation of aphids was clearly demonstrated, in contrast with their effects on the early population development. In addition to the predator-prey ratio and the coccinellid density, temperature also had a great influence on beneficial effects. At mean daily temperatures of < 20°C, the aphids benefitted from minimal activity of coccinellids, whereby the coccinellids clearly benefitted more at temperatures of > 22°C. This was also demonstrated in the computer simulations.

Although impeded by methodological problems and the limited ability to quantify individual predator effects, we are working on a means of including beneficial organisms in a new threshold concept for cereal aphids.

1. Introduction

Natural control of aphids in winter wheat has become a special, worldwide feature of integrated crop protection in arable farming. It has also been the subject of lively discussions on the ecological situation of major agricultural regions in Germany (Wetzel, 1993; Poehling et al., 1994). These discussions have shown how important, but difficult, it is to make realistic assessments of beneficial organisms. Problems arise when attempting to make representative measurements of the population density of stenophagous aphid antagonists and epigeous predatory arthropods. However, the population density is not the only problem. Now and in the past, the main problem has been in determining how to obtain a correct situation-related assessment of the effectiveness of predators in the field. Our current knowledge is still insufficient for this task. This is also true of coccinellids, although they are one of the most important enemies of aphids and although a large amount of scientific data on these organisms exists (Hodek, 1967; Baumgaertner et al., 1981; Ferran et al., 1986).

The primary goal of this several year long research project on the interactions between winter wheat, cereal aphids, and predators was to obtain data on the usefulness of coccinellids. Special attention was given to beneficial thresholds (Freier, 1994). The following questions on the usefulness of coccinellids were taken into consideration:

1. Does their predatory potential have different features in completely different agro-ecosystems?

2. How does the numerical response work?
3. Can their effects be quantified under field conditions?
4. How do coccinellids vary the injurious effects of cereal aphids?
5. Can the interaction between cereal aphids and coccinellids be depicted using a computer simulation model?
6. How can coccinellids and other beneficial organisms be included into control thresholds for cereal aphids?

Several interesting findings of the first two years of research in 1993 and 1994 will be presented in the following.

2. Material and Methods

Field counts on the population dynamics of cereal aphids and their antagonists: The studies were performed in winter wheat fields near Magdeburg (Magdeburger Börde, a very fertile and poorly stuctured site) and 50 km south of Berlin (North Fläming, moderately fertile and well structured site). The fields were labelled M93 (63 ha), M94 (54 ha), F93 (17 ha), and F94 (12 ha). Starting at stage EC 61, tillers on one side of each field and their corresponding soil areas were sampled at 5 checkpoints (20, 40, 60, 80, and 100 m from the edge of the field) once each week. Each checkpoint contained an average of 300 successive tillers in a drill row.

Methodological attempt to assess predators in winter wheat: In addition to the usual tiller counts, four 1 sqm areas were caged and completely harvested at both sites on two scoring dates in 1994. The arthropods in the enclosed crofts were collected using a D-VAC suction device, and the plants and remaining arthropods were removed and preserved. Additionally, the ground surface in the cage was roughened and suctioned off. The arthropods from a total of 16 collective samples were assessed in the laboratory.

Climate chamber experiments to determine the significance of temperature in interactions between cereal aphids and coccinellids: The experiments were performed 1994 in three climate chambers with a mean daily temperature of 1) 20°C, 2) 22°C, and 3) 25°C. All other conditions were standardized (day-to-night temperature difference of 9 K; day-to-night ratio of 16:8 hours; illumination of ca. 10,000 lux; relative humidity of 65%). Winter wheat plants (16 ear-bearing tillers) were set in vessels with *Sitobion avenae* (Fabr.). The starting population was 8 cereal aphids/tiller at stage EC 69. Each temperature stage had two variants, i.e., with and without 1 adult of *Coccinella septempunctata* L.

Cage experiments on the predatory efficiency of *Coccinella septempunctata* L.: Cages with a 2 sqm ground area were set up in winter wheat fields in stage EC 35. Early and late gradation was simulated by introducing the cereal aphids at different times (EC 61 and 69), whereby variations were produced using *Sitobion avenae* (Fabr.) and mixed populations of *Sitobion avenae* (Fabr.), *Rhopalosiphum padi* (L.), and *Metopolophium dirhodum* (Walk.). There were always 2 cages/variant. Six (1993) or ten (1994) adult *Coccinella septempunctata* L. (male to female ratio of 1:1) were placed in each cage.

Hunger experiments: Ten *Coccinella septempunctata* L. adults (male and female) were removed from fields F93 and F94 on 6 dates in 1993 and on 4 dates in 1994. The specimens were kept cool and transported to the laboratory. They were then placed in a climate chamber for three days, given a surplus of food (*Sitobion avenae* (Fabr.)), and weighed four times a day. The excrement of starved insects removed from the same fields was also weighed.

Experiments with the GTLAUS simulation model: The GTLAUS simulation model was developed for simulation of *Sitobion avenae* (Fabr.) in winter wheat, and contains the COCCISEP submodel for coccinellids. This model was used to perform scenario computations to predict the effect of predators on cereal aphids in winter wheat.

3. Results

Abundance dynamics of cereal aphids in the field

Figure 1 shows the abundance dynamics of cereal aphids in connection with the occurrence of predators. The infestation trends were studied on the basis of the following parameters: species spectrum, dominance, peak density, intrinsic rate, aphid index, and distribution. The results can be summarized as follows:

M93: Unusually late onset of infestation - first *Rhopalosiphum padi* (L.), then *Sitobion avenae* (Fabr.) - in conjunction with persistent milky ripeness due to the cold.

F93: Typical pattern of infestation with a relatively great increase from the beginning of the flowering period on; dominance of *Sitobion avenae* (Fabr.); peak occurred late due to persistent milky ripeness due to the cold.

M94: Typical but dampened pattern of infestation which was dominated by *Metopolophium dirhodum* (Walk.), and later by *Sitobion avenae* (Fabr.); somewhat premature peak due to unusually hot weather.

F94: Extremely early infestation by *Rhopalosiphum padi* (L.) and breakdown in the flowering period during unstable weather prior to the heat wave.

Thus, two completely different trends were observed over the course of the two years. Late leaf-ear infestation was seen in 1993, compared to early leaf infestation in 1994. These trends affected wide regions of Germany. The abundance dynamics data for cereal aphids in the four investigated wheat fields showed absolutely no influence of beneficials in M93, a moderate influence in F93 and M94, and an tremendous influence in F94. The question is, what effect did the antagonists actually have on the population dynamics of the cereal aphids?

Occurence of antagonists in the field

This analysis focused on coccinellids and the other classical predators of aphids because they were the predominant antagonists. Since the degree of parasitization was less than 1.1 % in each case, this was not an effective differentiation factor. Mould formation in the aphids was not measured precisely. Our estimates showed that this had virtually no effect in fields M93 and F93, and only little effect in M94. However, mould formation in the *Rhopalosiphum padi* (L.) population in F94 was unusually high.

The dominance ratios hardly differed between the two sites but clearly between the two years. One third of all antagonists observed were polyphagous predators (carabids, staphylinids and spiders). Except of field M94 the coccinellids always were the predominant predatory group (with 53 %, 35 %, 30 % (syrphids 33 %), and 25 %).

Figure 1 shows the results of field counts for stenophagous predators in comparison to the abundance dynamics of cereal aphids. In 1993 *Coccinella septempunctata* L. was the predominant species, in 1994 this was the case for *Propylaea quatuordecimpunctata* (L.). Other observed species were *Coccinula quatuordecimpustulata* (L.), *Synharmonia conglobata* (L.), *Coccinella quinquepunctata* L. and *Adalia bipunctata* (L.). These species had no importance at all.

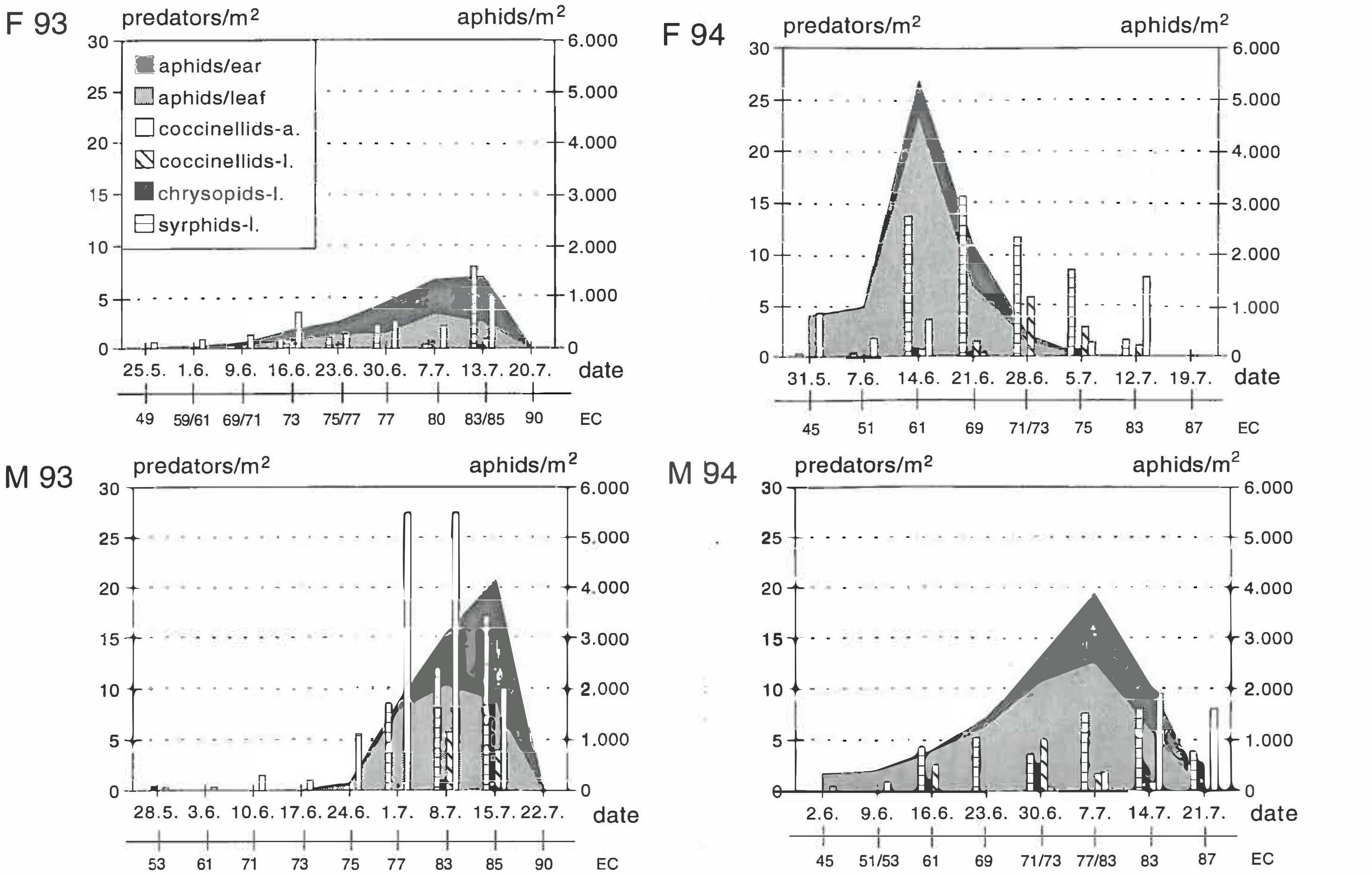


Figure 1: Occurence of stenophagous predators in winter wheat fields 1993 and 1994 (l. - larvae, a. - adult)

Methodological problems in density determination

Because no method of applied entomology is capable of precisely determining the predator density, the weaknesses of any given method must be assessed before the abundance dynamics data can be used to estimate the predator efficiency. Even the field counts presented here, which were obtained with a relativley high degree of time and effort, are not free of error. This was shown in the results of the methodical attempt to directly compare the field count data with the sqm of removed crop samples (Table 1). The data show that around 40 % of coccinellid adults, 63 % of coccinellid larvae, 48 % of syrphid adults, and 58 % of the chrysophid larvae were overlooked. Larvae in the early stages of development were most often overlooked. However, because only the last stage of larvae development affects the predatory effect in all stenophagous predators, this oversight was not expected to cause dramatic errors in the calculation of predatory efficiency.

Table 1: Comparison of the relative individual numbers derived from each method of density assessment "sqm - method" and "field count method" at the fields P94 and M94 (each at EC 69 and EC 75)

Method	Aphids	Coccinellid Larvae	Coccinellid Adults	Syrphid Larvae	Chrysophid Larvae
sqm	1.00	1.00	1.00	1.00	1.00
field count	1.31	0.37	0.60	0.52	0.42

Estimation of predator efficiency

The predator-prey ratio (PPR) is not always suitable for estimating predator efficiency. The effect of each predator group must be calculated different, and the PPR must be used in conjunction with population density data. If the abundance is low, predator larvae can starve to death, even at a PPR of 1:1. We therefore employed the following simplified, combined computation method:

1. The larvae of stenophagous aphid predators were assigned a factor of 1 (= **predator unit**), and adult coccinellids a factor of 2. Polyphagous carabides, spiders, and staphylinids were not taken into consideration, due to the conflicting data in the literature.

2. Using this predator unit, and according to Freier (1994), we defined the **effective predator potential** to be a PPR of less than 1:80 with a predator abundance of over 15 predator units/sqm. This definition already includes considerations for the above-mentioned error in density determination. The following assessments were thus made (Fig. 2):

M93: Since the predator density remained insignificant until EC 75, the extremely low PPR remained ineffective. Thereafter, a tremendous increase in the coccinellid population was observed (> 25 individuals/sqm). Because the PPR remained low, we concluded that the predator potential from EC 75 until the period of dough stage was effective. However, we were surprised to find that this had no effect on the course of gradation.

F93: Although the PPR was very low, the low predator density did not appear to have any decisive beneficial effects until the milky ripeness. Thereafter, the PPR became less favorable. It was only during EC 83/85 that the predator density and the PPR changed, so as to create an effective predator potential.

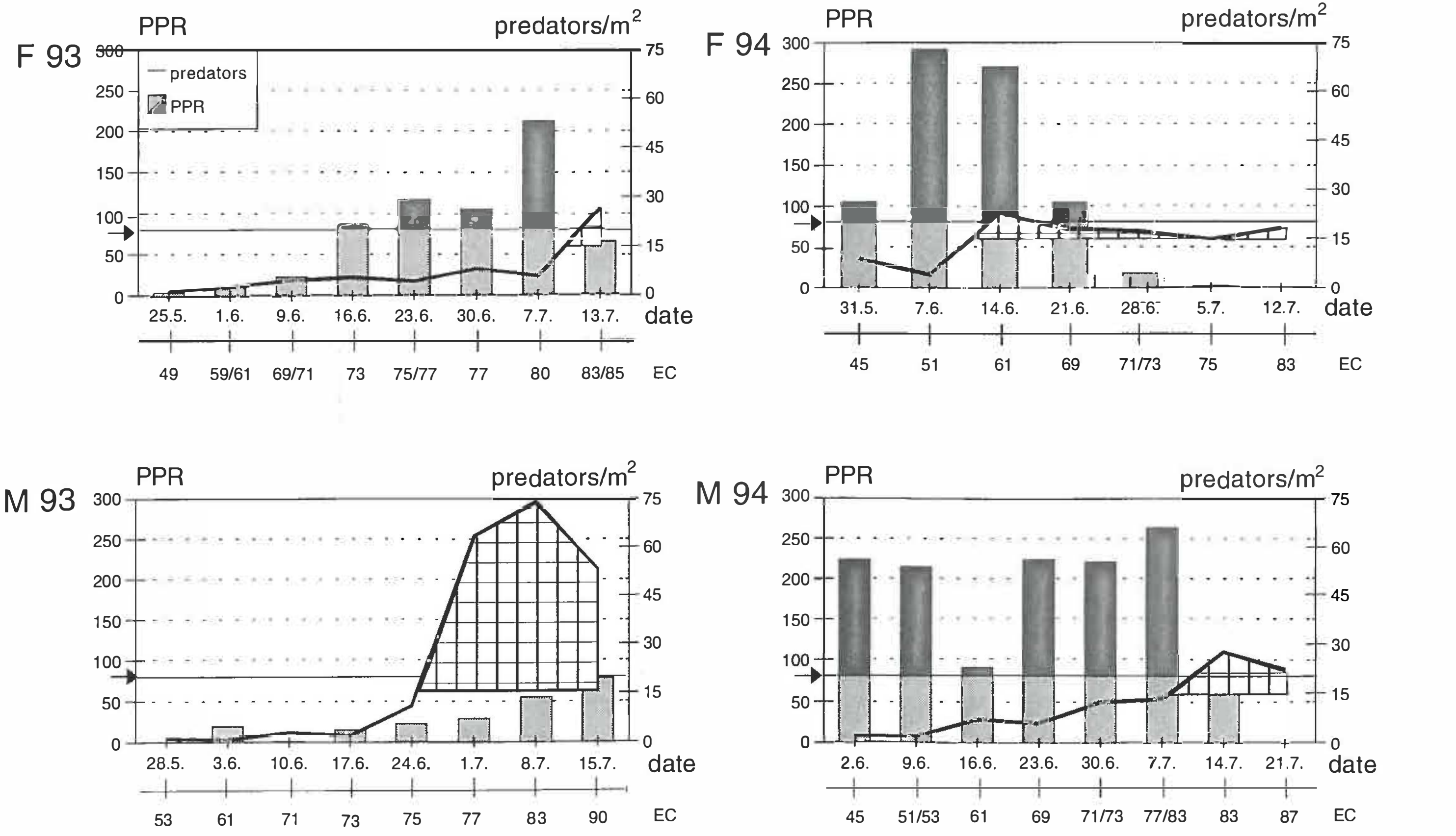


Figure 2: Predator-prey-ratio (PPR) and occurence of stenophagous predators (coccinellid adults = 2) in winter wheat fields 1993 and 1994

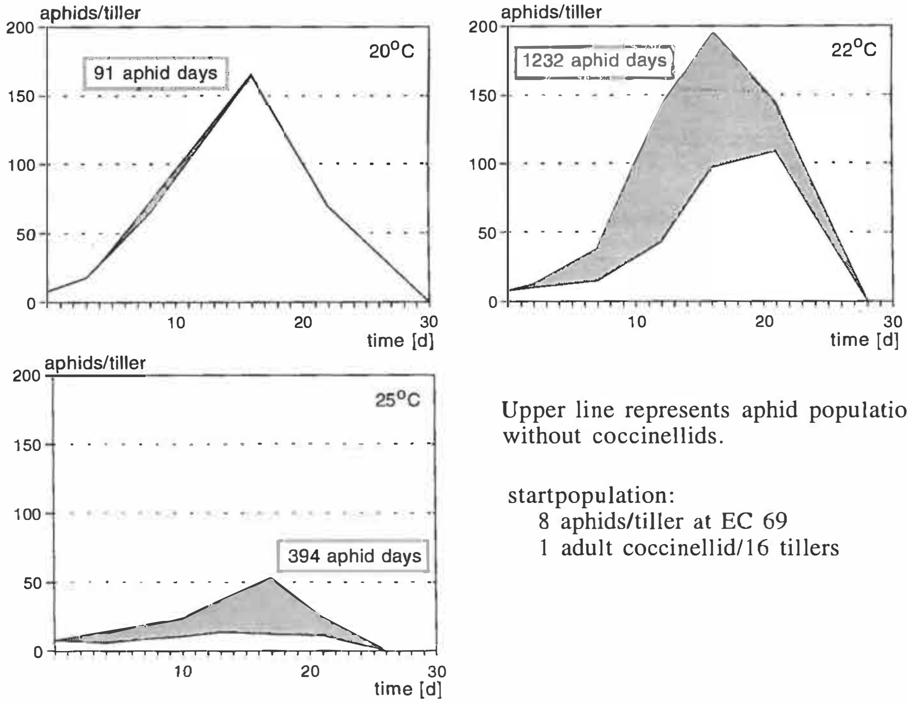
M93: Neither the predator density nor the PPR gave any indication of beneficial effects until the dough stage. It was only in the final phases of infestation, during EC 83-87, that the field data showed an effective predator potential.

F94: Until the beginning of flowering, the situation was characterized by an increasing presence of predators, but an unfavorable PPR. At the end of flowering, however, a high predator density and a low PPR produced a long-lasting and effective predator potential that lasted until the end of infestation.

The significant influence of the effective predator potential (particularly larvae and adults of coccinellids and larvae of syrphids) on the course of aphid gradation was clearly visible in fields F93, M94, and F94. But why wasn't aphid infestation in M93 inhibited? This will be discussed in the following.

Effects of temperature on interactions between cereal aphids and coccinellids

One must assume that, in addition to the density of predators and their individual predatory efficiency, other factors also contribute to the beneficial effect of coccinellids. Our data on the effects of temperature on the life processes of coccinellids and cereal aphids is rather good, but we know little about how the overall predator-prey system reacts during temperature changes. The question is: Which party in the system profits from temperature changes? In order to answer this question, we performed several climate chamber model studies.



Upper line represents aphid population without coccinellids.

startpopulation:
8 aphids/tiller at EC 69
1 adult coccinellid/16 tillers

Figure 3: Experiments in climate chambers to quantify the impact of *Coccinella septempunctata* L. on population development of *Sitobion avenae* (Fabr.) on winter wheat at changing temperatures (day:night = 16h:8h with 9 K difference)

Figure 3 shows the effects of three temperature regimes (temperature variation at intervals of 9 K) in otherwise completely identical test conditions. We found that the actually measurable effect, namely the reduction in aphid days, was extremely temperature-dependent. Whereas the course of infestation was hardly affected at 20°C, both the aphids and the coccinellids, which reduced the infestation by half, benefitted from temperatures of 22°C. At temperatures of 25°C, the coccinellids had the greatest relative benefit, and the small aphid population was almost completely consumed.

Numerical response in the field

We were particularly interested in studying the density feedback between the cereal aphids and their predators. Regression analyses of a total of 8 relationships were performed. We thereby asked 1) whether the occurrence of aphids tended to affect the density, density changes, and egg-laying of the predators and 2) whether the occurrence of the predators determined the aphid density, i.e., the course of infestation. The results were unsatisfactory. We observed a weak linear trend (the more aphids/sqm, the more predators ($p > 0.05$). Contrary to our expectations, egg-laying of the coccinellids was not found to be determined by the degree of infestation. The only findings from a comparison of frequency classes were that the average density when no coccinellid eggs were found was 111 aphids/sqm and 1312 aphids/sqm on days when eggs were counted. This suggests that the threshold density of the aphid population for egg laying is < 200 aphids/sqm.

Effects of hunger on numerical response

1993: The three-day feeding experiments with adult *Coccinella septempunctata* L. showed that the voracity of the females tended to increase as the number of eggs produced/day increased and the voracity of the males decreased. The increase in voracity of the females (x) was directly proportional to the number of eggs/day (y): $y = 3.86 + 1.09\ x$ ($r = 0.986$, $p < 0.05$). We did not find any indication of different levels of hunger, i.e., dependent on the degree of aphid infestation in the field. In 1994 we therefore attempted to find out whether hunger phenomena can be observed from the 1st day of removal from the field on.

1994: Clear hunger reactions were observed in the males (weight adjustment with overreactions) within 8 hours at temperatures of 23°C; stabilization followed (Fig. 4). This pattern was not as easily recognizable in the females. In males, the fecal production experiment showed a direct correlation between the density of aphids in the wheat field and the subsequent fecal production in the laboratory. At densities of around 2 aphids/tiller or 1200 aphids/sqm and more, the daily fecal production in males did not increase significantly (0.34 mg/male). This is suggestive of satiation. Up to a maximum infestation level of 3.5 aphids/tiller, the daily fecal production increased to 0.59 mg/individuals in older, egg-laying females.

Conclusions: A relatively low level of aphid infestation (ca. 2 individuals/tiller) ensures sufficient supply in males, whereas the hunger reaction in female *Coccinella septempunctata* L. was still clearly evident, even when the level of aphid infestation was twice as high.

Effects of *Coccinella septempunctata* L. in cages

The two-year cage experiments proved to have extremely complex methodological problems. There were four different infestation constellations. Each constellation had to be produced in an extra cage, both with and without coccinellids (double variation), with exactly defined starting conditions for the desired course of gradation.

