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The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). XXXI. Simulation studies of population growth of greenhouse whitefly on tomato.

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Abstract

Population growth of the greenhouse whitefly, *Trialeurodes vaporariorum*, on tomatoes was simulated using the model developed by Hulspas-Jordaan and Van Lenteren (in press). After some technical improvements, a sensitivity analysis was performed to evaluate the effects of temperature and several life-history components on population growth. Whitefly populations increase almost exponentially. The population growth rate is strongly influenced by temperature, duration of development, oviposition frequency and female sex ratio, whereas the influence of other life-history components – mortality in developmental stages, maturation period for adults and mean longevity of adults – is not strong.

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1. Introduction

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Homoptera, Aleyrodidae) is one of the most important pests in greenhouses worldwide (Van Lenteren and Woets, 1988). This pest is efficiently controlled by seasonal inoculative releases of the aphelinid parasite *Encarsia formosa* Gahan, mainly in European countries (Vet et al., 1980; Eggenkamp-Rotteveel Mansveld et al., 1982; Van Lenteren and Woets, 1988). The current biological control program was developed to a large extent based on a trial – and – error method by tests in experimental and commercial greenhouses (Woets, 1978; Van Lenteren, 1983).

To develop optimal control programs in which parasites are released in right numbers at the best moment, a quantitative description of the host plant – host – parasite system is a necessity. To reach this goal, Hulspas-Jordaan and Van Lenteren (in press) developed a simulation model to describe the tomato – whitefly system. The model is a state variable model to simulate population growth of whitefly on tomato.

The aim of this paper is to report and discuss the results of simulations and a sensitivity analysis. With the sensitivity analysis, we can obtain insight in how strongly different components of the life history influence population growth. Further, it is a very useful tool for generating ideas how to develop efficient biological control programs, because a sensitivity analysis indicates changes of which parameters in the system have the largest influence on whitefly population growth reduction.

2. Improvement of the model developed by Hulspas-Jordaan and Van Lenteren

The details of the original CSMP model are given by Hulspas-Jordaan and Van Lenteren (in press). The development of the whitefly is described in a socalled boxcar train procedure (Goudriaan, 1986; De Wit and Goudriaan, 1978), whereas the ageing and oviposition process of adults are described in Fortran.

The model was improved to enable more efficient simulations. In the original model, the INDEX feature (De Wit and Goudriaan 1978) is frequently used. Although use of the INDEX feature is convenient in CSMP programming, it is not used commonly. The INDEX features in PARAMETER statements were removed by using TABLE statements. The INDEX feature is often used in boxcar train procedures in the original model. In addition, the boxcar train procedure is repeated six times in the original model. The repetition of the boxcar train procedure was simplified by using the subroutine BOXCAR. Since the subroutine is described in FORTRAN, all INDEX features were removed from boxcar train procedures.

Three kinds of boxcar trains are distinguished, i.e. the escalator boxcar train, the fixed boxcar train and the fractional boxcar train. Depending on the dispersion during development that should be mimicked, one of these methods should be used (Goudriaan 1986 and Goudriaan & van Roermund 1988). In the original model, the fixed boxcar train was used because relative dispersions of development at various temperatures were assumed to be constant. However, this assumption is not correct, therefore the model had to be adopted and the fractional boxcar train was introduced to mimick dispersion during development.

The final improvement of the model has been to rearrange a part of data input as an interactive program. This enables researchers to use the program without any knowledge about the details and the structure of the program. The only thing a user has to do is to introduce data of life history, temperature and initial conditions. The interactive program can be used not only for simulating the population growth of whiteflies on tomato but also on other crops.

3. Running the model

The revised model was verified by comparing the simulation results with the observed population growth of whiteflies on tomatoes and with the simulated numbers by the original model. The data on observed population growth were collected by De Ponti (unpublished data). Since the original model has already been verified, the verification of the revised model was done for only one example.



