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Epidemiology and simulation of population development of Sitobion avenae in winter wheat

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Abstract

The epidemiology of *Sitobion avenae* and its natural enemies in winter wheat was studied in 1975, 1976 and 1977. Immigration was important until the end of flowering. The alate immigrants had apterous offspring. These became the driving force in population growth. Their offspring were mostly alatae which usually left the field. A model of the epidemic was developed. Quantitative relations between the aphids and their environment were obtained from literature or established in laboratory trials. The model simulated population development and population composition from the beginning of June till the population peak at the end of June or early in July. Because quantitative data on relations between aphids and their natural enemies and pathogens are scarce, and since the knowledge on wing formation is still limited, the population collapse could not be predicted. In the future, prognosis over a period of three weeks seems possible.

Additional keywords: Aphidius uzbekistanicus, A. picipes, Chrysopa carnea, Coccinella septempunctata, Entomophthora, Metopolophium dirhodum, Praon volucre, Rhopalosiphum padi, Syrphus corrolae, simulation techniques.

1 Introduction

The increase in numbers of cereal aphids during the last decennia constitutes a serious problem in wheat growing. A comprehensive survey of literature can be found in Rautapää (1976).

He assumed that damage is a function of number and time (Rautapää, 1966); however the physiological bases for determination of damage is weak and thus a study to quantify the effect of aphids in terms of plant physiology and production ecology was undertaken by Vereyken (1979). His data on injury levels in course of time combined with a system of forecasting of aphid populations are needed to develop a reliable warning system.

In the Netherlands, usually three species are of economic importance: *Sitobion avenae*, *Metopolophium dirhodum* and *Rhopalosiphum padi*, the first being probably the most important because of its migration to the ear. Many field observations on the growth of cereal aphid populations under various conditions have been made but they have little explanatory value since they are not combined with a detailed analysis of the underlying physiological and ecological phenomena. Extrapolation to other situations is then impossible. A sensible forecasting system requires knowledge on how the aphid population and its natural enemies interact with each other and with the host plant, and how the system is influenced by temperature, humidity, rain and wind, and by various cultivation methods. The aim of the present study was to develop simulation models that explain the population movements of the most important aphid *S. avenae* and may be used for extrapolation and prognosis in the short run, approximately 3–5 weeks. This is done by an intensive combination of model construction, field and laboratory experiments.

The system studied comprises the wheat crop, *S. avenae* and its natural enemies. The population growth of the aphid and the natural enemies is simulated for changing biotic and abiotic conditions. All simulations refer to commercial fields with row culture of the winter wheat cvs. Caribo and Clement. The experimental fields were tended as those under the normal commercial system. Weeds were controlled with sprays of Mecoprop and bromefenoxim. Except for a CCC treatment, no other chemicals were applied. Field experiments were set up for three consecutive years (1975, 1976 and 1977) and models were verified during these periods.

2 Epidemiology

2.1. Methods

In 1975, *S. avenae* was sampled from about 1200 m^2 of a winter wheat field cv. Clement near Lienden, Betuwe. In 1976, a 1-ha field cv. Caribo was used and in 1977 0.5 ha of a 1-ha field. Both fields were situated near Wageningen. In 1975, counts were made on 0.3 m rows according to Dean and Luuring (1970). This method was combined with detailed counts on single tillers. The latter method of counting required usually less than half the number of tillers necessary for the 0.3 m technique, probably because of the contagious nature of aphid distribution. Many samples taken at different places reduced the standard deviation more than bigger samples from a limited number of spots, an accuracy level of $\sigma_{\bar{x}} < 0.1\ \mu$ being aimed at.

The single tiller technique was used in 1976 and 1977. All larval instars, alatae, apterae, mummified aphids, aphids infected by *Entomophthora* spp. as well as predators were recorded. Sample size was calculated with $N = S^2/(\mu^2 \times D^2)$ in which μ = mean density, S = standard deviation, D = accuracy level $= \sigma_{\bar{x}}/\mu < 0.1$.

During the greater part of the population growth, sample size diminished as the population distribution became less patchy (Karandinos, 1976). The sample taken was usually larger than necessary. However, the method caused difficulties in the beginning of the epidemic when populations were low and contagious. The maximum number of tillers that could be examined within the day was 600, while at the low levels over a thousand generally were necessary for the desired level of accuracy. however counting could not be extended for more than one day because aphid populations often doubled in less than 3 days, and thus approximately 25% more aphids could be expected after 1 day.

Embryo counts, indicating physiological age of adults, were made by dissecting in a physiological salt solution, adults collected at random in the field. In laboratory trials, the number of embryos and the offspring was determined with 5 aphids at each age. All visible swellings of the ovary were considered to be embryos.

Rearing experiments to determine rate of development, induction of wing formation

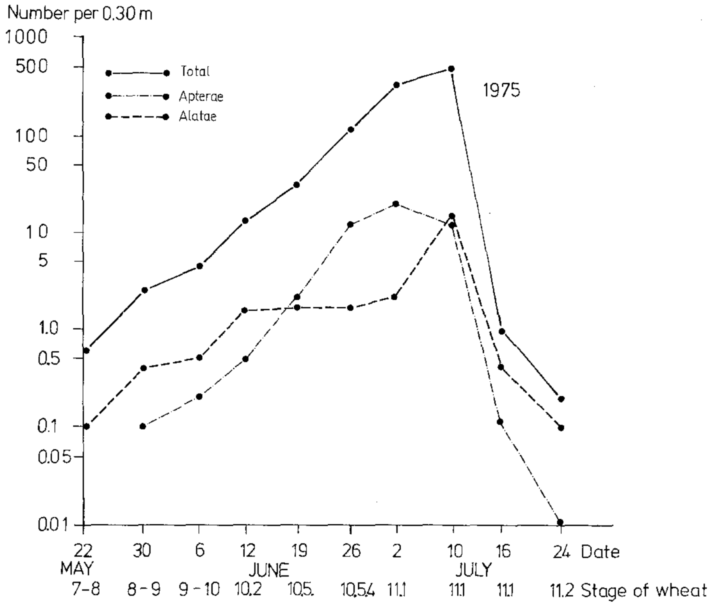


Fig. 1. Number of apterae, alatae and total number of living aphids in 1975. Counts per 0.3 m row.

Fig. 1. Aantal apteren, alaten en totaal aantal levende bladluizen in 1975. Telling per 0,3 m in de rij.

Fig. 2. Number of apterae, alatae, L_1 and total number of living aphids in 1976. Counts per tiller.

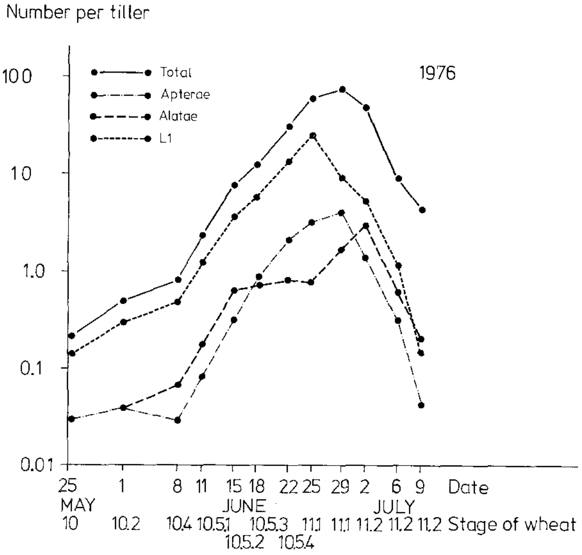


Fig. 2. Aantal apteren, alaten, L_1 en totaal aantal levende luizen in 1976. Telling per halm.

Fig. 3. Number of apterae, alatae, L_1 and total number of living aphids in 1977. Counts per tiller.

