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The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). XXXII. Simulation studies of the population growth of greenhouse whitefly on egg plant, cucumber, sweet pepper and gerbera.

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Contents

Abstract

Population growth of greenhouse whitefly, *Trialeurodes vaporariorum*, on eggplant, cucumber, sweet pepper and gerbera is simulated using the model by Hulspas-Jordaan and Van Lenteren (1988). A sensitivity analysis is used to evaluate the effects of changes in several life-history components and temperature. Based on the result of simulations, the feasibility of biological control by *Encarsia formosa* is estimated. The population growth rates from fast to slow on the different crops are in the following order: eggplant cucumber gerbera = tomato sweet pepper. The population growth rate is strongly influenced by duration of development, oviposition frequency and sex ratio for eggplant, cucumber and gerbera. On the other hand, it is sensitive to duration of development and immature mortality in developmental stages for sweet pepper, a host plant on which immature mortality is normally already very high. Based on these data and experience from tomato, we conclude that biological control seems promising on gerbera and sweet pepper, whereas difficulties are expected on cucumber and eggplant.

1. Introduction

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Homoptera, Aleyrodidae) is successfully controlled by seasonal inoculative releases of the parasite *Encarsia formosa* (Hymenoptera, Aphelinidae) on four greenhouse crops, in circa 15 countries and on a greenhouse area of circa 2300 hectares (Vet et al. 1980; Eggenkamp-Rotteveel Mansveld et al. 1982; Van Lenteren 1983; Van Lenteren and Woets 1988).

To develop optimal biological control programs, a quantitative description of the host plant-phytophagous insect-parasite system is necessary based on reliable biological information. Therefore, Hulspas-Jordaan and Van Lenteren (1988) developed a state-variable simulation model to simulate the population growth of whitefly on tomato. Yano et al. (1988) performed simulations of population growth on tomato using a slightly revised version of Hulspas-Jordaan and Van Lenteren's model. The whitefly population was shown to increase exponentially on tomato at normal greenhouse temperatures. A sensitivity analysis showed that the influence of changes in duration of development, ovipositon frequency, female sex ratio and temperature condition on the rate of population growth was significant.

The populaton growth of whitefly on other vegetables has not been studied as detailed as for tomato. Some data are available for cucumber (Xu 1982; Xu et al. 1984). Based on the limited population data available, it is difficult to estimate the control capability of *E. formosa* on other crops, although it is of high prioity to extend the area under biological control to other crops, such as cucumbers and ornamentals. The model by Hulspas-Jordaan and Van Lenteren (1988) can easily be modified to simulate the population growth on other crops if enough data about life history components are available. A large amount of data about the life history of whitefly on different crops and crop cultivars has been collected at the Department of Entomology, Agricultural University, Wageningen. Detailed data of the life history on gerbera are also available (Dorsman and Van de Vrie 1987).

Van Lenteren (1986, 1987) and Van Lenteren and Woets (1988) proposed characteristics which natural enemies should possess to be useful for seasonal inoculative releases in greenhouses. Their conclusion is that effective natural enemies should have a larger potential of population increase than the hosts, or, if host feeding also occurs, a larger hostkill rate (feeding + parasitization) than the rate of population increase of the host. On tomato, whitefly is currently controlled very effectively by *E. formosa*. The potential rate of population increase of *E. formosa* is higher than that of *T. vaporariorum* on tomato indeed (Van Lenteren and Hulspas-Jordaan 1983). Hence, use of *E. formosa* to control the whitefly on crops where the whitefly population increases more slowly than on tomato is promising unless physical or chemical properties of the host plant hamper the parasite (Li et al. 1987).

This paper reports the results of the simulation studies of the population growth of whitefly on different crops, i.e. eggplant, cucumber, sweet pepper and gerbera, in order to be able to estimate the control succuss of *E. formosa* on these crops. A sensitivity analysis was performed to evaluate the effects of life history components and temperature on the population growth of whitefly.

2. The model

In Hulspas-Jordaan and Van Lenteren's model (1988) the developmental process of whitefly is simulated using the so-called boxcar train method (Goudriaan 1986), whereas the ageing and egg laying process of adults are simulated with fixed delay functions. Yano et al. (1988) improved this model and performed a sensitivity analysis with this improved model to evaluate the effects on population growth of changing several life history components and temperature. The parameters and functions in the improved model were adapted to those for cucumber, egg plant, sweet pepper (two cultivars) and gerbera.

3. The data

All details of model functions and parameters are indicated in Tables 1-3 and Figs. 1-6. Data for all vegetables except for sweet pepper are from J.C. Van Lenteren and A. Van Vianen (unpublished), for gerbera from R. Dorsman (unpublished). Four sets of data for whiteflies on sweet pepper are used, i.e. data of Dutch whiteflies on Dutch sweet pepper (C.V. Tisana), Dutch whiteflies on Hungarian sweet pepper (C.V. Angeli), Hungarian whiteflies on Dutch sweet pepper and Hungarian whiteflies on Hungarian sweet pepper. These data were obtained from the Dutch-Hungarian whitefly profect conducted in 1985-1987 (Van Lenteren et al. in prep.) For convenience and to make comparison possible, functions and parameters for tomato are also indicated in the tables and figures.

