SIMULATION MODELS OF THE POPULATION DEVELOPMENT OF SITOBION AVENAE

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Abstract

Two models simulating the population development of Sitobion avenae are described. The output results from the models are compared with field observations from the Netherlands and England over a number of years. The agreement between the models and the field results is not always good but in several years the date and size of the peak density is accurately predicted. This indicates that most of the important processes are included in the model, but certain parts of the system are not fully understood. Sensitivity analysis shows that immigration and wing induction of the aphids on the crop are important processes acting on the population build-up and crash respectively. The models are reliable enough to be used for short term predictions.

Description

Two models simulating the population development of Sitobion avenae exist; one developed in England and written in FORTRAN IV (Carter, 1978; Carter et. al., in prep.), the other in the Netherlands and written in CSMP III (Rabbinge et. al., 1979).
The initial inputs for the two models are similar. They include the initial number of aphids, determined either from suction trap catches or from field counts respectively, the latitude of the site (this is used in the calculations of daylength), the initial crop development stage (metric scale), the natural enemy data, which is either the number of coccinellids and the percentage parasitism and disease or the number of syrphids respectively, and daily maximum and minimum temperatures.
Both models simulate population growth only on cereals. Temperature and crop development stage are the major driving variables. Temperature is calculated for each step using a sine curve passing through the minimum temperature at sunrise and the maximum temperature at 14.00. The step lengths of the two models are short, one hour for the English model and approximately 15 minutes for the Dutch one. These short steps are dictated by the rapid development of the aphids at optimum temperatures.
Immigration into the cereal crops depends on the size of the aerial population, whose origin is unknown. The settling behaviour of these alate aphids has not been studied but it probably depends on the crop development stage and the aphid density. In the English model it is assumed that the suction trap catches are an accurate representation of the aerial population and can be used to initialise the model. The trap catches are multiplied by two factors: the first can be called the Taylor-Palmer coefficient (Taylor and Palmer, 1972). In the model it is 64, ie. for each aphid caught in the trap 64 settle per million tillers. This assumes a flight duration of two hours, a density-height profile of -1.0 and one and a half million tillers per acre (or ca. four and a half million tillers per hectare).
The second factor, the concentration factor, is the increase in the number found in the crop to what is expected from the calculations of Taylor and Palmer. This factor is set at 40 and appears constant from year to year.
Development and survival is based on the data from Dean's work using barley

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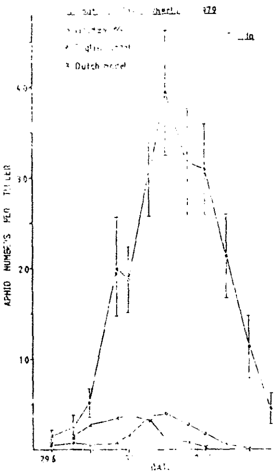
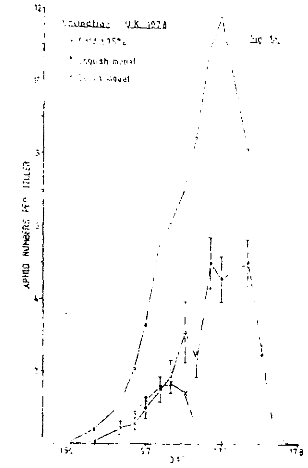

Dutch model
APHID NUMBERS PER TILLER
40
30
20
10
29 6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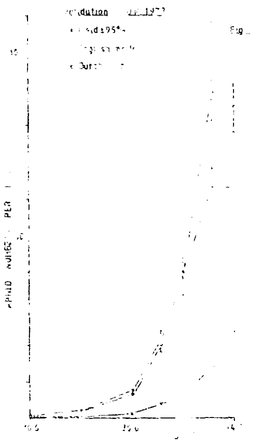
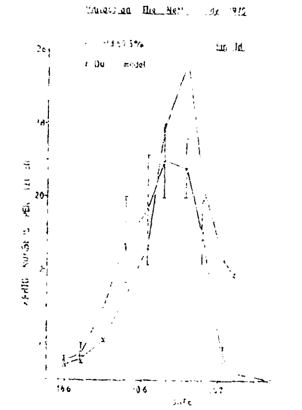
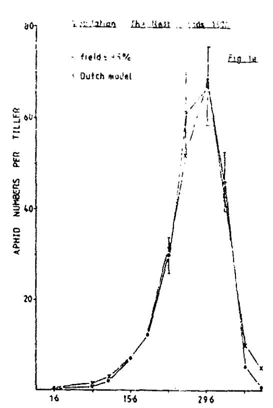
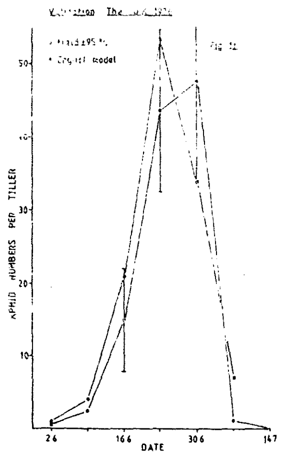





