Population dynamics of two leafminer pests (Liriomyza bryoniae and L. trifolii) and a parasitoid (Diglyphus isaea) in tomato; A simulation study.

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Contents

Summary

Two leafminer species, Liriomyza bryoniae and L. trifolii, can be a serious pest in greenhouse vegetables. A deterministic population model has been extended. The model simulates population growth of both leafminer species in tomato, population growth of a leafminer parasitoid, Diglyphus isaea, and interactions between the leafminer and the parasitoid population. In the model population growth is driven by two forcing variables, temperature and leaf nitrogen content. Differences in nitrogen content, as found in tomato plants during the season, can have a large influence on population growth. The multiplication factor between generations increases with increasing nitrogen content. The number of generations during the season is hardly affected. A sensitivity analysis of some life cycle variables has been carried out.

Validation has been carried out using data from a pilot greenhouse experiment. The experiment provides data on temperature, not on nitrogen content. There is good correpondance between simulated and experimental data for the first two generations. The third leafminer generation is overestimated by the model, even when a decreasing nitrogen content during the season is assumed. The parasitoid part of the model does not predict the percentage parasitism inflicted on the leafminer population well. Mechanisms possibly causing discrepancies between simulated and registered parasitism are discussed.

1 Introduction.

Culture of tomatoes in greenhouses in the Netherlands is confronted with the occurrence of leafminer pests. Two species are involved: Liriomyza bryoniae (Kaltenbach) and Liriomyza trifolii (Burgess) (Diptera: Agromyzidae). L.bryoniae has been found frequently in large numbers in Dutch greenhouse vegetables since 1976 and L. trifolii has appeared as a pest in greenhouses since 1980. Both leafminer species can be a pest on several vegetables and ornamentals. Females make feeding punctures on leaves by scraping the surface with their ovipositor. After puncturing the leaf, some juice is imbibed of the wounded tissue and oviposition sometimes takes place (Bethke & Parrella, 1985). Most damage is caused by the larvae however, mining the leaves (Minkenberg & v. Lenteren, 1986).

It is hard to control L. trifolii with insecticides. Resistance is developed readily (Leibee, 1981) and integrated control programs can be disturbed easily. Since 1972 the key pest in tomatoes in greenhouses, the white fly Trialeurodes vaporariorum (Westwood) is biologically controlled by the parasitoic wasp Encarsia formosa (Gahan). The development of a biological control method for leafminers is therefore very important (Minkenberg & v. Lenteren, 1986).

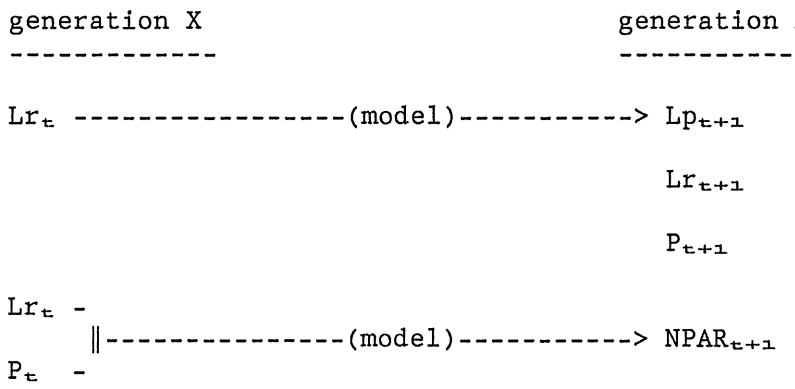
In 1983 the Department of Entomology of the Agricultural University at Wageningen has started a project titled: 'Development of a biological control program for leafminers in greenhouses' (Minkenberg, 1984). Research in the laboratory and in greenhouses on leafminers and several parasitoids of leafminers has produced data on the life cycle of both leafminers and a parasitoid, Diglyphus isaea (Walker) (Hymenoptera: Eulophidae). Using these data a simulation model can be developed which predicts the population development of the leafminers and the parasitoid.

At this moment it is still uncertain whether parasitoids can effectively control leafminer populations. After introduction of parasitoids a decreased population growth has been found. However without introduction also a decreased population growth of L. bryoniae has appeared. Conditions in greenhouses can be varying in such a way that a comparison between them is impossible.

To estimate the effectiveness of several parasitoid species, parasitoids will be introduced in greenhouses with well established leafminer populations. After each generation of leafminers two estimates will be made (Minkenberg, pers. com.):

(1) Mean number of larvae per plant during the last generation (Lr_t). A stratified random sampling method will be used (Southwood,1978a). This method gives good estimates (Jetten, 1986).
(2) Fraction of larvae parasitised during the last generation (P_t).

With a population-growth model the number of larvae in the next generation (Lp_{t+1}) can be predicted from the number of larvae of the previous generation (Lr_t, scheme below). By comparing the measured number of larvae (Lr_{t+1}) with the predicted number (Lp_{t+1}) mortality of leafminers due to the parasitoid, i.e. host feeding and parasitation, can be estimated. The fraction of larvae parasitised and the number of larvae will give information on the number of parasitoids in the next generation (NPAR).



A population growth model may help to predict the possible number of larvae in the next generation. Helderman (1986) has shown that a good prediction for the population growth can be made over the first 3 generations of L.bryoniae. The real number of larvae will be registered after every generation and predictions based on the model will only have to reach the next generation. Good predictions will probably be possible. A maximum error of 20% of the registered number of larvae will be strived for.

Only the first generations of leafminers will be separate. The generations will be overlapping soon. A population model may help, because it is not restricted to predictions from generation to generation. The actual number of eggs, larvae, pupae and flies can be predicted at any time.

In the population growth models of L. trifolii developed by Sanders & Mantel (1984) and Meijer (1986) and of L. bryoniae by Helderman (1986) only temperature is used as a forcing variable. Ottenheim (1985) has studied the relation between leaf nitrogen content and some life cycle components of L.trifolii. Rearing leaf miners on plants with a high nitrogen content appeared to increase the larval development rate and fecundity and to decrease mortality, compared to rearing on plants with a low nitrogen content. Increasing leaf nitrogen content can therefore result in an exponential increasing population growth rate (Minkenberg, 1988).

This study has 2 purposes:

(1) Increasing insight into the population dynamics of leafminers, L. bryoniae and L. trifolii, and their parasitoid D. isaea.

(2) Analysing the effect of leaf nitrogen content on the population dynamics of leafminers.

2 Biology of leafminers; data and assumptions used in the model.

Life history data of leafminers have been collected by Minkenberg (1988) for L. trifolii and Minkenberg & Helderman (1988) for L. bryoniae. Data are derived from these studies or original reports on which the mentioned studies are based. Data have been determined at constant temperatures (15°C, 20°C and 25°C). Development of L. bryoniae has been determined also at a fluctuating temperature (mean 19.5 °C). Values outside the 15-25 °C range have been extrapolated. For intermediate temperatures variables are determined by interpolation.

2.1 Development and mortality of immature stages.

Table 1 and 2 show the developmental periods of leafminer stages at different temperatures. The relations between the development rates (the inverses of the developmental periods) and temperature are nearly linear. In the model the regression lines shown in figure 2.1.1 and 2.1.2 are used. The regression lines are based on the mean values for each temperature. The total development rate from egg to adult as used in the model is compared with data from literature in figure 2.1.3. The model seems to overestimate the development rate a little at temperatures above 25 °C. For the standard deviation of the developmental period, the values from table 1 and 2 are used.

Table 1: Mean and s.d. of the developmental period of the different stages of L. bryoniae at different temperatures (mean, sd: days).

	Temperature (°C)							
Stage	15		19.5[a]		20		25	
Egg	6.1	0.5	3.9	0.2	4.1	0.2	2.8	0.3
L1	4.6	1.0	2.0	0.1	3.2	0.4	1.4	0.2
L2	3.7	0.7	3.0	0.5	2.6	0.4		
							3.6	0.4[b]
L3	4.0	0.8	3.1	0.5	2.7	0.4		
Pup	22.2	0.7	14.3	0.7	13.8	0.7	9.2	0.4

a: Average of fluctuating temperature; 16/22 °C.

b: For calculating the regression lines of L2 and L3 development with temperature the combined developmental period at 25°C is split up according to the average ratio found at other temperatures.

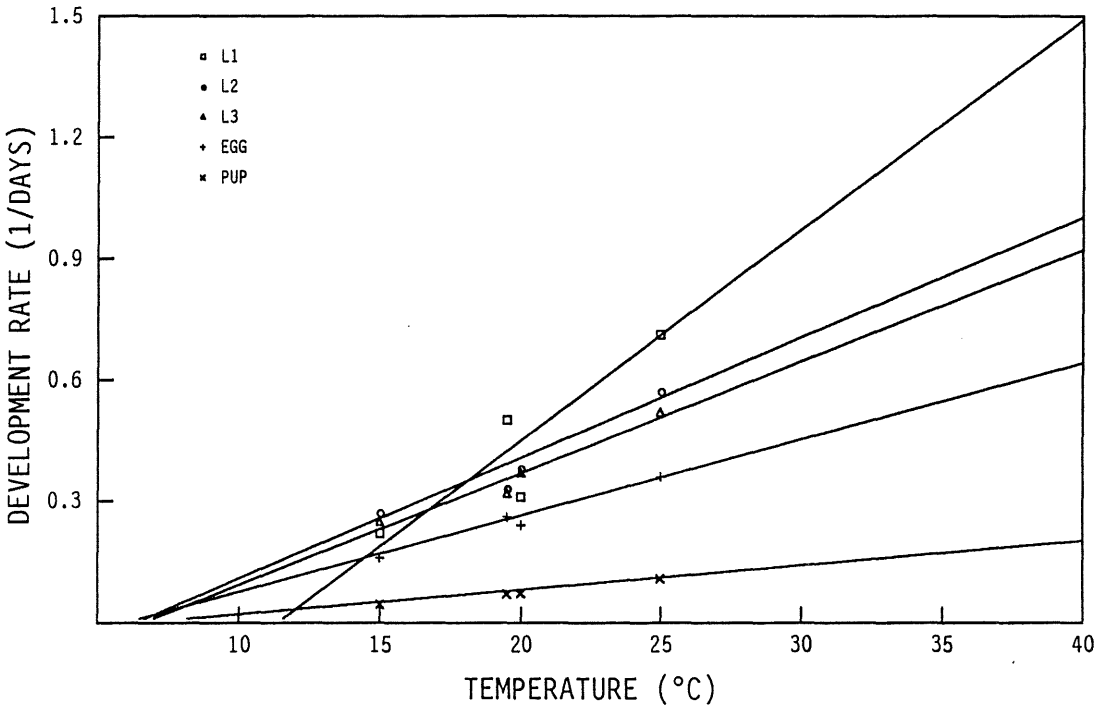


Figure 2.1.1: Temperature dependent development rates of L. bryoniae immature stages.

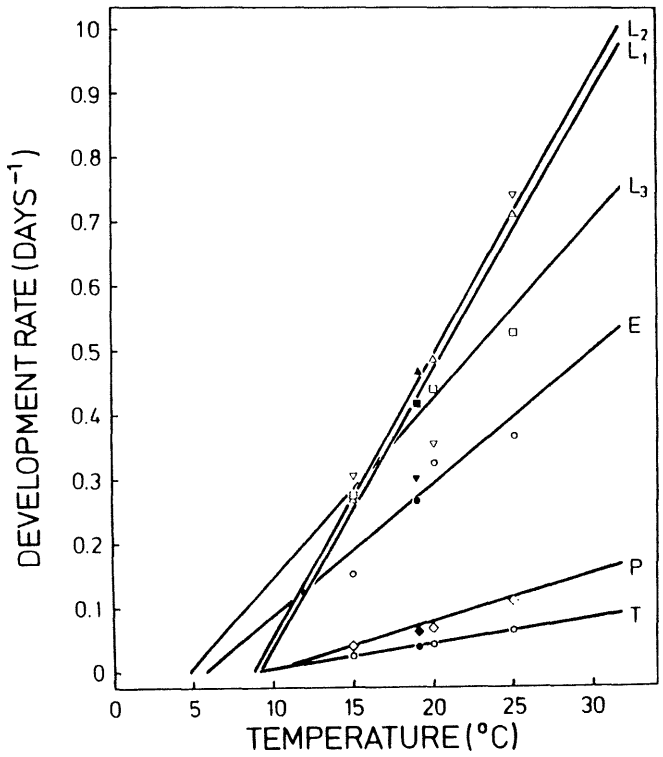


Figure 2.1.2: Temperature dependent development rates of L. trifolii immature stages.

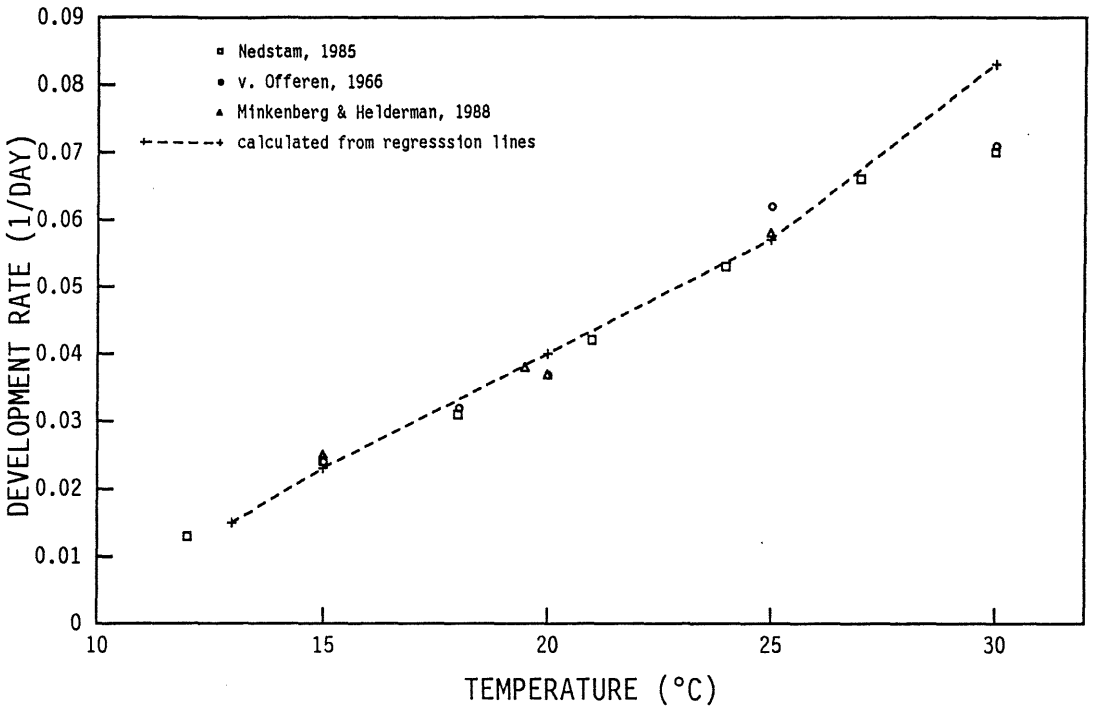


Figure 2.1.3: Development time from egg to adult of L.bryoniae on tomato plotted against temperature.

Table 2: Mean and s.d. of the developmental period of the different stages of L. trifolii at different temperatures (mean, sd: days).

Stage	Temperature (°C) 15		20		25	
Egg	6.6	0.2	3.1	0.1	2.7	0.1
L1	3.3	0.6	2.8	0.5	1.4	0.2
L2	3.7	0.9	2.1	0.4	1.4	0.3
L3	3.7	0.5	2.3	0.6	1.8	0.6
Pup	26.8	0.9	15.0	0.5	9.3	0.4

Mortality during a certain developmental stage is assumed proportional to the size of the population in that stage. The relative mortality rate can then be calculated from:

$$Y(I+1) = Y(I) * e^{-rmr*t}$$

$$rmr = (\ln Y(I) - \ln Y(I+1))/ t$$

with: Y(I) = number of animals beginning in stage I.
Y(I+1)= number of animals reaching stage I+1.
rmr = relative mortality rate.
t = average residence time in stage I+1.

Table 3 and 4 show the relative mortality rates of the different stages for L. bryoniae and L. trifolii.

Table 3: The relative mortality rate (day^{-1}) of L. bryoniae immature stages at different temperatures (°C).

stage	Temperature (°C) 5[a]	15	20	25	40[a]
Egg[b]	0	0.011	-	-	0
L1	0.50	0.202	0.009	0.020	0.1
L2	0.30	0.060	0.012	0.081	0.4
L3	0.05	0.009	0.012	0.028	0.15
Pup	0.02	0.021	0.025	0.022	0.02

a: Extrapolated values, added for simulation.

b: In the model egg mortality is set at zero. The model considers only viable eggs, i.e. eggs out of which a L1 larva develops.

Table 4: The relative mortality rate of L.trifolii immature stages at different temperatures (day^{-1}).

Stage	Temperature (°C) 5[a]	15	20	25	40[a]
Egg[b]	0	0.040	0.072	0.087	0
L1	0.30	0.181	0.089	0.142	0.24
L2	0.18	0.093	0.045	0.151	0.28
L3	0.11	0.000	0.004	0.052	0.12
Pup	0.05	0.003	0.005	0.017	0.07

a: Extrapolated values, added for simulation.

b: In the model egg mortality is set at zero. The model regards only viable eggs, i.e. eggs out of which a L1 larva develops.

2.2 Simulation of age-dependent reproduction and mortality

Senescence of the adult flies influences several parameters like the reproduction rate, the number of eggs per female per day, and the rate of mortality. The rate of senescence is temperature dependent. Therefore age, expressed in days, cannot be used to describe different stages of senescence. Physiological stages have to be distinguished in the model. Adult flies show no morphological differences, indicating certain physiological stages. Physiological stages are only indicated by changes in reproduction rate. An artificial classification must be made. The maximum longevity of the flies can be used to make such a classification. The maximum longevity is divided into a fixed number of classes, which represent physiological stages. Meijer (1986) defined the maximum longevity as the average longevity plus 3 times the standard deviation. At this age 99.9% of the adults had died. This method implies that at each temperature the same physiological stage is reached at a time which represents an equal fraction of the maximum longevity. This means that the shape of reproduction curves plotted against physiologic age should be similar. This is illustrated by Fig. 2.2.1, which shows how erroneous situations can occur. Fig. 2.2.1 shows reproduction plotted against time for 3 temperatures, a, b and c, with $T_a < T_b < T_c$. Using the maximum longevity for classification in physiological age classes will produce errors (fig. 2.2.1b). The shape of curve a is different from that of curve b and c. A rise in temperature from T_a to T_c will cause the reproduction rate to increase too much at early physiologic ages and to increase too little at late physiologic ages. A rise in temperature from T_a to T_b will even produce a decrease in reproduction rate at late physiological ages. Some reasons, which can cause dissimilar reproduction curves, can be marked. Maybe not every stage in the adults life responds just as strong to a change in temperature. For instance the age at which a fly reaches her maximum reproduction rate is not very sensitive for changes in temperature. The maximum longevity is more sensitive to changes in temperature. It is also possible that the potential number of stages is not reached. When for instance temperature decreases to

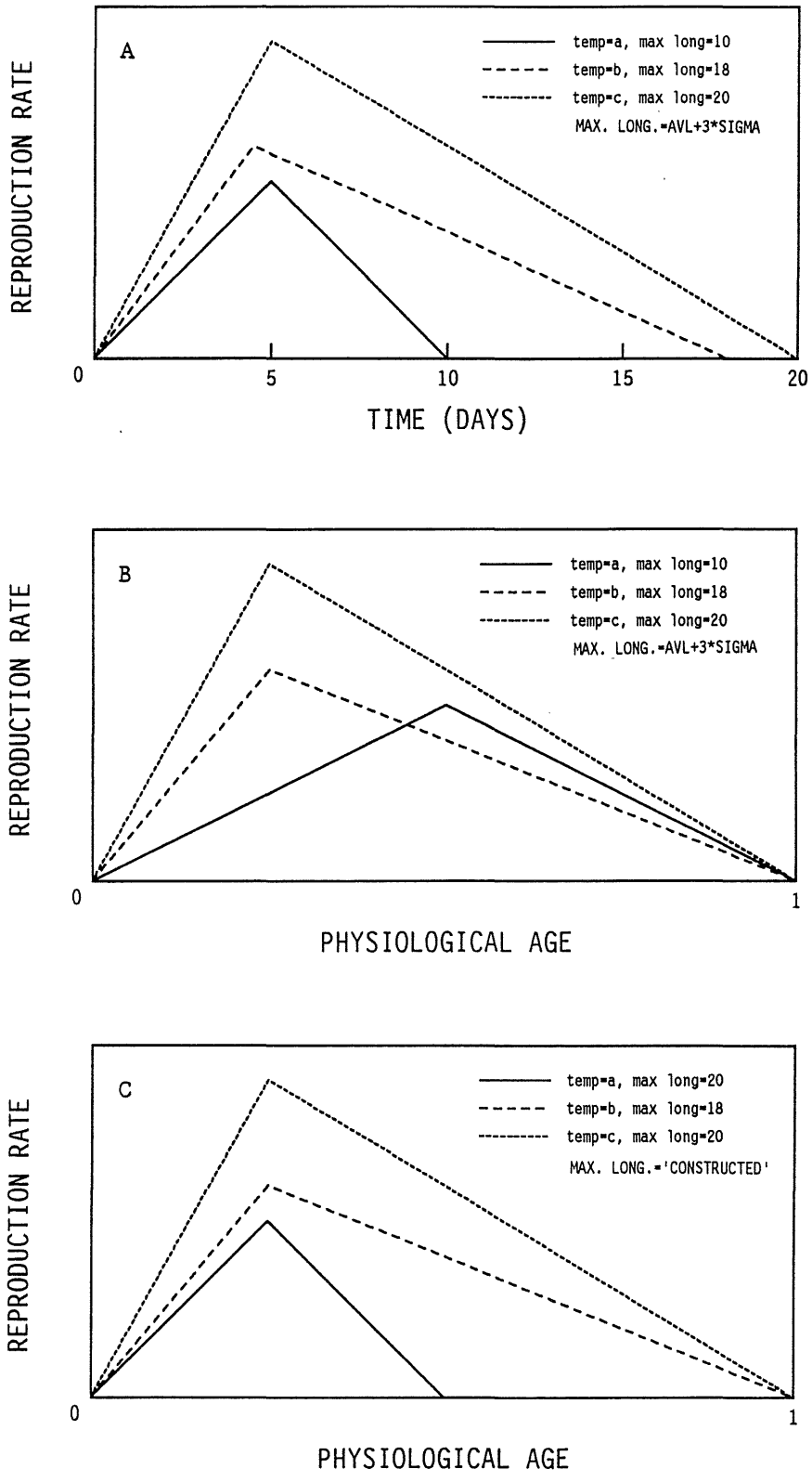


Figure 2.2.1: Example of relation between reproductive rate and age (A). Images B and C show relations between reproductive rate and physiologic age with classification based on the average longevity + 3*sigma (B) and classification based on the maximal reproductive rate (C) respectively.