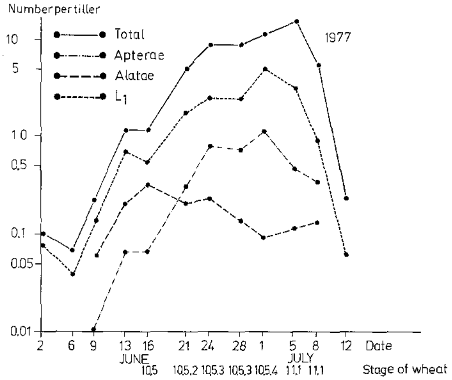


Fig. 3. Aantal apteren, alaten, L_1 en totaal aantal levende bladluizen in 1977. Telling per halm.

and reproduction rate were done in Perspex leaf cages, size 10 × 3 × 3 cm of the type described by Vereyken (1979) at light:dark (LD) 16:8 h and constant temperatures of 15, 20 and 25 °C and a varying temperature of 8 to 19 °C.

2.2 Results

The total number of aphids, L_1, apterae and alatae are presented in Figures 1–3. Aphid numbers are presented on a logarithmic scale, to reduce the length of the y-axis, and are plotted against calendar time and physiological stage of the plants according to Feekes (Large, 1954). They show a rapid increase in the total population for three to six weeks (doubling time about 3 days), a flattening of the curve for one to two weeks and then a rapid collapse of the population. This growth pattern was repeated in all three years but the levels were different. Table 1 gives the maximum number of total aphids found per tiller and per m².

The maximum number per tiller was lower in 1977 than in 1975 as a result of different plant densities but the number per m² was higher. The number of L_1 per adult is an indication of the vitality of the population. Figure 4 shows the decline in the ratio between L_1/total number and this means a gradually senescent population.

Table 1. Maximum number of aphids per tiller and per m² in 1975, 1976 and 1977.

Year	Number of aphids per		Number of tillers per m²
	tiller	m²	
1975	23.2	6000	259
1976	67.0	32000	472
1977	14.0	10000	748

Tabel 1. Maximum aantal bladluizen per halm en per m² in 1975, 1976 en 1977.

Fig. 4. Ratio L_1/total number of aphids in 1976 and 1977.

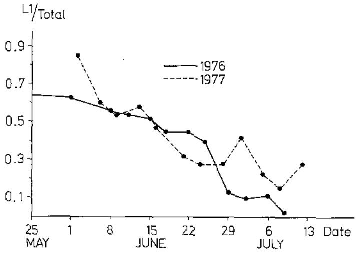


Fig. 4. Verhouding L_1/totaal aantal bladluizen in 1976 en 1977.

Fig. 5. Daily catches of alatae of *S. avenae* by the suction trap in 1976.

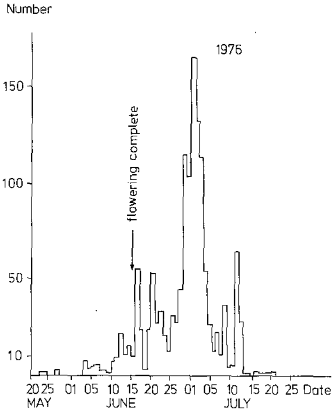


Fig. 5. Dagelijkse vangst van alaten van S. avenae door de zuigval in 1976.

Embryo counts (Table 2) indicate that in the field only part of the potential offspring are usually produced. Until the end of the epidemic, the number of embryos remains rather constant. In laboratory trials with aphids of known age and offspring, there was always a gradual decrease in number of embryos. It seems that the sum of embryos and offspring is rather constant.

At the start of the epidemics, at the end of May or early June, sometimes more apterae than alatae are found. But this situation soon changes and most of the time alatae predominate before flowering (Figs. 2 and 3). After the onset of flowering, immigration seems to stagnate as the number of alatae on the wheat remained constant. However the number of alatae caught in suction traps after 15 June was higher than before (Fig. 5). About two weeks later, the number of alatae increased again not because of immigration but because of moulting of alatiform L_4 (Fig. 6). The development of these alatiform L_4 marked the end of population growth. Soon afterwards populations collapsed, a phenomenon which was always amplified by the action of predators, parasites or *Entomophthora* spp. (Fig. 7). Then apterous adults diminished. The aphids present were still capable of rapid reproduction as can be seen from Table 3 showing the ratio of L_1/reproducing ♀♀. This ratio though not constant did not diminish at the end of the epidemic. It was different in the growth phase of the epidemic in 1976 and 1977. Embryo counts at the end of the epidemic also show the presence of well reproducing females (Table 2). The numbers of mummies increased in the second part of June. They declined sharply towards the end of the epidemic in 1977 but not in 1975 and 1976.

The parasites found in order of numbers in 1976 were a species resembling *Aphidius uzbekistanicus*, *Praon volucre* and *A. picipes*. In 1977, again in order of numbers the parasites were *A. ervi*, *A. picipes* and *A. uzbekistanicus*. Hyperparasites were numerous in 1976 but not in 1977. The predator *Syrphus corollae* was numerous in 1976 but not in

Table 2. Number of embryos in alatae and apterae in the field in 1975, and numbers of embryos found in *S. avenae* and their reproduction when reared at 13 °C and LD 16:8. Numbers of aphids investigated are given in parentheses.

Date	Field:		Laboratory				
	number of embryos		age	alatae: number of		apterae: number of	
	alatae	apterae	(days)	embryos	larvae	embryos	larvae
30 May	43.6(12)	70.0(1)	1	48.6	0	52.1	0
6 June	42.5(20)	48.0(1)	4	41.2	10.4	48.4	10.4
13 June	37.1(32)	43.3(9)	8	33.6	19.4	43.2	19.6
19 June	32.8(13)	59.1(44)	11	29.6	29.2	37.8	28.8
26 June	38.7(7)	56.4(31)	15	21.8	34.4	29.8	30.6
1 July	40.8(4)	52.0(33)	18	20.2	37.8	24.6	35.0
11 July	41.9(12)	32.3(17)	22	19.6	34.8	19.4	33.0

Tabel 2. Aantal embryonen gevonden in alaten en apteren uit het veld in 1975 en aantal embryonen en hun aantal nakomelingen gevonden bij bladluizen, gekweekt bij 13°C en LD 16:8. Tussen haakjes aantal onderzochte dieren.

Fig. 6. Number of L_4 apteriform and L_4 alatiform per tiller in 1976 and 1977.

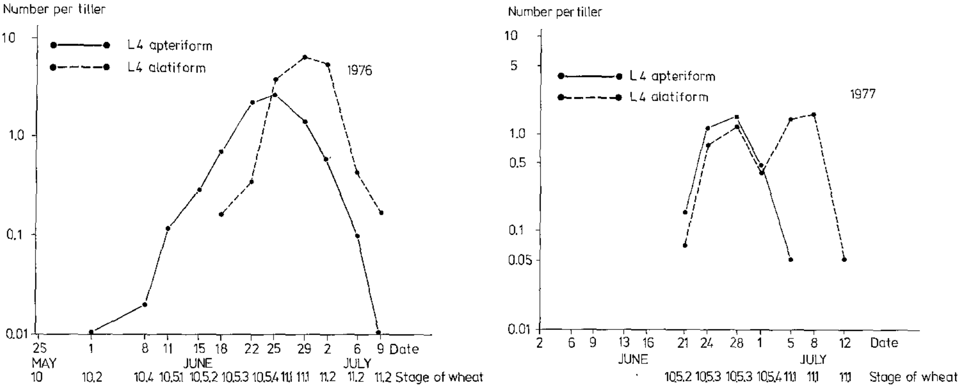


Fig. 6. Aantal L_4 apteriform en L_4 alatiform per halm in 1976 en 1977.

1977. The other major predators such as *Coccinella septempunctata* and *Chrysopa carnea* were far less numerous in all years.