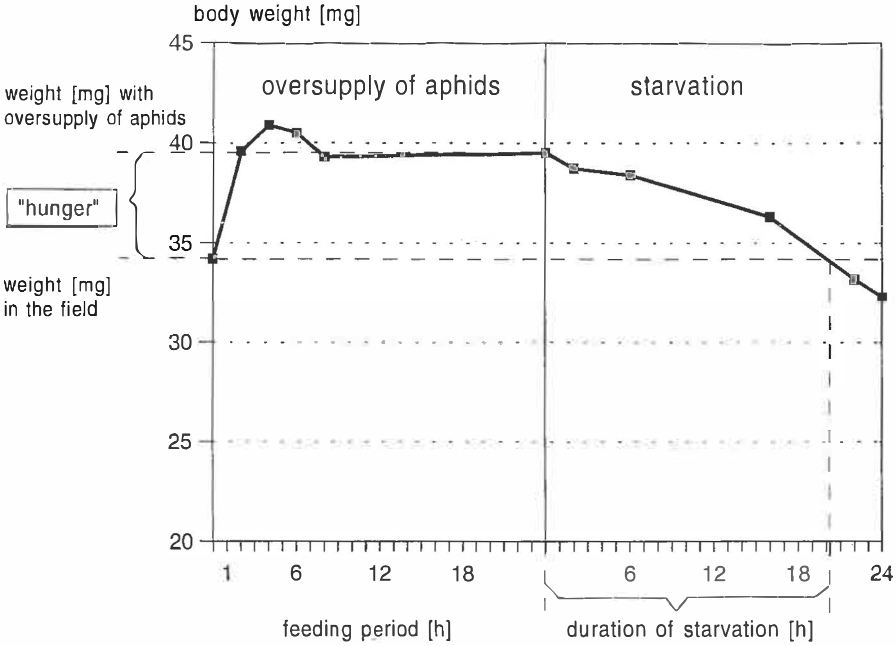


Figure 4: Measurement of hunger of adult coccinellids (*Coccinella septempunctata* L.) from a winter wheat field (F 94) by feeding with aphids (Sitobion avenae (Fabr.)) in climate chambers

In cooler weather, 3 (1993) and 5 (1994) adult *Coccinella septempunctata* L./sqm and their offspring were unable to prevent a tremendous increase in infestation in the cages, even though the initial level of infestation was within the range of the control threshold. The coccinellids decreased the aphid population increase only by 5 to 30 % in 1993 and by 0 to 66 % in 1994, depending on the constellation involved. A more interesting finding is that the aphid index (sum of all aphids/tiller on all days) was reduced by 15 to 54%. In all but one case, the number of reduced or consumed aphid days/tiller ranged from 1.7 to 3.8 (average 3.1) for each predator unit/sqm. Thus, one predator unit/sqm prevented approximately 2 % of the pest infestation (ca. 150 aphid days/tiller) during cooler weather conditions. Considering the temperature and other conditions, we therefore calculated that 30 to 50 predator units/sqm are needed to keep infestation under natural control.

GTLAUS simulation model

Using TURBO-PASCAL, the GTLAUS simulation model and integrated COCCISEP submodel for simulating the interactions between cereal aphids and coccinellids in winter wheat were implemented and validated at various stages. The simulation model contains 11 fixed equations and 30 regression equations. Even though we have worked with the model for several years, it would be unrealistic to believe that it is able to provide a realistic picture of every situation in the field. On the contrary, it merely helps us to gain insight into and find solutions for basic phenomena related to synecological interactions. We were thus able to confirm the impressive effect of temperature on the interaction of caged *Sitobion avenae* (Fabr.) and *Coccinella septempunctata* L.

Discussion and Theses

The international literature contains a wealth of information on the biology, behaviour, and importance of coccinellids in the regulation of aphid population. However, because it is so contradictory, the available literature still does not permit a situation-related assessment of the predatory efficiency of coccinellids in wheat fields. Our investigations were performed to promote such an assessment.

As we expected, greatly variable cereal aphid infestation patterns were seen in the four field surveys. Infestation remained sharply or slightly below the injury threshold. Only the infestation trends in field F94 indicated a strong beneficial effect, because a density growth factor of < 3 from stage EC 69 on, and an early infestation peak occuring prior to EC 77 are considered to be proof of effective natural control by antagonists (Holz & Wetzel, 1989, Holz et al., 1994).

Stenophagous predators such as hover fly larvae, and, in particular, the adults and larvae of *Coccinella septempunctata* L. and *Propylaea quatuordecimpunctata* (L.) comprised the dominant portion of the antagonist potential. It is remarkable that only these two species dominate the coccinellid community in wheat, although a total of 37 aphidophagous coccinellid species exist in Germany (Freier & Gruel, 1993). We found that polyphagous predators comprised one-third of all predators detected. However, it is very difficult to calculate their predatory efficiency (Volkmar et al., 1994).
Thesis: ***Coccinella septempunctata* L., *Propylaea quatuordecimpunctata* (L.) (adults and larvae), and Syrphid larvae are, numerically, the largest contributors to the antagonist potential against cereal aphids in Central Germany.**

A quantitative analysis of the efficiency of stenophagous predators that included the critical PPR and predator density using double assessment of adult coccinellids was able to demonstrate any significant predatory effects. However, methodological deficits do exist: Even with very painstaking field counts, many (up to 1 out of 2) young predator larvae are overlooked. This was also found by Lapkin et al. (1987), Iperti et al. (1988), and Holz (1993).
Thesis: **The determination of predatory density in cereal fields continues to be a problem in applied entomology. In coccinellids, representative field counts are possible only in adults and older larvae.**

The adverse effect of coccinellids on the late infestation phase, i.e. on retrogradation, was repeatedly demonstrated. It was more difficult to demonstrate how coccinellids retard the population growth of aphids in winter wheat on the basis of the available field data. We found that neither a high coccinellid density, e.g. much higher than 15 predator units (larvae and doubly assessed adults) /sqm nor a low PPR (< 1:80) gave any indication of particular predator efficiency. Temperature is doubtless an important factor. As was shown in the climate chamber experiments, slight temperature differences of 20°C to 23°C resulted in minor to major predatory effects.
Thesis: **Next to coccinellid population density and PPR, the temperature has the main influence on the predatory effect. At 20°C the coccinellid defence is still poor, and the aphids take advantage of the slow ripening of the cereal.**

Contrary to our expectations, our data analyses did not indicate any numerical response of the coccinellids, because the data pool was insufficient. We were only able to confirm the general assumption that delayed numerical response occurs during the final infestation phase in cereal aphids. An important and repeated observation was that surrounding areas with aphid infestation caused ladybirds to migrate from or abandon the wheat field.
Thesis: **The numerical response is the most important regulatory mechanism in the cereal aphid - stenophagous predator system. However, the density feedback is very difficult to quantify. Nearby aphid-infested fields and setaside land may counteract the density feedback and have a dramatic effect on the regulatory effect of aphidophagous predators in wheat.**

The hunger phenomenon was a special focus of attention. In experiments with *Coccinella septempunctata* L. performed under temperature conditions of an average summer, the coccinellids demonstrated unexpectedly quick adjustment to the food situation.
Thesis: **The hunger reactions of the ladybirds to different food situations are short-termed and, accordingly, they must be taken as a limited factor in numerical response calculations.**

The advantage of cage experiments is that they make it possible to study and quantitate the dynamics of cereal aphid-coccinellid interactions with precisely defined populations (Rautapää, 1975; Wetzel et al., 1981). On the other hand, the high intrinsic rate of caged aphids cannot be compared with that of aphids in actual field conditions. Still, our data was very interesting. We were able to clearly show a change in the course of infestation as a reduction in aphid days. In the two-year experiments with *Coccinella septempunctata* L., we measured an infestation-reducing effect of one predator unit/sqm (ca. 2000 aphid days/sqm or 3 aphid days/tiller). This can serve as a guide to determining the extent of natural control (Ferran et al., 1986).
We know that the predatory efficiency of coccinellids has to be weighted differently with respect to time. They are able to slow down the increase of the aphid population and, by their larvae, reduce later infestation. Climate chamber trials on wheat yield formation showed the following effect: the yield gain up to the stage of milky ripeness (resulting from predatory reduction of aphids) was twice as high as the same effect in the dough stage, because one aphid day during the flowering caused twice as much loss as one during dough stage.
Thesis: **From a point of view of Integrated Crop Protection, the predatory effect of coccinellids at the beginning of cereal aphid infestation is the most interesting finding. The coccinellids slow down the instrinsic rate of aphid population and thus reduce early infestation, which causes higher losses than late infestation.**

Given the extraordinary dynamics of cereal aphid-coccinellid interactions, simulation models are a very important means of gaining theoretical knowledge. The GTLAUS model has been improved on the basis of new findings, but still cannot accurately reflect reality, considering the concurrent effects of different beneficials or the complicated processes of migration and mortality.
Thesis: **Simulation models of cereal aphid-coccinellid interactions help us to understand important trends and phenomena.**

One of our central tasks was to define beneficial thresholds, i. e. densities of beneficials that keep a pest below the economic threshold. The trials showed that beneficial thresholds extend over a larger range of values than previously believed (Freier, 1994). It turned out that, under certain conditions, five adult *Coccinella septempunctata* L./sqm are enough to naturally control cereal aphids, while about 20 are needed in other situations.

In conclusion, it is a challenge for Integrated Crop Protection to include coccinellids and other antagonists into the threshold concept for cereal aphids. This is the subject of a current three-year investigation including farmers and extension service who are requested to make a basic assessment of the antagonist potential. Existing decision guidelines proceed from the principle of "the more beneficials, the higher the control threshold", and vice versa.

Acknowledgements

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STUDIES ON THE POPULATION ECOLOGY OF THE SPIDER *LEPTHYPHANTES TENUIS* (ARANEAE: LINYPHIIDAE) IN CEREALS

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ABSTRACT

Recent research into the population ecology of *Lepthyphantes tenuis* is reviewed. Consideration is given to its abundance, capacity for predation, development, reproduction, mortality, distribution and dispersal. It is found to be a species with considerable biocontrol potential because of its abundance, wide distribution and behavioural characteristics in relation to prey capture. It is well suited to life in agricultural environments, being an r-strategist with high reproductive capacity, long breeding season and high dispersal power.

INTRODUCTION

Spiders are acknowledged to be valuable predators of small pests in European agriculture (Riechert & Lockley 1984; Nyffeler & Benz 1987; Sunderland *et al.* 1986b, 1987). If pesticide inputs are to be reduced and more reliance put on biological control of pests, it becomes necessary to understand more about the population ecology of the common species of predator, so that they can be manipulated to Man's advantage. *Lepthyphantes tenuis* (Blackwall) is a common species in European agriculture with much potential as a biocontrol agent. The considerable amount of recent research focussed on this species is reviewed here, with attention being given to its abundance, capacity for predation (especially of pest species), development, reproduction, mortality, distribution and dispersal.

ABUNDANCE

Geographical distribution

The current distribution of *L. tenuis* includes Europe, North Africa, Chile, Argentina, New Zealand (Platnick 1993), North America (Edwards 1986) and Asia (Tanasevitch 1990). It is the dominant species in arable fields in parts of the North Island of New Zealand (C.J. Topping pers. comm.) and also occurs on the South Island (Ashby 1974). It is found in the middle-Asian region of the former USSR and is described by Tanasevitch (1990) as a basically holarctic species which has been introduced by the activities of man into other continents. It has been introduced recently into USA from Europe and did not occur in Washington State before 1950 (Edwards 1986). Found in all parts of the UK, it can be regarded as one of the most abundant species in that country (Bristowe 1958) but evidence to date suggests that it is not very numerous in Switzerland (papers by Nyffeler), Poland (papers by Luczak, Kajak) or Finland (papers by Huhta, Raatikainen).

Habitats

Because *L. tenuis* is a very dispersive species that occurs in many habitats, a full understanding of its role in agriculture cannot be obtained without also considering non-agricultural habitats that may form sources from which it can recolonise fields (Topping & Sunderland 1994bc). Its natural habitat in the UK, according to Duffey (1968) is "open herbaceous areas, both wet and dry, but it may also be found in woodlands". It has been recorded from UK oak woods (Turnbull 1960) and was the dominant linyphiid in a rush bed (*Juncus effusus* L.) where Linyphiidae formed 75% of total spiders (Rothschild 1966). Other European habitats include Danish beech woods (Toft 1976), Dutch peat bogs (Deeleman-Reinhold 1990) and islands off the west coast of Norway (Hauge *et al.* 1990). In general it appears to be one of the dominant aeronautic linyphiids over a large part of northwestern Europe (Sunderland 1987).

In agricultural habitats *L. tenuis* seems to favour tall, dense vegetation. It was found at 37 sites (upland and lowland) of intensively-managed agricultural grasslands in northern England (Rushton & Eyre 1989) and, based on multivariate analyses,Topping (1991) considered that it was more likely to be found at sites with tall vegetation. It also preferred dense to thinly-planted maize (Alderweireldt & Desender 1990).

Contribution to the arachnofauna

Table 1 shows that *L. tenuis* is one of the common species found in a wide range of European agricultural habitats. It probably contributes less to the arachnofauna of well vegetated non-agricultural habitats, but can be a dominant species in disturbed or ephemeral natural habitats, such as sand dunes and new polders (Table 1). Such conclusions must, however, be tentative until more data are available. Some caution is needed in interpreting Table 1 because many of the studies listed relied on pitfall trapping. Comparison of pitfall catches with "absolute" density (D-vac followed by ground search of the area just sampled) in winter wheat showed bias in sex and size of *L. tenuis* caught and a poor relationship between pitfall catch and true density (Topping & Sunderland 1992). Similar results were obtained by comparing D-vac and pitfall catch in German winter wheat (Dinter & Poehling 1992ab; Dinter 1995). *L. tenuis* will enter pitfall traps by lowering itself down from overhanging vegetation; it then moves around the inside of the trap and is only caught if it loses its footing. Trap avoidance, escape from traps and web-building within traps have all been observed. It was calculated that *L. tenuis* would need to encounter a mean of 26 traps before capture (Topping 1993).

Density

Density data are sparse, but adult density normally lies within the range 0.2 - 16.2 m^{-2} (Table 2); immatures ranged from 1.3 m^{-2} to 47.2 m^{-2} in winter wheat (Topping & Sunderland 1994b). Many of the studies in Table 2 relied on D-vac sampling to provide density estimates. The "absolute" density sampling method (above) provided an opportunity to assess the efficiency of the D-vac (ie numbers in D-vac as a percentage of numbers in D-vac plus ground search) As a foliage-inhabiting species, *L. tenuis* was sampled more efficiently (82-94%) than were ground-based Erigonine species (33-72%); D-vac efficiency also varied with site/year, season and degree of weed cover. Sampling precision for *L. tenuis* using the "absolute" method was 0.1- 0.3 and the coefficient of variation was 0.35 - 1.5 which compared favourably with other sampling methods (Sunderland & Topping

1995). Amongst adult *L. tenuis* , both males and females were caught more frequently in the D-vac part of the absolute density samples in both 1990 and 1991, presumably because they were more likely to be located in the vegetation than on the ground (Topping & Sunderland 1994a).

WEB CHARACTERISTICS AND WEB-SITE TENACITY

Linyphiids build horizontal, non-sticky, sheet or hammock webs (Bristowe 1958). *L. tenuis* walk on the undersides of their webs and web support is needed to keep the sagging central area above the soil in wind and rain and when the web is loaded with dew. For this reason webs are rarely found on bare soil but are usually supported by plants (Thornhill 1983). They are normally built 5 - 10 cm above ground in cereals and agricultural grassland (Sunderland *et al.* 1986a; Kennedy 1990; Topping 1991; Alderweireldt 1994b), with the exception that they can be built within holes in the ground if these are sufficiently large and deep (Thornhill 1983; Alderweireldt 1994a; Samu *et al.* unpublished). As a member of the subfamily Linyphiinae *L. tenuis* builds a much larger web than the majority of Erigoninae species, and it is the Linyphiinae that contribute most to the high coverage of ground (up to 50%) by webs recorded in cereal fields in the summer (Sunderland *et al.* 1986b). The mean size of adult webs appears to be *c.* 21 - 25 cm^2 on sand dunes (Duffey 1968) and in agricultural grassland (Topping 1991) but *c.* 62 - 75 cm^2 in sugar beet (Thornhill 1983), maize (Alderweireldt 1994b) and winter wheat (Sunderland *et al.* 1986a).

Webs can represent a considerable investment in time and energy for some linyphiid species (eg *Lepthyphantes zimmermanni* Bertkau (Ford 1977)), but this does not appear to be the case for *L. tenuis*, which often abandons its web within a few days (Fraser 1982). During a study in winter wheat, webs were observed to be abandoned by the original owner mainly because a larger adult female challenged the occupant and took over the web after a short contest (Samu *et al.* unpublished). Duffey (1956) offers an alternative explanation. He caught more adult females than males in pitfalls in grassland and many webs (presumed to belong to *L. tenuis*) were unoccupied; he hypothesised that during the breeding season females build a large number of webs in different places, remaining in each for only a short time if a male does not arrive. Merrett (1969) also caught more females than males in pitfalls in UK heathland. Meijer (1977) caught more females than males in window traps in a new Dutch polder, which raises the possibility that females may abandon their webs frequently and "balloon" (see below) to new habitats in order to allocate reproductive effort across a range of habitats, thus spreading the risk of local extinction (Den Boer 1968; Weyman 1993; Weyman *et al.* 1995). The converse of rapid web-site abandonment is that large numbers of spiders are mobile and searching for new web-sites. Holes in the ground (*c.* 10 cm diameter x 10 cm deep) seem to be highly favoured web-sites, and are occupied with a probability of 0.33 in the first day of availability (Samu *et al.* unpublished) by these vagrant individuals; artificial provision of such holes in fields can increase *L. tenuis* density from *c.* 1 m^{-2} to *c.* 20 m^{-2} (Alderweireldt 1994a).

PREDATION

Laboratory observations

L. tenuis appears to be totally dependent on its web for prey capture (Alderweireldt 1994b;

Sunderland *et al.* 1995a). This has allowed researchers to record predatory behaviour under controlled laboratory conditions, by observing the spider's responses to prey dropped into the web. The majority of such studies have focussed on pests, such as aphids and whiteflies, as prey. The large webs of adult females can exert a degree of pest control even when the spider is absent. The percentage of the cereal aphid *Sitobion avenae* (F.) escaping from webs of satiated adult females (which did not attack) within 4h at 20°C was related to size of the aphid, and ranged from 100% for adults down to only 3% for first instars (Sunderland *et al.* 1986b). Once they become hungry, adult *L. tenuis* are (for linyphiids) efficient and voracious predators. For example, after seven days starvation at 20°C adult females killed 18.7 whitefly (*Trialeurodes vaporariorum* (Westwood)) per day, which was significantly more than for adult females of the erigonine *Erigone atra* (Blackwall) (Fraser 1982). Similarly, capture efficiency of aphids (percentage of trials in which the aphid did not escape from the spider) by hungry adult *L. tenuis* females was greater than for hungry *E. atra* females and varied from 100% for first and second instars down to 30% for adult *S. avenae* (> 1 mg) (Sunderland *et al.* 1986b). Capture efficiency did not vary between the sexes or with temperature between 10°C and 20°C. When a first instar and adult *S. avenae* arrived in the web simultaneously, female *L. tenuis* preferred the adults. If an adult aphid arrived while the spider was feeding on a second instar the adult would be attacked even though the spider did not release remains of the first meal. These physiological and behavioural aspects of its predatory repertoire improve the value of *L. tenuis* as a biocontrol agent.

There is broad agreement between authors concerning the mean consumption rate (aphids day^{-1}) of *S. avenae* by adult *L. tenuis* under laboratory conditions; eg 9.8 first instars and 0.8 adults eaten by females and 5.3 first instars and 0.3 adults eaten by males at 16 - 18°C (Kennedy 1990); 1.7 third instars eaten by females at 20°C (0.09 mg dry weight per day) (Sunderland *et al.* 1986b). Sopp (1987) recorded a consumption of 0.14 mg wet weight *S. avenae* day^{-1} at 12°C and was able to detect, by ELISA, 0.10 - 0.13 mg *S. avenae* inside adult *L. tenuis* immediately after feeding at 10 - 16°C, using an antiserum specific to *S. avenae* (Sopp 1987).

Mansour & Heimbach (1993) investigated the capacity of spiders to reduce cereal aphid increase rates under laboratory conditions. *Rhopalosiphum padi* (L.) increased 12 fold over 13 days on small wheat plants in 5 l jars in the presence of an adult *L. tenuis* at 20°C but 18.5 fold in control jars with spiders absent. Type II functional response curves were recorded (using alate *R. padi* in 30 ml glass vessels) in relation to numbers of aphids *consumed*, but there was a linear relationship between number of aphids present and number *killed*, because the spiders displayed "wasteful killing". This is another feature of *L. tenuis* behaviour that is conducive to efficient pest control.

Fraser (1982) used the number of whitefly killed day^{-1} in the laboratory as a standard test to assay hunger level of spiders brought in from the field; 70% of Linyphiinae were beyond the hunger threshold at which predation is triggered and would therefore have attacked any aphid falling into the web in the field.

Predation in the field

This has been assessed directly by identifying prey taken from the chelicerae of *L. tenuis* adults in webs. Prey in UK winter wheat fields were mainly symphypleone Collembola and aphids, plus a few small Diptera and Acari (Sunderland *et al.* 1986a) and both sexes were observed feeding on aphids (Fraser 1982). Prey in Belgian maize and ryegrass fields were predominantly aphids, followed by Isotomidae (Collembola) and a few small Diptera and Acari (Alderweireldt 1994b). There was a mean of 2.8 prey per web (excluding zero values), but small adult Carabidae and Staphylinidae falling into webs were refused by the spiders after a quick check (Alderweireldt 1994b). Direct visual assessment of predation is extremely labour-intensive and, as a result, sample sizes are usually small. In addition, such assessments have, to date, only been made during the daytime, and only for adult *L. tenuis* (with an emphasis on females). The use of serological post-mortem methods overcomes some of these limitations (Sunderland 1988). Rothschild (1966) used the precipitin test to demonstrate that *L. tenuis* fed on the delphacid *Conomelus anceps* (Germar) in a rush bed (*Juncus effusus* L.). Janssens & De Clercq (1990) recorded feeding on cereal aphids by *L. tenuis* in Belgian winter wheat, using the antiserum of Crook & Sunderland (1984) in an ELISA. Sopp & Chiverton (1987) used ELISA to show that both *S. avenae* and *R. padi* were eaten in UK winter wheat in the autumn.

ELISA has also been used semi-quantitatively by recording the percentage of adult *L. tenuis* tested that gave positive reactions. In cereals, in Ireland, 92% of female and 76% of males collected by pooter were positive (using a cereal aphid antiserum), the equivalent values for pitfall-collected specimens being 77% and 43% respectively (Kennedy 1990). Sunderland *et al.* (1987) also recorded a significantly higher percentage positive for females than males in UK cereals. The percentage positive in cereals on two farms in southern England in two years ranged from 17 to 35%, and *L. tenuis* was one of the species positive when aphid density was very low (less than 10 m^{-2}) (Sopp 1987).

Values of the percentage positive in ELISA can be incorporated into predation indices (P). For example, Sunderland *et al.* (1987) reported that P values for *L. tenuis* were low before the start of flowering of the wheat crop (where P = [percentage positive/detection period] x mean predator density). Kennedy (1990) ranked adult *L. tenuis* as the second most important (coming after *Bathyphantes gracilis* (Blackwall)) linyphiid aphid predator in cereals; he used the formula of Kuperstein (1979) P = [percentage positive x predation rate in the laboratory x predator density]/detection period. The high ranking of *L. tenuis* was due to a high laboratory feeding rate combined with a high field density. Estimated consumption rates of *S. avenae* (m^{-2} day^{-1}) by this method were 3.2 first instars and 0.2 adults consumed by adult female *L. tenuis*, the equivalent values for males being 1.9 first instars and 0.2 adults (Kennedy 1990).

A calibration curve can be used to convert ELISA absorbance values to estimates of aphid biomass consumed by individual predators (Sopp *et al.* 1992). Using this method, consumption of *S. avenae* by adult *L. tenuis* in UK cereals was estimated to range from 0.0001 to 0.022 mg m^{-2} day^{-1}, and consumption rates per predator were 0.0033 - 0.0095 mg day^{-1} (Sopp 1987), ie considerably less than consumption rates recorded in the laboratory (see above). However, it should noted that immature *L. tenuis* were not included in this study and density estimates were based on D-vac and quadrat samples taken separately; density will, therefore, have been underestimated (Sunderland *et al.* 1995b). In addition, there are potential problems of ecological interpretation associated with this technology, such as the problems of scavenging and secondary predation (Sunderland 1995). The former may not apply to *L. tenuis*, because scavenging has not, so far, been observed in the laboratory (Sopp 1987; Sunderland *et al.* 1987).

DEVELOPMENT AND REPRODUCTION

Development

The mean period required for eggsac development (ie eclosion of spiderlings and their emergence from the eggsac) at ambient temperatures, in southern England, was 28 days (maximum 102 days) (Sunderland 1991). When rearing *L. tenuis*, individually, in Petri dishes in the laboratory, Sunderland (unpublished) made the following observations;

1. Eggsacs from which hatchlings had emerged (n = 42) were dissected and exuviae were found in all, indicating that at least one moult occurs within the eggsac.
2. The number of post-emergence moults, to adult, under experimental conditons, appeared to be variable. Five moults was uncommon (6.1%, n = 263) and may have been an artefact due to failure to remove exuviae from the rearing dishes on a few occasions. Four moults were recorded in 72.2% of cases and 3 moults in 21.7% of cases.
3. Number of moults was not strongly sex-related but females were slightly more likely (26.5%) than males (15.2%) to have three moults.

