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**Feeding and multiplication
of three cereal aphid species
and their effect on yield of winter wheat**

Proefschrift

ter verkrijging van de graad van
doctor in de landbouwetenschappen,
op gezag van de rector magnificus,
dr. H.C. van der Plas,
hoogleraar in de organische scheikunde,
in het openbaar te verdedigen
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ABSTRACT

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Sitobion avenae F. multiplies at a higher rate on winter wheat than *Rhopalosiphum padi* L. and *Metopolophium dirhodum* Wlk. Unlike the other two species *S. avenae* prefers the ear, where it multiplies twice as quickly as on the flag leaf. Infestation of the ear rather than of the leaves leads to reduction of the average grain weight. These results suggest that *S. avenae* is the most injurious. In 3 field trials with this aphid fungal growth on honeydew caused about half of the damage. After correction for the fungus effect, the loss in yield caused by *S. avenae* feeding on the ear did not differ much from that calculated from its energy budget. Therefore, it is concluded that stylet insertion and saliva injection have no important influence on the growth of grains.

From results with long living and highly productive crops it seems that honeydew can cause a more serious loss in yield if the crop does not prematurely ripen under the influence of various other yield-reducing factors.

Free descriptors: *Sitobion avenae* F., *Metopolophium dirhodum* Wlk., *Rhopalosiphum padi* L., *Triticum aestivum* L., host plant, crowding, wing formation, mortality, reproduction, migration, food utilization, honeydew, fungi, damage, economic threshold, warning system, integrated control.

Front cover:

alate fourth instar nymphs of *Sitobion avenae* F. sucking on a wheat ear.

Back cover:

artificial infection of wheat with cereal aphids in cages made of nylon gauze. These cages were useful to assess the damage caused by a single species attacking different growth stages of the plant under full field conditions.

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Dr. Brader, voormalig hoofd van de afdeling entomologie van het Instituut voor Plantenziektenkundig Onderzoek (IPO) stelde me het onderwerp voor, gaf me de gelegenheid aan zijn afdeling met het onderzoek te starten en voorzag me van een tijdelijk salaris.

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De professoren de Wilde en Brouwer wisten toen nog een aantal zwakke plekken in tekst en inhoud aan te wijzen, maar uiteindelijk kon Lies Lansink op haar voortvarende wijze de definitieve versie uittikken. De foto's die men hierin aantreft zijn van Albert Koedam en de grafieken komen van de vaste hand van Frits Scheffel.

De eindredactie van het proefschrift tenslotte berustte bij de hr. Aalpol.

CURRICULUM VITAE

De auteur werd geboren in Helmond op 31 januari 1948. Aan het Carolus Borromeus College aldaar behaalde hij in 1966 het diploma Gymnasium B. In 1972 werd aan de Katholieke Universiteit te Nijmegen met lof het doctoraal examen biologie afgelegd (met onderwisaantekening). Hoofdvak was zoölogie, waarin een fysiologisch en een ecologisch onderwerp werden bewerkt. Bijvakken waren chemische cytologie, en urbane en rurale sociologie.

Van 1972 t/m 1973 was hij leraar biologie aan het Christelijk Atheneum te Arnhem. In 1974 startte hij in Wageningen als gastmedewerker van de Landbouwhogeschool en het Instituut voor Plantenziektenkundig Onderzoek o.l.v. Prof. dr. de Wilde en Dr. Brader het huidige onderzoek, dat van september 1975 tot oktober 1978 is gesubsidieerd door de stichting Zuiver Wetenschappelijk Onderzoek.

Per 1 januari 1979 is hij aangesteld aan het Proefstation voor Akkerbouw en Groenteteelt in de Vollegrond als coördinator van het vergelijkend onderzoek naar gangbare, geïntegreerde en biologisch-dynamische landbouw op de Drie Organische Stofbedrijven te Nagele, gemeente Noordoostpolder.

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The general concern of growers about the occasionally explosive increase in grain aphids in past years resulted in world-wide research programmes. Current research started in 1974 at the Research Institute for Plant Protection in Wageningen. It aimed to clarify the main production-physiological and production-ecological aspects of the aphid-wheat relationship. It was considered that such fundamental research could yield knowledge necessary to develop schemes for supervised and integrated control. In a later stage researchers and students of the Agricultural University co-operated. The research programme was organized to answer the following questions. What is the significance in aphid population development of temperature, parasites, predators and pathogens, host plant and density-dependent effects? What factors are involved in loss of yield and what are the quantitative aspects of yield loss? Rabbinge et al. (1979) studied aphid population dynamics in relation to temperature, natural enemies and population density and prepared preliminary simulation models for population development and loss in yield. I studied the influence of age of the plant, nitrogen dressing and feeding site on population development (Chapter 2). I determined the influence of these factors and also that of aphid species and honeydew on loss of yield (Chapter 4). With *Sitobion avenae* (F.), which appeared to be the most injurious cereal aphid species the effect of density on population development (Chapter 3) and loss in yield (Chapter 5) was studied.

2 INFLUENCE OF THE HOST PLANT ON THE POPULATION DEVELOPMENT OF SITOBION AVENAE F., METOPOLOPHIUM DIRRHODUM WLK. AND RHOPALOSIPHUM PADI L.

2.1 INTRODUCTION

Sitobion avenae (F.), *Metopolophium dirhodum* (Wlk.) and *Rhopalosiphum padi* (L.) are known all over the world as pests in cereals (Kolbe, 1969). The 3 species differ much in their feeding behaviour. *S. avenae* has a marked preference for the ear and feeds on the rachis and on the bases of the spikelets. *M. dirhodum* usually settles on the abaxial surface of the leaf and is seldom found on the ear. *R. padi* prefers the pseudostem of plants in the vegetative stage, just above the ground and where the leaf blade changes into the leaf sheath. When the plant reaches the stage of stem extension, the stem seems less suitable as a feeding site and *R. padi* disperses over the whole plant. In Great Britain (Dean, 1973) and in the Netherlands (Hille Ris Lambers, pers. comm.) *R. padi* is less abundant in cereals, compared with the other 2 species, than could be expected from suction trap observations. In western Europe *S. avenae* is generally the most numerous species, reaching important numbers only after flowering (Dean, 1974a; Kolbe, 1973; Latteur, 1976; Remaudière et al., 1976; pers. obs.). Wheat and barley are the main cereals in this region. From the scarce information available, it seems that barley is attacked less than wheat in the Netherlands.

Based on these considerations, it was decided to study the performance of the 3 species on winter wheat from the stage of flowering on. In view of the marked differences in feeding behaviour between the 3 species, the influence of leaf and ear as substrate, the age of the plant and the nitrogen dressing were taken into consideration. For *S. avenae* also the influence of the last 3 factors on its efficiency of food utilization in general and of N, P and K in particular, was studied. Apart from the increase in biomass, also honeydew production and the N, P and K contents of honeydew and aphids were determined. When the biomass of aphids per tiller or per m² and the efficiency of food utilization are known, it should be possible to estimate the amount of dry matter the crop has lost as a consequence of the uptake of phloem sap by the aphids (Rabbinge & Vereijken, 1979). By comparing the estimated with the actual losses, it can be established whether the aphids also cause injury by stylet insertion and saliva injection, or the plant is able to compensate losses (Chapter 4).

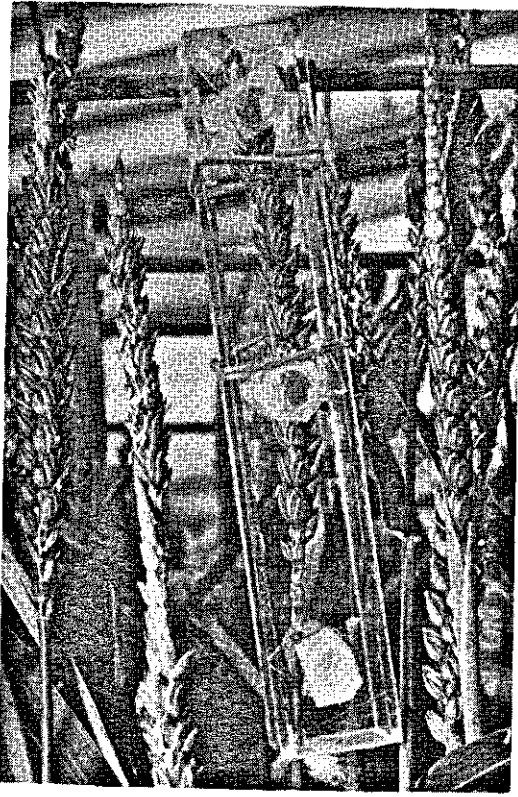


Fig. 1. Left: Perspex cage used for infection of the ear. See 2.2.1. Right: *Sitobion avenae* F., feeding on an ear.

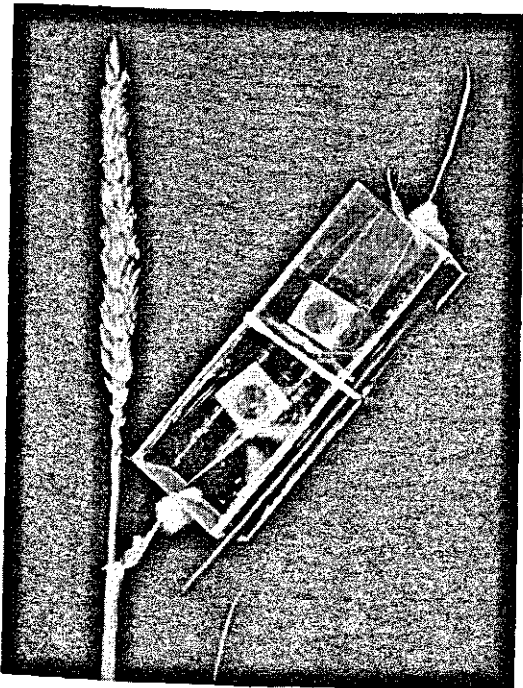


Fig. 2. Perspex cage used for infection of the leaf. See 2.2.1.

2.2 MATERIALS AND METHODS¹

2.2.1 Aphid culture

The aphids were reared on ears or on leaves in 2 mm thick Perspex cages of 100 mm x 30 mm x 25 mm and 180 mm x 25 mm x 20 mm, respectively (Fig. 1 and 2). The leaf cages had 2 ventilation holes of 1 cm diameter, covered with nylon gauze (0.3 mm mesh) on 3 sides. The ear cages had 3 ventilation holes in 2 opposite sides. The bottom and top of the cages were covered with the same nylon gauze. In the gauze covering the end of the leaf cages, a 2 cm groove was made through which the leaf could be passed. With small cotton wads, the grooves were made aphid tight. The gauze at the bottom of the ear cages was only partially glued. In the loose part a hole was made, big enough to contain the ear stem. From the edge of the loose end up to this hole, the gauze was cut. Via the bottom the ear was inserted into the cage and the loose gauze was fastened with adhesive tape. The gauze at the top of both types of cage was also kept partially loose to put the aphids on the encaged plant parts. The loose gauze was then glued to the Perspex with adhesive tape.

After incubation of the ears the adhesive tape at the bottom of the ear cages was loosened, the cages were taken carefully from the ear and the aphids were brushed from the ear into Petri dishes for quantification. With the leaf cages the adhesive tape at the top of the cage was loosened to brush the aphids from the leaf and the cage with the aphids was taken from the leaf.

The cages had the advantage that the honeydew production could be quantified and that emigration of alatae could be prevented. The disadvantages were that applying and removing the cages was very time consuming and that they became overcrowded and dirty if more than 2 generations were reared in them. Therefore the cages were not used in trials to study the population development of *S. avenae* on the ear for 4 weeks, i.e. 3 generations. Unlike alatae, few nymphs and apterae appeared to migrate in this situation. Most alatae settled on the light ceiling and died within a few days, or disappeared through the ventilation system.

The aphids with which the populations were started came from clones which had been conditioned in the climate room in colonies of 10 to 50 individuals for 2 or more generations. In the trial without cages apterae were used. In the trials with cages 3rd instar nymphs were used, which later appeared to be mostly alatae. Four to six days after rearing started, they became adults and began reproducing. Mortality occurred only during the nymphal stage. After 14 days rearing was stopped. The first-born nymphs were at that time 10 days old and not yet able to multiply. The number and weight of the surviving adults and nymphs was established. In this manner the differences in nymphal development rate and adult reproduction rate were not established separately, but combined.

The trials were set up as a split-plot scheme. So the separate effects and mutual

1. Details on plant culture are given in Chapter 4.

interactions of several factors could be tested at the same time by analysis of variance. In view of the large variation in the performance of the colonies, all treatments were done with as many replicates as possible, considering the available time and manpower.

2.2.2 Chemical analysis and determination of honeydew production

After the trial the aphid colonies and the Perspex cages were dried for 3 days at 70°C and weighed immediately after having been taken from the oven. The cages were cleaned and weighed again after 3 days of drying at 70°C. Thus the honeydew production could be calculated in mg dry matter per mg of weight increase of the aphid population. From the colonies of *S. avenae* on the ear and on the flag leaf about 25 mg of honeydew was collected and analysed together with the aphids and kernels of uninfected ears on N, P and K content (Novozamsky et al., 1975; Schouwenburg & Walinga, 1967 and 1975).

2.3 RESULTS

2.3.1 The influence of leaf and ear as substrate and of plant age

Table 1 shows how far the nature of the substrate i.e. leaf or ear combined with plant age influence the population of *R. padi* and *S. avenae* over a period of 2 weeks.

Of the 6 third-instar nymphs with which the colonies were started, an average of 19% of *S. avenae* and 37% of *R. padi* died before they reached the adult stage. On the young ear, from flowering until watery ripe (10.5.1 till 10.5.4, Feekes, 1941) mortality of *S. avenae* was hardly higher than on the flag leaf before flowering, although the aver-

Table 1. The significance of feeding site and plant growth stage for the population development of *Rhopalosiphum padi* (L.) and *Sitobion avenae* (F.) on winter wheat (cv. Clement). Data of R and S represent the mean performance during 14 days of 54 colonies, started with 6 third stage nymphs. Mortality in the initial number mainly occurred during the prereproductive period. Abbreviations; Fe = growth stage of the plant according to Feekes (1941). RS = mean performance of both aphid species. LSD = Least Significant Difference ($p = 0.05$), only listed if exceeded according to the analysis of variance.

Feeding site and plant growth stage	Mean % mortality in initial aphids			Mean multiplication in 14 days						Mean individual biomass in mg			Mean % of winged morphs		
				number			biomass in mg/mg								
	R	S	RS	R	S	RS	R	S	RS	R	S	RS	R	S	RS
flag leaf: Fe 10.1-10.5.1	23	14	18	12.6	11.8	12.2	14.2	15.3	14.8	0.19	0.35	0.27	30	81	56
ear: Fe 10.5.1-10.5.4	41	19	30	15.0	16.3	15.7	17.1	30.1	23.6	0.18	0.36	0.27	15	51	33
ear: Fe 10.5.4-11.1	48	24	36	10.0	13.1	11.6	9.2	26.5	17.9	0.15	0.31	0.23			
total mean	37	19		12.5	13.8		13.5	24.0		0.17	0.34		23	66	
LSD for total mean	5			1.3			2.6			not analysed			3		
LSD for RS	6			1.7			3.3			not analysed			5		
LSD for R and S	10			2.5			4.3			not analysed					

age colony on the ear was much larger than on the leaf. Moreover, the available feeding area of the leaf was 4 times as large as that of the ear. Mortality of *R. padi* was, on the young ear, almost twice as high as on the flag leaf before flowering. Mortality in both species increased somewhat as the plants grew older.

S. avenae increased in numbers more rapidly than *R. padi*, especially on the older ear from watery ripe to milky ripe (Fe 10.5.4 till 11.1). Considering the biomass, *S. avenae* multiplied twice as quickly as *R. padi*. The mean individual weight of *S. avenae* after 2 weeks, was twice as high as that of *R. padi*. Both species multiplied in numbers and in biomass more quickly on the young ear than on the flag leaf before flowering and also more quickly than on the older ear. *S. avenae* multiplied on the old ear at about the same rate as on the young ear and developed worst on the flag leaf before flowering: in biomass even less than half than on the young ear. *R. padi*, however, multiplied on the flag leaf before flowering just as well as on the young ear and developed worst on the old ear: in biomass almost half as quickly as on the young ear. Apart from that, there was little difference in the reproduction rates between the two species on the flag leaf before flowering.

On the young ear the percentages of nymphs with wing buds remained markedly lower than on the young leaf, whereas the reverse was expected in view of the colony densities. *S. avenae* appeared to be more quickly inclined to form wings than *R. padi*.

Table 2 shows to what extent the nature of the substrate, leaf or ear, and the age of the plant influenced the population development of *S. avenae* and *M. dirhodum*. Mortality of *S. avenae* on the ear was again not much higher than on the flag leaf, although the ear colonies were almost twice as large as those on the flag leaf. Mortality of *M. dirhodum* on the flag leaf was twice as high as that of *S. avenae*. On an average, mortality in both species during milky ripe was higher than during the period between flowering and milky ripe.