Entomophthora spp. were present in all three years but were only disastrous for the population in 1977 (Fig. 7).

Table 3. Ratio L_1/reproducing ♀♀.

1976			1977		
date	growth stage wheat	ratio	date	growth stage wheat	ratio
25 May	10	4.7			
1 June	10.2	3.9			
8 June	10.4	4.9	9 June		2.1
11 June	10.5.1	4.8	13 June		2.5
15 June	10.5.2	4.0	16 June	10.5	1.4
18 June	10.5.3	4.3	21 June	10.5.2	3.2
22 June	10.5.4	4.7	24 June	10.5.3	2.3
25 June	11.1	7.6	28 June	10.5.3	2.8
29 June	11.1	2.1	1 July	10.5.4	4.1
2 July	11.2	3.6	5 July	11.1	6.2
6 July	11.2	3.8	8 July	11.1	3.0
9 July	11.2	3.7			

Average: 3.5 ± 0.53
Average till 25 June 4.8 ± 0.14
(end of growing phase)

Average: 3.21 ± 0.34
Average till 28 June 2.3 ± 0.3
(end of growing phase)

Tabel 3. Verhouding L_1/reproducerende ♀♀.

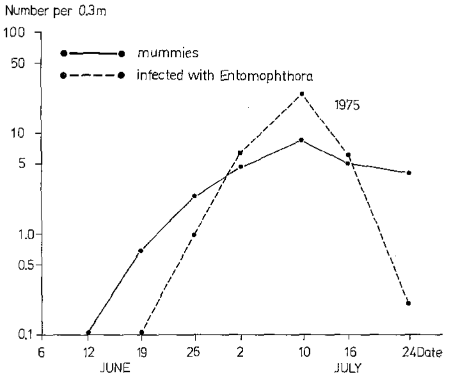
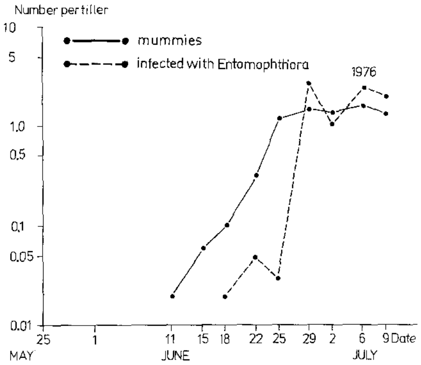
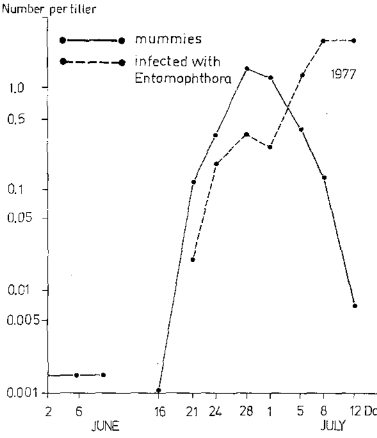


Fig. 7. Number of mummified aphids and number killed by *Entomophthora* spp. in 1975, 1976 and 1977. In 1975 numbers per 0.3 m and in 1976 and 1977 per tiller.

Fig. 7. Aantal gemummificeerde en door Entomophthora spp. gedode luizen in 1975, 1976 en 1977. In 1975 aantallen per 0,3 m en in 1976 en 1977 per halm.





2.3 Discussion

At the end of May, aphid population densities were extremely low. Increase is promoted by immigration of alatae from elsewhere. The absence of alatiform L_4 at this time (Fig. 6) in the wheat field indicates that their origin must be outside the wheat field. A possible source is all graminaceous plants in meadows or borders of roads. However, *S. avenae* was not numerous at that time and, as induction of wing formation strongly depends on crowding, this source does not seem plausible. On the other hand the area under grass is very large and could thus still produce at least part of the immigrants. Long-distance flight may also be of importance, but no data are yet available to support this hypothesis.

Immigration remains important until flowering (Figs. 1, 2, 3). At that time the number of alatae in the field no longer increases and immigration then almost compensates emigration and mortality of alatae. The large number of alatae found later should be regarded as future emigrants. They developed in the field as can be seen from the curves of alatiform L_4 (Fig. 6). We can therefore include in our system a limited period of immigration and emigration of all alatae produced. The apterae remain then as the only important driving force for reproduction.

Natural enemies usually arrive rather late. In early June, only a few parasitized

Fig. 8. Symbols of Forrester notation.

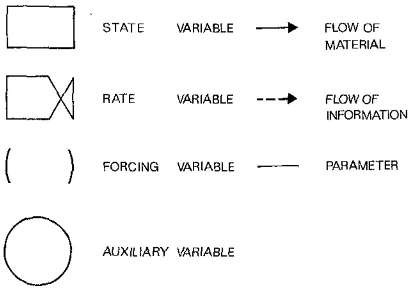


Fig. 8. Symbolen van de Forrester-notatie.

Fig. 9. Relational diagram of population growth and development of *S. avenae*.

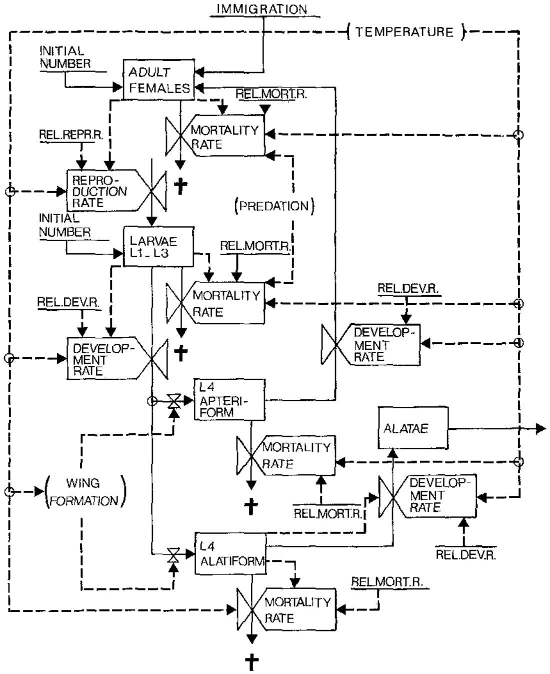


Fig. 9. Relatiediagram van populatiegroei en ontwikkeling van S. avenae.

Fig. 10. Relational diagram of population growth and development of *S. corollae*.

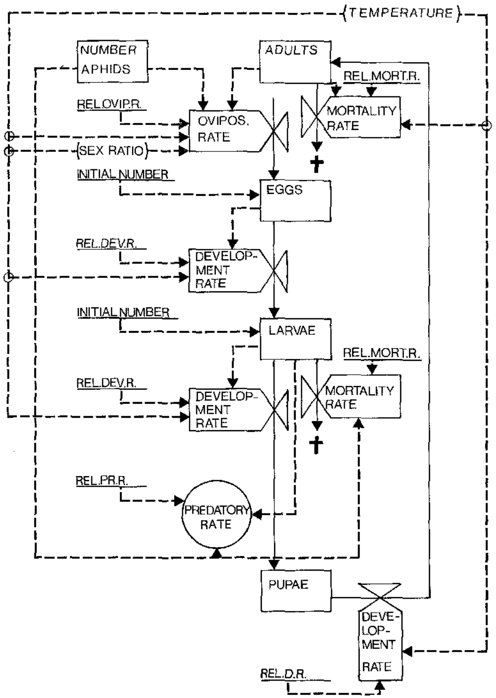


Fig. 10. Relatiediagram van populatiegroei en ontwikkeling van S. corollae.

aphids can be found. Since some of the mummies are alatae they help to disseminate the parasite. Estimation of the low initial number of parasites or predators is difficult because of the large samples needed.