Thus, four moults was the norm for *L. tenuis*, and this is also true for the majority of linyphiids (Toft 1976). The records for three moults might have been due to some individuals moulting twice within the eggsac or due to failure to record exuviae (eg the smaller exuviae can sometimes be difficult to detect amongst the prey in the dish and may be eaten by some prey species). Alternatively, *L.tenuis* may have a flexible, diet-related, moulting schedule, because 90% (n = 71) had four moults when reared on mixed Collembola *(Lepidocyrtus* spp. and *Isotoma* spp.), but only 66% (n = 192) had four moults when given stressful diets that did not support high survival rates (see below). Variable moulting schedules by spiders in relation to nutrition have been recorded previously (Bonnet 1930 cited in Turnbull 1962).

Reproduction

In southern England *L.tenuis* produces eggsacs in winter wheat crops between March and October (Topping & Sunderland 1994b) but some individuals have also been observed to construct eggsacs in cereals and grassland during mild winter periods (Sunderland 1991; Topping 1991). The mean number of hatchlings that emerge from individual eggsacs is *c.* 21- 24, depending on year and site, and the maximum recorded is 56 (Sunderland 1991; Topping & Sunderland 1994b). Females taken from winter wheat (captured initially as subadults, then mated after the matural moult), and given excess *Drosophila melanogaster* Meigen as food in the laboratory at 15°C, produced a mean of 3.3 eggsacs (range 1-10) during their reproductive life and had a mean fecundity of 77.2 (range 5-189) (Sunderland *et al.* 1995a). Food quality was found to have a considerable effect on reproduction under laboratory conditions. For example, adults reared from hatchlings on a diet of the Collembola *Lepidocyrtus* spp and *Isotoma* spp. (supplied in excess) produced eggsacs that yielded a mean of 20.8 hatchlings per eggsac, but on a diet of the Collembola *Folsomia candida* Willem (also supplied in excess) a mean of only 5.8 hatchlings per eggsac were produced (Sunderland *et al.* 1995a).

MORTALITY

Abiotic factors

Little information is available concerning the effects of physical factors on the mortality of *L. tenuis*, but survival rates appear to decline at temperature extremes and in relation to low humidity. Under near optimal conditions of 21°C and 100% RH in the laboratory hatchlings survived for a mean of 14 days without food, but only 7 days at 27-29°C (100%RH) and 5 days at < 50%RH (21°C) (Sunderland *et al.* 1995a). Adults taken from under stones with a snow cover and placed in tubes in the snow surface died within 10 minutes (Duffey 1962b).

Nutrition

Many spiders are physiologically adapted to survive extended periods of food shortage (Anderson 1970; Riechert & Harp 1987). In the case of *L. tenuis* , adult pre-breeding females, supplied with water but no food, survived for a mean of 42 days at ambient temperatures in southern England (Sunderland 1991) and even hatchlings can survive without food for a month at 9°C in the laboratory (Sunderland *et al.* 1995a). Survival rate can also be influenced by food quality. At 21°C in the laboratory only 1% of 292 hatchlings survived to become adult on a diet of *F. candida* compared with 60% of 100 hatchlings given a diet of *Lepidocyrtus* spp. and *Isotoma* spp. No hatchlings survived to adulthood when given *S. avenae* as food, in spite of care being taken to supply them with predominantly first instar aphids (Sunderland *et al.* 1995a). Toft (1995) found that first instar *E. atra* were unable to develop on a pure diet of *R. padi* and they died without moulting. Survival and reproduction of adult *L. tenuis* on aphid diets does not appear to have been investigated to date.

Parasitoids

Adult *L. tenuis* and their eggsacs can be attacked by hymenopteran parasitoids. *Acrodactyla degener* Hal. (Ichneumonidae) [and not *Polysphincta tuberosa* Grav. (Ichneumonidae) as mis-cited in Rollard 1984] is an ectoparasitoid attacking adults (Evans 1969; Hudson 1985), but there is no quantitative information about its effect on populations. In a winter wheat crop, in June and July, 3.4% of 383 eggsacs were parasitised, mainly by the scelionid egg parasitoid *Baeus* sp. and to a lesser extent by the ichneumonids *Aclastus* sp. and *Polyaulon* sp. (Van Baarlen *et al.* 1994). *Baeus* sp. is a tiny, wingless, wasp that enters the *L. tenuis* eggsac, by wriggling through the silk wall, and oviposits into individual eggs. More data are required to determine the variability of parasitism across sites, seasons and years.

Predation and cannibalism

Hyperpredation is a common and widespread phenomenon in agroecosystems and includes predation on spiders by a wide range of natural enemies (Sunderland 1995). In Petri dishes, in the laboratory, immature and adult *L. tenuis* were killed and eaten by the carabid beetles *Agonum dorsale* (Pont.) and *Demetrias atricapillus* (L.), the staphylinid beetle *Quedius tristis* (Grav.), the earwig *Forficula auricularia* L., the heteropteran bug *Nabis ferus* (L.), and also by other species of spider, Lycosidae imm., *Diplostyla concolor* (Wider) (Linyphiidae) and *Pachygnatha degeeri* Sundevall (Tetragnathidae) (Sunderland *et al.*

1994). Preliminary manipulative field experiments in winter wheat suggested that the density of immature *L. tenuis* can be reduced by increased numbers of Carabidae. It has not been determined whether this result was due to predation or a reproductive or aggregative numerical response to Collembola, which were more abundant where carabid numbers had been reduced (Sunderland *et al.* 1994). Cannibalism has been observed, not only by larger on smaller, but also amongst equal-sized hatchlings emerging from an eggsac (Sunderland *et al.* 1994). Cannibalism of adult female by adult female has also been observed in the field (F. Samu, pers. comm.).

Pesticides

Spiders are generally considered to be the group of polyphagous predators most sensitive to pesticides (eg Brown *et al.* 1983), and the Linyphiinae are especially exposed because of their higher vertical location in the crop (Jepson 1989). Pitfall catches of adult *L. tenuis* were reduced after fenvalerate and lambda-cyhalothrin (Wehling & Heimbach 1991) and endosulfan (Wehling & Heimbach 1994) applications to winter wheat. Similarly, a reduction of 72% was recorded for forty days after an application of lambdacyhalothrin to winter wheat (Brown *et al.* 1988) and the catch was reduced for seven weeks following an application of fenitrothion to oilseed rape (Everts *et al.* 1989). Dimethoate reduced the D-vac catch by 72% for six weeks in winter wheat and dead *L. tenuis* were found on the ground seven days after spraying (Vickerman & Sunderland 1977). Unfortunately, the majority of such studies do not quantify the factors underlying the reduced catch of spiders, which can be due to mortality, reduced activity or emigration in response to chemical repellency or food shortage. Recent studies in the laboratory (Weyman *et al.* 1994) and field (Weyman & Jepson 1994) have shown that some linyphiid species show a higher probability of ballooning under conditions of food shortage.

Overall mortality

Although it is very difficult to quantify the various components of mortality (above), the overall mortality of the egg and hatchling stages in a field of winter wheat in 1991 was estimated to be 96%. This figure was arrived at by comparing the actual density of hatchlings with the density expected in the absence of mortality. The calculation of expected density drew on information concerning migration rate, fecundity and development rate (Topping & Sunderland 1995a).

DISTRIBUTION & DISPERSAL

Within-habitat distribution

L. tenuis adults had an aggregated distribution (of pitfall catch) in winter wheat and oilseed rape, except for a period of six weeks after spraying with fenitrothion, when there was a random dispersion pattern (Everts *et al.* 1986). Kennedy (1990) found that adult females were uniformly distributed but males non-uniformly distributed in winter wheat. The pitfall catch was greater towards the edge of a maize field than in the middle (Alderweireldt & Desender 1990). However, patterns of horizontal distribution in agroecosystems are likely to be dynamic, responding to a wide range of factors (Powell *et al.* 1995), such as weed distribution (Topping & Sunderland 1994a) and soil moisture (Jagers op Akkerhuis 1993ab). Vertical distribution, on the other hand, is probably less dynamic, because there is less variability and heterogeneity in the vertical plane. Most studies have concluded that *L. tenuis* normally establishes itself on the vegetation above ground level. In a laboratory arena adult females moved onto vegetation and stayed there for a longer time than did *Erigone dentipalpis* (Wider) (Topping 1993). Similarly, *L. tenuis* frequented the upper strata of rush tussocks (Rothschild 1966). Duffey (1966) describes vertical stratification of the genus *Lepthyphantes* in herbaceous and woody vegetation less than 1.8 m high; *L. ericaeus* (Blackwall) is usually close to the ground, *L. mengei* Kulczynski in the middle zone and *L. tenuis* is usually in the upper zone. Duffey (1966) considers the relative size and colouring of these species correlates with their vertical location.

Dispersal

L. tenuis can disperse by walking over the ground or by "ballooning"through the air (ie passive transport attached to silken threads). Use of a short-term caging technique to prevent dispersal suggested that there was no large net immigration or emigration of spiders, by walking or ballooning, from a field of winter wheat during the early part of the growing season (Topping & Sunderland 1994a). However, in general, aerial dispersal is a very effective means of dispersal for this species.

L. tenuis is one of the nine commonest aeronaut species in the UK and was caught in nets on masts at 3 m, 59 m and 92 m (Freeman 1946) and in 12.2 m and 1.5 m suction traps in agricultural areas (Sunderland 1991). Owen & Le Gros (1954) recorded 238 *L. tenuis* taken in the air by swifts (*Apus apus*) in UK during July; 71% were taken on a single day and 96% were adults. It was one of the common aeronautic species caught on greased canes in grassland and near woodland (Duffey 1956) and it even appeared on the bare mineral surface of the blast zone of the Mount Saint Helens volcano (USA) within the first two summers of eruption (Edwards 1986). It constituted 11.2% of adults caught in deposition traps (design described in Topping & Sunderland 1995b) and 3.3% of adult ballooning spiders collected from fences at field edges (Thomas 1992). The number of adults caught per day per deposition trap ranged from 0.1 to 1.9 in UK agricultural grassland between November and August, and 0.1 to 3.3 in winter wheat between January and August (Weyman *et al.* 1995). A large rotory trap (Topping *et al.* 1992), suction traps and deposition traps all caught *L. tenuis* in a field of winter wheat in 1991, and the numbers of adult *L. tenuis* as a proportion of total spiders caught was also similar (*c.* 0.1) for the three trapping methods (Topping & Sunderland 1995b). To investigate the significance of such effective dispersal in the population ecology of this species required the construction of a spatial dynamics model that took account of dispersal in relation to the other population processes already discussed in this review.

Spatial dynamics model

A model was constructed to simulate *L. tenuis* population dynamics in a matrix of square plots using parameters from experiments and the literature. Changes in numbers of adults, juveniles and eggs were calculated annually based on monthly calculations of mortality, reproduction, maturation and emigration. Simulations suggested that asynchronous or non-contiguous perturbations would be less damaging to the metapopulation than synchronous or contiguous ones (Topping & Sunderland 1994b). Further simulations, for a 10 km^2 area of Lincolnshire, UK, suggested that *L. tenuis* density in crops would be raised if nonrotational set-aside were randomly distributed throughout this arable landscape (Topping & Sunderland 1994c). It is, however, emphasised that there are little or no data for spider density, mortality, reproduction or migration in the majority of agricultural habitats (the simulations above were modelled by analogy with the observed effects of farming practices on population dynamics parameters in winter wheat).

CONCLUSIONS

L. tenuis has a number of attributes suiting it to biocontrol, especially of aphids;

1. Wide geographical and habitat distribution
2. Usually numerous in agroecosystems
3. Highy mobile within and between fields, providing opportunity for encounter with pests
4. Can survive without food for long periods
5. Builds large webs that can kill some pests even in the absence of the spider
6. A high proportion are hungry in the field, ensuring that predatory behaviour towards pests entering the web will be triggered
7. Aphids are one of the most frequently caught prey types
8. Aphids are caught even at low aphid density
9. High capture efficiency and voracity
10. Can consume more than one aphid simultaneously
11. Exhibits "wasteful killing" at high aphid density
12. Well adapted to the exigencies of life in agroecosystems by being an r-strategist with high reproductive capacity, long breeding season and high dispersal power.

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Table 1. Contribution of Lepthyphantes tenuis to the arachnofauna

Author & (Country)	Sampling Method [1]	Habitat	Rank [2]	% [3]
AGRICULTURAL				
Kennedy 1990 (IRL)	P	wheat	in top 10	
Wehling & Heimbach 1991 (D)	P, PE	wheat		11
Sunderland et al. 1986 (UK)	Q	wheat	2-3	16-18
Sunderland & Topping 1993 (UK)	Q, D	wheat	1-2	28-31
Vickerman 1992 (UK)	D	wheat	in top 5	
Feeney & Kennedy 1988 (IRL)	P, Q, D	wheat	2-6	
Cottenie & De Clercq 1977 (B)	P	wheat	4-9	5-8
Volkmar et al. 1994 (D)	P, PE, D	wheat	in top 6	
Pietraszko & De Clercq 1982 (B)	P	wheat	7	6
Duffey 1978 (UK)	E	barley	2-4	
Toft 1989 (DK)	P	barley	10	0.5
Alderweireldt & Desender 1990 (B	P	maize	8	
Cocquempot & Chambon 1990 (F	P, Wa	cereals	2	
White & Hassall 1994 (UK)	P	cereal edge	7	
Kleinhenz & Buchs 1993 (D)	P, PE	sugar beet	4	5-7
Duffey 1978 (UK)	P	plough	1	
Duffey 1975 (UK)	P, Q	grass	3-5	
Gibson et al. 1992 (UK)	D	grass	3	
Edwards et al. 1976 (UK)	P	grass	9	
Asteraki et al. 1992 (UK)	P	grass	6	
Janssens & De Clercq 1986ab (B)	P	grass,beet	4	
Thornhill 1983 (UK)	P	barley,beet	4-6	
Thomas 1992 (UK)	D	cereal, grass		6-13
NON-AGRICULTURAL				
Duffey 1962a (UK)	P	grass	10	
Rushton 1988 (UK)	P	grass,scrub	1-6	
Vangsgaard et al. 1990 (DK)	P	forest,arable	15	
Merrett 1969 (UK)	P	heath	19	
Duffey 1968 (UK)	Q	sand dunes	3	
Meijer 1977 (NL)	P, Wi	new polder	1-2	

[1] Key to sampling methods: P = pitfalls, PE = photoeclector, Q = quadrats, D = D-vac, E = emergence traps, Wa = water traps, Wi = window traps

[2] Position in rank order of abundance of spider species in the sample

[3] Number of L.tenuis caught as % of total spiders caught

Table 2. Density of Lepthyphantes tenuis adults

Author & (Country)	Sampling Method [1]	Habitat	Density range (m-2)
Sopp 1987 (UK)	Q	wheat	0.3-1.5
Weyman et al. 1995 (UK)	D	wheat	0.2-1.8
Sunderland et al. 1987 (UK)	Q	wheat	0.8-3.4
Sunderland et al. 1987 (UK)	D	wheat	0.6-1.7
Sunderland 1991 (UK)	D	wheat	0.1-7.3
Dinter 1995 (D)	D, Q, Ex	wheat	1.0-6.8
Topping & Sunderland 1994b (UK	D, Q	wheat	1.3-16.2
Weyman et al. 1995 (UK)	D	grass	0.2-5.0
Meijer 1977 (NL)	Q	new polder	0.3-3.3

[1] Key to sampling methods: Q = quadrats, D = D-vac, Ex = heat extractor

Phenology and population density of predatory bugs (*Nabis* spp.; Heteroptera: Nabidae) in different fields of winter wheat in Germany, 1993/94

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Abstract

Studies took place in Schleswig-Holstein (near Kiel) and in Hesse (near Frankfurt/M.). According to the findings published so far and to the own studies, it seems, that *Nabis ferus* L. (and presumably also *N. pseudoferus* Rem.) reproduce mainly outside of wheat fields, in grassland or in field margins, where also hibernation takes place. So the time per year spent by *Nabis* spp. in wheat is very short, mainly July (and August) in Middle Europe. But extended studies are necessary to find out exactly the reproduction sites of populations of *Nabis* spp. in agricultural areas.

The numbers per m^2 of hygrophilous *Nabis* spp. in wheat fields are influenced by plant density and by field size. Highest numbers of (immigrated) predatory bugs were found in a small field (3 ha) in July (6 per m^2).

Average *Nabis* numbers per m^2 of fields with a size of 6 to 11 ha were 0,23 in early June and 0,34 in early/mid July. So the value of Nabidae for cereal aphid control will be limited in fields of winter wheat.

1. Introduction

Among the large number of different antagonists of cereal aphids, Nabidae have been mentioned rather rarely, as compared with other predator groups. It is known, that *Nabis* spp. are predators of cereal and other aphids, and of plant bugs (nymphs and eggs) (Kullenberg 1941, Benkó & Kiss 1989, Wetzel et al. 1991). Recently it was shown, that *Nabis ferus* L. is also a predator of linyphiid spiders (and others) (Sunderland et al. 1994), so that is should be regarded as a polyphagous predator. But the phenology of *Nabis* spp. in wheat fields is not fully understood yet, and figures on their population density are not available yet, since all studies in wheat published so far used sweep nets.

Nabis ferus L. is the predominant species in European wheat fields, followed by *N. pseudoferus* Rem., as has been shown for Northern Germany (Afscharpour 1960), for East Germany (Wetzel et al. 1991), for Hesse (Klumpp 1990) and for the Paris Bassin (France) (Chambon 1985).

In the course of studies on epigeal predators conducted on different fields of winter wheat near Kiel and near Frankfurt/M. (Germany), 1993/94, also *Nabis* spp. have been collected. The numbers found are presented here, compared with data published so far, and differences between the sites studied being tried to explain. So, in the end, a bit more of information should be available for one of the groups of cereal aphid antagonists.

2. Study sites and methods

Hesse: Pitfall traps, 50 m from the field margin, 10 m distant from each other (diameter 10 cm, trapping fluid 5 % Natrium benzoate plus detergent) were run at four sites in winter wheat, 10 to 20 traps per field, 30.4.-26.7.93 (harvest), being emptied weekly. The sites were: Friedberg-Dorheim (extensive), Bad Vilbel-Dottenfeld (biolocical-dynamic), Bad Vilbel-Gronau

("integrated", small fields) and Bad Vilbel-Massenheim (intense).
Square counts, also at least 50 m from the field margin, were conducted in 1994 weekly (May - July) at 3 sites at Bad Vilbel, the unit being 0,25 m^2, weekly four replicates. Procedure: a square tin frame (50 x 50 cm) was set to the soil. Wheat plants were first shaken to make insects fall down. Then the plants were cut off, shaken again and removed, so that insects could be counted on the ground. Pouring additionally 2 times 5 l of water per square was helpful, especially for other predators (Basedow et al. 1988).

Schleswig-Holstein: Square counts as above were conducted in 1993 and 1994, in early June and early July, 10 to 20 replicates per field, at two sites near Kiel: Brodersdorf (intense) and Passade (organic-biological).

Weeds and wheat ears per m^2 were measured in June/July (2 m^2 per field). Time and kind of insecticides sprayed were inquired of the farmer annually.

3. Results

3.1 Phenology

3.1.1 The present status of knowledge

For Europe, four publications on the phenology of *Nabis* spp. in agriculture are known.

1. Afscharpour (1960) studied with sweep nets the occurrence of *Nabis ferus* and *N. pseudoferus* in fields mainly of potatoes, wheat, clover/grass and *Lolium perenne* in Schleswig-Holstein. He gives summarizing figures on the phenology on all fields studied. After hibernation of the adults, the reproduction took place in May. Larvae (rare) were found in June and July. The peak densities of adults were observed in July and August. *N. ferus* was caught in highest numbers in fields of potatoes, wheat and grass, *N. pseudoferus* seemed to prefer grass (*L. perenne*).
Concerning the few larvae found: it cannot be seen from the text, tables or graphs, were the larvae occurred, in grassland or in wheat/potatoes (Afscharpour 1960).

2. Benkó & Kiss (1989) report for Hungary, that *Nabis* spp. colonize wheat fields in early June, as stated by sweep nets, when, besides of adults, also larvae ($L_2 + L_3$) occur soon.

3. Wetzel et al. (1991) have found by sweep net studies in East German fields of winter wheat, adult *Nabis* spp. only (*N. ferus* prevailing). They were rare in May, but numerous in July and August.

4. Morris (1990), using a D-Vac, reports, that *N. ferus* lives most time of the year in grassland, hibernating there as an adult, but being rare in July/August.

If these facts published so far are regarded together, it seems that at least the species *N. ferus*, but presumably also *N. pseudoferus*, are immigrating guests in wheat fields only, for a short time of the year, while not only hibernation (like in many other beneficials) but also reproduction mainly takes place in grassland or in field margins.

3.1.2 Recent findings

The observations on the phenology of *Nabis* spp. with pitfall traps in Hesse 1993 fit in the suspected cycle (fig. 1). Only adult *Nabis* individuals were caught in fields of winter wheat, rare in May, few in June, but with a peak density in July. The predators seem to leave the fields before harvest (presumably because the fields are too dry then, see below).

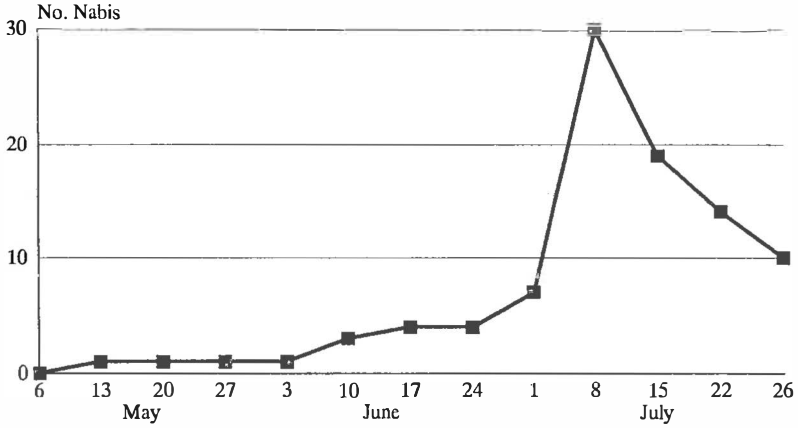

Fig. 1: Phenology of adult *Nabis* spp. on 4 fields of winter wheat in the Friedberg district (Hesse), 29.4.-26.7.1993 (50 pitfall traps)

3.2 Population density of *Nabis* adults in several fields of winter wheat, 1993/94

3.2.1 Population densities in July

The nine fields studied are arranged in table 1 according to field size, at Passade (where all fields were of equal form and size) according to plant density.

Numbers per m^2 were low in all cases in July (though it was the month of the highest activity), but some interesting tendencies can be derived from the findings.

All fields studied at Schleswig-Holstein were larger than those in Hesse. At Brodersdorf/Kiel, an area of high agricultural intensity (Basedow 1991), large fields (10 to 16,5 ha) were all sprayed with insecticides (table 1). No specimens of *Nabis* spp. could be found in these fields in July.

At Passade (5 km distant from Brodersdorf) studies took place on a farm managed organic-biological ("Bioland"), without input of pesticides etc. All fields (8 ha) were arranged rectangular there, each with hedges on two sides. No predatory bugs were found there in a field of winter Dinkel (`94 I), with a very low plant density. In the other two fields studied at Passade, with higher plant densities, *Nabis* spp. numbers per m^2 in July were 0,3 -0,4, i.e. rather low.

In Hesse, 1994, the population density of *Nabis* spp. adults in July increased with decreasing field size (table 1). Though, at Gronau, Pirimicarb was sprayed, end of June 1994, the density of the predatory bugs was fivefold higher in the small field than in a neighbouring large field managed biological-dynamic ("Demeter"; no pesticides etc. being used, either).