15°C, the mean longevity decreases for L. trifolii. This cannot be caused by an increasing rate of development. A lower rate of development will be expected at lower temperatures. The adults will probably die at an earlier physiological age.

The reproduction curves at different temperatures have different forms for both L.bryoniae, L.trifolii and D.isaea. Therefore errors may occur.

To reduce errors resulting from different shapes of the reproduction curves, the separation into physiological stages can be slightly changed. Classification can be based on the age at which the reproduction rate reaches its maximum. This age is supposed to be pointed at a fixed physiological stage, independent of temperature. This can be done by plotting the reproduction rate against a physiological time scale and changing the maximum longevities so, that the highest reproduction rate is reached at an equal physiological time (fig. 2.2.1c). So the value of the maximum longevity is constructed for modeling and does not necessarily correspond to the actual longevity. By this procedure errors are moved away from the classes with the highest reproduction (Figs. 2.3.1, 2.3.2, 3.2.1). Errors caused by different shapes of reproduction curves will still be present. The effects will be suppressed, however, because the flies responsible for the paramount part of reproduction will be in approximately equal physiological stage at all temperatures.

In fig. 2.2.2 the constructed maximum longevities used for classification based on the maximum reproduction rate are shown. One will expect that a certain developmental stage is reached earlier at higher temperatures, i.e. the maximum longevity is shorter at higher temperatures. This expectation is met for L. bryoniae. However with L. trifolii this is not the case. The constructed maximum longevity for L. trifolii is rather constant at the measured temperatures.

The two classification methods will be evaluated (see 6.1). The classification method based on the maximum reproduction rate may be more precise. The classification method based on the average longevity + 3*sigma has the advantage of using one parameter less, i.e. the constructed maximal longevity.

2.3 Reproduction of flies.

Reproduction of leafminers is age and temperature dependent. Age in the model is expressed in classes according to one of the methods described above. When the method is not mentioned explicitly, classification based on the mean longevity and its standard deviation is used. Reproduction is mimicked using the relations between age, temperature and reproduction rate measured. The curves shown in fig. 2.3.1 and 2.3.2 are the result of fitting the original data by hand. In a class the reproduction rate is considered constant. The values used in the model have been read from the curves at an age representing the median age in a class. (So for class 1 the physiological age 0.5 is used,

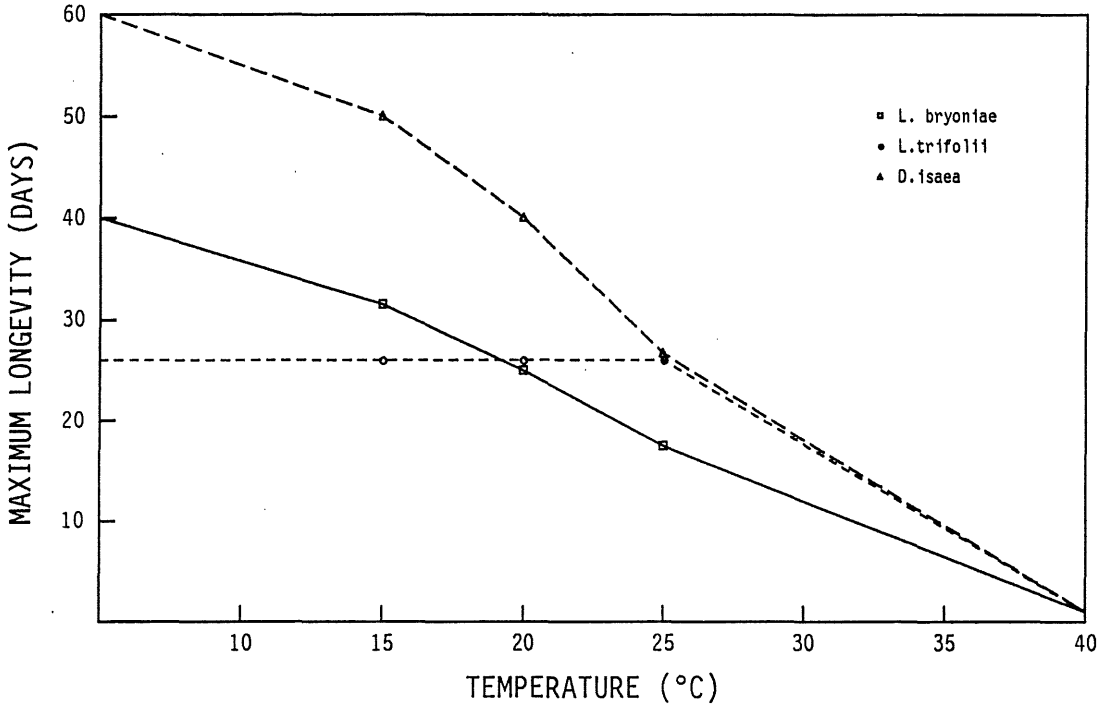


Figure 2.2.2: Constructed maximum longevity used when classification is based on the maximum reproduction rate for L. bryoniae, L. trifolii and D. isaea plotted against temperature.

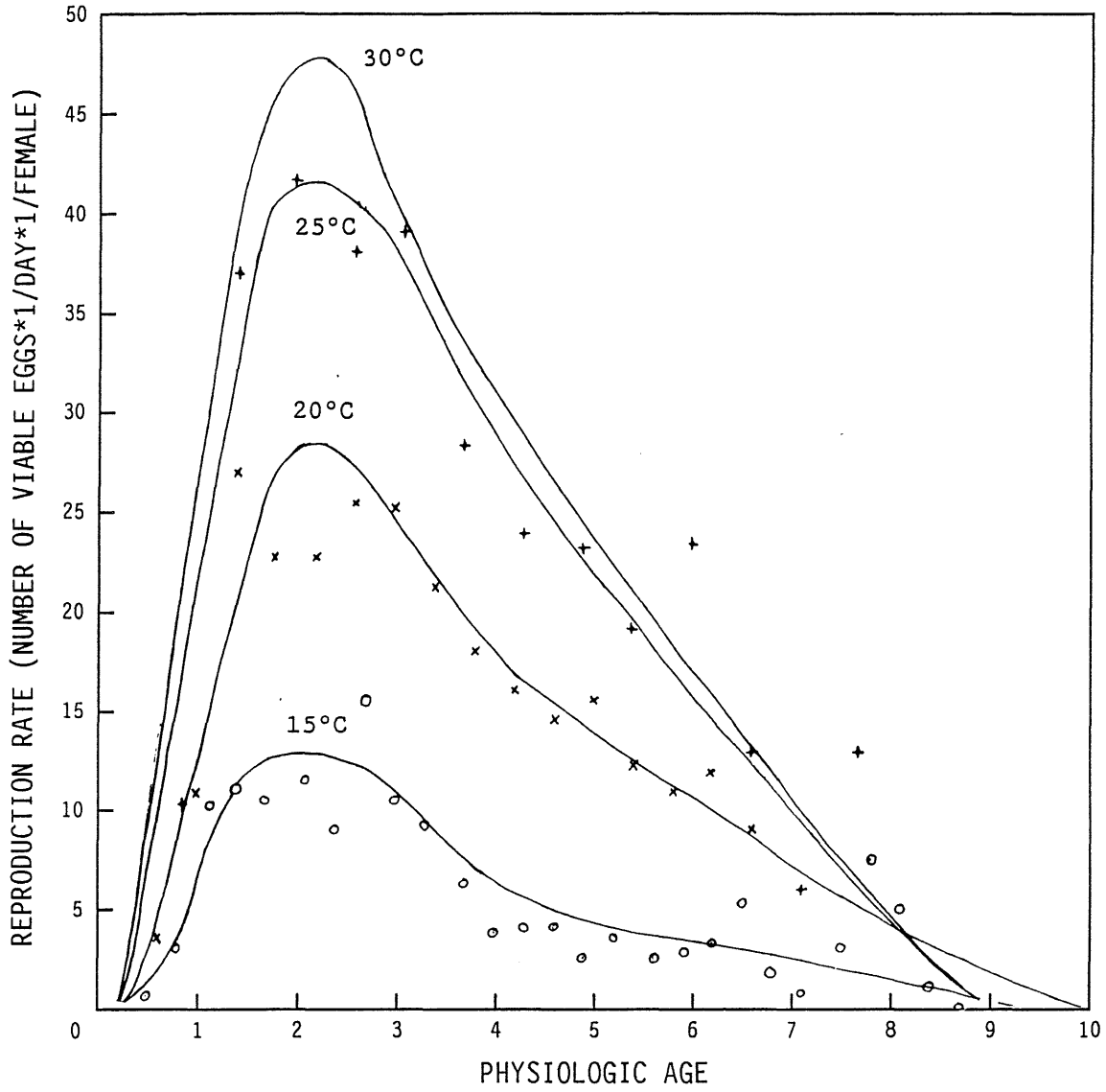


Figure 2.3.1: Reproduction rate of L. bryoniae for different temperatures plotted against physiologic age. At physiologic age = 10 the constructed maximum longevities (fig. 2.2.2) are reached.

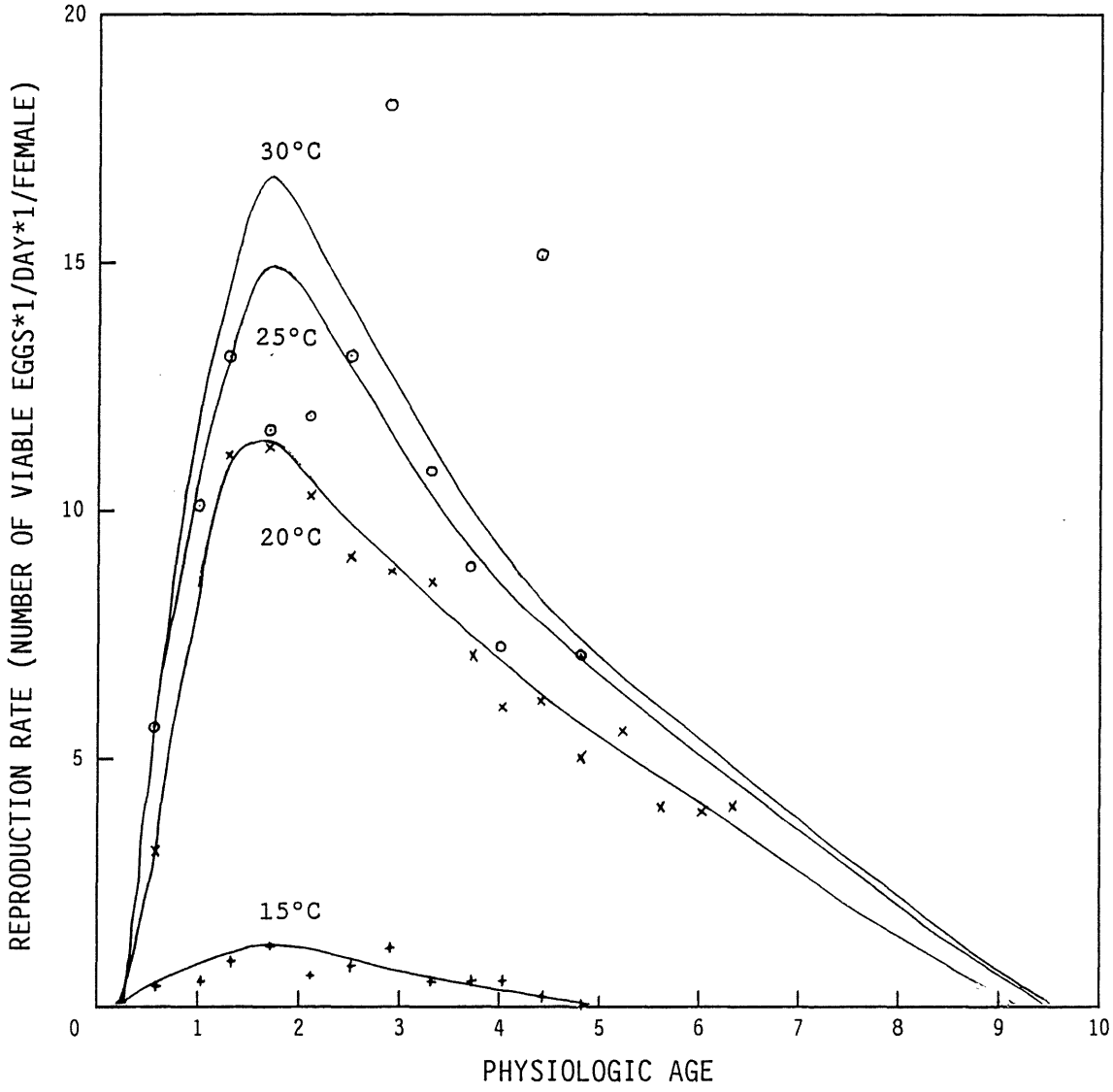


Figure 2.3.2: Reproduction rate of L. trifolii for different temperatures plotted against physiologic age. At physiologic age = 10 the constructed maximum longvities (fig. 2.2.2) are reached.

for class 2 an age of 1.5 etc.). Figs. 2.3.1 and 2.3.2 show curves when classification is based on the maximum reproduction rate. The same curves have also been used determining the reproduction rates in classes resulting from the other method. This can be done easily after adjusting the physiological time scale.

Only data for 15, 20 and 25 °C are available. The other curves drawn in fig. 2.3.1 and 2.3.2 are speculative. At higher temperatures the metabolism will speed up and the reproduction rate will increase to a maximum. Maybe L. trifolii will reach this maximum later than L. bryoniae because it is a more tropical species (Spencer, 1973). However this is not accountedfor in the model. In the model maximal reproduction rates are assumed to occur above 30 °C. The curves at temperatures above 30 °C are also shown in fig. 2.3.1 and 2.3.2. The maximum reproduction rate at 30 °C is set arbitrarily at a value representing the maximum reproduction rate at 25 °C + 0.5*δ(maximum reproduction rate 25,20 °C). At intermediate temperatures the reproduction rates are found by interpolation.

2.4 Mortality in the adult stage.

The cumulative mortality of flies is plotted against time on a probability scale in fig. 2.4.1 and 2.4.2. In all cases a linear relationship is found. Therefore, it can be assumed that describing the longevity of adults with a normal distribution will be adequate. The average longevity is found at f(average longevity)= 5 (50% of the flies are still living). The slope of the regression line represents -1/(standard deviation).

At any time t the slope of a cumulative mortality function (fig. 2.4.3) represents the mortality rate (adults* day^{-1}). Because the longevity of adults is assumed normally distributed, the probability density function for a normal distribution can be used calculating the mortality rate.

$$Mort(t) = 1/\sigma * (2*\pi)^{-0.5} * e^{-0.5*((t-\mu)/\sigma)^2} \qquad (2.4.1)$$

Mort(t)= Mortality rate at time=t (adults*day^{-1}).
μ = Average longevity (day).
σ = Standard deviation of the average longevity (day).

To find the relative mortality rate at time t, we have to divide the mortality rate by the adults still living at time t, viz. F(t). F(t) is represented by the integral of the probability density function for a normal distribution. In the model F(t) is read from a table mimicking a normal distribution.

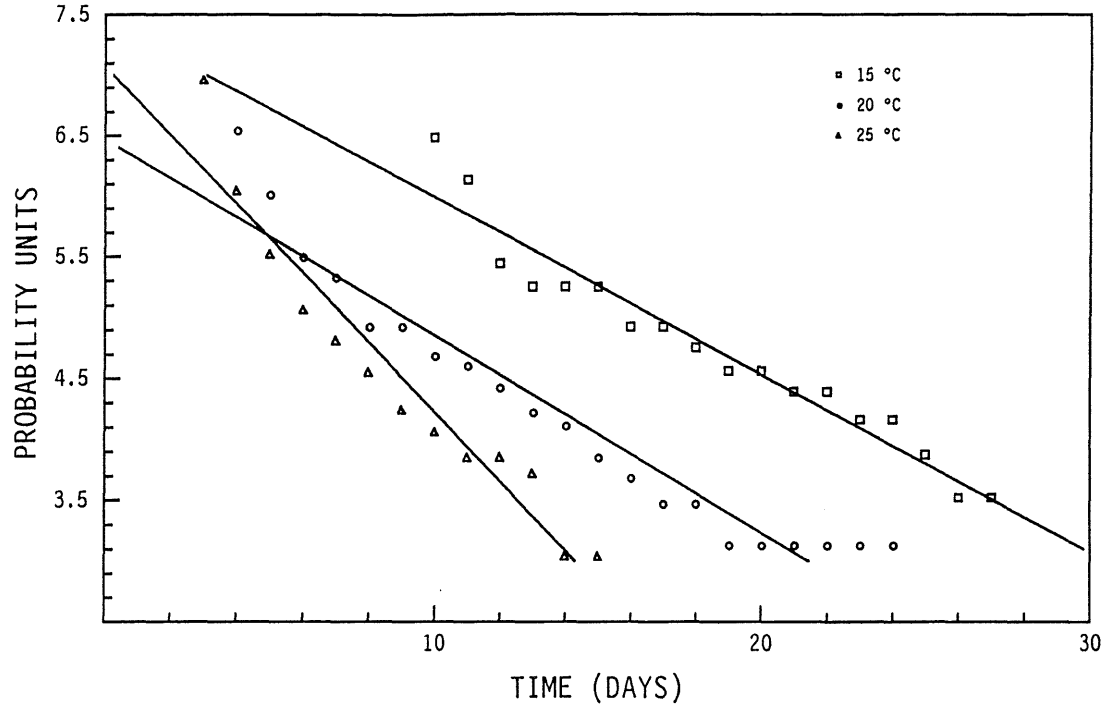


Figure 2.4.1: Survival of L. bryoniae (1 - cumulative mortality) in probability units (probits) plotted against time for different temperatures. The average longvity is found at probit=5. The standard deviation of the average longvity = -1/a, where a is the slope of the line.

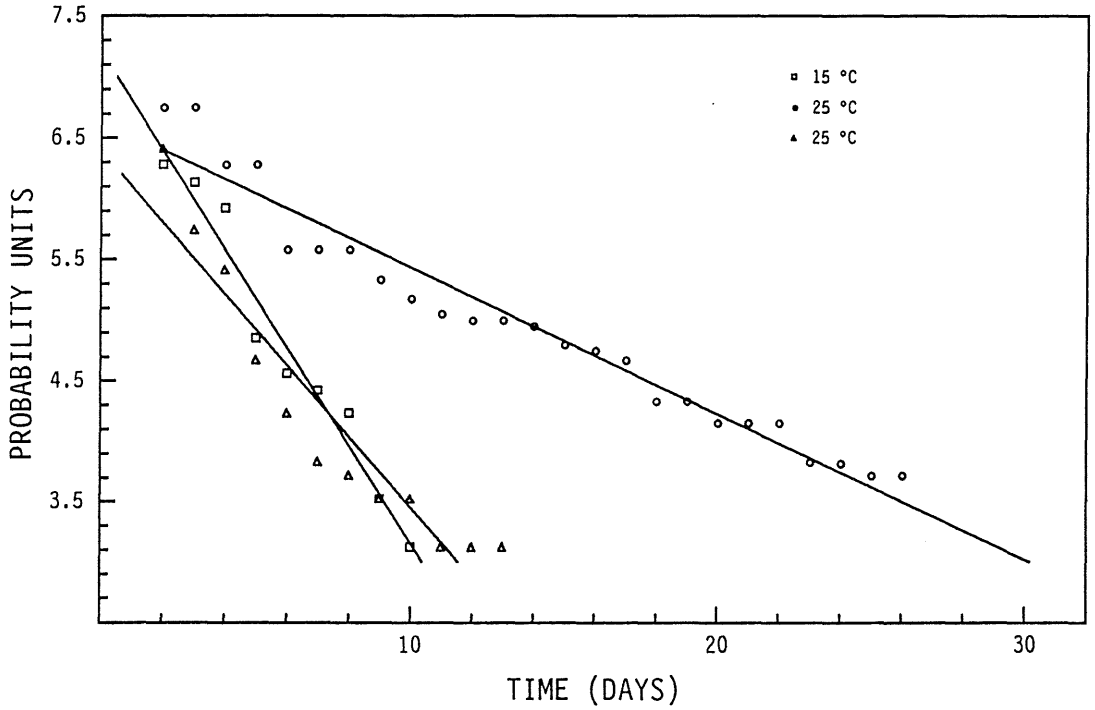


Figure 2.4.2: Survival of L. trifolii (1 - cumulative mortality) in probability units (probits) plotted against time for different temperatures. The average longvity is found at probit=5. The standard deviation of the average longvity = -1/a, where a is the slope of the line.

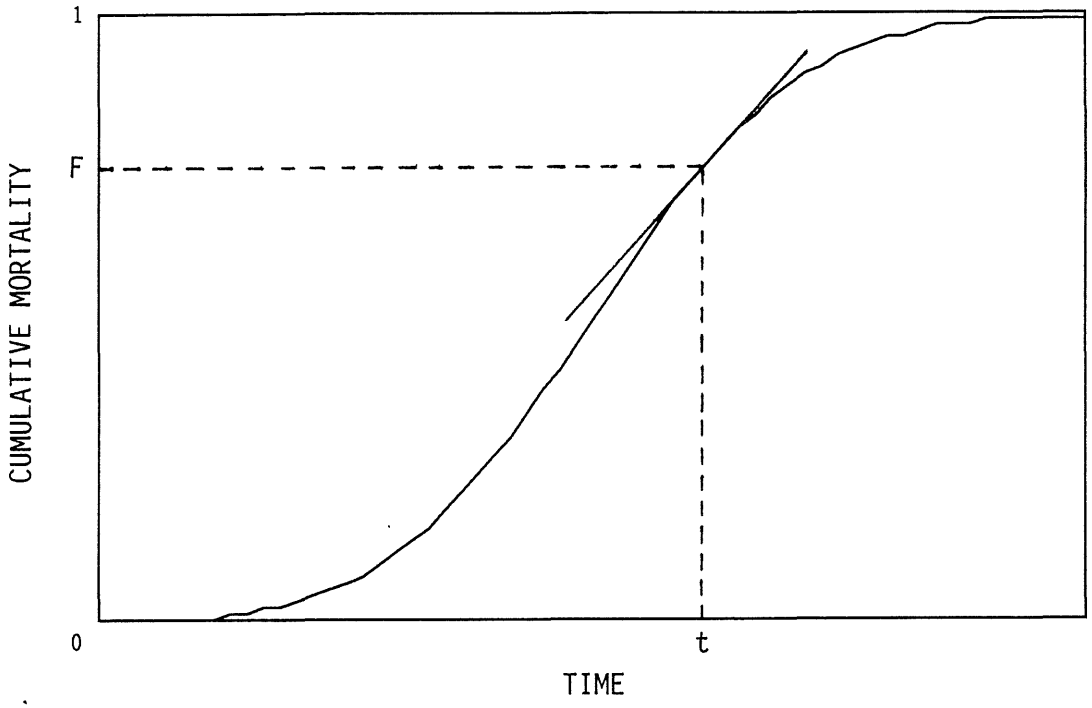


Figure 2.4.3: Example of a cumulative mortality function. The slope at time=t indicates the rate of mortality (RMORT) at time=t. The relative mortality rate is found by dividing the rate of mortality by the fraction of animals that survived till time=t: RMR_t = RMORT / (1-F).

