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

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Abstract

The construction of a state variable, temperature driven, explanatory, dynamic, deterministic simulation model to estimate within and between generation population development of the greenhouse whitefly on tomato is described. The selection of data used for the model is discussed and the formulation of equations presented. A program listing is provided with technical details on modelling with boxcar train systems. The verification of submodels and validation tests are given, as well as a preliminary sensitivity analysis. The simulations provide data that are corresponding well with experimental data. New experimental data have to be obtained for further verification and validation. The sensitivity analysis shows that changes in the developmental period have the greatest effect on the population growth rate, followed by the effect of changes in fecundity. Changes in mortality of immature stages, longevity of adults and maturation period have a weak influence.

1. Introduction

The greenhouse whitefly is a well-known pest on several glasshouse grown crops (Van Lenteren & Woets 1988). Mainly in view of the biological control of this pest with the parasitoid *Encarsia formosa*, much research has been conducted on the host plant-whitefly-parasitoid system (Eggenkamp-Rotteveel Mansveld et al. 1982; Hulspas-Jordaan et al. 1987; Vet et al. 1980).

Although a successful biological control program has been developed, this does not imply that all problems are overcome. The biological control on cucumber e.g. is still troublesome (Fransen 1987). It is therefore not only for theoretical reasons but also from a practical point of view important to acquire as much insight as possible into the host plant-whitefly-parasitoid system, in order to achieve improvements in situations where biological control is insufficient yet.

The development of a mathematical model is very suitable to that end. It offers a possibility to bring together the results of the extensive research conducted and to recognize possible gaps in our knowledge. Once the model has stood verification and validation tests, it can be used to obtain qualitative and quantitative information on the importance of certain relations or parameters, and it may serve to predict the reaction of the system on a change of the values of parameters, variables etc. With the development of a whitefly model it was tried to follow the methodology as described by Ruesink (1976) and worked out by Rabbinge and Carter (1983).

The (rather ambitious) objectives of the system analysis are already given above. At this point the objects within the system are to be defined. To begin with, the model was restricted to the host plant-whitefly subsystem. As the host plant has a main influence on the population growth rate of *T. vaporariorum* (Woets & van Lenteren 1976), it would get too complex for a start to involve several host-plant species. We therefore decided to restrict the model to one host-plant species, from which most experimental data were available, i.e. tomato (*Lycopersicon esculentum* L.). In subsequent articles the model will be extended and other host-plant species are included (Yano et al. 1988a, b).

Because an explanatory and dynamic model was desired, a simulation model was constructed. As will appear from the following, it is a deterministic model. A special simulation language was used to formulate the model, namely CSMP (Continuous System Modelling Program).

In the following paragraphs we will discuss successively the relational diagram that forms the basis of the model, the selection of the data to be used and the formulation of the equations, the program listing with some technical details, the verification of the submodels, and the validation tests. At the end of this paper a first, limited sensitivity analysis is given.

2. Life history put into a relational diagram

Based on our knowledge on the life history of the whitefly, a relational diagram is constructed (see figure 1). The immature whitefly period can be subdivided into several stages. The sizes mentioned beneath are derived from Hargreaves (1914), Weber (1931), Milliron (1940), Eijsackers (1969), Van Lenteren et al. (1976), Nechols and Tauber (1977a), Li et al. (1980) and Collman and All (1980).

The white eggs are laid by the whitefly females at the under surfaces of host-plant leaves. They are 0.21-0.24 mm. in length and 0.07-0.10 mm. in width. After one to four days (depending on temperature) they turn black (Weber 1931). As this darkening is not of interest in relation to *Ermosa*, the white and black eggs are put together in the model (EGG in figure 1).

The first instar larva that hatches from the egg is initially mobile. Its length and width are respectively 0.26-0.29 mm. and 0.11-0.15 mm. It crawls around, reaching no more than a few centimeters distance from its eggshell, till it settles down with its mouthparts inserted in the leaf tissue. The duration of this crawling period varies but is usually no longer than a few hours. It may take longer on leaves in bad condition or on less preferred host plants, where crawling may be restarted several times after short periods of probationary settling (Weber,

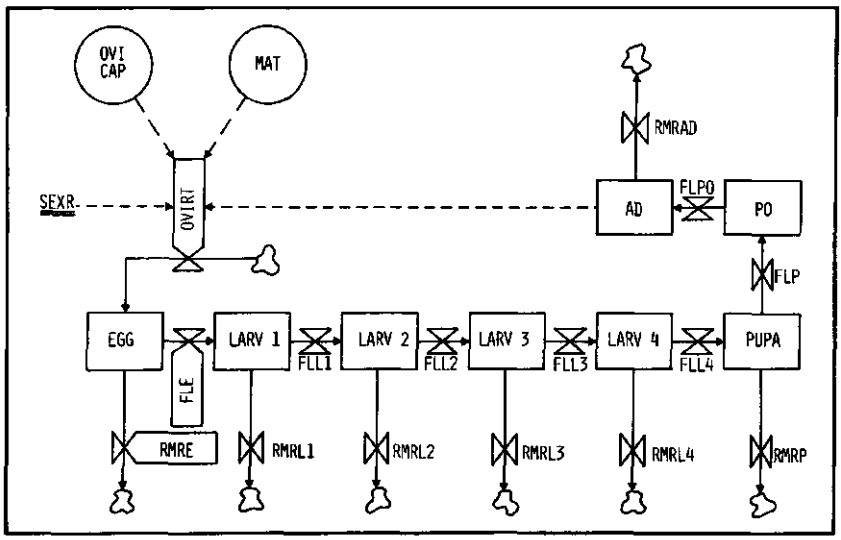

Fig. 1. Relation diagram for the population growth of *Trialeurodes vaporariorum*.

1931). It is therefore arbitrary to distinguish strictly a crawling and a settling period. For this reason and mainly because crawling takes only a very small part of the total first instar period, crawling and settled first instar larvae are put together in the model (LARV1). The settled larva is covered with a thin layer of wax and it remains on the chosen spot through all the immature stages that follow.

There are three moults leading to respectively the second, third and fourth instar larva (LARV2, LARV3 and LARV4). The second and third instar larvae differ hardly from each other except for their sizes. The second instar is 0.32-0.39 mm. in length and 0.19-0.23 mm. in width, while the third instar measures 0.42-0.55 mm. by 0.26-0.33 mm. The fourth instar larva is flat at first, like the previous larval stages. Its size is 0.62-0.82 mm. by 0.37-0.48 mm. During its development it thickens and produces waxy rods that form a palisade around it and dorsal and lateral waxy spines are formed. Some time before emergence of the adult one can see its red pigmented eyes through the waxy layer.

As Nechols and Tauber (1977a) already noticed, there is no uniform terminology for the stage between the third-instar moult and adult emergence. Table 1 lists the various terms used, with their authors. There are indeed only four larval stages and no pupal stage in the usual sense of the word. As Nell et al. (1976) showed, there is a considerable difference in acceptability for *Ermosa* between the fourth larval instar before the red eyes are visible (their prepupa) and the fourth larval instar with pigmented eyes (their pupa). It is therefore necessary to distinguish between these instars. Because the term 'pupa' is used throughout the whitefly literature and because the thickened fourth larval instar with visible pigmented eyes can technically be regarded as a pupa (Hinton 1963) we will also use this term (PUPA in figure 1). The sizes given for the pupa, prepupa or pseudopupa are 0.66-0.76 mm. by 0.39-0.48 mm.

The adult emerges through a slit-like opening in the pupal skin. After the

Table 1. Terms used for last *T. vaporariorum* developmental stage. (L4 = fourth larval stage)

Author	Flattened, translucent to opaque-whitish	Expanded, wax-ensheathed opaque-white with dorsal and lateral waxy spines	Red eyes visible beneath waxy larval integument
Hargreaves 1915	pupa	pupa	pupa
Weber 1931	L4	L4	L4
Burnett 1949	L4	L4/pupa	pupa
Eijsackers 1969	L4	L4	pupa
Van Lenteren et al. 1976-1	L4	prepupa	pupa
Nechols & Tauber 1977-1	early L4	L4, transitional sub-stage	L4, pharate adult sub-stage
Li et al. 1980	pseudopupa	pseudopupa	pseudopupa
This paper	L4	L4	pupa

wings have been unfolded, a white waxy secretion from ventral abdominal glands is spread all over the body except for the eyes. While the males are sexually mature at eclosion, the females are not. During the period that the females are not yet able to lay eggs, the adults in the model are called pre-oviposition adults (PO). From the start of the oviposition period they are indicated with 'AD'. Unmated females lay haploid eggs from which males develop. Mated females lay either diploid eggs, which produce females, or haploid eggs. In the model the sex ratio (SEXR) is fixed, in accordance with literature data.

The number of eggs laid per female per day changes during the oviposition period. In the first days it gradually increases until a level is reached that is maintained during almost the rest of the females' life. Only shortly before dying the female lays a decreasing number of eggs per day (Van Sas et al. 1978). The duration of the period of increase is determined by the auxiliary variable 'MAT' (maturation), while the height of the maximum oviposition capacity is given by 'OVICAP' (see figure 1). The developmental rate from one stage to the next stage is indicated with 'FL' (flow). 'FLL3' e.g. is the rate with which larvae in the third stage develop into fourth instar larvae. 'OVIRT' is the total oviposition rate, which is determined by the number of adults present, their sex ratio, their maximal oviposition capacity (OVICAP) and the extent to which this maximal capacity is reached (MAT). During every stage mortality may occur, indicated with 'RMR' (relative mortality rate). During the pre-oviposition period no mortality is assumed.

The rates mentioned may be influenced by abiotic factors like humidity, light intensity and temperature. Data on the role of humidity are very scarce and are reviewed by Vet et al. (1980). They mainly concern the performance of *Ermosa*. Humidity is therefore not included in the model as a driving variable.

Data on the influence of light intensity, so far as they are available, are discussed in the following paragraphs. They do not lead to the inclusion of light intensity as a driving variable too.

Temperature is known to have a great influence on most of the rates mentioned above. In the following paragraphs much attention will be paid to the role of temperature and it is included in many of the equations as a driving variable.

3. Data selection and formulation of equations

3.1 Developmental rates of whiteflies in pre-adult stages

Data on the developmental periods of immature whiteflies on tomato are available from several authors. Weber (1931), Burnett (1949), Hussey and Gurney (1957), Eijsackers (1969), Kraaijenbrink (1972) and Van Evert and Schutte (1983) all performed their experiments at constant temperatures. Their results are shown in figure 2. Christochowitz and Van der Fluit (1981), Kraaijenbrink (1972) and Van Evert and Schutte (1983) determined developmental periods of whiteflies in the various stages at fluctuating temperatures.

As figure 2 shows, most experiments were done at temperatures around 22 °C. Van Evert and Schutte (1983) investigated development at extreme temperatures to extend earlier studies. They could not determine developmental durations at 35 °C for eggs and pupae because of a 100% mortality of individuals in these stages at that temperature. They also investigated the developmental durations in all stages at a low temperature of 7 °C, but after a period of 25-34 days hardly any of the larvae had moulted, nor had the fourth instar larvae turned into pupae. Only 1/3 of the second instar larvae moulted, after a mean period of

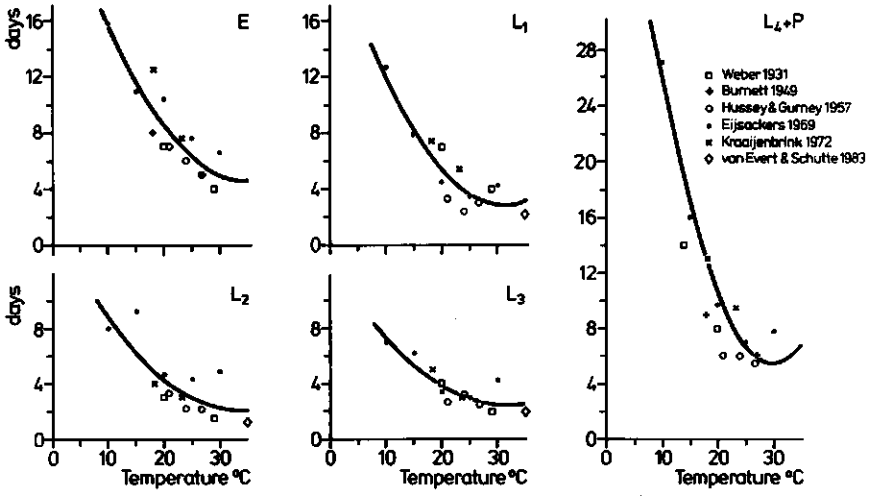

Fig. 2. Developmental period in days against temperature in °C for *Trialeurodes vaporariorum* eggs (E), and first-fourth (including pupa) larval stages (L1-L4+P). For values for second-grade polynomes see figure 3.