Table 1: Population density of *Nabis* spp. (adults, average of July) in different fields of winter wheat (Passade `94 I: winter Dinkel) in two regions of Germany, 1993/94

* B = Brodersdorf (intense), P = Passade (organic-biol.),
M = Massenheim (intense), D = Dottenfeld (biol.-dynamic),
G = Gronau ("integrated", small fields)

Land, district	Location*, year	Insecticide, (end of June)	field size (ha)	ears per m^2	weeds per m^2	*Nabis* per m^2 (July)
Schleswig-Hostein, Plön	B `93 I	Oxydemeton-M.	16,5	642	< 1	0.0
	B `93 II	Pirimicarb	10,5	534	< 1	0,0
	B `94	Pirimicarb	10,0	494	< 1	0,0
	P `94 I	./.	8,0	294	14,4	0,0
	P `93	./.	8,0	355	5,5	0,4
	P `94 II (after 5 yr fallow)	./.	8,0	336	62,0 +44 clover	0,3
Hesse, Friedberg	M `94	Cyhalothrin	6,3	624	< 1	0,3
	D `94	./.	5,6	344	?	0,5
	G `94	Pirimicarb	3,0	401	< 1	2,5

3.2.2 The development of the population density within wheat fields from June to July

The seven cases studied are listed in table 2. In large fields managed intensely (plus insecticide), predatory bugs were missing in June and July. In another large field, treated with Pirimicarb, predator numbers dropped from 1 to 0 per m^2 (Brodersdorf 1993).
But in a small field, in spite of a Pirimicarb spray, bug numbers increased enormously from 0 in June to 6 per m^2 in mid July. In larger fields, managed ecologically (Passade 1993/94, Dottenfeld 1994), the rate of predaor increase was low, or the population density remained at the same level, June and July (table 2).

From table 2 the following average population densities of *Nabis* spp. in wheat fields can be derived:

Early June, field size 5,6 to 10,5 ha: 0,23 per m^2.

Early/mid July, field size 5,6 to 10,5 ha: 0,34 per m^2; field size 3,0 ha: 6,0 per m^2.

Table 2: Population density of *Nabis* spp. adults per m^2 on different fields of winter wheat near Kiel (Germany), early June and early July, 1993/94, and near Frankfurt/M. (Germany), mid June and mid July, 1994

site, year	field size (ha)	ears per m^2	insecticide (end of June)	*Nabis* spp. per m^2	
				3.6.93	8.7.93
Brodersdorf, intense, 1993	16,5	642	Oxydemeton-M.	0,0	0,0
	10,5	534	Pirimicarb	0,1	0,0
Passade organic-biol. 1993	8,0	355	./.	0,05	0,4
				1.6.94	5.7.94
1994	8,0	336	./.	0,0	0,3
				14.6.94	12.7.94
Massenheim, 1994 intense	6,3	624	Cyhalothrin	0,0	0,0
Dottenfeld, 1994 biol.-dynamic	5,6	344	./.	1,0	1,0
Gronau, 1994 "integrated"	3,0	401	Pirimicarb	0	6,0

4. Discussion

4.1 Phenology

The phenology, as shown in fig. 1, but especially the rates of population increase from 0 to medium or high numbers (Passade 1993/94 and Gronau 1994, Table 2), without that larvae had been observed in the field before, support strongly the hypothesis formulated in section 3.1.1: the reproduction and propagation on *Nabis* spp. populations seems to take place outside of wheat fields. So specimens found within wheat fields in July are presumably only short-time guests there.

But since, during the present studies, no search for *Nabis* specimens was conducted in other areas than wheat fields, the suspected main habitats cannot be named, and so the hypothesis remains a hypothesis so far.

4.2 Attractive fields

Penth (1952) has shown, that *Nabis pseudoferus* is very hygrophilous. If it is assumed, that the same is true for *N. ferus*, it would explain the fact, that fields with a low plant density, were humidity is low (Basedow & Rzehak 1988), are not colonized by Nabidae (e.g. Passade 1994 I). Hygrophily would also explain the fact, that Nabidae leave drying wheat fields before harvest (fig. 1).

But most attractive, i.e. easily to colonize, are apparently small fields with broad adjacent grassy field margins (e.g. Gronau 1994). The Gronau area is rich of field margins as hibernation sites for predatory insects (Basedow 1990). Presumably the Nabidae colonize the wheat fields, because they are attracted by the availability of prey, there. This should explain changes in predator density from June to July, but since the availability of prey was not quantified during the present study, it is impossible to explain the observed differences safely.

But also the migratory capacity of Nabidae, unknown so far, might influence the colonization of fields by this group. If the capacity would be low, this fact could help to explain the differences between large and small fields concerning population density.

From the studies presented, not experimental, it is impossible to clarify the role of the diferent insecticides used. It seems, however, reasonable to say, that the population density of *Nabis* spp. is affected more by the field size than by selective aphicides.

4.3 Population density and importance of *Nabis* spp. in wheat fields

Figures on *Nabis* numbers per m^2 of wheat fields in Middle Europe have not been published so far, since frequency of the bugs was measured by sweep nets, only.

For fields of at present normal size in West Germany (6-10 ha), average *Nabis* numbers per m^2 to relie on will be rather low with 0,23 in June and 0, 34 in July. So, in spite of a rather high consumption capacity (15 aphids per specimen and day; Wetzel et al. 1991), the significane of Nabidae in natural aphid control in wheat will be limited. But nevertheless Nabidae are part of the large spectrum of aphid antagonists, worth to enhance. If large fields cannot be divided, they could perhaps be divided by grass strips, which is favourable for a lot of predator groups (Nentwig 1989, Lys et al. 1994)). It might also enhance Nabidae.

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Studies on the ecology and control of maize aphids in Catalonia

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SUMMARY: Antecedents, main aims and some provisional results of the current research on maize aphids conducted in the Lleida basin are presented. Maximum temperatures usually occurring in Lleida may have a negative effect on aphids, especially *S.avenae*, causing mortality and reducing their performance after the first peak population in June. Anthocorids were the most frequent epigeal predators, and carabids and spiders the main component of the soil predatory fauna. Delaying the sowing date reduces or prevents the colonization of aphids and may reduce the probability of virus infection. The use of sistemic soil insecticides (carbofuran) was not sufficient to kill aphids and to prevent virus transmission.

Maize is one of the most important arable crops in the irrigated basin of Lleida (NE Spain). Although the area devoted to this crop has been reduced in recent years, it is still important. The traditional rotation of arable crops in the region is alfalfa - winter cereals - maize or sunflower. The maize surface is devoted almost exclusively to grain production.

Aphids constitute one of the primary pests of maize in Spain, with a high potential for injury, but their incidence in time and space is variable (Castañera, 1986). In Lleida, the study of aphids on maize was started in 1984, and two periods may be distinguished: the first lasted from 1984 to 1990, and the second started in 1993 and is still open.

1984-1990:

The aim in this period was to determine the role played by maize in cereal aphid biology and in BYDV epidemiology. Some results and observations can be outlined:

1) Maize is the main host of cereal aphids and the most important reservoir of BYDV in the summer and early autumn (Pons *et al.* 1989; Comas *et al.*, 1993).
2) The aphid species composition varies from spring to autumn: whereas *Rhopalosiphum padi* L., *Sitobion avenae* F. and *Metopolophium dirhodum* (Walker) are the predominant species in spring, *R.padi* and, to a lesser extent, *S.avenae* are the most frequent in autumn (Pons *et al.*, in press).
3) In this period the population dynamics of aphids was also determinated (Pons *et al.*, 1989). Aphids colonize maize in May and their densities increases until they reach a peak in June. Populations at this time are basically composed of alate adults and young nymphs. Soon after the June peak, the population collapses, and population levels through the

summer are very low. Temperature, plant phenology and natural enemies have been suggested as possible factors determining the population dynamics of aphids on maize at this time (Pons and Albajes, 1986), but their actual effects on the maize aphid populations are not well known. At the end of August, an increase in populations levels occurs and densities in autumn are again high, especially for *R.padi*.

4) Aphids living on maize may be vectors of maize dwarf mosaic virus (MDMV), the most serious virus disease affecting maize (Achón, 1993).

5) One of the regular practices in maize crop management in the study area is to apply a soil insecticide at seeding to prevent damage by Elateridae (wireworms), Noctuidae (cutworms) and other soil pests. Systemic soil insecticides are also seen as a good controllers of aphids, and farmers apply them to prevent MDMV infection as well. A preliminary experiment conducted in small plots in Lleida (Albajes *et al.* 1985) showed that plots treated with one of these insecticides did not differ in aphid and MDMV incidence from those not treated.

Project started in 1993

With these antecedents, a three-year research project was started in 1993 in order to better understand the maize aphid ecology and the effects that some practices could have on it. The objectives of this project are:

1) To determine the effect of temperature and crop phenology on the performance of aphids in order to establish whether these factors may be decisives in the decline of population levels soon after the June peak.

2) To discover which natural enemies are present in our maize ecosystems, their relative importance and their influence on aphid populations.

3) To evaluate the influence of the sowing date on the population dynamics of aphids.

4) To determine the effect of treatment with systemic soil insecticides on the maize aphid populations and natural enemies.

Some aspects of the methodology.

1.- *The effect of temperature on aphid performance*

The experiment was carried out with one clone of *R.padi* and one of *S.avenae*, in a chamber at 16:8 h (L:D) photoperiod and constant temperature. The temperatures tested were 18, 22, 25, 27.5 and 30 °C, a range of temperatures usual in June and July in the study area. The experiment was started with 70-80 alatiform nymphs (F_0 generation) that were placed individually in a cylindrical plastic cage (5.3 cm diameter and 3.2 cm height) with a 4 cm piece of fourth or fifth leaf of maize. Plants used were in the six leaf stage (stage 1.5 of Hanway (1971)). The resulting alatae (F_0) were left in the cage until they produced five or six offspring (F_1 generation). Measurements of aphid performance were made in this offspring daily up to the onset of reproduction, when several of the resulting apterous adults were individualized and data about their reproductive capacity were recorded. Developmental time, nymphal mortality, reproductive rate, fecundity and intrinsic rate of increase were some of the performance parameters determined.

2.- *Beneficial fauna present in maize ecosystems*

Data about epigeal fauna were obtained by visual sampling performed regularly on maize plants in commercial fields and experimental plots (see points 3 and 4).

Data about predators living in the soil were obtained by displaying pitfall traps in the same commercial fields and experimental plots. Pitfall traps were collected and replaced every week on the same day as visual sampling for aphids and epigeal predators.

3.- *The effect of the sowing date*

The experiment was conducted in commercial fields sown at different dates. The distance between fields was never more than 1 km. The minimum size of fields was 2 ha. Three sowing dates were chosen: an "early" sowing date (in April), a "medium" sowing date (in May) and a "late" sowing date (in June). Fields were divided into several plots following the soil terraces (or into regular divisions where there were none), and each was taken as a replication. The number of plants sampled in each replication varied from 15 to 25 according to the size. Plants were sampled visually once a week and aphid species and number of individuals and instars present were recorded.

4.- *The effect of soil systemic insecticides*

The experiment was a randomized block with 4 replications (blocks) and three kinds of insecticide treatment: i) plots treated with carbofuran (Curraterr Forte®), applied at the sowing line at the seeding, in a dose of 15 kg/ha; ii) plots treated with granular lindane at the seeding, in a dose of 20 kg/ha; iii) untreated plots. The experiment was carried out in a commercial field. Elemental plot size was never lower than 0.4 ha. Sampling began when maize emerged and ended 10 weeks later. Plants were visually sampled twice a week during the first month and once a week later. The number of plants sampled in each plot was always 25. Aphid species present, the number of individuals and the instar of each species were recorded. The experiment has been carried out in two sites for two years.

Some provisional results and discussion

As part of the work is not finished, the results presented are provisional.

1.- *The effect of temperature on aphid performance*

For *R.padi*, developmental time was shorter, and fecundity, reproductive rate and intrinsic rate of increase higher at 27.5 °C than at the other tested temperatures. Nymphal mortality was higher at 30 °C, and at this temperature many F_1 adults did not reproduce or gave dead offsprings.

In the case of *S.avenae*, developmental time was shorter at 25 °C but time to onset of reproduction and intrinsic rate of increase were not significatively different at 22 and 25 °C. Reproductive rate was higher at 22 °C. The lowest intrinsic rate of increase was achieved at 27.5 °C, and at 30 °C nymphal mortality was nearly 100 %.

Maximum temperatures in the Lleida basin in June range from 23 to 34 °C with 28.7 °C as an average. According to the data obtained, these temperatures can have a negative effect on *S.avenae*, acting as a mortality factor and reducing its performance. The effect on *R.padi* seems to be lower and other factors will have to be evaluated.

2.- *Beneficial fauna present in maize ecosystems*

Table 1 shows the proportion of main groups of epigeal predators found on maize plants in visual samplings. Anthocoridae were the most frequent group in June, July and August, *Orius* sp. being the main genera. The proportion of spiders and other Arachnida was quite high during the crop cicle, especially at the beginning and at the end.

Table 1.- Monthly proportion of epigeal predators found on maize plants sampled visually.

	Percentage of presence on plants					
Predator	May	June	July	August	September	October
Coccinellidae	13.6	8.2	5.9	6.4	3.1	4.9
Carabidae	39.6	5.8	5.5	1.0	1.3	1.9
Anthocoridae	9.3	41.9	57.0	67.6	30.8	20.4
Nabidae	1.4	4.1	4.4	2.3	4.7	13.6
Miridae	0.0	7.4	3.2	3.7	6.1	4.9
Chrysopidae	0.0	0.2	1.7	4.4	3.0	0.0
Arachnida	34.2	25.3	19.5	13.9	49.4	53.4
Others	1.9	7.1	2.8	0.7	1.6	0.9
Total predators	591	3008	5466	3545	686	103

The number of mummies detected in the field sampling was always very low. The number of parasitized aphids increased in September and October when aphid populations increased as well.

Table 2 shows the percentage of different predator groups caught in pitfall traps in maize fields. Arachnida and Carabidae were the most frequent predators, although the percentage of Dermaptera was also high throughout the crop cycle.

Table 2.- Monthly proportion of predators caught in pitfall traps in maize fields.

	Percentage of presence in pitfall traps					
Predator	May	June	July	August	September	October
Arachnida	40.8	66.4	31.9	25.8	28.7	35.3
Carabidae	28.3	19.5	34.6	42.7	40.6	35.9
Staphylinidae	12.3	3.1	1.1	1.0	5.5	6.3
Dermaptera	16.6	10.4	32.0	28.5	24.2	21.7
Others	2.0	0.6	0.4	2.0	1.0	0.8
Total predators	2308	17022	10023	8625	4321	1246

3.- *The effect of the sowing date*

Fields sown late escaped the spring aphid colonization. When the colonization of these fields occured, plants were at a more avanced development stage than plants from early sowings when their colonization occurred in spring. This may be important for the reduction of damage produced by viruses in maize.

However, the aphid population peaks in fields sown at different times coincided in many cases, increasing the risk of direct or honeydew damage in late sown plants, as they are younger.

4.- *The effect of soil systemic insecticides*

Plots treated with carbofuran showed lower population levels of aphids than lindane or untreated plots during the first week after maize emergence. However, at that time, densities were very low (<3 aphids/plant). Later, there were no significant differences between plots treated with carbofuran and lindane, or untreated. Soil treatment did not affect the development of populations. These results show that carbofuran was not useful in the prevention of MDMV transmission, and confirm the preliminary results obtained in the study area (Albajes *et al.* 1985). No consistent significant differences were found in population levels of predators on plants and in pitfall traps in treated and untreated plots, although a more detailed analysis of data should be made.

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Analysis of the flight activity of *Rhopalosiphum padi* males in relation with a population biology model

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1. Summary

A population biology model was applied to a cereal aphid species, Rhopalosiphum padi for which different reproductive patterns may occur in the same region. This model predicted the different proportions of these strategies of reproduction. Knowledge of these proportions is of major importance to estimate accurately the risk of BYDV infection by aphids.

Following this model, assumptions were made concerning the variability of the male proportions depending on climatic and geographical situations.

Males, which are a flying sexual morph, are continuously monitored by the use of suction traps in France and Britain. These data were analysed in order to point out interesting information on the dominant life cycle at a specified site during a specified autumn. The relationships between "sex ratio " (number of males/total catches of R. padi) and dominant reproductive strategies or temperature of previous winter were therefore described.

The geographical and yearly variations observed for this ratio were partially explained. Nevertheless, the monitoring of only one of the two sexual morphs was insufficient to validate completely the population biology model. The limit of this primary model were also discussed.

2. Introduction

Several life cycles and reproductive patterns may occur within a species in the same area. This is the case for a major cereal aphid species, *Rhopalosiphum padi* (Dedryver et Gellé, 1982, Leather *et al*, 1992, Simon *et al*, 1991a). Some clones are holocyclic: they produce alate sexual morphs in the autumn, gynoparae and males, in theoretically equal proportions. Other clones are androcyclic: they produce virginoparae and males. The proportion of males in the offspring vary from 0 (anholocyclic clones) to approximatively 30% (Simon *et al*, 1991a).

The extreme strategies to reproduce or multiply are pure holocycly or pure anholocycly. The occurrence of both strategies depends on the distribution of the primary host plant, *Prunus padus*, and on the winter climate. Viviparous androcyclic clones cannot overwinter in case of very low temperatures, unlike holocyclic clones that overwinter as cold resistant eggs.

In some areas where cold and mid winters alternate, both holocyclic and androcyclic clones may coexist in various proportions and androcyclic males may therefore mate with holocyclic females and transmit their genes.

In order to simulate the balance between holocyclic strategy and its asexual derivatives under different frequencies of cold winters, theoretical population biology models have been developped (Rispe, 1994). These models calculated the theoretical

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proportions of males, gynoparae and virginoparae during a succession of cold or mild winters. These simulated results can be compared to field results provided by the counting of sexual alate morphs in aerial sampling.

Since males are easily distinguishable sexual morphs while gynoparae are not, the present study was limited to the counting of males at different sites over a long period of time. It consisted in checking if monitoring of males could provide interesting information on the dominant life cycle strategy at a specified site during a specified year.

3. Material and methods

Yearly aphid counting of *R. padi* males and no males (virginoparae and gynoparae merged) were provided by the French suction trap network, AGRAPHID. These traps have been operating from 1978 (fig 1). Only data from 1981 to 1988 were presented in details in this paper. British data supplied by the Rothamsted Insect Survey were also used.

Temperature data were provided by INRA-STEFCE.

For the sites of Le Rheu, Arras and Colmar, the rate *p* of androcycly was estimated following the ratio emigrant/alate exule at the end of winter (Simon *et al*, 1991b).

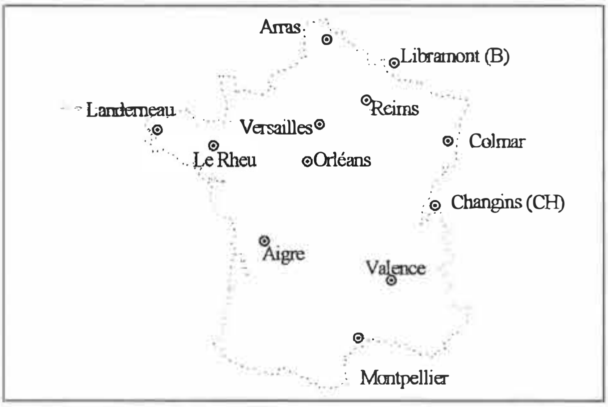

Figure 1: Agraphid Network of Suction Traps

4. Results

4.1. The Population Biology model

Androcycly and holocycly were considered as two alternative strategies in competition within a population. Every year, the winter climate determined the relative fitness of each strategies. The holocyclic clones might provide a reproductive success (g) low but safe as being independant of the severity of winter. Androcyclic clones might afford a higher reproductive success (G) after a mild winter or be radically eliminated after a cold one. After a cold winter, the proportion of holocycly might therefore increase in the population. If there were only cold winters and no migration, population should included only holocyclic clones. After a mild winter, androcyclic clones might be more numerous because of a higher fitness (fig. 2). Males were produced by holocyclic and androcyclic clones. Models predicted that the proportion of males varied between 50% (versus gynoparae in case of holocycly) and 30% at most (versus virginoparae in case of androcycly). Models predicted therefore that at a specified site the number of males was dependant on the dynamic of populations and that the proportion of males was dependant on the dominant reproductive strategy (fig. 3). In the model, the transition from holocycly to androcycly was slower than the shift from androcycly to holocycly.

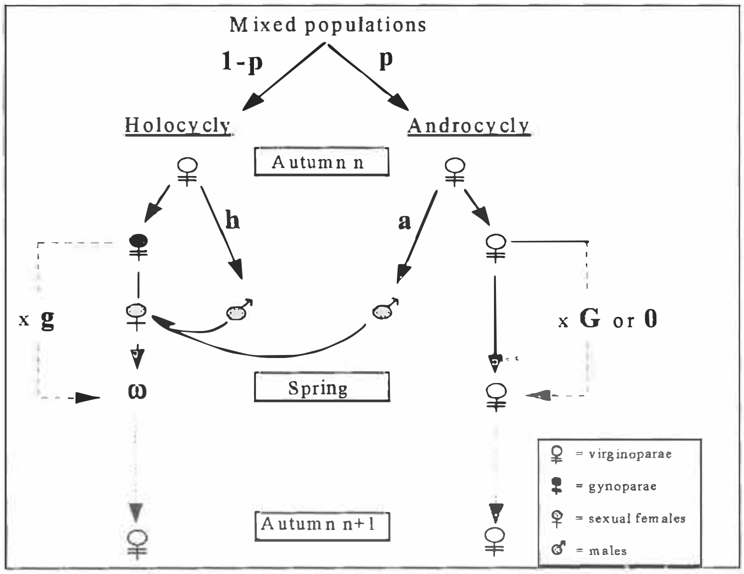

Figure 2: Parameters of the population biology model: **p** proportion of androcyclic clones in mixed populations, **h** proportion of males produced by holocyclic clones, **a** proportion of males produced by androcyclic clones, **g** fitness of hocyclic clones, **G** fitness of androcyclic clones after a mild winter, **O** fitness of androcyclic clones after a cold winter. The dashed lines correspond to several parthenogenetic generations

4.2. *The flight activity of R. padi males*

The percentage of males varied from one site to another between 2 and 45%. The lowest percentages were observed in West (Rennes, Aigre, Landerneau) and South (Aigre, Montpellier) and at Libramont in Belgium. The highest percentages were observed in East (Reims, Changins) and North (Caen, Arras) (Table I). These results were globally in harmony with the model, as a gradient from androcycly to holocycly probably exists from South-West to North-East of France.

At sites where androcycly is dominant percentages varied between 8 and 10%, and at sites where holocycly is dominant between 17 and 28%. The highest percentages were observed at Arras where a mixed strategy generally occurs. This last result was in contradiction with the model which predicted there a mixed population and therefore an intermediate proportion of males.

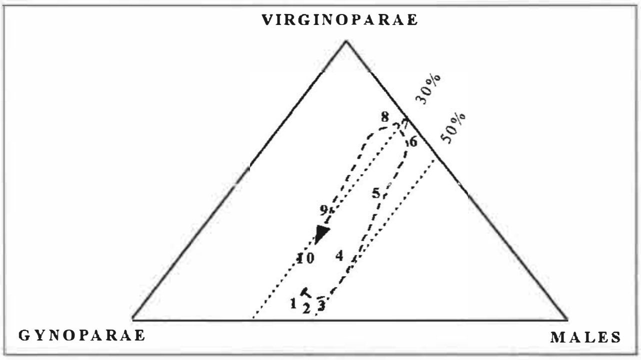

Figure 3: Frequencies of the different morphs produced in the autumn along 10 successive winters (1,2, 3 cold winters, 4,5,6,7,8 mild winters, 9 and 10 cold winters): 1: initial frequencies : 40% of males, 50 % of gynoparae and 10% of virginoparae corresponding to a dominant holocycly. 8: 25% of males, 5% of gynoparae and 70% of virginoparae corresponding to a dominant androcycly due to 5 previous mild winters. 9 and 10: decreasing proportion of androcycly involving a rapid increase of gynoparae. The dashed lines represent 30% and 50% of males, the two values of *a* and *h* predicted by the model respectively for androcycly and for holocycly.

Percentages of males in suction trap catches were significantly lower than estimated by the model, particularly at Colmar or Libramont.

The mean percentage of males was negatively correlated with the mean temperature of previous winter but not significantly ($r = -0.39$) mainly because of the year 1987 which was caracterized by a cold previous winter and a low percentage of males. The mean percentage of males caught during the autumn was estimated for Britain, France, Belgium and Switzerland using catches of at least 9 years per suction trap. The highest proportions of males were not observed in regions where holocycly is dominant and where *Prunus padus* are numerous (such as Scotland or Eastern France) but in Northern France and South-East of Britain, regions where both andro- and holocycly may occur and where winters are milder than in Scotland or in eastern France (Fig. 4).

Following the model, the number of males M_{ij} for a given year i at a site j could be estimated as being equal to $N_{ij} * \left[a* p + h* (1-p)\right]$, N_{ij} being the total number of individuals caught during the autumn. The proportions p of androcycly and *1-p* of holocycly were estimated at the end of winter using the abundance of individuals identified as emigrants and exules in suction trap catches from 1985 to 1988 at three sites, Rennes, Arras, Colmar representing a range of reproductive strategies from dominant androcycly to dominant holocycly. The average proportions of males observed at Rennes and Colmar, respectively 0.08 and 0.17, were used as estimators of *a*, the proportion of males produced by androcycly and *h*, the proportion of males produced by holocycly. The theoretical proportions *a* (0.30) and *h* (0.50) given by the model were also tested.