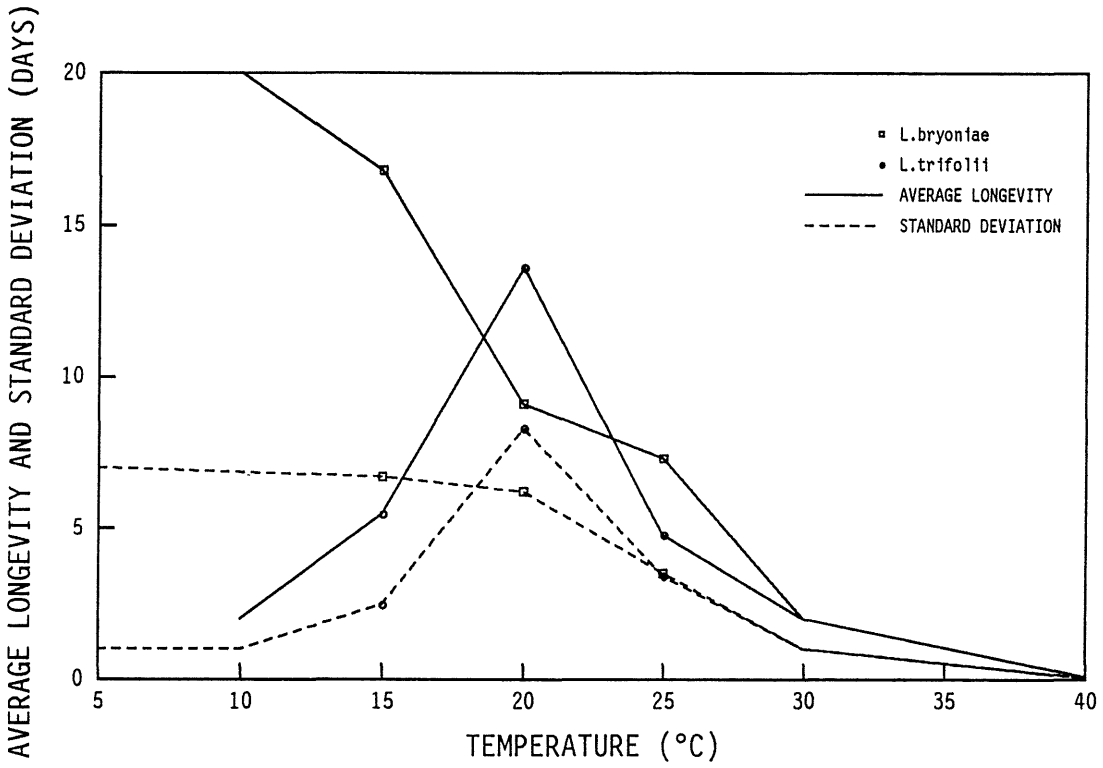


Figure 2.4.4: Average longevity and its standard deviation plotted against temperature. The values are derived from fig. 2.4.1 and 2.4.2 for L. bryoniae and L. trifolii respectively.

$$rmr(t) = \frac{Mort(t)}{F(t)} \qquad (2.4.2)$$

rmr(t) = Relative mortality rate at time=t (1/day).
Mort(t)= Mortality rate at time=t (adults/day).
F(t) = Adults still living at time=t (adults).

$$F(t) = \int_0^t 1/\sigma * 2*\pi^{-0.5} * e^{-0.5*((t-\mu)/\sigma)^2} \qquad (2.4.3)$$

Using this method the mortality can easily be adjusted by changing 2 variables, the average longevity and its s.d., instead of introducing new tables describing relative mortality in the classes.

The average longevity and its standard deviation, necessary to calculate the relative mortality rate, are calculated from fig. 2.4.1 and 2.4.2. The relative mortality rate is calculated at the average age of each class and assumed constant in that class. The average longevity and its standard deviation as used in the model is plotted against temperature (fig. 2.4.4). Only for 15, 20 and 25 °C data are available. The average longevity is supposed to decrease with increasing temperature, because senescence will speed up due to a faster metabolic rate. The curve of L. trifolii shows an optimum at 20 °C. Other mortality factors than senescence are probably determining the average longevity below 20 °C. However data on the average longevity of L.trifolii on celery, Apius graveolens, (Leibee, 1984) and Chrysanthemum morifolium (Parrella, 1984; see also fig 8.3) have shown a decreasing curve in the total temperature range, similar to L. bryoniae.

3 Biology of Diglyphus isaea; Data and assumptions used in the model.

3.1 The development from egg to adult

Most data on D. isaea have been taken from Meijer (1986). The total developmental period from egg to adult is used to describe development of immature stages of D. isaea. Table 5 shows the developmental period of D. isaea immature stages. A linear relation between development rate (the inverse of developmental period) and temperature is assumed. The regression line shown in fig. 3.1.1 is used in the model. The values from table 5 are used for the standard deviation of the developmental period. Values outside the 15-25 °C range are extrapolated.

Table 5: Developmental period of Diglyphus isaea from egg to adult at different temperatures.

	Temperature (°C)		
	15	20	25
devel.period	26.0	16.6	10.5
s.d (days)	1.4	0.6	0.7

The relative mortality rates at different temperatures are shown in table 6. The values have been calculated with the same method as the relative mortality rates of leafminer immature stages. Values outside the 15-25 °C range are extrapolated.

Table 6: Relative mortality rate of the immature stages of D.isaea at different temperatures.

	Temperature (°C)				
	5[a]	15	20	25	40[a]
Relative mort. rate (day^{-1})	0.04	0.030	0.012	0.025	0.05

a: Extrapolated values, added for simulation.

3.2 Senescence, reproduction and mortality of D. isaea adults.

Senescence of D. isaea is similar to senescence of leafminers and therefore simulated accordingly. The constructed maximum longevity with classification based on the maximum reproduction, is plotted against temperature in fig. 2.2.2. Fig. 3.2.1 shows the reproduction rate at different temperatures, plotted on a physiologic time scale. The values found for 20 °C are allmost similar to the values found

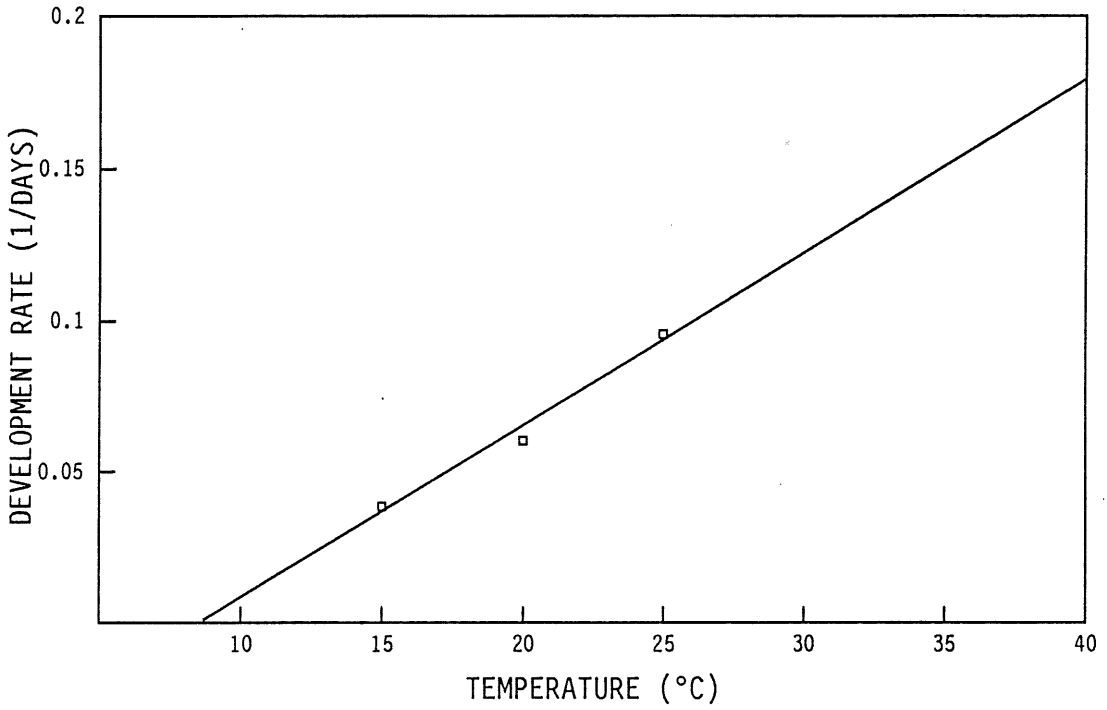


Figure 3.1.1: Temperature dependent development rate of D. isaea immature stages.

for 15 °C, though we would expect them to lie between those for 15 °C and 25 °C. This is probably caused by different experimental circumstances. The 20 °C experiment (Meijer & Westerman, 1985) was not carried out together with the 15 and 25 °C experiments (Reytenbagh & Smidt, 1985) and for instance seasonal changes in plant quality may have had their influence. Therefore the maximum reproduction rate in the artificial curves at 30 °C and 10 °C is estimated using the difference between the 15 and the 25 °C curve (maximum reproduction rate 30 °C=maximum reproduction rate 25 °C + 0.25*δ(maximum reproduction rate 15 and 25 °C). At 15 °C the reproduction rate is still high, so also a curve for 10 °C is added in the model (maximum reproduction rate 10 °C=maximum reproduction rate 25 °C - δ(maximum reproduction rate 15 and 25 °C). Data used in the model to calculate mortality are shown in fig. 3.2.2 and 3.2.3.

3.3 The parasitation process.

About the parasitation process of D.isaea little quantitative information is available. Therefore assumptions have been made. The rate of successful encounters between parasitoids and leafminer larvae is assumed density dependent according to a 'type 2' functional response (Holling, 1959):

$$RENC = A * DENS * RENMAX/(A * DENS + RENMAX)$$

RENC = Rate of successful encounters (Larvae*Day^{-1}).
A = Searching efficiency (Plants*Day^{-1}).
RENMAX = Maximum rate of successful encounters (Larvae*Day^{-1}).

During an encounter two possible reactions are supposed to occur:
1- The parasitoid attacks the larvae for parasitation. During each parasitation approximately 1 egg will be laid by D. isaea (Minkenberg & v. Lenteren, 1986).
2- The parasitoid kills the larvae for host feeding.

L1 larvae are much less attractive to D. isaea then L2 and L3 larvae. Therefore it is assumed that parasitoids ignore 7/8 of the L1 larvae present. To achieve this, 1/8 of the L1 larvae is used for calculating leafminer density used in the functional response formula. A fixed fraction is used for distributing the successful encounters over host feeding and parasitation. Meijer (1986) has found ca. 80% parasitation under experimental conditions with L3 larvae. Westerman (1986) found ca. 50 % parasitation in a greenhouse experiment. About the same fraction was reported by Ibrahim & Madge (1978) for the leafminer Chromatomyia syngenesiae. Host feeding in the greenhouse has probably been more numerous, because larvae of all stages were present. During host feeding a larva is totally consumed except cuticle (Ibrahim & Madge, 1978). To meet her nutritional requirements, a parasitoid will probably spend more successful encounters on host feeding when larvae are small,

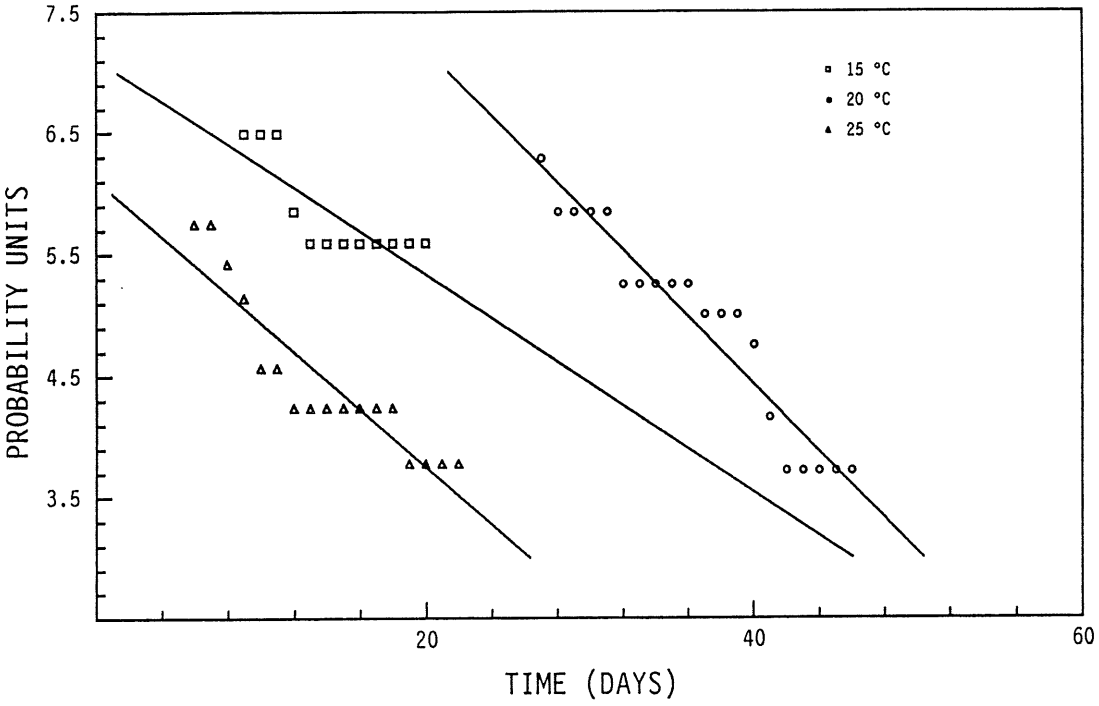


Figure 3.2.2: Survival of D. isaea (1 - cumulative mortality) in probability units (probits) plotted against time for different temperatures. The average longvity is found at probit=5. The standard deviation of the average longvity = -1/a, where a is the slope of the line.

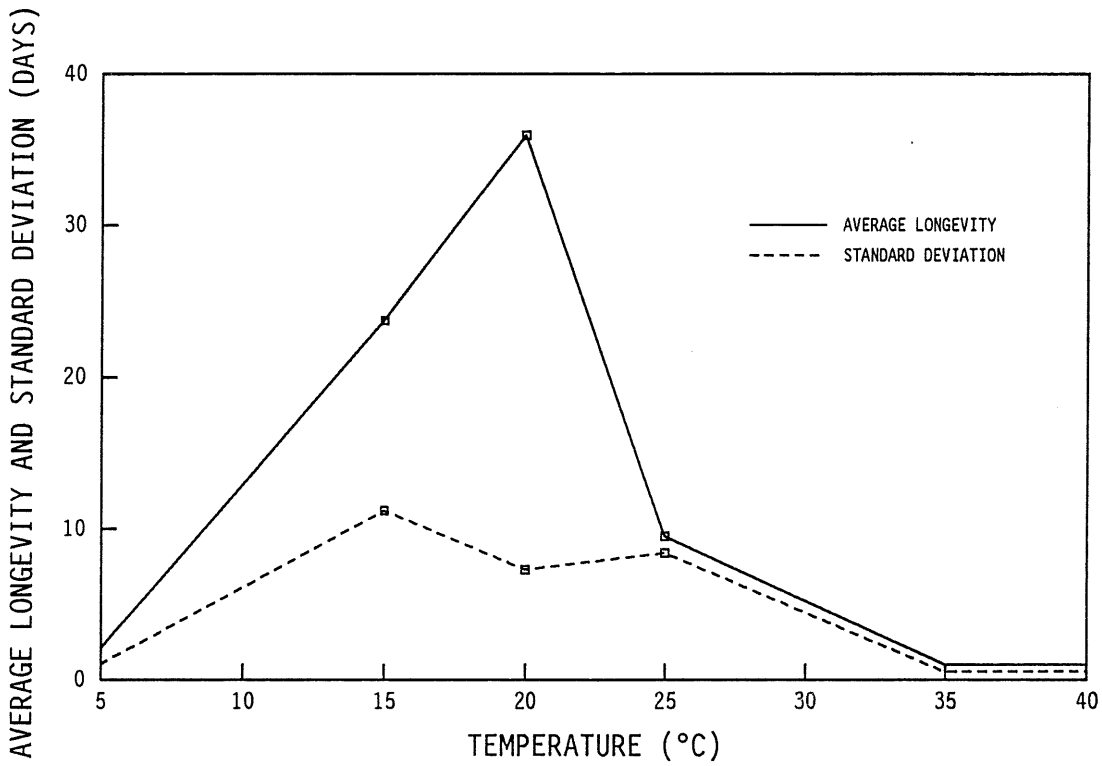


Figure 3.2.3: Average longevity of D.isaea and its standard deviation plotted against temperature. The values are derived from fig. 3.2.2.

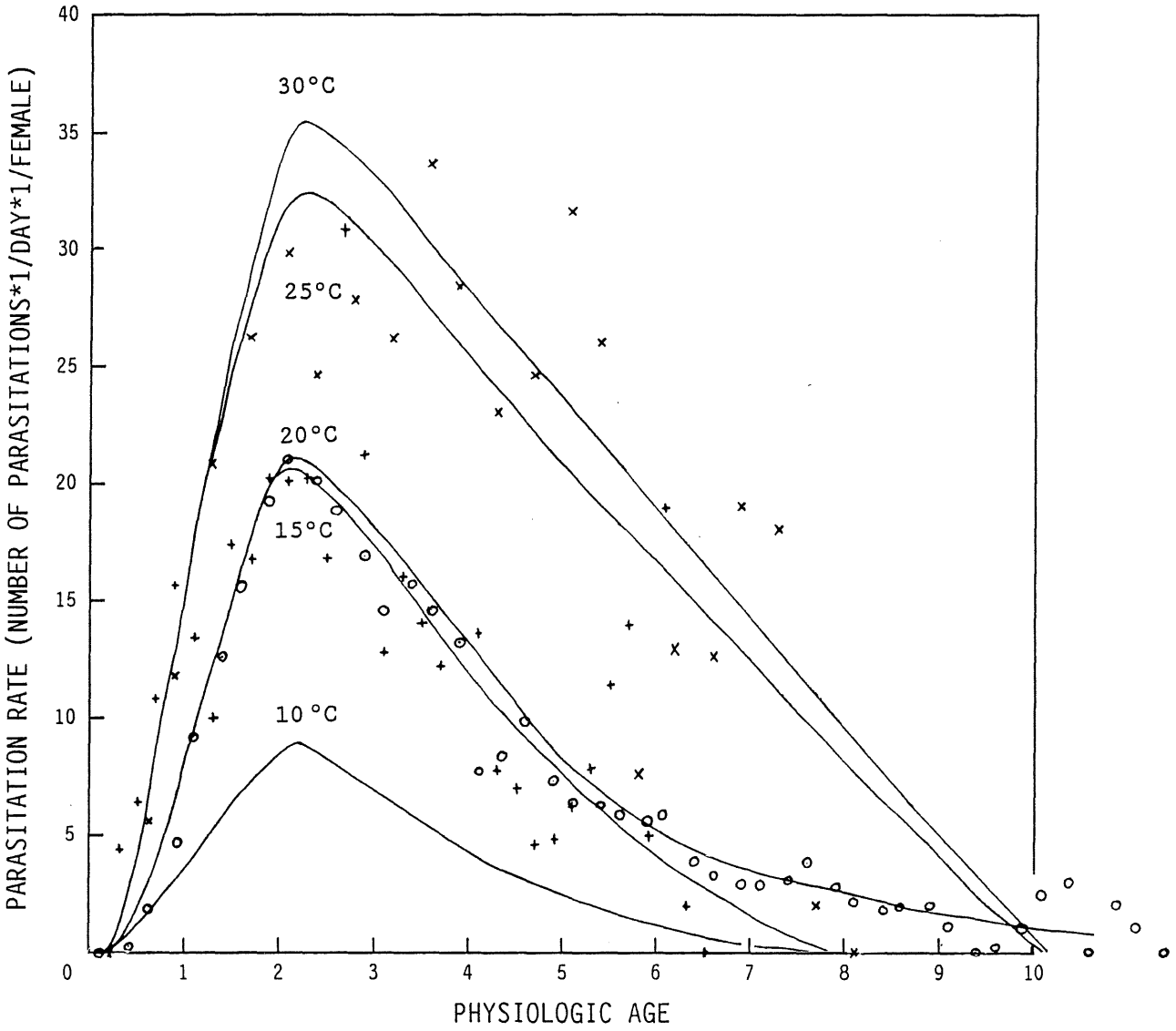


Figure 3.2.1: Maximum parasitation rate of D. isaea for different temperatures plotted against physiologic age. At physiologic age =10 the constructed maximum longevities are reached (fig. 2.2.2).

The maximum rate of successful encounters is calculated from the maximum rate of parasitation (fig. 3.2.1). These parasitation rates have been determined when abundant L3 larvae were available and can be considered as maximal (Meijer, 1986). Larvae killed by host feeding numbered approximately 25% of larvae killed by parasitation. The maximum rate of successful encounters can therefore be calculated as 5/4 * parasition rates from fig. 3.2.1. The searching efficiency A is the most difficult parameter of the functional response formula to estimate (Meijer, 1986). Estimates of A depend on plant size, fraction of the plant in which parasitoids search for hosts and the total searching period per day. Meijer used $A=2.3$ plants$*day^{-1}$ and Helderman (1986) $A=0.2$ plants$*day^{-1}$.