field ± 95%
Dutch model
APHID NUMBERS PER TILLER
80
60
40
20
1 6
15 6
29 6
DATE


English model
APHID NUMBERS PER TILLER
50
40
30
20
10
2 6
16 6
30 6
14 7
DATE

leaf discs (Dean, 1974), although this is supplemented in the Dutch model by measurement on whole plants (Ankersmit, unpubl.). More experimental data on these processes are however needed. Development is dependent solely on temperature while survival depends on temperature and crop development stage (see Watt, 1979). In the Dutch model development is handled in a more complicated way; instead of using the mean values for development it uses an associated standard deviation to mimic dispersion. The data for reproduction come from Dean's work (English model) or from Ankersmit (unpub.) (for the Dutch model). In the English model it depends, not only on temperature but also on crop development stage and this latter factor has now also been incorporated into the Dutch one. Much of the information for this comes from Watt (1979). Crop condition is however not included. Morph determination in the English model occurs at birth and is controlled by a multiple regression equation dependent on crop development stage and aphid density. This equation has been calculated directly from field data and this aspect of the system is in need of further experimentation. A similar approach is used in the Dutch model. After the alatiform nymphs have moulted to the adult stage they emigrate immediately without making any reproductive contribution.
The natural enemies are treated in a simple way. In the English model actual field observations are used in the model, while in the Dutch one predation by syrphids is calculated using a simple functional response curve. The numerical response of the syrphids is handled in a simplified way too, assuming an aphid density dependent reproduction rate. The role of natural enemies in controlling aphid population growth is still a controversial subject and will remain so until detailed quantitative experiments are carried out. Crop development is carried out by integration of development rate over time dependent on temperature.
Output from both models is daily (although this can easily be changed to give more or less frequent output) providing information on the number of aphids (morphs and instars), the number of natural enemies or the number of aphids killed, and crop development stage. These results can be compared directly with field results to validate the models or can be used to provide information which is not measureable in the field. Obviously this latter process can only be used if the model has been shown to be reliable and accurate.

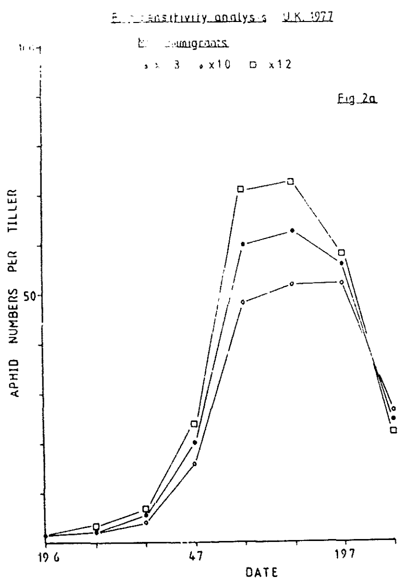
Validation

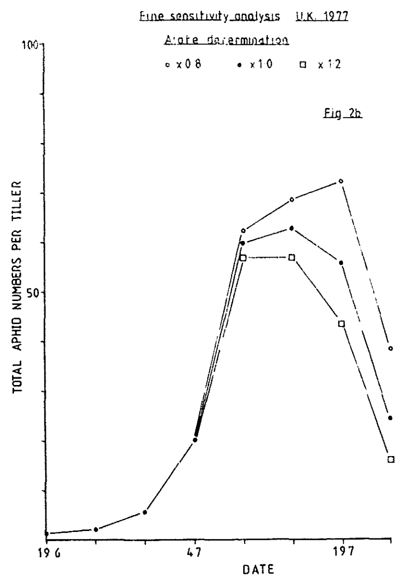
The simplest way to validate a model is to compare output with independent field observations. This has been done with the two cereal aphid models. Both were compared with the results from field observations in England (1977 and 1978) and the Netherlands (1979). The Dutch model is also compared with Dutch field results from 1975 and 1976 and the English model with English field results from 1976.
As the English model uses suction trap catches to initialise it this section of the model has to be validated in detail. This was done by comparing the alate numbers in the model with those in the field (U.K. 1977). The fit is reasonable, with the model predicting the correct number of alates early in the season. Later in the season many of the alates are produced on the crop, thus the model will underestimate this level. This is only important if these alates remain and make a major contribution to reproduction.
Both models underestimate the field results from the Netherlands (1979) by an order of magnitude (fig. 1a). Problems were encountered with the crop development sub-model in both models as the crop ripened much quicker than in the field. The sub-model has been changed in the English version but not in the Dutch one at present. This is reflected in the early decline