Table I: Percentages of *Rhopalosiphum padi males* observed in suction traps during the autumn from 1985 to 1988 and mean temperature of previous winter (from november to march)

	1981	***1982***	***1983***	***1984***	***1985***	***1986***	***1987***	***1988***	***avg***
Rennes	5	11	8	9	2	13	2	11	**8**
Aigre	4	21	12	8		11	2		**10**
Montpellier	19	4	14	1	28	15	14	5	**12**
Libramont			15	21	8	7	21	4	**13**
Landerneau		15	14	11	9	13	19	13	**14**
Orléans	21	8	13	16	11	16	16	21	**15**
Valence	29	8	10	16	13	23	14	19	**16**
Versailles				12	22	18	11	20	**17**
Colmar	11	24	25	19	8	13	21	18	**17**
Changins			**16**	16	19	26	27	38	**24**
Caen						16	29	36	**27**
Reims					25	18	29	39	**28**
Arras	41	47	29	32	30	24	35	45	**35**
avg	**19**	**17**	**15**	**15**	**16**	**16**	**18**	**22**	
temperature in °C	**5.6**	**6.2**	**5.8**	**5.6**	**5.4**	**5**	**4.4**	**5**	

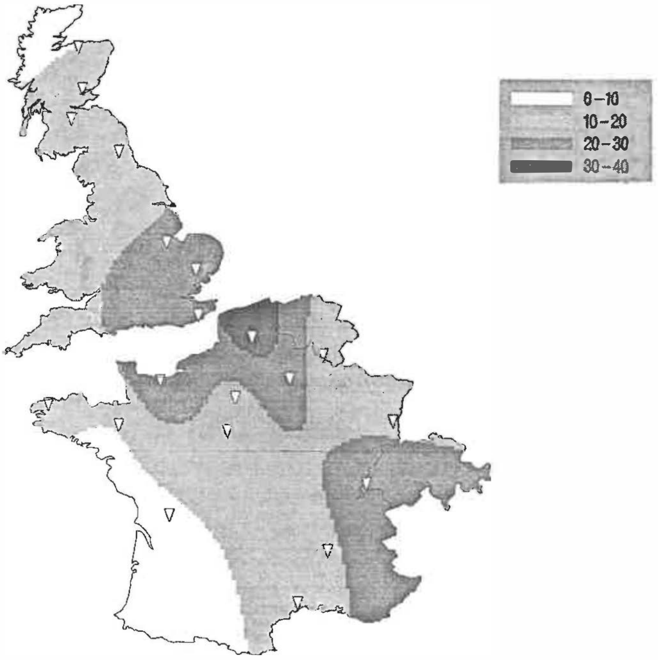

Figure 4: distribution of the proportion of males of *Rhopalosiphum padi* estimated from autumn mean catches provided by the Rothamsted Insect Survey and AGRAPHID networks. (British sites are from North to South: Elgin, Dundee, East Craigs, Newcastle, Kirton, Broom's barn and Wye)

When compared to the theoretical values, the observed number of males showed a deficit mainly at sites where holocycly is dominant such as Colmar. When compared to estimated values, this « male » deficit was lower and number of males was even underestimated at Arras. As total numbers of *R. padi* were also higher at holocyclic sites, the model used was very sensitive to the value of ***h***.

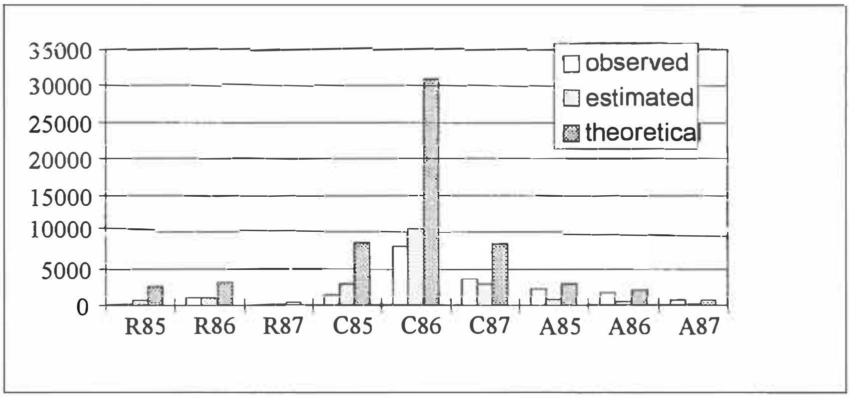

Figure 5: Number of males at 3 sites (R: Le Rheu, C: Colmar, A: Arras) during 3 years (1985-1987), using the biology population model; **observed**: really counted in suction traps, **estimated**: with rates *a* and *h* respectively equal to 0.08 and 0.17 as calculated from data, **theoretical**: with *a* and *h* respectively equal to 0.30 and 0.50 as given by the model

5. Discussion

The monitoring of males of *R. padi* is insufficient on its own to explain all the variability of reproductive strategies expected in nature. The theoretical population biology model generally overestimated the proportions of males which were really observed in suction traps, especially in regions where holocycly is supposed to be dominant. Several assumptions could be made.

One hypothesis is based on the mortality of sexuparae. Their offspring begin with a batch of gynoparae and after 3 weeks the first males appear. The cumulative sex-ratio reaches 50% only if the sexuparae stay in life long enough (Fig. 6). The hypothesis is that mortality of sexuparae is lower in oceanic region than in Scotland or Eastern France. The sex ratio is then higher in these oceanic regions. Our population biology model did not take this disparity into account.

Other hypothesis could be the migration of aphids with a diffusion of holocyclic clones from their areas of production. This hypothesis is being tested by Rispe using a reaction/diffusion model. Another assumption involves the higher mobility of males whose estimation could be biased in suction traps.

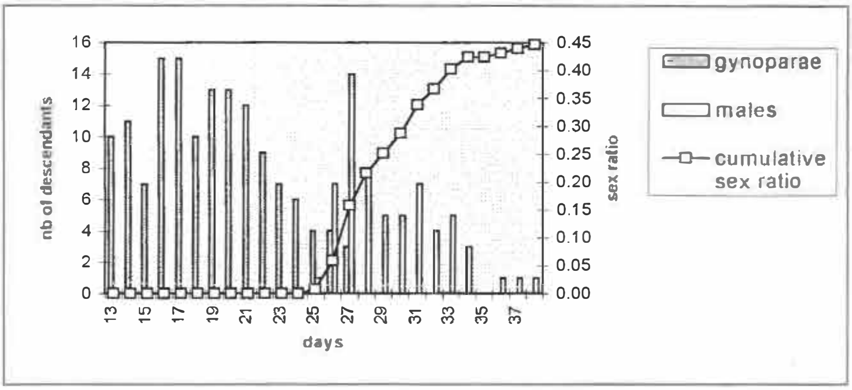

Figure 6: cumulative sex ratio in the offspring of a sexuparae of *R. padi* (after Simon, 1991b)

Other hypotheses are based on a female biased ratio in host alterning species depending on the decline of the population on the summer hosts and the delays of reproduction through males and females.

In any case, the differenciation between gynoparae and virginoparae will be necessary to validate completely these population biology model,.

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EFFECTS OF PESTICIDES AND USE OF PERENNIAL STRIPS ON THE VEGETATION-LIVING INSECTS IN CEREAL FIELD

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ABSTRACT

The ecological effects of two pesticide regimes (C=conventional and D=reduced) and two types of cultivation systems (A=customary, B=lighter technique) and permanent perennial strips were studied in a large-scale field experiment. Study objects were the vegetation-living insects, which were sampled with a vacuum sampler and by sweep netting during the growth season.

Only short-term effects of pesticides on numbers of Diptera, Hymenoptera, Auchenorrhyncha, Heteroptera, Thysanoptera and Aphididae were observed. Differences were usually found only in the first samples taken after insecticide applications, and later the populations recovered. The numbers of any non-target arthropod group were obviously higher in perennial strips than in cereal field, whereas the cereal pests, aphids and thrips, were more abundant in adjacent cereal fields. The pesticide use in the fields did not have any detrimental effect on the arthropod fauna in the perennial strips. The possible repellent effect of pesticides increased the numbers of Thysanoptera in perennial strips adjacent to treated plots after pesticide application.

Although the effects of pesticides on vegetation-living insects were transient and short-term, under Finnish conditions with a short growth season, the effects on the agroecosystem may be remarkable, because pesticide spraying is done during the active period of animals (arthropods and vertebrates).

INTRODUCTION

The effects of pesticides, mainly insecticides, on non-target organisms have been extensively documented (e.g. Jepson 1989, Croft 1990). Especially the effects of pesticides on the polyphagous epigeal arthropods (Carabidae, Araneae) and stenophagous aphid predators (Coccinellidae, Chrysopidae and Syrphidae) have been shown in many studies (see Theiling & Croft 1988). However, there are less studies on the decline of numbers of vegetation-living insects after pesticide use, although they are very important organisms in the agroecosystem. They are food for other animals (e.g. Sotherton & Moreby 1992) and pollinators, and they partly maintain the stability of the community.

We suggest that vegetation-living insects are more exposured than epigeal arthropods because a higher proportion of applied pesticide usually remains on the vegetation layer, not penetrating to the ground surface (Cilgi & Jepson 1992). On the other hand, because of the basic physiological similarities between arthropod groups (target organisms, their natural enemies or other non-target organisms) pesticides often inflict high mortality in all arthropod groups (Croft 1990).

Diversification of agricultural systems is a more and more popular aspect of the agricultural landscape. The importance of all kinds of created habitats, perennial strips, weed strips, beetle banks, conservation headlands and other semi-natural habitats as reservoirs of predatory arthropods and ecological corridors in the agroecosystem have been studied extensively (Nentwig 1988, Sotherton 1992, Thomas & Wratten 1990, Thomas *et al.* 1992). Diversification of habitats aims at increasing biodiversity of agroecosystems. However, pesticide use may reduce also the numbers of animals in field margins or adjacent unsprayed fields directly and indirectly (Cilgi *et al.* 1994). Levels of adjacent field margins may also change via migration as a result of repellent or attractive impact of pesticides. Effects of pesticide drift on invertebrates have been shown e.g. in butterflies (Davis *et al.* 1991, Cilgi & Jepson 1995) and ground beetles (Cilgi *et al.* 1994), but vegetation-living insects as totality have not been studied.

The aims of this study are to clarify
1) the differences in abundance of arthropods between perennial strips and cereal fields and
2) the effects of pesticide use on vegetation-living non-target arthropods in cereal fields and unsprayed perennial strips.

MATERIAL AND METHODS

Experimental design

Use of plant protection chemicals and intensity of farming have been studied within the Nummela project, which started in 1992 at the Institute of Plant Protection, Agricultural Research Centre of Finland (ARC). The ecological effects of two pesticide regimes (C=conventional, D=reduced) on the field ecosystem are evaluated. The plant protection programmes are contrasted with two types of cultivation systems (A=customary, B=lighter technique). The permanent shelter belts (perennial green fallow strips) at the margins of the treatment plots and the completely untreated blocks provide additional elements.

The experimental field is situated on the Nummela Experimental Farm of ARC in Jokioinen (60°52' N, 23°25'E) about 120 km northwest of Helsinki. Before the field experiment, fields were under conventional grain and grass production and cattle pasture. Plot size was 52*132 m (0.7 ha). There were six replicates (blocks) and the treatments were fully randomised in blocks.

The experiment consisted two Cultivation system treatments as follows

A=customary farming practice
(deep ploughing, no undergrowth)

B=light (integrated) farming practice:
(soil treatment with cultivator only,
reduced use of fertilizers (2/3 of the fertilizers applied on A),
green undergrowth (a mixture of timothy and red clover)

and three Pesticide regimes

C=conventional (prophylactic) treatment with pesticides
(high pesticide pressure)

D=reduced plant protection programme
(low pesticide pressure)

0=no pesticides, '0-control'

Plots of the conventional pesticide regime were sprayed with herbicides, insecticides, fungicides and growth regulators annually. The plots on reduced pesticide regime were treated only when the control thresholds were exceeded. Use of pesticides in 1993-1994 is given in Table 1.

In 1993, the crop was barley (cv. Arra) and in 1994 spring wheat (cv. Satu). Shelter belts (12 m wide perennial strips) were located at the shorter ends of each plot, and were sown in 1991 with a mixture of timothy, meadow fescue and red and white clover. The perennial strips were not cut or renewed after the establishment. A 4 m wide strip of *Phacelia tanacetifolia* was added beside the shelter belts in 1992. Sowing of the *Phacelia* strip was repeated annually.

Monitoring of arthropods

The vegetation-living insects in the experimental fields were collected with sweeping nets and a vacuum sampler. Furthermore, the incidence of aphids was determined annually. In addition, epigeal arthropods were collected with pitfall traps, but the results are not presented here.

One sweep net sample consisted of 60 sweeps. Annually the sweep net samples were taken from each C and D plot and from the shelter belts next to each plot. 0 plots of three replicates (3, 5 and 6) were also swept.

Vacuum sampling was done with a Ryobi vacuum sampler (Macleod *et al.* 1994). One sample consisted of two 0.2 m^2 (30 s) suctions. Annually each C and D plot and the adjacent shelter belts were sampled. Samples of 0 plots were taken from three replicates (3, 5 and 6).

Vacuum sampling was started before the first spraying (early June), but sweeping was not possible until the plant stand was about 20 cm high (end of June). Details of the arthropod sampling programme are given in Table 2.

Study objects

The arthropods were identified at the order level, and flies (Diptera), parasitic Hymenoptera (Hymenoptera: Parasitica), leafhoppers (Homoptera: Auchenorrhyncha), bugs (Heteroptera), aphids (Homoptera: Aphididae) and thrips (Thysanoptera) were counted. Leafhoppers will be identified at the species level later, and used as bioindicator group of vegetation-living insects, whereas ground beetles are the main objects of epigeal arthropods. Possible cereal pest species belonging to these groups were *Rhopalosiphum padi* (Homoptera: Aphididae), *Javesella pellucida* (Homoptera: Auchenorrhyncha) and *Limothrips denticornis* (Thysanoptera).

Table 1. Use of pesticides in 1993-1994 in the Nummela project. (H=herbicide, G=growth regulator, F=fungicide I=insecticide).

		Conventional (C)	Reduced (D)
1993			
Seed coating	F	Carboxin+Imazalil (Täyssato S)	-
1st spraying	H	Chlorsulfuron (Glean 20 DF) A plots	-
(10.6.)	H	MCPA+Bentazone (Basagran MCPA) B plots	-
	I	Dimethoate (Roxion)	-
2nd spraying	G	Etefon (Cerone)	-
(28.6.)	F	Propiconazole (Tilt)	-
1994			
Seed coating	F	Carboxin+Imazalil (Täyssato S)	-
1st spraying (16.6.)	H	MCPA+Mecoprop-P A plots (Hormoprop Duplosan)	MCPA+Mecoprop-P (Hormoprop Duplosan)
	H	MCPA+Bentazone (Basagran MCPA) B plots	MCPA+Bentazone (Basagran MCPA)
	I	Dimethoate (Roxion)	-
2nd spraying	G	Etefon (Cerone)	-
(13.7.)	F	Propiconazole (Tilt)	-
	I	Deltamethrin (Decis)	-

Table 2. Sampling programme of the vegetation-living arthropods in 1993-94 in the Nummela project. t= time from 1st insecticide treatment, ( )= time after 2nd treatment.

	Sampling time	Vacuum sampler		Sweep nets	
		date	t	date	t
1993	1	08.6.	-2	30.06.	20
	2	12.6.	2	09.07.	29
	3	21.6.	11	20.07.	40
	4	29.6.	19	30.07.	50
1994	1	09.6.	-7	29.06.	13
	2	17.6.	1	14.07.	27 (1)
	3	28.6.	11	25.07.	38 (12)
	4	15.7.	28 (2)	12.08.	56 (30)
	5	27.7.	40 (14)		

Statistical analyses

The differences in numbers of animals between treatments after pesticide use were assessed using repeated measures of analysis of variance (ANOVAR) with balanced complete block design (SAS/PROC GLM; Littell *et al.* 1991). REPLICATE, PESTICIDE TREATMENT (PT), CULTIVATION TREATMENT (CT), TIME and their interactions were included in the models. The significance levels adjusted by Greenhouse-Geisser corrections were used (Potvin *et al.* 1990). Whenever catches were too small for analysis, the sampling times were omitted. To find out the duration of pesticide effects on the animal numbers, we calculated contrasts between pesticide treatments at each sampling time (Satterwaite approximation for the deminator degrees of freedom was taken into account). Effects of pesticide use on insects of perennial strips were analysed only on the first samples after insecticide applications.

The values were usually log-transformed before analysis, but original medians are shown in figures.

RESULTS

Dominant groups in vacuum and sweep net catches were Diptera, Hymenoptera: Parasitica, Auchennorrhyncha, Thysanoptera and Aphididae. In sweep net catches, Heteroptera were also common. Aphid-specific predators, like Coccinellidae, Syrphidae and Chrysopidae, were rare in the catches, with mean numbers below one per sample. The numbers of Araneae, Coleoptera and Lepidoptera were also too low for analysis.

Pesticide treatments

In 1993, the number of Thysanoptera declined after pesticide spraying in conventional pesticide plots (C plots), but at the last sampling (19 days after treatment) it increased (Fig. 1). The number of Auchenorrhyncha were higher in vacuum samples from reduced pesticide plots than from conventional plots, but the difference was not statistically significant. In numbers of Diptera no statistically significant difference between treatments was found. Numbers of other insect groups in vacuum samples were too low for analysis. In 1993, no statistically significant difference was found in insect numbers between pesticide regimes in sweep net samples, except numbers of Heteroptera were higher in C plots in last samples.

In 1994, the plots of reduced plant protection (D) were not sprayed with insecticides, but conventional plots were sprayed with dimethoate in June and with deltamethrin in July (Table 1). The differences in the numbers of Diptera were significant between high pesticide pressure plots (C plots) and D plots in vacuum samples (Table 3), but the difference changed with time (greatest after the second spraying). Even the numbers of Thysanoptera and Hymenoptera were higher in vacuum samples from D plots than in C plots, except in catches of the last sampling (14 days after second treatment).

After second pesticide treatment in sweep net catches, the number of Diptera was higher in reduced pesticide plots than in conventional plots immediately after the spraying, but later no difference was found (Fig. 2). Likewise, in numbers of Hymenoptera, Auchenorrhyncha and Thysanoptera the effect of the second spraying was detected only at first sampling after application, but later differences were not found or they were even opposite. Numbers of Aphididae were high enough for analysis only just before and after the second spraying, and the sampling times were analysed separately. Numbers of aphids immediately after the second spraying were significantly higher in reduced pesticide plots than in conventional plots, but the difference was detected only in customary farming practice plots.

In general, the effects of pesticides were short term. Differences in animal numbers in relation to pesticide treatment were normally found during the first week after spraying. Later populations recovered.

Perennial strips

The numbers of any non-target arthropod group were obviously higher in perennial strips than in cereal fields, whereas the cereal pests, aphids and thrips, were more abundant in adjacent cereal fields (Fig. 3). Species compositions of the study groups differed between perennial strips and cereal fields. For instance, micropterous Auchenorrhyncha occurred more frequently in perennial strips than in the cereal field.

Effects of pesticide use on insect numbers in perennial strips were tested on the first samples taken after pesticide applications if the numbers were high enough for analysis, but no detrimental effect of pesticide use on the arthropod fauna of perennial strips was found. However, in 1993 the numbers of Thysanoptera were higher in vacuum samples from perennial strips adjacent to insectide treated plots than from strips adjacent to untreated plots, which may result from the repellent effect of pesticide. At the same time, numbers of Thysanoptera in treated plots declined as compared with untreated plots.

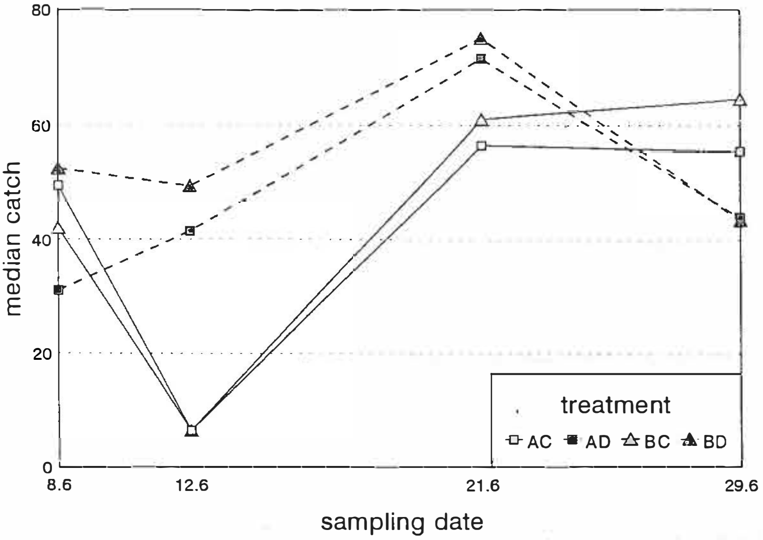

Fig. 1. Vacuum sample catches of Thysanoptera in 1993. Dimethoate spray was applied only in the conventional pesticide regime (C) on 10 June. (C=solid line, D=broken line).

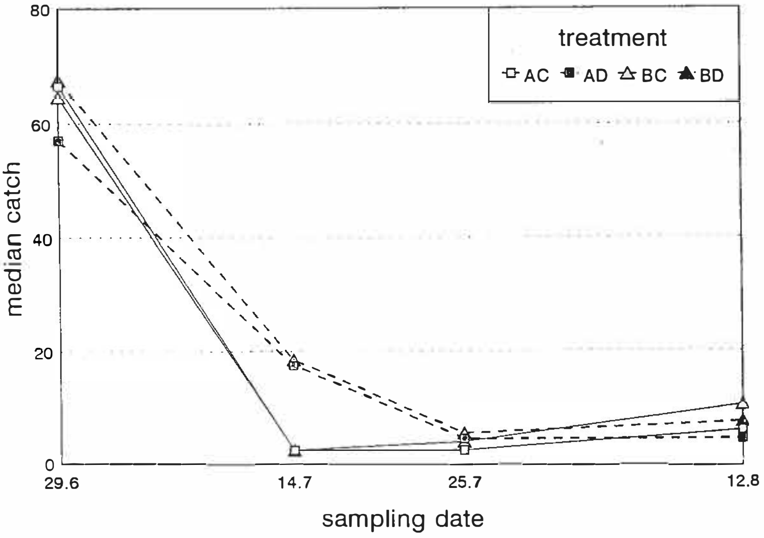

Fig. 2. Median catches of Diptera in sweep net samples in 1994. Dimethoate spary was applied on 16 June and deltamethrin on 13 July in the conventional pesticide regime (C). (C=solid line, D=broken line).

Table 3. The effects of PESTICIDE TREATMENT (PT), CULTIVATION TREATMENT (CT) and TIME on the animal numbers in 1993 and 1994. The studied animal taxa were Diptera, Hym.:Parasitica, Auchenorrhyncha, Heteroptera, Aphididae and Thysanoptera. Only statistically significant effects (P < 0.1) are presented. The repeated MANOVA (See Methods) was used. (- = not analysed; o = P < 0.1, * = P < 0.05, ** = P < 0.01, *** = P < 0.001).

	Vacuum sampling	Sweep nets
1993		
Diptera	(times 3-4)	(times 2-4)
PT		
Thysanoptera	(times 1-4)	(times 1-4)
PT	41.32 ***	
PT*TIME	27.58 ***	
Heteroptera		(times 2-4)
PT*TIME	-	3.54*
Auchenorrhyncha	(times 3-4)	(times 1-4)
PT		
1994		
Diptera	(times 3-5)	(times 1-4)
PT	22.74 ***	24.59 **
PT*TIME	9.07 **	58.24 ***
Hym.:Parasitica	(times 3-5)	(times 1-2)
PT	4.03 o	3.79 o
PT*TIME	18.35 ***	4.81 *
Auchenorrhyncha		(times 1-2)
PT*TIME	-	18.94 ***
CT*TIME	-	3.73 o
Aphididae	(times 3-5)	(times 1-2)
CT	3.55 o	
CT*TIME	3.94 o	7.73 *
PT*CT*TIME		5.22 *
Thysanoptera	(times 3-5)	(times 1-2)
PT		26.18 ***
PT*TIME	8.50 **	33.47 ***
CT*TIME	2.96 o	

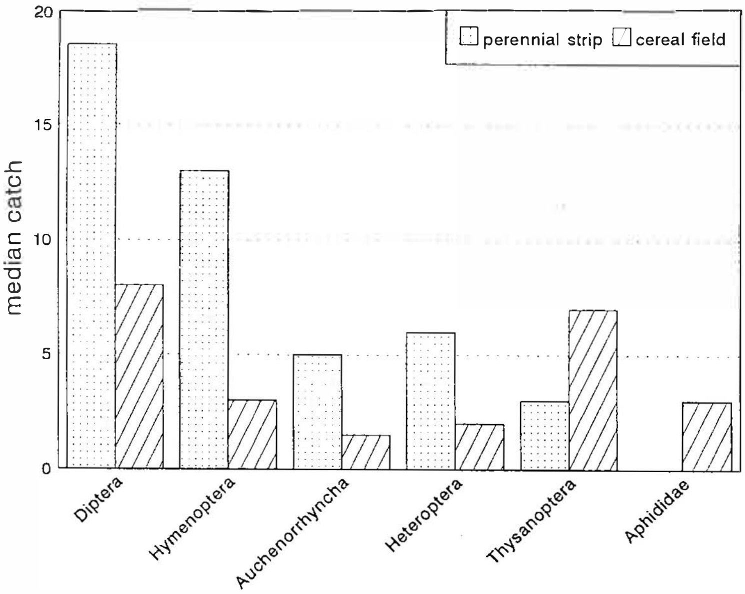

Fig. 3. Sweep net catches of the vegetation-living insects in the perennial strips and in the the wheat field in 1994.