Host feeding and parasitation will be distributed over the larval stages of the leafminers. L1 larvae are unsuitable for oviposition (Minkenberg, pers. com.). Therefore, a fixed ratio between host feeding and parasitation cannot be kept when L1 larvae are relative abundant. L2 and L3 larvae are suitable for both host feeding and parasitation. It is likely that preferences for one of the stages will exist. Preferences are not modelled however, because both host feeding and parasitation result in mortality.

4 Influence of leaf nitrogen content on leafminer development.

The suitability of the host plant strongly affects the performance of herbivorous insects (Tabashnik & Slansky 1987). The suitability of host plants is determined by their chemical composition and fysical properties. Nitrogen has been found to be one of the major factors determining host plant suitability (Scriber 1984, Tabashnik & Slansky 1987). This has also been found by Ottenheim (1985), who studied the development of L. trifolii on plants with different nitrogen contents. He found that leaf nitrogen content influences several parameters of the leafminer life cycle.

Other physical and chemical factors may influence plant quality besides nitrogen content. Tomato plants contain allelochemicals, for instance the alkaloid tomatine (Kennedy, 1986). These allelochemicals might reduce the relative growth rate substantially (Scriber 1984). Physical changes of the leaves may occur due to senescence of the plants. However the influence of most of these factors on leafminers is still obscure.

Nitrogen content is not necessarily the causal factor in the experiments of Ottenheim (1985), however. The changes in different life cycle parameters may have been caused by other factors, which change parallel to the nitrogen content. By introducing nitrogen as a variable all these other factors are supposed to remain coupled to nitrogen in the same way as in Ottenheims experiments.

Ottenheims data have been determined at 25°C. For the other temperatures, the life cycle parameters are supposed to perform the same relative changes due to changes of leaf nitrogen content. These parameters were calculated according to:

$$P(T,N) = P(T,N_{ref}) * \frac{P(25,N)}{P(25,N_{ref})}$$

with: P(T,N) = Life cycle parameter at temperature T and leaf nitrogen content N (percentage nitrogen of dry weight). N_{ref} is the nitrogen level at which the parameter values of Minkenberg (1988) and Minkenberg & Helderman (1988) are supposed to be determined.

N-content of the host plants, used for estimation of life cycle parameters, has not been determined (Minkenberg, 1988; Minkenberg & Helderman, 1988). Later measurements have shown a range of 4.8-8% N (dry weight) for comparable plants (pers. comm. O. Minkenberg). It is therefore supposed that N-content has been 6% in the experiments to determine life cycle parameters of both L. trifolii and L. bryoniae. An exception is made, however, for mortality of L. trifolii. The mortality found by Minkenberg (1988) is much higher than can be expected at 6% N on the basis of Ottenheims results. (fig 4.1.2). This may be caused by the

period the experiments have been carried out, being November for Minkenberg and June for Ottenheim. It is a general phenomenon that the performance during winter is poor in insect breeding, though the reason for this is unknow. The reference nitrogen level for L. trifolii is found by fitting the value of Minkenberg (1988) into the curve of Ottenheim (1985) (fig 4.1.2).

4.1 Influence on larval development

For several fytophagous insects the relative growth rate has been found to increase with N content of their food. This increase might cause a shorter developmental period and/or an increase in pupal size, depending on the species (Scriber, 1984).

Ottenheim (1985) has shown a decrease of the developmental period from egg to pupae with an increasing nitrogen content of the leaves for L. trifolii. The developmental period of the eggs is supposed to be independent of leaf nitrogen content. Therefore the developmental period from L1 to pupae is calculated by subtracting the mean developmental period of the eggs found by Minkenberg (1988). The developmental periods from L1 to pupae as used in the model are plotted against leaf nitrogen content in fig 4.1.1. To calculate the developmental period for each separate stage, the relative change of the developmental period in each stage is supposed to be the same and therefore equal to the relative change of the developmental period from L1 to pupae.

Mortality during the larval stages is also influenced by the N content of the leaves (fig 4.1.2; Ottenheim, 1985). Ottenheim gives the mortality during the period from L1 to pupae. The model however uses the mortality during each separate stage. To calculate these, a constant relative change of the RMR (relative mortality rate) in each separate stage is supposed. Because of relation (4.1.1) the relative change in the $RMR_{L1-pupae}$ value is the same as the relative change of the mortality for the separate stages.

$$RMR_{L1-pupae}*DVP_{L1-pupae} = RMR_{L1}*DVP_{L1} + RMR_{L2}*DVP_{L2} + ... \qquad (4.1.1)$$

So

$$A*RMR_{L1-pupae}*DVP_{L1-pupae} = A(RMR_{L1}*DVP_{L1} + RMR_{L2}*DVP_{L2} + ...)$$

$$= A*RMR_{L1}*DVP_{L1} + A*RMR_{L2}*DVP_{L2} + ...$$

because the relative change of RMR is supposed to be equal for each stage.

4.2 Influence on the adult stage

The effect of the nitrogen content on the adult stage may be caused in two ways. Firstly the adults feed during their lives on mesophile of the leaves (Minkenberg & v. Lenteren, 1986). When

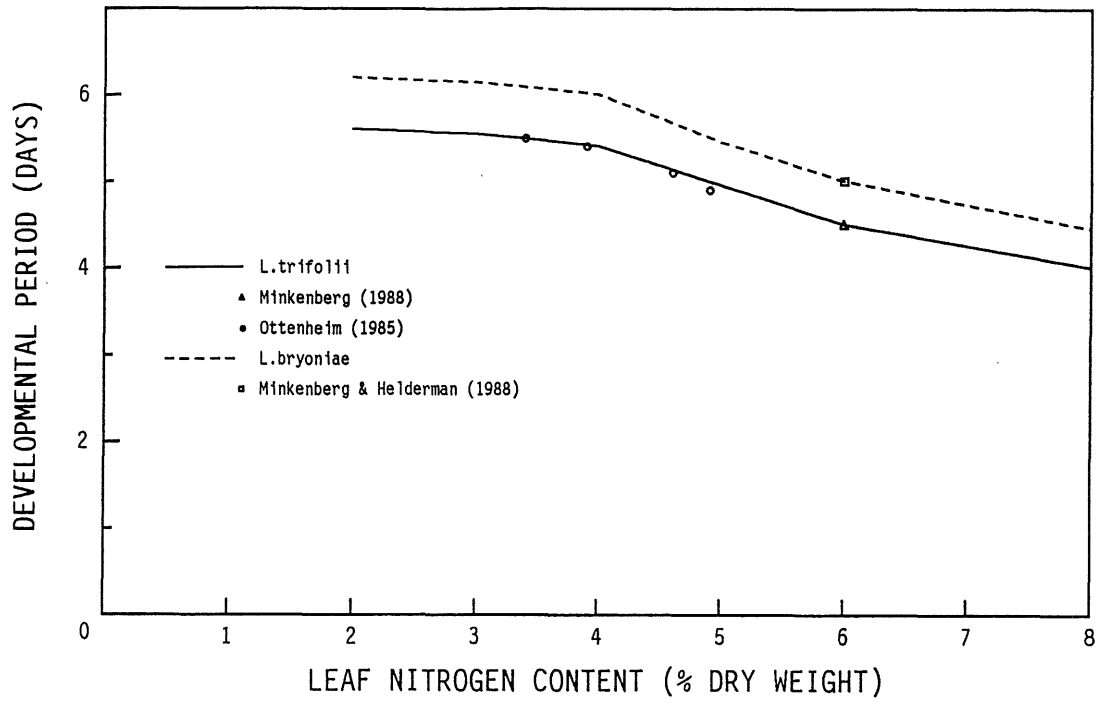


Figure 4.1.1: Developmental period from L1 to pupa at 25°C as used in the model plotted against leaf nitrogen content for L.trifolii and L.bryoniae. Data from Ottenheim (1985), Minkenberg (1988) and Minkenberg & Helderman (1988) are shown.

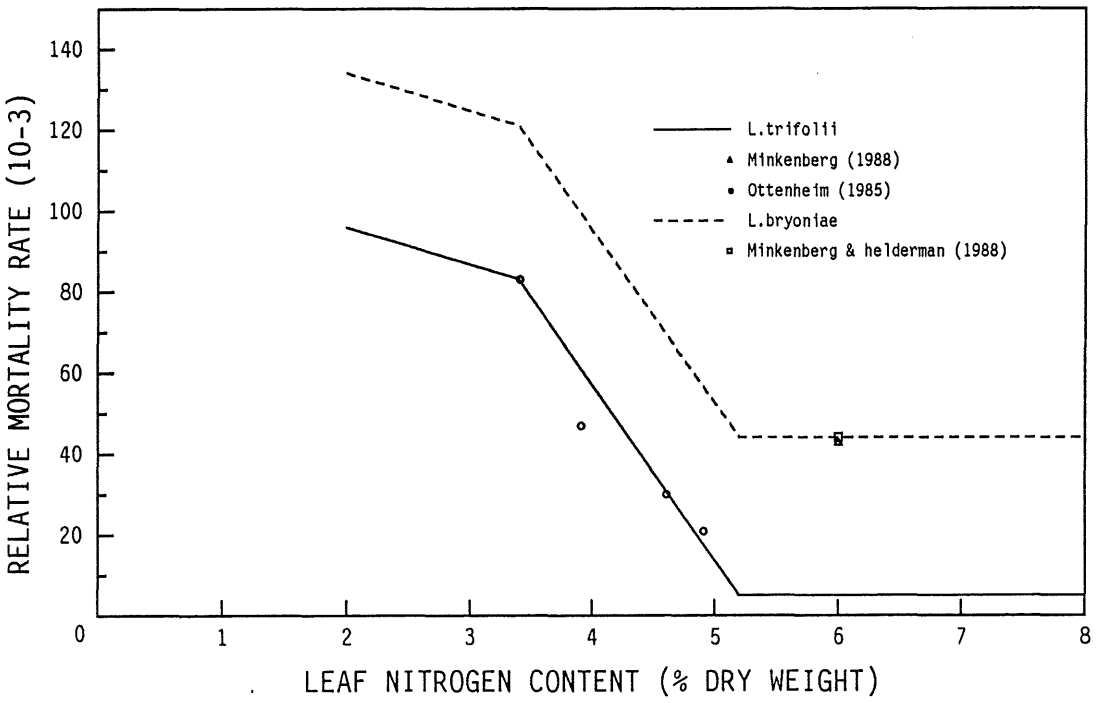


Figure 4.1.2: Relative mortality rate from L1 to adult at 25°C as used in the model plotted against leaf nitrogen content for L.trifolii and L.bryoniae. Data from Ottenheim (1985), Minkenberg (1988) and Minkenberg & Helderman (1988) are shown.

held on plants with a higher nitrogen content, the food contains more nitrogen. Secondly the better growth of the larvae on leaves with a higher nitrogen content causes the pupae to be significant larger (Ottenheim, 1985). Parrella (1983) has found that the length of the pupae is a positive indicator for the average longevity and fecundity of L. trifolii on Chrysanthemum morifolium.

Ottenheim (1985) has studied the relation between the nitrogen content of the leaves and the fecundity. He found an increasing mean fecundity when nitrogen content increased from 4.3 to 4.9% (fig 4.2.2), together with an increase in average longevity (fig 4.2.1). A higher fecundity, i.e. the total number of eggs per female, results from the combined effect of changes in the average longevity and the reproduction rate, i.e. the number of eggs per female per day. The average longevity is plotted against leaf nitrogen content in figure 4.2.1. The line represents the relationship as used in the model. There are no data concerning nitrogen dependent changes in the standard deviation of the average longevity. It is therefore assumed that the relative change in the standard deviation is equal to the relative change in the average longevity as found for different temperatures.

The determination of the effect on the reproduction rate is explained in figure 4.2.2. It is assumed that there is a linear relationship between the mean egg capacity and leaf nitrogen content (line A). Line A was chosen in such a way that the original value for the mean egg capacity is reached at N=6%. This has been achieved by forcing a linear regression of Ottenheims data through this point. Line B shows the effect of the changing average longevity at different leaf nitrogen levels while keeping the reproduction rate constant. The difference between the two lines is caused by the nitrogen effect on the reproduction rate and as such introduced in the model. The relative change in reproduction rate is assumed equal for every class of females.

In the model the longevity of adults, calculated as the average longevity + 3*sigma, is used for dividing the flies into classes. Introducing leaf nitrogen content as a forcing variable would also mean a leaf nitrogen dependent longevity. However we chose to make longevity nitrogen independent. So it is only driven by temperature. It is possible to do this because the nitrogen independent average longevity, i.e. at N=6%, is maximal. The number of flies in the last class will only get smaller as a result of leaf nitrogen. This method implies that the maximum reproduction is always reached at the same age at equal temperatures. Making the longevity leaf nitrogen dependent implies that the maximum reproduction is reached at equal physiologic age. Both methods have been compared to evaluate the possible effects on the simulation of the leafminer population (see 6.3).

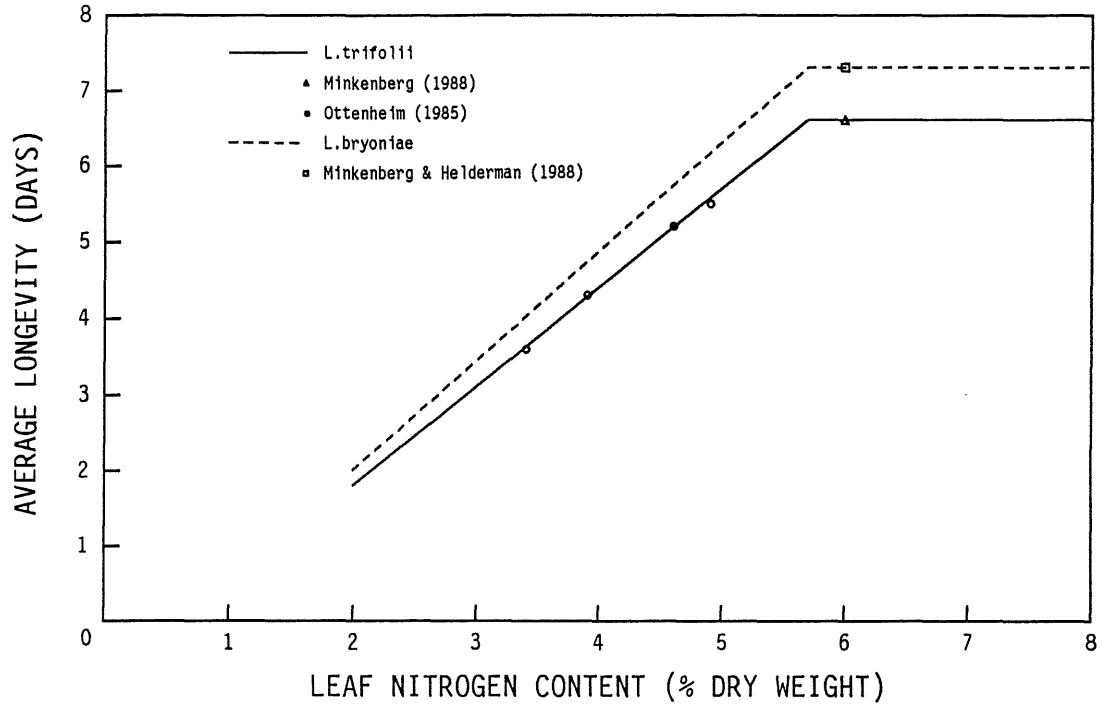


Figure 4.2.1: Average longevity of flies at 25°C as used in the model plotted against leaf nitrogen content for L.trifolii and L.bryoniae. Data from Ottenheim (1985), Minkenberg (1988) and Minkenberg & Helderman (1988) are shown.

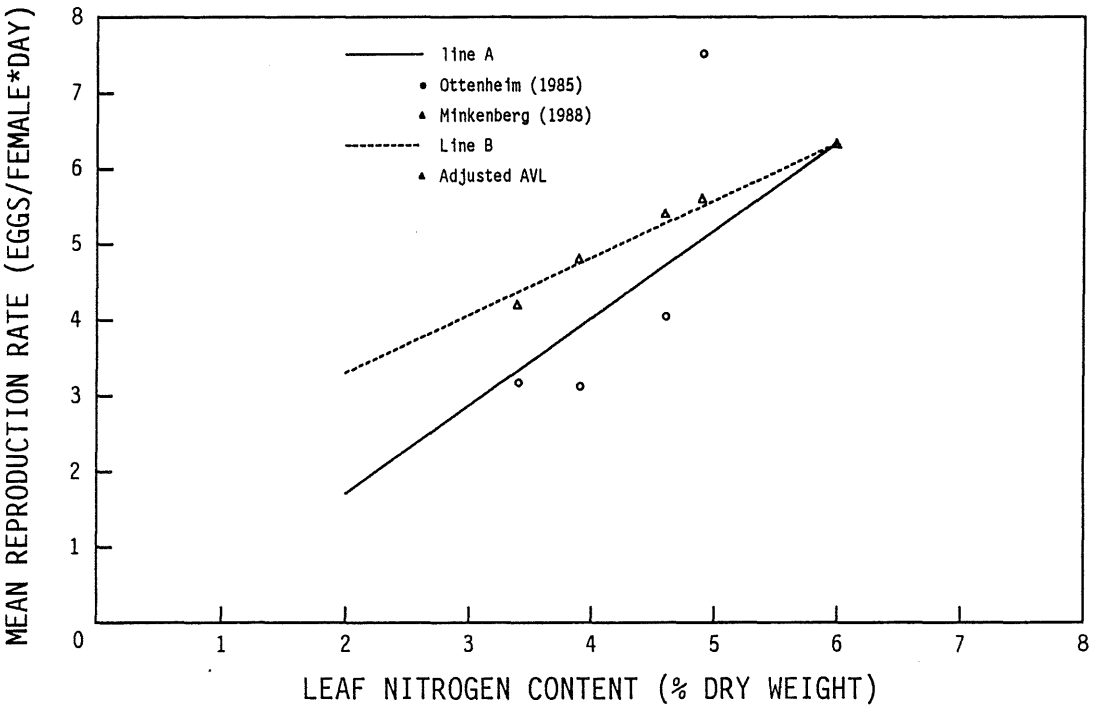


Figure 4.2.2: Mean reproduction rate plotted against leaf nitrogen content. For further explanation see text.

4.3 Influence on different Liriomyza species

No data are available on the influence of leaf nitrogen content on L. bryoniae . The relative changes in the different parameters of the life cycle caused by a change in nitrogen content in the leaves are therefore supposed to be equal to those for L. trifolii. Thus, the values for the life cycle parameters at a certain nitrogen content of the leaves are calculated using:

$$P(bryo,T,N) = P(bryo,T,6) * \frac{P(tri,T,n)}{P(tri,T,6)}$$

with: P(spec,T,N) = Life cycle parameter for species SPEC at temperature T and leaf nitrogen content N.

Using this method mortality of L. bryoniae larval stages will be very high at N=2%, because mortality at the reference nitrogen content is much higher for L. bryoniae compared to L. trifolii The slope of the curve increases to the eightfold of L.trifolii's curve. There seems to be no biological reason for this strong increase. Therefore a curve parallel to the RMR-curve of L.trifolii is used for L.bryoniae (fig 4.1.2).

4.4 Vertical distribution of leafminer species

The leafminer species are partly vertically separated on tomato plants. L. bryoniae and L. trifolii are most frequently found around the 15th and 7th leaf from the top respectively (Westerman & Minkenberg, 1986; Schuster & Beck, 1981; Ledieu & Helyer, 1985). Because of this separation the circumstances will be different for the different species. Differences have been found in nitrogen and tomatine content between young and mature leaves (Siregar & Schmiermann, 1985). In the model the vertical distribution is not taken into account.

5 Description of the model

In appendix A the complete model is given.