3 Description of the system, cereal-aphids-natural enemies

The system is presented by so-called 'relational diagrams' (Fig. 9 and 10). These give a schematized representation of the whole system or parts of it. In these relational diagrams the conventions of Forrester (1961) are used (Fig. 8). A more detailed explanation of the technique of system analysis and simulation and their application in applied entomology is given by De Wit and Goudriaan (1978) and Rabbinge (1976).

The model is divided into four sections. The first concerns the abiotic conditions, the second describes the development, ageing and reproduction of the aphids, the third comprises the subsystem wheat plant, here assumed to be an unlimited food resource and only characterized by physiological age and in the fourth the natural enemies of the aphids are given. The description of the system is short both qualitatively and quantitatively. The predators and parasites involved and their interrelations are scarcely known. Incorporation of these relations in the models was mainly based on guesses and assumptions. Fungi may also be important but lack of knowledge of their mode of action made their introduction in the models speculative.

3.1 Abiotic factors

Nearly all biological processes in the system are affected by temperature and as temperature within a crop may vary, accurate measurements seem desirable. However, such measurements and their introduction in the model are time- consuming. Therefore these measurements are only justified when the effects of small changes in temperature are of major importance on the population development of the aphid. To determine these effects, a sensitivity test with a computer model was executed. The results of these calculations are given in 4.2.2 and, as a consequence, it suffices to use the air temperature measured in a Stevenson screen at 1.50 m in the immediate surrounding of the field as a forcing variable. Only the daily minimum and maximum temperature are needed, the actual temperatures being calculated from a sinusoid through both these temperatures. The form of this sinusoid depends on time of sunrise and sunset, which are calculated from day of the year and latitude of the site. Humidity is not considered in this model, since its effect on the different phenomena is not known. However it may play a major role in the development of *Entomophthora* spp. epidemics, it may affect the development of secondary pathogens on the honeydew produced by the aphids (Vereyken, 1979) and it may interfere with the development of the aphid. If these effects are of quantitative importance, humidity should also be introduced as a forcing variable.

3.2 The aphid, Sitobion avenae, its development, ageing and reproduction

Figure 9 gives a simple diagram for the development of *S. avenae*. Juvenile aphids with three larval stages develop into alatiform or apteriform L_4. The maturing apterous females may produce a new generation of aphids, whereas the alatae emigrate and disappear from the system. Wing formation is a result of the combined effects of temperature, crowding and also physiological condition and stage of the plant. These effects were estimated by giving a 24-h crowding stimulus in small glass vials to not more than one-day-old adults kept separately since the L_4 stage. During this crowding period, the aphids were not allowed to feed (Lees, 1967). The results of these experiments given in Table 4a and b are erratic. Temperature seems of less importance for wing formation than crowding. Crowded alatae produce only few alatae. This is confirmed by tests with aphids collected in the field (Table 4c). Apterae from the field produce mainly alatae and alatae produce mostly apterae. Effects of physiological stage and condition of the host plants are likely but they are not yet quantified. The data of Table 4 are introduced as such into the model.

The influence on rate of development of juveniles by temperature (Dean, 1974), is shown in the relational diagrams by the arrows from the forcing variable temperature to the rates. Dean's data were largely confirmed by our experiments using young wheat plants as a food source instead of barley leaf disks on wet cotton wool (Table 5). However in our trials made at 11 °C instead of 10 °C a much lower rate was found. Moreover we determined that development reacted momentaneously to fluctuations in temperature. The total development period at a constant temperature of 13 °C is 14.2 ± 0.16 days and when temperature fluctuates between 8 and 19 °C, such that the average temperature is 13.5 °C it amounts to 14.05 days. Differences between development period for aphids reared on leaf or on ear are minor, grown on leaves 14.05 days and on ear 14.7 days at 13.5 °C. Thus, directly temperature dependent rates could be introduced in the computer models and history effects could be neglected.

After a while, dispersion in development occurs. Measurements indicated that the relative dispersion, i.e. ratio of standard deviation to mean, decreased with temperature increase. The simulation model on population growth involves these effects; they are mimicked using a method developed by Goudriaan (1973). This method is used throughout the present model. It basically comprises the distinction of age classes that are passed by the developing animals. The mortality rates due to abiotic factors were determined from experiments on duration of development. The mortality rates were

Table 4a. Percentage alatae produced in the first week by alatae and their apterous first and second generation offspring under the influence of crowding at 13 °C and LD 16:8 in three experiments.

Treatment	Parents								
	alatae: experiment			first generation: experiment			second generation: experiment		
	I	II	III	I	II	III	I	II	III
No crowding	0	0	0	32	29	0	1	84	21
Crowding	4	0	0	99	90	50	39	100	15

Tabel 4a. Percentage alaten dat in de eerste week werd geproduceerd onder invloed van 'crowding' bij 13 °C en LD 16:8 door alaten en hun aptere nakomelingen in de eerste en tweede generatie in 3 proeven.

Table 4b. Effect of temperature and number of crowded aphids during crowding on the percentage alate offspring of alatae when reared afterwards at 20°C and LD 16:8.

Number crowded	Crowding temperature	
	13°C	20°C
1	24	44
1	24	50
2	40	53
10	38	63
10	41	63
18	49	53

Tabel 4b. Invloed van de temperatuur gedurende de crowding en het aantal 'crowded' bladluizen op het percentage alate nakomelingen van alaten wanneer ze daarna bij 20°C en LD16:8 werden gekweekt.

Table 4c. Type of offspring produced in 5 days by alatae and apterae collected in the field and reared separately in cages at 13°C and LD 16:8.

Date of collecting	Parents apterous number of			Parents alate: number of		
	parents	alate offspring	%	parents	alate offspring	%
22 June 1977	6	77	81	10	6	6
30 June 1977	27	297	95	27	68	42
6 July 1977	4	38	90			

Tabel 4c. Type nakomelingen geproduceerd in 5 dagen door alaten en apteren die in het veld waren verzameld en in afzonderlijke kooitjes gekweekt bij 13°C en LD 16:8.

Table 5. Development period in days of *S. avenae* at various constant temperatures (Dean, 1974).

Leaf		Temperature				
		10	15	20	25	27.5
Larvae stage 4	$\bar{x}$	4.1	2.76	2.25	2.0	2.3
	σ	0.5	0.4	0.33	0.5	0.4
Larvae stages 1–3	$\bar{x}$	11.36	7.64	5.84	5.07	6.09
	σ	3.46	2.46	1.0	1.25	1.42
Total until reproducing	$\bar{x}$	16.8	11.4	8.8	8.4	10.2

Tabel 5. Ontwikkelingsduur in dagen van S. avenae bij verschillende constante temperaturen.

proportional to the actual number present and thus mortality can be expressed in relative rate of mortality (day^{-1}). This relative rate of mortality at various temperatures is calculated with

$$RMOR = (\ln N_t - \ln N_{t+1}) / \Delta t$$

in which N_t is the number of living animals at time t and N_{t+1} the number of living animals at time t + 1. The data in Table 6 show that the relative mortality is negligible between 10°C and 30°C.

The apterous females mature during a temperature-dependent period. The rate of reproduction and the fecundity depend again on temperature. These effects were determined in individual rearing experiments at various constant temperatures and with fluctuating temperatures. The results of these experiments on complete plants are presented in Table 7. The rate of reproduction and the fecundity depend strongly on temperature, they decrease considerably below and above the range 15°C–25°C. Rate of ageing and dispersion during ageing are also strongly dependent on temperature (Table 7).

The effect of temperature on ageing is incorporated in the model in a similar way as the effect of temperature on dispersion during development. The alate females are supposed to emigrate before they start reproducing and non-fliers are not considered. Their contribution to a new generation in the system is therefore ignored.