17.2 days. The rest of them had not moulted when the experiment was stopped after 29 days. With the eggs the experiment lasted 40 days, at the end of which not a single egg had hatched. Most of these eggs did hatch, however, when they were put at higher temperatures. Weber (1931) states that the egg development is stopped at temperatures of 8 °C and lower. According to him, approximately this also applies to the development of the first, second and third instar larvae. For fourth instar larvae the temperature at which no development takes place, as given by Weber, is even lower (0-4 °C) and he supposed that emergence of the adults will not occur at temperatures below some point between 5 and 15 °C.

Only Eijsackers (1969) and Van Evert and Schutte (1983) subdivided the last developmental stage in the way we decided to do it. Their data were used therefore to describe the relationship between the developmental period of fourth instar larvae and of pupae and temperature (see figure 3). With regard to total developmental time of whiteflies in these substages, the data from Eijsackers fit well in between those of other authors (see figure 2).

In most cases (except for the first and third larval stages) a second grade polyn-

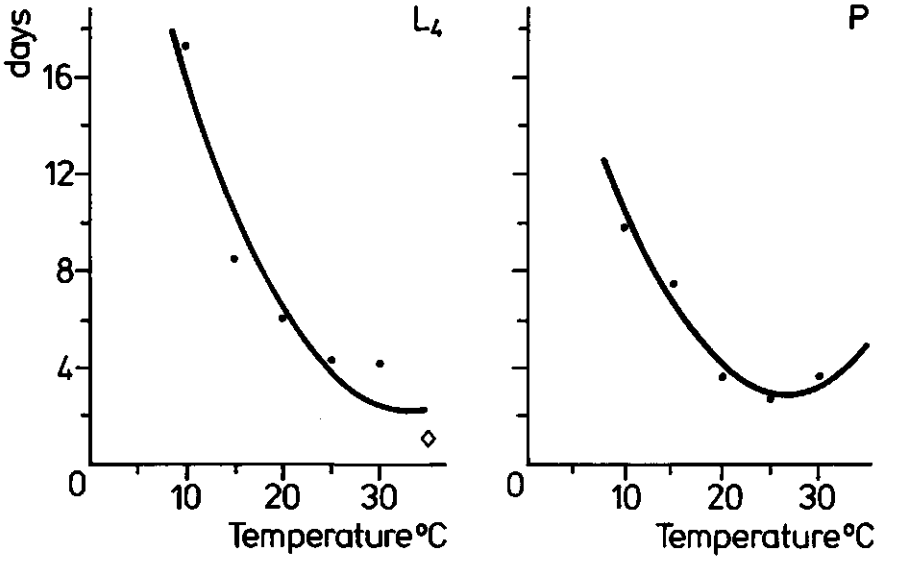

Fig. 3. Developmental period in days against temperature in °C for *Trialeurodes vaporariorum* fourth larval stage (L4) and pupa (P).
Data from Eijsackers (1969) and Van Evert & Schutte (1983).
The curves are the best fitting second-grade polynomes.

(DU = developmental period in days, T = temperature in °C)

DU E	$= 26.35-1.25T+0.018T^2$	DU L4+P	$= 52.50-3.16\,T+0.053T^2$
DU L1	$= 23.71-1.34T+0.022T^2$	DU L4	$= 30.78-1.74\,T+0.027T^2$
DU L2	$= 16.10-0.85T+0.013T^2$	DU P	$= 21.72-1.42\,T+0.027T^2$
DU L3	$= 12.94-0.66T+0.010T^2$		

ome did not fit the data significantly better than did a first-grade polynome. Eijsackers, however, using the widest temperature range, showed that at high temperatures the developmental period was sub-optimal. Because this is also achieved with second grade polynomes, we decided to use those to describe the developmental period/temperature relationships for all stages. These curves are also given in figures 2 and 3. The curve drawn through the L4+P-data in figure 2 is a combination of the curves of figure 3. At 8 °C these curves end, because the developmental rates at temperatures of 8 °C and lower are all set to zero, to fit in with the data from Weber (1931) and Van Evert and Schutte (1983).

Kraaijenbrink (1972) showed that the developmental periods of whiteflies in the various stages at temperatures fluctuating between 15 and 20 °C and between 20 and 25 °C did not differ from those determined at constant mean temperatures. This is not surprising because the developmental rate/temperature relationship can be regarded as linear over the short temperature ranges used. To see whether the temperature summation method of the model, based on developmental durations determined at constant temperatures, could also be used at fluctuating temperatures that reach more extreme values, simulation results were compared with data from Christochowits and Van der Fluit (1981) for the low temperature zone and with data from Van Evert and Schutte (1983) for the high temperature region

3.2 Mortality rates during development

The mortality of the whitefly in its various developmental stages has been determined by assessing the percentage of individuals of a certain stage that reached the next stage. Hardly anything is known about the course of mortality during a stage. Weber (1931) noticed that the first instar larva is especially vulnerable to drought during its wandering period. He also states that the fourth instar larva during the second phase of its existence (presumably from thickening onwards) is less vulnerable to desiccation of the host plant as well as to dry air than younger larvae. A few lines later, however, Weber mentions that on living plants humidity of the air had more influence on the vitality of whiteflies in the fourth larval stage than on that of individuals in previous stages.

We found no justification in the literature to built into the model a separate moulting mortality as Rodolphe et al. (1977) did in their model on Aleyrodids. In our model mortality of whiteflies in the various developmental stages is build in as a constant relative mortality rate. Data on mortality on tomato are given by Curry and Pimentel (1971), Burnett (1949), Van de Merendonk (1978), Jansen (1974), Van Sas et al. (1978), Kraaijenbrink (1972), Kajita (1980), Elzinga (1982) and Van Evert and Schutte (1983). From Curry and Pimentel (1971) we can only use egg mortality because the older stages are not subdivided by them and mortality due to parasitization by *Ermosa* is included in their data. Burnett (1949) only determined total mortality during development from egg to adult. He does point out that at 27 °C most of the deaths occurred in the pupal stage.

Van Sas et al. (1978) and Elzinga (1982) measured mortality only roughly and their data will not be included therefore. Kajita (1980) reports about a field experiment with presumably strongly fluctuating temperatures. His data will be disregarded too. Van Evert and Schutte (1983) filled a gap that existed in our knowledge on mortality at a high temperature (35 °C).

Except for the remarks of Weber (1931), given above, no information on the influence of humidity is available. Some experiments have been done concerning the relation between density and mortality. Jansen (1974) found no correlation between the density of the eggs and the mortality during the pre-adult period on tomato. Egg densities varied from 0.25 to 23.2 eggs per cm^2. Zebitz (1978) working with egg densities of 2 to 100 eggs per 7.5 cm^2 of tobacco leaves, found only a very slight increase in mortality with increasing density in a climate room at 25 °C, but in a small glasshouse with temperatures fluctuating between 16 °C and 25 °C he found no correlation at all. XU et al. (1984) did find positive correlations between egg density and mortality from egg to third larval stage and between third larval instar density and mortality from the third larval stage to adult emergence. They show however that this effect is negligable at densities under 8 eggs per cm^2 and 0.5 third instar larva per cm^2 of suitable cucumber leaves. These high densities will hardly ever be reached under normal growing conditions, when *E. formosa* is used for whitefly control. Based on these literature data, in the model the mortality is supposed to be density independent.

The relation between mortality during development and temperature is shown in figure 4. Mortality during the egg stage is independent of temperature, if constant temperatures between 20 and 25 °C are regarded. Yano (1981) found a very low mortality, varying between 0 and 6%, on tobacco at temperatures ranging from 15 to 30 °C. According to Weber (1931) no eggs will hatch at constant temperatures of 32 °C and higher. Van Evert and Schutte (1983) obtained indeed a 100% mortality of the eggs at 35 °C. Weber (1931) points out that the harm from these high temperatures sets in only after at least one day. As in north-western Europe temperatures in glasshouses with tomato crops hardly ever remain over 30 °C for longer than a few hours, the mortality is kept low at high temperatures in the model. As far as temperatures below 15 °C concern, we know from Stenseth (1983) that the eggs are very cold resistent. Sixty percent of the eggs survived a period of 20 days at 6 °C. O'Reilly (1974) even found that 41% of the eggs survived a period of 7 days at 1 °C. We decided to include in the model an egg mortality of 6.1% (the mean of the data in figure 4) independent of temperature.

Figure 4 shows that the mortality of the first instar larvae on tomato is also very low. Yano (1981), working with tobacco plants, found that at high and low temperatures mortality was higher than at moderate temperatures. Van Evert and Schutte (1983) showed that on tomato this was not the case for high temperatures. Weber (1931) states that first instar larvae are as sensitive for high temperatures as the eggs, which means that only continuous high temperatures will harm. About low temperatures Weber remarks that, provided that they are above −4 °C, they are only harmful when the plant too is damaged.

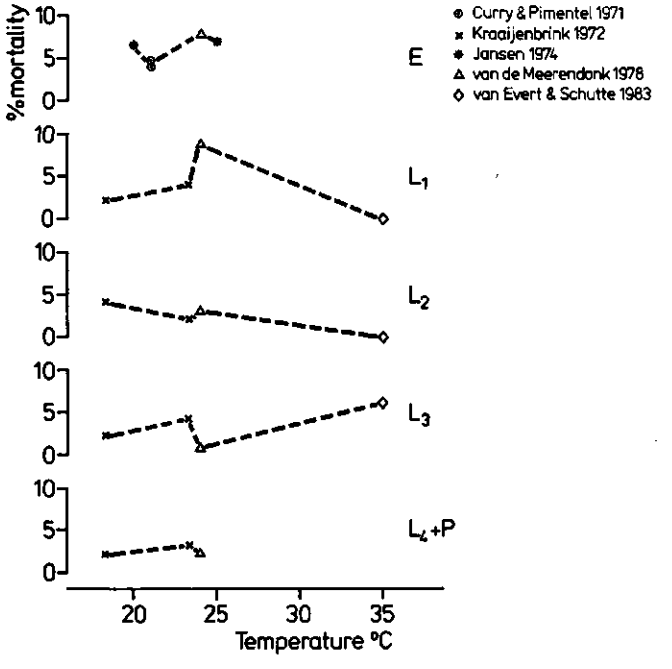

Fig. 4. Mortality of *Trialeurodes vaporariorum* developmental stages on tomato against temperature.

We therefore will use a mortality of 3.7% (the mean of the data in figure 4) independent of temperature.

The data on mortality of second and third instar larvae do not show a temperature dependence too. Weber (1931) states that these instars are even less sensitive to high temperatures and that, like the eggs, they stand low temperatures better than the plants do. The mortalities included in the model are the means of the data given in figure 4, i.e. 2.3% and 3.3% for second and third instar larvae respectively.

Figure 4 also shows data on mortality of fourth instar larvae including pupae. Van Evert and Schutte (1983) subdivided the last developmental stage into fourth instar larva and pupa in the way it is done in our model. They found that at a constant temperature of 35 °C the mortality of the fourth instar larvae was only 4%, whereas 100% of the pupae died. Burnett (1949) states that at a high temperature (27 °C) the mortality was mainly pupal mortality. Yano (1981) and Weber (1931), using tobacco as host plant, also found very high mortalities for whiteflies in the last developmental stage at temperatures of respectively 30 °C and 32 and 37 °C, namely 95.5, 92.1 and 100%. They both did not differentiate between fourth instar larvae and pupae. Weber remarks that the damaging effect sets in quickly and he shows that this high mortality at high temperatures is not caused by a change in humidity. At low temperatures

Weber found a very low mortality (5% after 12 days at 5 °C). We rather arbitrarily split the data on the joined fourth instar substages in such a way that the mortality of the fourth instar larvae was smaller than the mortality of the pupae, in accordance with the findings of Madueke (1979) on mortality on bean plants. In the model we included a mortality for fourth instar larvae of 1.5% (the mean of the partial mortalities and the mortality found by Van Evert and Schutte (1983)) independent of temperature. For the pupal stage the mortality at temperatures up to 30 °C is fixed at 1.9% (the mean of the partial mortalities) and for higher temperatures we included a 96.9% mortality in the model, i.e. the mean of the data from Yano (1981), Weber (1931) and Van Evert and Schutte (1983).

All this leads to a total mortality during development of 17.5% at temperatures up to 30 °C, which fits in well with the literature data on total mortality as presented in table 2.

Temperature independence of the mortality during development is also suggested by data obtained with other host plants, like bean (Madueke 1979) and cucumber (Kraaijenbrink 1972 and Van de Merendonk 1978). On tobacco the mortality also does not show a clear relationship with temperature (except for pupae) but it is very variable (Weber 1931, Nechols and Tauber 1977b and Yano 1981).