5.1 Forcing variables

The actual temperature is calculated by a function generator TEMPT during the first 47 days. From time=47 temperature is read from an external file by the subroutine READ (AIRTMP.DAT). File AIRTMP.DAT contains the measurements of Helderman (1986) of air temperature. The corrections described by Helderman (1986) have been carried out. Within hours temperature is calculated using a interpolation algorithm. Soil temperature GTMP was 0.9°C higher than air temperature (Helderman 1986). Leaf nitrogen content NPERC is calculated by a function generator NPERCT.

```
      FIXED K,M
      M=TIME
      KL=TIME-M
      IF(TIME.GT.47.)THEN
          K=(TIME-47.)*24.
          TMP=AIRTMP(K)+((TIME-47.)*24.-K)*(AIRTMP(K+1.)-
              AIRTMP(K))
          TEMP=TMP/10.
      ELSE
          TEMP=AFGEN(TEMPT,KL)
      ENDIF
      GTMP=TEMP+0.9

NPERC=AFGEN(NPERCT,TIME)
```

5.2 Development of the leafminers

The development of the leafminers is simulated by the subroutine BOXCAR (De Wit & Goudriaan, 1978). It mimicks the dispersion SD(E-P) of the larval development. The variables OVIP and OUT(E-P) are the in- and outflows from the different developmental stages. EGG, LAR(1-3) and PUP are the contents of the stages, with an initial value of EGGI, LARI(1-3) and PUPI at time STINTA. RES(E-P) are the residence times in each developmental stage. RME, TRM(1-3) and RMP are the relative mortality rates of the stages. Leafminers are introduced at time STINTA.

```
OUTE,EGG=BOXCAR(EGGI,RESE,SDE,RME,OVIP,N1,STINTA)
OUT1,LAR1=BOXCAR(LAR1I,RES1,SD1,TRM1,OUTE,N2,STINTA)
OUT2,LAR2=BOXCAR(LAR2I,RES2,SD2,TRM2,OUT1,N3,STINTA)
OUT3,LAR3=BOXCAR(LAR3I,RES3,SD3,TRM3,OUT2,N4,STINTA)
OUTP,PUP =BOXCAR(PUPI ,RESP,SDP,RMP ,OUT3,N5,STINTA)

DVRE=AFGEN(DVRET,TEMP)
DVR1=AFGEN(DVR1T,TEMP)
DVR2=AFGEN(DVR2T,TEMP)
DVR3=AFGEN(DVR3T,TEMP)
DVRP=AFGEN(DVRPT,GTMP)
```

The residence time is calculated as the inverse of the development rate DVR(E-P). The residence time and relative mortality are adjusted to the actual leaf nitrogen content by FRES and FRM.

```
RESE=1./DVRE
RES1=FRES/DVR1
RES2=FRES/DVR2
RES3=FRES/DVR3
RESP=1./DVRP

FRES=AFGEN(FREST,NPERC)

SDE=AFGEN(SDET,TEMP)
SD1=AFGEN(SD1T,TEMP)
SD2=AFGEN(SD2T,TEMP)
SD3=AFGEN(SD3T,TEMP)
SDP=AFGEN(SDPT,GTMP)

RME=AFGEN(RMET,TEMP)
NIRM1=AFGEN(RM1T,TEMP)
RM1=NIRM1*FRM
NIRM2=AFGEN(RM2T,TEMP)
RM2=NIRM2*FRM
NIRM3=AFGEN(RM3T,TEMP)
RM3=NIRM3*FRM
RMP=AFGEN(RMPT,GTMP)

FRM=AFGEN(FRMT,NPERC)
```

The total rate of mortality is calculated by summarising rate of host-feeding RMHFL(1-3), rate of parasitation RMPAR(2-3) and mortality due to other causes RM(1-3). The rates of host-feeding and parasitation are calculated in a different section.

```
TRM1 = AMIN1(RM1+RMHFL1,1./DELT)
TRM2 = AMIN1(RM2+RMHFL2+RMPAR2,1./DELT)
TRM3 = AMIN1(RM3+RMHFL3+RMPAR3,1./DELT)
```

5.3 Senescence of the adult flies

Senescence is simulated by a boxcar-train without dispersion (De Wit and Goudriaan, 1978; Goudriaan, 1986). The relative mortality rate of the adult females is calculated by subroutine CALCRM.

```
FAVL=AFGEN(FAVLT,NPERC)
RMA,MORTA,CUMPA,NILONG=CALCRM(TEMP,CUMPT,AVLT,SIGMT,FAVL)
DO 50 I=1,10
    IF (RMA(I).GT.1./DELT) THEN
        RMA(I)=1./DELT
    ENDIF
50 CONTINUE
```

By putting the emerging females from the pupal stage FLOW0 (=OUTP*SEXR) in the first class of the boxcar-train, a lumping error will be created. The average age in the first class will be 0.25* REST (REST= residence time in a class), REST + 0.25*REST in the second class, etc. To get an average age of 0.5* REST etc., a preclass can be used. The preclass AF0 will get FLOW0 and will have an outflow FLOW1 with a relative rate of 1/ 0.5* REST. Helderman (1986) has modeled the same effect by building an impulse statement in the model which lumps the inflow once a day in the first class. By doing so he modeled a discrete emergence from the pup stage, which is registered in nature. Emergence mostly occurs during the morning hours (Charlton & Allen, 1981). Using this method the residence time in a class has to be exactly 1 day. In this model the residence time in the classes is varying with temperature. Therefore we can not simulate the discrete emergence of leafminers. The effect however will be negligible, because emergence of leafminers is only discrete over 1 day and most parameters are not varying much over such a short period.

```
AF0=INTGRL(AFI0,FLOW0-FLOW1)
SEXR=0.5
FLOW0=OUTP*SEXR
FLOW1=AF0*AMIN1(2./(NILONG*1./10.),1./DELT)
```

The content of a development stage is pushed into the next stage after a period of 0.1*NILONG. This shift is controlled by PUSHA. It pushes when the integral SEN reaches value 0.1*NILONG.

```
PUSHA=INSW(SEN-1./10.,0.,1./DELT)
RSEN=1./NILONG
SEN=INTGRL(0.,RSEN-PUSHA/10.)
```

The net change in a stage NTFL (inflow-outflow-mortality) is calculated by subroutine NETFLW. The content AF of the different stages is calculated by subroutine ARRINT. SUMA calculates the total number of adult females TAF.

```
NTFL,FLOW11=NETFLW(AFI,FLOW1,PUSHA,AF,RMA,DELT)
AF,DUM=ARRINT(10,AFI,NTFL,DELT,TIME,STINTA)
TAF,DUM=SUMA(AF,10)
```

The rate of reproduction REP is calculated by multiplying the number of adult females of the stages AF, the relative reproduction of the physiologic stages RRE and FCAP. FCAP adjusts REP for the actual leaf nitrogen content.

```
RRE(1)=AFGEN(RRT1,TEMP)
RRE(2)=AFGEN(RRT2,TEMP)
RRE(3)=AFGEN(RRT3,TEMP)
RRE(4)=AFGEN(RRT4,TEMP)
RRE(5)=AFGEN(RRT5,TEMP)
RRE(6)=AFGEN(RRT6,TEMP)
RRE(7)=AFGEN(RRT7,TEMP)
RRE(8)=AFGEN(RRT8,TEMP)
RRE(9)=AFGEN(RRT9,TEMP)
```

```
RRE(10)=AFGEN(RRT10,TEMP)
FCAP=AFGEN(FCAPT,NPERC)
DO 10 I=1,10
    REP(I)=RRE(I)*AF(I)*FCAP
10 CONTINUE
```

The total reproduction TREP is put into the buffer REPBUF. REPBUF is emptied once a day in state variable EGG by OVIP at 8.00h (TIME = 0.35)

```
TREP,DUM=SUMA(REP,10)
REPBUF=INTGRL(0.,TREP-OVIP)
OVIP=PUSHOV*(REPBUF/DELT +TREP)
PUSHOV=IMPULS(0.35,1.)
```

5.4 Development of the parasitoid

The parasitoid-part of the model is started after introduction of wasps.

```
IF (TIME.GE.START-DELT/2..AND.INWASP.GT.0.) THEN
```

The larval development of the parasitoid is simulated using subroutine BOXCAR (De Wit & Goudriaan,1978) to mimic dispersion in development time (see 5.3).

```
DVRPAR = AFGEN(DVRPRT,TEMP)
RMLP = AFGEN(RMLPT,TEMP)
SDPAR = AFGEN(SDPART,TEMP)
RESLP = 1/DVRPAR
OUTPAR,LPAR=BOXCAR(LPARI,RESLP,SDPAR,RMLP,TRPAR,10,START)
```

5.5 Senescence of the adult parasitoids

Mortality during the adult stages is calculated using subroutine CALCRM. Because leaf nitrogen content is supposed not to influence the parasitoid, FAVL is set at 1

```
FAVL=1.
RDR,MORTP,CUMPP,REST=CALCRM(TEMP,CUMPT,AVLTP,SIGMTP,FAVL)
```

To simulate senescence of the adult parasitoids a boxcar-train without dispersion is used. The number of females in preclass FLP0 is calculated by multiplying the number of emerging parasitoids OUTPAR by the sex ratio SR. At TIME = START the number of females in the first adult stage is set at INWASP.

```
IF (TIME.GT.START-DELT/2..AND.TIME.LT.START+DELT/2.) THEN
    FLP1=INWASP/DELT
    H0=0.
ELSE
    FLP0  =OUTPAR*SR
    FLP1=H0*AMIN1(2./(REST*1./10.),1./DELT)
    H0=INTGRL(HI0,FLP0-FLP1)]
ENDIF
```

The content of a developmental stage is pushed into the next stage after a period of 0.1*REST. This shift is controlled by PUSHP. It pushes when the integral SENP reaches value 0.1*REST.

```
RSENP   =1./REST
PUSHP   =INSW(SENP-1./10.,0.,1./DELT)
SENP    =INTGRL(0.,RSENP-PUSHP/10.)
```

The net change in a stage NTFLP (inflow-outflow-mortality) is calculated by subroutine NETFLW. The content of the different developmental stages is calculated by subroutine ARRINT. SUMA calculates the total number of adult female parasitoids SUMH.

```
NTFLP,FLWP11=NETFLW(HI,FLP1,PUSHP,H,RDR,DELT)
STINTH=START
H,DUM=ARRINT(10,HI,NTFLP,DELT,TIME,STINTH)
SUMH,DUM=SUMA(H,10)
```

5.6 Parasitation and host-feeding by D.isaea.

The rate of successful encounters by D.isaea with its hosts is calculated for every class according to a 'type 2' functional response (Holling, 1959). Searching efficiency A is calculated by a function generator. The density of larvae suitable to attack DENS is calculated by dividing the number of larvae suitable to attack NOLARP by the number of plants NOPLA. The third parameter needed to calculate the rate of successful encounters is the maximal number of larvae which can be parasitised by a single parasitoid PRM. PRM is temperature and physiological stage dependent. The rates of successful encounters RENC are calculated by subroutine ENCOUN. The total rate of successful encounters TRENC is calculated using subroutine SUMA.

```
A = AFGEN(AT,TEMP)
NOLARP=LAR1/8.+LAR2+LAR3
DENS=NOLARP/NOPLA

PRM(1)=AFGEN(PRMT1,TEMP)
PRM(2)=AFGEN(PRMT2,TEMP)
PRM(3)=AFGEN(PRMT3,TEMP)
PRM(4)=AFGEN(PRMT4,TEMP)
PRM(5)=AFGEN(PRMT5,TEMP)
PRM(6)=AFGEN(PRMT6,TEMP)
PRM(7)=AFGEN(PRMT7,TEMP)
PRM(8)=AFGEN(PRMT8,TEMP)
PRM(9)=AFGEN(PRMT9,TEMP)
PRM(10)=AFGEN(PRMT10,TEMP)

RENC,DUM=ENCOUN(PRM,A,DENS,H)
TRENC,DUM=SUMA(RENC,10)
```

The total rate of successful encounters is distributed over host-feeding and parasitation. First the rate of mortality of L1 larvae is calculated. The rate of mortality of the L1 larvae considered suitable for successful encounters with parsitoids (1/8 part; see 3.3) is TRENC/NOLARP. RMHFL1 is the relative mortality of the total number of L1 larvae, however, so TRENC/NOLARP has to be divided by 8.

```
IF (LAR1.GT.1.) THEN
    RMHFL1=TRENC/(8*NOLARP)
ELSE
    RMHFL1=0.
ENDIF
```

The relative rate of successful encounters of L2 and L3 larvae is the total rate of successful encounters TRENC divided by the total number of larvae suitable for attacking NOLARP. The fraction FACT is the fraction of the L2 and L3 larvae which should be parasitised to get an overall (L1, L2 and L3 larvae) fraction parasitation PREFPR. When L2 and L3 are very small, F1 will become larger than 1. FACT however can not become larger than 1 (=100%). So when F1 becomes larger than 1, the overall fraction parasitation PREFPR can not be realised.

```
F1=PREFPR*(LAR1/8+LAR2+LAR3)/(LAR2+LAR3+0.1)

    IF (F1.GT.1.) THEN
        FACT=1.
    ELSE
        FACT=F1
    ENDIF

        RMHFL2=(1-FACT)*TRENC/NOLARP
        RMPAR2=FACT*TRENC/NOLARP

        RMHFL3=(1-FACT)*TRENC/NOLARP
        RMPAR3=FACT*TRENC/NOLARP
```

The total rate of host-feeding is found by summarising the rates of host-feeding for each larval stage. The same holds for the total rate of parasitation.

```
TRHF=RMHFL1*LAR1+RMHFL2*LAR2+RMHFL3*LAR3
TRPAR=RMPAR2*LAR2+RMPAR3*LAR3
```

5.7 Subroutines

5.7.1 Subroutine READ

The subroutine READ reads temperatures out of file AIRTMP.DAT. X1,X2 and X3 are other variables in file AIRTMP.DAT, which can be ignored. The temperatures are stored in array AIRTMP with a maximum of 2400 values.

```
      SUBROUTINE READ(AIRTMP)
      IMPLICIT REAL(A-Z)
      INTEGER I
      DIMENSION  AIRTMP(2400)

      OPEN (UNIT=21,FILE='AIRTMP.DAT')

      I=0
10    FORMAT(4F)
5     READ(21,*,END=20) X1,X2,X3,X4
      AIRTMP(I)=X4
      I=I+1
      GOTO 5

20    CONTINUE
      CLOSE(UNIT=21)
      RETURN
      END
```

5.7.2 Subroutine NETFLW

The subroutine NETFLW calculates the netto change of the classes of leafminer and parasitoid adults. The netto rate of change NTFL of stage i is calculated as the inflow from stage i-1 to stage i minus the outflow from stage i to stage i+1 minus the rate of mortality, calculated by multiplying the number of adults in stage i AF(I) by the relative rate of mortality RMA(I). The flow into stage 1 is calculated in the main program. The flows are controlled by PUSHA, which pushes the content of the stages into the next stage.

```
      SUBROUTINE NETFLW(AFI,FLOW1,PUSHA,AF,RMA,DELT,NTFL,FLOW11)
      IMPLICIT REAL (A-Z)
      INTEGER I
      DIMENSION AFI(10),AF(10),RMA(10),NTFL(10),FLOW(11)

      DO 10 I=1,10
          FLOW(1)=FLOW1
          FLOW(I+1)=PUSHA*(AF(I)-RMA(I)*AF(I)*DELT)
          NTFL(I)=FLOW(I)-FLOW(I+1)-AF(I)*RMA(I)
10    CONTINUE
      FLOW11=FLOW(11)
      RETURN
      END
```

5.7.3 Subroutine CALCRM

Subroutine CALCRM calculates the relative mortality per class of leafminer and parasitoid adults. The method used to calculate mortality is discussed in 2.4. The average longevity AVL and its dispersion SIGMA are calculated by a function generator AVLT and SIGMT and adjusted to the actual leaf nitrogen content by FAVL. AVL and SIGMA are expressed as fractions of the maximal longevity NILONG by MU and SIGML. By expressing MU and SIGML as fractions of NILONG the mortality of the every physiological age, expressed as a fraction of NILONG (I-0.5)/10, can be calculated. The rate of mortality MORT is calculated according to formula 2.4.1 for each adult stage. Using formula 2.4.1, the rate of mortality is expressed per NILONG. The rate of mortality must be divided by NILONG to get the mortality per day. The integral of formula 2.4.1 is calculated using afgen function CUMPT, mimicking a cumulative standard normal distribution function.

```
      SUBROUTINE CALCRM(NLOC,TEMP,CUMPT,AVLT,SIGMT,FAVL,RMA,
     $MORT,CUMP,NILONG)
      IMPLICIT REAL (A-Z)
      INTEGER NLOC,I
      DIMENSION RMA(10),MORT(10),A(10),Q(10),CUMP(10)

      NIAVL=AFGEN(NLOC,AVLT,TEMP)
      AVL=NIAVL*FAVL
      NISIGM=AFGEN(NLOC+5,SIGMT,TEMP)
      NILONG=NIAVL+3.*NISIGM
      SIGMA=NISIGM*FAVL
      MU=AVL/NILONG
      SIGML=SIGMA/NILONG

      DO 100 I=1,10
          A(I)=((2.*3.1416)**-.5)/SIGMA
          MORT(I)=A(I)*EXP(-.5*(((I-0.5)/10.-MU)/SIGML)**2.)
          Q(I)=((I-0.5)/10.-MU)/SIGML
          CUMP(I)=AFGEN(NLOC+15,CUMPT,Q(I))
          RMA(I)=MORT(I)/CUMP(I)
100   CONTINUE

      RETURN
      END
```

5.7.4 Subroutine ENCOUN

Subroutine ENCOUN calculates the rate of successful encounters with hosts by each of the adult parasitoid physiological stages. A 'type 2' functional response described by Holling (1959) has been supposed, using searching efficiency A (plants per day), density of its hosts DENS (larvae per plant) and the maximal number of successful encounters PRM*5/4 (see 3.3). The relative rate of successful encounters is multiplied by the number of adult parasitoids to get the rate of successful encounters.

```
      SUBROUTINE ENCOUN(PRM,A,DENS,H,RENC,DUM)
      IMPLICIT REAL (A-Z)
      INTEGER I
      DIMENSION PRM(10),RER(10),RENC(10)
      DIMENSION H(10)

      DO 10 I=1,10
          IF (PRM(I).LT.0.1) THEN
              RENC(I)=0.
          ELSE

              RER(I)=((A*DENS*PRM(I)*5/4)/(A*DENS+PRM(I)*5/4))
              RENC(I)=RER(I)*H(I)

          ENDIF
10    CONTINUE

      RETURN
      END
```

5.7.5 Subroutine SUMA

Subroutine SUMA summarises the elements of array ARR, containing N elements. The result is put in variable SUM.

```
      SUBROUTINE SUMA(ARR,N,SUM,DUM)

      IMPLICIT REAL (A-Z)
      INTEGER I,N
      DIMENSION ARR(N)

      SUM=0.
      DO 10 I=1,N
          SUM=SUM+ARR(I)
10    CONTINUE
      RETURN
      END
```

5.7.6 Subroutine ARRINT

Subroutine ARRINT integrates the elements of array Y, using the rectangular method. N is the number of elements of array Y. Array YI contains the initial values of Y. The integration is initialised at TIME = STINT. Array X contains the rate of change of the elements of Y.

```
      SUBROUTINE ARRINT(N,YI,X,DELT,TIME,STINT,Y,DUM)
      IMPLICIT REAL (A-Z)
      INTEGER N
      DIMENSION Y(N),YI(N),X(N)

      DO 10 I=1,N
          IF (TIME.EQ.STINT) THEN
              Y(I)=YI(I) + X(I)*DELT
          END IF
          IF (TIME.GT.STINT) THEN
               Y(I)=Y(I)+X(I)*DELT
          END IF
10    CONTINUE
      RETURN
      END
```

5.8 The time constant of the model.

The time constant of the model is determined by the largest relative rate used (De Wit & Goudriaan, 1978). In table 7 the relative rates potentially determining the time constant are summarised. In most cases the relative rates are temperature dependent. The temperature at which the largest relative rate can be expected is given. At extreme temperatures some relative rates appear to be very large. However it will not be right to adjust the time constant according to these values. The temperature in greenhouses stays normally within the 10-30 °C range. Temperatures outside this range will be scarce.

For the leafminers L. bryoniae and L. trifolii FLOW1/AF0 is limiting the time constant: 1.7 day^{-1} and 1.1 day^{-1} at 30 °C respectively. The RMA values exceed these values in the late adult stages. These stages contain only a small part of the total number of adults, however. Limited exceeding is therefore of minor importance. For the parasitoid FLP1/H0 is limiting the time constant: 1.1 day^{-1} at 30 °C. A time constant of 0.1 days seems reasonable both for simulation with and without parasitoids. To avoid negative values the relative rates should not surpass 1/(time constant). Therefore the relative rates potentially surpassing this limit in exceptional cases are restricted to this value.

Table 7: Relative rates used in the model.

name of rel. rate	rel. rate (1/ day) L. bryoniae	L. trifolii
DVRE 40 °C	0.64	0.78
DVR1 40 °C	1.49	1.70
DVR2 40 °C	1.00	1.59
DVR3 40 °C	0.92	1.08
DVRP 40 °C	0.20	0.28
RME	0	0
RM1 5 °C	0.50	0.30
RM2 40 °C	0.40	0.28
RM3 40 °C	0.15	0.12
RMP 40 °C	0.02	0.07

	30°C	40°C	30°C	40°C
RMA(1)	0.19	3.8	0.19	
RMA(2)	0.20	4.1	0.20	
RMA(3)	0.39	7.8	0.39	
RMA(4)	0.64	12.9	0.64	
RMA(5)	0.97	19.3	0.97	
RMA(6)	1.33	26.6	1.33	
RMA(7)	1.72	34.4	1.72	
RMA(8)	2.09	41.8	2.09	
RMA(9)	2.56	51.3	2.56	
RMA(10)	1.44	28.8	1.44	
FLOW1/AF0	1.7	20	1.1	20
TRM1[a]	∞		∞	
TRM2[a]	∞		∞	
TRM3[a]	∞		∞	

	D. isaea
DVRPAR 40 °C	0.181
RMLP 40 °C	0.05

	30°C	40°C
RDR(1)	0.07	0.4
RDR(2)	0.11	0.4
RDR(3)	0.16	0.8
RDR(4)	0.22	1.3
RDR(5)	0.29	1.9
RDR(6)	0.36	2.7
RDR(7)	0.42	3.4
RDR(8)	0.50	4.2
RDR(9)	0.57	5.1
RDR(10)	0.30	2.9
FLP1/H0	1.1	20

a: When parasitoids are incorporated in the model.

6 Simulations.

6.1 Comparison of two methods for classification of adult flies and parasitoids.

Two methods for classification of adults are described in chapter 2.2 . The first method is based on the average longevity and its standard deviation. The second method is based on the maximum reproduction rate. These methods have been compared by running the model. The model is initialised with 100 L3 larvae (LAR3I=100.) and all other state variables are set at zero. For comparison of parasitoids 10 female parasitoids are introduced at the 20th day (START=20., INWASP=10.). Temperature is varying daily according to a sinus curve with an average temperature of 20 °C and an amplitude of 5 °C.

Figs. 6.1.1-6.1.3 show that the numbers are not influenced by the method of classification. The small differences that occur are probably the result of reading the reproduction rates used in the classes at different time intervals. This is illustrated by calculating the net reproduction of a female[a] at constant temperatures. Between both methods differences of more than 10% are normal, though the values should be equal (table 8).

Table 8: Net reproduction for L. trifolii, L. bryoniae and D. isaea, using different adult classification methods.

Species	basis of classification method	netto reproduction (eggs/female) 15 °C	25 °C
L. trifolii	AVL + 3*SIGMA	3.9	41.8
	Max. reproduction	3.5	45.6
L. bryoniae	AVL + 3*SIGMA	80.9	203.1
	Max. reproduction	101.3	182.4
D. isaea	AVL + 3*SIGMA	235.3	198.1
	Max. reproduction	222.6	197.6

Because the method does not influence the results, further simulations are carried out using the first method. Using this method the maximum longevities of flies and parasitoids (LONG and REST) can be calculated by the model and need not be given in a function statement.

a: The net reproduction rate of a female is defined as the mean number of viable eggs of a female during her life. To get this value the reproduction rate in every class is multiplied by the class width (days) and the fraction of survivors in that class. Then the netto reproduction rates of the classes are added.