Fig. 1 shows the temperature-dependent functions for development of whiteflies on tomato, cucumber, eggplant, and sweet pepper. Only one set of data at a constant temperature or only one series of data at variable temperature were available, therefore the functions that describe the relation between temperature and development on the various crops were extrapolated using the functions for the development on tomato. First, the ratio of the duration of development on a crop to the corresponding duration on tomato was calculated. Then, the temperature-dependent function for the development on tomato was multiplied bij the ratio. Fig. 2 shows the temperature-dependent functions for the development on gerbera with respect to different developmental stages.

Relative dispersions of development and number of boxcars of developmental stages and of adults in pre-oviposition period are given in Table 1 (for further explanation see Hulspas-Jordaan and Van Lenteren 1988 and Yano et al. 1988). Relative dispersions during development of whitefly on sweet pepper and on gerbera were calculated from the original data. For cucumber and eggplant, data on dispersion of duration of development are not available, therefore the data of whitefly on tomato were used. The numbers of boxcars were basically calculated as 0.75/ (relative dispersion). Mortalities of developmental stages on tomato, cucumber, eggplant and sweet pepper are given in Table 2. Temperature-independent mortalities of developmental stages are assumed on these crops (Hulspas-Jordaan and Van Lenteren 1988). On the other hand, temperature-dependent mortalities of developmental stages are used for the development on gerbera (Fig. 3).

The temperature-dependent functions of mean longevity of adults are shown in Fig. 4 and the relative dispersions are given in Table 3. Except for gerbera, the functions were extrapolated according to the method used to calculate the functions for development. In the simulation process of adult ageing, the longevity of adults is assumed to follow a normal distribution with a constant relative

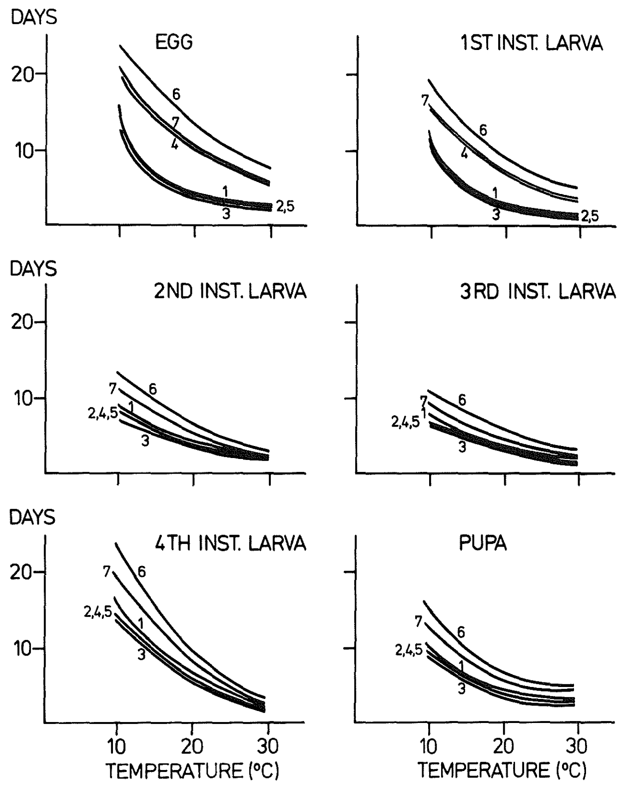


Fig. 1. Developmental period of the whitefly on tomato (1), cucumber (2), eggplant (3) and sweet pepper (4-7: 4 = Dutch whiteflies on Dutch sweet pepper (DW-DSP); 5 = Dutch whiteflies on Hungarian sweet pepper (DW-HSP); 6 = Hungarian whiteflies on Dutch sweet pepper (HW-DSP); 7 = Hungarian whiteflies on Hungarian sweet pepper (HWHSP)).

dispersion. Therefore, the relative dispersion of adult longevity is one of the constant parameters of the model.

In the model the egg laying process of adults is characterized by three basic parameters, i.e. pre-oviposition period, maturation period and oviposition frequency. The definitoins of the parameters are given bij Hulspas-Jordaan and Van Lenteren (1988). The data on pre-oviposition periods are very scarce, so that 1.3 days are taken as a constant preoviposition period of adults on all crops but except for gerbera. On gerbera, a constant pre-oviposition period of 1.0 day is assumed. Figs. 5 and 6 show the temperature-dependent functions of oviposition frequency and maturation period, respectively. Except for gerbera, all the functions were extrapolated from the functions for tomato in the same way as for development and adult longevity.