As adults *S. avenae* weighed 20% and as nymphs 40% more on the ear than on the flag leaf. During the milky ripe stage, the weight of the adult *S. avenae* on the ear remained 25% below that during the previous period. Adults of *M. dirhodum* became just as heavy on the flag leaf as adults of *S. avenae* on the ear.

Before milky ripe *S. avenae* multiplied more quickly on the ear than on the flag leaf, twice as quickly in numbers and more than 3 times as quickly in biomass. On the flag leaf *M. dirhodum* multiplied during this period twice as rapidly in numbers and in biomass almost 3 times as rapidly as *S. avenae*.

During the milky ripe stage *S. avenae* multiplied more slowly on the ear and somewhat more quickly on the flag leaf than in the preceding period. Consequently multiplication in biomass on the ear progressed only half more quickly than on the flag leaf. *M. dirhodum* multiplied during milky ripe on the flag leaf more slowly than before, especially in biomass, so that the difference from *S. avenae* on the flag leaf diminished.

Honeydew production by *S. avenae* expressed in mg dry matter per mg aphid biomass was on the flag leaf 1.7 times as high as on the ear. The fact that the biomass on the ear increased 2.7 times as quickly as on the flag leaf is apparently correlated with the difference in concentration of essential nutrients between flag leaf and ear, assuming that the feeding rates on both plant parts are equal. The ageing flag leaf was of better

Table 2. The significance of plant growth stage and feeding site for the population development of *Metopolophium dirhodum* Wlk. and *Sitobion avenae* F. on winter wheat (cv. Cyrano). Data of M, SL and SE represent the mean performance during 14 days of 30 colonies, started from 8 third stage nymphs. Mortality in the initial number mainly occurred during the prereproductive period. Abbreviations: Fe = growth stage of the plant according to Feekes (1941). M = *M. dirhodum*. SL = *S. avenae* on flag leaf. SE = *S. avenae* on ear. MS = mean performance of M, SL and SE. LSD = Least Significant Difference ($p = 0.05$), only listed if exceeded according to the analysis of variance.

Growth stage of the plant	Mean mortality in initial aphids			Mean weight of surviving adults in mg			Mean multiplication in 14 days			Mean individual biomass after 14 days in mg			Mean honeydew production in mg winged dry mass/mg produced biomass			Mean % of																
	M	SL	SE	M	SL	SE	M	SL	SE	M	SL	SE	M	SL	SE	M	SL	SE														
	MS	MS	MS	MS	MS	MS	MS	MS	MS	MS	MS	MS	MS	MS	MS	MS	MS	MS														
Fe 10.5.2-11.1	32	18	19	23	0.78	0.65	0.85	0.76	10.1	5.2	10.8	8.7	15.6	5.9	20.2	13.9	0.22	0.25	0.40	0.29	2.2	3.2	1.2	2.2	3.2	1.2	2.2	3.2	1.2	36	82	71
Fe 11.1-11.2	37	17	31	28	0.71	0.57	0.63	0.64	8.0	6.1	8.0	7.4	9.3	7.3	10.9	9.2	0.23	0.29	0.35	0.29	2.0	1.9	1.7	1.9	1.9	1.9	1.9	1.9	. . .			
total mean	35	18	25	. . .	0.74	0.61	0.74	. . .	9.1	5.7	9.4	. . .	12.5	6.6	15.5	. . .	0.23	0.27	0.38	2.1	2.5	1.5				
LSD for total mean	6				0.04				0.7			1.4					not analysed			0.8												
LSD for MS	5				0.05				0.8			1.7					not analysed			. . .												
LSD for M, SL, SE	. . .				0.06				1.2			3.5					not analysed			1.3												

Table 3. The significance of plant growth stage and feeding site for *S. avenae*, *R. padi* and *M. dirhodum*: Summary of tables 1 and 2. Data are expressed as percentages of the performance of *S. avenae* on the flag leaf before the milky ripe stage.

	Nymphal mortality	Multiplication in		Honeydew production	Wing formation
		numbers	biomass		
<i>S. avenae</i> on flag leaf before Fe 11.1 (I)	100	100	100	100	100
<i>S. avenae</i> on flag leaf during Fe 11.1 (II)	95	115	125	60	.
<i>S. avenae</i> on ear I	120	175	270	40	80
<i>S. avenae</i> on ear II	170	135	180	55	.
<i>R. padi</i> on flag leaf I	165	105	95	.	40
<i>R. padi</i> on flag leaf II
<i>R. padi</i> on ear I	290	125	110	.	20
<i>R. padi</i> on ear II	345	85	60	.	.
<i>M. dirhodum</i> on flag leaf I	180	195	265	70	45
<i>M. dirhodum</i> on flag leaf II	205	155	160	65	.

feeding quality for *S. avenae* than the young flag leaf.

M. dirhodum reacted more slowly with wing formation on crowding than *S. avenae*. Again *S. avenae* developed more alatae on the leaf than on the ear, even though higher densities were reached on the ear.

Table 3 summarizes the main results of Tables 1 and 2.

2.3.2 The influence of the nitrogen dressing

The population development of *S. avenae* was studied on ears of plants, which had grown on 3 levels of nitrogen dressing. The basic dressing was 30 mg of N per tiller (N1), which is equivalent to about 135 kg of N/ha. During the stage of stem extension, the plants received an extra 5 mg of N (N2) or 10 mg of N (N3) per tiller by adding NH_4NO_3 via the water supply. After the crop had ripened the average yield per tiller was for N1, N2 and N3 : 1.58, 1.52 and 1.51 g of dry matter, with an N content of 1.45, 1.64 and 1.88% (LSD = 0.20%), respectively. In practice the N content varies between 1.70 and 2.00%.

As *S. avenae* feeds only some millimetres in front of the developing grains, it was assumed that the ingested phloem sap would contain N, P and K in the same ratio as they occur in the grain. Fig. 3 shows to what extent this variation in the food influenced the population development in *S. avenae*, starting from one apterous adult. The mortality of the adults was for N1, N2 and N3 during the first week: 8, 4 and 20% (LSD = 10% with $p = 0.05$), respectively. During the 4th week mortality was 10%, 37% and 57% (LSD = 14% with $p = 0.05$), respectively. Undoubtedly the increase in mortality during the first week was caused by a change in food quality, but during the 4th week the differences in average population density under the influence of the various N levels also played an important role. Assuming that the reproduction rate during the first week was constant (Wratten, 1977), that mortality of the initial adults during the second week was negligible and that

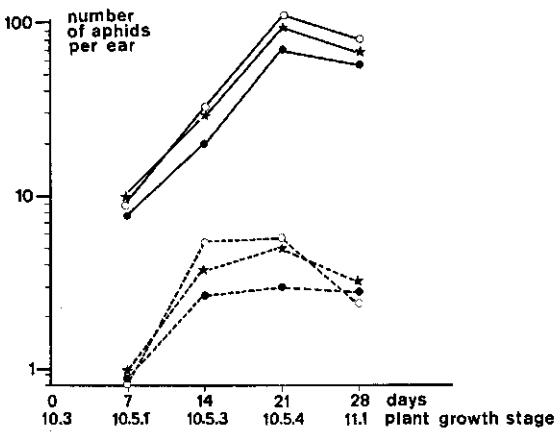


Fig. 3. Population development of *Sitobion avenae* from 1 adult per ear at 3 levels of nitrogen dressing: N1 (●) N2 (★) N3 (○). ---Adults. —Total number. Each point represents the average of 24 colonies.

the nymphs after 10.5 days became adults, it appeared that the apterous population after 14 days consisted of surviving initial adults and young adults born during the first half of the first week. So, the ratio of wing development in nymphs that were born during the first 3.5 days can be expressed as $1 - (A_{14} - A_7) / (0.5 L_7)$, where L_7 is the number of nymphs on the 7th day and A is the number of apterous adults.

On plants dressed with N1, N2 and N3: 59%, 45% and 0% of the nymphs became alatae. The average number of observed apterae was at the end of the 2nd week 2.7, 3.6 and 5.2 (LSD = 1.7 with $p = 0.05$), respectively and at the end of the 3rd week 3.0, 5.0 and 5.6 (LSD = 1.2 with $p = 0.05$), respectively.

Nearly all alatae left the ear after their last moult. The number of alatae remaining in the colony was largest at the end of the 3rd week. At that time an average of 0.9, 1.2 and 0.6 alatae per ear were present. The repression of wing formation in the 1st generation by the extra nitrogen and consequently the development of more apterae finally resulted in an increase in the total number of aphids in the 2nd generation. At the end of the 3rd week, the total number of aphids per ear in N1, N2 and N3 was 64, 85 and 104 (LSD = 29 with $p = 0.05$), respectively.

Table 4 shows to what extent leaf and ear as substrate and also the nitrogen dressing influenced the production of biomass and honeydew and also food utilization in *S. avenae*. From 5 alatae per tiller, 2.4 times as much biomass consisting of $31.5 \pm 1.5\%$ dry matter developed in 3 weeks on the ear as on the leaf. Per mg dry matter aphid production 2.4 times as much dry matter honeydew was produced on the leaf as on the ear. Again this indicated that the increase in biomass of aphids is closely correlated with the concentration of nutrients in the ingested phloem sap and that sap from the rachis contains twice as much nutrient value as that from the flag leaf. The efficiency with which the aphids take up N and P compounds from the sap appeared to be similar at both feeding sites, considering the equal amounts of N and P in the honeydew from flag leaf and ear. The nitrogen dressing did not influence this. The extra nitrogen dressing did effectuate a strong decrease in honeydew production via enhancement of the N and P concentration and possibly by a decrease in the K concentration in the phloem sap. As the cages

Table 4. Production of honeydew and biomass (31.5 + 1.5% dry mass) and food utilization by *Sitobion avenae* on winter wheat (cv. Cyrano), as influenced by feeding site and nitrogen dressing. N1 = basic nitrogen gift of 30 mg N/tiller; N2-3 = extra nitrogen gift during stem extension and heading 5-10 mg N/tiller. Aphid populations, in cages, started with 5 alatae/tiller after flowering, were sampled after 3 weeks. Data of N1-3 represent the averages over 5 tillers (colonies). Between brackets: standard deviation

	Dry mass per tiller in mg (for honeydew: dry mass per tiller/mg aphids)	% N	% P	% K
Kernel yield of untreated tillers				
N1	1415	1.51	0.38	0.67
N2	1091	1.57	0.43	0.59
N3	1170	1.81	0.44	0.54
LSD (p=0.05)	190	0.20	0.16	0.04
N123	1225	1.63	0.41	0.60
Aphid production on				
flag leaf				
N1	8.9			
N2	10.6			
N3	12.9			
N123	11.0 ¹ (2.9)			
ear				
N1	30.6	6.46	0.88	0.99
N2	25.4	6.59	0.89	1.00
N3	23.6	6.72	0.88	1.03
N123	26.5 ¹ (9.5)	6.59	0.88	1.01
Honeydew production on				
flag leaf				
N1	10.2	0.50	0.09	0.96
N2	7.9	0.40	0.11	1.02
N3	8.9	0.30	0.12	1.10
N123	9.1 ² (2.2)	0.40	0.11	1.03
ear				
N1	4.8 ³ (1.2)	0.39	0.19	1.11
N2	3.6	0.37	0.16	1.09
N3	3.0 ³ (1.0)	0.34	0.16	0.94
N123	3.8 ² (1.4)	0.37	0.17	1.05
Utilization: $\frac{\text{mg N, P, K in aphids}}{\text{mg N, P, K in aphids + honeydew}} \times 100\%$ on				
flag leaf				
N1		56	48	9
N2		68	51	11
N3		72	44	10
N123		65	48	10
ear				
N1		78	49	16
N2		83	61	20
N3		87	65	27
N123		83	58	21

1), 2) and 3) Corresponding data showing significant difference at 5% level according to Students t-test.

avoided migration, the restricted wing formation under the influence of the extra nitrogen applied was not expressed in a higher biomass production compared with the normal dressing. The increase in mortality and possibly also the decrease in kernel yield brought about by the extra nitrogen dressing even led to a somewhat lower biomass production on the ear. From Table 4 it can be deduced that from the 3 elements in the sap, N, P and K, the first was utilized most. Thus the concentration of organic nitrogen compounds limits the nutrient value of the phloem sap.

2.4 DISCUSSION

The number of replicates in the various trials was not excessive because even considerable differences between 2 averages were often hardly larger than the LSD.

Half the number of nymphs of *R. padi* that were on the ear died before they reached the reproductive stage. It was surprising that young alatae did not seem to be able to settle again after a flight period of some days. This seems to confirm the supposition of Dean (1973) that *R. padi*, at least as alata, has an "aversion" to cereals and only settles on this crop on a small scale.

Contrary to the findings of Dean (1974b), who reared his aphids on young barley, the 3 species did not multiply at the same rate at the given temperature. *M. dirhodum* multiplied on the flag leaf by far the most quickly, in spite of its high nymphal mortality. Still *S. avenae* is best adapted to wheat, because this species settles in the field mainly on the ear, where it has a lower nymphal mortality, a higher efficiency of food utilization and a quicker multiplication based on biomass, than *M. dirhodum* on the leaf (Table 3). Moreover, *S. avenae* reacts sooner with wing formation on crowding than the other two species and is thus better adapted to the rapid senescence of the plant in the course of the milky ripe stage, when the populations usually reach their peak. As the ear generally remains physiologically active longer than the leaf, *S. avenae* can maintain itself longest in the crop (Lattour, 1976; pers. obs.). These conclusions are confirmed by the general observation that in Western Europe *S. avenae* is usually the most numerous aphid in wheat (Dean, 1974a; Kolbe, 1973; Lattour, 1976; Remaudière et al., 1976; pers. obs.).

The fact that *S. avenae* has become a serious pest in large parts of the world during recent years, could have been caused to a large extent by the enhanced nitrogen dressing. An extra nitrogen application to the plant, generally applied during the phase of stem extension, appears to stimulate the multiplication rate of *S. avenae* by limiting wing formation and consequently the emigration of alatae. Moreover, senescence of the plant is slowed down by the application of nitrogen in combination with fungicides, thus giving the aphids the opportunity to prolong their multiplication, which increases the chance of reaching the economic threshold.

Mittler (1958) assumed on the basis of his results with *Tuberolachmus salignus* (Gmelin), that an increase in N content in the phloem sap enhances the growth rate of the aphid and diminishes its excretion rate. Hertel & Kunkel (1976) found that 4th instar nymphs of *Myzus persicae* (Sulzer), feeding on an artificial diet containing less than half the concentration of amino acids of the standard diet (Mittler et al., 1970), excreted

22-40% more carbohydrates and lost 35% in growth rate, compared with the standard diet. Llewellyn et al. (1974) showed with *Tuberolachmus salignus* that honeydew production has a negative correlation with growth rate.

Extra nitrogen dressing caused an increase in N and P content and a decrease in K content in the grains and consequently in the phloem sap in the rachis. At the same time the honeydew production decreased sharply in *S. avenae*. However, the increase in efficiency of food utilization was not followed by an enhanced biomass production. This could have been caused by an increase in mortality and a decrease in plant production under the influence of the extra nitrogen dressing, which enabled the plant to keep forming new side tillers until after flowering. Because of the suboptimal radiation intensity in the growth room, this happened to the detriment of the kernel content in the existing tillers. In previous trials, where the plant production remained the same or even increased a little under the influence of an extra nitrogen dressing, faster growth of the aphids again could not be established. Probably other growth-limiting factors play also a role.

Of the N, P and K present in the food, *S. avenae* utilized N best by far: for 65% from the sap of the flag leaf and for 83% from that of the rachis. Other aphid species show the following N-utilization percentages. *Aphis fabae* Scop. in *Vicia faba* (L.) 50-70% (Banks & Macaulay, 1965), *Megoura viciae* Buckt. on *Vicia faba* (L.) more than 50% (Ehrhardt, 1962), *Myzus persicae* (Sulzer) on an artificial diet 50% (Mittler, 1970) and 64-70% (Kunkel & Hertel, 1975).

S. avenae multiplies twice as quickly on the ear as on the flag leaf. This fact is coupled with a honeydew production per mg biomass production on the ear, which is twice as low as on the leaf. So the phloem sap stream in the rachis has a nutrient value which is two times higher than that in the flag leaf. We can easily understand this observation because the wheat plant accumulates in the grain in 4 weeks about 50% of its dry matter and 90% of its N and P supply.

Alatae as well as apterae show a marked preference for the ear (Chapter 3). In view of the above data, this adaptation has a great survival value. The fact that *S. avenae* usually reaches high numbers after flowering (Chapter 3), seems to me very much correlated to the high nutrient value of the ear and its preference for this feeding site.

It is common practice to estimate the efficiency of food utilization on the basis of the energy budget. Thus for aphids the caloric value of the food taken up is equalised by the caloric value of honeydew and biomass (including exuviae) and the metabolic heat loss (respiration).

Llewellyn (1972) found for *Eucallipterus tiliac* a caloric value of 5.6 cal/mg dry matter² and Llewellyn & Quereshi (1978) found for *Aphis fabae* Scop. a caloric value of 5.5 cal/mg dry matter. From results of Kunkel & Hertel (1975) it could be calculated that 3rd instar alatforms of *Myzus persicae* contained 5.8 cal/mg dry matter. From their data it could also be calculated that the ratio between increase in biomass and metabolic heat loss at 15°C amounts to 1 : 2, approximately.