Fig. 1. Simulated population growth of different developmental stages for 30 days (a), 60 days (b) and 90 days (c) at $22^{\circ}C$ constant. The simulation was started with 100 eggs in the first boxcar for the egg stage.

Table 1 shows the result of this verification. The calculated numbers of empty pupae in the revised model were in the range of 1.6% of those in the original model. Therefore, the revised model is expected to have the same ability of prediction as the original model.

To figure out the trend of the population growth of whiteflies, the population growth at 22 °C constant was simulated using the revised model. Numbers of eggs, first, second, third and fourth instar larvae, pupae and adults were calculated for 90 days. The simulation was started with 100 eggs in the first boxcar for eggs. The population of each developmental stage showed an oscillating increase for about two generations (Fig. 1a, b), and then showed an almost exponential growth (Fig. 1c).

Table 1. Verification of the revised model. The numbers are observed data of empty pupae on glasshouse tomatoes and calculated values using the original model and the revised model.

| | Observed | original model | revised model | |
|--------|---------------------|----------------|---------------|--|
| Day 40 | 4,134 | 4,060 | 3,996 | |
| Day 61 | 14,990 | 17,870 | 17,969 | |
| Day 83 | 310,808- 474,227 | 296,620 | 298,519 | |

4. Sensitivity analysis

Sensitivity analysis is the systematic investigation of the effect of changing the values of parameters in a model to find the sources of variation in behaviour of the model.

Sensitivity analysis was performed on the following variables for the life history: duration of development (DU), mortality of developmental stages (TMR), oviposition frequency of adults (OVI), mean longevity of adults (LON), maturation period of adults (MAT), and female sex ratio (SEX). In the sensitivity analysis, the original value of one of the parameters was multiplied by multiplication factors (MF), whereas other parameters were not changed. Values of multiplication factors for duration of development were 1.2, 1.1, 0.9 and 0.8, while for other parameters, they were 1.5, 1.2, 0.8 and 0.5. These values were selected, as they cover about 67-95% of the confidence interval of the original values for the parameters. All simulations were initiated with 100 eggs in the first boxcar for the egg stage. The simulations were performed for 80 days under a constant temperature of 22 °C.

Another sensitivity analysis was carried out to evaluate the effect of the variation in temperature, which is the most dominant driving variable for whitefly population growth. Simulations were performed under temperature conditions of 15, 20, 25 and 30 °C constant. All other conditions of the simulations were the same as for the sensitivity analysis of the variables of life history.

The results of the sensitivity analyses are shown in Fig. 2-8 and summarized in Table 2 and 3. The figures show the population growth in terms of the total population numbers (the total number of eggs, larvae, pupae and adults). The tables show the total population numbers at the end of the simulations. Fig. 2-7 show that variations in duration of development, oviposition frequency and female sex ratio have the strongest effects on the population growth rate, whereas variations in mortality of developmental stages, mean longevity of adults and maturation period of adults have slight effects. However, the trends of exponential growth are consistent at least in the later part of the simulations, so that the final values indicated in Table 2 and 3 are considered to reflect the population growth rate. Table 2 also includes the relative differences in each run from the reference model. The behaviour of the model was most sensitive to the variations in duration of development, then to oviposition frequency of female adults, and sex ratio and was almost not sensitive to the variations in mortality of developmental stages, mean longevity of adults and maturation period of adults. The results of changes in oviposition frequency and sex ratio were identical for the same multiplication factors. Fig. 8 and Table 3 show the result of sensitivity analysis to evaluate the effect of temperature. The variation in temperature has a large effect on the population growth. For example, the

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decrease in temperature from 22 °C to 20 °C resulted in a 63%-reduction in the numbers at day 80.



Fig. 2. Simulation results for the total population number of whitefly when the duration of development is multiplied by 0.8, 0.9, 1.0 (reference model), 1.1 and 1.2.



Fig. 3. Simulation results for the total population number of whitefly when the mortality of developmental stages is multiplied by 0.5, 0.8, 1.0 (reference model), 1.2 and 1.5.