3.3 Sex ratio

Data on the sex ratio of *T.vaporariorum* are given by Weber (1931), Burnett (1949), Di Pietro (1977), Van Rongen (1979), Madueke (1979), Van Boxtel (1980) and Collmann and All (1980). Most of them found a sex ratio of approximately 1:1.

Weber (1931, p.657) only mentions that the sex ratio in his rearing stock was always approximately 1:1. Burnett (1949) shows that the sex ratio varies around equal numbers of both sexes when the progenies are considered of groups of adults that were allowed to oviposit for 18 hours at 18, 21, 24 and 27 °C. He also states that in large populations of *T.vaporariorum* the sex ratio appears

Table 2. Total mortality of *T. vaporariorum* developmental stages at constant temperatures on tomato.

Author	Temperature (C)	Mortality (%)
Burnett 1949	18	6.6
Jansen 1974	20	≤22.1
Burnett 1949	24	16.6
Van de Merendonk et al. 1978	24	21.2
Jansen 1974	25	≤ 8.7
Burnett 1949	27	32.4

to range from a preponderance of one sex to a preponderance of the other. This, he writes, is apparently caused in part by the sampling method used, for the adult males have a tendency to remain on the lower leaves (on which they emerged) while the females predominate on the upper leaves of the host plants.

Madueke (1979, p.51) asserts that counts made during glasshouse experiments showed that the male:female ratio was approximately 2:3. She does not describe her counting method, however, nor does she give the numbers counted.

Di Pietro (1977), Van Rongen (1979) and Van Boxtel (1980) determined the sex ratio of newly hatched adults. Di Pietro using tobacco as host plant, found a 1:1 sex ratio at 17 °C as well as 22 °C (n was 203 and 564 respectively, originating from numerous parent whiteflies). Van Rongen determined the sex ratio of adults that hatched from pupae which he sampled from a rearing stock (n was 1178) and found it to be not significantly different from 1:1. Van Boxtel found the same sex ratio with several host plants, namely tomato, cucumber, eggplant and sweet pepper (n was 1956, 3033, 6589 and 9 respectively, originating from 9, 9, 13 and 20 parental couples). He reports that the 1:1 sex ratio is the overall result when the progenies of all females are combined. Per female the sex ratio of the offspring is extremely variable.

Collmann and All found a female: male ratio that varied depending upon the time of the year the oviposition took place, from 0.71 in March to 2.86 in July. They used very small samples (n was 18 to 111) which may also account for this variability.

In the model we introduced a 1:1 sex ratio by stating that only half of the adults after the pre-oviposition period (AD in figure 1) contributes to egg production.

3.4 Pre-oviposition period

Literature data on the pre-oviposition period of *T.vaporariorum* are given in table 3.

All authors recorded daily for individual whitefly females whether they had started ovipositing. The figures in table 3 with two decimals suggest indeed an accuracy that cannot be achieved with daily recordings. The data from Lloyd (1922) are too inaccurate to be used.

The data from Madueke (1979) and Di Pietro (1977) clearly show a decrease of the pre-oviposition period with increasing temperature, whereas the data from Burnett (1949) do not. Burnett's results are based on twice respectively three times as many whiteflies as those of Di Pietro and Madueke. Stenseth (1971) reports that female whiteflies started ovipositing 24-48 hours after emerging, both at 18 and 24 °C.

We chose to introduce into the model a temperature-independent pre-oviposition period (giving a temperature-independent rate, FLPO in figure 1) of 1.3 days, which is the mean of the rounded off figures from Burnett, given in table

Table 3. Pre-oviposition period of *T. vaporariorum*

Author	Duration (days)	Temp. (C)	Host Plant	n
Lloyd 1922	2-5	variable	several	?
Burnett 1949	1.16	18	tomato	56
,,	1.88	21	,,	57
,,	0.40	24	,,	57
,,	1.57	27	,,	44
Stenseth 1971	1-2	18	bean	?
,,	1-2	24	,,	?
Di Pietro 1977	2.95	17	eggplant	20
,,	0.93	22	,,	30
,,	0.51	27	,,	35
Madueke 1979	2.2	18	bean	15
,,	0.8	22.5	,,	15
,,	0.6	27	,,	17

3. His research was the only one in which tomato was used as host plant. Taking the mean of all figures from table 3 (except those of Lloyd) would give the same result.

3.5 Adult longevity

The longevity of the adult *T.vaporariorum* determines the ageing rate that is used in the model. Literature data on longevity on tomato, assessed at constant temperatures, are shown in figure 5. As can be seen from this figure, most experiments were conducted at about 22°C. Specifications of these experiments are given in table 4.

Curry and Pimentel (1971) used two different tomato varieties and found a longevity on one twice as long as on the other. Van Boxtel (1980), partly published by Van Boxtel et al. (1978), did his experiment twice, during November-December and during January-March. In the second period the mean whitefly longevity was twice as long as in the first period. In another experiment, which was set up to assess the number of offspring of whitefly couples, Van Boxtel (1980) found a longevity for females of 29 days and for males of 11 days. Van Evert and Schutte (1983) determined 50% survival periods at the same temperature as Van Boxtel used and did not find a significant difference in longevity between males and females. We should consider thereby that the mean lifetime in their experiment must have been longer than 32 days because their longevity distribution was skewed to the right.

Van Sas (1978), partly published by Van Sas et al. (1978), compared the longevities of female whiteflies in small leaf cages that were transferred to another leaf every two days, with the longevities of female whiteflies that had a whole

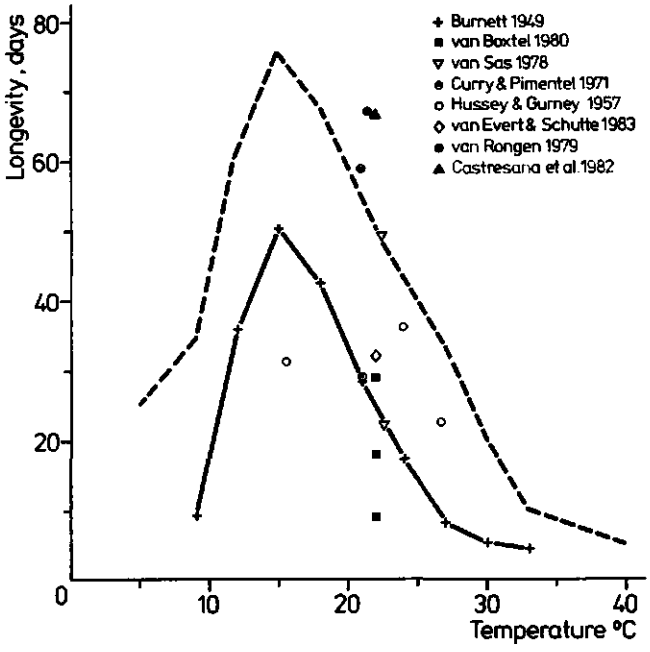

Fig. 5. Longevity of *Trialeurodes vaporariorum* on tomato against temperature. Interrupted line is curve included in model.

plant to their disposal and were transferred to a new plant only once per 2.5 weeks. Under the former circumstances the mean longevity was less than half of that under the latter circumstances.

Van Rongen (1979) transferred his female whiteflies once a week and found a mean longevity of 67 days. He included only the females that survived the first week and did not count the week of death.

Castresana et al. (1982) put couples of whiteflies in cages with a small plant and counted and removed the eggs laid, once a week. Whenever a whitefly was found dead at daily inspection, it was removed and sexed. They found a mean longevity of 66.6 days for the females and about the same for the males.

Curry and Pimentel (1971) conclude that the tomato variety strongly influences the longevity. This is not unlikely and would make it impossible to construct a generally valid tomato model, if differences in longevity as presented here would have a great impact on the total population growth rate. This will be discussed later with the parameter sensitivity analysis of the model.

Van Boxtel (1980) suggests that the time of the year influences the experimental results. However, the experiment Van Sas (1978) conducted from November till January, which was the same as Van Boxtel's, gave even longer lifetimes than Van Boxtel found during January-March.

Table 4. Experiments on *T. vaporariorum* longevity at 21 - 22.5 °C.

Author	mean longevity (days)	tomato variety	transfer every	leaf area per ♀	date	no. ♀♀	anaesthetized at transfer
Van Boxtel 1980	9	moneymaker	2 days	∅ 2 cm	XI-XII	37	no
Van Boxtel 1980	18	moneymaker	2 days	∅ 2 cm	I-III	41	no
Van Sas 1978	21.9	moneymaker	2 days	∅ 2 cm	XI-I	21	no
Burnett 1949	28.5*	bonnie best	1 day	½ leaflet	–	57	–
Curry & Pimentel 1971	29.1	delicious	4-5 days	∅ 2.5 cm	–	40	no
Van Boxtel 1980	29	moneymaker	3 weeks	1 plant	I-V	9	no
Van Evert & Schutte '83	32**	moneydor	2.5 weeks	∅ 2 cm	I-II	44	no
Van Sas 1978	49.3	moneymaker	2.5 weeks	1 plant	I-V	8	no
Curry & Pimentel 1971	58.7	tiny tim	4-5 days	∅ 2.5 cm	–	44	no
Castresana et al. 1982	66.6	–	1 week	1 plant	–	–	no
Van Rongen 1979	67	moneydor	1 week	∅ 2 cm	I-IV	34	yes

* median ** 50% survival

When we look at table 4, column 5, it does not seem to matter whether the whiteflies have a whole plant to their disposal or are confined to a very restricted leaf area. Short as well as long lifetimes are found, using small leaf cages.

Column 8 shows that anaesthesia is not likely to shorten longevity as the only experiment in which the whiteflies were regularly anaesthetized (be it only once per week) rendered the longest lifetimes. Some authors do mention that they used CO_2 anaesthesia to sex the adults at the beginning of the experiments.

Column 4 gives some support to the conclusion of Van Sas (1978) that frequent disturbance of the whiteflies shortens their longevities. The longevity found by Van Boxtel with little disturbance, is rather low but he used a very small sample, as did Van Sas too indeed in her experiment with little disturbance. Under normal growing conditions the whiteflies will not very often be forced to move to another spot and therefore we decided to fix the longevity at 22 °C at the mean of the figures given in table 4, except for the first four figures and that from Van Evert and Schutte. This resulted in a 50 days longevity at 22 °C.

Concerning the relationship between longevity and temperature, we have given data from Burnett (1949) and Hussey and Gurney (1957) in figure 5. Both found a decrease of the longevity when temperature increased from 24 °C onwards. This is confirmed by experiments of Van Evert and Schutte (1983). They determined the median longevity not only at a constant temperature of 22 °C, but also at other temperature regimes.

When they raised the temperature to 30 °C during 4 hours per day, while it was kept at 22 °C during the rest of the time, the longevity of female whiteflies was shortened to 15 days. They also tried temperatures of 33 °C during 2 hours per day, 35 °C during 1 hour and 41.5 °C during half an hour. These resulted in longevities of respectively 17, 9 and 10 days. The high rate with which the temperature was changed might have contributed to this effect. The assertion of Lloyd (1922), that 95% of adult whiteflies cannot survive a 5 minutes period at 40-43 °C was disproved by the experiment of Van Evert and Schutte.

At increasing temperatures within the region of 15-24 °C, Burnett (1949) found a decreasing longevity, while Hussey and Gurney (1957) found it slightly increasing. For temperatures below 15 °C only the data from Burnett are available. For a comparison table 5 lists data on longevity in relation to temperature for other host plants than tomato.

Concerning the course of the longevity curve at temperatures above 15 °C, the data of Di Pietro (1977) and Madueke (1979) are in agreement with those of Burnett. The results of Yano (1981), who found the longest lifetimes at 21 °C, seem to link up better with the data of Hussey and Gurney. Weber (1931) suggests that maximal longevity is reached at some temperature between 5 and 22 °C, and according to his figure 37 this should be at approximately 13 °C.

Since Burnett used the widest temperature range and his longevity curve is supported by most of the other literature data, we adopted the shape of his curve. Because we decided earlier that the longevity at 22 °C should be 50 days, we shifted this curve upwards. This however would lead to a longevity of some 30 days at 30 and 33 °C. From the data of Van Evert and Schutte (1983) an

Table 5. Longevity of *T. vaporariorum* on other host plants than tomato in relation to temperature.

Author	Mean longevity (days)	Temperature (C)	Host plant
Weber 1931	49	5	tobacco
,,	42	22	,,
,,	4	32	,,
,,	0.5	36	,,
Di Pietro 1977	52.8	17	eggplant
,,	38.3	22	,,
,,	18.1	27	,,
Madueke 1979	37.3	18	bean
,,	25.3	22.5	,,
,,	14.8	27	,,
Yano 1981	29	15	tobacco
,,	25	18	,,
,,	40	21	,,
,,	33	24	,,
,,	25	27	,,
,,	16	30	,,

ageing rate of 0.24 per day at 30 °C can be calculated, giving a longevity of 4.1 days at a constant temperature of 30 °C, and an ageing rate of 0.36 per day at 33 °C, giving a longevity of 2.8 days at a constant temperature of 33 °C.