3.3 *The plant*

In the present model, the plant is considered an unlimited food resource. This implies that effects of the changing condition of the plant on reproduction and wing formation are ignored. Although this assumption may hold for the presented simulations it appears from many experiments in practice that the physiological condition of the plant may affect the process of wing formation considerably (Vereyken, 1979; Rabbinge and Vereyken, 1979).

Also the morphological stage of the plant may affect the biometrical parameters of the aphid. Since the nutritive value of ears may be different from that of the leaves the reproduction rate of the aphid may be higher when it is living on the ear than on the leaves. Moreover, the process of wing induction may be influenced directly by the physiological stage of the plant. Quantitative data on these effects are not yet available and the results of preliminary experiments indicate that the physiological stage of the plant is of minor importance for wing formation. Nevertheless knowledge of the physiological stage seems an important characteristic of the system: – plant – aphids – natural enemies. Therefore the physiological stage of the plant expressed in the Feekes

Table 6. Relative rate of mortality (day^{-1}) of *S. avenae* during development in relation to temperature.

Temperature	10	15	20	25	30
L_1–L_4	0.0005	0.0004	0.0006	0.05	0.85

Tabel 6. Relative sterftesnelheid (dag^{-1}) van S. avenae gedurende de ontwikkeling in afhankelijkheid van de temperatuur.

Table 7. Rate of reproduction, fecundity, ageing and mortality in dependence of temperature for *S. avenae*.

	Temperature (°C)					
Rate of reproduction in age classes	10	15	20	25	30	35
1	0	1.5	1.05	0.25	0	0
2	0.1	2.2	4.63	2.7	0	0
3	1.7	2.38	2.88	2.45	0	0
4	1.6	1.78	2.08	1.35	0	0
5	0.95	0.45	0.7	0.65	0	0
6	0.35	0.05	0.1	0.15	0	0
7	0.05	0.01	0.01	0.03	0	0
8	0.01	0	0	0	0	0
9	0	0	0	0	0	0
10	0	0	0	0	0	0
Fecundity	33	46	61	33	0	0
Maximum life span in days	75	82	55	45	15.8	5
Length of each age class in days	7.5	8.2	5.5	4.5	1.58	0.5
Relative rate of mortality (day^{-1}) in age classes						
1	0.002	0.0184	0.001	0.002	0.08	0.1
2	0.004	0.017	0.002	0.006	0.1	0.2
3	0.014	0.028	0.007	0.016	0.146	0.3
4	0.027	0.046	0.029	0.038	0.11	0.22
5	0.047	0.064	0.058	0.076	0.46	0.9
6	0.084	0.079	0.094	0.131	0.34	0.7
7	0.146	0.100	0.168	0.169	0.60	1.6
8	0.103	0.136	0.228	0.252	0.81	1.2
9	0.185	0.156	0.252	0.334	0.65	1.3
10	0.7	0.7	0.7	0.64	0.69	1.4

Tabel 7. Snelheid van reproduktie, reproduktiecpaciteit, veroudering en sterfte in afhankelijkheid van de temperatuur bij S. avenae.

scale is conserved in a state variable that changes with a temperature-dependent development rate of the plant. The data for this dependence on temperature are given by Robertson (1968).

The rate of development increases linearly with temperature and during development the slope of this linear temperature relation has a breaking point at flowering. During the stages before flowering, the slope has the value 0.0007 development units per °C, and from flowering up to doughy ripeness the value of the slope amounts to 0.0024 where Feekes scale 11.2 corresponds with development stage 2 and flowering stage 10.5.1 with development stage 1.

3.4 Natural enemies

Available data on natural enemies are limited. Nevertheless, a first attempt is made to involve them in this preliminary explanatory model.

In Figure 10, the relational diagram for the predator *Syrphus corollae* is given to show how predators and parasites may be introduced into the model. The life cycle of the animal is given; adult females produce eggs that hatch into larvae. These larvae develop into pupae that give rise to a new generation of adult females and males.

Similar to the prey, development rates, reproduction rate and fecundity are affected strongly by temperature. These effects are described by Barlow (1961) and Wahbi (1967) and their data are used to quantify the different relations (Table 8). These authors only supplied data at temperatures of 15, 20 and 25 °C and the values of reproduction rate, development rate and fecundity at temperature values below or above this range were determined by extrapolation. The rate of predation is principally determined by the prey and predator density and by the relative predation rate which is dependent on temperature and area (Rabbinge, 1976). These relations are derived from the rough data on predation of *S. corollae* supplied by Bombosch (1962). The maximum predation rate of larvae of *S. corollae* amounts to 200 larvae L_1–L_3 of *S. avenae* per day and 100 adults or fourth instar larvae. The relative predation rate per predator is defined as predation rate divided by the actual prey density. In the model, the total predation rate is calculated each time interval by multiplying the prey density per tiller by predator density per tiller and this product by the relative predation rate. At low prey densities, predation decreases due to inevitable searching time of the predator. This functional response is accounted for by a dependency of the relative predation rate on the prey density. Figure 11 presents this dependency, the breaking point being based

Table 8. Developmental period and rate of reproduction of *S. corollae* in relation to temperature and prey density.

		Temperature					
		0	10	15	20	25	35
Developmental period in days							
Egg	$\bar{x}$	10	8	5	4	3	3
	σ	3.2	2.8	2.2	2.0	1.7	1.7
Larvae	$\bar{x}$	60	80	15	10	7	7
	σ	7.7	8.9	3.9	3.2	2.6	2.6
Pupae	$\bar{x}$	50	30	20	12	7	6
Longevity	σ	7.0	5.5	4.5	3.5	2.6	2.4
Adult	$\bar{x}$	80	80	70	50	30	10
	σ	8.9	8.9	8.4	7.1	5.5	3.2
Rate of reproduction							
$\bar{x}$ food unlimited $>$ 10 *S. avenae* per tiller		0	3.6	7.5	18	30	30
$\bar{x}$ when $<$ 10 *S. avenae* per tiller		0	v × 3.6	v × 7.5	v × 18	v × 30	v × 30

v = 0.1 × total number of *S. avenae* per tiller

Tabel 8. Ontwikkelingsduur en reproduktiesnelheid van S. corollae in afhankelijkheid van temperatuur en prooidichtheid.

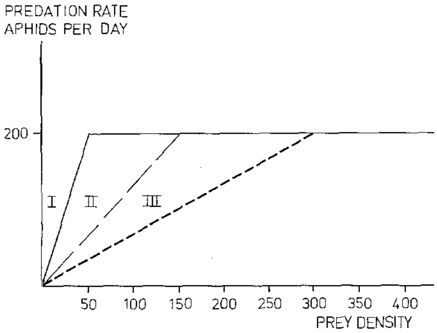


Fig. 11. Functional response curve of *S. corollae*, maximum predation rate 200 aphids/day. Breaking point at an aphid density of I = 50 aphids/tiller, II = 150 aphids/tiller and III = 300 aphids/tiller.

Fig. 11. Functionele reactiecurve van S. corollae, maximum predatiesnelheid 200 luizen/dag. Breekpunt van de functionele responscurve bij I = 50 luizen/halm, II = 150 luizen/halm en III = 300 luizen/halm.

on guesses since sound quantitative data are lacking. The sensitivity analysis in 4.2.2 shows the importance of this type of knowledge.

Another effect of prey-predator interaction is the numerical response which expresses the enhanced or reduced reproduction rate of the predator in relation to the prey density. Data of Bombosch (1962) and Wahbi (1967) showed that the reproduction rate of the predator may decrease drastically when insufficient food is available. Their data supplemented with guesses are introduced in the computer model (Table 8).

An extensive computer listing that gives the quantitative information on all relations described is available on request.

4 Validation of the model

During model construction and experimentation several hypotheses, assumptions and guesses on qualitative and quantitative relations within the system and on effects of forcing variables were made. To verify the structure of the model and the incorporated relations a comparison with the results of independent experiments has to be made. Moreover, the relative impact of different relations used has to be determined.