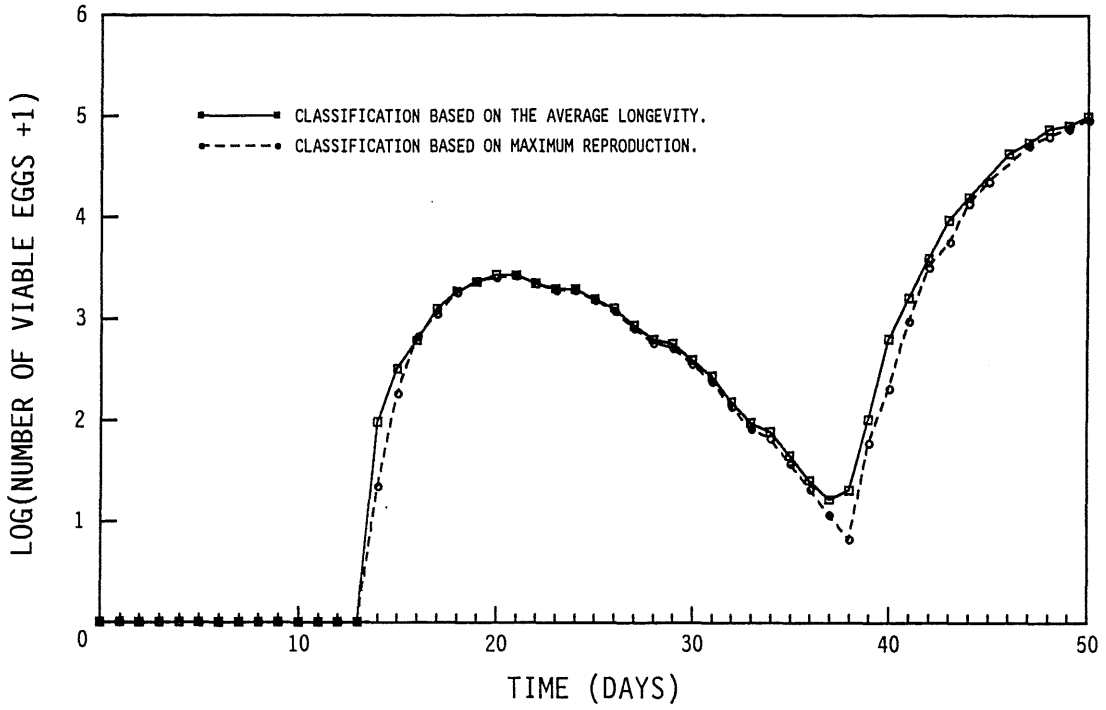


Figure 6.1.1: Simulated number of viable eggs of L.bryoniae plotted against time for two different ways of classifying the development of the adult stage (simulation conditions, see text).

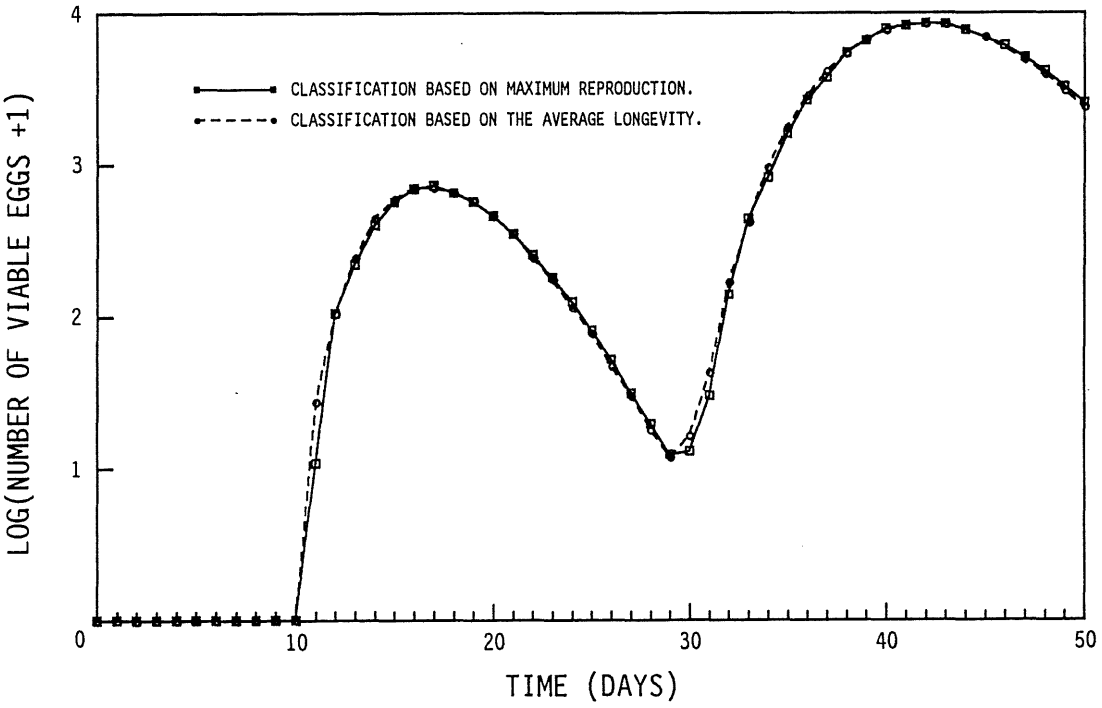


Figure 6.1.2: Simulated number of viable eggs of L.trifolii plotted against time for two different ways of classifying the development of the adult stage (simulation conditions, see text).

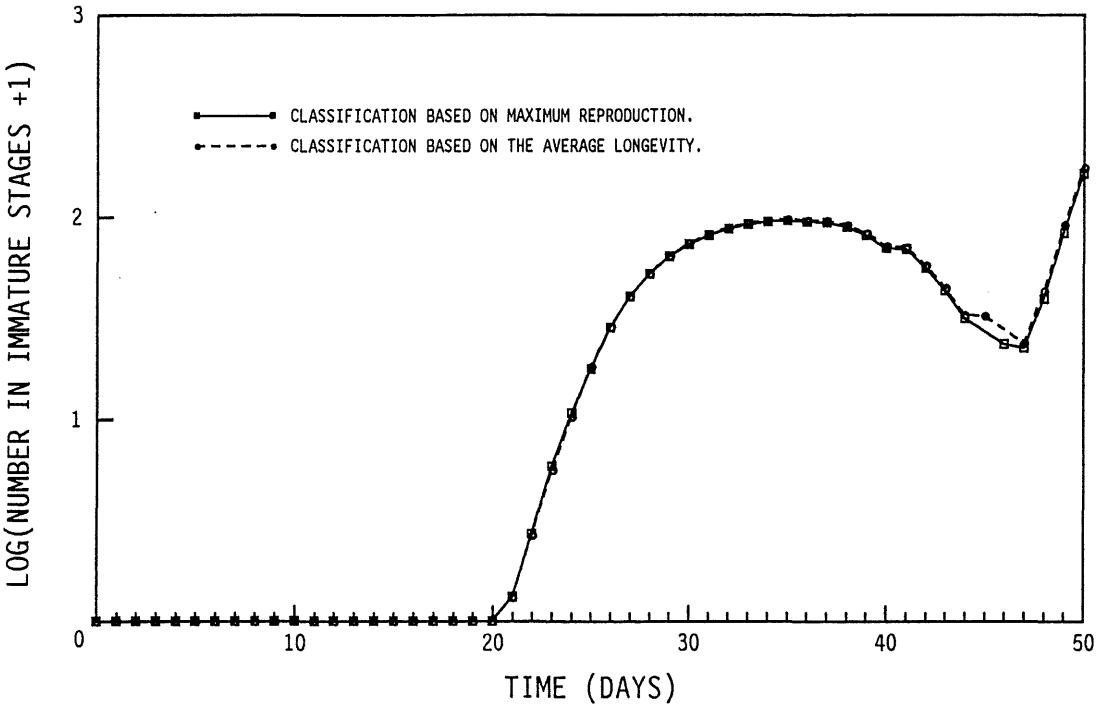


Figure 6.1.3: Simulated number of immatures of D.isaea plotted against time for two different ways of classifying the development of the adult stage (simulation conditions, see text).

It can be understood that the classification method does not influence the results. Using classification based on the maximum longevity, errors occur by changes of temperature. The structure of the leafminer population can vary a lot during the season, which is illustrated by the occurence of distinguishable generations. However the fluctuations will at least comprise a week. To evaluate effects of varying temperature in this system, 3 possibilities can be marked. Firstly the fluctuation period of temperature can be much smaller then the fluctuation period of the leafminer population. The population of leafminers can be considered constant during a fluctuation in temperature. The maximum reproduction rate may be shifted from one class to another, forwards and backwards dependent on temperature fluctuations. Eventual errors will be compensated because the number of flies is approximately constant during the shifting. This situation actually occurs here, because temperature fluctuates over one day in a greenhouse. Secondly the fluctuation period of temperature can be in the same order of magnitude as the fluctuation period of leafminer populations. In this case there can be considerable effects because shifting the maximum reproduction rate between classes may coincide with changes in the number of flies, which prevents eventual errors to be compensated later. In such circumstances classification based on the maximum reproduction rate would be preferable to avoid errors. Situations like this are imaginable in the open field. Then fluctuations in temperature can occur over larger periods besides fluctuations over 1 day. Thirdly the fluctuation period of temperature can be much larger then the fluctuation period of leafminer populations. Now the temperature can be considered constant during a fluctuation of the leafminer population and no effects can be expected.

6.2 Sensitivity analysis of leaf nitrogen content for L. bryoniae.

In the model nitrogen content of the leaves influences the leafminer population in 4 different ways:
1- higher nitrogen levels cause lower larval mortality.
2- higher nitrogen levels cause larger larval developmental rates.
3- higher nitrogen levels cause longer lifespans of adult flies.
4- higher nitrogen levels cause a larger reproduction rate of the flies.

To evaluate the overall effects on the leafminer population a sensitivity analysis is carried out. The model is initialised with 100 eggs (EGGI=100.) and all other state variables are set at zero. In the model parasitoids are not introduced, because they are not influenced by leaf nitrogen content. Temperature fluctuates daily according to a sinus curve with an average of 20°C and an amplitude of 5°C. The cumulative number of mines and the daily number of pupations give information on population growth (fig. 6.2.1) and changes in population structure (fig. 6.2.2) respectively.

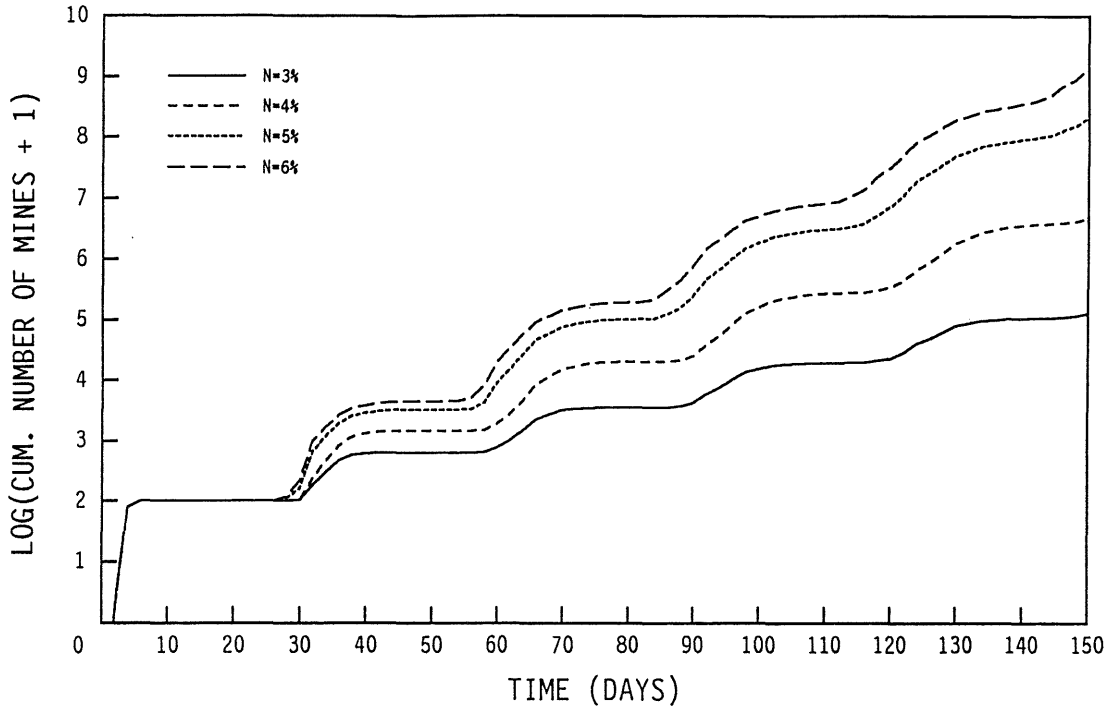


Figure 6.2.1: Simulated cumulative number of mines of L.bryoniae plotted against time for four different levels of leaf nitrogen (% dry weight). For simulation conditions, see text.

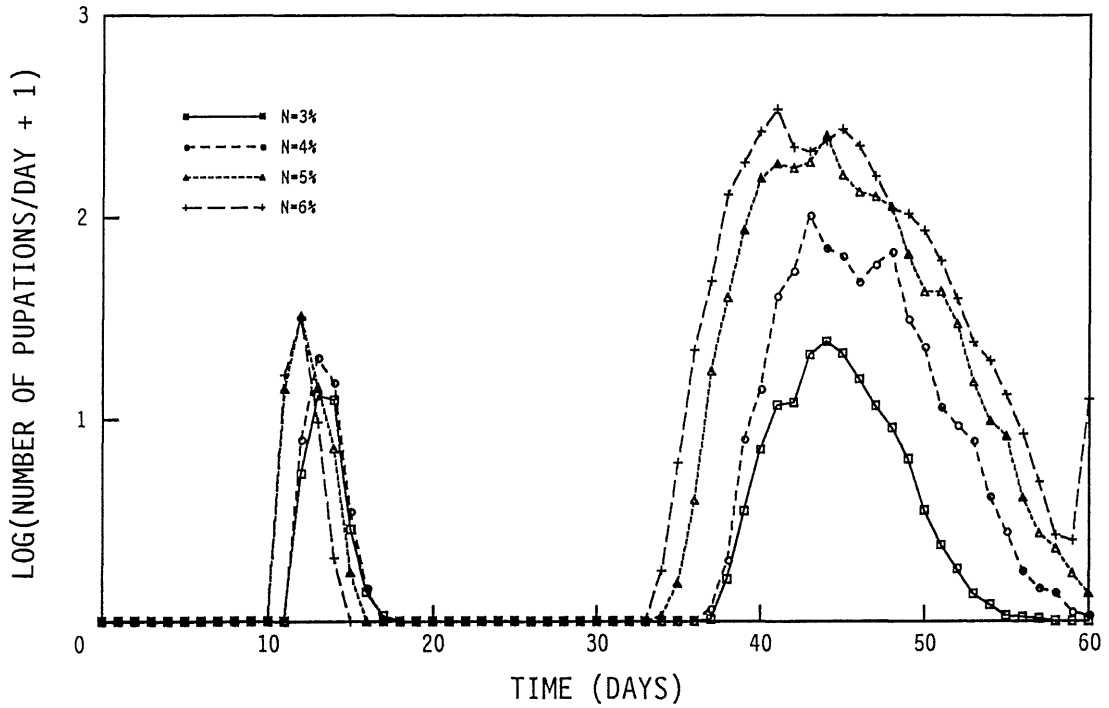


Figure 6.2.2: Simulated number of pupations per day of L.bryoniae plotted against time for four different levels of leaf nitrogen (% dry weight). For simulation conditions, see text.

The cumulative number of mines changes periodically. First the eggs introduced in the model hatch and bring the cumulative number of mines at 100. The leafminers develop and a few days after the production of the first eggs the cumulative number of mines starts to increase rapidly. This increase will stop or become very small until a new generation comes to development. The multiplication factor between generations can be calculated from the difference in the number of mines, which represents the number of L1 larvae of a generation.

Table 9 summarises the effect of leaf nitrogen content on the multiplication factor of the population between generations and the cumulative number of mines after 150 days. From these data the number of generations in 150 days can be calculated (n.b. the first increase in number of mines caused by the hatching of the initial eggs is not counted as a generation):

$$100 * F^{a} = Min - Min/F^{*} \Rightarrow$$

$$a = [\log(Min *(F-1)/F) - \log(100)]/ \log(F)$$

F = Multiplication factor in 1st generation.
a = Number of generations.
Min = cumulative number of mines.

*: Because Min is the cumulative number of mines, terms of previous generations have to be subtracted. One term is sufficient. The influence of the earlier generations on the cumulative number of mines will be negligible.

Table 9: The multiplication factor between generations, the cumulative number of mines and the number of generations after 150 days at different leaf nitrogen levels.

leaf nitrogen in % N of dry weigh	multiplication factor between generations	cumulative number of mines (t=150)	number of generations (t=150)
3	5.3	$1.24*10^5$	4.1
4	13.3	$4.53*10^6$	4.1
5	30.9	$2.07*10^8$	4.2
6	42.8	$1.34*10^9$	4.4

The number of generations over 150 days is hardly influenced by leaf nitrogen content. The large differences in the cumulative number of mines are almost completely caused by the differences in multiplication factor between generations.

The effect of leaf nitrogen content on the population structure can be seen in figure 6.2.2. A decrease in leaf nitrogen content decreases the average longevity of flies. This is reflected by the sharper peak of daily number of pupations. At

low leaf nitrogen levels the different generations of leafminers will be more distinct. The residence time in the larval stages is larger at low nitrogen than at high nitrogen levels, increasing the generation time. This effect is counteracted by the shorter average longevity of flies at low nitrogen levels. The generation time, being the result of both larval and adult stages, is therefore hardly influenced by nitrogen content.

Leaf nitrogen content can be an important forcing variable. In commercial greenhouses a decrease of 1-2 % N can be registered in tomatoes during the season (january-july; Sonneveld, Naaldwijk, pers. com.). In april the leaf nitrogen content measures about 5 % (Boot, 1987).

6.3 Effects of a leaf nitrogen dependent or leaf nitrogen independent longevity of the adult stages of L. bryoniae.

The longevity of adults is only used for dividing the flies into classes and does not influence the numbers of flies of a certain age. That parameter is influenced by the average longevity (AVL) and its standard deviation (SIGMA). The longevity can be made leaf nitrogen independent (calculated as AVL + 3*SIGMA, for N=6%) or leaf nitrogen dependent (calculated as AVL + 3*SIGMA, for N='actual %'). Effects of the different longevities as classification criterion will be zero with a leaf nitrogen content of 6% and with decreasing nitrogen levels the possible effects will increase. The model is initialised with 100 L3 larvae (L3I=100.). Nitrogen content is set at 3%. Other conditions are the same as used in 6.2.

Figure 6.3.2 shows the effect of the different longevities. The peak of pupal emergence with nitrogen independent longevity appears to be broader than the other one. There is only a small effect however. Figure 6.3.1 illustrates that maximum reproduction is shifted to another adult age (days) by changes in longevity. Making longevity nitrogen dependent a greater part of the reproduction will be shifted to the first days in the adult life at lower leaf nitrogen levels than 6 %. The peak of daily number of pupations will be sharper and the generation time will be slightly smaller.

It is doubtful if the maximum reproduction rate will be reached earlier with decreasing leaf nitrogen values, which is a consequence of making longevity nitrogen dependent. Maybe the period until the maximum is only dependent on temperature. The opposite possibility seems also very likely; the period until the maximum reproduction rate can be longer with decreasing nitrogen levels as a result of a slower development. We have chosen a nitrogen independent period until the maximum reproduction rate. Longevity based on the average longevity and its standard deviation at N=6% is used in all other simulations.

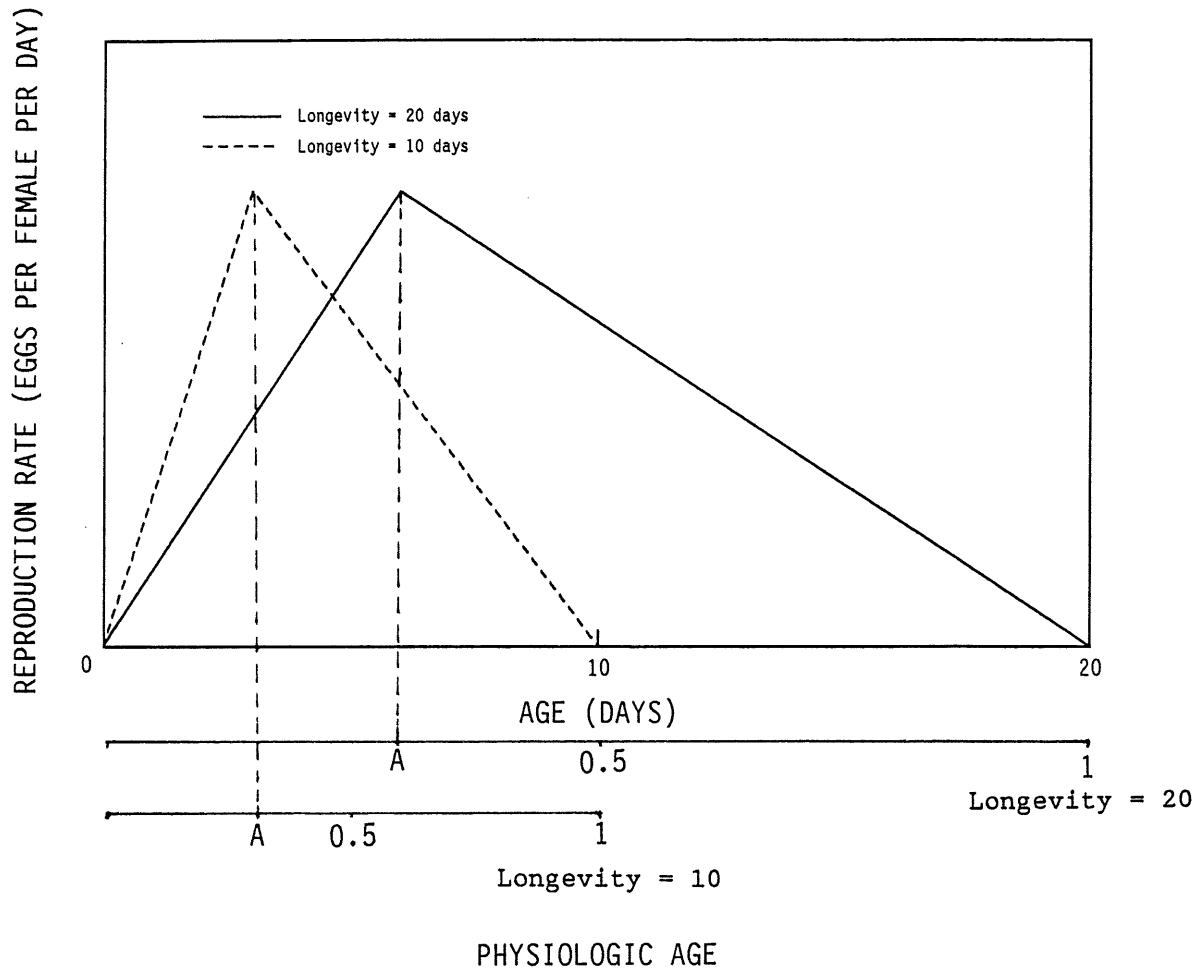


Figure 6.3.1: Example of the mechanism of shifting the maximum reproduction to a different age (in days) by changing longevity.