These values are even lower than the median longevities Burnett found at these temperatures. We mentioned already that the high rate with which Van Evert and Schutte changed the temperature, might have had an additional effect. As we mentioned above, Lloyd (1922) also found very low longevity values at high temperatures. He does not describe, however, how he performed his experiment. Weber (1931) kept adults of unknown starting age on picked tobacco leaves and found very short lifetimes at high temperatures (see table 5). The unknown starting age and the presumably bad condition of the host-plant leaves at these temperatures render these figures rather useless. We decided to fix the longevities at 30 °C and higher temperatures at values somewhat above those from Burnett and Van Evert and Schutte. As concerns temperatures below 9 °C, Weber (1931) mentions a 49 days longevity at 5 °C.This is even longer than at 22 °C, but he also suggests the optimum temperature for longevity to be about 13 °C. We arbitrarily fixed the longevity at 5 °C at 25 days.

In figure 5 the total longevity/temperature curve that is included in the model is indicated. The parameter sensitivity analysis of the model, should indicate whether this rough approximation is acceptable.

3.6 Oviposition frequency

Data on oviposition frequency, determined at constant temperatures on tomato, are shown in figure 6. As with the longevity data, most of these have been determined at about 22 °C. The results at this temperature are again very variable. Table 6 lists specifications of these experiments in order of increasing oviposition frequency.

The results of Van Boxtel (1980) obtained in November-December and in January-March with the same experimental set-up, differ much. Hussey and Gurney (1959), testing the oviposition rate from October to June found it to be rather constant, except for a decline during November-January. Differences only in light intensity or in duration of the diurnal period of light did not have this effect, so they ascribe this reduction of the oviposition rate to a change

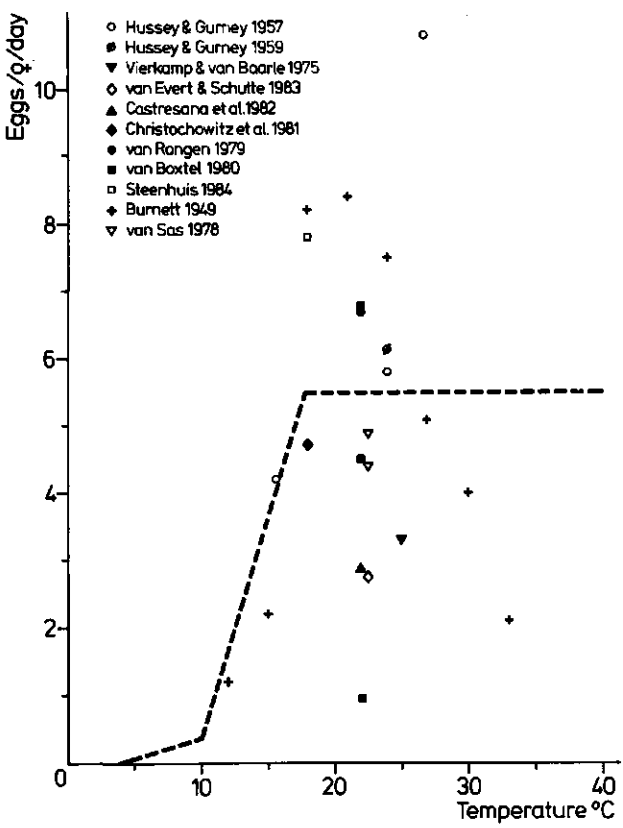

Fig. 6. Oviposition capacity of *Trialeurodes vaporariorum* on tomato against temperature. Interrupted line is curve included in model.

Table 6. Experiments on *T. vaporariorum* oviposition frequency at 21-24 °C.

Author	mean oviposition frequency (eggs/♀/day)	experiment duration	tomato variety	transfer every	leaf area per ♀	date	no. ♀♀
Van Boxtel 1980	0.96	life-span	moneymaker	2 days	∅ 2 cm	XI-XII	37
Van Evert & Schutte 1983	2.74	8 hours	moneydor	8 hours	∅ 2 cm:5	I-III	648
Castresana et al. 1982	2.84	life-span	–	1 week	1 plant	–	–
Van Sas 1978	4.4	life-span	moneymaker	2 days	∅ 2 cm	XI-I	21
Van Boxtel 1980	4.5	life-span	moneymaker	2 days	∅ 2 cm	I-III	41
Van Sas 1978	4.9	life-span	moneymaker	2.5 weeks	1 plant	I-IV	8
Hussey & Gurney 1957	5.8	life-span?	–	–	1 leaflet	–	7
Hussey & Gurney 1959	6.15	4 days	–	4 days	1 leaflet:4	–	–
Van Rongen 1979	6.7	day 8-15	moneydor	1 week	∅ 2 cm	I-IV	34
Van Boxtel 1980	6.8	day 11-19	moneydor	2 days	∅ 2 cm	III-IV	13
Burnett 1949	7.5	life-span	bonnie best	1 day	leaflet	–	57
Burnett 1949	8.4	life-span	bonnie best	1 day	leaflet	–	57

in the products of metabolism in the host plant under winter conditions. However, they seem to have controlled only the minimum temperature of the greenhouse during their first mentioned experiment, so that it cannot be excluded that they measured a temperature effect.

Van Sas (1978) determined the oviposition frequency in exactly the same way as Van Boxtel did. She found in November-January the same rates as Van Boxtel found in January-March. Van Sas found almost the same rates too in an experiment with less disturbance of the whiteflies than in the abovementioned experiment and without confinement of the whiteflies to a very restricted leaf area.

Van Evert and Schutte (1983) worked with whiteflies that originated from and had been feeding on another tomato variety ('Sonatine') than used during the experiment. They found a very low oviposition rate of 0.8 eggs per female per day. When they used whiteflies originating from the experimental tomato variety, they found a much higher oviposition frequency, as given in table 6. This might indicate that the origin of the whitefly females influences their oviposition frequencies, as was also found by Van Boxtel et al. (1978) using tomato, cucumber and sweet pepper as host plants or as plants of origin. Because in practice we have mainly to do with whiteflies originating from the crop concerned, we will disregard this effect in our model.

From the data given in table 6, it is impossible to draw any conclusions on the influence of the host-plant variety on the oviposition frequency. But, as with the whitefly longevity, it is not unlikely that among the commercially grown tomato varieties there are more and less suitable ones with regard to oviposition frequency. As can be seen in table 6 and table 4, Dutch researchers usually worked with the variety named 'Moneydor' or the closely related variety 'Moneymaker'.

Van Evert and Schutte (1983) also showed that there was no difference in oviposition rate between whiteflies that were previously anaesthetized with CO_2 and those that were not. Whitefly females appear to recover very quickly from anaesthesia, certainly if we consider that Van Evert and Schutte allowed them to oviposit for only 8 hours.

Hussey and Gurney (1957 and 1959) used detached leaflets for their oviposition experiments and showed the oviposition frequency to decrease as the leaflets offered for oviposition aged. This was also found by Burnett (1949) at 18 °C. Because whitefly females are mostly found on young leaves when they can make their own choise, as in practice (Milliron 1940, Hussey and Gurney 1959, Di Pietro 1977, Vaishampayan et al. 1975, Verschoor-van der Poel and Van Lenteren 1978, Noldus et al. 1985, 1986) we will disregard the oviposition values determined with older leaflets for the model. Van Evert and Schutte (1983) and Hussey and Gurney (1959) used whiteflies of unknown age, which they took from top leaves of their host plants. Van Rongen (1979) and Van Boxtel (1980) however, determined the oviposition frequency during a restricted, but well known, period of adult life. As can be seen from table 6, it made no difference for the oviposition rate whether the whiteflies were transferred every two days (as Van Boxtel did) or were left undisturbed for a week (as Van Rongen did).

To compare the oviposition frequencies measured over the total life span, with those determined during a restricted period, we should know how the oviposition rate changes during a female's lifetime.

Oviposition curves (number of eggs per living female per day, counted regularly during lifetime) are given by Van Boxtel (1980), Van Sas (1978) and Steenhuis (1984) at constant temperatures on tomato. The pattern of daily oviposition is roughly described by Burnett (1949). Van der Laan et al. (1982) determined the oviposition curve at a temperature regime of 18 °C by day and 7 °C at night on tomato. From all these experiments we can conclude that the oviposition rate increases during the first days of the oviposition period, remains at a certain level during the next period and decreases shortly before the adults die. Yano (1981) presents oviposition curves determined on tobacco at 15, 24 and 30 °C. They do not show distinct periods of increase.

According to Burnett (1949) the period of decrease in daily oviposition is relatively long. This is not confirmed by the other researchers. Burnett also states that the period of increase in daily oviposition is shortened as the temperature is increased. This is supported by the following data. Van Boxtel and Van Sas found a period of increase of about 3 days at 22 °C, while from the data of Steenhuis a mean period of increase of 4.75 days at 18 °C can be calculated. As appears from the data of Burggraaf-van Nierop and Van der Laan (1983), the mean period of increase at a temperature regime of 18 °C by day and 7 °C at night is 11.0 days.

Into the model we introduced a period of increase in daily oviposition, the duration of which is negatively correlated with temperature (figure 7) and a temperature dependent daily oviposition rate that is reached after this period of increase. This oviposition level is supposed to be kept up till death. This last simplification is acceptable because the period of decrease in daily oviposition is relatively short, and mainly because we know from life-history tactics theory that eggs laid at the end of a female's lifetime do hardly contribute to the population growth rate (Stearns, 1976).

The height of the oviposition level at 22 °C is fixed at the mean of the data from table 6, because we had no good reason to select any of these. Because the data based on life-span research are systematically too low as a measure for the oviposition level, the mean (5.14) is rounded off upwards to 5.5 eggs per female per day.

As the relationship between oviposition rate and temperature concerns, we have data from Burnett (1949) and from Hussey and Gurney (1957) (figure 6). Burnett found a bell-shaped curve with the top at 21 °C, whereas Hussey and Gurney found the oviposition rate to be positively correlated with temperature in the region from 15 to 27 °C. For a comparison, figure 8 shows data on oviposition frequency in relation to temperature, determined with other host plants. The data from Madueke (1979) and Di Pietro (1977) suggest a top rate at about 22 °C, while Yano (1981) found the oviposition frequency not to change significantly when temperature increased from 21 to 30 °C.

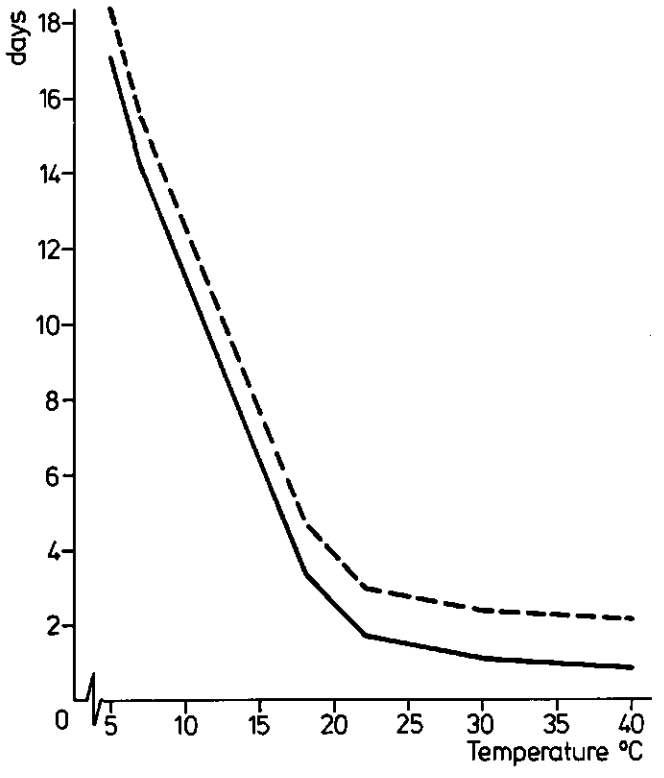

Fig. 7. Period of increase of daily oviposition of *Trialeurodes vaporariorum* (–), the pre-oviposition period included (– –) against temperature.

As it was hard to decide what should be introduced into the model with these data, we performed a new experiment.

Materials and methods.