4.1 Comparison of field experiments and model output

Models have to be verified at different levels of integration. Data on field level were available while data to verify the implicit hypotheses and model outcomes at lower levels of integration are still being collected. The population density curve of the aphids divided over their different development stages is calculated by numeric integration using intervals of 0.01 days (about one quarter of an hour). This interval is determined by the smallest time coefficient of the system, here the development period at 30 °C.

Figure 12 shows the model output in comparison with field observations for three years, the latter data being given with confidence intervals (95%). For each year the simulated and observed total population density curves are in good correspondence during the phase of rapid growth. Also for every year, the period of flattening is in reasonable agreement, although the collapse of the aphid population curve in 1977 due to *Entomophthora* spp. has not been simulated because of the absence of this pathogen in the model. In 1975 and 1976, the collapse of the epidemic is reasonably simulated with exception of the very last part of the population curve. At this phase, parasitism,

Table 9. Disappearance of aphids in numbers per tiller in 1976 caused by predation, abiotic mortality, and emigration based on model calculations.

Date	Time	Growthstage plant[1]	Mortality		Emigrants (winged females)	Actual number of aphids (total)
			predation and parasitism	abiotic		
24 May	5	10	0	0.001	0	0.3
29 May	10	10.1	0	0.004	0	0.4
	15	10.2	0	0.03	0	1.5
	20	10.3	0	0.05	0	5.6
	25	10.5.1	0.2	0.3	0.02	13.6
	30	10.5.2	4.0	1.0	0.27	40.6
	35	10.5.3	25.0	5.9	5.4	68.4
	40	11.1	99.8	12.2	20.0	22.3
9 July	45	11.1	119.6	13.3	24.1	5.0
	50	11.2	121.3	13.4	26.0	4.1

[1] Feekes scale.

Tabel 9. Verdwijnen van de bladluizen in aantal per halm in 1976 veroorzaakt door predatie, abiotische mortaliteit en emigratie volgens berekeningen van het simulatiemodel.

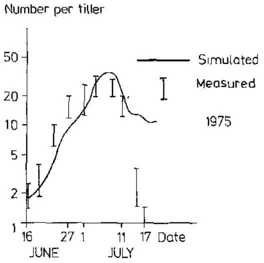
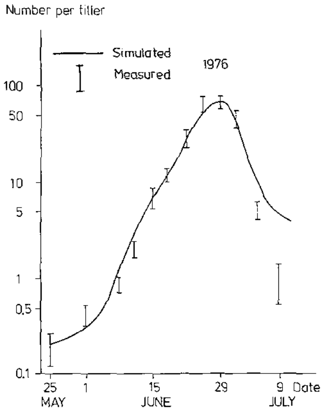
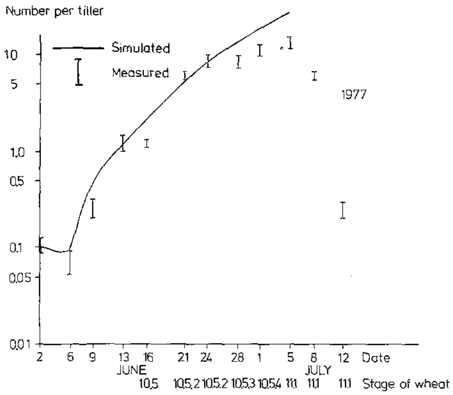


Fig. 12. Simulated and counted total number of *S. avenae* in 1975, 1976 and 1977. The control numbers are given in terms of 95% confidence intervals.

Fig. 12. Gesimuleerd en geteld totaal aantal S. avenae in 1975, 1976 en 1977. De getelde aantallen zijn gegeven met 95% betrouwbaarheidsinterval.





predation, *Entomophthora* spp. and emigration seem very important and the overestimation of the aphid population density in the calculations is probably due to omitting them from the model. However, this seems of minor importance because the incorporated processes like predation and emigration explain most of the population collapse. The population collapse triggered by emigration of alatae is amplified by biotic mortality factors. The absence of exact data on predation rate, parasitization rate and *Entomophthora* spp. epidemics makes a detailed incorporation of these aspects in the model impossible. Nevertheless the preliminary simulations of the predator density of *S. corollae* in 1976 correspond reasonably well with field observations (Fig. 13). This is encouraging, but it should be emphasized that the introduced relations on predation rate and numerical response of the predator given in Table 8 are based on estimates and incomplete data of Bombosch (1962).

Another aspect of comparison of simulated and observed population density curves is the age distribution of the aphid population. The number of reproducing females was determined by considering the alatae before physiological plant stage 10.5.1 as immigrants, and those after that stage as alatae developed within the system and thus emigrating from the system. In all three years simulated and observed age distribution of the populations correspond fairly well. The results for 1976 (Fig. 14) agree well with the observations, especially the agreement in the appearance of the first alatiform L_4 is

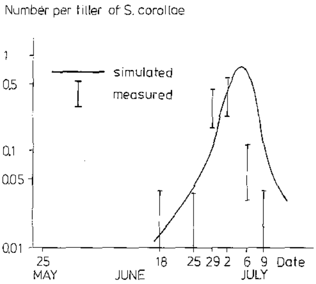


Fig. 13. Simulated and counted number of Syrphid larvae in 1976. The counted numbers are given in terms of 95% confidence intervals.

Fig. 13. Gesimuleerd en geteld aantal zweefvlieglarven in 1976. De getelde aantallen zijn gegeven met 95% betrouwbaarheidsinterval.

Fig. 14. Simulated and counted number of reproducing adults, L_4 and L_1-L_3. The counted numbers are given in terms of 95% confidence intervals.

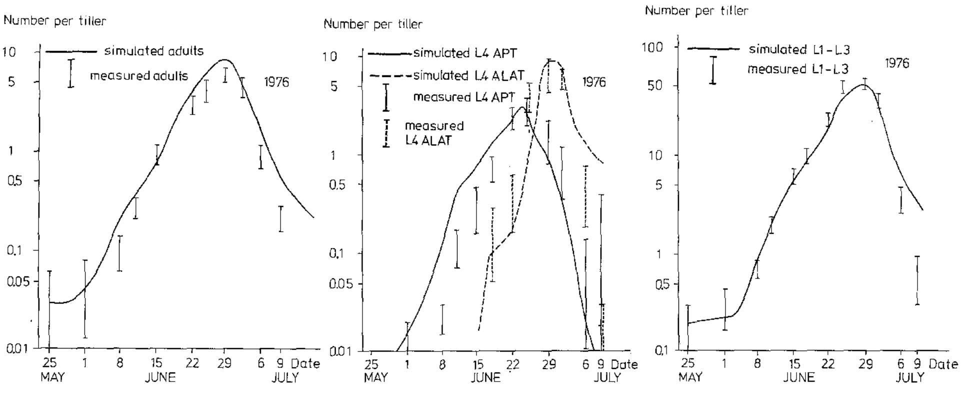


Fig. 14. Gesimuleerd en geteld aantal reproducerende volwassen bladluizen, L_4 en L_1-L_3. De getelde aantallen zijn gegeven met 95% betrouwbaarheidsinterval.

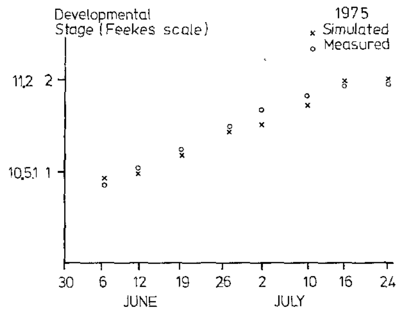


Fig. 15. Simulated and observed development of winter wheat in 1975 on the experimental field. Development expressed in Feekes scale.