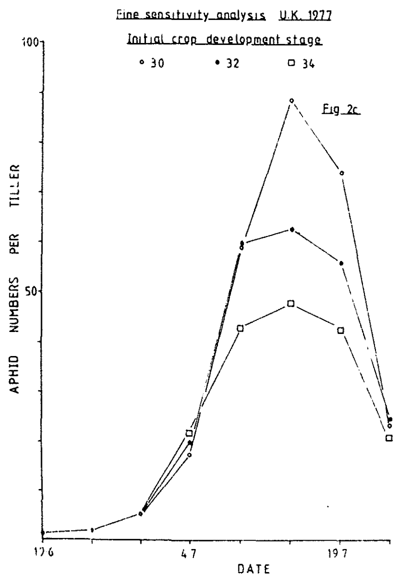
in the Dutch model. This also occurs with the results from England in 1978 (fig. 1b). The Dutch model gives an accurate prediction of the observed results at the beginning of the season (unlike the English model which overestimates the population development) but declines early as the crop, in the model, ripens too quickly. The English model simulates reasonably well the shape of the curve of the observed results. Validation of the models using the field results from England in 1977 presents a further problem. The English model gives a reasonable fit to the data but the Dutch model underestimates the population growth. (fig. 1c). This is due to the lengthy continuous immigration period in this year, which is not taken into account in this simulation. In other years, when this is taken into account, the Dutch model gives better predictions eg. in the Netherlands 1975 (fig. 1d), 1976 (fig. 1e), while the English model gives a reasonable fit to the English data from 1976 (fig. 1f). This indicates that although our knowledge of the system is not complete we do know enough to gain insight by using the models.

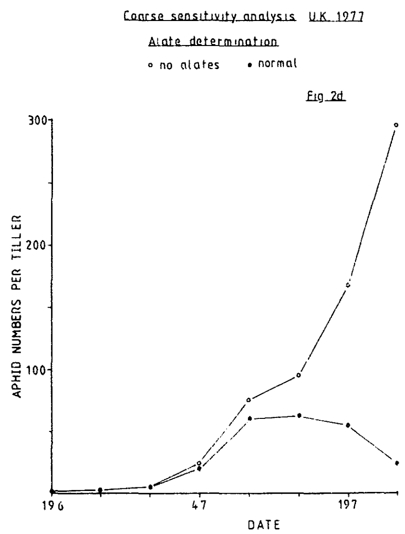
Sensitivity Analysis

Sensitivity analysis can only be carried out with models which have been validated, otherwise the conclusions are not very meaningful. It can be done in two ways; by making small changes (the size of which is dictated by the standard deviation of the observed results) to initial conditions, rates, variables and parameters (fine sensitivity analysis) or by omitting processes from the system (coarse sensitivity analysis). Sensitivity analysis determines the importance of processes in the system so that research can be concentrated on the main ones. By increasing and decreasing values the symmetry of the response can be evaluated - if the response is asymmetrical then that variable has a complicated effect in the system. Firstly the effect of dispersion of development in the Dutch model was evaluated. This was done by running the model with and without it. The effect of removing the process is insignificant and this is explained by the small standard deviations associated with the development rates. It is therefore not necessary to include dispersion in the English model. The rest of the sensitivity analysis concentrates on the English model using the 1977 English field results (as this combination gives a good fit). There were very few predators and parasitoids in this year so the system is basically a host plant-aphid one. Attention is centred on the role of alates in the population build-up and collapse.
Carter et. al. (in prep.) and Rabbinge et. al. (1979) discuss the results of sensitivity analysis on other processes, such as reproduction, survival and development. The sensitivity of the system to small changes in immigration was tested by altering the number of immigrating alates by +/- 20%. Next the initial crop development stage was changed by +/- 2.0. This studies the effect of the timing of immigration in relation to the crop development stage. It is important to know how sensitive the system is to these changes as all the crops in an area will not be synchronous. The other important process concerning alates is the determination of the alatiform:apteriform ratio. This was tested in two ways; by altering the proportion of alatiform nymphs by +/- 20% and by removing the process (wing induction) from the system. It must be remembered however that there are no intra-specific competition effects in the model at present. If these were present then the effect of removing the alatiform section of the model would be smaller.
Altering the number of immigrants and the proportion of alatiform nymphs has much the same effect (fig. 2a, b). The timing and size of the peak density is affected. By decreasing immigration or the proportion of alatiform nymphs the data of the peak is delayed by over one week. This is