In a climate room at 20 °C, whitefly pupae on tomato leaves (*Lycopersicon esculentum* L., c.v. Moneydor) were put into a cage with a tomato plant of the same variety. Lights were on from 7 a.m. to 9 p.m.. After 24 hours the leaves were removed and the adults that had hatched were left on the plant for 7 days. A number of adults was then sucked off the plant and sexed under CO_2 anaesthesia. About 30 female whiteflies were individually put into leaf cages , that were attached to the leaves of new host plants. These plants were put into another climate room, with the same light regime, in which the temperature was slowly (during 24 hours) changed from 20 °C to the experimental temperature. The leaf cages were then transferred to younger leaves of the same host plant. The

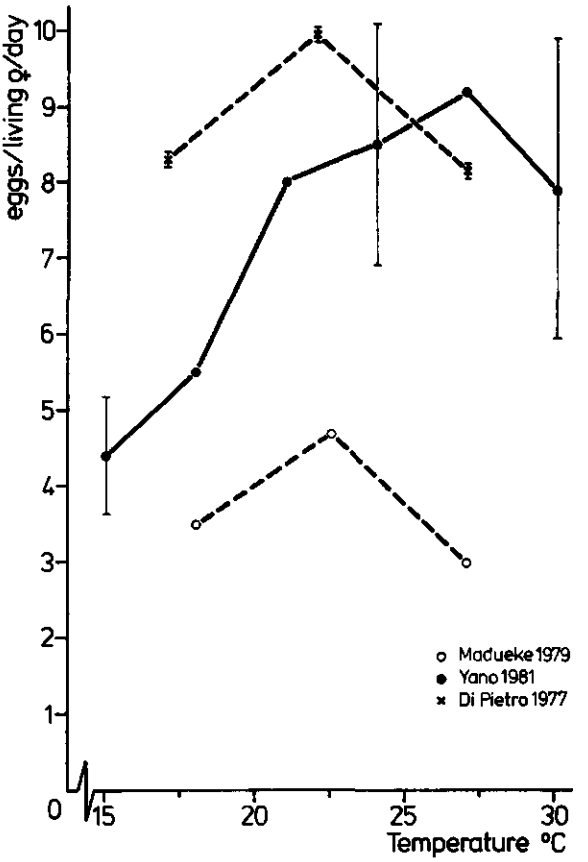

Fig. 8. Oviposition frequency with standard error of *Trialeurodes vaporariorum* on other host plants than tomato in relation to temperature. (Madueke = bean; Yano = tobacco; Di Pietro = egg plant).

whiteflies were anaesthetized for a few seconds for this transfer. While the temperature was kept stationary, the whiteflies were again allowed to oviposit for 24 hours. At transfer and at the end of the second period of 24 hours we recorded the number of adults that survived and the number of eggs laid.

The experimental temperatures were 10, 15, 20, 25, 30 and 35°C in random order.

Results.

The results are shown in table 7. The oviposition rates found are also given in figure 9. The rates found at the changing temperatures are given with the

Table 7. Oviposition rate of *T. vaporariorum* on tomato at various temperatures

Temperature in °C	20/10	10	20/15	15	20/20	20	20/25	25	20/30	30	20/35	35
No. of ♀♀ surviving	25	25	23	23	30	29	27	26	29	26	31	17
% of ♀♀ surviving	83.3	100	76.7	100	100	96.7	90.0	96.3	96.7	89.7	100	54.8
Mean no. of eggs laid per day per surviving ♀	0.48	0.12	1.26	1.13	2.20	1.93	1.41	1.73	1.48	1.69	3.39	1.94
% of surviving ♀♀ that did not oviposit	68.0	88.0	26.1	43.5	26.7	20.7	22.2	34.6	31.0	19.2	3.2	23.5

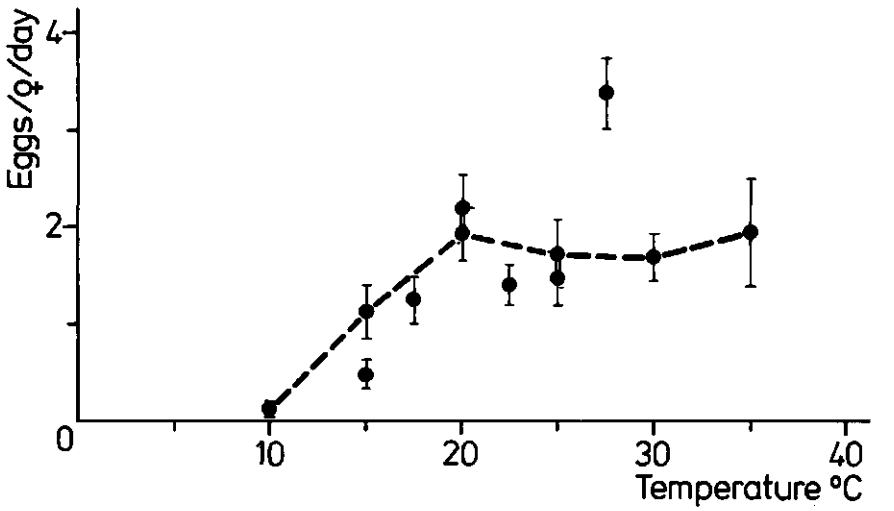

Fig. 9. Mean oviposition rates of *Trialeurodes vaporariorum* with standard errors at various temperatures.

mean temperatures. Regarding the oviposition rate at constant temperatures, we found the following. At 10 °C the rate appeared to be significantly lower than at higher temperatures. At 15 °C the rate is significantly lower than at 20 °C, but does not differ from those at still higher temperatures. The oviposition rates at 20, 25, 30 and 35 °C do not differ among themselves.

As we can see from table 7, very low temperatures do not influence the mortality of the adults so quickly, but they do affect the percentage of the female whiteflies that actually oviposits. A very high temperature of 35 °C in contrast, kills many adults but does not change the proportion ovipositing of those that survive. The number of eggs laid per ovipositing female increases with temperature from 1 at 10 °C to 3.5 at 35 °C. During the 24 hours that the temperature was changed from 20 to 35 °C, the number of eggs laid is the largest by far. This is mainly due to the fact that almost all whiteflies participated in ovipositing.

Discussion.

All oviposition rates found (except for the rate at 20-35 °C) are very low compared to those given in figure 6. The experimental set-up resembles that of Van Boxtel (1980) who used whiteflies of 11-19 days old. In the beginning of his experiment the whiteflies were almost of the same age as they were here. We used the same tomato variety and the same leaf cages. The differences were that he conducted his experiment in a small glasshouse, during March-April

(our experiment was in October-November) and transferred the whiteflies every 2 days. Alas, literature data on the effect of the date of the experiment and of the extent of the disturbance as given above, are rather contradictory.

Considering only the relative values, we may conclude that the oviposition frequency per living female whitefly decreases when temperature decreases from 20 °C downwards. This is in accordance with all literature data known to us. When temperature increases from 20 °C onwards, the oviposition frequency is hardly changed, up to and including a temperature of 35 °C. This is in contradiction with the data presented in figure 7 from Burnett and with those from Madueke and Di Pietro in figure 8. It does agree however, with the findings of Yano (figure 8).

Burnett (1949) remarks that fewer females oviposited at high and low temperatures than in the medium temperature range. In this latter range, most of the females oviposited except at 27 °C, where 18% did not. This suggests that the difference between his and our results at high temperatures are mainly due to the fact that in his experiment the percentage of females that oviposited was low at these temperatures, while in our experiment it was at least as high as at medium temperatures. The reason for this is unknown, but possibly the condition of his picked leaves was more affected by the high temperatures than the condition of our complete plants were.

We decided to introduce into the model an oviposition rate of 5.5 eggs per female per day at temperatures of 18 °C and higher. As this is about three times as high as we found in our experiment, we fixed the rates at lower temperatures also at three times the rates we found.

Weber (1931) mentions that the threshold for egg maturation is 4 °C. At that temperature the oviposition frequency is therefore fixed to zero. At intermediate temperatures the oviposition rate is interpolated in the model. The oviposition curve introduced is indicated in figure 6.

4. The computer program with remarks on technical details

In the preceding paragraphs 3.1-3.6 the data are given to fill up the rates, parameter and auxiliary variables of the relational diagram discussed in paragraph 2. In this paragraph the computer program that was made with these data, will be discussed.

Figure 10 (appendix 1) shows the listing of the first part of the program. It includes a short description of the program and the initial situation of the whitefly population. To run the program a temperature-time table is inserted between this first part of the program and the next one.

Figure 11 (appendix 2) shows the listing of the second part of the program. It consists of several subprograms. The first of these, models the development of the eggs. Then the submodels for the development of the four larval stages and the pupa follow. For all these submodels the boxcar train method as described by De Wit and Goudriaan (1978) is used. Using this boxcar train simulation method implies that one assumes that there is no correlation between the development time in one stage and that in the other stages per individual. This was checked using data from Christochowitz and Van der Fluit (1981). The Kendall coefficient of concordance showed no association between the development times of the second, third, and fourth larval stage and the pupal stage. The Spearman rank correlation test ($\alpha = 0.01$) showed that there was no correlation between the durations of the successive stages L2-L3, L3-L4, and L4-P. With $\alpha = 0.05$ the only significant correlation was a negative one between the duration of the second and third larval stage. This gave no reason to us not to use the boxcar train simulation method.

The relative dispersion of the development that one wants to achieve in the model, determines the number of development classes that has to be chosen for each stage and the type of boxcar train model that should be used. Data on the relative dispersion of the development on tomato can be derived from the studies of Eijsackers (1969) and Christochowitz and Van der Fluit (1981). Table 8 gives the results of our calculations. The relative dispersions based on the data of Eijsackers do not suggest any temperature dependence. To see whether the relative dispersion at fluctuating temperature differs from that at constant temperatures, we compared the relative dispersions derived from Christochowitz and Van der Fluit with the mean relative dispersions of Eijsackers (table 8). Using the one-tailed utest ($\alpha = 0.05$), we found no differences between them, except in case of the fourth larval stage.

More information on the relative dispersion of development of whiteflies in relation with temperature can be gained from the studies of Madueke (1979), Stenseth (1971) and Li et al. (1980), who all used bean as host plant. The relative

Appendix 1

Figure 10

```
TITLE A SIMULATION MODEL OF WHITEFLIES ON A TOMATO CROP
*          THE DEVELOPMENTAL STAGES ARE SIMULATED AS A BOXCAR TRAIN WITH
*          CONSTANT RELATIVE DISPERSION, EXCEPT FOR THE EGG STAGE WHERE A
*          BOXCAR TRAIN WITH CONTROLLED DISPERSION IS USED.
*          THE MORTALITY OF THE DEVELOPMENTAL STAGES IS SIMULATED AS
*          REL.MORT.RATE =(LN Y(N) - LN Y(N+1))/DT.
*          THE OVIPOSITING ADULTS ARE SIMULATED WITH A FORTRAN PROCEDURE
*          IN WHICH THE NUMBERS ARE UPDATED EVERY 1/4 DAY.
*****
       STORAGE AD(600),AGE(600),MAT(600),SUAD(600)
       TABLE AD(1-600)=8.,8.4,8.9,10.,11.4,13.3,16.,20.,20.,591*0.
*          INITIAL NUMBER OF OVIPOSITING ADULTS
       TABLE AGE(1-600)=0.,0.1775,0.36,0.58,0.738,0.8735,1.,1.1265,...
                        1.262,591*0.
*          CORRESPONDING INITIAL AGES OF OVIPOSITING ADULTS
       TABLE MAT(1-600)=0.,0.5,598*1.
*          CORRESPONDING INITIAL EXTENTS OF MATURITY
FIXED I,J,K
*****
INITIAL
PARAM INE'1,12'=12*50.
PARAM INL1'1,13'=13*15.
PARAM INL2'1,7'=6*81.,88.
PARAM INL3'1,4'=10.,20.,30.,159.
```

Figure 10-1

```
PARAM INL4'1,6'=98.,5*88.
PARAM INP'1,9'=20.,2*10.,6*0.
*          INITIAL NUMBERS OF EGGS, L1, L2, L3, L4 AND PUPAE
PARAM F=0.79
*          FRACTION USED IN MODELLING EGG DEVELOPMENT
PARAM INPO'1,4'=4*1.
*          INITIAL NUMBER OF PRE-OVIPOSITION ADULTS
PARAM INAGE=0.
PARAM INMAT=0.
PARAM INWAD=0.
PARAM AGED=0.
PARAM SUADS=70.
PARAM ETOT=0.
*          PARAMETERS BEGINNING WITH 'X' ARE MULTIPLICATION FACTORS
*          USED IN SENSITIVITY ANALYSIS
PARAM XDU=1.
PARAM XRMR=1.
PARAM XOVI=1.
PARAM XLON=1.
PARAM XMAT=1.
PARAM XSEX=1.
PARAM TEMPTO=0.
*
*****
DYNAMIC
       TEMP=TEMPTO+AFGEN(TEMPTB,TIME)
```

Figure 10-2

Fig. 10. Listing of the first part of the whitefly-population-growth model.