Fig. 15. Gesimuleerde en waargenomen ontwikkeling van wintertarwe in 1975 op het proefveld. Ontwikkeling uitgedrukt in Feekes-schaal.

important, as it predicts the beginning of emigration. This correspondence shows that the simulation model may explain the population growth during the first phases of the epidemic rather well. The data from the laboratory trials are apparently sufficient to give model outcomes that agree well with the independent field observations.

There is a similar agreement for the verification of the growth of plants. The way plant development in relation to temperature is introduced is rather primitive. However there is good correspondence between the simulated and observed physiological stages (Fig. 15) and this is another encouraging aspect of the comparison of model output and real data.

4.2 Sensitivity analysis

The correspondence between preliminary model calculations and field observations enables a first sensitivity analysis to be carried out with the model and some testing of hypothesis on the causes of population movements formulated in Section 2. The structure of the system as described in Section 3.2 may be tested by model calculations by omitting some elements. After these calculations, the relative importance of the involved relations on model outputs was determined by changing rates or initial conditions. This sensitivity analysis may help to improve the insight in the system and guide management and further detail studies or field experiments.

4.2.1 Structure of the system. Runs with the model to test structural changes were executed for 1976 and in some cases also for other years.

a) Immigration. From our field observations we can conclude (Fig. 1,2 and 3) that even with a continued aphid flight (Fig. 5) the number of alatae does not increase and immigration comes apparently almost to a stand after flowering. Then immigration only compensates for mortality and no relation between number of alatae and number of L_1 exists. Once the immigration wave has elapsed, the stage for the coming events seems set. The number of alatae per m^2 at flowering stage 10.5.1–10.5.2 calculated from the data of Fig. 1 and Table 1 ranged for $2 \times 10 = 20$ in 1975, $0.65 \times 472 = 307$ in 1976 to $0.32 \times 748 = 239$ in 1977. During the stage before flowering the difference in density between the apterae and the alatae was relatively small in 1976. Moreover the absolute number per m^2 of apterae at flowering stage were rather high in 1976 (180 in 1976, 44 in 1977 and 5 in 1975). Thus the relative importance of the immigrants seems smaller in 1976 than in 1975 and 1977. This reasoning is strengthened by the rapid increase of the density of the apterae in 1976 in comparison with 1975 and 1977 and confirmed by

Fig. 16. Effect of immigration on total number of aphids in 1976 according to the simulation model.

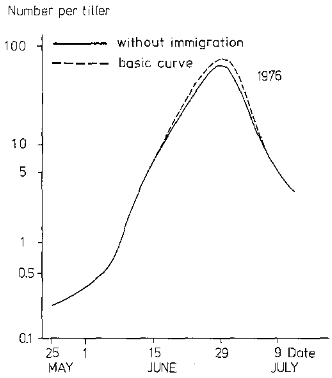


Fig. 16. Invloed van immigratie op het totale aantal bladluizen in 1976 volgens het simulatiemodel.

Fig. 17. Effect of immigration on total number of aphids in 1977 according to the simulation model.

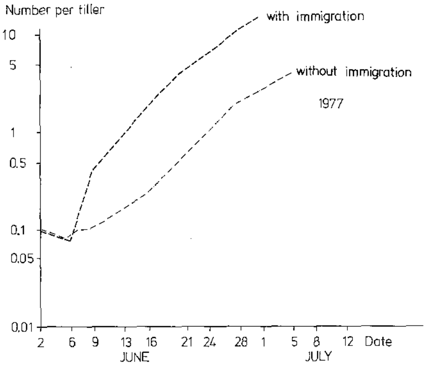


Fig. 17. Invloed van immigratie op het totale aantal bladluizen in 1977 volgens het simulatiemodel.

model calculations. Figure 16 shows that in 1976 ignoring immigration has only a slight effect on the population density curve. In 1977, the immigrants are major factors in the start of the upsurge of the population (Fig. 17).

b) Emigration. The offspring of alatae tend to be apterous like those of non-crowded apterae (Table 4). They constitute the driving force for population growth. The reproduction visualised by the ratio L_1/reproducing females (Table 3) follows closely the trend of number of apterae. These L_1 largely become alatae. The questions are: do these alatae stay in the original field, do they infest new wheat fields and can they be considered as emigrants from the system? Field observations indicate a positive answer to the last question for most of them. No correlation could be found between the huge number of alatae swarming above the crop and the number of L_1 in the crop.

Absence of emigration can only be compensated by predation or other natural enemies when they are already present in considerable numbers in an early stage of population growth.

c) Besides immigration and emigration, the reproduction rate throughout the epidemic may affect the size and composition of the population considerably. Is this rate affected by quality changes in the host plant or by aphid density effects, of by changes in the age of reproducing aphids?

When we consider the ratios between numbers of L_1 to numbers of reproducing females (Table 3) as a measure of reproductive activity, we can see that this ratio remains rather constant throughout the epidemic. A small peak in ratio can be observed near the population peak period, but this is still unexplicable. No indications can be seen that on the older host plant fewer L_1 per adult are produced than on the younger plant. Thus the population collapse cannot be caused by a reduction in reproduction per aphid. Moreover, preliminary results of experiments on reproduction on leaves or on the ear do not indicate that any difference in reproduction rate and fecundity of the aphids exists. Detailed studies of Vereyken (1979) on this subject show that plant condition may affect the reproduction rate considerably. The physiological stage of the plant is in our model considered to be of minor importance. Thus values independent of plant stage can be used for reproduction and temperature is the only driving force.

Age distribution is constantly shifting to populations (Fig. 4) in which older stages predominate. This shift might imply the occurrence of gradually older females with a lower reproduction rate (Dean, 1974). The embryo counts (Table 2), however, indicate that only in the final stage of the epidemic the number of embryos found per female declines. Throughout the major part of the epidemic, this number remains the same. In laboratory trials, the number of embryos steadily declines when more larvae are deposited. The sum of larvae and embryos remains more or less constant (Table 2). Thus the embryo counts give information on the physiological age of the adults. Only young females are present, all still in the phase of their maximum reproductivity rate.

d) Predation and other biotic factors. From field observations alone the effect of predation is difficult to evaluate. *S. corollae*, *C. septempunctata* and *C. carnea* were always present, but usually in rather low numbers except in 1976. Then almost 40% of the tillers contained larvae of *S. corollae*. In our model calculations, the effect of predation is clearer (Fig. 18). During the initial phase of population growth, the influence of predators is negligible but the phase of flattening and collapse is delayed considerably by their absence. The contribution of predation becomes still clearer from Table 9 where the simulated numbers of aphids lost per ear due to predation are given.

The parasites too can be of importance. Their effect seems clear in 1977 when the decrease in the number of adult aphids on 28 June coincides with a high number of mummified aphids (Fig. 7). If we add this number to that of the number of apterae, we come close to the expected number of 2.5 when the population grows unhampered. We can then estimate parasitism at 60 to 70% of the adults. This causes an immediate decline in L_1 production. But for unknown reasons the parasite attack lessened and the aphid population recovered a little before the final collapse.

Hyperparasites may have had an effect on the population collapse of the parasites but since on 30 June not more than 14 hyperparasites and 27 Aphidiids emerged from 41 mummies, hyperparasites may only give a partial explanation. Another explanation

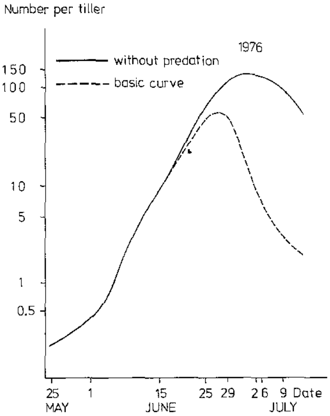


Fig. 18. Effect of predation on total number of aphids in 1976 according to the simulation model.