Assuming that on the basis of dry matter the energy content of *S. avenae* is 6 cal/mg and that of phloem sap and honeydew is 4 cal/mg (wheaten flour and saccharose: 4 cal/mg)

2. 1 cal = 4,1868 J.

and that the heat loss is 3 cal/mg of aphid production, then we can estimate the energy budget of *S. avenae* as follows. *S. avenae* on the ear: caloric value of ingested sap = caloric value of biomass production and of honeydew (contaminated with exuviae) plus metabolic heat loss = $6 + (3 \times 4) + 3 = 21$ Cal. The efficiency of food utilization is $6/21 = 29\%$. For the production of 1 mg of aphid $21/4 \approx 5$ mg of phloem sap is needed of which 3 mg is excreted as honeydew. *S. avenae* on leaf: caloric value of ingested sap = $6 + (9 \times 4) + 3 = 45$ cal. The efficiency of food utilization is $6/45 = 13\%$. For the production of 1 mg of aphid $45/4 \approx 11$ mg of phloem sap is needed of which 9 mg is excreted again. For these estimates the honeydew production at the highest nitrogen level (Table 4) is considered to be the most representative for the honeydew production in the field. At this fertilising level, the N content of the grains was 1.9%, in the field an N content of 1.7-2.0% is normal.

M. dirhodum (Table 2) produces on the flag leaf $2.1/2.5 \times 100\% = 84\%$ of the amount of honeydew that is produced by *S. avenae*. So for *M. dirhodum* it can be stated that on the flag leaf the caloric value of the ingested sap = $6 + (7.5 \times 4) + 3 = 39$ cal. The efficiency of food utilization is $6/39 = 15\%$. To produce 1 mg of *M. dirhodum* $39/4 \approx 10$ mg of phloem sap is needed, of which 7.5 mg is excreted again.

Table 5 presents a review of the energy budgets of 9 species of aphids. It appears that with regard to efficiency of food utilization, grain aphids take an intermediate position. The value of the data shown in this table should not be overestimated, however. Factors like age of the plant and leaf, feeding site and nitrogen dressing undoubtedly were of strong influence.

Table 5. Energy budgets of 9 aphid species.

Aphid species	Host plant	Percentage energy in		Author(s)	
		growth	respiration honeydew		
<i>Aphis fabae</i>	<i>Vicia faba</i>	20	10	70	Dixon (1971)
<i>Aphis fabae</i>	<i>Vicia faba</i> feeding on mature tissue	56	7	37	Llewellyn & Qureshi (1978)
	feeding on young tissue	47	6	47	
<i>Aphis fabae</i> 1st and 2nd instar	<i>Vicia faba</i> artificial diet	54	4	42	Llewellyn & Leckstein (1978)
		26	4	70	
<i>Megoura viciae</i>	<i>Vicia faba</i>	67(!)	20	13	Dixon (1971)
<i>Acyrtosiphon pisum</i>	<i>Pisum sativum</i>	22	22	56	Barlow et al. (1977)
<i>Myzus persicae</i> 3rd instar apteriform	artificial diet	17	20	63	Kunkel & Hertel (1975)
3rd instar alatiform		35	24	41	
<i>Sitobion avenae</i>	winterwheat(cv.Cyrano) feeding on ear	29	15	56	present paper
	feeding on flag leaf	13	7	80	
<i>Metopolophium dirhodum</i>	winterwheat(cv.Cyrano) feeding on flag leaf	15	8	77	present paper
<i>Eucallipterus tiliae</i>	<i>Tilia x Vulgaris</i>	6	4	90	Llewellyn (1972)
<i>Drepanosiphum platanoides</i>	<i>Acer pseudoplatanus</i>	4	5	91	Dixon (1971)
<i>Tuberolachnus salignus</i>	<i>Salix</i> ?	6	4	90	Dixon (1971)

3 POPULATION DEVELOPMENT OF SITOBION AVENAE F., ESPECIALLY IN RELATION TO CROWDING

3.1 INTRODUCTION

Sitobion avenae F. lives on many host plants, almost all belonging to the Gramineae and shows a specific preference for the panicle (Hille Ris Lambers, 1939; Latteur, 1976). In spring and in summer, reproduction is parthenogenetic and viviparous. At temperatures between 15°C and 20°C, nymphal development (4 stages) is completed in about 10 days. One apterous adult can produce 20 to 40 nymphs in 2 weeks, depending on its size.

"Crowding" ("effect de groupe", Bonnemaison, 1951) can result in the production of alatae, which is very important for the survival of the species. Overpopulation is thus avoided and when the quality of the host plant deteriorates, the aphids are capable of migrating to another host. With *Aphis fabae* Scop. (Way & Banks, 1967; Dixon & Wratten, 1971) it was found that crowding decreases the size, which results in a lower fecundity of the individuals. According to Taylor (1975) size influences fecundity mainly through reproduction rate and longevity.

This section first describes the population development of *S. avenae* in the field in general terms and alate production and migration in detail. Then it discusses trials on the effects of crowding, which were done in the laboratory where natural enemies are absent and climate is under control.

3.2 MATERIALS AND METHODS³

Field trials were done near the Research Institute for Plant Protection (IPO) in Wageningen. In 1974 and 1975, the population development was studied by taking random samples weekly. The average number of aphids per tiller and per leaf was recorded. The rapid population increase and decline, the pattern of dispersion and the change in age composition required more detailed observations. Therefore in 1976 and 1977 samples were taken twice a week and the numbers of aphids were quantified according to seven age and morph classes: 1st, 2nd and 3rd instar, 4th instar alatiform or apteriform, alate or apterous adult. The various nymphal instars were distinguished by size and wing dimorphism. Apteræ were distinguished from 4th instar nymphs without wing buds by the length of the cauda or by dorsal pigmentation. From climate room observations it was assumed that those alatae that did not suck with their heads down on the rachis or on the base of the spikelets, as all other aphids did, would eventually migrate. As they would not

3. Details of aphid and plant culture are given in Chapters 2 and 4, respectively.

function as reproductive adults in the colony, they were classified as 4th instar alati-forms. In this way a realistic evaluation could be made of the total number of reproduc-ing adults and of the ratio between alatae and apterae.

The primary purpose of the observations was to obtain an insight in the factors de-termining population development, especially those involved in density-dependent effects. Therefore it was considered to be sufficient to follow the level and composition of the population on 100 tillers, well distributed in a field of 2500 m². To avoid loss of aphids, the ears were not touched during counting.

3.3 RESULTS

3.3.1 Field observations

3.3.1.1 Migration to the crop

Alatae were observed for the first time during the period of stem extension. In 1976, (Fig. 4) their number increased before flowering started (Fe 10.5.1) and remained more or less steady until growth stage watery ripe (Fe 10.5.4). In 1977, (Fig. 5) a strong migra-

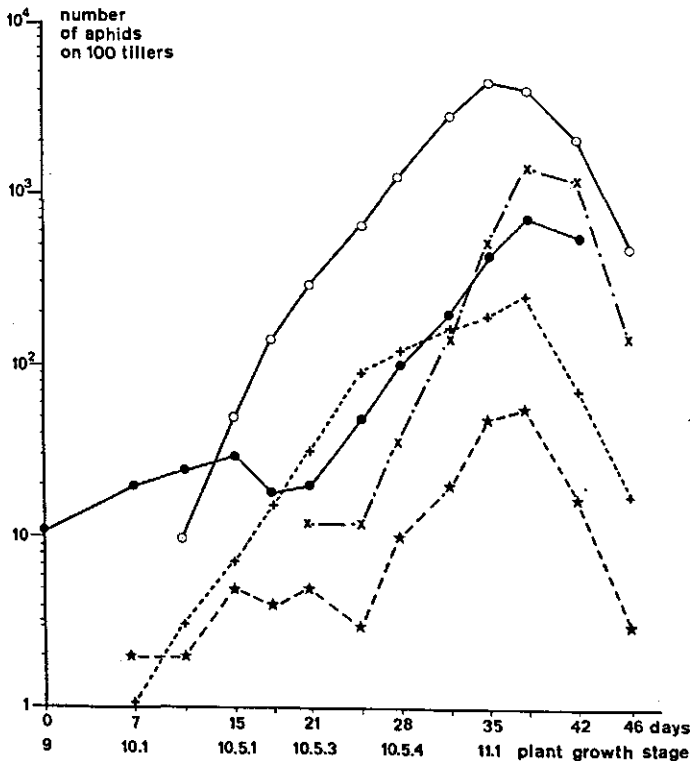


Fig. 4. 1976. Population development of *Sitobion avenae*. Observations were made on 100 marked tillers, twice a week from 24 Mai (Fe.9) till 9 July (Fe.11.2). (○) Total number on ears. (●) Total number on leaves. (+) Apteræ. (✱) Alatae. (✕) Nymphs of 4th stage, alati-form.

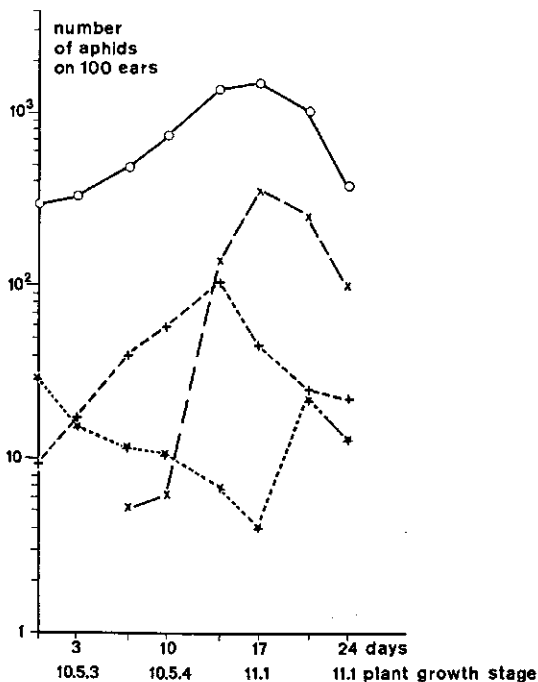


Fig. 5. 1977. Population development of *Sitobion avenae*. Observations were made on 100 marked ears, twice a week from 17 June (Fe.10.5.2) till 11 July (Fe.11.1). (○) Total number. (+) Apteræ. (*) Alatae. (X) Nymphs of 4th stage, alatiform.

tion had already taken place before flowering and then the number of alatae decreased rapidly until the beginning of the milky ripe stage (Fe 11.1). In 1976, the number of alatae increased strongly from Fe 10.5.4 and in 1977 from the beginning of Fe 11.1. Probably most of these alatae originated from winter wheat, where usually a massive migration occurs in this period (Figs 4 and 5, 4th instar, alatiform). The number of alatae, however, remained much smaller than the number of apterae, so that this second migration wave can be considered relatively unimportant. In 1976, an average of 1.4 aphids was present per ear during flowering, of which 3% were alatae and 37% of the ears were occupied. In 1977, the corresponding figures were 0.9, 32% and 78%, respectively. Thus the speed with which the available ears are colonised seems to depend on the rate of immigration of alatae.

3.3.1.2 Migration within the crop

It was established in laboratory trials that nymphs hardly migrate if they are not disturbed. Only after the last moult do they become restive and move in the direction of the light source. Alatae soon start to fly and apterae settle down at the top of the plant. Once having started reproduction, the adults usually stay where they are.

The observations in 1976 confirmed these findings. From Fig. 6 it appears that apterae had already colonised the ears, when they were only partly visible (Fe 10.4).

No 3rd and 4th instar nymphs were present yet, so reproduction had just started. At the beginning of flowering, the preference for the ear of both alatae and apterae resulted in a sharp decrease in reproduction on the leaves causing the two oldest nymphal stages to be the most numerous. At the same time more apterae than 3rd and 4th instar nymphs were present on the ears. This migration from the leaves to the ears resulted in 1976 in a decrease in percentage of tillers with leaf infection from 17 before flowering to 10 at the end of flowering, whereas in this period the percentage of tillers with ear infestation increased from 0-53%. Fig. 4 shows that temporarily the total number of aphids on the leaves even slightly decreased. After flowering in 1976, the percentage of tillers with leaf infestation increased to almost 100% at the end of the milky ripe stage. In my opinion this mainly resulted from disturbance of ear colonies, caused by wind (rain was absent), coccinellids and nymphs of syrphids. Many times I saw that the presence of a predator in a dense ear colony caused especially 4th instar nymphs and adults to drop down. Undoubtedly a number of the fallen aphids settled again on the leaves. After flowering in 1976, the average number of 1st instar nymphs per adult was 3.3 in leaf populations and 5.0 in ear populations. These values indicate that the rate of reproduction on leaves is lower than on ears, which was also found in the laboratory (Chapter 2). The growth rate of total leaf and ear populations, however, was the same (Fig. 4). This suggests that the aphids present on the leaves after flowering mainly originate from the ears.

3.3.1.3 Influence of migration and temperature on population growth

In 1976, the population showed an exponential growth during the 3 weeks from Fe 10.4 to Fe 11.1 (Fig. 4). In this period the population kept pace with the number of adults, mostly apterae. From Fe 10.5.4 the number of adults started to grow less rapidly because an increasing proportion of the nymphs developed wings and migrated as soon as they reached the adult stage. Fig. 4 shows that the population as a whole kept on growing for 10 days with approximately the same speed, apparently because the reproduction rate increased strongly. This probably happened under the influence of a sharp rise in temperature. In 10 days the temperature rose steadily from 14.5°C to 24°C.

In 1977, the population growth during flowering was hardly noticeable (Fig. 5) because of the sharp decrease in the number of alatae, which were in fact the largest fraction of reproducing adults. However, the number of apterae did increase during flowering, so that by the end of flowering (Fe 10.5.3) they outnumbered the alatae. From that moment on, the population started to grow more rapidly and kept pace with the number of apterae. Even though the number of adults started to decrease before milky ripe because more and more nymphs developed wings and migrated after their last moult, the population still increased for a few days because the reproduction rate increased, probably induced by a rise in temperature from 15°C to 20°C.

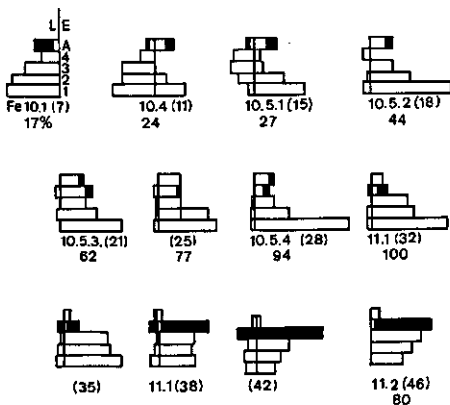


Fig. 6. 1976. Age composition of the population at successive dates. Frequencies of the 5 age classes are presented as percentage of the total number. Symbols used: L, E = Leaf, Ear population. 1 - 4 = 1st - 4th nymphal stage. A = adult. () = Day of observation. % = Percentage of colonized tillers. Unwinged, winged aphids.

3.3.1.4 Analysis of population development based on age and morph composition

The various phases in the development of aphid populations become visible in the ratio of numbers between the separate age classes on subsequent dates. In Fig. 6 an overall picture of the population development in 1976 is shown. On Day 8 (Fe 10.1) the first ears were occupied, and the production of the 1st generation started. The majority of the parent generation on the ear was apterous and therefore originated from the leaf. Because before and after flowering little migration occurred, colonisation of the crop progressed gradually. Only on Day 30 (Fe 10.5.4) all ears were occupied. On Day 15 (Fe 10.5.1) for the first time 4th instar nymphs of the first generation were present on the ear. On the base of the results of Dean (1974) it could be estimated that the first nymphs of the second generation were born around Day 19 (Fe 10.5.2) and reached the 4th instar around Day 25 (Fe 10.5.4). On this day for the first time 4th instar alate nymphs were observed. In all probability these were the first nymphs of the second generation, because they belonged to the oldest and thereby largest colonies, where the strongest incentive to wing formation existed (see wing formation). So, migration of second generation alatae started after Day 25, which is also indicated by the less rapid increase in the number of apterae after this day (Fig. 4). It kept on increasing, however, for 2 weeks and even tripled during this period. This steady increase was caused by the very gradual colonisation of the crop. Because the last ears were colonized only around Day 28 (Fe 10.5.4), apterae from the 1st generation could join the population at least until Day 38 (see wing formation).

In 1977, population development on the ear progressed mainly in a similar manner, and can be described as follows (Fig. 7). Owing to an intensive immigration before flowering, 80% of the ears were colonised at the beginning of flowering. As a consequence, the majority of the parent generation adults were winged. The presence of 4th instar nymphs of the first generation on Day 0 (Fe 10.5.2) showed that reproduction on the ear had started about 8 days earlier (Fe 10.5). Around Day 3 (Fe 10.5.3) the first nymphs

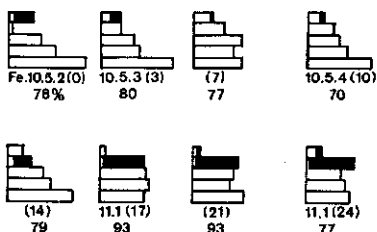


Fig. 7. 1977. Age composition of the population at successive dates. For further details see fig. 6.

of the 2nd generation were born and reached the 4th instar around Day 10 (Fe 10.5.4). At that moment 5% of the 4th instar nymphs were alatiform and 4 days later this percentage was 80. So again the second generation was mainly winged.