Appendix 2

Figure 11

```
*                          HATCHING OF THE EGGS
      EO=INTGRL(0.,OVIRT-FLEO-RMRE*EO)
*          A PRECLASS IS CONSTRUCTED TO PROCESS THE BIRTH RATE
      E'1,12'=INTGRL(INE'1,12',FLE'0,11'-FLE'1,12'-RMRE*E'1,12')
      OVIRT=NWEGG/DELT
      FLE'0,12'=INSW(E'0,12'-1.E-20,0.,FWE'0,12')
*          TO PREVENT 'UNDERFLOWS'
      FWEO=EO*(1.-RMRE*DELT)*2./(F*RESTE)
      FWE'1,12'=E'1,12'*(1.-RMRE*DELT)*F*PUSH
*          THE FLOWS OF FRACTIONS F OF THE CONTENTS OF EACH CLASS TO THE
*          NEXT CLASSES OF EGGS
      PUSH=INSW(DEV-1.,0.,1./DELT)
      DEV=INTGRL(0.,1./(F*RESTE)-PUSH)
*          THE CONTENTS OF THE CLASSES ARE ONLY SHIFTED EVERY FRACTION F OF
*          THE RESIDENCE TIME
      RMRE=XRMR*(0.063/DUE)
*          THE RELATIVE MORTALITY RATE OF THE EGG-STAGE
      RESTE=DUE/12.
*          RESIDENCE TIME PER EGG-CLASS
      DUE=XDU*(26.35-1.25*TEMP+0.018*TEMP**2.)
*          MEAN DURATION OF EGG-STAGE DEPENDENT ON TEMPERATURE
      EGG=SUM1(E'0,12')
*          TOTAL NUMBER OF EGGS
*****
```

Figure 11-1

```
*                          DEVELOPMENT OF L1
      L11=INTGRL(INL11,FLE12-FLL11-RMRL1*L11)
*          FIRST L1-CLASS IS FILLED WITH HATCHED EGGS
      L1'2,13'=INTGRL(INL1'2,13',FLL1'1,12'-FLL1'2,13'-RMRL1*L1'2,13')
      FWL1'1,13'=L1'1,13'*(1.-RMRL1)/RESTL1
*          THE CONTINUOUS FLOWS TO THE NEXT CLASSES OF L1
      FLL1'1,13'=INSW(L1'1,13'-1.E-20,0.,FWL1'1,13')
*          TO PREVENT 'UNDERFLOWS'
      RMRL1=XRMR*(0.038/DUL1)
*          THE RELATIVE MORTALITY RATE OF L1
      RESTL1=DUL1/13.
*          RESIDENCE TIME PER L1-CLASS
      DUL1=XDU*(23.71-1.34*TEMP+0.022*TEMP**2.)
*          MEAN DURATION OF L1-STAGE DEPENDENT ON TEMPERATURE
      LARV1=SUM1(L1'1,13')
*          TOTAL NUMBER OF L1'S
*****
*                          DEVELOPMENT OF L2
      L21=INTGRL(INL21,FLL113-FLL21-RMRL2*L21)
*          FIRST L2-CLASS IS FILLED WITH MOULTED L1'S
      L2'2,7'=INTGRL(INL2'2,7',FLL2'1,6'-FLL2'2,7'-RMRL2*L2'2,7')
      FWL2'1,7'=L2'1,7'*(1.-RMRL2)/RESTL2
*          THE CONTINUOUS FLOWS TO THE NEXT CLASSES OF L2
      FLL2'1,7'=INSW(L2'1,7'-1.E-20,0.,FWL2'1,7')
*          TO PREVENT 'UNDERFLOWS'
      RMRL2=XRMR*(0.023/DUL2)
*          RELATIVE MORTALITY RATE OF L2
```

Figure 11-2

```
      RESTL2=DUL2/7.
*          RESIDENCE TIME PER L2-CLASS
      DUL2=XDU*(16.10-0.85*TEMP+0.013*TEMP**2.)
*          MEAN DURATION OF L2-STAGE DEPENDENT ON TEMPERATURE
      LARV2=SUM1(L2'1,7')
*          TOTAL NUMBER OF L2'S
*****
*                              DEVELOPMENT OF L3
      L31=INTGRL(INL31,FLL27-FLL31-RMRL3*L31)
*          FIRST L3-CLASS IS FILLED WITH MOULTED L2'S
      L3'2,4'=INTGRL(INL3'2,4',FLL3'1,3'-FLL3'2,4'-RMRL3*L3'2,4')
      FWL3'1,4'=L3'1,4'*(1.-RMRL3)/RESTL3
*          THE CONTINUOUS FLOWS TO THE NEXT CLASSES OF L3
      FLL3'1,4'=INSW(L3'1,4'-1.E-20,0.,FWL3'1,4')
*          TO PREVENT 'UNDERFLOWS'
      RMRL3=XRMR*(0.034/DUL3)
*          RELATIVE MORTALITY RATE OF L3
      RESTL3=DUL3/4.
*          RESIDENCE TIME PER L3-CLASS
      DUL3=XDU*(12.94-0.66*TEMP+0.010*TEMP**2.)
*          MEAN DURATION OF L3-STAGE DEPENDENT ON TEMPERATURE
      LARV3=SUM1(L3'1,4')
*          TOTAL NUMBER OF L3'S
*****
*                              DEVELOPMENT OF L4
      L41=INTGRL(INL41,FLL34-FLL41-RMRL4*L41)
*          FIRST L4-CLASS IS FILLED WITH MOULTED L3'S
```

Figure 11-3

```
      L4'2,6'=INTGRL(INL4'2,6',FLL4'1,5'-FLL4'2,6'-RMRL4*L4'2,6')
      FWL4'1,6'=L4'1,6'*(1.-RMRL4)/RESTL4
*          THE CONTINUOUS FLOWS TO THE NEXT CLASSES OF L4
      FLL4'1,6'=INSW(L4'1,6'-1.E-20,0.,FWL4'1,6')
*          TO PREVENT 'UNDERFLOWS'
      RMRL4=XRMR*(0.015/DUL4)
*          RELATIVE MORTALITY RATE OF L4
      RESTL4=DUL4/6.
*          RESIDENCE TIME PER L4-CLASS
      DUL4=XDU*(30.78-1.745*TEMP+0.027*TEMP**2.)
*          MEAN DURATION OF L4-STAGE DEPENDENT ON TEMPERATURE
      LARV4=SUM1(L4'1,6')
*          TOTAL NUMBER OF L4'S
*****
*                              DEVELOPMENT OF PUPA
      P1=INTGRL(INP1,FLL46-FLP1-RMRP*P1)
*          FIRST PUPA-CLASS IS FILLED WITH MOULTED L4'S
      P'2,9'=INTGRL(INP'2,9',FLP'1,8'-FLP'2,9'-RMRP*P'2,9')
      FWP'1,9'=P'1,9'*(1.-RMRP)/RESTP
*          THE CONTINUOUS FLOWS TO THE NEXT CLASSES OF P
      FLP'1,9'=INSW(P'1,9'-1.E-20,0.,FWP'1,9')
*          TO PREVENT 'UNDERFLOWS'
      RMRP=XRMR*(0.019/DUP)
*          RELATIVE MORTALITY RATE OF P
      RESTP=DUP/9.
*          RESIDENCE TIME PER PUPA-CLASS
      DUP=XDU*(21.72-1.42*TEMP+0.027*TEMP**2.)
```

Figure 11-4

```
*          MEAN DURATION OF PUPA-STAGE DEPENDENT ON TEMPERATURE
      PUPA=SUM1(P'1,9')
*          TOTAL NUMBER OF PUPAE
      SURVP=INTGRL(8.,FLP9)
*          CUMULATIVE NUMBER EMERGING FROM PUPA (EMPTY SCALES)
      LARVP=LARV4+PUPA
```

Figure 11-5

Fig. 11. Listing of the second part of the whitefly-population-growth model: the developmental stages.

Table 8. Relative dispersions of the developmental periods of immature whitefly stages on tomato, calculated from literature data.

Data from	Temp, °C	Egg	L1	L2	L3	L4	Pupa
Christochowitz & v.d.Fluit 1981	D18/N8	0.07	–	0.26	0.19	0.16	0.14
Eijsackers 1969	10	0.11	0.35	0.18	0.32	0.39	0.42
	15	0.15	0.26	0.25	0.54	0.29	0.19
	20	0.13	0.24	0.76	0.46	0.62	0.54
	25	0.20	0.29	0.46	0.89	0.32	0.17
	30	0.07	0.24	0.28	0.28	0.48	0.35
mean		0.13	0.28	0.39	0.50	0.42	0.33

dispersions we calculated using data of Madueke are given in table 9. Stenseth presents in his table 1 the number of days after which 10% and 90% of the whiteflies had reached a particular stage. As an indication of the relative dispersion, we calculated the difference between these two data and divided that by the mean of them. The results of those calculations are also given in table 9. In his figure 1, Stenseth shows cumulative frequencies of development at fluctuating temperatures (24 D / 18 N, mean 21 °C and 24 D / 15 N, mean 19.5 °C). As the duration of egg development concerns, one may conclude from this figure that the relative dispersions at fluctuating temperatures do not or hardly differ from those at the mean constant temperatures. The other curves given in the figure do not allow to draw conclusions on the separate following stages, as the dispersions of development of previous stages is included in these curves. Li et al. present the mean, minimum and maximum development times at fluctuating temperatures. As an indication of the relative dispersion, we calculated the difference between the minimum and maximum development times and divided that by the mean development time. The results are given in table 9.

The figures derived from Stenseth and Li et al. support the conclusion, based on data from Eijsackers that the relative dispersion is not temperature dependent. The figures from Madueke show only a slight increase of the relative dispersion with increasing temperature. For our model the boxcar train with constant relative dispersion seems most suitable therefore. The mean relative dispersions from Eijsackers have been used to determine the number of development classes per stage ($N = \left(\frac{1}{\text{rel.disp}}\right)^2$. For the six stages, from egg to pupa, this leads to respectively 57, 13, 7, 4, 6, and 9 classes. Except at the egg stage, these numbers can be found in the program listing (figure 11). To reduce the number of classes for the egg stage, the boxcar train method with controlled dispersion can be used. This means that a fraction F of the contents of each class is shifted once every fraction F of the residence time in a class. The number of classes (N) and F can be calculated from : $F = 1\text{-}N \times \text{rel.disp}^2$. One of the possible solutions, namely $N = 12$ and $F = 0.79$, is chosen and can be found in the program listing.

Table 9. 'Relative dispersions' of the developmental periods of immature whitefly stages on bean, calculated from literature data.

Data from	Temp, °C	Egg	L1	L2	L3	L4	Pupa
Madueke 1979	18	0.03	0.11	0.18	0.20	0.15	0.15
	22.5	0.08	0.22	0.24	0.24	0.12	0.16
	27	0.12	0.25	0.31	0.26	0.18	0.25
Stenseth 1971	9	0.34	–	–		–	
	12	0.17	0.16	0.53		0.48	
	15	0.23	0.33	0.38		0.26	
	18	0.25	0.43	0.23		0.38	
	21	0.31	0.67	0.35		0.43	
	24	0.14	0.46	0.45		0.33	
	30	0.20	0.40	0.58		0.33	
Li et al. 1980	10-15	0.05	0.31	0.22	0.15	0.21	
	10-21.5	0.06	0.12	0.54	0.36	0.44	
	14-25	0.35	0.33	0.60	0.49	0.33	
	21-25	0.27	0.36	0.40	0.25	0.33	
	20-30.5	0.46	0.44	0.44	0.67	0.33	
	22-30.5	0.54	0.67	0.86	0.80	0.41	

Table 9 continued.

The figures given are relative dispersions (Madueke), the difference between the periods of 10% and 90% development, divided by the mean of them (Stenseth) and the difference between the maximum and minimum periods of development, divided by the mean development time (Li et al.).

The last mentioned method leads to a discontinuous simulation curve, in contrast with the former method, and forces the modeller to use the rectilinear integration method.

The method used for modelling the egg development gives rise to a new problem. The first development class is filled with a continuous inflow of newly laid eggs (OVIRT in figures 11 and 1). Only the eggs that enter the class directly after the shifting mentioned above has taken place, stay in the class for the intended residence time. Eggs entering later will have a residence time that is too short. The mean residence time in the first class will be short by half of the

shifting interval $\frac{\text{FxRESTE}}{2}$. To correct this a preclass is constructed with an average residence time of $\frac{\text{FxRESTE}}{2}$.

Each subprogram in figure 11 contains an equation that describes the relation between duration of development (DU) and temperature for the whitefly stage concerned. These second-grade polynomes are discussed in paragraph 3.1 and shown in figures 2 and 3. After validation tests, however, the developmental

rates were not set to zero at temperatures of 8 °C and lower. At these temperatures too the polynome values are used.