sensitivity analysis U.K. 1977
x10 x12
Fig 2a
APHID NUMBERS PER TILLER
50
19 6
47
19 7
DATE


Fine sensitivity analysis U.K. 1977
Alate determination
x 0 8 x 1 0 x 12
Fig 2b
TOTAL APHID NUMBERS PER TILLER
100
50
19 6
47
19 7
DATE


Fine sensitivity analysis U.K. 1977
Initial crop development stage
30 32 34
Fig 2c
APHID NUMBERS PER TILLER
100
50
17 6
4 7
19 7
DATE


Coarse sensitivity analysis U.K. 1977
Alate determination
no alates normal
Fig 2d
APHID NUMBERS PER TILLER
300
200
100
19 6
47
197
DATE

probably because in the original simulation the data of the peak is not very distinct. The aphids maintain a constant density for over one week. Increasing immigration or the proportion of alatiform nymphs does not alter the data of the peak. The peak density is changed by +/- 15% for a 20% change in immigration but the response to changes in the proportion of alatiform nymphs is asymmetrical. Decreasing the proportion increases the peak by 15% but increasing the proportion leads to a reduction of only 5%. This is because a proportion of 1.0 in the original model remains at 1.0 in the sensitivity analysis, ie. a proportion of 1.2 would lead to an artificial increase in reproduction. Altering the initial crop development stage changes the size of the peak density and its timing (fig. 2c). With the latter the response is complicated as both changes lead to a delay in the peak density. This is due to the dependence of alatiform determination on aphid density and crop development stage, and the effect of the latter on other processes in aphid biology, ie. reproduction and survival. The peak densities occur at different crop development stages. The peak density is altered asymmetrically, a lower initial development stage increases the peak density by 45% while a higher initial stage reduces the peak by 23%. Removing alate determination from the system has a very dramatic effect. The peak density is increased by more than five times and its timing is delayed by over one week (fig. 2d). Thus this is very important in determining the decline of the population.

Discussion

The models do not always give a good fit to data from a number of different places in different years. This is because several parts of the system are in need of further study, ie. aphid biology on wheat, the role of natural enemies and the effect of crop development. Simulation models are not an end in themselves but only a means to an end; and we believe the only means for a thorough aphid study. The models have already helped with experimental work. The English model has demonstrated the usefulness of the suction traps in determining the timing and size of immigration. The models also indicate the importance of alate determination in the decline of the aphid populations. This process can only be studied in the field by counting the number of apteriform and alatiform fourth instar aphids. It is unreliable to use counts of adult alates to measure this process as it appears that the alates leave the crop soon after moulting. As our knowledge of the system improves so the predictive value and usefulness of the models will increase. Simulation models are not a replacement of field and laboratory studies but they do help to pinpoint areas where attention should be centred. The models are reliable enough to be used for short term prediction purposes.

REFERENCES

Carter, N. (1978), Unpub. Ph.D. thesis, University of East Anglia.
Carter, N., Rabbinge, R. and Dixon A.F.G. (in prep.) Simulation Monograph series, PUDOC, The Netherlands.
Dean, G.J. (1974), Ann. appl. Biol. 76: 1-7.
Rabbinge, R., Ankersmit, G.W. and Pak, G.A. (1979), Neth. J. Pl. Path. 85: 197-220.
Taylor, L.R. and Palmer, J.M.P. (1972), in Aphid Technology (ed. H.F. van Emden), Academic Press, London, 189-234.
Watt, A.D. (1979), Ann. appl. Biol. 91: 147-157.