3.3.1.5 Wing formation

Only at the 4th nymphal stage is wing formation clearly visible with the naked eye. In 1976 and in 1977 (Figs 6 and 7) the first alatiformae were observed 7 days later than apteriformae. Thus both alatae and apterae had unwinged progeny during the first week after the start of the ear colony, notwithstanding their previous history. Apparently wing formation in *S. avenae* depends on the circumstances prevailing just before birth or during the first days of nymphal life. Results of climate room trials (3.3.2) confirmed this. For 1 date in 1976 and for 2 dates in 1977 separate ear colonies were studied to find a correlation between the percentages of nymphs with wing buds in the 4th instar and the size of the colony just after their birth, so 7 days earlier. On these 3 dates the percentages of alatiformae were well distributed between 0 and 100 and more than 10 colonies, a minimum for correlation analysis, satisfied the following 2 conditions: (a) there should be at least 2 nymphs of the 4th instar and (b) 1 adult should have been present 7 days earlier or at least 2 nymphs should have been in the 1st instar. These conditions were applied to exclude colonies which were disturbed during the last 7 days or were founded by fallen aphids. The rank correlation coefficient according to Spearman was calculated, because it is less sensitive to random variation. The results were 0.63, 0.68 and 0.82, respectively. Every time the probability that no correlation existed was less than 0.01. In view of these reliable indications for a direct influence of the size of the colony on wing formation, their coherence has been tested in all observation data in 1976 and in 1977 until the population maximum was reached. A strong correlation ($r = 0.95$) was apparent between the percentage of nymphs with wing buds in the 4th instar converted into probits and the logarithm of the colony size 7 days earlier (Fig. 8). These calculations showed that *S. avenae* forms wings at very low population densities. According to Ankersmit (pers. comm.) the green *S. avenae* is apt to develop wings earlier than the dark, brown one. In the current trials the majority of aphids were green.

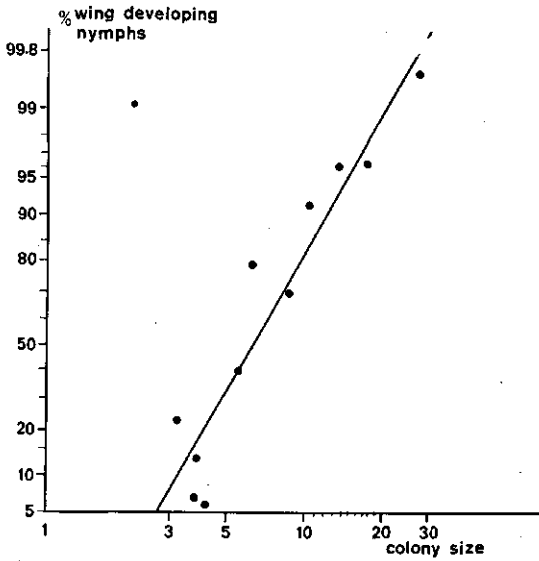


Fig. 8. 1976 and 1977. Percentage of wing developing nymphs in the 4th stage as influenced by colony size at time of birth (one week before). Each point represents the average over 100 marked ears at a certain date. $n = 11$, $r = 0.95$. Regression formula : $\text{probit } y = 4.53 \log x + 1.36$.

3.3.2 Climate room trials

Table 6 shows that there were big differences in the development of *S. avenae* populations in Perspex cages starting with 4 and 8 individuals of the 3rd instar per ear. After 14 days the increase in biomass from starting density 8 was 49% less than that from starting density 4. Approximately 10% of this effect was caused by a higher mortality in the initial number, 60% by a lower increase in numbers and 30% by a lower average weight of the nymphs.

In 2 trials the population development was studied during 4 weeks starting with the lowest possible initial densities i.e. 1, 2 and 3 apterae per ear (Figs 9 and 10). In the first trial, smaller and consequently less productive adults were used than in the second trial. During the first week more than 10% of the adults died in Trial 1, but in Trial 2

Table 6. The significance of initial density for the population development of *Sitobion avenae* on the ear of winter wheat (cv. Clement). Data represent the mean performance of 27 colonies in perspex cages, started with 3rd instar larvae, over 14 days during the period from 'flowering' until 'watery ripe'. All differences between the two densities are significant at 5%. Between brackets: relative performance of initial number 8.

Initial number	Initial biomass	Mean survival in initial aphids	Mean multiplication in			
			number		biomass	
			corrected for mortality			
			-	+	-	+
4	0.78 mg	91%	19.5	20.4	41.0	43.0
8	1.68 mg	76%	13.6	15.5	21.1	24.0
			(70%)	(76%)	(51%)	(56%)

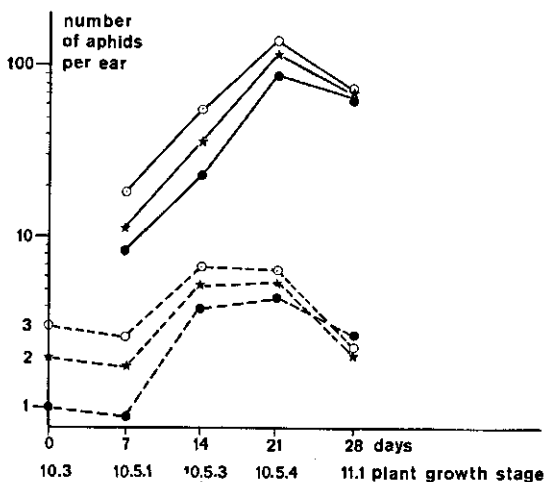


Fig. 9. Lab.exp. 1. Population development of *Sitobion avenae* from 3 initial densities : 1 (●), 2 (★) and 3 (○) adults per ear. --- Adults. — Total number. Each point represents the average over 72 colonies.

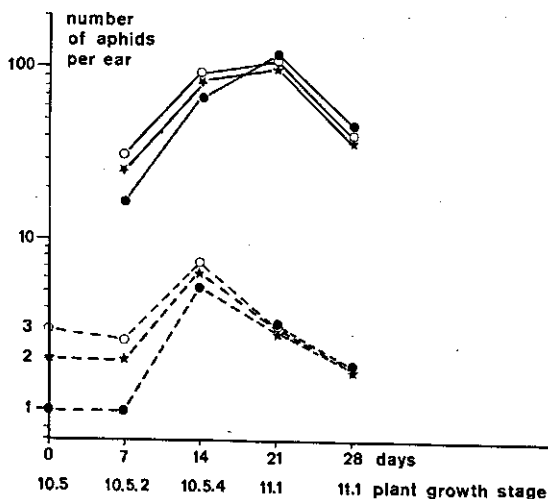


Fig. 10. Lab.exp. 2. See Fig. 9 for details.

some mortality occurred only at density 3. After 1 week there were 50% less nymphs present in Trial 1 than in Trial 2. Corrected for mortality the reproduction rate (nymphs/adult per day) during the first week with density 1 was in both trials significantly higher than with the other densities. On an average over the two trials the reproduction rates for densities 1, 2 and 3 were 1.66, 1.22 and 1.13 nymphs/adult per day, respectively. The least significant difference was 0.23 ($p = 0.05$). Ten days after the start of the population development the first nymphs became adults. Two days later the first alatae were observed against the light ceiling of the climate room. Migration increased during the next weeks. It was striking that the majority of the alatae did not return to the crop and died after a few days. Only in the milky ripe stage did a number of alatae settle on the yellowing leaves and form colonies.

From Figs 9 and 10 it can be deduced that although during the first week in Trial 1 less than half the number of nymphs were born compared with that in Trial 2, the number of young apterae was nearly equal in both trials after 14 days. Apparently a stronger wing development occurred in the young nymphs in Trial 2 owing to higher colony densities. Assuming that the reproduction rate during the first week was constant (Wratten, 1977), that mortality of the initial adults during the second week was ignorable and that the nymphs after 10.5 days became adults, it appeared that the apterous population after 14 days consisted of surviving initial adults and young adults born during the first half of the first week. So, the ratio of wing development in nymphs that were born during the first 3.5 days can be expressed as $1 - (A_{14}-A_7)/(0.5 L_7)$, where L_7 is the number of nymphs on the 7th day and A is the number of apterous adults.

The first trial yielded 34% and the second 56% alatae. From the two trials together, a marked relation seemed to exist between the average percentages of wing formation and the average colony size in the middle of the first week: the correlation coefficient was 0.98. Assuming that the remaining initial adults all died in the 3rd week, the number of apterae of the second generation increased during the 3rd week by 40% in Trial 1 and decreased in Trial 2 by 26%. Of the nymphs born in the second half of the first week approximately 65% in Trial 1 and 100% in Trial 2 were winged. Crowding most likely caused mortality and possibly some migration of the 2nd generation apterae during the 3rd week. Owing to the decrease in number of apterae, the total number of aphids in Trial 2 increased only slightly during the 3rd week, so that the maximum number after 21 days was equal in both trials. Only in Trial 1 was levelling between the total numbers of the 3 densities not yet complete at this time. During the 4th week the total number of aphids decreased in both trials as a consequence of ageing, mortality of apterae and continuing migration of alatae.

3.4 DISCUSSION

Until now it has generally been assumed (Lateur, 1976; Sparrow, 1974; Wetzel et al., 1975) that, apart from action by *Entomophthora*, the decrease in population is caused by ageing of the host plant together with an increasing activity of natural enemies. The reproduction rate of *S. avenae* on the ear does indeed decrease under the influence of host plant ageing (Chapter 2) but this occurs only in the second half of the milky ripe stage, whereas the population in the field frequently reaches its maximum before that. The fact that aphids usually attain their maximum density a few days before their natural enemies does not only indicate that the second phenomenon causes the first one, the reverse can also occur and may be even more relevant. The current results show that the typical population development consisting of: build up, rapid multiplication, slow down, stagnation and quick decrease is in the first place regulated by intraspecific factors.

Development of winged forms depending on the size of the colony followed by emigration in itself can not only restrain the population growth, but can even reduce it to less than half. In practice the natural enemies and the senescence of the host will subsequently enhance a further decrease. The strong preference for the panicle and the sharp reaction to crowding normally seem to result in an ear population of not more than 2 ge-

nerations, of which the last one is almost entirely winged.

It was striking that the reproduction rate of a single adult on the ear was 30% higher than that of 2 or 3 adults living together on one ear. So, contrary to Taylor's (1975) findings with *Aphis fabae* Scop. it seems that with *S. avenae* the density does not only influence the rate of reproduction by way of the body size but also directly. The effect of density on the individual size and longevity seems hardly relevant to the population development in cereals. Nymphs with a retarded growth as a result of crowding will undoubtedly form wings at an early stage and migrate after the last moult. In the laboratory even the adult stage of small individuals in a dense colony lasts at least 7 days. Periodic observations of marked tillers revealed that in the field the duration of the adult stage is usually shorter than 7 days, because of natural enemies and climate. Thus in the field most aphids do not get the chance to die from physiological ageing or from the effects of overpopulation.

4 INJURY AND DAMAGE TO WHEAT, CAUSED BY SITOBION AVENAE F., RHOPALOSIPHUM PADI L. AND METOPOLOPHIUM DIRHODUM WLK.

4.1 INTRODUCTION

Strickland & Bardner (1967) defined injury and damage as follows. "Injury is the effect of insect feeding or other activities on the growth or appearance of crop plants. Damage is injury resulting in measurable loss of yield or reduction in quality". Uptake of phloem sap, injection of toxic saliva, pollution of the plant with honeydew and transmission of virus are the most obvious causes of aphid injury. To what extent injury leads to damage is a complex matter. According to Bardner & Fletcher (1974) it depends on the nature, the site and intensity of the injury, the condition of the plant and environmental factors. To investigate the relation between injury and damage they recommended a study of crop physiology, especially analysis of plant growth in terms of effective photosynthetic area, production of dry matter and its distribution between the various parts of the plant.

From several studies it appears that the dry matter of the grains is formed more than 90% after flowering mainly in the flag leaf, peduncle and ear, and that the yield level depends on the size and duration of the photosynthetic area and environmental factors such as radiation, temperature and moisture content of the soil (see reviews by Thorne, 1974; Yoshida, 1972).

Particularly in the period after flowering aphids usually attain large numbers (Chapter 3). Therefore the effect of aphids on yield was only determined in this phase. In climate room trials I investigated to what extent aphid species, site and time of infestation and nitrogen dressing influenced the damage. The light and temperature regime and the moisture content of the soil were not varied, although these factors are possibly relevant to the damage. The nitrogen dressing was varied because it strongly determines the size and duration of the photosynthetic area and thereby the yield level. Moreover, the efficiency of food utilization seemed to increase through the extra fertilization with nitrogen (Chapter 2).

From a known quantity of biomass of *S. avenae* it could be estimated on the basis of its energy budget, how much dry matter was withdrawn from the plant. If the calculated loss in yield would appear higher than the established loss in yield it would indicate that the plant is able to compensate for the loss. The reverse would indicate that stylet penetration and saliva injection in the plant also contribute to damage. In these climate room trials fouling of the plant by honeydew and black moulds could be neglected because the honeydew dried out and remained as small and fungus free crystals on the plant as a result of the intensive ventilation and low humidity of the air.

However, in the field honeydew deposited on the plant can cause a severe fungus infestation. As this phenomenon often occurs during the period in which the grains are

still developing, it was assumed that it would affect the yield negatively. By determining the effect of aphids on yield in the field with and without treating the crop with a broad spectrum fungicide, I tried to establish the ratio between "feeding damage" and "honeydew damage". The possible direct influence of honeydew on plant production is being investigated by Rabbinge et al.

The significance of the intensity of infestation for the damage will be discussed together with the possibilities of control (Chapter 5).

Because transmission of virus seems only locally important in wheat culture in western Europe, this source of injury has not been included in this study.

4.2 MATERIAL AND METHODS

4.2.1 *Laboratory trials*

4.2.1.1 Plant culture (Fig. 11)

Germinated grains of winter wheat cv. Cyrano were put on moist filterpaper and vernalised in Petri dishes for 6 weeks at 2°C. They were then planted in 2 rows of 25 grains each in boxes of 50 cm x 20 cm x 20 cm, in a soil mixture of 10 kg of sand, 8 kg of potting compost, 5 kg of light clay and 4 l of water which saturated the water capacity for



Fig. 11. Wheat culture in the climate room.
See 4.2.1.1.

60%. In each box 3 porous filter candles with a total volume of 600 ml were put at a depth of 10 cm. They were connected to a water reservoir under the box with a rubber tube having an inner diameter of 2 mm. Loss of water in the soil mixture was constantly compensated by the capillary action of the tube. To each box the following quantities of "slow release fertilizers" were added: 5 g of CaCO_3 , 5 g of MgO , 10 g of P_2O_5 , 2 g of K_2O and 3.5 g of N.

The first 6 weeks, during the tillering phase, the climate was regulated as follows: daylength 15 h, day and night temperature 15°C and 9°C respectively. After that daylength was 16 h and day and night temperatures were 18°C and 12°C . Relative humidity was 70%. The light intensity at the top of the crop was constantly kept at 20.000 lux (62 W/m^2) by adjusting the distance between the crop and the TL-33 ceiling. Under these circumstances 50 main tillers and 60 to 80 sidetillers per box started flowering after 13 weeks. The available quantity of nitrogen per tiller was about the same as in the field. The average yield/tiller was 1.75 g with a moisture content of 17% and the mean kernel weight was 44 mg, which equals the average in practice.

4.2.1.2 Aphid culture

Details on aphid culture were given in Chapter 2. Before each trial a sample of the aphids was put on oat seedlings, to see if they were still free of Barley Yellow Dwarf Virus. Beemster, virologist at the Research Institute for Plant Protection, taught me the symptoms which normally become visible after some 10 days. Unlike samples from the field, samples from the laboratory never reacted positive.

4.2.2 Field trials

The field trials were done with winter wheat cv. Caribo on the experimental fields of the Research Institute for Plant Protection in Wageningen. The maintain was to find out to what extent fungal growth on honeydew led to damage. In statistical terms the question was: is there an interaction between an aphicidal and a fungicidal treatment? To solve this problem a split-plot scheme seemed most appropriate. As I was more interested in the effects of aphids and their control than in the effects of fungicides, it was decided to consider the aphicidal treatment as a split factor. Based on experience from previous years and on the expected extent of the effect, the trials were set up in 10 blocks. Each block consisted of 2 sub-blocks of which one was treated with a fungicide mixture comprising maneb 42.5% and carbendazim, 6% a.i. 4 kg/ha, at the start of flowering. In the 1976 trial cages made of nylon gauze (.3 mm mesh) were used, with a diameter of 44 cm and 150 cm high. The nylon gauze was put around a frame of coarse plastic metal gauze, which was fixed to the ground with iron pins. Earth was piled up against the lower part of the cage to prevent insects to crawl through. All plants 15 cm around the cages were removed allowing the encaged plants more light, which appeared to compensate for the 10-20% reflection and absorption by the gauze. In each cage 40 to 70 tillers were present and their yield was similar to that of the full field tillers. The nylon gauze was attached at the time the ears just became visible. The same day and

4 days later the plants in the cages were treated with a short term phosphoric ester to kill the aphids and the natural enemies present. At the start of flowering in each sub-block which comprised 4 cages, 4 treatments were allocated at random: *S. avenae*, *M. dirhodum*, *R. padi* and control. In each cage 40 4th instar nymphs and adults were released, originating from a laboratory culture. Four weeks later, at the end of the milky ripe stage, the gauze was removed. The aphids present on 10 tillers per cage, randomly chosen, were counted and the plants sprayed with a short term insecticide. After the crop had ripened the total grain yield, the number of tillers and the average grain weight per cage was determined and the average number of grains per ear was calculated. On the total yield and on each of its three components an analysis of variance was made.