The mortality percentages that are discussed in paragraph 3.2 are converted to relative mortality rates (RMR). When the mortality during a stage is m%, the relative mortality rate can be calculated as RMR =

$$\frac{-\ln\left(1-\frac{m}{100}\right)}{DU}.$$

The high mortality for pupae at temperatures of 30 °C and higher is not found in the model listing. This is based on validation tests that will be discussed later.

In figure 12 (appendix 3) the third part of the program is given. It concerns the adult whiteflies and starts with their pre-oviposition period. As with the developmental periods, the boxcar train simulation method is used for modelling. The number of classes should again be determined by the relative dispersion. Because there are no accurate data available, we used the relative dispersion of the mean pre-oviposition periods found by Burnett (1949) (table 3). This lead to four classes.

For the construction of the model it was important to have information on the distribution of the longevity. Survival curves of whiteflies on tomato are given by Van Rongen (1979), Van Boxtel (1980) and Van Sas (1978). Yano (1981) shows survival curves on tobacco.

The distribution of the longevity as given by Van Rongen was found to be not different from a normal distribution with $\sigma = 0.3\mu$. Van Boxtel and Van Sas performed series of experiments on several host plants, among which tomato. Of the distributions found, by far the most do not differ from a normal distribution. The standard deviations average 0.6 times the means. The curves given by Yano do also not differ from normal distributions, while his standard deviations average 0.4 times the means. Based on these data we assumed the longevity to be normally distributed with $\sigma = 0.5\mu$. The adult life after the pre-oviposition period is modelled using a Fortran procedure. Every 1/4 of a day, the adults that have come out of the preoviposition boxcar during those six hours (NWAD) enter the first compartment of an array (AD1). This array consists of 600 compartments, in each of which the adults may stay for 1/4 of a day, after which they are shifted to the next compartment. This implies that in total a lifetime after the pre-oviposition period of 150 days at most can be simulated. The longest mean lifetime that may be realized is 74.5 days (see figure 5). The longevity is regarded as normally distributed with $\sigma = 0.5\mu$ (see above), so that even in the most extreme situation only 2% of the population is lost in the end in the model (97.7% will have died after $\mu + 2\sigma$ days, i.e. 149 days). The adults that enter the first compartment of the array are considered to be on the average 1.3 days of age, i.e. the mean duration of the pre-oviposition period. The residence time of six hours at most in NWAD is neglected.

During the six hours between two shiftings the adults grow older. Besides, during the first part of the oviposition period the female whiteflies mature untill

Appendix 3

Figure 12

```
*                              AGEING OF THE ADULTS
*                              PRE-OVIPOSITION PERIOD
      PO1=INTGRL(INPO1,FLP9-FLPO1)
      PO'2,4'=INTGRL(INPO'2,4',FLPO'1,3'-FLPO'2,4')
      FLPO'1,4'=INSW(PO'1,4'-1.E-20,0.,FWPO'1,4')
*          TO PREVENT 'UNDERFLOWS'
      FWPO'1,4'=PO'1,4'/0.325
*          RESIDENCE TIME PER PRE-OVIPOSITION CLASS IS 0.325
      PO=SUM1(PO'1,4')
*****
*                              OVIPOSITION PERIOD
      NWAD=INTGRL(INWAD,FLPO4)
*          IN NWAD THE CONTINUOUS OUTFLOW FROM THE PRE-OVIPOSITION PERIOD
*          IS GATHERED DURING 1/4 DAY
      TRIG=IMPULS(0.25,0.25)
*          TRIGGER FOR THE PROCEDURE WITH WHICH THE OVIPOSITING ADULTS ARE
*          SIMULATED TO BE RUN EVERY 1/4 DAY
      FLAGE=INTGRL(INAGE,AGERT)
*          THE AGEING RATE IS INTEGRATED DURING 1/4 DAY. THE RESULT IS
*          ADDED TO THE AGES STORED IN THE PROCEDURE AND THEN RESET TO 0.
      AGERT=1./LONAD
      LONAD=XLON*AFGEN(LONTAB,TEMP)
      FUNCTION LONTAB=(5.,23.7),(9.,33.2),(12.,60.),(15.,74.5),...
                      (18.,66.5),(22.,48.7),(24.,41.2),(27.,32.3),...
```

Figure 12-1

```
                    (30.,18.7),(33.,8.7),(40.,3.7)
*       MEAN DURATION OF OVIPOSITION PERIOD (LONGEVITY MINUS 1.3 DAYS
*       PRE-OVIPOSITION PERIOD) DEPENDENT ON TEMPERATURE
      OVIFQ=XOVI*AFGEN(OVITAB,TEMP)
      FUNCTION OVITAB=(4.,0.),(10.,0.09),(15.,0.847),(18.,1.375),...
                    (40.,1.375)
*       OVIPOSITION FREQUENCY IN EGGS PER FEMALE PER 1/4 DAY,
*       DEPENDENT ON TEMPERATURE
      FLMAT=INTGRL(INMAT,MATRT)
*       THE MATURATION RATE IS INTEGRATED DURING 1/4 DAY, THE RESULT IS
*       ADDED TO THE MATURATION STORED IN THE PROCEDURE AND THEN RESET
*       TO 0.
      MATRT=1./MATDU
      MATDU=XMAT*AFGEN(MATTAB,TEMP)
      FUNCTION MATTAB=(5.,17.1),(7.,14.2),(18.,3.4),(22.,1.7),...
                    (30.,1.1),(40.,0.85)
*       DURATION OF THE PERIOD FROM HATCHING TO FULL MATURATION
*       (I.E. MAXIMUM DAILY EGG PRODUCTION) MINUS 1.3 DAYS OF THE
*       PRE-OVIPOSITION PERIOD
      ADULT=PO+NWAD+SUADS
PROC SUADS,NWEGG=LIFE(TRIG,FLAGE,FLMAT,NWAD,XSEX,OVIFQ)
      IF (KEEP.NE.1.) GOTO 888
      IF (TRIG.NE.1.) GOTO 777
      DO 10 I=1,599
*       THE CONTENTS OF THE ADULT-TABLE IS MOVED UP BY ONE 1/4-DAY-
*       COMPARTMENT. THE FIRST COMPARTMENT IS NEWLY FILLED.
      K=600.-I
```

Figure 12-2

```
      AD(K+1)=AD(K)
      AGE(K+1)=AGE(K)
      MAT(K+1)=MAT(K)
   10 CONTINUE
      AD(1)=NWAD
      AGE(1)=0.
      MAT(1)=0.
      DO 20 I=2,600
*         THE AGES AND MATURITIES ARE ADJUSTED ACCORDING TO THE CHANGES
*         DURING THE LAST 1/4 DAY
      AGE(I)=AGE(I)+FLAGE
      MAT(I)=MAT(I)+FLMAT
      IF (MAT(I).GT.1.) MAT(I)=1.
   20 CONTINUE
      FLAGE=0.
      FLMAT=0.
      NWAD=0.
      SUADS=0.
      NWEGG=0.
      SEXR=0.5*XSEX
*         SEX RATIO AS FEMALE FRACTION OF TOTAL POPULATION
      DO 30 I=1,600
      AGED=AGE(I)
      SURVX=AFGEN(SURVTB,AGED)
      FUNCTION SURVTB=(0.,1.),(0.01,0.976),(0.1775,0.95),...
          (0.28,0.925),(0.36,0.9),(0.4815,0.85),(0.58,0.8),...
          (0.6625,0.75),(0.738,0.7),(0.8075,0.65),(0.8735,0.6),...
```

Figure 12-3

```
            (0.937,0.55),(1.,0.5),(1.063,0.45),(1.1265,0.4),...
            (1.1925,0.35),(1.262,0.3),(1.3375,0.25),(1.42,0.2),...
            (1.5185,0.15),(1.64,0.1),(2.165,0.01),(2.2875,0.005),...
            (2.5,0.0),(5.0,0.0)
*           PERCENTAGE SURVIVAL DEPENDENT ON AGE, BASED ON THE ASSUMPTION
*           OF A NORMALLY DISTRIBUTED LONGEVITY WITH SIGMA=0.5*MU
        IF (SURVX.EQ.0.) GOTO 888
        SUAD(I)=AD(I)*SURVX
        SUADS=SUADS+SUAD(I)
        NWEGG=NWEGG+(SUAD(I)*SEXR*OVIFQ*MAT(I))
     30 CONTINUE
        GOTO 888
    777 NWEGG=0.
    888 CONTINUE
ENDPROC
PROC ETOT=SUM(TRIG,NWEGG)
        IF (KEEP.NE.1.) GOTO 999
        IF (TRIG.NE.1.) GOTO 999
        ETOT=ETOT+NWEGG
*           THE TOTAL NUMBER OF EGGS PRODUCED
    999 CONTINUE
ENDPROC
*****
        TOTPOP=EGG+LARV1+LARV2+LARV3+LARVP+ADULT
PREPAR TOTPOP,EGG,LARV1,LARV2,LARV3,LARV4,PUPA,LARVP,SURVP,ADULT,...
        NWEGG,ETOT,TEMP
*****
```

Figure 12-4

```
METHOD RECT
TIMER FINTIM=38.,OUTDEL=2.,PRDEL=2.,DELT=0.05
END
STOP
ENDJOB
```

Figure 12-5

Fig. 12. Listing of the last part of the whitefly-population-growth model: the adult whiteflies.

they have reached their maximum daily oviposition level, as was discussed in paragraph 3.6.. The ageing and maturation are calculated in the model by integration of the temperature-dependent ageing and maturation rates. The ageing rate (AGERT) is the inverse of the longevity minus the 1.3 days of the pre-oviposition period (LONAD). The maturation rate (MATRT) is the inverse of the period from the end of the pre-oviposition period till the moment of maximum daily oviposition (MATDU). Every 1/4 of a day the Fortran procedure is run. The contents of the array compartments are shifted and the ages and maturities of the whiteflies are adjusted, according to the changes during the last six hours. Next, with a table based on a normal distribution with $\sigma = 0.5\mu$, the survival percentages of the initial numbers of adults at the given ages is determined (SURVX) and the number of surviving adults per compartment is calculated (SUAD(I)).

Then the number of eggs laid is calculated. Per compartment the oviposition frequency is determined by multiplying the oviposition level (OVIFQ) by the maturation (MAT(I)). This oviposition frequency multiplied with the number of surviving adults and the sex ratio (SEXR, the female fraction of the total population) gives the number of new eggs laid (NWEGG). This modelling method made it possible to achieve as much detailedness as was desired and to keep the amount of computing time needed within acceptable limits.

At the end of the listing of figure 12 the total population is defined (TOTPOP). Erroneously the variable NWEGG is not included in this definition.

5. Verification and validation

Running the whitefly model program and accurately controlling its operation revealed that it operated as intended.

The time interval of integration (DELT) that is used in the model is 0.05 (i.e. 0.05 of 24 hours, which is 1 hour and 12 minutes). This should be much smaller than the time constant of the system modelled, because it is assumed that the changing rate of the system is constant during the interval (Rabbinge 1978). However, if DELT is chosen smaller than necessary, it will take much more time to run the program and thereby make a run needlessly expensive. The efficiency of the DELT chosen was tested by rerunning the model, after a successful validation run, with DELT = 0.15 and DELT = 0.005. With DELT = 0.15 the results differ much from those obtained with DELT = 0.05. Using DELT = 0.005 led to results that were almost the same as with DELT = 0.05. We decided to keep DELT at 0.05.

To validate the model, we first tested the part of it that describes the developmental period. There were two data sets available to compare the model results with. One came from an experiment conducted by Christochowitz and Van der Fluit (1981). They followed the development of second instar larvae at a temperature regime of 7 N / 18 D. The results of their experiment and of the model are given in figures 13a and 13b. The developmental rate in the experiment was higher than in the simulated results, even in spite of the fact that the developmen-

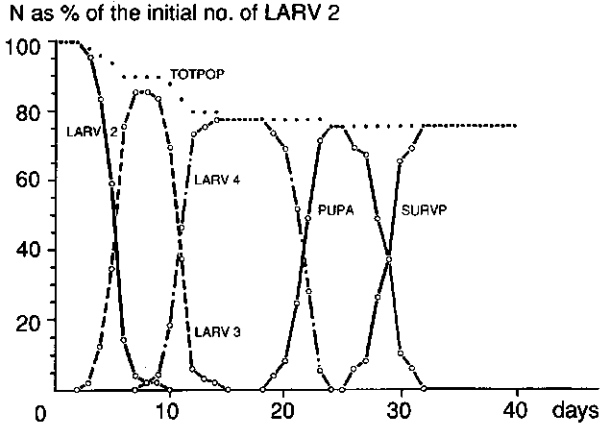

Fig. 13a. Numbers of whitefly larvae and empty pupae from an experiment of Christochowitz and Van der Fluit (1981) at a temperature regime of 7N/18D.