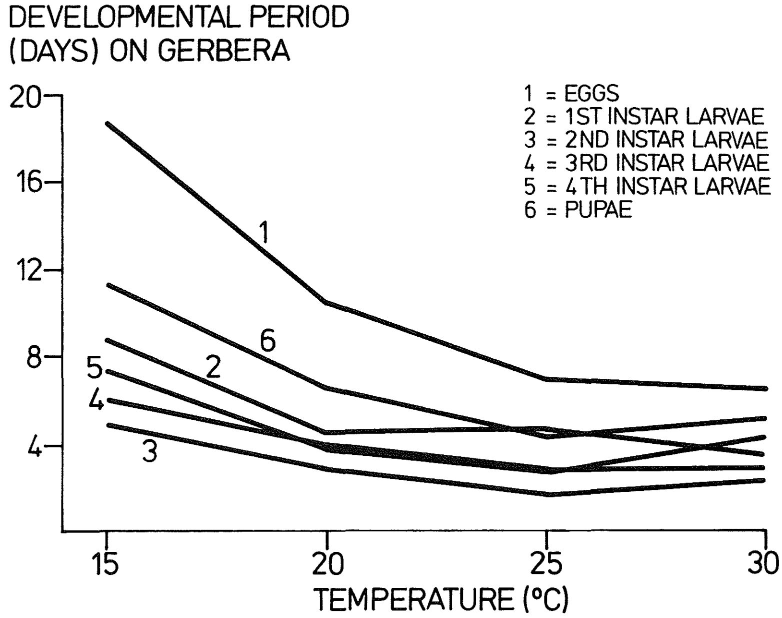


Fig. 2. Developmental period of eggs, 1st, 2nd, 3rd and 4th instar larvae and pupae of whiteflies on gerbera.

Table 1. Relative dispersions, number of boxcars (in parentheses) of different developmental stages. E = egg; L1, L2, L3, L4 = 1st, 2nd, 3rd and 4th instar larva; P = pupa; PRE-OVI = pre-oviposition period of adult

Crop	E	L1	L2	L3	L4	P	PRE-OVI
Tomato	0.13	0.28	0.39	0.50	0.42	0.33	0.50
	(12)	(10)	(5)	(3)	(4)	(7)	(3)
Cucumber	0.13	0.28	0.39	0.50	0.42	0.33	0.50
	(12)	(10)	(5)	(3)	(4)	(7)	(3)
Egg plant	0.13	0.28	0.39	0.50	0.42	0.33	0.50
	(12)	(10)	(5)	(3)	(4)	(7)	(3)
DW - DSP	0.11	0.11	0.44	0.37	0.35	0.35	0.50
	(15)	(8)	(4)	(5)	(6)	(6)	(3)
DW - HSP	0.09	0.09	0.67	0.37	0.29	0.67	0.50
	(15)	(9)	(2)	(5)	(9)	(2)	(3)
HW - DSP	0.09	0.09	0.61	0.59	0.51	0.37	0.50
	(15)	(7)	(2)	(2)	(3)	(5)	(3)
HW - HSP	0.12	0.12	0.36	0.35	0.23	0.27	0.50
	(15)	(6)	(6)	(6)	(14)	(10)	(3)
Gerbera	0.05	0.19	0.30	0.21	0.21	0.18	0.50
	(10)	(7)	(4)	(6)	(8)	(10)	(3)

Table 2. Percentage of mortality of developmental stages on different host plants or cultivars. Mortality is expressed as a percentage of the number entering the developmental stage. E = egg; L1, L2, L3, L4 = 1st, 2nd, 3rd, 4th instar larva; P = pupa.

	E	L1	L2	L3	L4	P	E - P
Tomato	6.1	3.7	2.3	3.3	1.5	1.9	17.5
Cucumber	7.0	2.5	0.0	0.0	0.6	0.6	10.4
Egg plant	4.2	2.2	0.0	0.0	0.0	2.8	8.9
DW - DSP	13.7	7.3	32.7	27.0	11.2	16.7	70.9
DW - HSP	38.1	25.4	25.4	27.5	6.1	14.5	79.9
HW - DSP	13.1	6.6	32.7	66.5	63.8	6.7	93.6
HW - HSP	6.4	3.6	4.3	8.3	15.9	2.7	35.2