In 1977 another 2 trials were made likewise. One comprised 10 blocks with each 2 sub-blocks. A sub-block consisted of 2 plots of 6 x 5 m. Again per block one sub-block was treated with a fungicide. In each sub-block one plot was treated with the selective aphicide pirimicarb at the beginning of flowering and again 10 days later, to avoid a natural infestation with *S. avenae*. In the untreated plots the population development was established by counting the number of aphids on 10 ears per plot twice a week. To avoid migration and in case the natural population remained too low, another trial was set up in cages with artificial infestation. This would permit the calculation of the loss of dry weight of the plant according to biomass production by the aphids and their energy budget. The trial consisted of 8 blocks and again in each block one sub-block was treated with a fungicide at the beginning of flowering. A sub-block comprised 2 cages, one of which was infested before flowering with 100 4th instar nymphs and adults of *S. avenae* and the other remained uninfested. After 3 weeks 10 tillers per cage were examined for aphid and fungus infestation and for the percentage of physiological yellowing (Ubels & van der Vliet, 1979). These observations were also done in the full field trial.

4.3 RESULTS

4.3.1 Climate room trials

Using Perspex leaf and ear cages, the effect of *S. avenae* and *R. padi* on the yield of winter wheat cv. Clement was determined with a variation in the following factors: (a) infection site combined with the infection period (aphids on the flag leaf from Fe 10.1 to Fe 10.5.1, on the ear from Fe 10.5.1 to Fe 10.5.4 or from Fe 10.5.4 to Fe 11.1) and (b) the nitrogen dressing of the plant at 3 levels: 40, 50 and 60 mg of N/tiller. On an average in both aphid species, most biomass was produced on the ear during the 2 weeks the trial lasted: 60% more than on the flag leaf before flowering and 30% more than on the more developed ear. This had no demonstrable effect on the loss of yield. At the 3 N-levels the average kernel yield per ear was 1630 mg, 1810 mg and 1840 mg, respectively. This did not influence the aphid production or the loss in yield. Table 7 shows that aphid production in numbers was the same in both species, but that biomass production ($31.5\% \pm 1.5\%$ dry matter) of *S. avenae* was more than two times higher than that of *R. padi*. Nevertheless, no significant differences could be detected in the effect the two species had on the yield. Table 7 also shows that on an average in both species only the

Table 7. The effect of *S. avenae* and *R. padi* on the yield of winter wheat (cv. Clement) C = untreated; R = *R. padi*; S = *S. avenae*; RS = mean of R and S. The aphids were kept in cages around the flag leaf or ear during 2 weeks starting with 6 third stage nymphs per tiller. Data of C, R and S represent the mean of 162 tillers. One third of these had aphids on the flag leaf during Feekes 10.1 - 10.5.1, another third had aphids on the ear during Fe 10.5.1 - 10.5.4 and the remainder had aphids on the ear during Fe 10.5.4 - 11.1. LSD = Least Significant Difference ($p = 0.05$), only listed if exceeded according to the analysis of variance.

	Aphid production per tiller				Plant dry matter production per tiller in mg					
	number		dry matter in mg		number of kernels per ear		kernels per ear in mg		average kernel weight per ear	
	R	S	R	S	C	RS	C	RS	C	RS
mean	75	81	4.3	9.2	47.3	46.9	1800	1730	38.1	36.9
LSD			0.9						0.7	

mean kernel weight per ear had decreased significantly, namely with 3% by 78 aphids with a total dry weight of 6.8 mg. Per mg of aphid, loss of dry weight per ear was $\{(38.1 - 36.9) \times 46.9\} / 6.8 = 8.2$ mg.

In a second trial, using Perspex cages, the effect of *S. avenae* and *M. dirhodum* on the yield of winter wheat cv. Cyrano was studied with variations in infection site (flag leaf or ear) and in the period the infection took place (from Fe 10.5.2 to Fe 11.1 or from Fe 11.1 to Fe 11.2). On an average in both species, aphid production in the first infection period was 20% higher in numbers and 50% higher in biomass than in the second infection period. Nevertheless no effect could be found on loss of yield. Table 8 shows that *S. avenae* on the ear produced twice as much biomass as *S. avenae* and *M. dirhodum* on the flag leaf. The differences between these 3 treatments in quantities of dry matter extracted from the plant, were much less because *S. avenae* on the ear utilized its food better as was apparent from honeydew production. Perspex cages on the ear compared with cages on the flag leaf significantly reduced the number of grains/ear by 5% and the average weight of the grains by 7%. Similar to the previous trial, aphid infestation had no detectable effect on the number of grains per ear nor on the yield per ear. A 5% reduction in average grain weight occurred only when the ear was infested with *S. avenae*. Per mg of dry aphid matter, the loss of dry grain matter was $\{(37.9 - 35.9) \times 36\} / 8 = 9.0$ mg. *S. avenae* on the ear hardly reduced the amount of N per grain. It was striking that under the influence of aphid infestation, the dry weight of the infected leaf or ear (Table 8 columns 9 and 10) increased significantly. *M. dirhodum* and *S. avenae*, feeding on the flag leaf increased the dry weight of that leaf by 8 and 9% respectively, and *S. avenae* on the ear enhanced the dry weight of that plant part without grains with 9%.

In a third trial I determined the effect of *S. avenae* on the yield of winter wheat cv. Cyrano, when the aphids were allowed to develop on the ear during 4 weeks from Fe 10.3 to Fe 11.1. The ears were infested with 2 apterae per ear and no cages were used. In this trial again the influence of N dressing of the plant on the effect of aphid infestation was established. As basic dressing 30 mg of N per tiller (N1) was used. During the phase of stem extension the plants were given an extra dressing of 5 mg of N (N2) or 10 mg of N (N3). After the crop was harvested no significant differences in average yield of dry

Table 9. The effect of *S. avenae* on the yield of winter wheat (cv. Cyrano) at 3 levels of nitrogen dressing, (N1-N3). C = untreated; S = *S. avenae*. Aphids were kept on the ear during 4 weeks (Fe 10.5-11.1), starting with 2 apterae/ear. Data of C and S represent the mean of 144 ears. LSD = Least Significant Difference, only listed if exceeded according to the analysis of variance.

Level of nitrogen dressing	Aphid production in mg dry matter per ear		Number of kernels per ear		Dry kernels per ear in mg		Average kernel weight per ear in mg		N in kernels in %			N per kernel in mg	
	C	S	C	S	C	S	C	S	C	S	CS	C	S
N1	-	28	41.9	39.5	1500	1106	35.8	28.0	1.48	1.72	1.60	0.53	0.48
N2	-	32	36.3	38.6	1308	1020	36.0	26.4	1.61	1.86	1.74	0.58	0.49
N3	-	35	39.0	38.2	1341	995	34.4	26.1	1.85	2.06	1.96	0.64	0.54
mean	-	32	39.1	38.8	1383	1040	35.4	26.8	1.65	1.88		0.58	0.50
LSD mean	1.9		0.08				not analysed
LSD CS			0.14				not analysed

grain matter per ear nor in average grain weight per ear in the 3 N levels could be found. Table 9 shows that there was a significant difference in N content of the grains, where $N3 > N2 > N1$. Aphid production increased somewhat with the increasing amount of N, but this effect was not significant. The N dressing had no demonstrable effect on the damage which was 24% of the average grain weight. Aphid infestation had again no influence on the number of grains per ear. In a random sample I found that the average dry weight of the aphids was about 0.3 mg. Per mg of aphid production, the yield of dry grain matter per ear was reduced in the N1-3 levels with 11.- mg, 11.6 mg and 9.1 mg, respectively. Aphid-infested ears had an N content in the grains which was 14% higher than in the control. Consequently the reduction in the total amount of N per grain was limited to 13%. The speed with which the flag leaf yellowed was not influenced by aphid infestation.

4.3.2 Field trials

Table 10 shows the results of a trial in 1976. At Fe 10.1 eighty nylon gauze cages were placed in the crop distributed over 10 blocks. At the start of flowering half of each block was randomly treated with fungicides. Three days later each of the 4 cages in one half block received one of the following treatments; no aphids, *S. avenae*, *M. dirhodum* and *R. padi*. After 4 weeks, at the end of the milky ripe stage, the average aphid population had developed into 14, 154, 85 and 5 aphids per tiller respectively. Of these numbers 86%, 74%, 0% and 19% were present on the ear. The fungicide treatment did not seem to have demonstrably affected the ultimate number of aphids. During mass rearing in the laboratory an Entomophthora infection had developed in *R. padi*, which caused this species to remain at a very low level during the field trial. So low in fact, that it was not further involved in the observations. Of the 3 yield components, the number of ears per area, the number of grains per ear and the average grain weight, only the last one seemed to be influenced by the aphids. as was also found in the climate room trials. Over all plots, only *S. avenae* reduced the average grain weight significantly, by 9.5%. *M. dirhodum* and the fungicide had no detectable influence on the yield. There was a clear interaction between fungicide and aphid treatment. In the crop not treated with fungicide,

Table 10. 1976. The effect of *S. avenae*, *M. dirhodum* and *R. padi* on the yield of winter wheat cv. Caribo as influenced by fungicide treatment (maneb/carbendazim, 42.5%/6% a.i., 4 kg/ha). Round nylon cages (diameter 44 cm), 10 per aphid treatment, were placed over the plants at Fe 10.1. Plants were treated with TEPP at Fe 10.4, with fungicide at 10.5.1, and with 40 aphids/cage (4th instar larvae and adults) at Fe 10.5.2. After 4 weeks at Fe 11.1-11.2, cages were removed, aphids were counted and plants were treated with TEPP. Plants were harvested after ripening. Data represent the mean of 10 cages. Symbols used: F = treated with fungicide, OF = mean of untreated and treated with fungicide. LSD = Least Significant Difference, only listed if exceeded according to the analysis of variance

	Aphids per tiller		Dry kernels per cage in g		Tillers per cage		Kernels per ear		Average kernel weight in mg		% N in kernels							
	O	F	O	F	O	F	O	F	O	F	O	F	OF					
control	11	16	14	78.7	76.0	77.4	62.6	60.2	61.4	29.4	30.3	29.9	42.8	41.7	42.3	1.96	1.94	1.95
<i>S. avenae</i>	151	157	154	70.6	69.5	70.1	60.2	62.4	61.3	31.1	28.7	29.9	37.7	38.8	38.3	1.89	1.82	1.86
<i>M. dirhodum</i>	80	89	85	76.6	79.2	77.9	58.6	61.7	60.2	31.9	30.8	31.4	41.0	41.7	41.4	1.86	1.88	1.87
<i>R. padi</i>	3	6	5	80.4	77.5	79.0	64.5	63.2	63.9	29.5	28.8	29.2	42.2	42.6	42.4			
mean	61	67		76.6	75.5		61.5	61.9		30.5	29.7		40.9	41.2		1.90	1.88	
LSD OF	not analysed		4.9										1.0				0.07	
LSD O and F	not analysed												1.5					

S. avenae and *M. dirhodum* reduced the average grain weight significantly with 12% and 4% respectively. In the fungicide treated area the loss yield was 7% and 0% only. On the whole *S. avenae* and *M. dirhodum* reduced the N content of the grains by more than 4%. A random sample of 100 aphids from 3 cages showed that the average dry weight of *S. avenae* at the end of the trial was 0.20 mg. So in the fungicide treated crop an average of $0.74 \times 157 \times 0.20 \text{ mg} = 23.2 \text{ mg}$ of dry aphid matter had been developed. Corrected for the light infestation in the control, this figure becomes 20.8 mg. Yield loss was calculated to be 7% = 84 mg per ear. So per mg of aphid production on the ear, 4.0 mg of dry plant matter was lost. In the same manner I calculated that in the crop not treated with fungicides, 7.8 mg of dry plant matter was lost per mg of aphid production. Consequently the fungicides had reduced the losses per mg of aphids by 49%.

Table 11 shows the results of a trial in 1977. At Fe 10.1, forty nylon cages were distributed over 10 blocks. At Fe 10.5.1 half of each block was treated with a fungicide. At 10.5.2 one cage in each half block was infested with *S. avenae*. After 3 weeks at Fe 11.1, I found that in mean in the crop not treated with fungicide 165 aphids per ear had developed and in the treated crop 122 aphids. The number of aphids on the leaves was estimated to be 10 to 15 per tiller in average. Over the whole trial *S. avenae* signifi-

Table 11. 1977. The effect of *S. avenae* on the yield of winter wheat cv. Caribo, as influenced by fungicide treatment, (maneb/carbendazim, 42.5/6% a.i., 4 kg/ha). Round nylon cages (diameter 44 cm), 8 per aphid treatment, were placed over the plants at Fe 10.1. Plants were treated with TEPP at Fe 10.4, with fungicide at Fe 10.5.1 and with 100 aphids/cage (4th instar larvae and adults) at Fe 10.5.2. After 3 weeks, at Fe 11.1, cages were removed, aphids were counted and plants were treated with TEPP. Plants were harvested after ripening. The data represent the average of 8 cages. Symbols used: see Table 10.

	Production of <i>S. avenae</i> per ear			Dry kernels per cage in g			Ears per cage			Kernels per ear			Average kernel weight in mg		
	O	F	OF	O	F	OF	O	F	OF	O	F	OF	O	F	OF
control	-	-	-	96.9	92.4	94.7	45.5	44.1	44.8	44.2	44.0	44.1	48.2	47.6	47.9
<i>S. avenae</i>	165	122	144	93.0	95.4	94.2	46.9	43.4	45.2	45.5	47.6	46.6	43.6	46.2	44.9
mean				95.0	93.9	.	46.2	43.8	.	44.9	45.8	.	45.9	46.9	.
LSD mean					
LSD OF				.			.			.			1.6		
LSD O and F				.			.			.			2.3		

	Dry matter in mg of						Observation on diseases at Fe 11.1-11.2											
	ear without kernels			top internodium with flag leaf			% covered with black moulds			% dead or yellow								
	O	F	OF	O	F	OF	ear	flag	leaf	ear	flag	leaf	ear	flag	leaf			
control	465	462	464	542	526	534	2	0	1	2	2	2	18	17	18	37	35	36
<i>S. avenae</i>	482	499	491	546	560	553	17	7	12	22	12	17	12	12	12	30	33	32
mean	474	481		544	543		10	4		12	7		15	15		34	34	
LSD mean							3			3								
LSD OF			18				3			3			2					
LSD O and F						34	4			4								

cantly reduced the mean kernel weight with an average of 6.5% and fungicide treatment had no detectable effect. Again there was a clear interaction between fungicide and aphid treatment. In the fungicide treated crop *S. avenae* reduced grain weight by 3% only, but this figure is not significant. However, in the untreated crop *S. avenae* reduced grain weight significantly by 9.5%. In the crop not infested with aphids, fungicide treatment had no demonstrable effect. It did enhance grain weight significantly by 6%, however, in aphid infested crop. On the whole, aphid infestation caused a significant increase of 6% in the dry weight of the ear without grains. In the fungicide treated crop aphid infestation also caused a significant increase of 6.5% in the dry weight of the top internode (peduncle) plus flag leaf.

At the end of Fe 11.1, it appeared that the aphids strongly had enhanced the development of black mould on flag leaf and ear and that the fungicide had reduced it. The two treatments obviously interacted. The fungicide reduced the black mould significantly in the presence of aphids only. The average dry weight of *S. avenae* at the end of the trial was 0.09 mg, calculated from a random sample of 100 aphids taken from 5 cages. So in the fungicide-treated crop an average of 11.- mg of dry aphid matter per ear had been developed, which led to a loss in yield of 3% = 56 mg per ear. This implies that per mg of aphid production on the ear, 5.1 mg dry grain matter was lost. In analogy it was calculated that the corresponding figure in the untreated crop was 12.3 mg, so the fungicide had reduced the losses per mg of aphids by 58%.