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Fig. 4. Simulation results for the total population number of whitefly when the oviposition frequency is multiplied by 0.5, 0.8, 1.0 (reference model), 1.2 and 1.5.



Fig. 5. Simulation results for the total population number of whitefly when the mean longevity of adults is multiplied by 0.5, 0.8, 1.0 (reference model), 1.2 and 1.5.

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Fig. 6. Simulation results for the total population number of whitefly when the maturation period of adults is multiplied by 0.5, 0.8, 1.0 (reference model), 1.2 and 1.5.



Fig. 7. Simulation results for the total population number of whitefly when the female sex ratio is multiplied by 0.5, 0.8, 1.0 (reference model), 1.2 and 1.5.

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Fig. 8. Simulation results for the total population number of whitefly under different constant temperature conditions of 15°C, 20°C, 22°C (reference model), 25°C and 30°C.

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Table 2. Sensitivity analysis to evaluate the variation of life history parameters, DU = duration of development; TMR = mortality of developmental stages; OVI = oviposition frequency; LON = mean longevity of adult; MAT = maturation period of adults; SEX = female sex ratio. MF = value of the multiplication factor. Simulations were started with 100 eggs in the first boxcar for eggs. Numbers indicate the total population number at day 80. The numbers in parentheses are relative differences expressed as percentage from the values in the reference model.

| MF | DU | TMR | 0VI | LON | MAT | SEX |
|-----|--------------------|--------------------|--------------------|-------------------|--------------------|--------------------|
| 0.5 | | 115,304 (+23%) | 25,203 (-73%) | 78,931 (-16%) | 100,686 (+7.8%) | 25,203 (-73%) |
| 0.8 | 301,177 (+222%) | 101,669 (+8.8%) | 60,953 (-35%) | 90,261 (-3.4%) | 96,260 (+3.0%) | 60,953 (-35%) |
| 0.9 | 149,091 (+60%) | | | | | |
| 1.0 | 93,416 | 93,416 | 93,416 | 93,416 | 93,416 | 93,416 |
| 1.1 | 55,737 (-40%) | | | | | |
| 1.2 | 29,948 (-68%) | 85,778 (-8.2%) | 132,793 (+42%) | 95,258 (+2.0%) | 90,613 (-3.0%) | 132,793 (+42%) |
| 1.5 | | 75,385 (-19%) | 204,851 (+119%) | 96,861 (+3.7%) | 86,516 (-7.4%) | 204,851 (+119%) |

Table 3. Population growth of the whitefly on tomatoes under different temperature conditions. The numbers show the total population number at day 80, and the ratio to the value at 22° C expressed as percentage.

| | Temperature (°C) | | | | | |
|---|------------------|--------|--------|---------|---------|--|
| | 15 | 20 | 22 | 25 | 30 | |
| Number at day 80 | 3,340.5 | 34,568 | 93,416 | 262,332 | 999,182 | |
| Ratio to the value at $22^{\circ}C(\%)$ | 3.58 | 37.0 | | 281 | 1,070 | |

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5. Discussion

The population growth of whiteflies at constant temperatures first showed an oscillating increase and then an exponential growth. It seems likely that it is realistic up to a certain extent, because the model lacks any effects of density dependence or any effects of age of host plant or deterioration of the host plant due to high whitefly densities. As the final aim of the model is to generate whitefly and *Encarsia formosa* population dynamics, we have not yet included effects that occur at extremely high whitefly densities. Such densities are usually not reached when Encarsia formosa is applied as a biological control agent. In the present model, temperature is the only driving variable. The kind of agestructured population system modelled here can be compared with the socalled Leslie matrix model (Leslie 1945). In the matrix model, the numbers of organisms in various age classes are described by a vector and this vector is changed by multiplication with a transition matrix. If all elements of the matrix are constant, which means constant parameter values of life history, the matrix model shows almost the same behaviour as that of the system in this study (e.g. Emlen, 1984). However, constant environmental conditions may not always occur and thus the transition matrix has to be adopted at every multiplication. This is a complicated affair and therefore the more flexible method using the boxcar procedure seems more appropriate. In the greenhouse, temperature is more constant than in the field and threshold temperatures for whitefly development are usually not reached. Hence, we can expect exponential population growth of whiteflies in the greenhouse until density effects in whiteflies show up.