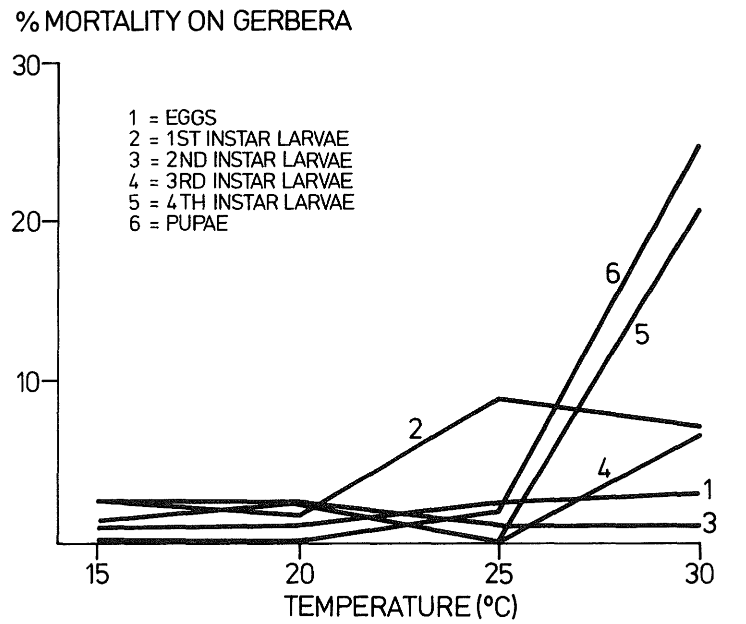


Fig. 3. Percentage mortality of eggs, 1st, 2nd, 3rd and 4th instar larvae and pupae of whiteflies on gerbera.

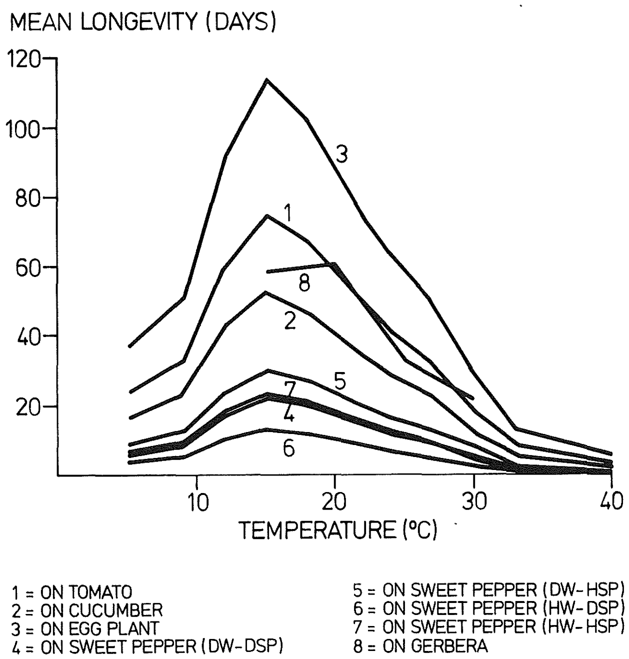
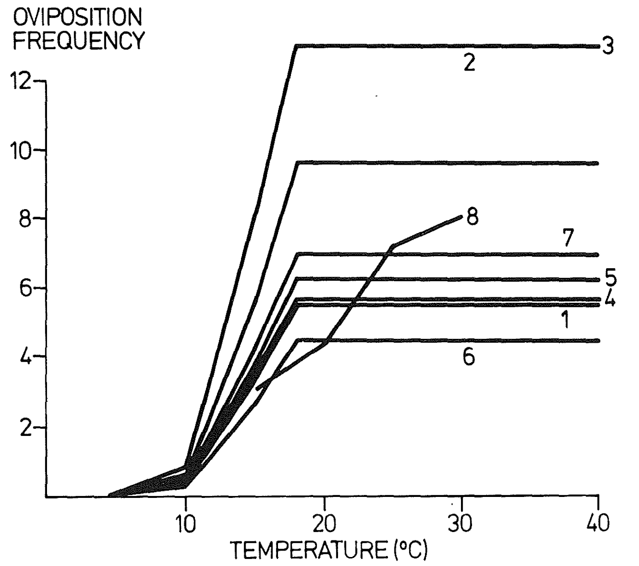


Fig. 4. Mean longevity of adults on tomato, cucumber, eggplant, sweet pepper and gerbera.

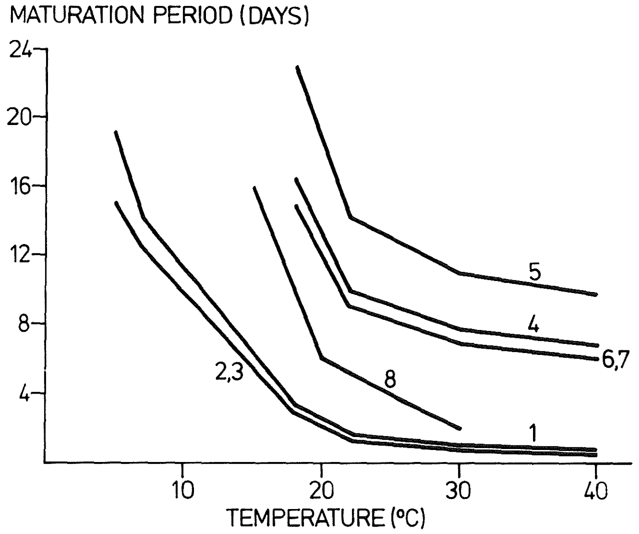
Table 3. Relative dispersions of adult longevity on different crops

	Tomato	Cucumber	Egg plant	DW-DSP	DW-HSP	HW-DSP	HW-HSP	Gerbera
Relative dispersion	0.5	0.4	0.5	1.0	1.0	0.5	0.7	0.5



1 = ON TOMATO
2 = ON CUCUMBER
3 = ON EGG PLANT
4 = ON SWEET PEPPER (DW-DSP)
5 = ON SWEET PEPPER (DW-HSP)
6 = ON SWEET PEPPER (HW-DSP)
7 = ON SWEET PEPPER (HW-HSP)
8 = ON GERBERA

Fig. 5. Ovipositon frequency of adults on tomato, cucumber, eggplant, sweet pepper and gerbera.