Table 12 shows the results of a field trial in 1977. The experimental design was similar to the one described previously. At Fe 10.5.1 half of the plot was treated with an aphicide against natural populations of *S. avenae*. At this time there was an average of only 2 aphids per ear. At the beginning of Fe 11.1 the population in the untreated plot reached a maximum of 15 aphids per ear in the crop without fungicide and 9 aphids per ear where it had been treated with a fungicide. This significant difference suggests aphicidal properties of the fungicide, which is also found by Vickermann (1977). Over all

Table 12. The effect of *S. avenae* on the yield of winter wheat cv. Caribo, as influenced by fungicide treatment, (maneb/carbendazim, 42.5%/6% a.i., 4 kg/ha). Net plots: 6 x 5 m. Data represent the mean of the 10 replicates per treatment. Fungicide treatment at Fe 10.5.1. Aphicide treatment at Fe 10.5.1 and Fe 10.5.4. Symbols used: see Table 10.

	Max. number of <i>S. avenae</i> /ear			Dry kernels in kg/ha			Average dry weight of kernels in mg			Observations on diseases at Fe 11.1-11.2											
										% covered with black mould						% dead or yellow					
										ear		flag leaf		ear		flag leaf					
O	F	OF	O	F	OF	O	F	OF	O	F	OF										
control	15	9	12	4325	4500	4415	38.3	40.8	39.6	3	1	2	4	2	3	7	7	7	34	27	31
pirimicarb	-	-	-	4410	4725	4570	41.4	41.9	41.7	0	0	0	0	0	0	7	7	7	30	25	28
mean				4370	4615	.	39.9	41.4	.	2	1	.	2	1	.	7	7	.	32	26	.
LSD mean						
LSD OF				.			0.9			1		1				.		.			
LSD O and F 5				.			1.3			2		2				.		.			

plots the fungicide treatment had no significantly positive effect on the average grain weight (3.5%), contrary to aphicide treatment (5.5%). Fungicide and aphicide influenced each other again. In plots where no aphicide was used, fungicide treatment did result in a significant increase in yield (6.5%) and where fungicide was used, aphicide treatment could not enhance yield significantly (2.5%).

At the end of Fe 11.1 I found again that the development of black moulds was clearly stimulated by the aphids. Where no aphicide was used the fungicides restrained the development of the black moulds significantly.

The fungicide reduced the loss in yield by 65%. Corrected for the slight insecticidal action of the compound used, the reduction in loss per mg of aphids amounted to 44%.

4.4 DISCUSSION

4.4.1 *The three components of yield*

In western Europe, *S. avenae*, the most numerous aphid species in cereals, usually attains economically important numbers only after flowering of the crop (Dean, 1974a; Latteur, 1976; Breniaux et al., 1976; unpubl. pers. obs.). From trials with winter wheat in the open field and in climate rooms, it was found that in this phase of plant growth, the aphids can only cause a decrease in average grain weight and not in numbers of grains per ear nor in numbers of tillers per area. This agrees with the results of Wratten & Redhead (1976) and Freier & Wetzell (1976). However, Rautapaa (1966) and Hinz & Daebeler (1976) found in field trials with *S. avenae* in cages and on encaged ears, that because of infection from the time the ears appeared or from the time the flowering started, the number of grains per ear was also reduced in winter wheat. It seems to me that they kept the aphids for such a long time in the cages preventing emigration, predation and parasitization, that their numbers reached unnaturally high levels, causing a reduction in yield between 40% and 90%. With such a severe loss in yield an important part of the grains is so small that it is lost during harvesting. Possibly also abortion of seeds took place by such a heavy nutrient drain.

Still, I noticed that in practice a moderate attack by *S. avenae* may cause loss of grains on an indirect manner. When kernel weight is lowered some 5% to 10% by the aphids and the crop is not very dry yet the combine harvester may lose an important fraction of the minor grains.

4.4.2 *N content of the wheat*

The N content of wheat grains is important to its baking quality. Wratten (1975, 1976, 1978) found that infestation of leaves below the flag leaf, where in the field mainly *M. dirhodum* is involved, can reduce the N content of the grains. According to this author, the loss of N as a result of sap uptake by the aphids is detrimental to the transport of N to the grains. Moreover, the uptake of N from the soil is limited as a result of premature senescence of the infected leaves. (In my opinion this only happens when predation, parasitization and migration are prevented by cages and the

aphids reach abnormally high numbers.) Transport of carbohydrates to the grains is not inhibited by this kind of infestation because it takes place from the flag leaf, peduncle and ear (Thorne, 1974; Yoshida, 1972). So only infestation of the lower leaves leads to a reduction of the N content of the grains. In the opinion of Wratten, infestation of flag leaf and ear, where in the field mainly *S. avenae* is involved, keeps the N content of the grains steady because the uptake of phloem sap by the aphids equally reduces the flow of carbohydrates and N compounds to the grains. This does not explain the increase in N content that Wratten sometimes found. Sofield et al. (1977) showed that during the first days of grain growth, the ratio of incorporation between N compounds and carbohydrates is clearly higher than in the subsequent period. In grains collected 1 week after flowering, I found indeed a N content which was 40% higher than that in grains a week older. These results are understandable when one realises that the peripheral layers of the grain, especially the aleuron layer and the outer part of the endosperm, which are first filled up, have a much higher N content than the centrally located endosperm (Pomeranz, 1972). With an ear infestation most of the dry matter will be withdrawn during the milky ripe stage because at that time the aphids will have attained their highest numbers. As the growth of the central endosperm will then especially be limited, the N content of the infested grain will remain higher than that of the uninfested grain. A climate room trial showed indeed that the development of 105 specimens of *S. avenae* on the ear in the period from Fe 10.3 to Fe 11.1, limited the accumulation of dry matter in the endosperm to such an extent (24%), that the N content of the resulting grain was 14% higher than in the control (Table 9). An infestation of the flag leaf after flowering by 65 specimens of *M. dirhodum* and 38 of *S. avenae* and an infestation of the ear by 67 *S. avenae* did not have a detectable effect on the N content (Table 8). In this trial the average grain weight was almost equal to that of the control. In a field trial (Table 10) it was found that an infestation of 155 specimens of *S. avenae* and 85 of *M. dirhodum* per tiller, of which numbers 25 and 100% were present on the leaves, reduced the N content significantly by about 6%. The average grain weight was reduced by 9.5 and 2% respectively. These results agree with those found by Wratten. The economic importance of *M. dirhodum* emphasized by this author, however, should not be overestimated. To reduce the protein content of the grains from 11% to 10% some 70 aphids should be present per tiller (Wratten, 1975), a population level I seldom observed or heard of in the Netherlands during the past 5 years.

4.4.3 Time and site of infection

It could not be concluded from the trials, that from Fe 10. on, the character and rate of loss in yield depends on the period in which the infection occurs. It is clear, however, that ear infection leads to heavier damage than flag leaf or leaf infection (Tables 8 and 10). Wratten (1975, 1976, 1978) concluded already that flag leaf and ear infection give rise to higher losses than infections on other leaves. This is easy to understand if the opinion of the plant physiologists is taken into account, that the dry grain matter is mainly produced by flag leaf, peduncle and ear. Why then does flag leaf infection result in less loss of yield than ear infection? Rawson & Evans (1970) found

that sterilization of florets in the middle spikelets led to larger number of grains per ear, bigger grains in the upper and lower spikelets and a markedly improved yield per ear. According to these authors the grains in the middle spikelets would adversely influence the formation and size of the other grains because they develop sooner and more quickly. They found that assimilates from the flag leaf accumulate especially in these grains. In my opinion uptake of phloem sap from the flag leaf could also have a beneficial effect on the growth of the grains in the upper and lower spikelets, which could compensate for the loss in weight of the grains in the middle spikelets.

4.4.4 Nitrogen dressing

In Section 2 it was concluded that extra N dressing leads to larger numbers of aphids because wing formation is reduced and maybe also because the plant ages less quickly, provided fungicide application checks the development of fungi. Moreover, the efficiency of food utilization of *S. avenae* on the ear increases with the extra nitrogen dressing. From the current research it could not be concluded that the N dressing influences the rate of loss in yield. It should be kept in mind, however, that it was not possible to obtain a significant rise in yield in the climate room with an extra N dressing, due to sub-optimal light intensity.

4.4.5 Aphid species

In the only trial where *R. padi* and *S. avenae* were compared, no difference in their effect on yield was found (Table 7). There was also no detectable difference between *M. dirhodum* and *S. avenae* in their effect on yield, when the flag leaf was infested (Table 8). It seems that *M. dirhodum* causes some damage only when at least 50 aphids have developed per tiller and the crop has not been protected with a fungicide against growth of fungi on honeydew (Table 10).

4.4.6 Honeydew damage

From the results of 3 field trials it was concluded that 49%, 59% and 44% of the losses were caused by fungi growing on honeydew which could be prevented by treatment of the crop with a fungicide (Table 10-12). In particular fungi of the so called black mould complex thrive on honeydew. Laboratory research of Ubels & Fokkema (unpubl. results) showed, however, that *Septoria nodorum* and red and white yeast also grow well on honeydew.

In 1976 it rained only 1 day in the period flowering until mealy ripe, so all honeydew remained on the leaves, whereas in 1977 it rained frequently in the same period and hardly any honeydew on the leaves was visible. Notwithstanding this and the fact that in 1976 3 times as many aphids developed per tiller as in 1977, the relative as well as the absolute share in the damage of fungal growth on honeydew remained almost the same (Table 10 and 11). In 1976 honeydew was strongly crystallized, covering only a small part of the leaves. On the crystals no black moulds developed. In 1977

honeydew possibly remained on the plant as a thin film, especially on the remote parts where its concentration was high enough to promote attachment and germination of spores and the first growth of mycelia. Honeydew and fungi covering green area, could lower the photosynthetic rate by reflection and absorption of radiation and by reduction of transpiration and carbon dioxide diffusion via the stomata, due to the high osmotic value of the honeydew which may cause loss of turgor or even plasmolysis and necrosis of plant cells. Water stress, hot and sunny weather and the activity of microorganisms on the leaves damaging cuticula and epidermis could enhance the latter effect. Through the developing lesions fungi could furthermore penetrate into the plant. The final result of all these actions would be that honeydew in combination with fungi also reduces leaf area duration.

Feeding on the ear, *S. avenae* can shoot away its honeydew pellets over 4-8 cm. Based on an average of 500 tillers per m^2 , which stand in rows lying as distance of 25 cm from each other, an estimated 30% of the honeydew drops on the ear, 35% on the flag leaf, 20% on the second leaf and 10% on the third leaf. Honeydew damage by *M. dirhodum* seems less important since this aphid mainly feeds at the bottom of the second, third and fourth leaf.

4.4.7 Feeding damage: stylet insertion, saliva injection and sap uptake

From 3 field trials (Tables 10-12) it can be concluded that at the current level of yield, damage caused by feeding is about as important as damage caused by fouling the plant with honeydew which stimulates the development of fungi. From laboratory trials it could be deduced that, depending on the N content of the grains which was in these cases 1.51%, 1.57% and 1.81%, *S. avenae* took up 7.1 mg, 5.9 mg and 5.3 mg of dry phloem sap matter per mg of aphid production (Chapter 2). In 3 climate room trials (Table 7-9) where grains of the control plants contained 1.61%, 1.54% and 1.65% N, the loss in yield per mg of aphid production of *S. avenae* on the ear was 8.2 mg, 9.0 mg and 10.6 mg of dry matter respectively. So the losses were about 50% higher than was expected from the efficiency of food utilization of the aphids. In 2 field trials (Tables 10 and 11) where the crop was treated with a fungicide and the grains from control plants contained 1.94 and 1.74% N, the loss in yield caused by *S. avenae* infestation on the ear was, based on dry matter, 4.0 and 5.1 mg per mg of aphid production. These losses agreed with those expected from the efficiency of food utilization of the aphids. These results justify the conclusion that stylet insertion and saliva injection by *S. avenae* do not markedly influence the physiology of the grains. It was remarkable, however, that after ripening the infected leaves and ears (without grains) had a higher dry weight than the controls (Tables 8 and 11). Wratten (1978) found that infected leaves had a higher N content at death. This may be caused by a stagnation in the phloem transport as a result of plugging of the sieve plates of punctured sieve tubes (Evert et al., 1968) or by the stimulating effect of aphid saliva on the growth and differentiation of plant cells (Miles, 1968).

5 QUANTITATIVE ASPECTS OF ATTACK BY *SITOBION AVENAE* F. AND ITS EFFECT ON YIELD; THEIR RELEVANCE TO SUPERVISED AND INTEGRATED CONTROL

5.1 INTRODUCTION

Ecologically a crop forms with its pests and diseases, as well as their antagonists, parasites and predators one dynamic biosystem, which, in turn, is in close relation with the cultural conditions.

In the latter, climate and soil are combined with cultural practices to form a complex, which is subject to manipulation. From this point of view the concept of integrated control has been developed (Stern et al., 1959). It is based on the idea that regulation of pests and diseases first of all can and should take place by the plant itself, by antagonists, pathogens, parasites and predators and also by the use of appropriate cultural techniques: choice of crop and variety, crop rotation, soil cultivation, sowing date, quantity of seed, quality and quantity of manure etc. Chemical control is only allowed as a last resort, on the condition that the chemical spares as much as possible the natural limiting factors of the harmful organism.

On the base of early research data the gap between preventive chemical control and integrated control can be bridged by a system of supervised control. This can briefly be characterized as chemical control guided by experts, aiming at the use of chemicals in the most efficient way.

In both supervised and integrated control the use of the chemical should be based on a good understanding of the phenology of the insect and on a prognosis of its population development and the damage it may cause. A scheme of regular observations on the population dynamics of the pest is required. In case of an integrated control programme, the population dynamics of parasites and predators have to be included. The decision to spray is taken as soon as the population reaches the economic threshold, i.e. the population level, resulting in economic injury to the crop. Economic injury is the damage, expressed in terms of money, clearly higher than the costs of a control treatment (costs of the chemical, application and possible damage by the treatment).

The purpose of the present work was to develop a system of supervised control of cereal aphids, especially *S. avenae* in winter wheat. A prerequisite to the successful introduction of such a system in practice is that it fulfils the following demands: it has to offer the growers clear advantages over applying an insecticide prevently in combination with a routine treatment with fungicides, there must be no risk for important economic damage and the method of observation has to be simple and not time consuming. On meetings and in professional magazines of growers and the extension service I mentioned the advantages of supervised control; the development of great numbers of polyphagous natural enemies also reducing the need for control in other crops, less chance for resistance of the pest against the insecticides and for an explosive increase in the

number of aphids in prematurely treated fields. These positive effects balance the possible extra costs.

To meet the grower's demands, it was necessary to study extensively the relation between attack and damage and to find safe and quick methods of observation, warning and control.

5.2 TRIALS AND RESULTS

5.2.1 Methods in observation and warning

Attack by cereal aphids can be quantified on several ways. A field trial was set up to find a both quick and reliable method. Its results are summarized in Table 13. The mean dry grain weight per tiller of 100 tillers kept aphid free with pirimicarb was 42.1 ± 1.8 mg which was 6% higher than the weight of the infected tillers. Because the average effect of the aphids was hardly bigger than the random variation in yield per tiller, little coherence was found between attack and yield. The numeric integral of the population level in the course of time showed the poorest correlation. Probably this was due to predation by syrphids and coccinellids which were present in large numbers especially just after the aphid populations had reached their peak. Predators and traces of predation were present at that time in more than half of the ear colonies. For the ears where predation had taken place the integral calculation underestimated the intensity of attack, whereas the maximum number was much less influenced by predation. It is obvious from Table 13 that this parameter correlated most with the yield. The maximum biomass correlated less because it is a more momentary observation and consequently less representative for the population development than the maximum number. The maximum number per tiller was not more correlated with the yield than the maximum number per ear, because leaf infestation was relatively low and moreover leads less quickly to damage than ear infestation (Chapter 4).

In the Netherlands a warning system has functioned from 1974 on. Every year time

Table 13. Correlation between mean dry grain weight per tiller of 40 tillers of winter wheat cv. Caribo and different parameters for the intensity of attack by *S. avenae* and *M. dirhodum*. Population development including age distribution of the aphids was observed twice a week from Fe 9 till Fe 11.2. On the base of laboratory observations the biomass of the 4 nymphal stages and adults was determined at 0.1 mg, 0.2 mg, 0.4 mg, 0.8 mg and 1.0 mg respectively. Numeric integrals were calculated with a computer following time steps of 1 day. After ripening the mean dry grain weight per tiller was established, averaging 40.2 mg over the 40 tillers with a standard deviation (SD) of 2.1. All correlations were significant at 5%.