DISCUSSION

The abundance of vegetation-living insect groups declined after insecticide (dimethoate in 1993, and dimethoate and deltamethrin in 1994) applications. The decrease after pesticide treatment arises from deaths or emigration as a result of chemical or indirect effects on food supply or habitat (Brown 1989). In our study, the decline of insect abundance lasted usually one or two weeks. After that, differences were not found or the insects even increased. The explanation for the fast recovery may be that insects found in the last catches were not exposured pesticides, or the pesticides had no effect or they dispersed from untreated areas. For example nymphs of Thysanoptera were not exposured to pesticides because they live under the shelter of vegetation, thus avoiding contact with pesticides.

We found only short-term effects of pesticides on the numbers of vegetation-living insects at the order level. In epigeal arthropods, the effects of insecticides have been found to last even a month (Jepson & Thacker 1990, own unpubl. data). Thus, the effects of pesticides differ between arthropod groups. In addition, we suggest that the effects probably differ within the studied groups. We agree with Croft's (1990) that the overall pesticide impact is very difficult to predict because there are great variations in the effects of pesticides between arthropod species, and the interaction between arthropod species is unknown. In our experiment, the numbers of many interesting insect groups (f.ex. Syrphidae, Coccinellidae, Chrysopidae) in catches were so low that any differences after treatments was impossible to notice. Consequently, the numbers of individual species would have been absolutely too low for analysis.

We suggest that many vegetation-living insect groups have a better dispersal ability than epigeal arthropods and, consequently, they recover faster after exposure. The rate of recolonisation depends on the sources of recolonisation (surrounding habitats) and size of treated area. Our trial plots were under 1 hectare. So, our results may underestimate the effects in relation to normal field conditions (see Jepson & Sherratt 1991). However, the duration of pesticide effects and the recovery may differ between families, species and even between biotypes. For example, macropterous and micropterous biotypes may differ in their dispersal ability and recovery.

Although the decline in arthropod abundance would last only some weeks, it may have dramatic effects in northern agroecosystems because use of pesticides coincides with the active period of animals (e.g. arthropods and vertebrates).

Insects occurred more abundantly in perennial strips than in adjacent cereal field plots. Only the numbers of cereal pests were higher in the field. Higher insect diversity in perennial strips may result from higher plant species and plant architecture diversity of perennial strips. Structural diversity components, like plant species, foliage height, growth form and plant density diversity were obviously higher in perennial strips. However, the effects of structural diversity are often impossible to distinguish from the direct effects of plant species richness (Lawton 1983). Furthermore, the perennial strips are more permanent and unchangeable habitats than fields, which may maintain a high insect diversity in perennial stips.

We did not observe any detrimental effects of pesticide use in the fields on arthropod fauna of the perennial strips. However, the possible repellent effect of pesticide caused an increase in the numbers of Thysanoptera in perennial strips adjacent to treated plots after pesticide application.

More detailed results (especially concerning leafhoppers) will be published later.

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Species diversity and activity densities of epigaeic and flower visiting arthropods in sown weed strips and adjacent fields

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Abstract

In 1992 and 1993 epigaeic (Araneae, Carabidae) and flower visiting arthropods (Syrphidae, Lepidoptera, Apoidea, Sphecidae) were investigated in sown weed strips of different age, in the adjacent fields and a field boundary. Epigaeic arthropods were caught by pitfall traps and flower visiting insects were observed quantitatively and caught by yellow traps. The weed strips contained more species of spiders and ground beetles than the fields and for many abundant species dispersal tendencies from the weed strips into the adjacent fields could be observed. In all groups of flower visiting insects numbers of species and individuals were higher in the weed strips than in the fields. Twelve percent of all species of these insect groups belonged to endangered species. Apart from increasing predators within arable fields weed strips can also serve as new habitats for several species in agricultural areas, poor in natural structures and can therefore contribute to biodiversity in arable landscapes.

1. Introduction

Natural habitat structures like weed strips in arable land provide a new habitat for species which, together with those natural structures, had previously disappeared from agricultural areas. Weed strips have a high diversity of plants which is a prerequisite for athropod communities rich in species (Heitzmann-Hofmann 1993). Weed strips help to increase the number of predatory species (Nentwig 1988) and proved to be very attractive hibernation sites for different beneficial arthropods (Bürki & Hausammann 1993; Lys & Nentwig 1994).

Although natural habitats lying on field edges serve as a reservoir of predators (Basedow 1988) the immigration of predators into adjacent fields is spatially limited. Therefore the sowing of weed strips inside fields is recommended to enable the predators to disperse into all areas of the field. The dispersal of spiders and ground beetles from weed strips into adjacent fields is significant because these epigaeic predators can become very numerous in agricultural areas and they then make an important contribution to integrated pest management (Sunderland et al. 1985; Hance 1987).

This paper evaluated species diversity and activity densities of spiders and ground beetles in weed strips and adjacent fields. Further the dispersal of spiders and ground beetles from weed strips into fields was investigated. Since still little is known about the attractiveness of weed strips on flower visiting insects (Frank & Nentwig, in press) numbers of species and individuals in hoverflies, butterflies, wild bees and thread-waisted wasps in weed strips and adjacent fields were examined. Moreover the appearance of endangered flower visiting insects in weed strips was illustrated.

2. Material and Methods

In 1992 and 1993 three sown weed strips of different age (1-3 years old) were investigated in the Swiss plateau near Bern. The weed strips were 1.5 m wide and between 155-212 m long. Two of the weed strips were sown in spring 1992 shortly before the study began. These weed strips were called one-year-old strips in 1992. The third weed strip was sown in spring 1991

and was called a two-year-old strip in 1992. On the adjacent fields rape, maize and wheat were growing. The investigation took place in the weed strips, in the adjacent fields (13 m and 50 m from the strips) and in a grass-dominated field boundary which bordered on one of the fields.
Spiders and ground beetles were caught by four pitfall traps at each site. Ground beetles were evaluated in both years but spiders were considered only in 1992. In both years hoverflies were observed in plots of 2 m^2 which were chosen at random. Additionally they were caught by two yellow traps at each site in 1992. Butterflies were recorded by walking through the sites in both years. In 1992 wild bees and thread-waisted wasps were caught by yellow traps and in 1993 the number of individuals of wild bees was counted in plots of 1 m^2 being chosen at random.

3. Results and Discussion

3. 1. Araneae

The two-year-old weed strip showed the highest number of species, followed by the rape site close to this strip and the field boundary in 1992. The high number of species in the two-year-old weed strip was due to a dense and richly structured vegetation as well as the assumption that this site served as a place of hibernation for many species. The lower species diversities in the one-year-old weed strips were due to a less structured covering by weeds and the fact that spiders could not hibernate in the one-year-old weed strips. From the two-year-old weed strip to the rape centre a decrease in number of species by one third was seen. Also from the one-year-old weed strip in the wheat field towards the field centre number of species decreased by one quarter. The field sites close to the weed strips (13 m to the strips) contained more species than the field centres (50 m to the strips).

The number of individuals was highest in the two-year-old weed strip followed by those two field sites which were next to this strip. This reflects a particularly high enrichment in individuals of adjacent fields caused by the two-year-old weed strip. From the two-year-old weed strip to the rape centre a decrease in number of individuals (like in number of species) was observed. The same dispersal tendencies were obtained by Katz et al. (1989) for a natural meadow.

Both numbers of species and individuals decreased with increasing distance from the weed strips. This shows that weed strips enrich their adjacent field parts in species diversity and activity density - a fact which is of great importance for the augmentation of spiders in fields.

Five of the nine most abundant species (*Erigone atra*, *E. dentipalpis*, *Oedothorax apicatus*, *Pardosa agrestis*, *P. palustris*) showed a dispersal from the weed strips into the adjacent fields, i. e. in spring more individuals were in the weed strips, but as the season progressed more individuals were in the fields. Thus weed strips can augment spider densities in adjacent fields. Between the weed strips and the adjacent fields an exchange in dominant species could be observed, whereas the field boundary revealed a high degree of autonomy. Three of the five dominant species (*Pachygnatha degeeri*, *Dicymbium nigrum*, *Trochosa ruricola*) were not dominant at any other site which emphasizes the above mentioned autonomy of the grass-dominated field boundary.

3. 2. Carabidae

With regard to species diversity in ground beetles similar trends were obtained as in spiders, because in both years numbers of species found in weed strips were higher than those in adjacent fields and also numbers of species in the fields decreased with increasing distance from the weed strips. Also Lys & Nentwig (1992) found more species of ground beetles in weed strips than in adjacent wheat fields. Klinger (1987) captured more species in margin strips than in adjacent wheat fields and observed a species enrichment in the field parts close to the strips. The field sites comprised higher numbers of species in 1993 than in 1992. The numbers of species inside the fields increased distinctly which might be either due to a general species enrichment caused by the weed strips from the second year on or to crop rotation.

Dispersal from the weed strips into the adjacent fields could be seen in several abundant species, e. g. *Clivina fossor*, *Harpalus affinis*, *Platynus dorsalis*, *Pterostichus anthracinus*, *P. vernalis*. The number of ground beetles dispersing from weed strips into adjacent fields was much higher in two-year-old than in one-year-old weed strips. This could be referred to the fact that two-year-old weed strips already served as hibernation sites from where the beetles dispersed into the fields. The dispersive ability of ground beetles (and spiders too) from weed strips into adjacent fields could be an important component of integrated pest management.

3. 3. Syrphidae and Lepidoptera

In both years higher numbers of species were observed in the weed strips than in the fields in hoverflies and butterflies. In 1992 the two-year-old weed strip comprised the most species of hoverflies and butterflies, whereas in 1993 the other weed strips (already two-year-old in 93) showed an equal or higher species diversity than the older weed strip. The higher species diversity in the older weed strip in the first year of the investigation was most likely due to the more diverse supply of flowers because in the two-year-old weed strip not only annuals but also perennials were flowering. Thus it seems that two-year-old weed strips generally attract more species of flower visiting insects than one-year-old weed strips.

The weed strips and also the field boundary were very attractive sites for hoverflies because in both years conspicuously more species as well as individuals were observed in these sites than in the fields. Also Weiss & Stettmer (1991) and Salveter & Nentwig (1993) found high densities of hoverflies in weed strips. On the whole more adult hoverflies with aphidophagous larvae were observed in the weed strips than in the fields. But aphidophagous hoverflies reached a higher percentage in the fields than in the weed strips and the field boundary. Adult hoverflies having been recorded in the field sites were almost entirely confined to species with aphidophagous larvae. Yet in the weed strips and the field boundary also species with aquatic larvae and big adults were abundant. In 1992 much more individuals with aquatic larvae were found in the two-year-old weed strip than in the two one-year-old weed strips, namely in a ratio of 7 to 1.5 to 1. But in 1993 numbers of individuals with aquatic larvae showed almost no difference between all three weed strips. This markedly higher percentage of big aquatic hovervflies in the older weed strip compared with the younger strips in 1992 in contrast to 1993 was due to the fact that many attractive plants with big inflorescences were only flowering in the two-year-old weed strip in 92 but in 93 they were also flowering in the other weed strips.

Weed strips provided much nectar and therefore proved to be attractive feeding places for butterflies. Many species could have used the weed strips as breeding sites because larval host plants of many species occurred there. Yet although larval development was not part of this investigation some caterpillars of *Papilio machaon* could be observed in the weed strips. Some other species used the weed strips as mating places, e. g. *Pieris napi* and *Aglais urticae*. Thus weed strips served some species not only as feeding places, but also as places for mating and oviposition.

3. 4. Apoidea and Sphecidae

Weed strips proved to be very attractive sites for wild bees because highly significantly more individuals were observed in the weed strips than in the fields and the field boundary. In 1993 wild bees were completely absent from the wheat sites.

Yellow trap captures of thread-waisted wasps showed markedly higher numbers of species and individuals in the weed strips and the field boundary than in the fields. In this group the high number of species compared with individuals was striking, because the ratio between individuals and species was merely 4 to 1. In other studies meadows, fallows and margin strips turned out to be very attractive sites for wild bees and thread-waisted wasps containing many species (Amiet 1973; Gathmann & Tscharntke 1993; Lagerlöf & Wallin 1993).

Although weed strips were used primarily by unendangered species also endangered species could be found in all investigated groups of flower visiting insects. On the whole twelve percent of the species of flower visiting insects were endangered ones. Weed strips are of great importance for providing suitable habitats for endangered and still common species of the agricultural landscape. Thus weed strips play a significant role in species conservation which must include still widespread species and might not be restricted to already endangered species.

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The effects of sown weed strips on pests and beneficial arthropods in winter wheat fields

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Abstract

In two winter wheat fields with a sown weed strip and in one field without a strip pests and beneficial arthropods were investigated at different distances from the weed strip respectively from the field edge in 1993 and 1994. The dominant pest insects were cereal aphids and leaf beetles. The infestation of aphids was always below the economic damage threshold and did not show any differences between the edge and the middle of the fields. The cereal leaf beetles *Oulema* sp. were more numerous in the middle of the field than near the weed strip and their population was higher in the field without strip than in the strip-managed fields. Polyphagous predators and parasitic Hymenoptera were caught in larger number near the weed strips than far from them. The population of aphidophagous predators was higher in the field with a weed strip than in the control field. These results might be due to an enhancing effect of the weed strips. Cereal crop did not seem to be more infested by pest insects near the weed strip than in the rest of the field.

1. Introduction

One aim of the integrated pest management is the protection and augmentation of natural enemies. Cultivated areas with weeds and natural border vegetation could enhance beneficial arthropods like Carabidae, Staphylinidae and Araneae (Altieri & Letourneau 1984). Studies by Klingler (1987) and Nentwig (1988) showed an increase of the abundance and diversity of predatory arthropods by strip-management in cereal fields and sown meadows. Sown weed strips within large fields or at the field edges could be a useful element to enhance the diversity of the agroecological system. Therefore strip-management might be a possibility to hold pest insects below the economic damage threshold. Not only predatory but also phytophagous arthropods could be enhanced by weed strips. This study deals with the effects of sown weed strips on pest and beneficial arthropods in winter wheat.

2. Materials and methods

The investigation took place 1993/94 in the area of an agricultural school 6 km north of Berne, Switzerland. In 1993 two winter wheat fields (0.5 ha and 0.4 ha) with sown weed strips (1.5 m wide, 25 herbaceous plant species as described in Heitzmann, 1994) and a field without weed strip (2.5 ha and an adjacent sown meadow) as control area were investigated. In 1994 a 6 ha winter wheat field with a sown weed strip was studied (variety Arina in all studied fields). From May to July the arthropods in the wheat fields were counted weekly on the tillers and caught by sweep netting. In the first year the strip-managed fields were only 27 m wide and the investigated distances from the weed strips were 3, 6 and 10 m. The same distances were investigated in the control field. 1994 the arthropods were studied at 3, 6, 10, 25, 50 and 75 m distances from the weed strip.

3. Results

The following wheat pests were found: the aphids *Sitobion avenae*, *Metopolophium dirhodum* and *Rhopalosiphum padi* and the cereal leaf beetles *Oulema melanopus* and *Oulema lichenis*. In 1993 the maximum of the aphid infestation was 4 aphids / tiller in EC 71. 1994 the maximum was already reached in EC 51 with 4.5 aphids / tiller. In both years aphids did not reach the economic damage threshold and no significant differences between the distances from the weed strip were found. In 1993 *Oulema* sp. did not show any significant differences between the investigated distances either. But the population in the control field was significantly higher than in the strip-managed fields. In 1994 the number of cereal leaf beetles was lower at the 3 m distance than at the other distances on the first two sampling days. Later in the year the population was spread nearly equally in the field.

The aphidophagous predators did not show any differences between the investigated distances. But in the strip-managed fields more Coccinellidae and Syrphidae were found than in the control field. Araneae, Empididae and Nabidae were the dominant generalist predators. Furthermore Staphylinidae, Cantharidae and Dolichopodidae were caught. In the first year of the investigation they were more numerous at the 3 m than at the 10 m distance of the strip-managed and the control field. Towards the end of June in 1994 more predators were found near the weed strip than at the 25 m distance and in the middle of the field. The parasitic Hymenoptera showed the same tendencies in their distribution in the field.

4. Discussion

In Switzerland aphids are only occasionally harmful in cereals. The economic damage threshold is given when 50 % of ears and flag leaves in EC 59 are infested (Häni et al. 1988). In both years of the investigation the aphids did not reach this threshold. Their infestation of the wheat close to the weed strip and in the middle of the field did not differ which might be due to the low infestation or the small size of the field.

The valid economic damage threshold of *Oulema* sp. (var. Arina, conventional management, EC 55: 0.45 larvae / tiller) (Schärer 1994) was only reached in the control field. It might be that potential predators had been enhanced in the strip-managed field. Schärer (1994) observed the following predators in his investigations: Coccinellidae eating eggs, Nabidae and larvae of *Chrysopa carnea* eating small larvae and eggs of *Oulema* sp. In the western region of Switzerland an increased mortality of the cereal leaf beetles near a weed strip could also be found (Chassot in prep.).

The high number of flowering plants in the weed strips were expected to attract parasitic Hymenoptera, which need flowers for their ovification. Van Emden (1964) observed that they could be attracted especially with umbelliferous flowers. Nevertheless the number of parasitoids caught did not differ significantly between the investigated distances close to the weed strips and the middle of the field. This might be due to the possibility of their spreading out easily in the whole field.

The aphidophagous predators were not found to be accumulated near the weed strip either. Chambers & Adams (1986) and Poehling (1988) showed in their studies that stenophagous predators act according to their prey. In this investigation the aphidophagous were equally distributed in the whole field as the aphids. Pest insects on the wheat could never be observed in a higher number close to the weed strips than in the rest of the field. Therefore we can conclude that the sown weed strips do not accumulate pests, but an enhancing effect for polyphagous predators might exist.

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'Beyond the Infectivity Index.'

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Abstract

The infectivity index as a system for forecasting the need for control of vectors of BYDV is reviewed. Methods for improvement are suggested and current research on BYDV epidemiology at Rothamsted is described.

Introduction

Barley yellow dwarf viruses (BYDV) are a group of luteoviruses which can cause serious losses to cereals in the UK, the extent of which varies annually and spatially. A forecasting system is being developed to prevent prophylactic spraying of autumn sown cereal crops to control the main aphid vectors, *Sitobion avenae* (Fabricius) and *Rhopalosiphum padi* (L.),

Interest in BYDV at Rothamsted Experimental Station continues from an early forecasting technique termed the 'infectivity index' (Plumb *et al.* 1981). This is calculated from the total number of each species of cereal aphid caught in the Rothamsted 12.2m suction trap (Macaulay *et al.* 1988, Taylor 1986) multiplied by the proportion of these species, caught alive in a 1.5m trap in the same area, that subsequently transmit the virus to test cereal seedlings. The index was highly correlated with virus incidence in autumn cereal crops in the south-east of England but failed to predict BYDV outbreaks in southwest England (Kendall & Chinn 1990), or in southwest Scotland (Foster *et al.* 1993). A seven year study at four sites throughout England showed variable correlations between the infectivity index and virus incidence (Tatchell *et al.* 1994).

A problem with the infectivity index is that it includes numbers of males and gynoparae of *R. padi*, which pose little threat to cereals (Kendall & Chinn 1990) while virginoparae of *R. padi* caught at the same time are very important vectors in the autumn. It also fails to allow for secondary spread of the virus, which, in a mild winter, can contribute greatly to the final virus incidence (Foster *et al.* 1993).

This paper details a new method for rapidly separating the different autumn morphs of *R. padi* and describes experiments which will lead to improved predictions of secondary spread within the crop.

Separation of the autumn morphs of *R. padi*.

In the UK, *R. padi* is mainly holocyclic; most clones produce pre-sexual and sexual morphs (gynoparae and males) in autumn which leave the summer graminaceous hosts to colonise the bird cherry tree (*Prunus padus* L.). A few clones continue to produce virginoparae which may move to autumn-drilled cereal crops, to introduce and spread the virus. Males are easily identified but gynoparae and virginoparae are morphologically indistinguishable (Stroyan

1984). They can be separated by a simple test in which the aphids are presented with equal areas of leaves of the alternative host plants, gynoparae choosing *P. padus* and virginoparae choosing barley on which to feed and reproduce (Tatchell *et al.* 1988). However, this is time consuming and requires living aphids. Gynoparae and virginoparae can now be separated using a simple, cheap and rapid "squash blot" test (Lowles 1995). This method is more accurate than the choice test method of separating these morphs and enables gynoparae to be omitted easily from the assessment of the infectivity index.

The proportion of gynoparae to virginoparae varies annually and there is some evidence that the differences are related to the temperature in the previous winter, with fewer virginoparae in autumns following severe winters. Initial data collected at Rothamsted show (Fig. 1) that there is a threshold of approximately 20 day-degrees, accumulated below 0°C between December and February below which a high proportion of virginoparae are produced (Harrington *et al.* 1995). This becomes important in mild autumns following mild winters when large proportions of virginoparae could lead to much initial infection and extensive secondary spread.

Measuring primary infection in autumn

Transmission of the virus can be separated into three periods: a) the acquisition access period, during which the vector has access to the virus source plant although is not necessarily feeding; b) the latent period, i.e. the time after the vector has acquired the virus but before it becomes infective; and c) the inoculation threshold period, that is the minimum time necessary for a vector to feed on a healthy plant before inoculation occurs (Federation of British Plant Pathologists 1973). Work is being done to quantify these different periods using alate aphids, at temperatures common in the autumn in the UK.

Details follow of a series of experiments on the inoculation threshold period of two species of aphids with two isolates of the virus, *S. avenae* transmitting the MAV-like isolate, and *R. padi* transmitting the PAV-like isolate to oats (cv. Dula). The proportion of plants infected for six inoculation access periods (2, 6, 12, 24, 48 and 72 hours) at each of four temperatures, 6°C, 12°C, 18°C and 23°C were compared. Each species/isolate combination was tested separately and each experiment was replicated five times. In each experiment a batch of ten viruliferous aphids were used at each temperature/inoculation access period combination. Uninfected aphids were placed on ten control plants at each temperature and removed after 72 hours.

After a 72-hour acquisition feed, single winged aphids were placed on the oat seedlings for the required time. The aphids and any nymphs were then squashed to prevent further inoculation and the plants removed to a glasshouse. The plants were assessed for visual symptoms of virus at 17 and 24 days, and any plants with indistinct symptoms were tested by double antibody sandwich ELISA (Lister & Rochow 1979).

There was no further increase in the proportion of plants with virus after a 24 hour inoculation period for either the MAV- or PAV-like isolates (Fig. 2a). For the PAV-like isolate there was no difference between the proportion of plants infected at 12°C, 18°C or 23°C, but at 6°C the proportion was significantly smaller (Fig. 2b). For the MAV-like isolate, there is a weak positive relation between the proportion of plants infected and temperature. These results, and those for the acquisition and latent period experiments yet to be completed, will be used to estimate the time taken at a certain temperature for an infective aphid to transmit the virus, and thereby improve future prediction models.

Results for virus transmission are more useful when combined with data on aphid movement. The time an aphid stays on a plant at a given temperature, when combined with data on transmission of the virus by apterous aphids, facilitates understanding of the of movement of aphids and its relation to the spread of virus within a crop over a given period.

Quantifying factors affecting aphid movement

A major problem with the infectivity index is its failure to account for secondary spread during winter months. This is of particular importance under mild winter conditions, when transmission is more efficient and increased aphid survival and movement enhances spread of the virus through the crop. *Sitobion avenae*, which overwinters more successfully than *R. padi* (Dewar and Carter, 1984; Tatchell *et al*, 1994), is thought to be the prime contributor to secondary spread of the virus. An accurate prediction of disease progression during the winter relies on an understanding of how biotic and abiotic factors determine vector movement. Some of these including temperature and aphid density, were investigated in a series of laboratory experiments.