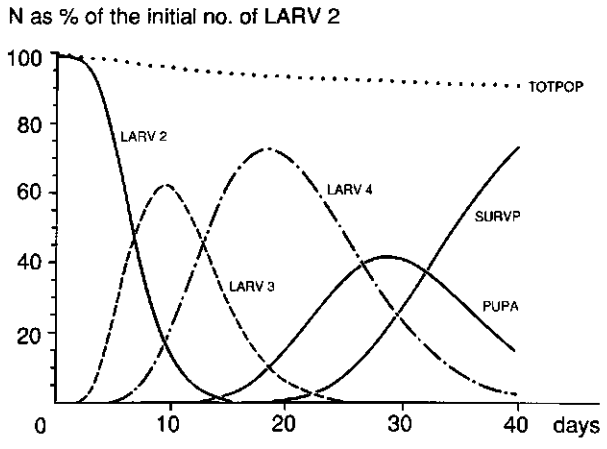

Fig. 13b. Results of the simulation of the experiment shown in figure 13a.

tal rate at temperatures of 8 °C and lower was not set to zero. We decided therefore not to build into the model a zero for the developmental rate but to use the polynomes as given in figures 2 and 3 at all temperatures. Of the adult whiteflies 50% had hatched after 29 days in the experiment, while it takes almost 33 days in the simulation. Also the deviations in developmental times are smaller in the experiment than in the simulated results. The mortality was much higher than simulated, particularly during the second and third larval stages. It must be mentioned, however, that the host plants used in the experiment did not very well stand the low temperature regime. Only a few of them survived the experiment. The whitefly population represented in figure 13a was found on these few plants. The high mortality seen in figure 13a might have been caused by the condition of the host plants. Besides, it is very well possible that the larvae included in figure 13a constitute a select, strong group out of the total population. No further changes were therefore introduced into the model based on this validation experiment.

The second experiment with which the simulation results could be compared was conducted by Van Evert and Schutte (1983). They followed the development of 127 whitefly eggs on tomato at a temperature regime that is normal for Dutch glasshouses in summer (lowest night temperature 17.8 °C, highest day temperature 34.6 °C). Their results and those of the simulation are presented in figures 14a and 14b. To obtain the results of figure 14b, the model was changed in one respect. According to what was discussed in paragraph 3.2, the pupal mortality at temperatures from 30 °C onwards was initially set at 96.9%. This led to a tremendous decrease in numbers in the simulation from the moment that pupae appeared. As can be seen in figure 14a, this high mortality did not occur in reality. When we fixed the pupal mortality at 1.9% for all temperatures, this led to the results shown in figure 14b. The correspondence with the experimental

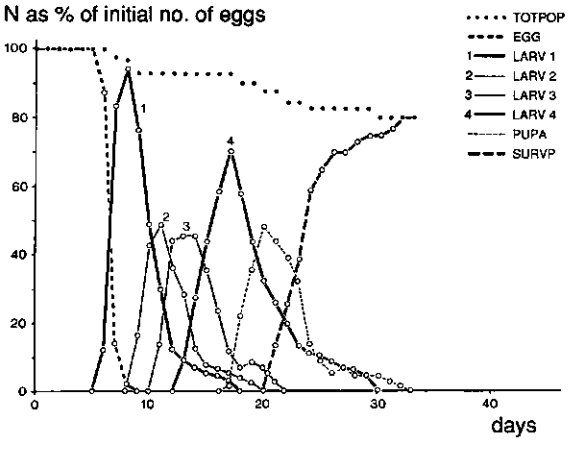

Fig. 14a. Numbers of whitefly eggs, larvae and empty pupae, from an experiment of Van Evert and Schutte (1983) at a normal summer temperature regime.

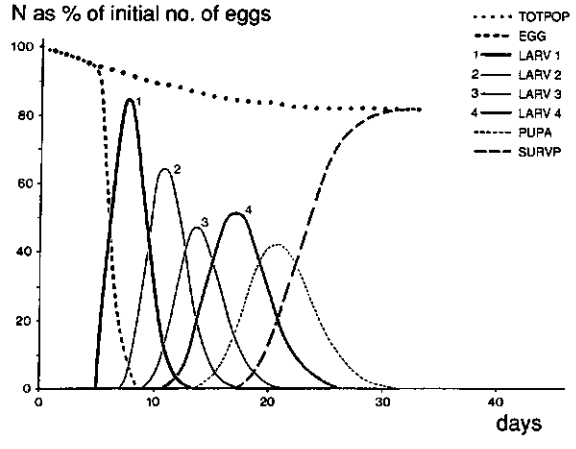

Fig. 14b. Results of the simulation of the experiment shown in figure 14a.

data is very good and does not give rise to further changes of the model.

To validate the total model, we gratefully used data provided by Dr. O.M.B. De Ponti of the Institute for Horticultural Plant Breeding in Wageningen. They were data of development of whitefly on the tomato variety 'Allround' in experiments on whitefly resistance. In glasshouse compartments whitefly adults were introduced on 5 to 15 tomato plants. The numbers of empty pupae were counted

as a measure for total population size after some time. The temperature was recorded with thermographs. When we introduced into the model the same initial number of adults and the same temperature regime, this led to the curves given in figures 15a-f.

Some remarks have to be made on the experimental data. Unless indicated otherwise, the numbers given are the numbers of empty pupae that were determined by checking all leaves of all plants in the experiment concerned. In experiment 'a', 2 out of 15 plants were checked for empty pupae on day 92. The dots in figure 15a indicate the estimated total numbers, assuming that the ratios (counted plant: total) were the same as on day 54. In the experiments 'b' and 'c', 1 out of 10 plants was checked on day 83. The estimates of the total numbers on day 83 were made with the assumption that the ratio (counted plant : total) was the same as on day 40 or day 61. In figure 15f the results of 3 experiments are combined. Those experiments were conducted in 3 compartments of the same glasshouse and there was one temperature registration available. On day 44 adults were trapped and counted to get an impression of the infestation. Respectively 97, 147 and 286 adults were thus removed. On day 47 the numbers of empty pupae were counted on 2 leaflets of each leaf. According to earlier findings

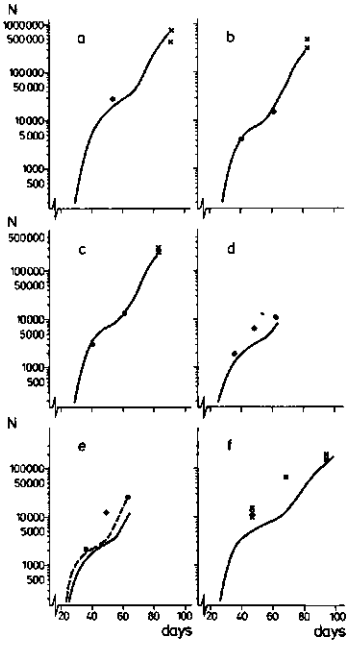

Fig. 15. Simulated and experimental numbers of *Trialeurodes vaporariorum* empty pupae in population experiments on tomato.
• = counted numbers, x = estimated numbers, ¯ = simulated numbers, ---- = simulated numbers with a 2°C higher temperature.

of the Institute for Horticultural Plant Breeding, one gets a reliable estimate for the total numbers present, by multiplying the numbers thus found by 3. On day 47 the estimates for the 3 glasshouse compartments are given. In one of the compartments the last count was made on day 69, while in the other compartments the numbers of empty pupae were counted on day 90 till day 95.

When we compare the experimental results with the simulation curves, we may conclude that in three out of these six cases their correspondence is good (15a, b and c). In figure 15d, e and f the experimental numbers are all above the simulated curves. The experimental results in these last three cases suggest that the levelling off of the simulation curves till about day 60 is not realistic. However, we do find such a course in the experimental data of figure 15b and c. The experiments were all done with the same host plant variety in almost the same way. The temperatures varied between the same limits (about 16–19 °C at night and 20–38 °C in the afternoon).

In the beginning of the experiments, the afternoon temperatures of experiments 'd', 'e' and 'f' were higher (35–38 °C) than those of experiments 'a', 'b' and 'c'. This might suggest that the whitefly model underestimates the population growth rate at the higher temperatures. Of all rates in the model, the ageing rate (based on longevity data) was fixed somewhat arbitrary at high temperatures. It is not impossible that the mean longevity at these temperatures was chosen too low (see paragraph 3e). Therefore a rerun was made for experiment 'e' with a mean oviposition period of 13 days at 33 °C (instead of 8.7 days) and 10 days at 40 °C (instead of 3.7 days). This resulted in a population curve that had the same course and was only slightly higher than the curve given in figure 15e.

The temperature registration during the experiments, with thermographs, is not very accurate. The temperature table in the model contains three or four temperature-time data per 24 hours, while the data between them were found by linear interpolation. Thus only a rough description of the temperature course is obtained. To get an impression of the effect of deviations in temperature, a rerun was made for experiment 'e' raising the temperature with 2 °C. The resulting curve is also given in figure 15e. There is a substantial effect, but the course of the curve remains almost the same.

As a last remark, it must be mentioned that it is not impossible that the plants used in the experiments were already unintentionally infected at the beginning. The Institute for Horticultural Plant Breeding as well as ourselves have experienced that it is almost impossible to keep plants free of whiteflies, while in the neighbourhood whiteflies are present for other experiments. If not very accurately searched for, whitefly eggs and young instars are easily overlooked.

Of course more control data with replicates are needed, so that it can really be tested further whether the simulation results are within the confidence intervals of the experimental data. The first simulation results over two to three generations are, however, hopeful.

6. Sensitivity analysis

For a preliminary evaluation of the relative importance of various life history components for the population growth rate, a limited sensitivity analysis was done. We determined the effect of a 10% increase or decrease of several life-history components on the end result of the simulation. The simulation of experiment 'c' (figure 15c) was used as a reference, because this fitted the experimental data best.

The following components were varied : developmental period (from egg to adult), fecundity, relative mortality rate of the developmental stages, adult longevity and the duration of what we have named 'maturation period'. We must point out that changing the adult longevity did not imply a change of the pre-oviposition period, nor a change of the maturation rate. The results are shown in figure 16. On the left of the zero-line we see the relative change in total population size after 84 days, when the component concerned was set to 90% of the value used in the reference model. On the right of the zero-line the same is shown for 110% of the reference value. A 10% decrease of the developmental period thus led to a 68.8% increase of the total population size. A 10% increase of the developmental time led to a total population size that was 42.8% smaller than the reference value. By decreasing the fecundity with 10%, the total population size was decreased with 25.5%, while increasing the fecundity with 10% led to a total population size that was 30.8% larger than the reference value. As can be seen from figure 16, changing of the developmental period has far the greatest effect, followed by a proportionally equivalent change in fecundity. This is in agreement with theoretical publications on the relative importance

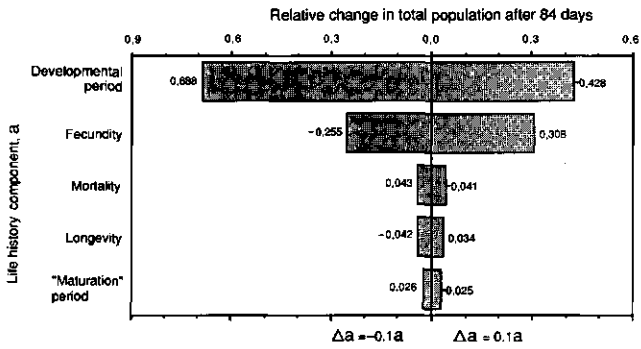

Fig. 16. Sensitivity analysis of *Trialeurodes vaporariorum* population growth-model.

of life-history components for the population growth rate (Lewontin 1965; Snell 1978; Caswell and Hastings 1980).

In paragraph 3.5 the influence of the tomato variety on the whitefly longevity was discussed. Figure 16 shows that a change in longevity will not strongly affect the population growth rate. Of course this only holds when the fecundity, and especially the oviposition frequency in the beginning of the oviposition period, is not changed too much at the same time.

The rather rough approximation that was used to determine the longevity/temperature curve (paragraph 3.5) seems not unacceptable, at least in the temperature region used in this analysis (16–38 °C).

The data given in figure 16 should of course only be regarded in relation with one another. Regarded absolutely they only apply to the initial situation of this case, the temperature course that was introduced and the period after which the total population size was determined. Probably also the relative results of such a sensitivity analysis will be different when another temperature regime is introduced. The sensitivity analysis given should only be considered a first, preliminary analysis. More extensive analyses can be found in Yano et al. 1988 a,b.

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