Intensity of attack parameter	Coefficient of correlation with		
	mean per tiller	SD	mean dry grain weight per tiller
maximum number on the ear	51 aphids	36	-0.45
max. number on ear and leaves	64 aphids	38	-0.46
max. biomass on the ear	21 mg	13	-0.39
max. biomass on ear and leaves	25 mg	15	-0.38
numeric integral numbers on ear	520 aphid days	370	-0.35
num. int. numbers on ear and leaves	685 aphid days	405	-0.33

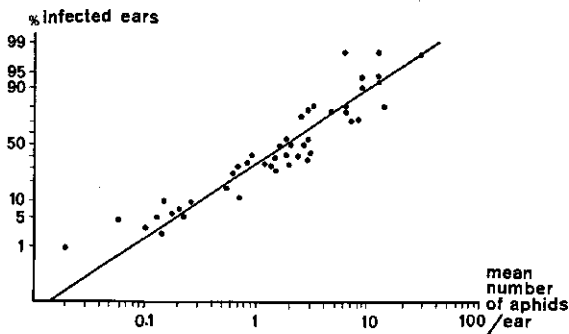


Fig. 12. The percentage of infected ears as a function of the average number of aphids/ear before the population maximum. Correlation coefficient $R = 0.94$. Regression formulas; $\text{probit } y = 1.58 + 1.52 \log 100 x$, $\log 100 x = -0.69 + 0.59 \text{ probit } y$. Calculations were made on 49 samples of 100 ears, taken in the years 1973-1977.

and intensity of infestation appeared to differ strongly from region to region, probably because of differences in climate and landscape. However, also within the various regions large differences were found, even between adjacent fields. So factors like site of the field, variety of wheat and fertilization could also play a role. These facts emphasize the importance of the regionalization of the warning system and of the principle that after a warning the intensity of attack in each field ought to be determined before a decision regarding control is taken. In each region of 10-30.000 ha wheat about 10-30 well distributed fields are sampled weekly from the moment the ears become visible. Regional specialists from the extension service count in every field the aphids on 25 ears taken at random. The size of the samples is based on the available time and manpower.

The call to the growers to inspect the crop before starting to spray, which was broadcast together with a radio warning, seemed not to have had the expected result. A large part of the growers considered counting aphids on 25 ears per field too difficult and time consuming. These objections could be met by relating the current threshold of control of 15 aphids per ear to 95% of the ears infected. This new criterion is based on the strong correlation ($r = 0.94$) between the mean number of aphids per ear and the percentage of infected ears, which was found in 49 samples of 100 ears per field taken in the years 1973-1977 (Fig. 12).

5.2.2 The effect of chemical control on yield

Between 1973 and 1977 eleven trials were performed to investigate the benefit of control with the selective aphicide pirimicarb, which is recommended by the extension service and increasingly used by the growers. A trial comprised 10 blocks of 2 fields each, one of which was kept aphid free. In the untreated fields the ear infestation was determined weekly. The difference in yield between treated and untreated was well correlated with the maximum number of aphids per ear during the milky ripe stage ($r = 0.61$) contrary to the number of aphids at the start of flowering ($r = 0.04$). This population was not connected to the maximum number 3 or 4 weeks later ($r = 0.06$) because of the varying influence of climate, migration and natural enemies. The correlation between

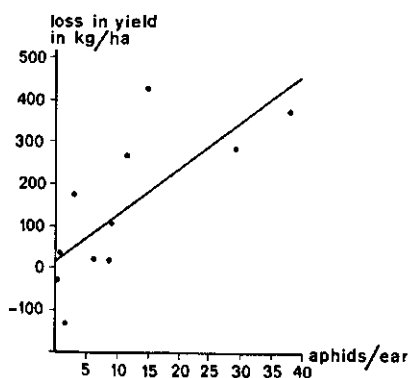


Fig. 13. The loss in yield as a function of the peak number of aphids per ear. Correlation coefficient $r = 0.75$. Regression formula; $y = 15.51 + 10.97 x$. Calculations were made with the results of 11 trials, done in the years 1973-1977. A trial comprised 10 blocks of 2 plots of which 1 was kept aphid free by 1 or 2 treatments with a selective aphicide. Aphid population development in untreated plots was followed weekly by random sampling 10 ears per plot.

attack and yield was considerably higher ($r = 0.75$, see Fig. 13) when it was not expressed as the mean difference in total yield in kg/ha between treated and untreated fields, but as the mean proportional difference in average grain weight multiplied by the average total yield in kg per untreated ha. In Chapter 4 it has already been shown that the average grain weight is the only component of the total yield that is normally influenced. So, the increase in correlation is due to the loss in random variation, caused by differences in the number of ears per area and the numbers of kernels per ear.

5.3 DISCUSSION

5.3.1 Methods in observation and warning

Rautapaa (1966) and later Latteur (1976) expressed the intensity of attack in the so-called aphid-index, which is the numeric integral of the number in course of time. Table 13 demonstrates that this parameter correlated less with yield than the maximal number of aphids per ear, which also in the 11 trials with pirimicarb was well correlated with the loss in yield ($r = 0.75$, Fig. 13). If in these trials the intensity of attack was expressed in the aphid-index, the correlation coefficient remained the same. Latteur (1976) found in 32 trials with the aphicide menazon, that the aphid-index calculated on the numbers of *S. avenae* on the ear was obviously related with loss in yield ($r = 0.74$). From his data, however, I could calculate that the maximal numbers per ear were equally well correlated to the loss in yield ($r = 0.73$). Based on these considerations it seems to me that the maximal number per ear is a more suitable parameter for aphid attack than the aphid-index. The maximal number does not have to be calculated and is equally accurate.

Because a clear relation could be demonstrated between the percentage of ears colonized by *S. avenae* and the average size of the colonies (Fig. 12) the threshold of

control of 15 aphids per ear could be replaced by 95% of the ears infected, which is more easily and quickly determined and as such more acceptable to the growers. As the method is quick, the sample size can be brought from 25 to 50 ears per field which enhances the reliability of the estimates. Fig. 12 also shows that there is still a considerable variation in the relation between the two parameters: for example the number of aphids per ear corresponding with 90% of the ears infected may vary from 6 to 20 approximately. Since the regional warnings are based on the average of 10 or more observations, this variation only plays a role with the observations by the individual growers. In my opinion it is of relative importance as the numbers per ear may double in 3 days (Chapter 3), the growers generally count inaccurately and the benefit of control depends less on the number of aphids at the time of spraying than on the further increase of the aphids in case the crop was not sprayed !

Freier and Wetzel (1978) also found a clear correlation ($r = 0.89$) between the percentage of colonized ears and the average colony density. Their results are in a long range of infestation in marked agreement with ours (Table 14). From our analysis it seemed that a sigmoid curve represents the relation best. Above the level of 5 aphids per ear Freier & Wetzel disposed of relatively little observations and supposed that the relation kept being purely exponential, so from here their results diverge increasingly. The growing divergence of the results of the Dutch extension service from ours is probably based on the phenomenon that less experienced observers are more likely to underestimate the numbers the higher they become. Nevertheless, Table 14 demonstrates clearly, that in the relevant range of infestation the percentage of colonized ears is on average a reliable indication of the number of aphids per ear.

Because infestation varies strongly from region to region and even within the regions from field to field the warning system is regionalized and with every warning the farmers are asked to check their fields first before they decide to spray. For the same reason it could be useful to warn even when the control threshold is reached in only half of the observation fields. This reduces the chance that the worst infected fields are treated too late. Moreover, the growers will be less inclined to spray without a preceding observation.

Table 14. The average number of *S. avenae* per ear as a function of the percentage of infected ears, a comparison of the results from 3 sources of observation. Sample size was 50, 100 and 25 ears respectively. The number of samples was 296, 49 and 212 and the coefficient of correlation was 0.89, 0.94 and 0.83 respectively.

Percentage of infected ears	Freier & Wetzel (1978)	Author (Fig. 1)	Dutch extension service (De Boer, unp. res.)
50	2.2	1.8	1.6
60	2.9	2.6	2.1
70	3.8	3.7	2.9
80	4.8	5.7	4.3
85	5.3	7.5	5.4
90	5.9	10.4	7.1
95	6.5	16.9	10.9

5.3.2 Economic injury and economic threshold

In general a threshold of control of 15 aphids per ear is recommended in western Europe, which is mainly based on the work of Latteur (1976). He considers control only justified if aphids threaten to cause a damage of at least twice the costs of control because normally in his country the capital output in wheat is two times as large as the input. Thus he states that in Belgium the economic damage varies between 260 and 570 kg/ha, depending on the costs of control. A statistic model allowed him to calculate for infestation during the watery ripe stage, the probability of a population development resulting in economic damage. He found that in 50% of the cases populations of *S. avenae* consisting at this stage of 6 to 18 specimens per ear exceeded the lower or upper threshold of economic damage. On these grounds he has put the economic threshold at 15 aphids per ear. This is somewhat above average, but it enhances the chance for a remunerative control. Some points in Latteur's ideas are debatable. The tremendous variation in the effect of the aphids is not taken into account. He states that a loss of 570 kg/ha is caused by an aphid-index of 280, but it seems from his data that this infestation leads to a loss of 570 ± 340 kg/ha ($p = 0.1$). Not many growers will accept such a risk. Current practice in chemical control shows that most growers prefer to invest a relatively small amount of money with the chance to lose it partly or all, than doing nothing with the chance of losing a multiple of this amount. Another point is, that many growers are content with a lower ratio between output and input and will consequently put the economic threshold at a much lower level. For this reason the economic threshold in Great Britain (George, pers. commun.) and in the D.D.R. (Wetzel et al., 1978) has been put at 5 aphids per ear. In the D.D.R. it is raised to 8 aphids per ear during the milky ripe stage. The threshold of control in the Netherlands was rather arbitrarily put at 10 aphids per tiller in 1974 and was at my proposal increased to 15 aphids per ear in 1976. It appeared from the available data that such an infestation causes a loss in yield that stays within the limits of the costs of control equalling 100-250 kg/ha. Fig. 13 shows that 15 aphids per ear cause a damage of 180 ± 230 kg/ha ($p = 0.1$), which is estimated to be reduced by 50% however, if the crop is treated with fungicides before flowering (Chapter 4). In our experience this level of infestation would normally not be reached, so this threshold of control would strongly reduce the use of insecticides.

In my opinion no real economic threshold can be drawn at the moment, because population development and subsequent damage can as yet not be predicted accurately. Possibly simulation models like that of Rabbinge et al. (in press) will provide such predictions in the near future. In particular the damage needs much more research. Its strong variation appears from the fact that *S. avenae* populations with a maximum number of 15 per ear cause a loss in yield of 460 ± 340 kg/ha ($p = 0.1$) according to Latteur (1976) and 180 ± 230 kg/ha ($p = 0.1$) according to us (Fig. 13). The 3 main causes for this discrepancy are in the first place that the regression is calculated over a limited number of observations. In the second place the maximal number of aphids per ear is just an estimate of the number of aphids that really develop to the detriment of the yield. In particular migration, parasitism and predation cause a variable

number of aphids to elude observation. The most important cause in my opinion is that the damage per aphid is not constant. The damage resulting from feeding is usually slight and more or less stable (Chapter 4), but the effect of honeydew seems highly variable. Theoretically honeydew in combination with fungi can reduce the rate of photosynthesis, the available green area and the duration of this area. Since also factors like variety, availability of water and minerals, weather and attack by diseases influence these yield determining magnitudes, the honeydew damage depends on the time and the intensity with which it and the other stress factors occur. It can be readily supposed that the honeydew damage is maximal when the other production limiting factors are absent. This was indicated by the results of a team of Dutch researchers investigating the possibilities to bridge the gap between the average yield in practice of 5.5 t/ha and the potential yield of approximately 10 t/ha of winter wheat. Two field trials in 1978, a year when stress factors as drought, heat, lodging or diseases were on the whole unimportant, yielded each 7 t/ha without any use of pesticides. Owing to the cold and wet weather *S. avenae* developed slowly and just reached a moderate maximum number of 12 and 20 per ear (Mantel, pers. commun.) However, in the plots kept aphid free with pirimicarb yield was 1.4 and 1.1 t/ha higher (de Vos, pers. commun.)! In present-day crops honeydew action normally coincides with a number of other production reducing factors, so its ultimate effect is limited (Chapter 4 and Fig. 13). When in the future growing techniques, especially control of diseases are optimized, the mean production level will rise considerably and grain aphids will undoubtedly become more important. Not only because they remain one of the last yield reducing factors, but also because they will have the chance to reach higher numbers in these long-growing and highly productive crops. Moreover, a species like *M. dirhodum*, which is still relatively unimportant in our regions, may also reach a pest status because it seems to favour crops with high densities of tillers and leaves. In 1978 Rijdsdijk (pers. commun.) found in a sample of 120 wheat fields with an average yield of 7.4 t/ha that in some 15% of the fields an insecticidal treatment was combined with the routine application of fungicides before flowering which lead to a mean increase in yield of almost 1 t/ha. Considering the fact that the maximum number of aphids per ear was 0 to 20 (Mantel, pers. commun.) it must be concluded that the current threshold of control of 15 aphids per ear is too high. The only solution seems to be to lower the threshold of control to reduce the risk for serious yield loss. In my opinion a threshold of 80% of the ears infected, equalling an average of 5 aphids per ear will be satisfactory for the period before the milky ripe stage. After that the threshold must be raised to 90% of the ears infected, equalling a mean of about 10 aphids per ear (Table 4). A threshold of 5 aphids per ear during the stage of milky ripe will be exceeded almost every year over the whole country and will certainly bring most growers to the conclusion that they might as well mix the insecticide with the fungicide. This will enhance the risk of reinfection and the need for a second treatment. It may also lead to resistance of the aphids and increase of other noxious insects, because natural enemies are wiped out over large areas.

1978 also showed that it is too risky to count on the collapse of the aphid populations around the middle of the milky ripe stage (Chapter 3) and to advise a-

gainst control from then on. Migration of alatae appeared to be reduced by the long period of cold and wet weather and since crop development was also retarded the aphid populations kept increasing until the end of the milky ripe stage. Possibly also wing induction was reduced in these exceptional circumstances. Still it seems useful to avoid treatments against populations which are near their top or are already declining, because they are a waste of money and lead to the well-known side effects. Therefore, treatments from the time the third and second leaf start yellowing are ill-advised, as at that time one can be sure that the productivity of the crop is rapidly decreasing and aphids will not be able to increase much more.

Current results suggest that *Sitobion avenae* is the most injurious cereal aphid species as a consequence of its strong preference for the ear in contrast to the other two species. The high nutrient value of the phloem sap in the rachis enables *S. avenae* to multiply at a higher rate than the others, which explains why it is generally the most numerous species in wheat. Secondly, infestation of the ear leads to loss in yield at lower aphid densities than infestation of the leaves. Thirdly, the honeydew excreted by *S. avenae* is mainly deposited on the ear and upper leaves, which are the very organs to produce the dry matter for the kernels. Honeydew caused in three field trials about half of the damage by stimulating fungal growth.

After correction for the fungus effect, the established losses caused by *S. avenae* feeding on the ear did not differ much from those calculated on the basis of its energy budget. Therefore, it was concluded that stylet insertion and saliva injection have no important influence on the growth of the grains.

Until 1978 I assumed that the damage by *S. avenae* was more or less predictable based on biomass production and efficiency of food utilization. The fungus effect could be neglected because a fungicide treatment of the wheat at the beginning of flowering was a routine measure in the Netherlands. The results of a Dutch research group on the improvement of wheat yield (de Vos, pers. commun.) and the results of the Dutch growers in 1978 (Rijsdijk, pers. commun.) changed my point of view. For the first time I was confronted with crops that did not ripen prematurely under the influence of diseases, heat or lack of minerals and water and thereby yielded 2-3 t/ha more than the average 5-6 t/ha. Only in these long living crops honeydew was allowed the time to realize its full yield-reducing capacity, considering the unexpected high losses caused by but moderate infestations. This effect suggested that honeydew has also a direct effect on production. In my trials with the usual crops the honeydew effect was apparently neutralized for the major part by the combined effect of various other yield-depressing factors.

The conclusion is that aphid damage is interrelated with a complex of other stress factors. This implicates that the damage will only be predictable if except aphid population development also crop growth can be predicted, depending on factors such as availability of water and minerals, weather, diseases and honeydew. The simulation model approach seems very promising in forecasting but is still lacking much quantitative information.

Growing techniques are improving rapidly and so is yield. Consequently, an increasing significance of honeydew can be expected. Therefore, I finally suggest that the current criterion of control should be lowered from 15 aphids per ear to 5 and 10 aphids per ear equalling 80% and 90% of the ears infected for the period before and during the

milky ripe stage, respectively. Until the above models are available, this advice may serve as a preliminary compromise with the demand of the growers, not to risk a serious loss in yield and the demand of the environment to make minimal use of pesticides.

SUMMARY

Influence of the host plant on the population development of Sitobion avenae F., Metopolophium dirhodum Wlk., and Rhopalosiphum padi L.

In trials in a climate room the population development of 3 cereal aphid species on wheat was studied from the time the ear became visible. At the same time the possible influence of flag leaf and ear as substrate, the age of the plant and nitrogen dressing was established. Special attention was paid to the efficiency of food utilization by *S. avenae*.

Before the milky ripe stage, *M. dirhodum* multiplied on the flag leaf in numbers twice as quickly and in biomass 3 times as quickly as *S. avenae* and *R. padi*. On the ear, however, *S. avenae* multiplied twice in numbers and more than 3 times in biomass more quickly than on the flag leaf. On the ear *R. padi* multiplied in biomass less than half as quickly as *S. avenae*. In the course of the milky ripe stage, the multiplication rate on the flag leaf decreased strongly with *M. dirhodum* and hardly changed with *S. avenae*. On the ear, the multiplication rate decreased both with *R. padi* and with *S. avenae*, but with *R. padi* the decrease was stronger. In the second half of the milky ripe stage, the multiplication rate of *S. avenae* on the ear had diminished by half.