To determine the probability of an aphid leaving a plant and the distance it subsequently moved, *S. avenae* were released on the central plant of a 9 x 9 grid of oat seedlings at growth stage 12, planted at a spacing of 6 cm. Densities of 2, 8, 16, and 24 aphids per plant and temperatures of 5, 12, 18 and 25°C were compared. Aphids were contained on the plant by clip-cages for 24 hours before being released. After a further 48 hours all plants were thoroughly searched and aphid positions noted. The proportion of aphids which had left the central plant and the mean distance they moved were calculated.

There was very little movement of aphids away from the central plant at densities of 2 per plant (Fig. 3a & 3b) and these data were not analysed. For all other densities the proportion of aphids that moved increased with temperature and, for any given temperature, increased with density. These two relationships did not interact. The average distance moved also increased significantly with temperature and with density although the latter effect was not consistent for all temperatures at low densities, whereas at temperatures of 18°C and 25°C there was little difference among densities.

High aphid densities are a strong stimulus for dispersal, but at low aphid densities (2 per plant or less) as might occur during winter months, aphid density is not important. Temperature had a clear effect, with movement increasing with temperature. At 5°C very little movement occurred, indicating that the threshold for movement may be around that point. Data presented will be useful in predicting aphid movement during the winter based on ambient temperatures, particularly when combined with results on virus transmission.

Modelling secondary spread of BYDV

Suitable methods for determining the amount and distribution of primary inoculum are still being assessed. These involve developments of the infectivity-index concept combined with field sampling. Sampling to account for secondary spread becomes increasingly difficult as the winter progresses, so a minimal number of field visits is desirable in any advisory system for vector control. A mechanistic model of secondary spread, including relationships such as those described above, and driven by routinely available meteorological data, should remove the need for sampling, once an accurate means of assessment of the final levels of primary inoculum has been achieved. The model should include the effects of temperature on aphid development, reproduction and survival; the effects of temperature, wind, rain, plant density, plant age, aphid density and aphid age on aphid movement; and the effects of temperature, plant age and aphid age on virus transmission characteristics.

The ultimate objective of the research programme is to provide a decision support system for the use of insecticides to control the aphid vectors.

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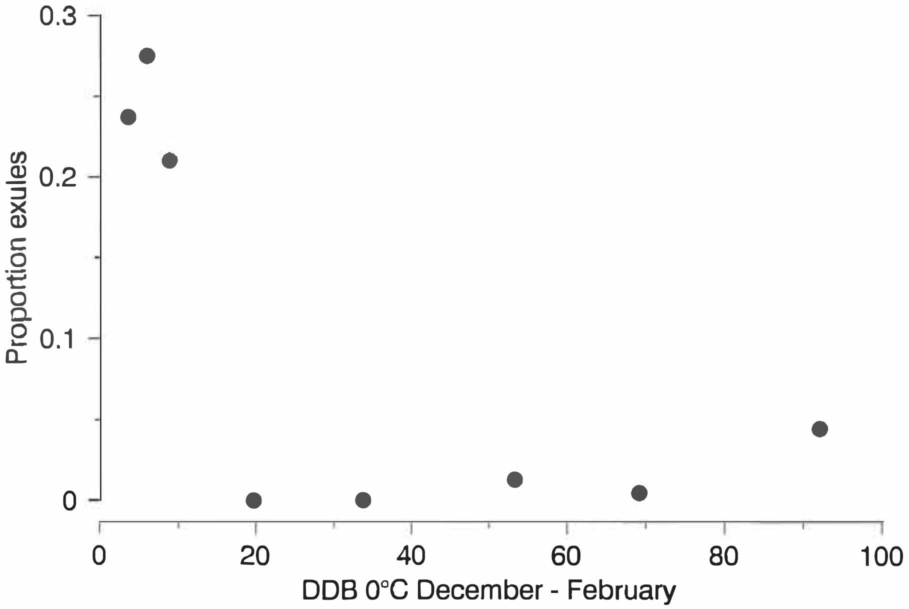
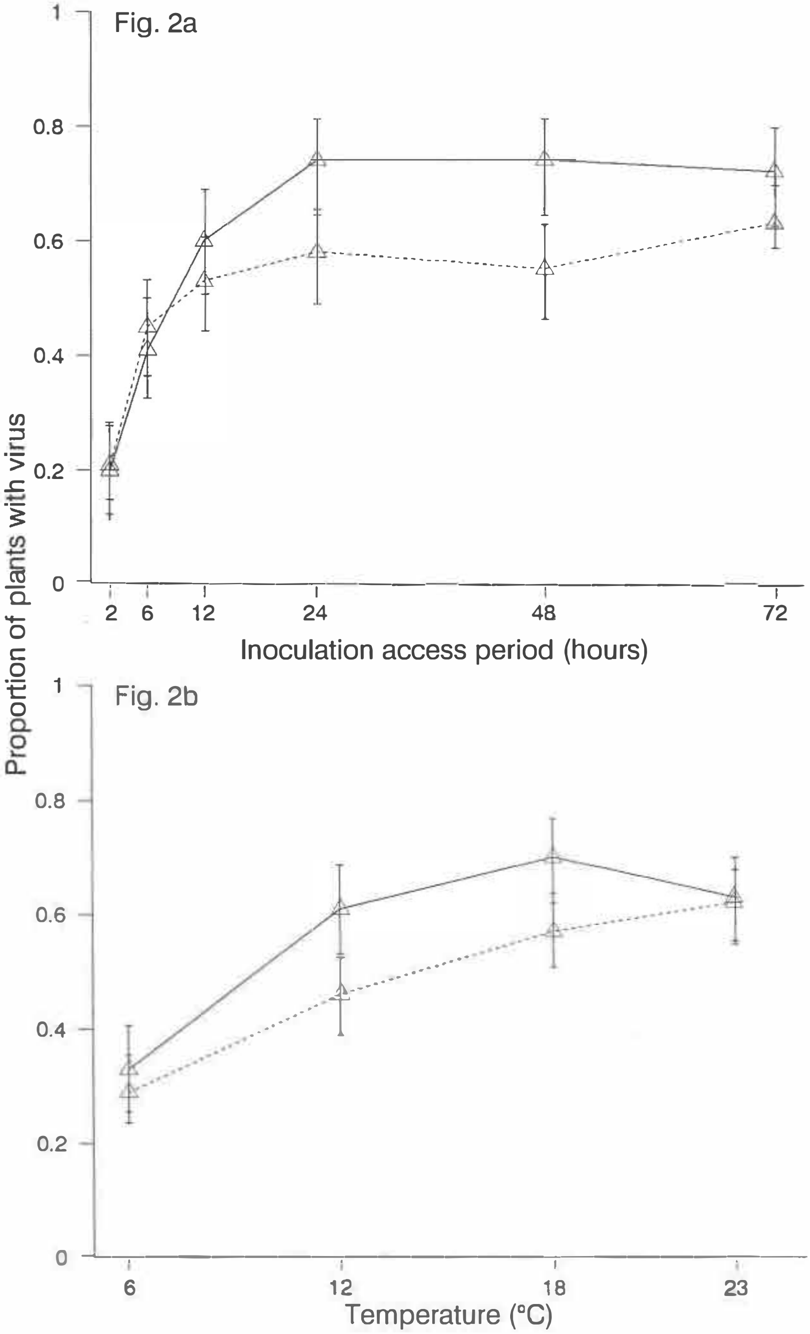


Fig. 1. Proportion of *R. padi* from holocyclic clones in samples from the Rothamsted 12.2m suction trap in autumns (from 1st October) 1986-1993 in relation to temperature (day degrees below zero) the previous winter (December to February).

Proportion of plants with virus for each access period (Fig. 2a) and each temperature (Fig. 2b), with approximate 95% confidence limits, for MAV-like (----) and PAV-like (—) isolates.



Proportion of aphids moving at each temperature (Fig. 3a) and mean distance moved at each temperature (Fig. 3b). Bars show S.E. of mean.

Fig. 3a

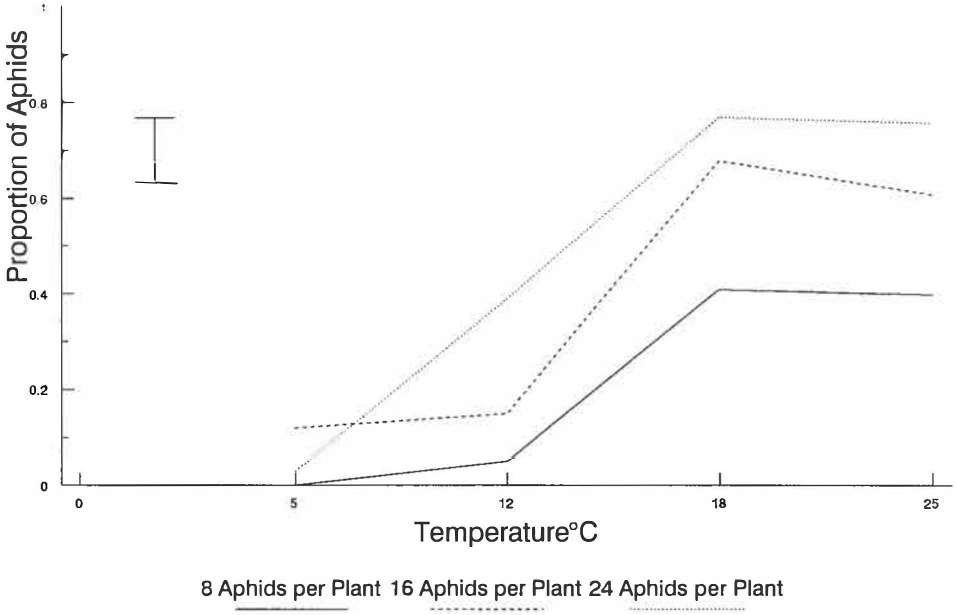
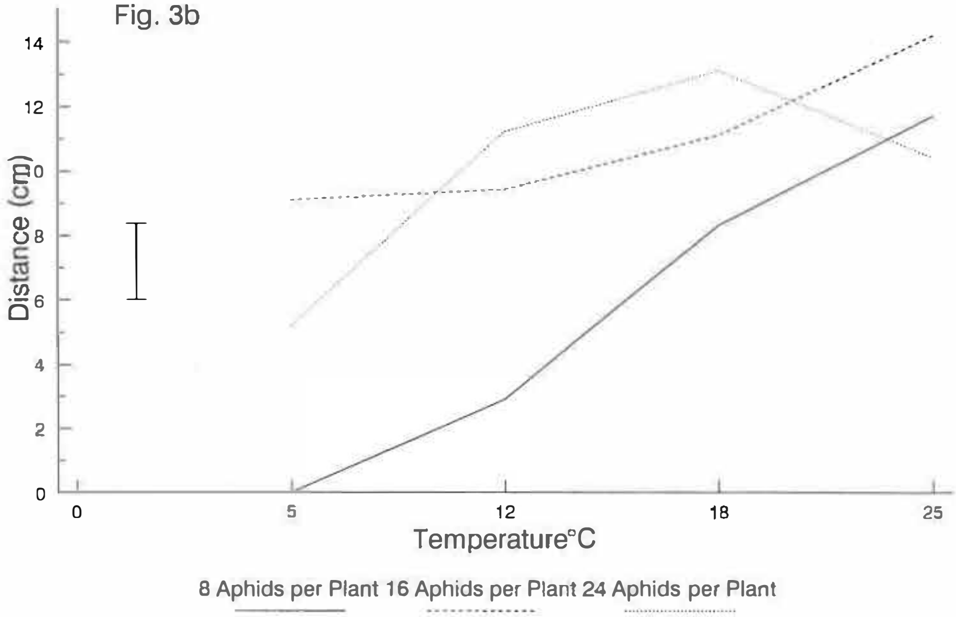


Fig. 3b



Studies on the movement and dispersal of apterous *Sitobion avenae* in winter barley and a new simulation model on secondary spread

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SUMMARY

A new approach on modelling aphid spread in autumn sown cereals is presented. The model is derived from results of mark/release trials and of semi-field tests. Linear regression analysis with single climatic parameters failed to predict the movement of apterous *Sitobion avenae* accurately. Multiple regression models gave better fits. Here the thermal time and the rain index, a measure of rain intensity that has been shown also being responsible for aphid mortality in autumn in other studies, was found to have the main positive effect on aphid spread. Wind speed as well as the number of hours with rainfall had a negative effect on aphid movement. In semi-field trials the first two larval stages moved to a very low extent. The relation of the mobility between the different stages relate to 1:0.529:0.622:0.052 (apterous adults : 4th instar : 3rd instar : both first instars). A computer based simulation program gave good approximations if field data of counts at mid November as the start input were taken.

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1. INTRODUCTION

Forecasting BYDV in Germany is at present just the same as before the epidemic outbreaks during the last ten years. No model is available. The main concern in this studys is the investigation of the secondary spread inducing factors. The secondary spread is assumed to be the most important part of the epidemiology in Northern Germany (BORGEMEISTER & POEHLING 1991). In this manner the mild winter temperatures were responsible that the virus was spread by anholocyclicly overwintering aphids to a severe extent. Except these years no problems with BYDV occurred so that primary infections are not of greater significance.

Scientists in England developed two models to predict an outbreak: The first one has been recently introduced by KENDALL et.al. (1992). It is a dynamic model based on the NACHMANN part of the Poisson prabability function. It includes as well primary infections by alatae as secondary spread by apterous aphids. Remarkable is the accurate approximation of field data in several years. The disadvantages of this model type are its complexity, the partly unknown biologic background and therefore the impossibility to explain the reasons for failure in some years. The infectivity index derived from suction trap catches is another way (PLUMB 1986). It is an easy approach that relies only on that catches so that it ignores secondary spread. But there has been carried out some research to improve it with the future goal of an index based on both primary infections and secondary spread (MANN et al. in press, LOWLES et al. in press). Furthermore the main vector involved in secondary spread of BYDV in Germany is *Sitobion avenae*. It occurres hardly in suction trap catches in autumn. Therefore, both approaches are not assumed to be qualified to predict an outbreak in Germany with a certain reliability.

Other studies modelling movement only with laboratory data lead to an misinterpretation of the situation in the field and predicted a clear underestimation of the virus spread (MORGAN 1990).

2. METHODS

To get the recquired informations two different studies were carried out. At first flourescent powder marked apterous adult *S. avenae* of two different clones were released in a winter barley field (cv. Sonja). POWER (1991) applied this method with success. All released aphids were taken from a synchronized culture at 10 °C. The movement events and the number of progeny were monitored. At the first of October 1992 (growth stage EC 11) 86 virusfree individuals of an anholocyclic clone and 40 individuals of a brown coloured holocyclic clone were released with a distance of four meters between each aphid. 43 and 25 aphids resp. were investigated on the following day. Aphid search was carried out daily. Ten days later only 16 and 15 aphids resp. were found and the trial was not continued. At the 15th of October 35 individuals of both clones were released. One day later 27 and 24 resp. were investigated. Aphids were monitored again for 11 days. The movement events, the distance moved, the movement type and the number of larvae were noted. The movement types are classified as given in fig.1. Movements of type I and II are movements within a plant row, towards the nearest plant or towards the plant following the nearest one. Type VI is a collection of movements within one plant row over more far distances. Type III is the most straightforward way towards a plant in one of the two neighboured plant rows. Types IV and V are diagonal movements as described. Finally type VII is a collection of all other diagonal movements and of movements towards plants in other rows.

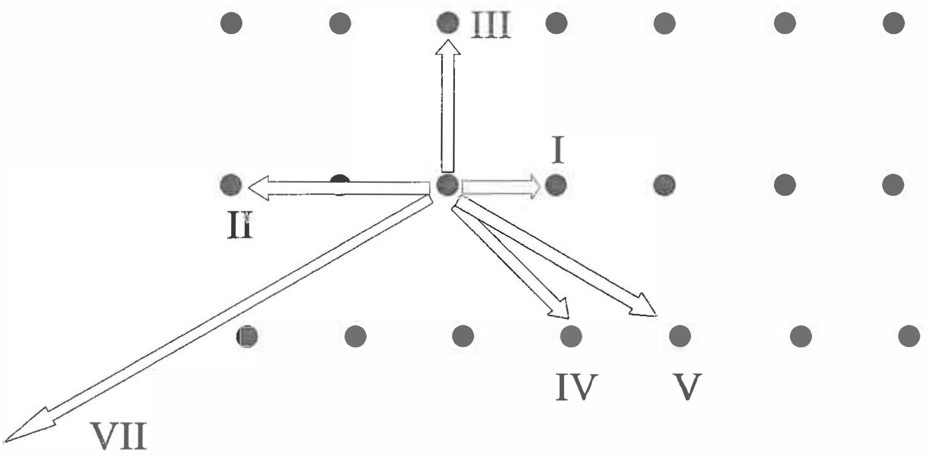

Fig. 1: Movement type classification (for description see text)

The daily movement rates of both mark/release trials were calculated for each clone seperately. A linear regression analysis was carried out using SAS vers. 6.03 proc CORR and proc REG. All data of each clone had been pooled and accumulated to n=17.

In a semi-field triald the informations of differences between the stages were determined. To derive these data under natural conditions natural colonies were investigated in 1994. At October 5 ten natural colonies i.e. plants with one winged *S. avenae* and one to four larvae were enclosed with acryl tubes. At October 13 ten enclosures with a diameter of 52 cm and a height 30 cm were arranged around the colonized center plant. It included plants of five rows. After removing the tubes all enclosures were covered with gauze. This trial ended at the 15th of November.

From each of 5 replications three larvae of the fourt stage were removed and again enclosed in tubes. Nine days later all aphids had moulted to adults, were marked with different colours and released in the arranged enclosures as described before. Counts ended up at December 6. Before the aphids were released, for the first trial the plant number was reduced uniformly to 42 plants and for the second trial to 32 plants. This was necessary to facilitate aphid counts and to prevent disturbing aphids during the counts. Aphid dispersal was monitored almost daily. All plants of each replication were mapped, numbered and marked in case of colonizing aphids. It was not differed between the first and the second larval instars. The movement type was also noted.

3. RESULTS

The frequencies of the selected movement types of the adult aphids in the different trials are give in fig. 2. The first impression viewing this figure leads to the assumption that movement type I is the most favoured one. In the mark/release trial there are differences both between the two trials and the two clones. The anholocyclic clone preferred twice as much the nearest plant as the holocyclic clone did in the first trial. That clone showed no particular preference of a special movement type in the first trial.

In the second trial only movements within one row of short distances could be monitored. In the semi-field trials the movement of the adult aphids patterns revealed a greater variability. The spatial movement patterns of the larvae were similar to the described patterns except of both first and second instar. These instars selected virtually only movement types I and II. In the above described model differences between the stages were neglected and not presented here in more detail.

There were found clear differences of the movement frequencies between the different aphid stages in the first semi-field trial. Movement activity of the third and fourth instars relates to 52.9 % and 62.2 % percent of the adult activity. Both first instars hardly moved in this trial (5.2 %). In the second trial larval instars developed only to the second stage. Along with it, not any larval movement activity was monitored.

The movement rate should be related to climatic data. In a regression analysis at first single weather variables were selected and tested against the movement rate as the dependant variable (tab. 1). For both clones only low or no correlation was found between thermal time and the movement rate resp between wind factors and the movement rate. The wind gust index - that is the difference between the average wind speed and the maximum wind speed - takes into account that aphids could adapt to average wind speed.

Better correlation provide the rain amount and the number of hours with rainfall here termed as rain time. A rain index gave the best fit in testing single weather variables against the movement rate. This index is an expression of the rain intensity and was introduced by KLEINHENZ (1994) to calculate rain mortality. It is calculated with the squared rain amount multiplied by 10 and devided by the number of hours with rainfall. The rain index multiplied by the thermal time gave no better fit. Testing a waether factor multiplied by the thermal time takes into account that an aphid that breaks feeding and pulls the stylet out of the plant might be easier removed by wind or rain than a feeding one. Those breaks could be dependant from the temperature.

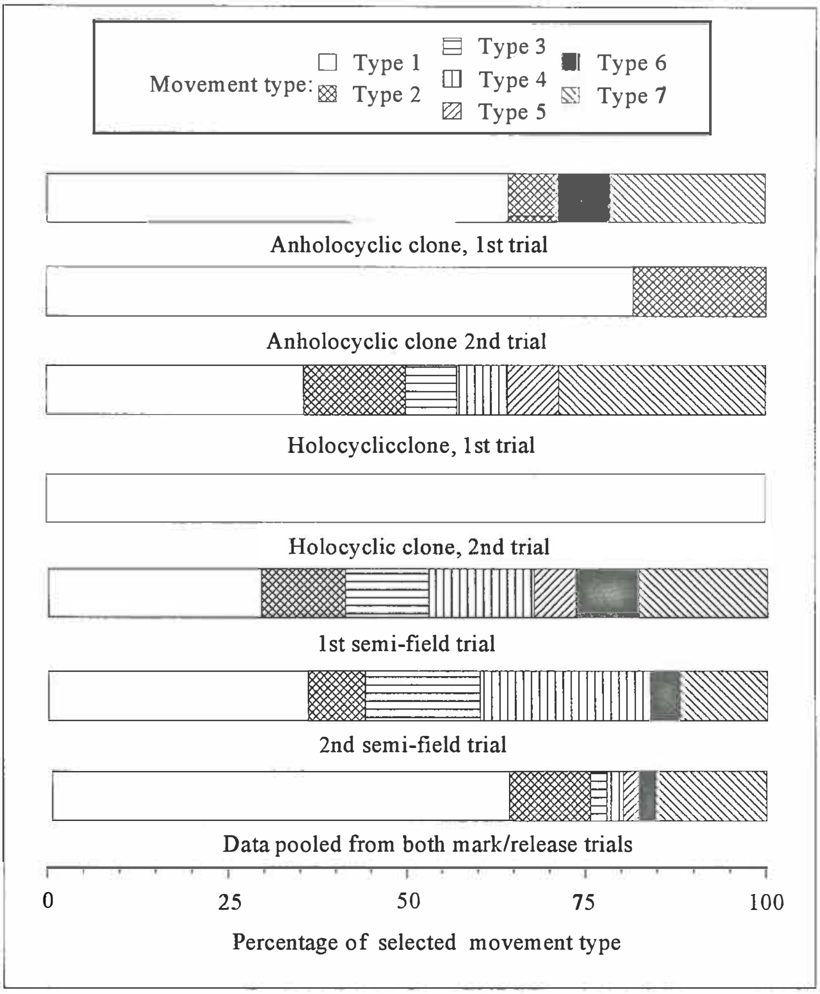

Fig. 2: Frequencies of the selected movement types (for description of movement types see fig. 1 and text)

It is remarkable that except the maximum wind speed model every regression using data of the anholocyclic clone gave better fits than using those of the holocyclic one.

Multiple regression models gave better approximations. Three formulas were found from a wide range of tested combinations that fits the values of both clones with still acceptable

Tab. 1: Linear regression between the movement rate (dependant variable) and single climatic variables

Clone	Variable	Intercept	Slope	Probability a)	Coefficient of determination
Anholocycl..	Thermal time	-0.0921	0.0148	0.0420	0.221* b)
Holocycl.	[°C/d]	-0.013	0.0102	0.0757	0.174
Anholocycl..	Average wind speed	-0.0504	0.0525	0.2156	0.089
Holocycl.	[m/s]	0.0289	0.0300	0.3703	0.047
Anholocycl..	Max. wind speed	0.0433	0.0035	0.8248	0.003
Holocycl.	[m/s]	0.1166	-0.0051	0.4232	0.010
Anholocycl..	Wind gust index	0.0755	-0.0058	0.7766	0.000
Holocycl.	[m/s]	0.1328	-0.0152	0.3346	0.000
Anholocycl..	Rain	0.0103	0.0524	0.2156	0.472**
Holocycl.	[mm]	0.0612	0.0103	0.0157	0.298
Anholocycl..	Rain duration time	0.0085	0.0093	0.0082	0.346**
Holocycl.	[h]	0.0591	0.0060	0.0374	0.231
Anholocycl..	Regenindex	0.0179	0.0035	0.0001	0.710***
Holocycl.	[mm^2/h]	0.0655	0.0022	0.0013	0.464
Anholocycl..	Rain index × thermal	0.0185	0.0002	0.0001	0.710***
Holocycl.	time [mm^2 × °C/h × d]	0.0667	0.0001	0.0009	0.488

a) significance of testing the slope against 0

b) *** : $p \leq 0.001$, ** : $p \leq 0.01$, * : $p \leq 0.05$

Tab. 2: Three multiple regression models fitting the movement rate of two clones of *S. avenae* and of pooled data

Clone	Model a)	Coefficient of determination
Anholocycl.	0.0344+(0.0187 TT)+(0.0016 RI TT)-(0.0242 RI)-(0.0048 W)-(0.0006 WM)	0.835*** b)
Holocycl.	0.1034-(0.0013 TT)+(0.00135 RI TT)-(0.0206 RI)+(0.0372 W)-(0.017 WM)	0.651***
Anholocycl.	-0.004+(0.006 TT)+(0.0002 RI TT)-(0.0151 W TT)	0.766***
Holocycl.	0.0467+(0.0074 TT)+(0.00014 RI TT)-(0.0023 W TT)	0.578**
Anholocycl.	0.0001+(0.008 TT)-(0.0096 RT)+(0.0055 RI)-(0.00145 WM TT)	0.832***
Holocycl.	0.0485+(0.0087 TT)-(0.0057 RT)+(0.0035 RI)-(0.002244 WM TT)	0.613***
Pooled data	0.0689+(0.00026 TT)+(0.00149 RI TT)-(0.0224 RI)+(0.0163 W)-(0.009 WM)	0.716***
Pooled data	0.0045+(0.0038 TT)+(0.0014 RI TT)-(0.00092 W TT)	0.716***
Pooled data	0.0248+(0.00843 TT)-(0.0077 RT)+(0.0451 RI)-(0.0019 WM TT)	0.701***

a) TT: thermal time, W: wind speed, WM: maximum wind speed, RT: rain time, RI: rain index

b) *** : $p \leq 0.001$, ** : $p \leq 0.01$

accuracy (tab. 2). The first model includes the thermal time, the rainindex multiplied by the thermal time, the wind speed and the maximum windspeed. The last three partial regression components have a negative effect on the outcome. In all models at least one of the wind components has a negative sign. The second model included also the thermal time and the rain index multiplied by the thermal time. Another component is the wind speed multiplied by the thermal time. The third model includes the thermal time and the rain index as positive components, the maximum wind speed multiplied by thermal time and the rain time as negative components. In consistency with the other regressions in tab. 1 the response of the holocyclic clone to weather parameters is slighter.