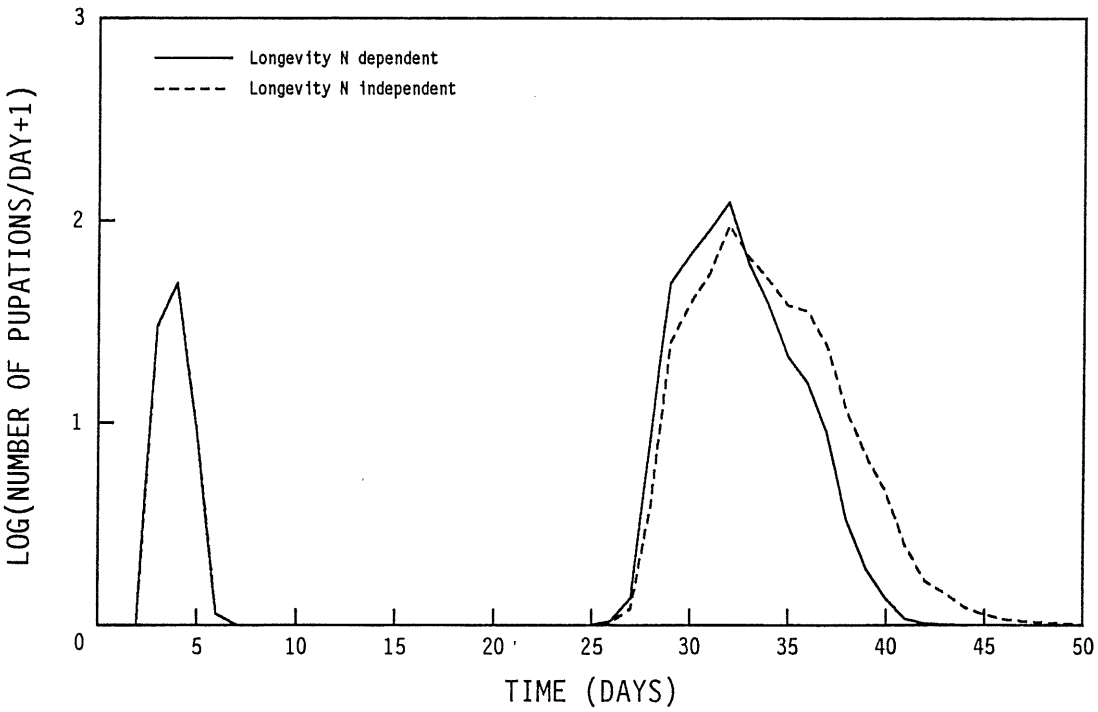


Figure 6.3.2: Simulated number of pupations per day plotted against time, when longevity is dependent or independent of leaf nitrogen content (simulation conditions, see text).

6.4 Sensitivity analysis of some important parameters in the leafminer population model of L. bryoniae.

Four parameters have been submitted to a sensitivity analysis:
1 Residence time in the larval stages (RES1-3).
2 Mortality in the larval stages (RMR1-3).
3 Average longevity of the adult flies (AVL).
4 Reproduction rate of the adult flies (REP(I)).

The original parameters are changed in two ways (1) According to a fixed fraction of 25%. (2) According to the coefficient of variation found for these parameters. The parameters have been reduced and enlarged with the standard deviation measured. Because relative mortality is only determined once, no dispersion can be determined. Therefore relative mortality of immature stages can only be tested using a fixed fraction. To determine variation of the average longevity and the reproduction rate, data from Ottenheim (1985) on the mean fecundity are used. Mean fecundity depends on longevity and the reproduction rate of the adult fly. Dispersion of the reproduction rate has therefore been determined as the rest variance of a linear regression between longevity and mean egg capacity, as determined by Ottenheim (1985). Ottenheim (1985) has studied L. trifolii, however, not L. bryoniae. It is assumed that variation of the reproduction rate and longevity are similar for both leafminer species. Coefficients of variation of residence time, average longevity and the reproduction rate are 12%, 15% and 50% of the mean value, respectively. The model is initialised with 100 eggs (EGGI=100.) and temperature fluctuates daily according to a sinus curve with an average temperature of 20 °C and an amplitude of 5 °C. Leaf nitrogen is kept constant at N=6%.

Changes of relative mortality in the larval stages have just a slight effect on the multiplication factor and no effect on generation time. Changes in residence time in the larval stages have a much stronger effect. Reduction of residence time causes besides a decreasing mortality, a reduction of the generation time. After 150 days there is a difference of 0.8 generation between the runs with an enlarged and a reduced residence time (fixed fraction). Because mortality has little effect, this will be the major aspect of changes in residence time. The reproduction rate has a major effect on the multiplication factor. Average longevity has little effect, probably because it has no effect on reproduction of the early adult stages, during which most of the reproduction takes place.

Table 10: The multiplication factor between generations, the cumulative number of mines and the number of generations after 150 days as a result of changes in life history parameters.

	multiplication factor between generations	cumulative number of mines (t=150)	number of generations (t=150)
Original parameters	42.8	$1.34*10^9$	4.4
0.75*RES1-3	46.7	$9.47*10^9$	4.8
1.25*RES1-3	39.2	$2.60*10^8$	4.0
0.75*RMR1-3	46.7	$1.99*10^9$	4.4
1.25*RMR1-3	39.3	$9.05*10^8$	4.4
0.75*AVL	35.4	$9.48*10^8$	4.5
1.25*AVL	52.2	$2.30*10^9$	4.3
0.75*REP(I)	31.1	$3.48*10^8$	4.3
1.25*REP(I)	53.5	$3.87*10^9$	4.4
$(1-\sigma)$*RES1-3	44.6	$3.83*10^9$	4.6
$(1+\sigma)$*RES1-3	41.0	$4.76*10^8$	4.1
$(1-\sigma)$*AVL	38.7	$1.13*10^9$	4.4
$(1+\sigma)$*AVL	48.2	$1.86*10^9$	4.3
$(1-\sigma)$*REP	21.4	$5.38*10^7$	4.3
$(1+\sigma)$*REP	64.3	$9.25*10^9$	4.4

7 Validation

7.1 Validation of the leafminer model.

A greenhouse experiment (Westerman, 1986; Helderman, 1986) is available to validate the model. During this experiment temperature has been recorded every hour and is incorporated in the model. Leaf nitrogen content, however, being the other forcing variable has not been determined.

Simulation is started with 30 L3 larvae (LAR3I=30.). T=0 is corresponding with 08-02-86. Temperature has been recorded from 28-03-86 (T=47), so during the first 48 days temperature is described by a function generator (Helderman, 1986). Runs have been made with a constant leaf nitrogen content of 6%, i.e. temperature is the only forcing variable. In greenhouses a decrease of leaf nitrogen content from 6% to 4.5% dry weight can be expected (pers. comm. Sonneveld, Naaldwijk). Therefore runs have been made assuming a continuously decreasing leaf nitrogen content from 6% at T=0 to 4.5 % at T=142. The daily number of pupations and the cumulative number of mines have been printed (fig. 7.1.1 & 7.1.2).

Figure 7.1.1 gives a good impression of the consecutive generations. Measured values from the greenhouse experiment are shown. These values have a relative nature. They cannot be used as an absolute indication of the daily number of pupations. Still they are important as a means for detecting consecutive generations. The succession of generations in time is predicted well.

Figure 7.1.2 shows the cumulative number of mines together with measured values. The numbers after the first 2 generations are predicted well by the simulation with constant nitrogen at 6% as well as by the simulation with decreasing nitrogen content. The number of mines after the 3rd generation however is overestimated compared to the actual measured values. Multiplication factors between consecutive generations have been calculated and are summarised in table 11.

Table 11: Multiplication factors between consecutive generations for L. bryoniae. Values based on simulations and measurements.

	multiplication factors				
	simulation		measured values[a]		
generation	fixed N (6%)	decreasing N (6%-4.5%)	D. isaea section	C. parksi section	control section
1-2	48.2	46.5	59	100	49
2-3	30.0	25.4	33	24	25
3-4	31.6	24.0	13	12	13
4-5	22.5	13.0			

a: Westerman & Minkenberg (1986), corrected for host-feeding and parasitation

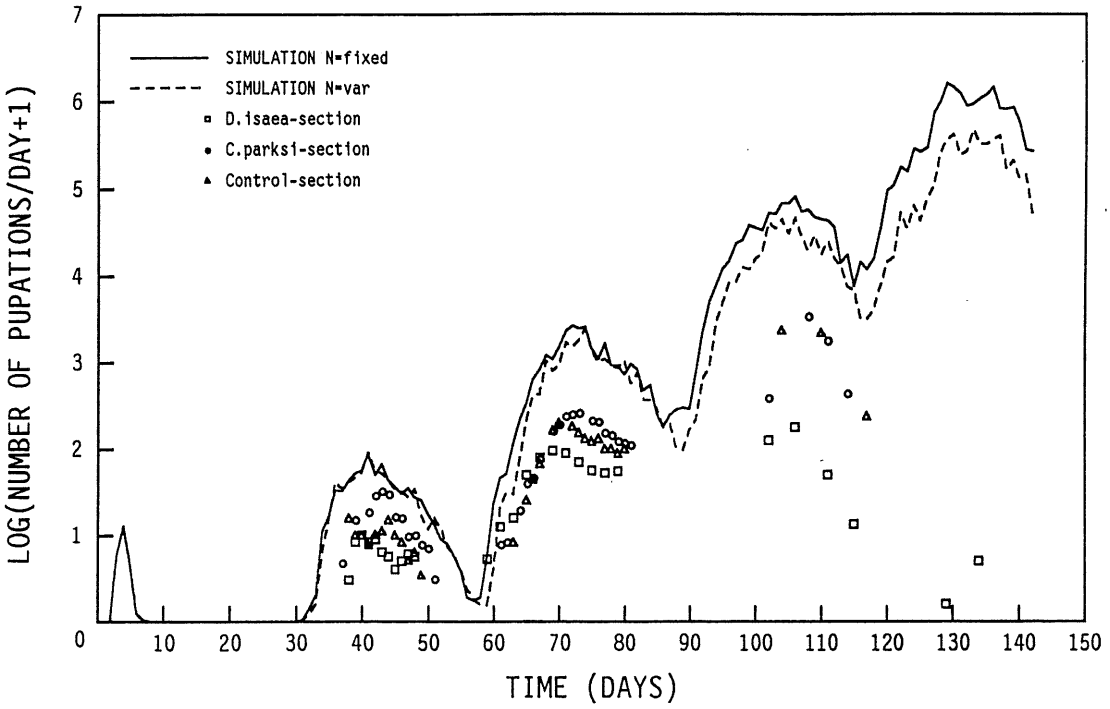


Figure 7.1.1: Number of pupations per day plotted against time. Simulated values, using a fixed (N=6%) or a variable (N=6%->4.5%) leaf nitrogen content (simulation conditions, see text), and measured values (Westerman, 1986) are shown.

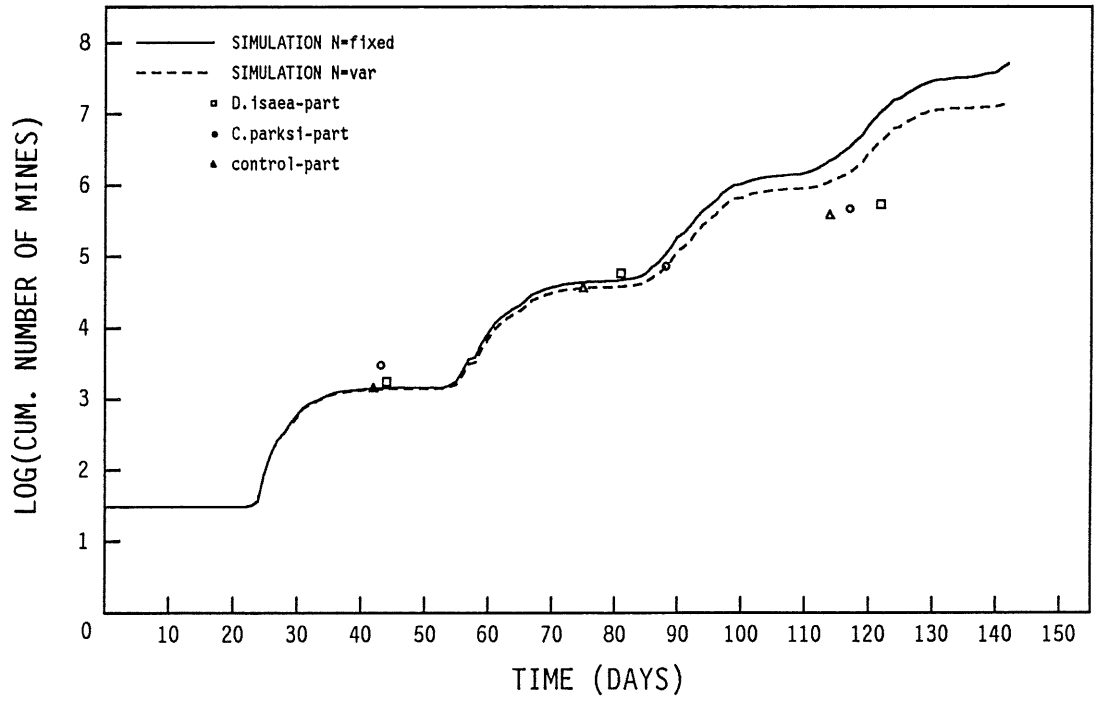


Figure 7.1.2: Cumulative number of mines plotted against time. Simulated values, using a fixed (N=6%) or a variable (N=6%->4.5%) leaf nitrogen content (simulation conditions, see text), and measured values (Westerman, 1986) are shown.

The measured multiplication factor between the first and the second generation is rather variable. The experiment has been started with only 30 L3 larvae. A small variation in for instance sex ratio can result in big differences after the first generation. Some days in June temperature has increased to 40°C around noon. It is unknown what the effect on the population is of such high temperatures. In the model the interval of 25 to 40°C is extrapolated for all relations. At such extreme temperatures, mortality has been supposed to increase rapidly for both immature and adult stages. This increase may cause the low multiplication factor from the fourth to the fifth generation of L.bryoniae (simulation). The decrease in multiplication factor from the third to the fourth generation (measured) cannot be explained by temperature as forcing variable. A model which assumes decreasing nitrogen content levels during the season improves the fit with measured values a little but is still unable to explain the registered decrease of the multiplication factor.

Simulation runs can also be carried out using L. trifolii life history parameters. In fig. 7.1.3 and 7.1.4 simulations of L. trifolii and L. bryoniae are compared. The measured temperatures from the greenhouse experiment have been used and temperature is the only forcing variable (N=6%). The multiplication factors between generations of L. trifolii (table 12) are much smaller then L. bryoniae's multiplication factors. The generation time however is shorter for L. trifolii. L. trifolii has 1 complete generation more in the simulated 142 days. The shorter generation time is not enough to catch up with L. bryoniae's population development in the end though. Table 12 shows another interesting feature. The multiplication factors between generations for L. trifolii stay rather constant during the season. L. bryoniae's multiplication factors show a decreasing tendency. So measured temperatures have had a negative influence on population growth later in the season. Population growth of L. trifolii is unaffected. This is consistent with greenhouse observations that L. trifolii is mainly a problem in summer (Frijters et al., 1986).

Table 12: Multiplication factors between consecutive generations of L. trifolii; Values are calculated from simulations.

generation	multiplication factor	
	L.trifolii	L.bryoniae
1-2	9.2	48.2
2-3	15.7	30.0
3-4	11.0	31.6
4-5	12.8	22.5

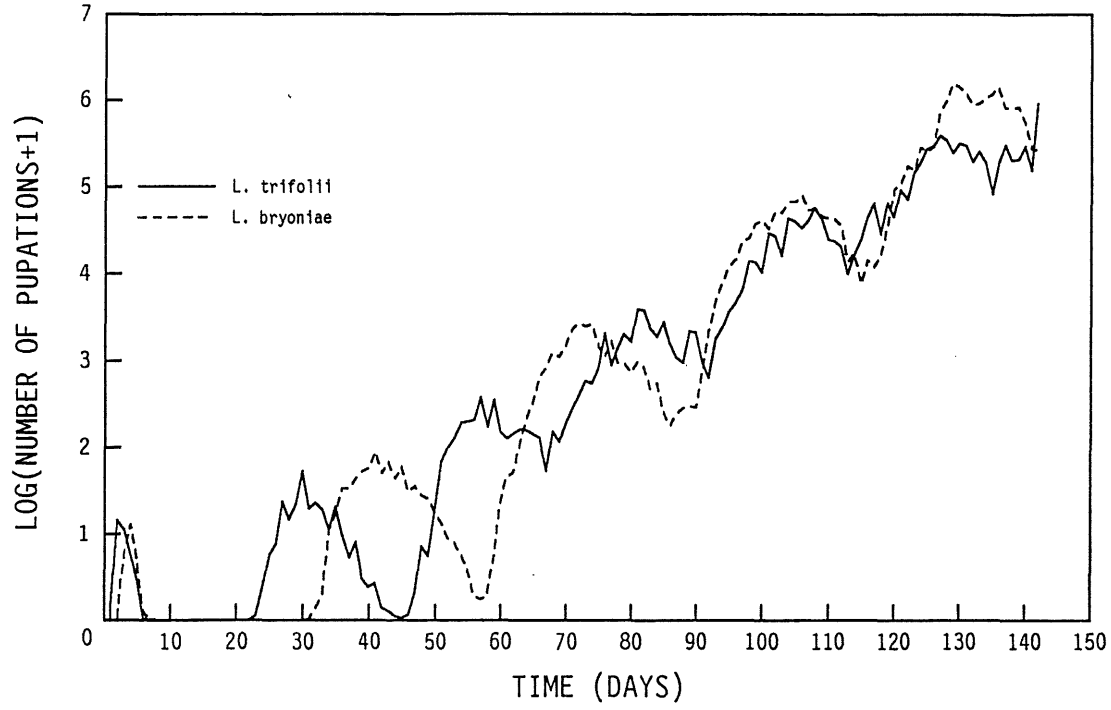


Figure 7.1.3: Simulated number of pupations per day plotted against time for L.trifolii and L.bryoniae (simulation conditions, see text).

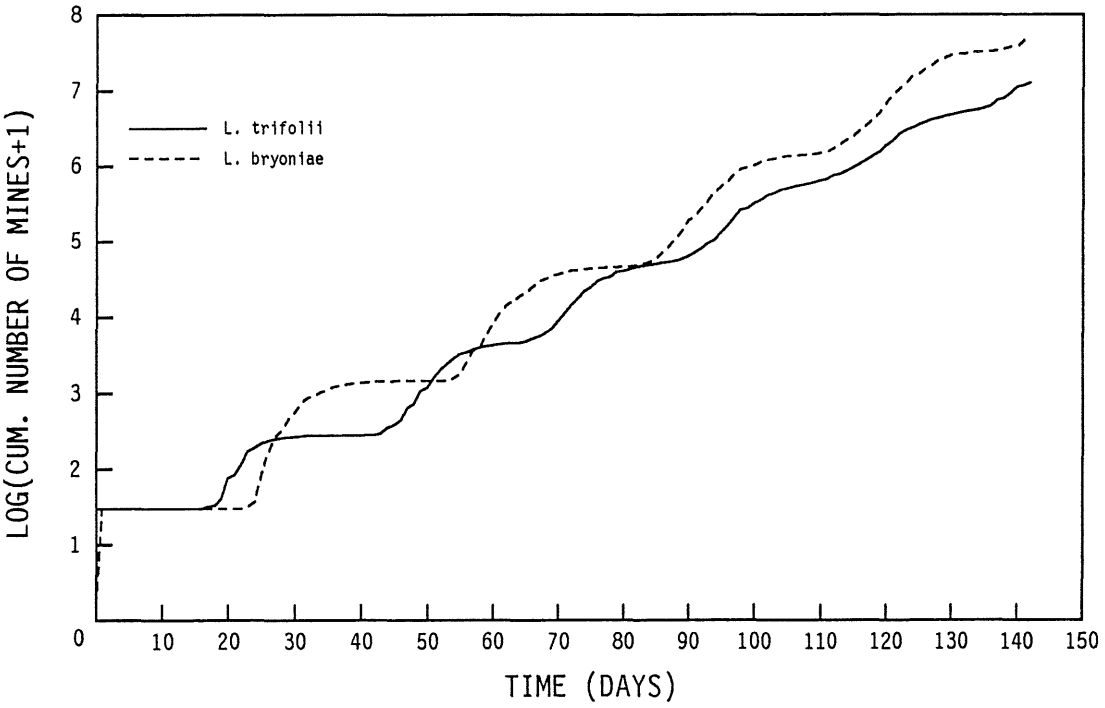


Figure 7.1.4: Simulated cumulative number of mines plotted against time for L.trifolii and L.bryoniae (simulation conditions, see text).

7.2 Validation of the parasitoid model.

The greenhouse experiment of Westerman (1986) also provides some data to validate the parasitoid model. The parasitoid population growth is determined by temperature and numbers of its host. So when parasitoids are introduced in the leafminer model wrong simulations of the host population can create errors and validation will be hard. To make a good validation possible the input in the leafminer model has been slightly adjusted to get a population development resembling the measured data (Table 13). Doing so, the leafminer model will become a leafminer density generator instead of an explanatory model.

Table 13: Measured cumulative number of mines after generations and acquired cumulative number of mines after generations with adjusted model input.

generation	log(cum. number of mines measured[a])	log(cum. number of mines simulated (adj. input)
1	3.24	3.29
2	4.78	4.78
3	5.92	5.97

a: Values derived from Westerman (1986).

Simulation is started with 40 L3 larvae (LAR3I=40.). Leaf nitrogen content is set at 6% from T=0 to T=75 and set at 4% from T=75 to T=142. At T=61 200 females of D.isaea have been introduced. The parasitoids are supposed to parasitise 65% of the number of encountered leafminer larvae (PREF=0.65), using the rest for host feeding. No reliable estimation exist on searching efficiency. Simulation runs are therefore carried out for 3 different searching efficiencies (A=0.2, A=1.0, A=2.3). The A-value of 2.3 has been determined by Meijer (1986) for the host L.trifolii, but seems to be an overestimation, because only L3 larvae have been used (see discussion). The other values have been chosen arbitrarily. The daily number of pupations (leafminers) and the number of parasitoids have been printed.