In *M. dirhodum* and *R. padi* alate production in reaction to crowding was less rapid than in *S. avenae*, which produced alatae sooner on the flag leaf than on the ear. Nymphal mortality in *M. dirhodum* and *R. padi* was twice as high as in *S. avenae*.

On the flag leaf, *S. avenae* produced 2 to 3 times as much honeydew as on the ear. Of the nitrogen, phosphorus and potassium present in the food, nitrogen was utilized best: for 65% from the flag leaf sap and for 83% from the rachis sap. In view of the energy budget of *S. avenae*, it was estimated that for the production of 1 mg of aphid, 5 mg of phloem sap from the ear and 11 mg of phloem sap from the flag leaf was needed, based on dry matter. Based on caloric value, 29% and 13% of this sap would be converted into aphid dry matter, respectively. *M. dirhodum* feeding on the flag leaf, utilized its food about as efficiently as *S. avenae* at the same feeding site. Efficiency of food utilization by *S. avenae* on the ear increased and alate production and consequently migration decreased, when the plant was given an extra nitrogen dressing. Though there was also a rise in mortality, the increase in the number of apterous adults in the colonies led to a markedly higher population level in the next generation.

Population development of Sitobion avenae F., especially in relation to crowding

In the river-clay area in the environment of Wageningen, field observations were made in the years 1974 to 1977. Migrants of *Sitobion avenae* colonized winter wheat especially during heading and flowering. Immigration reached its peak in the weeks after flower-

ing. In view of the large number of apterous adults subsequently born in the crop, immigration in this phase could hardly contribute any more to population growth.

From field observations and laboratory trials, the following general conclusions could be drawn. As soon as the ears are visible, the immigrants prefer to settle on them. Apterous adults developing on the leaves also move to the ear. On the leaves a relatively small number of aphids remains. *S. avenae* is very susceptible to crowding: in colonies with an average of 5 or 15 individuals, 50% or 95% of the newborn nymphs develop wings. Consequently the second generation developing on the ear is already mostly winged. The majority of the young alatae emigrate so the number of adults increases less strongly. At a certain moment more adults die than are added to the colony which reaches its maximum density when the rapidly accumulating sum of emigration and mortality is balanced by the decreasing birth rate. After that, a quick population decrease takes place.

From laboratory research, it seems that crowding also adversely effects longevity, weight and thereby rate of reproduction. However, the rate of reproduction is also directly reduced. If the influence of natural enemies and the ripening of the ear are not taken into account, wing formation followed by emigration does not only limit population growth but can even effect a population decrease of more than half.

Injury and damage to wheat, caused by Sitobion avenae F., Rhopalosiphum padi L. and Metopolophium dirhodum Wlk.

Field and laboratory trials on injury and damage were performed with wheat from the stage of flowering onwards. Aphid infestation can lead to a decrease in the average weight of the grains. Normally the number of grains is not influenced. Comparing the effect on yield of *R. padi* and *S. avenae* both feeding on the ear, or the effect of *M. dirhodum* and *S. avenae* feeding on the flag leaf, no difference could be demonstrated. Infestation of the ear leads to loss in yield at lower population densities than infestation of the flag leaf. *S. avenae* lives mainly on the ear, in contrast to the two other species, and is therefore comparatively the most injurious. There was no effect of time of infection and nitrogen dressing on the decrease in yield at comparable densities.

Honeydew on the plant stimulates the development of fungi, especially black moulds.

In 3 field trials with *S. avenae* this caused about as much damage as the uptake of sap. After correction for the mould effect, the established losses caused by *S. avenae* did not differ much from those calculated on the basis of its energy budget. Therefore, it can be concluded that stylet insertion and injection of saliva have no important influence on the growth of the grains.

Quantitative aspects of attack by Sitobion avenae F. and its effect on yield; their relevance to supervised and integrated control

The so-called aphid-index of Rautapaa is less suitable to relate damage to the intensity of attack. It is better to use the aphid population maximum, which is correlated to damage to the same extent but does not have to be calculated.

In a system of supervised control the criterion for treatment can best be expressed

as the percentage of infected ears. It is strongly correlated with the average number of aphids per ear and can be determined relatively simply and quickly.

Aphid damage shows a strong variation, which mainly seems to be caused by the effect of honeydew depending on the presence and intensity of a number of factors, which also reduce plant production. Because much quantitative information on the population dynamics of the aphids, the production of the crop and the influence of the honeydew is still lacking, no predictions concerning damage can be made yet. Hence no satisfactory economic threshold can be drawn.

An insufficient warning system may lead to loss of goodwill to the extension service and to supervised control. Therefore a low risk criterion for control seems to be the most appropriate solution for the time being. 80% and 90% of the ears infected are safe thresholds for the periods before and during the stage of milky ripe, respectively.

De algemene bezorgdheid onder de telers over de soms explosieve toename van graanbladluizen in de afgelopen jaren gaf over de gehele wereld aanleiding tot onderzoek. Mijn onderzoek startte in 1974 aan het Instituut voor Plantenziektenkundig Onderzoek te Wageningen. Het was bedoeld om de voornaamste produktiefysiologische en produktieecologische aspecten van de bladluis-tarwe-relatie op te helderen. Een dergelijk fundamenteel onderzoek werd geacht de kennis te kunnen opleveren die nodig is voor de ontwikkeling van geleide en geïntegreerde bestrijdingsschema's. In een later stadium kwam samenwerking tot stand met onderzoekers en studenten van de Landbouwhogeschool.

Het onderzoekprogramma werd opgezet rond de volgende vragen. Wat is de betekenis van temperatuur, parasieten, predatoren en pathogenen, waardplant en dichtheidsafhankelijke effecten voor de populatieontwikkeling van de bladluizen? Welke factoren zijn betrokken bij het verlies aan opbrengst en wat zijn de kwantitatieve aspecten van de opbrengstderving? Rabbinge et al. (1979) bestudeerden de populatiedynamiek van de bladluizen met betrekking tot temperatuur, natuurlijke vijanden en populatiedichtheid, en maakten simulatiemodellen voor de populatieontwikkeling en de opbrengstderving. Ik onderzocht de invloed van stikstofbemesting, groeistadium van de plant en plaats van aantasting op de populatieontwikkeling (hoofdstuk 2). Ik bepaalde tevens de invloed van deze factoren en ook van de soort bladluis en de honingdauwafscheiding op het verlies aan opbrengst (hoofdstuk 4). Uit dit onderzoek bleek dat de grote graanluis (*Sitobion avenae* F.) de meest schadelijke soort was. Daarom werd van deze bladluis het effect van de dichtheid op de populatieontwikkeling (hoofdstuk 3) en op de schade (hoofdstuk 5) nader bestudeerd.

De invloed van de waardplant op de populatieontwikkeling van Sitobion avenae F., Metopolophium dirhodum Wlk. en Rhopalosiphum padi L.

In klimaatkamerexperimenten werd de populatieontwikkeling van de 3 soorten bladluizen op wintertarwe bestudeerd. Hierbij werd nagegaan in hoeverre vlagblad en aar als substraat, de leeftijd van de plant en de stikstofbemesting van invloed waren. Van *S. avenae* werd het voedingsrendement onderzocht.

Vóór het melkrijpe stadium vermeerderde *M. dirhodum* zich op het vlagblad in aantal tweemaal zo snel en in biomassa bijna driemaal zo snel als *S. avenae* en *R. padi*. Op de aar vermeerderde *S. avenae* zich echter in aantal tweemaal en in biomassa ruim driemaal zo snel als op het vlagblad. Op deze voedingsplaats vermeerderde *R. padi* zich in aantal even snel als *S. avenae*, maar in biomassa bijna de helft langzamer.

In de loop van het melkrijpe stadium bleef de vermeerderingssnelheid op het vlagblad bij *S. avenae* vrijwel ongewijzigd en nam deze bij *M. dirhodum* sterk af. De vermeerderingssnelheid nam bij *S. avenae* en *R. padi* op de aar eveneens af, maar bij *R. padi* was de afname groter. Aan het einde van het melkrijpe stadium was bij *S. avenae* op de aar de vermeerderingssnelheid tot de helft gedaald.

R. padi en *M. dirhodum* bleken veel minder snel met produktie van gevleugelde adulten te reageren op toename in dichtheid dan *S. avenae*. *S. avenae* werd op het vlagblad eerder tot vleugelvorming geprikkeld dan op de aar. Bij *R. padi* en *M. dirhodum* was de larvale sterfte tweemaal zo hoog als bij *S. avenae*.

Op het vlagblad produceerde *S. avenae* twee à drie maal zoveel honingdauw als op de aar. Van de stikstof, fosfor en kalium in het voedsel werd de stikstof het meest benut: voor 65% uit het zeefvatsap van het vlagblad en voor 83% uit het zeefvatsap in de aarspil. Op grond van het energiebudget van *S. avenae* werd geschat dat op basis van droge stof voor de produktie van 1 mg bladluis 5 mg zeefvatsap uit de aar en 11 mg zeefvatsap uit het vlagblad benodigd is. Van het onttrokken zeefvatsap zou op basis van de energetische waarde 29 resp. 13% worden omgezet in bladluisbiomassa. Naar schatting was op het vlagblad het voedingsrendement van *M. dirhodum* ongeveer gelijk aan dat van *S. avenae*.

Extra bemesting van de plant met stikstof verhoogde bij *S. avenae* het voedingsrendement op de aar, remde de vleugelvorming en als gevolg daarvan ook de emigratie. Alhoewel ook de sterfte toenam, leidde de stijging van het aantal ongevleugelde adulten toch tot een duidelijk toename in het totaal aantal bladluizen van de volgende generatie.

De populatieontwikkeling van Sitobion avenae F. met name de invloed van de dichtheid

In de jaren 1974-1977 werden veldwaarnemingen verricht in het rivierkleigebied in de omgeving van Wageningen. *Migrantes* koloniseerden de wintertarwe voornamelijk gedurende de periode van het in-de-aar-komen en de bloei.

De immigratie bereikte een top in de periode na de bloei. Gezien het reeds aanwezige aantal ter plaatse geboren ongevleugelde adulten droeg in deze fase immigratie nauwelijks meer bij tot de populatiegroei.

Mede op grond van laboratoriumexperimenten konden de volgende algemene conclusies worden getrokken. Zodra de aren zichtbaar worden, vestigen zich de immigrantes bij voorkeur hierop. De ongevleugelde adulten die zich op de bladeren ontwikkelen begeven zich ook naar de aar. Op de bladeren blijft een relatief klein aantal bladluizen aanwezig.

S. avenae is zéér gevoelig voor toename in dichtheid: in kolonies van 5 respectievelijk 15 individuen ontwikkelt 50% respectievelijk 95% van de nieuwgeboren larven vleugels. Daardoor is reeds de tweede generatie die zich op de aar ontwikkelt grotendeels gevleugeld. Jonge gevleugelde adulten hebben de neiging te emigreren. Daardoor neemt het aantal adulten in de kolonie steeds minder toe. Op een gegeven moment verdwijnen er meer adulten dan erbij komen. De populatie bereikt een piek wanneer de snel groeiende som van emigratie en sterfte in balans is gekomen met de afnemende geboorte. Daarna volgt een snelle afname.

Uit laboratoriumonderzoek bleek verder dat toename in dichtheid tot gevolg heeft dat de levensduur, het gewicht en de snelheid van vermeerdering afnemen. De vermeerderingssnelheid wordt zowel via het gewicht als rechtstreeks beïnvloed. Onafhankelijk van de in-

vloed van natuurlijke vijanden en de afrijping van de aar blijkt de produktie van gevleugelde dieren onder laboratoriumomstandigheden niet alleen tot een verminderde populatiegroei maar zelfs tot een populatieafname van meer dan de helft te kunnen leiden.

Schade aan de tarweopbrengst als gevolg van aantasting door Sitobion avenae F., Metopolosiphum dirhodum Wlk. en Rhopalosiphum padi L.

De experimenten werden uitgevoerd met wintertarwe van het stadium van de bloei af. Aantasting door graanbladluizen bleek te kunnen leiden tot een verlaging van het gemiddeld gewicht van de graankorrels. Het aantal korrels per aar werd niet beïnvloed. Er kon géén verschil in schadelijkheid worden aangetoond bij aantasting van de aar tussen *S. avenae* en *R. padi* en evenmin bij aantasting van het vlagblad tussen *S. avenae* en *M. dirhodum*, die niet op de aar voorkomt.

Aantasting van de aar bleek bij lagere dichtheden tot opbrengstverlies te leiden dan aantasting van het vlagblad. Omdat *S. avenae* in tegenstelling tot de andere twee soorten voornamelijk op de aar voorkomt is deze soort naar verhouding dus het meest schadelijk.

De betekenis van tijdstip van infectie en stikstofbemesting voor de schade bij gelijkblijvende dichtheid kon niet worden aangetoond.

Honingdauw op de plant stimuleert de ontwikkeling van met name zwartschimmels. Dit veroorzaakte in een drietal veldproeven met *S. avenae* ongeveer evenveel schade als de opname van sap. Na correctie voor de schimmelinvloed bleken de geconstateerde verliezen weinig af te wijken van de verliezen berekend op grond van het energiebudget. Hieruit kon worden geconcludeerd dat het aanprikken van de plant en de injectie van speeksel door *S. avenae* op de aar geen belangrijke invloed hebben op de groei van de korrels.

Kwantitatieve aspecten van aantasting en schade door Sitobion avenae F. hun betekenis voor geleide en geïntegreerde bestrijding

De zogenaamde bladluisindex van Rautapaa is minder geschikt om de schade in verband te brengen met de mate van aantasting. Men kan hiervoor beter het maximum aantal van de bladluispopulatie gebruiken, dat een even goede samenhang met de schade bezit maar niet hoeft te worden berekend.

In een systeem van geleide bestrijding kan het bestrijdingscriterium het beste worden uitgedrukt in het percentage aangetaste aren. Het is sterk gecorreleerd aan het gemiddeld aantal bladluizen per aar en kan naar verhouding eenvoudig en snel worden vastgesteld.

De bladluisschade is zeer wisselend. De voornaamste oorzaak hiervan lijkt het effect van de honingdauw, dat afhangt van de aanwezigheid en intensiteit van een aantal andere factoren die ook opbrengstverlagend werken. Omdat er nog onvoldoende kwantitatieve informatie over de populatiedynamiek van de luizen, de produktie van het gewas en de invloed van de honingdauw beschikbaar is, kunnen nog géén voorspellingen over de schade worden gedaan. Daarom kan ook nog géén bevredigende economische schadedrempel worden aangegeven.

Een onvolkomen waarschuwingssysteem kan leiden tot verlies aan goodwill voor de voorlichtingsdienst en geleide bestrijding. Om deze reden lijkt een bestrijdingscriterium, dat weinig gevaar inhoudt voor opbrengstderving voorlopig de meest geschikte oplossing. Een aantasting van 80% van de aren is een veilig bestrijdingscriterium voor de periode vóór het melkrijpe stadium. Tijdens het melkrijpe stadium mag een aantasting van 90% van de aren worden getolereerd.

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STELLINGEN

1. Van de drie meest algemene soorten graanbladluizen is de grote graanluis (*Sitobion avenae* F.) het schadelijkst.

Dit proefschrift.

2. Overbemesting van tarwe met stikstof stimuleert de grote graanluis tot het bereiken van hogere aantallen.

Dit proefschrift.

3. Graanbladluizen moet men meer vrezen om hun honingdauwafscheiding dan om hun voedingsgedrag. Dit geldt temeer naarmate de korrelvullingsperiode van het gewas langer wordt.

Dit proefschrift.

4. De voorkeur die de grote graanluis vertoont voor de aar is van grote waarde voor het voortbestaan van deze soort.

Dit proefschrift.

5. Het efficiënt bestrijden van graanbladluizen heeft tot gevolg dat de bestrijding van afrijpingsziekten minder winst oplevert.

6. Preventieve bestrijding van graanbladluizen tijdens de bloei van het gewas houdt belangrijke ecologische en financiële risico's in en moet derhalve worden afgeraden.

7. Geïntegreerde bestrijding maakt de landbouw minder kwetsbaar voor schaarste aan energie en grondstoffen en creëert tegelijk "schone" werkgelegenheid voor de middelbare en hogere opleidingsniveau's.

8. Als het de overheid ernst is met het bevorderen van geïntegreerde bestrijding dient zij zich niet alleen met het onderzoek maar ook met de introductie van deze benadering bezig te houden.

9. Het toepassen van het principe "de vervuiler betaalt" op de vervaardiging en het gebruik van bestrijdingsmiddelen in de landbouw verdient als beleidsinstrument aanbeveling.

10. Alternatieve landbouwmethoden behoren alleen al in stand te worden gehouden omdat ze onmiskenbaar een bron van inspiratie en geluk vormen voor de velen die ze beoefenen.

11. Het poneren van stellingen is een achterhaalde vorm van imponeergedrag, zeker als de promovendus niet in rok verschijnt.

Proefschrift van P.H. Vereijken
Performance of *Sitobion avenae* F., *Metopolophium dirhodum* Wlk. and *Rhopalosiphum padi* L.,
and their effect on yield of winter wheat.
Wageningen, 14 maart 1979