In the last three rows of the table the regression outcomes were given using the three described models applied to the pooled data. There was no other model which could explain more than 70 % of the variability of the movement rate.

The model

At first a population dynamic model with an acceptable accuracy is necessary. Analysis of the aggregation patterns influenced by movement activity is senseless without reliably predicted abundance data. A deterministic model derived from the data and formulas of KLEINHEINZ (1994) should meet this need. The overall mortality probability is caused by a spontanous rate and a rain intensity induced effect in accordance to KLEINHENZ (1994). This model was extended by a partial mortality probability due to subzero temperatures according to BALE *et al.* (1987). Here the frost mortality is assumed to correspond to the thermal time below 0 °C (i.e. cooling degree days). The supercooling point - the temperature where no aphid survival is possible - is at -22 °C. In the model a straight line across the 0 and the supercooling point predicts aphid losses due to frost. The LT_{50} for adult *S. avenae* is at -11.3 °C if aphids are exposed for 24 h (relates to 11 cooling degree days). This temperature is closedly related to the model prediction. No field derived data that could model survival with changing temperatures are available.

The basic model input should be data derived directly from field samples. This approach may be termed as virtual space model. Virtual aphids disperse in a virtual space, between virtual plants. Each aphid is here treated separately. The model takes some knowledge about basic behavioural traits for granted. The accuracy of the model fits may be tested with aggragation analysis, for instance with the index of dispersion or a variogram analysis. The prediction of virus spread can not be compared with field evaluations, because no data from the outbreak years are available. Therefore BYDV transmission procedures are not presented here. But with spatial data it is possible to perform a virus gradient analysis (THRESH 1976). The model is also complex, but it is easier to understand than the dynamic model mentioned before. All model assumptions rely on accurate abundance predictions based on also accurate field samples. Along with it, however, arises a problem: The behaviour of the alatae in the field is unpredictable. Those can leave without any reproduction, can produce a wide range of larvae and can move to another plant or stay on that plant or flight to another field out of the system in the model respectively. Furthermore abundance estimates in the field are often difficult because one can not count enough plants achieving the recquired accuracy. The simuluation should therefore refer to later population estimates at the end of the aphid flight.

For the model the last multiple regression equation was used to predict aphid movement. It is the most reasonable approach because it takes all exspectable effects of weather factors into account. The included rain time should greatly influence the time of wetness on the leaves that is reported to have an inhibiting effect on aphid dispersal following HARRINGTON & CHENG (1984).

Spatial orientation of between plants moving aphids relates to a standardized movemnt pattern as given in the lowermost bar of fig. 2. Movement types 6 and 7 were pooled and added to type 5.

To run a simulation it is necessary to get the recquired probabilities and clima variables. A first program written in Borland Turbo Pascal vers. 7.0 calculates the thermal time below a base temperature of 0 °C i.e. the cooling degree days for the mortality probability. It also calculates the thermal time above a base temperature of 0 °C for a movement algorithm and above 3 °C for the reproduction algorithm. The output is the daily thermal time for the reproduction algorithm, the movement and the mortality probabilities. The output is the input for the simulation program. It calculates the population dynamics using the informations of published work as mentioned before. Aphid growth is confined to 5000 individuals. The virtual space has to be regarded as a part of a field with 20000 plants arranged in 50 rows with 400 plants in each row. It is far apart the field margins. The virtual space is an open system: emigrating aphids were added on the other side of the virtual area, aphid losses caused by movement are impossible. The output of the present algorithm version gives the number of the different stages of each day, the number of aphid infested plants and the variance. With the variance and the mean it is possible to calculate the index of dispersion (PIELOU 1977) also known as FISHER index.

In fig. 3 the results of two simulation runs are described. The first run started at the 21th September. This refers to the day of crop emergence in the field trial. At the beginning of October only 1 from 500 plants infested with one winged *S. avenae*. This start population was extended to 20000 plants. The 40 apterous aphids were assumed to enter the virtual plants on the first four days.

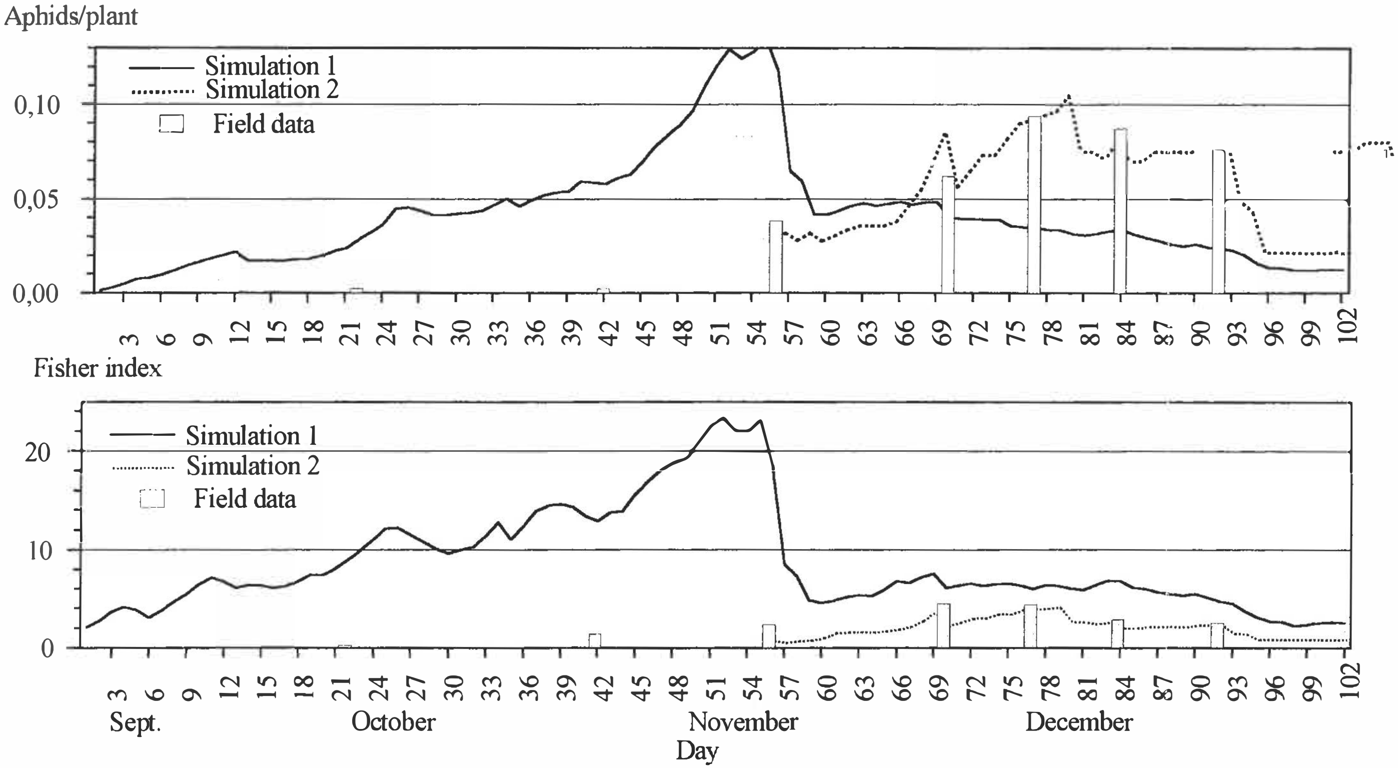

Fig. 3: Aphid abundance and Fisher index during autumn 1994 in a winter barley field and in two simulations

At the 14th of November a density of 7 aphids on 200 plants was found. The input referred exactly to the field situation. But due to computer memory problems the virtual space was reduced to 5000 plants. The first simulation did not fit the field data, but the second one did it more or less accurately. Fig. 4 shows the index of dispersion. This index is expressed by the variance that becomes devided by the mean. It becomes the higher the more aggregated the aphids are. Zero indicates a regular distribution, 1 refers to a random distribution. A dispersal pattern is the result of movement, reproduction and mortality. The field data are fitted as well with acceptable accuracy. Heavy rainfall around the start date induced an index closed to 1 in the modelled data. Afterwards in the field and in the simulation an appreciable bildup of aggregation could be found.
Fig. 4 reveales the calculated rain mortality including the spontanous mortality and the the rain induced part of the movement probability. The rain induced movement probability is always higher than the rain mortality.

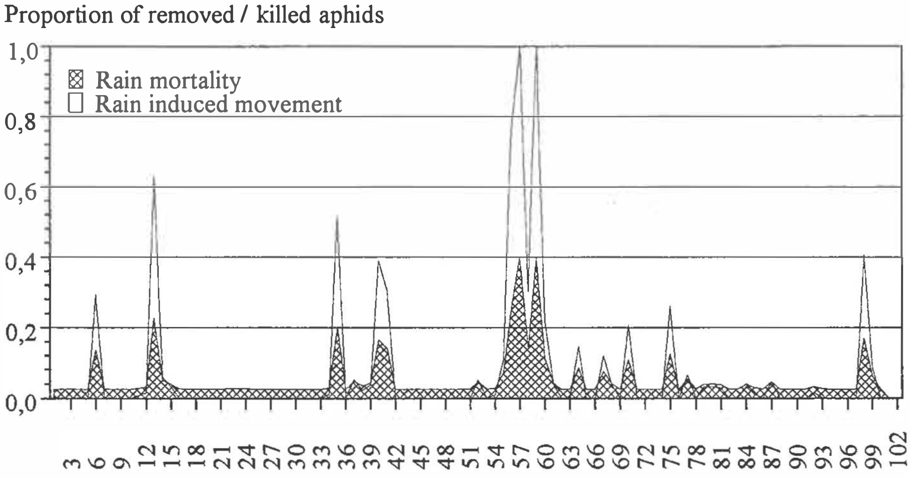

Fig. 4: Calculated rain mortality including spontanous mortality and rain induced movement activity in autumn 1994

4. DISCUSSION

The movement of *S. avenae* in the field is correlated with some weather factors. Thermal time and rain intensity have positive effects on the movement. The rain intensity also influences the mortality of aphids (KLEINHENZ 1994). This compound effect was also shown by MANN *et al.* (in press). By way of contrast, however, there was a slightly negative correlation between wind and the movement rate. The movement forcing effect of wind was found in the experiments of MANN *et al.* under laboratory conditions. During the field experiments described here there occurred no wind at gale force that may have a positive effect. Further field research is necessary to quantify the wind effects. A wind index (e.g. squared wind speed) could be reasonable.

The rain duration time tested in multiple regression had a negative effect on the movement activity. This is in consistency with HARRINGTON & CHENG (1984), who described the same effect in *Myzus persicae*.

The responses of the to different clones on the tested abiotic factors were not uniform. The spatial orientation during movement of a brown coloured holocyclic clone was more variable than that of an anholocyclic clone. With only two clones the outcomes should not be generalized. But clonal variability might also be involved in movement patterns and movement activity and this outcome should give raise to further studies.

There was only short distance movement within a plant row monitored in a second trial. The reason for the difference between the two trials should be differences in host plant quality depending from the growth stage that is assumed to decrease during autumn and winter (KLEINHENZ 1994). Therefore, in accordance to NIKU (1979) the distance moved by aphids should be closedly related to the host plant quality of the source plant: Decreased plant quality results in short distance movement.

The spatial orientation of aphids in both semi-field trials may be influenced by reduced light intensity caused by the gauze and by the reduced number of plants. The results were not included in model assumptions. These trials revealed great differences in the movement frequencies between the different stages. But this differences that have been taken as model assumptions may be also influenced by the gauze in an unpredictable manner. The rain intensity that can induce movement activity may be decreased by the gauze. Therefore some field trials with different stages are necessary to confirm or to improve the model assumptions.

Modelling secondary spread of aphids during winter under the climatic circumstances of Northern Germany is connected with some specific difficulties. At first there are problems with the accuracy of the sample. To meet the need for accurate sampling there is a need for a high sample size according to sampling theory. The number of samples with a standard error of the mean below 5 percent is foremost too high to achieve it with a realistic personal equipment in the field. Nevertheless a simulation run based on a sample in November gave encouraging outcomes in terms of the calculated population dynamics and the index of dispersion. But there are limits of the benefits in comparing field data with simulation outcomes using a mean/variance derived index. If at low temperatures very few aphids occurr that are not aggregated movement activity may hardly influence the index of dispersion. For this case a variogram analysis detecting spatial dependance or an index derived from distances between the aphids may be of greater help. But this needs a special sampling design in the field. SCHOTZKO & KNUDSEN (1992) used also a variogram analysis to compare laboratory trial derived dispersal data of *Schizaphis graminum* with simulation run outcomes.

If the abundance and the dispersal predictions are accurate, the spread of BYDV can be included. For every simulation run it is necessary to confirm the accuracy of the three model sections. If e.g. the abundance is inaccurately predicted, necessarily the secondary spread cannot be predicted. To improve the model there are data of many years necessary that can be compared with simulation outcomes. That work is in progress.

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Approach to Barley yellow dwarf (BYD) epidemiology in Catalonia (NE of Spain): a case study

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Abstract

In the irrigated area growing cereals in the Lleida basin BYDV is widespread. MAV-like and PAV-like isolates of BYDV are the most common in cultivated Poaceae. In forage cereals, and cereal volunteers, the incidence of BYDV isolates is fairly stable being PAV-like isolates predominant. In winter cereals the incidence of MAV-like isolates is more stable than that of PAV-like isolates. In winter cereals the incidence of PAV-like isolates is more variable than that in forage cereals. Maize is an important reservoir specially for MAV-like serotypes. *R. padi* is the most important species to be considered in the epidemiology of PAV-like serotypes while *S. avenae* does not efficiently transmit this strain of BYDV. Epidemiology of MAV-like isolates depents on both *S. avenae* and *R. padi*.

Introduction

In Spain, barley yellow dwarf virus (BYDV) was first detected in 1979 on the east coast in rice and in the northeast in winter cereals. These identifications were made by transmissions tests using *R. padi* as the vector (Alfaro and Montes 1984). The first surveys for BYDV based on the enzyme linked immunosorbent assay (ELISA) technique were made in 1985-1989 in the main cereal growing regions (Fereres *et al.* 1989, Moriones and García-Arenal 1991).

Samples from the 1985-1986 surveys were sent to Dr R.M. Lister, Purdue University (USA) where standard double antibody ELISA tests were done. The antisera used were a polyclonal serum produced at Cornell University against a MAV isolate and polyclonal antisera produced at Purdue University against the Purdue PAV isolate (P-PAV) and RPV. The ELISA results showed that PAV-, MAV-, and RPV- like isolates of BYDV were present (Fereres *et al.* 1989).

Samples from the 1987-89 surveys were tested at the Universidad Politécnica de Madrid, Dep. de Patologia Vegetal. BYDV infection was determined using an indirect ELISA. The trapping antibodies were those of the polyclonal antiserum KY (Doupnik *et al.* 1982). Trapped antigens were detected with monoclonal antibodies (MAb) produced in rats, to a RPV- and a PAV-like isolate from the United Kingdom (Torrance *et al.* 1986). Both PAV- and RPV-like isolates were found in all regions surveyed (Moriones and García-Arenal 1991).

Objective

In the Lleida basin (northeast Spain), where maize, forage cereals and winter cereals overlap in autumn, and winter cereals and maize overlap in spring, cereal aphids survive year round on cultivated *Poaceae* (Pons and Albajes 1987, Pons *et al.* in press). Under these circumstances it is probable that BYDV isolates are also maintained in the region all the year. To try and test this an extensive survey for BYDV, using ELISA, was made of forage cereals, winter cereals and maize in the Lleida basin during 1987-1990.

Since *R. padi* and *S. avenae* are the most important species colonizing winter cereals in autumn and maize in spring, and since BYDV isolates are transmitted from crop to crop by cereal aphids, the infectivity of alate *R. padi* and *S. avenae* in autumn and in spring was determined in order to contribute to an explanation of BYDV epidemiology in the region.

Materials and Methods

Samples were collected in the irrigated area growing cereals in the Lleida basin. This area covers over 5,000 km^2 being the surface devoted to cereals about 45%. Barley and wheat are the most important cereals (125,000 and 70,000 ha, respectively). Forage cereals (usually oats or barley associated with vetch) is over 3,000 ha, but is widely spread all over the region. Maize is the main cereal in summer, with over 20,000 ha.

Forage and winter cereals samples

Samples from forage cereals (oat and barley) were collected the winters of 1987/8, 1988/9 and 1989/90 from commercial fields. Samples from winter cereals (barley and wheat) were collected the springs of 1988, 1989 and 1990. For each sample a single young but fully expanded leaf was collected at random.

Maize samples

Samples were collected in 1988, 1989 and 1990. Each sample was of leaves taken from just above the cob from plants chosen at random in commercial fields during September when the crop was maturing.

Alate aphids samples

In autumn on winter cereals, and in spring on maize, during 1987/88, 1988/89 and 1989/90, colonizing alates of *R. padi* and *S. avenae* were collected to determine their infectivity. Samples in autumn were taken in October-November when cereals were at GS 10-12 (Zadoks *et al.* 1974), samples in spring were taken in May when maize plants had 1-2 leaves. Alates were collected from plants using forceps or a fine brush. Individuals collected were transported quickly in glass vials to the laboratory where were identified before being tested for infectivity test. Time between capture and infectivity test was less than 3 hours.

Diagnosis

Leaves were kept at -40°C and dried at room temperature before being tested by ELISA. Diagnosis was done at the Plant Pathology Department, Rhothamsted Experimental Station, Institute of Arable Crops Research, Harpenden, UK and in the Àrea de Protecció de Conreus, Centre UdL-IRTA, Lleida, Spain. BYDV was detected by serology using an indirect enzyme-linked immunosorbent assay (ELISA). The trapping antibodies were those of the polyclonal antiserum KY (Doupnik *et al.* 1982), which was kindly provided by T.P. Pirone, University of Kentucky, Lexington, USA, and the polyclonal antisera RES-F and RES-R568 prepared at Rothamsted Experimental Station. The detecting antibodies were the monoclonal antibodies MAC-91 (for PAV-like isolates), MAC-92 (for RPV-like isolates) and MAFF-2 (for MAV-like isolates) (Torrance *et al.* 1986), supplied by the Central Science Laboratory, Ministry of Agriculture, Fisheries and Food, UK. With some samples BYDV was detected also by immunospecific electron microscopy (ISEM), which was used as a check on the ELISA diagnosis. ISEM was done as described by Forde (1989), using the polyclonal antibodies RES-F and RES-568, and the monoclonal antibodies MAC-91, MAC-92 and MAFF-2. The grids were examined using a Siemens 102 transmissions electron microscope at a magnification of x40,000. Numbers of BYDV particles per field were counted from several randomly chosen fields of each grid.

Infectivity test

Infectivity tests were done in a glasshouse using *Triticum durum* var. *turgidum* (cv Mexa) inside cilindrical (32.5 cm diameter and 45 cm height) muslin insect proof cages. Each cage contained one pot (9 cm diameter and 9 cm height) containing a single test plant. Each test plant was infested with a single aphid at GS=10-11 (Zadoks *et al.* 1974). Aphids were kept on the test plants for 7-10 days. After that, test plants were sprayed with pirimicarb to kill the aphids and then were left in the glasshouse for 30-40 days in insect proof conditions. Finally plants were kept in the fridge at -30 °C until diagnosis.

Results and Discussion

Forage cereals

In the three years of study the proportion of isolates in the infected samples of forage cereals was relatively stable. With approximately 30% of samples infected with PAV-like isolates, 30% with double infections of PAV and MAV-like isolates, 15% were infective for MAV-like isolates and 8% of the infected samples were positive for mixed infections of all three isolates (Comas *et al.* in press).

Winter cereals

In winter cereals PAV- and MAV-like isolates were widespread, but there were few RPV-like isolates. The proportion of samples infected with PAV-like isolates in single or in mixed infections with MAV-like isolates was much more variable (52% in 1988, 7% in 1989 and 26% in 1990) than that in forage cereals. However, the incidence of MAV-like isolates in single or mixed infections with PAV-like isolates was more stable (28% in 1988, 27% in 1989 and 31% in 1990), irrespective of the frequency of occurrence of PAV-like isolates and mixed PAV-MAV infection (Comas *et al.* in press).

Maize

BYDV was widespread and MAV-like isolates ware especially common (52 % in 1988, 50 % in 1989 and 43 % in 1990). The incidence of RPV-like and PAV-like isolates was more variable from year to year, and their incidence in the fields surveyed was much less than for the MAV-like isolates (Comas *et al.* 1993) When samples were tested by ELISA and ISEM, the results from ISEM generally supported the ELISA diagnosis (Comas *et al.* 1993).

Alate infectivity

Alates collected on winter cereals

Plants infested with alates of *R. padi* were mainly positive for PAV-like isolates. In the autumn of 1988 some plants infested with *R. padi* were also positive for MAV-like serotypes in mixed infections with PAV-like isolates. *S. avenae* alates were infective, almost exclusively, with MAV-like isolates (Comas *et al.* in preparation).

Alates collected on maize

Test plants infested with *R. padi* were positive mainly for PAV serotypes in single or in mixed infections with MAV serotypes. Test plants infested with *S. avenae* were mainly infected with single infections of MAV-like isolates (Comas *et al.* in preparation).

The results of the relationship between BYDV isolates and aphid species observed in the present research agree with what has been established in the literature (Rochow 1969, 1979). However, two features have to be emphasized as of particular relevance to BYDV epidemiology in our region:

1. *S. avenae* did not transmit efficiently PAV-like isolates particularly in autumn. An important feature is that in our region the transmission of PAV serotypes depends, almost exclusively, on the presence of *R. padi* and not on the presence of *S. avenae.*

2. MAV-like isolates were consistently transmited by *R. padi*, a non specific vector, mainly in mixed infections with PAV-like serotypes. That *R. padi* is able to transmit, is some proportion, MAV-like isolates is important from the epidemiological point of view because it ensures the passing of MAV-like inoculum from crop to crop even in the absence of *S. avenae* alates, and again emphasizes the role of *R. padi* in BYDV epidemiology in NE Spain.

Conclusions

BYDV is widespread in the irrigated area growing cereals in the Lleida basin. MAV-like and PAV-like isolates of BYDV are the most common in cultivated Poaceae. The incidence of RPV-like isolates is less important.

In forage cereals and cereal volunteers the incidence of BYDV is fairly stable. The proportion of isolates is also relatively stable.

In winter cereals the incidence of MAV-like isolates is more stable than the incidence of PAV-like isolates. The incidence of PAV-like isolates differs from year to year.

Maize is an important reservoir for BYDV isolates, especially for MAV serotypes. The incidence of PAV serotypes differs from year to year.

Epidemiology of MAV serotypes depends on both *S. avenae* and *R. padi*.

R. padi is the most important species to be considered in the epidemiology of PAV-like serotypes in the northeast of Spain while *S. avenae* does not efficiently transmit this strain of BYDV.

A key role is played by forage cereals and cereal volunteers as a bridge for aphids and for the maintenance of BYDV inoculum between maize and winter cereals.

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