1 = ON TOMATO
2 = ON CUCUMBER
3 = ON EGG PLANT
4 = ON SWEET PEPPER (DW-DSP)
5 = ON SWEET PEPPER (DW-HSP)
6 = ON SWEET PEPPER (HW-DSP)
7 = ON SWEET PEPPER (HW-HSP)
8 = ON GERBERA

Fig. 6. Maturation period of adults on tomato, cucumber, eggplant, sweet pepper and gerbera.

4. Population growth of whiteflies on different crops

Population growth on different crops was simulated for 80 days at a constant temperature of 22 °C. All simulations were started with 100 eggs in the first boxcar for eggs. Fig. 7 shows the temporal changes in the total population numbers (the total number of eggs, larvae, pupae an adults) on different crops expressed on a logarithmic scale. The order of the rate of population growth on the different crops is from high to low: eggplant cucumber gerbera = tomato Hungarian whitefly on Hungarian sweet pepper (HW-HSP) Dutch whitefly on Hungarian sweet pepper (DW-HSP) = Dutch whitefly on Dutch sweet pepper (DW-DSP) Hungarian whitefly on Dutch sweet pepper (HW-DSP). On eggplant, cucumber, gerbera and tomato, whiteflies increase almost exponentially at least in the later half of the simulation period. In contrast, on sweet peppers, whitefly population numbers show oscillations. HW-HSP, DW-HSP and DW-DSP show an oscillating increase, HW-DSP does not increase. The numbers after 80 days and the ratio to the number on tomato are shown in Table 4. There are large differences between the population growth rates on different crops and cuiltivars.

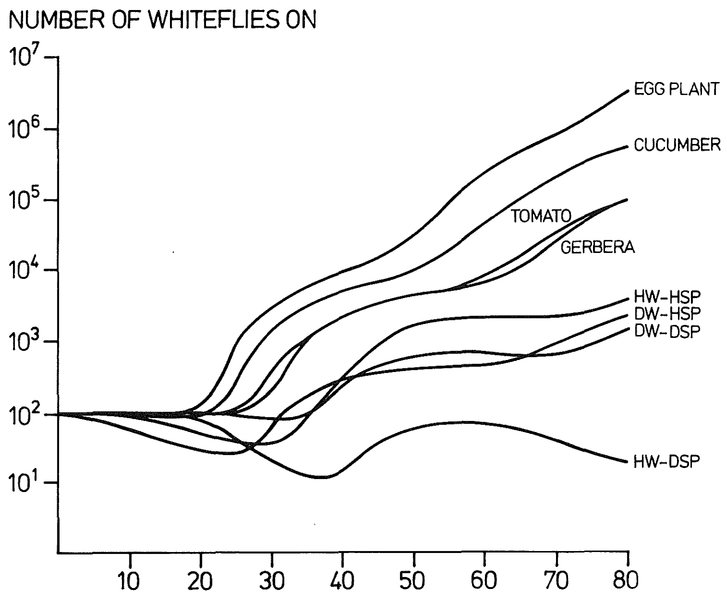


Fig. 7. Population growth of whiteflies on different crops at 22 °C constant. The initial condition is 100 eggs in the first boxcar for eggs.

Table 4. Population growth of whiteflies on different kinds of crops at 22 °C constant. The numbers show the total population numbers (the total numbers of eggs, larvae, pupae and adults) at day 80.

	Tomato	Cucumber	Egg plant	DW-DSP
Number	93,416	537,436	3,270,820	1,473.9
Ratio to the number on tomato (%)	–	575	3,501	1.6
	DW-HSP	HW-DSP	HW-HSP	Gerbera
Number	1,804.2	18.5	3,440.1	94,414
Ratio to the number on tomato (%)	1.9	0.002	3.7	101.1

5. Sensitivity analysis

A sensitivity analysis was performed for evaluating the effects of life-history components and temperature on the rate of population increase. According to the method used for the analysis on tomato (Yano et al. 1988), the influence of change in six life-history components, i.e. duration of development, immature mortality, oviposition frequency, mean longevity of adults, maturation period of adults and sex ratio were evaluated in the sensitivity analysis. Because of lack of data about the normal range of variations in the life-history components, the sensitivity analysis was performed with only two multiplication factors, 1.2 and 0.8. The selection of multiplication factors is based on the values for tomato. The sensitivity analysis for the influence of changes in temperature was performed only in the case of population growth on gerbera at 15, 20, 25 and 30 °C. In the model for cucumber, eggplant and sweet pepper, similarly shaped temperature-dependent functions were used as those for tomato. Therefore almost the same effects of variation in temperature are expected. All simulations in the sensitivity analysis were performed for 80 days under a constant temperature of 22 °C. The initial condition was 100 individuals in the first boxcar of the egg stage.