Fig. 18. Invloed van predatie op het totale aantal bladluizen in 1976 volgens het simulatiemodel.

could be the *Entomophthora* spp. outbreak. From sectioning we found however, that the number of parasitized adults decreased before the sharp increase in *Entomophthora* spp. between 30 June and 6 July. There was no decrease in numbers of mummies in 1975 and 1976 (Fig. 7). In 1976, the mummified aphids at the end of the epidemic were mostly hyperparasitized. Such mummies tend to remain longer on the plant so that population changes of the parasites may be obscured. The role of *Entomophthora* spp. was extremely important in 1977. In all three years, they became apparent only in a late stage of development of the epidemic and consequently contributed most to the collapse but not to the determination of the peak of the population. The epizootic character of the attack by *Entomophthora* spp. seems to explain the sudden population collapse in 1977.

4.2.2 Initial conditions and quantitative relations within the system. The results of the simulations for testing the effect of initial conditions and different rates are presented in comparison with the unchanged model output for 1976. Unless otherwise stated the tendencies determined in this analysis are the same for the other two years.

a. Initialization. Initial population densities may vary by at least 20% without having a considerable effect on the population growth during the rest of the season, as was found from a test with the model in which initial conditions were varied. Populations reach a peak earlier with higher initial numbers and somewhat later with lower initial numbers of aphids. Changes in initial predator densities have a greater effect. A small change in their initial numbers may delay or enhance the collapse of the aphid populations.

b. Rates. Changes in reproduction rate and development rate of the aphids were made within the confidence interval of their measurements. These changes had only a small effect on the course of the population density curves. An increase in reproduction or development rates transferred the total population curve somewhat forward, a decrease caused the reverse effect. Of more importance is the relation between the relative rate of predation and population density. Changes in the place of the breaking point of the functional response curve (Fig. 11) considerably affect the population density curve of the aphids and the syrphid larvae (Fig. 19 and 20). This result emphasizes the importance of more detailed knowledge of the effects of predators and parasites and also shows that the breaking point in the predation rate curve should be determined first.

Tests of changes in the forcing variable temperature showed that a decrease in temperature causes a delay in population growth but that populations finally reach higher densities (Fig. 21). These results may be due to the difference in response to temperature, of development rate of the plant and of the aphid population development rate. Lower temperatures cause a slower development of the plant but not a proportional decrease in population growth so that the latter may continue a little further. A systematic increase in temperature of 2 °C enhances population growth. Thus it is concluded that although temperature deviations may affect the population curve, the effect is only important when there are considerable differences from normal conditions. A difference of 2°C for a monthly average may already be considered as high. The similarity in the results of the field experiments in 1975, 1976 and 1977 in which the average temperatures differed, confirms this statement.

Besides the biotic mortality, abiotic mortality may play a role. Sensitivity runs, in

Fig. 19. Effect of different values for breaking point in functional response curve of *S. corollae* on total number of aphids per tiller.

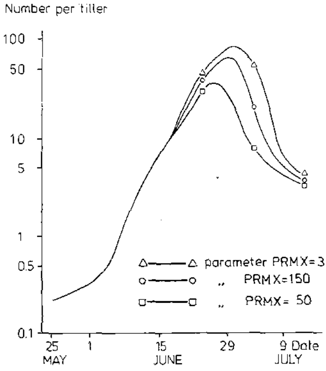


Fig. 19. Invloed van verschillende waarden voor het breekpunt in de functionele reactiecurve van S. corollae op het totale aantal bladluizen per halm.

Fig. 20. Effect of different values for breaking point in functional response curve of *S. corollae* on number of syrphid larvae per tiller.

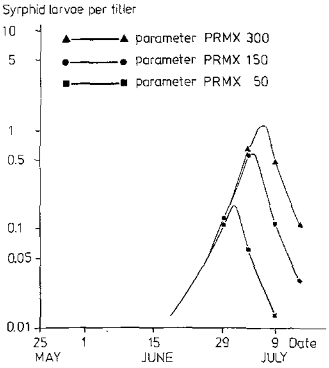


Fig. 20. Invloed van verschillende waarden voor het breekpunt in de functionele reactiecurve van S. corollae op het aantal syrphidelarven per halm.

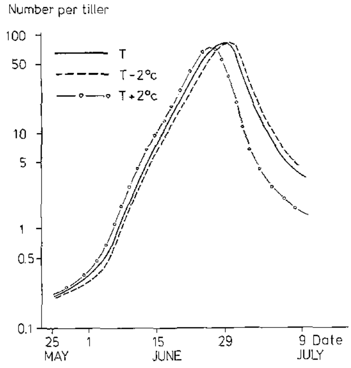


Fig. 21. Effect of temperature on population growth of *S. avenae* in 1976 according to the simulation model.

Fig. 21. Invloed van de temperatuur op de populatiegroei van S. avenae in 1976 volgens het simulatiemodel.

which abiotic mortality was changed by 100%, did not result in large deviations (not more than 5%) of the basic population density curve, probably because the effect of this abiotic mortality in the model was very small. Although the moment of wing induction and alatae formation described by the model is in good correspondence with field observations, the absence of accurate data on this process makes its introduction dangerous. Small changes in the wing induction function dependent on crowding, temperature and physiological age and condition of the plant may strongly influence the population curve.

4.3 Future prospects

Conclusions are difficult because of the lack of knowledge about how the major processes in the system operate; predation, parasitism, epidemics of *Entomophthora* spp., emigration and immigration. All these elements play a role in the course of aphid population growth and their relative contribution may vary. More experimental data on these basic processes are required before the model can be validated more thoroughly. As confidence in the model increases it should be possible to use the model for making forecasts in the field. The preliminary results presented are encouraging but not yet sufficient for decisive statements. The model is not an end in itself but may help to integrate the fragmentary knowledge and guide the necessary experiments. The final aim of model construction is to enable the development of simple formulae that may be used by the extension service or farmers in their planning of crop protection measures. Advice based on extrapolations with the model are possible but still rather inaccurate. But although these forecasts are not very reliable, they are still better than the speculative prognoses which are used today.

Samenvatting

Epidemiologie en simulatie van de populatieontwikkeling van Sitobion avenae op wintertarwe

De toenemende betekenis van graanbladluizen (vooral *Sitobion avenae*), gepaard gaande met een sterke toename van het gebruik van insecticiden op granen maakte verbetering van de prognose over het schadelijk optreden wenselijk. Door gedetailleerde tellingen in het veld (Fig. 1–7) werden gegevens verkregen over het verloop van de epidemie en het optreden van natuurlijke vijanden in 1975, 1976 en 1977.

Een immigratieperiode tot in de bloei kon worden vastgesteld. Daarna lijkt de aantrekkelijkheid van het gewas voor alate luizen te verminderen. De alate immigranten krijgen aptere nakomelingen. Deze vormen de stuwende kracht van de populatiegroei. De nakomelingen van apteren zijn merendeels alaat. Zij verlaten het gewas.

Een model van de populatieontwikkeling gedurende de epidemie werd opgesteld. De relatiediagrammen Fig. 9 en 10 laten groei en ontwikkeling van *S. avenae* en een predator (*Syrphus corollae*) zien. Kwantificering van de betrekkingen werd mogelijk door literatuurgegevens en laboratoriumexperimenten.

Met het model kon de populatieontwikkeling van *S. avenae* vanaf begin juni tot aan de populatiepiek in 1975, 1976 en 1977 vrij goed worden gesimuleerd (Fig. 12). Ook de populatieopbouw kon worden gesimuleerd (Fig. 14). De teruggang van de populatiedichtheid blijkt moeilijker te voorspellen door het ontbreken van gegevens over natuurlijke vijanden.

Het lijkt waarschijnlijk dat in de toekomst met het model een prognose over de piek van de bladluispopulatie circa 3 weken tevoren mogelijk zal zijn.

Acknowledgements

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