The importance of the comparison of the innate capacity of population increase between the host and the natural enemy is stressed in the evaluation program of natural enemies used for seasonal inoculative releases, the type of biological control applied in greenhouses (Van Lenteren 1986, 1987). In such release programs effective natural enemies must, besides other characteristics, have a larger potential of population increase than the hosts. An interesting deduction from this hypothesis is that biological control will be more feasible if the population growth rate of the host is reduced by factors other than parasitization, on the assumption that the natural enemy still keeps the same potential of population increase. The results of the sensitivity analyses indicate which components of the life history of whitefly are having a large effect on changes in population increase.

Duration of development, oviposition frequency, female sex ratio and temperature were shown to be such important components in the sensitivity analysis. The dominant effect of the speed of development on the rate of population increase has already been demonstrated in theoretical works (e.g. Caswell and Hastings 1981). However, the observed variation in duration of development

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in greenhouse and laboratory tests, and in literature data is usually smaller than the observed variation in other components. The standard deviation is usually less than 20% of the mean. Therefore, it might not be easy to find or select a tomato cultivar on which whiteflies develop very slowly. On the other hand, observed variations in oviposition frequency are large. Actually, Hulspas-Jordaan and Van Lenteren (in press) provided data that show the oviposition frequency of whitefly adults to vary in the range of 1 to 9 at 20-25°C. Female sex ratio is assumed to be 50% in the model given by Hulspas-Jordaan and Van Lenteren (in press). This assumption seems to be valid for tomatoes but on other crops, it does not necessarily hold. Li and Li (1983) reported a female biased sex ratio of whiteflies on cucumbers. Yano (unpublished data) also found a female biased sex ratio of whiteflies on tobacco plants. Van Vianen (personal communication) observed different sex ratios of whiteflies on different crops. If the female sex ratio is higher on a crop, it is an additional factor which might make biological control on the crop more difficult. The sensitivity analysis for oviposition frequency and female sex ratio yielded identical results. This is because both factors have the same effect on determining the daily production of eggs which develop into female adults later. Ordinary control measures, including chemical control and biological control, are concerned only with the control of mortality in the developmental stages and of the adults. The sensitivity analysis clearly shows that control via the mortality is not the most efficient way for depressing population growth unless a very high mortality can be realized. It further shows that manipulation of host-plant resistance factors influencing rate of development and oviposition frequency might be a worthwhile new research line. The population growth rate is strongly dependent on temperature. This is also expected from the values of the intrinsic rate of natural increase (r_m) measured in the glasshouse. Work by Van Lenteren and Hulspas-Jordaan (1983a, b) demonstrated that there is a positive linear relationship between the temperature and r_m of the whitefly and the parasite *Encarsia formosa*.

One of the most interesting result of this study is the suggestion to develop partially resistant crops to whiteflies. Breeders should focus on rate of development, oviposition frequency and sex ratio in breeding resistant plants. Biological control of the whitefly by *Encarsia formosa* was considered to be difficult at low temperature (Burnett, 1949; Milliron, 1940). Recently, this picture has changed and a sufficient efficiency of the parasite at low temperature was concluded based on results of fundamental studies (Van Lenteren and Hulspas-Jordaan, 1983b) and control experiments (Eggenkamp – Rotteveel Mansveld et al., 1982; Hulspas-Jordaan et al., 1987). The intrinsic rate of natural increase of *Encarsia formosa* is always larger than that of the whitefly above 12° C. The sensitivity analysis for temperature supports that biological control of whiteflies by *E. formosa* should be possible because the population growth rate of whiteflies is very low and the parasite still has the ability to increase faster than the host.

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