As the trends of the simulations in the sensitivity analyses – not the population numbers were similar for cucumber, eggplant and gerbera, only data for cucumber are given in figure 8. Population growth is most sensitive to changes in duration of development followed by changes in oviposition frequency and sex ratio on cucumber, eggplant and gerbera. The effects of other life-history components are slight. On the other hand, population growth on sweet pepper is sensitive to changes in all the life history components (Figs. 9 and 10). Changes in mortality of developmental stages is the next important factor to duration of development for DW-SDP, DW-HSP and HW-HSP (Table 5). The effects of changes in oviposition frequency and sex ratio are less important compared with the results for other crops.

Table 5 summarizes the results of the sensitivity analysis. The values for duration of development do not reflect the effect of this parameter correctly because of the effect of phase differences in population oscillations. However, variations in duration of development influence population growth most strongly. The influence of changes in oviposition frequency and female sex ratio on population growth on tomato, cucumber, egg plant and gerbera is also demonstrated. Effect of changes in mortality of developmental stages is significant only on sweet pepper. Fig. 11 and Table 6 show the results of evaluation of the effects of changes in temperature on the population growth on gerbera. The population growth rate for gerbera is highest at 25 °C. Temperature strongly influences population growth on gerbera as well as on tomato.

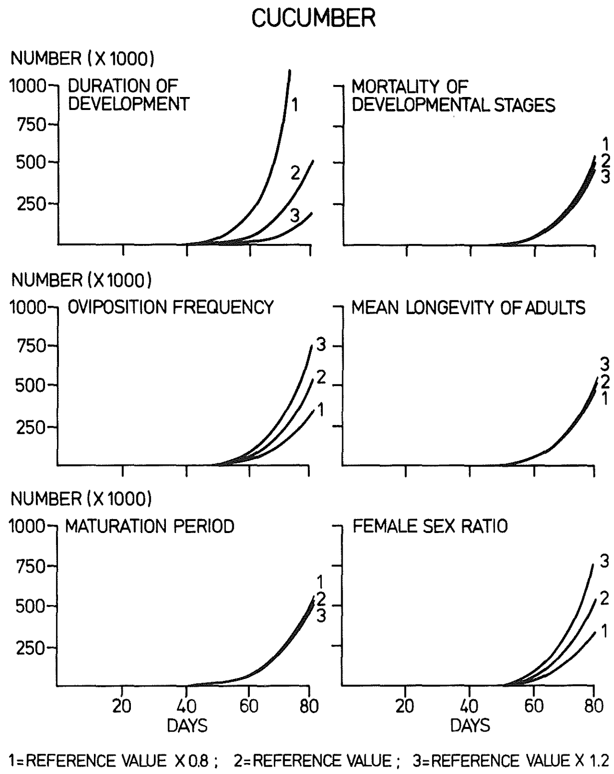


Fig. 8. Simulation results for the total population number (the total number of eggs, larvae, pupae and adults) of whiteflies on cucumber. Duration of development, mortality of developmental stages, oviposition frequency, mean longevity of adults, maturaton period and female sex ratio are multiplied by 0.8 (1), 1.0 (2, reference model) and 1.2 (3).

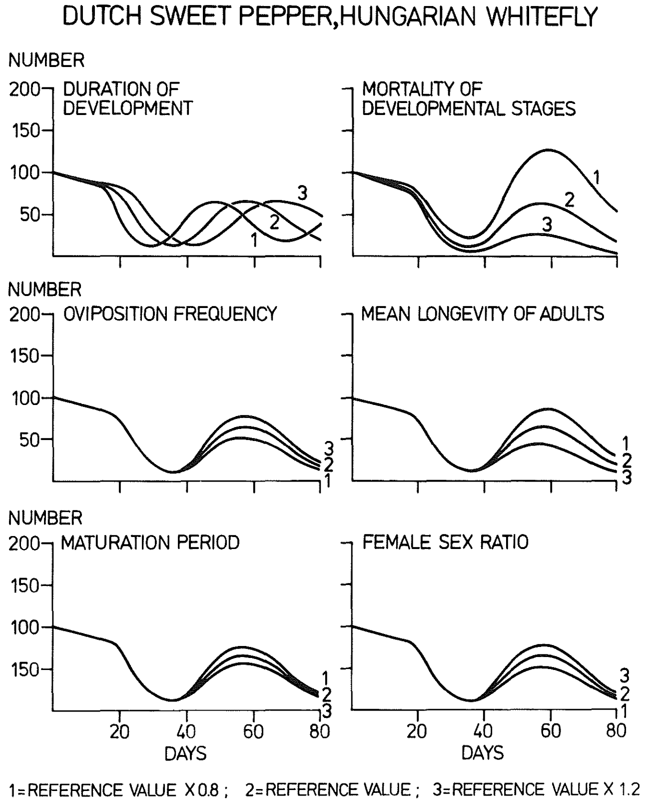


Fig. 9. Simulation results for the total population number of Hungarian whiteflies on Dutch sweet pepper. Duration of development, mortality of developmental stages, oviposition frequency, mean longevity of adults, maturation period and female sex ratio are multiplied by 0.8 (1), 1.0 (2) and 1.2 (3).

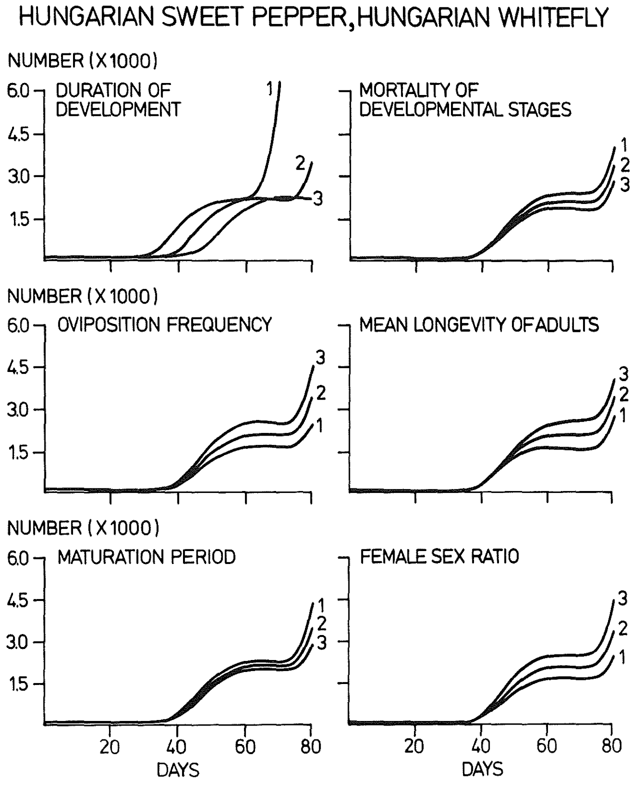


Fig. 10. Simulation results for the total population number of Hungarian whiteflies on Hungarian sweet pepper. Duration of development, mortality of developmental stages, oviposition frequency, mean longevity of adults, maturation period and female sex ratio are multiplied by 0.8 (1), 1.0 (2) and 1.2 (3).

Table 5. Sensitivity analysis of life-history components of whitefly on different kinds of crops. The percentages indicate relative differences of the total population numbers at day 80 to those of reference values.

Crop	Reference value	MF[1]	DU[2]	TMR[3]	OVI[4]	LON[5]	MAT[6]	SEX[7]
Tomato	93,416	0.8	+222%	+ 8.8%	−35%	− 3.4%	+ 3.0%	−35%
		1.2	− 68%	− 8.2%	+42%	+ 2.0%	− 3.0%	+42%
Cucumber	537,436	0.8	+637%	+ 6.0%	−37%	− 6.6%	+ 3.9%	−37%
		1.2	− 61%	− 5.7%	+47%	+ 3.6%	− 3.6%	+47%
Egg plant	3,270,820	0.8	+781%	+ 4.1%	−43%	− 1.3%	+ 7.2%	−43%
		1.2	− 76%	− 4.0%	+59%	+ 0.8%	− 6.5%	+59%
DW-DSP	1,473.9	0.8	+198%	+ 65%	−32%	−20%	+29%	−32%
		1.2	− 60%	− 41%	+39%	+18%	−21%	+39%
DW-HSP	1,804.2	0.8	+ 87%	+115%	−34%	−22%	+27%	−34%
		1.2	− 55%	− 56%	+41%	+17%	−21%	+41%
HW-DSP	18.5	0.8	+101%	+193%	−22%	−41%	+16%	−22%
		1.2	+156%	− 76%	+23%	+52%	−13%	+23%
HW-HSP	3,440.1	0.8	+552%	+ 18%	−28%	−20%	+26%	−28%
		1.2	− 39%	− 15%	+32%	+19%	−17%	+32%
Gerbera	94,414	0.8	+166%	+ 4.4%	−35%	− 3.3%	+11%	−35%
		1.2	− 76%	− 4.3%	+42%	+ 1.9%	−10%	+42%

1 multiplication factor
2 duration of development
3 mortality of developmental
4 oviposition frequency
5 mean longevity of adults
6 maturation period
7 female sex ratio

Table 6. Population growth of whiteflies on tomato and gerbera under different temperature conditions. The numbers show the total population numbers (the total numbers of eggs, larvae, pupae and adults) at day 80.
of eggs, 1st, 2nd, 3rd and 4th instar larvae and pupae of whiteflies on gerbera.

	Temperature (°C)				
	15	20	22	25	30
Tomato	3,340.5	34,568	93,416	262,332	999,182
Gerbera	1,681.4	23,239	94,414	483,340	118,825

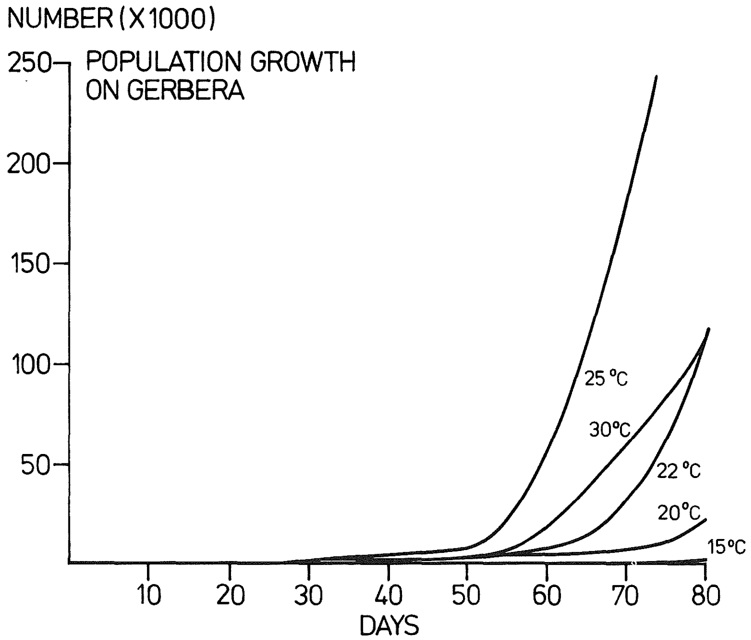


Fig. 11. Simulation results for the total population number of whiteflies on gerbera at constant temperatures of 15, 20, 22, 25 and 30 °C.

6. Discussion

The simulations predicted the following order in growth rats: eggplant cucumber gerbera = tomato HW-HSP DW-HSP = DW-DSP HW-HSP. Comparison of population growth rates is also possible by comparing the intrincic rate of natural increase (r_m). Van Lenteren and Hulspas-Jordaan (1983) calculated the r_m values of whitefly on tomato, and Dorsman and Van de Vrie (1987) on gerbera. The r_m values for these crops are almost the same, which is in agreement with results of this study.

When we apply the hypothesis that, in seasonal inoculative releases, a natural enemy should have a larger r_m or kill rate than the rate of population increase of the host (Van Lenteren 1986, 1987), to the simulation data in this paper, biological control of whiteflies by *Encarsia formosa* shoud be successful on sweet pepper and gerbera. On sweet pepper, practical experience is in line with this prediction. For gerbera too few data from commercial greenhouses are available to conclude whether *E. formosa* can be used.

On the other hand, the model predicts that it is not easy to obtain good biological control on cucumber and eggplant, a conclusion which is also supported by data from commercial greenhouses. Of course, the hypothesis is only concerned with one of the necessary basic conditions for successful biological control. It does not mean automatically that when this conditon is met, biological control on a certain crop is possible. Other factors such as searching efficiency or dispersal ability of parasites etc., which might be influenced by crop architecture should also be considered, e.g. Dutch scientists are presently trying to develop cucumber cultivars with fewer hairs to enhance the searching efficiency of the parasite on leaf surfaces (Van Lenteren et al. 1987).

A quite special case forms sweet pepper: whitefly is a pest of this crop in Hungary and not in the Netherlands (Van Vianen et al. 1987). In Hungary, this pest situation is mainly caused by whiteflies that immigrate into a sweet pepper house from neighbouring crops (e.g. cucumber, sunflower). Biological control of whiteflies by *E. formosa* on sweet pepper in Hungary is successful. The simulation results indicate that control of Hungarian whitefly on Hungarian sweet pepper should be easy, indeed.

Large differences are observed for parameters that influence population growth on sweet pepper and other crops. The system on sweet peppers is sensitive to all parameters, in contrast with other crops where only a few parameters have a strong influence. In general, population growth seems to be more sensitive to any changes of parameters of life-history components on unsuitable host plants than on suitable ones.

An important finding is that the system on sweet pepper is very sensitive to changes in mortality of developmental stages. This is a meaningful result because most pest control measures aim at the increase of immature mortality. In case of other crops, changes in immature mortality are not so important. Therefore, once the immature mortality becomes large, the system also becomes sensitive to additional changes in mortality. This indicates the usefulness of integrated control where several control measures are used in a harmonic way. For example, in sweet pepper, breeders for resistant cultivars should concentrate on increasing the immature mortality of whitefly.

The sensitivity analysis for other crops indicates that in general, duration of development, oviposition frequency and sex ratio are the important factors to aim at in the development of resistant crops.

The present simulation program can easily be adapted to other host plants. Further, it is intended to make an interactive version of the model so that it can be used by those having little experience with computer programs.

Acknowledgements

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