The percentage of larvae used for host feeding and parasitation in a generation can be calculated from the increase of the cumulative number of mines and the increase of the cumulative number of host feedings or parasitations in the generation (Table 14).

Table 14: Percentage host feeding and parasitation caused by D. isaea. Wasps have been introduced in the second generation; Values from simulations.

searching efficiency (A) (plants/day)	host feeding (%)	parasitation (%)	total (%)
generation 3:			
0.2	5.9	11.1	17.0
1.0	13.6	25.4	39.0
2.3	17.2	31.9	49.1
generation 4:			
0.2	16.4	29.9	46.3
1.0	65.0	14.0	79.0
2.3	83.9	4.1	88.0

Westerman (1986) has determined the percentage parasitation by D. isaea. The percentage parasitation in the third and the fourth generation of leafminers numbered 15.2% and 58.7% respectively. The increase in percentage parasitation from the third to the fourth generation is rather big. The model cannot simulate an increase equal to the greenhouse data. In the model there will be no leafminer larvae surviving the fourth (A=1.0 and A=2.3) or the fifth generation (A=0.2) (figure 7.2.1). Such a strong effect of D. isaea has not been found in the greenhouse experiment, although mortality due to parasitoids was high in the fourth generation. Westerman (1986) estimated a mortality of 98% in the fourth generation. This value is very high however. Even when no larvae reach the pupal stage in simulations, mortality due to parasitoids is not that high because a part of the larvae will be killed by other causes before parasitoids can act.

When A=1.0 or A=2.3 pressure on the leafminer population will be very high. In the third generation, the second generation after wasp introduction, the majority of successful encounters will be with L1 larvae. Therefore mortality will be due mainly to host feeding. Westerman (1986) has shown however that over 50% of the killed hosts were parasitised both in the 3rd and 4th generation. Figure 7.2.2 shows the simulated population growth of parasitoids in time. The population only increases for 2 generations (only 1 when A=2.3). The leafminer population will be extinct and parasitoid population will decrease rapidly.

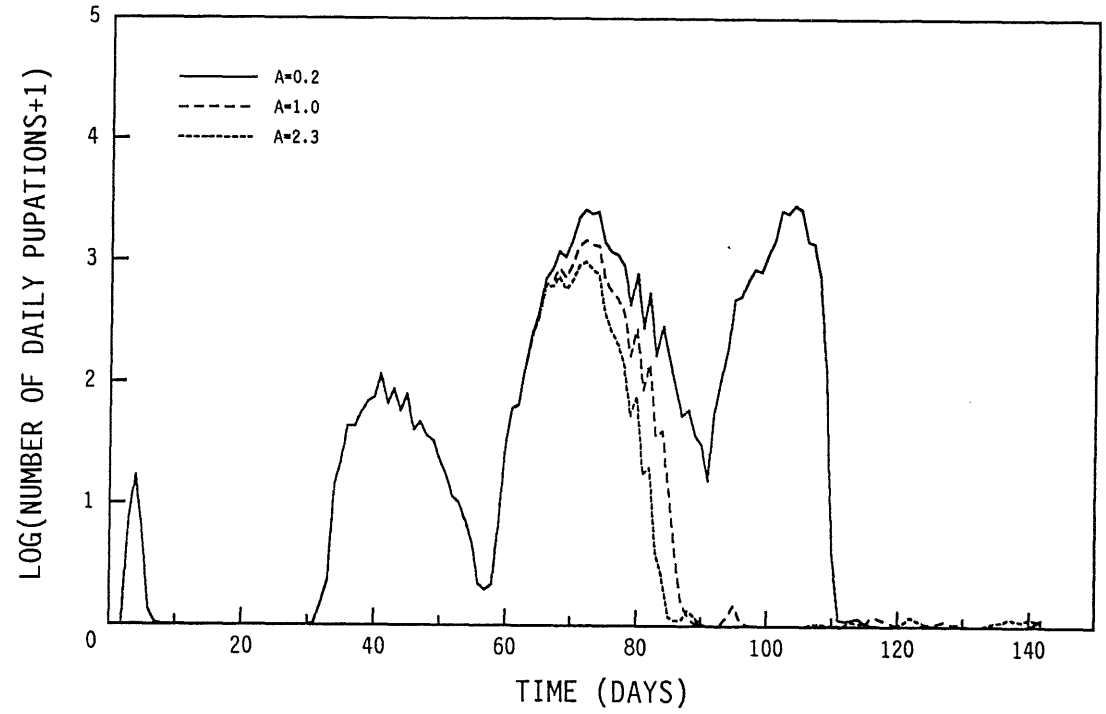


Figure 7.2.1: Simulated number of pupations per day of L.bryoniae plotted against time when parasitoids are introduced with different searching efficiencies A (simulation conditions, see text).

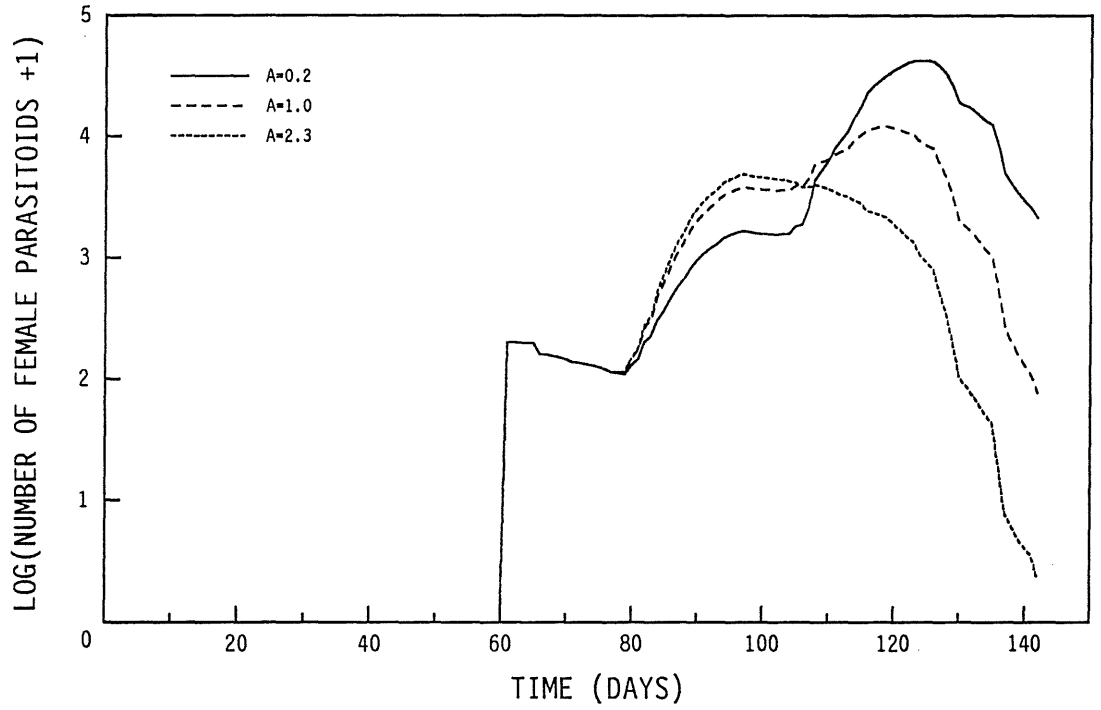


Figure 7.2.2: Simulated number of adult female parasitoids when introduced in L.bryoniae population for different searching efficiencies (simulation conditions, see text)

8 Discussion

The model is based on some general assumptions which may not be true. Life history variables have been determined on small tomato plants, still in the vegetative stage with 7 -10 leaves. It is not sure whether the determined values can be applied to a system with full grown tomato plants. For the relations between leaf nitrogen content and life history variables there is an additional problem. Data have been determined on L. trifolii. It is questionable whether the same relationships hold for L. bryoniae. Another general assumption is made about influences of forcing variables. The response to these variables is supposed to be instantaneous: fluctuating temperatures have the same effect as a constant temperature (Rabbinge & Carter, 1983). There is little evidence that this assumption holds for highly fluctuating forcing variables in nature. However effects of fluctuating temperatures (16 °C/ 22 °C) can be explained reasonably by the mean temperature for L. bryoniae (Minkenberg & Helderman, 1988).

When 2 forcing variables are used (temperature and leaf nitrogen content), another assumption is made: the relations between life history variables and each forcing variable are independent of each other. This means that when a life history variable is plotted against a forcing variable for different levels of another forcing variable, the shape of the curves has to be approximately equal. Figures 8.1-8.3 give examples from literature where a few life history variables are plotted against temperature. Figures have been plotted from data summarised by Minkenberg & v. Lenteren (1986). The different measurements can be conceived as different levels of the forcing variable 'plant quality'. 'Plant quality' summarises all possible other forcing variables like for instance leaf nitrogen content. The developmental period of immature stages and the fecundity per day have approximately the same shape, though studies of egg capacity are scarce. The relationship between temperature and these life history variables may be conceived as independent of other forcing variables. For longevity of females this picture does not hold. The curve drawn from Minkenberg (1988) has a different shape compared to curves drawn from data from the other studies (fig 8.3).

The model describes the actual data of a pilot greenhouse experiment fairly well during the early generations. Later in the season the model overestimates the population growth. There is no marked indication that introducing leaf nitrogen content as a forcing variable gives a better description of population growth. However with nitrogen levels decreasing 1-2% during the season, it may have a large impact on population growth. No data exist yet to validate the model with leaf nitrogen content included as a forcing variable. Measurements are carried out during the first half year of 1988 in a commercial greenhouse, which will make validation possible (Minkenberg, pers. com.).

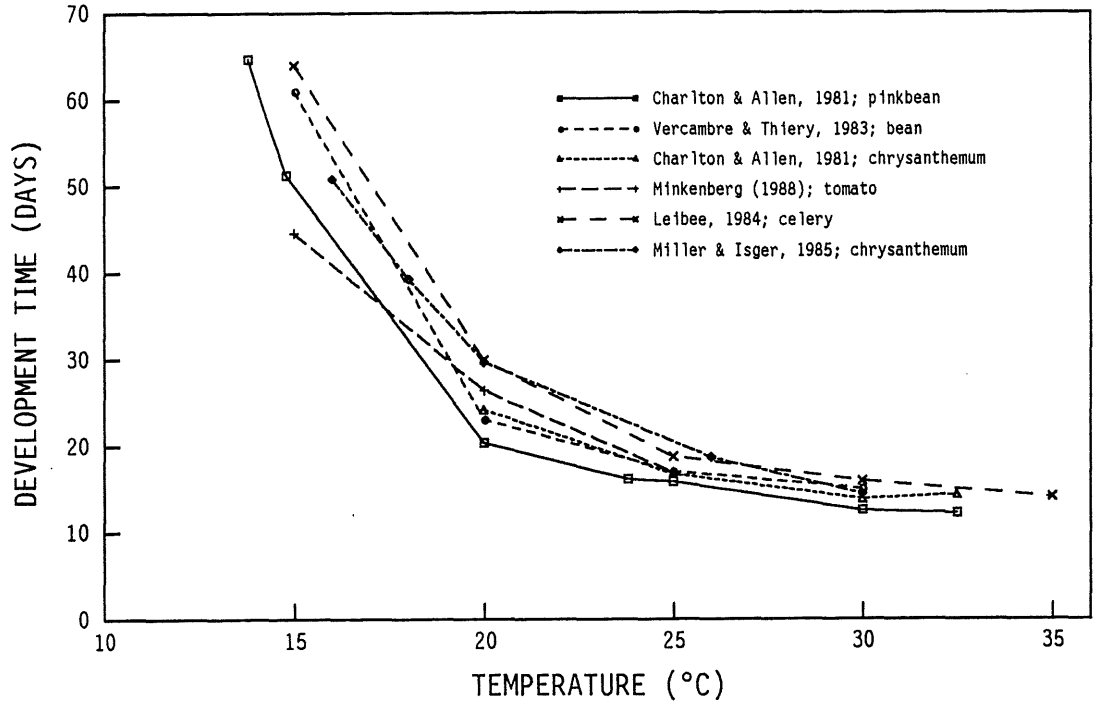


Figure 8.1: Development time from egg to adult of L.trifolii on different host plants plotted against temperature.

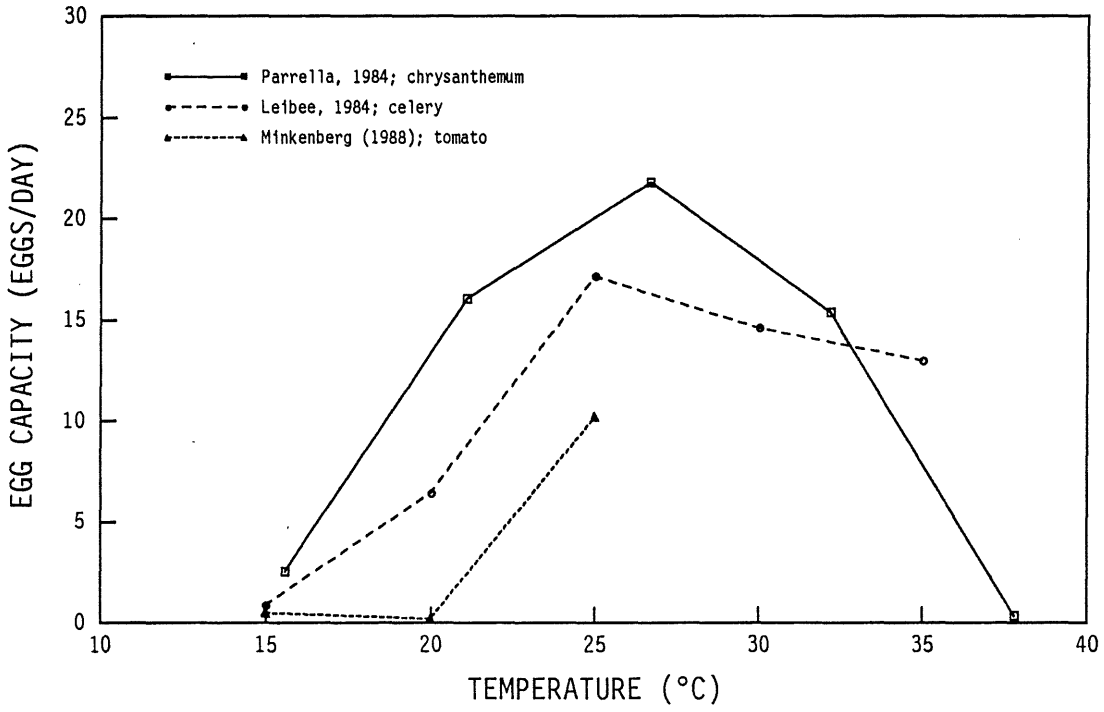


Figure 8.2: Mean fecundity per day of L.trifolii on different host plants plotted against temperature.

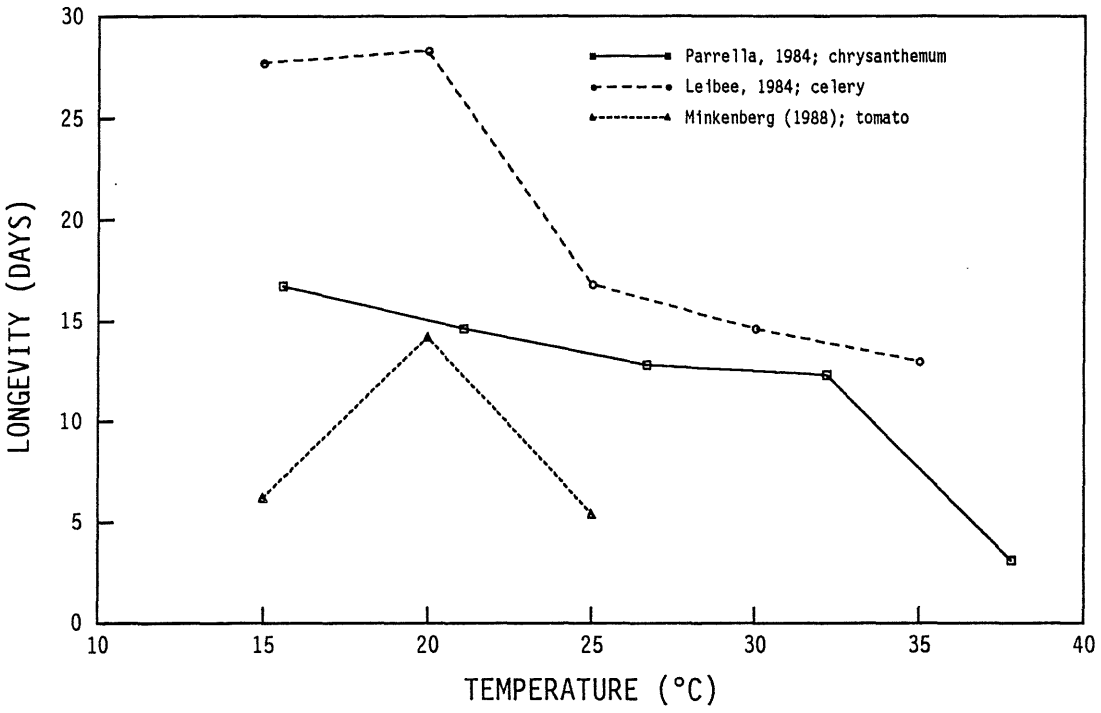


Figure 8.3: Longevity of adult stage of L.trifolii on different host plants plotted against temperature.

The parasitoid model gives no proper description of the parasitation process. Apart from the lack of a good estimation of the searching efficiency, the increase of parasitation in the 4th generation is not simulated well. The model predicts an extinction of hosts and parasitoids in a few generations. In nature intricate mechanisms are probably preventing such a strong effect. The model used is probably too simple. A number of limitations and possible errors are summarised below.

To describe the parasitation process, a 'type 2' functional response (Holling, 1959) has been supposed. The actual type of D. isaea's functional response is not known. 'Type 2' responses can describe experimental data of many examined species fairly well (Hassell et al., 1976), though v. Lenteren & Bakker (1976) have supposed that 'type 3' responses may occur more often.

After the decision to use a type 2 functional response the problem arises to estimate its parameters. A number of assumptions have been made which are known to be false actually in at least a number of documented cases. In the model parasitoids search with a constant overall searching efficiency for the 3 larval host stages. However Bal (1985) showed for D. isaea that larval stages of L. trifolii have different chances of being found, which means different searching efficiencies. The search for L1, L2 and L3 stages will not be independent, so using an overall searching efficiency is inevitable. Making searching efficiency dependent on the relative densities of the different larval stages may be a possible improvement.

It is often stated that interference between parasitoids may play an important role (Hassell, 1971; Hassell et al., 1976). Interference can arise from increasing parasitoid density. Encounters will occur more frequently and during these encounters parasitoids may show a behavioural response resulting in a decreased searching efficiency or increased handling time (in this model handling time is expressed in the maximum parasitation rate, RPARmax = 1/Th). Possibly interference is also arising from encounters between parasitoids and already parasitised hosts. The functional response may also be influenced by interactions like superparasitism, time spent on already parasitised hosts and host feeding on parasitised larvae, when parasitoid density is relatively high. In the system modeled these interrelations seem likely to arise since parasitism is very high in a few generations (Westerman & Minkenberg, 1986). Interrelations may even be intensified by aggregation of parasitoids.

The numerical response of the parasitoid is another important component of arthropod parasitation (Beddington et al., 1976). The numerical response consists of 2 major aspects: the numerical changes brought about when parasitoids aggregate in response to a clumped host distribution and the influence of the host death rate to numerical changes of the parasitoid population (Holling, 1966).

The model assumes a homogenous distribution of parasitoids and hosts. This does not hold in a greenhouse however; At least the distribution of leafminers is found to be aggregated (Frijters et al., 1986; Schuster & Beck, 1981). Aggregation of parasitoids and hosts can influence the outcomes of the model when curvilinear density dependent relationships are present (When density dependent relationships are linear the mean density can be used for calculations). The present model contains only 1 curvilinear density dependent relationship: the functional response. Effects of clumped distributions may be analysed by dividing space into patches, distributing parasitoids and leafminers over these patches and applying the model for every patch (Kroon & Driessen, 1982; Rabbinge et al., 1984).

The relationship between the host death rate and numerical changes of parasitoids is relatively simple. A parasitised host gives in general rise to a constant number of parasitoids in the next generation (Beddington et al., 1976). Several remarks can be made however.

Larval development of wasps has been supposed to be independent of the developmental stage of the host. Smaller hosts may cause an increased mortality of the parasitoid's larval stages, however. Parasitoids emerging from small hosts have a reduced size, possibly causing a lower fecundity (Charnov et al., 1981). When parasitoid numbers increase compared to the number of leafminers, a smaller percentage of the L2 larvae will reach the L3 stage, causing a decrease in mean host size. Host plant suitability may influence the suitability of the leafminer as a host (Vinson & Barbosa, 1987). During the season leaf nitrogen content will decrease (pers. comm. Sonneveld, Naaldwijk), causing a reduction of host size (Ottenheim, 1985). Host suitability will be less due to a reduction of mean host size. A decreasing parasitation rate during the season may be expected.

Sex ratio has been supposed to be 0.5. Hymenopteran parasitoids possess a haplo-diploid reproductive system. Fertilised eggs become females while unfertilised eggs become males. Sex ratio can be regulated by regulation of the fertilisation of eggs (Waage & Hassell, 1982). Sex ratio may shift towards male production by reduction of host size (Reeve, 1987; Charnov et al., 1981) or interference between parasitoids (Waage, 1982; Wylie, 1976). A change in sex ratio will have a major influence on the parasitation rate because male parasitoids have hardly any influence on the host population.

The number of parasitoids searching for hosts is possibly influenced by host density. When host density is small compared to parasitoid density interference or lack of hosts may lead to dispersal out of the greenhouse (migration). Trying to escape from unfavourable circumstances by migration is a general phenomenon in insect behaviour (Southwood, 1978b). D. isaea host

feeds on its host, in this way obtaining nutrients for production of eggs and other functions. Therefore fecundity and survival is possibly also influenced by host density (Beddington et al, 1976).

Another parameter directly influencing the numerical response is the host feeding/parasitation ratio, i.e. which part of the encounters is used for host feeding and parasitation respectively. The model supposes no difference between host feeding of L1, L2 and L3 larvae. However it is clear that the larger larvae account for a greater amount of food. D. isaea consumes host fed larvae totally (Ibrahim & Madge, 1978). The ratio will therefore not be a constant but will be varying, depending on available host stages. It may be possible to correct the host feeding/parasitation ratio for changes in available host stages by taking the weight of different host stages as a relative indication of its nutritional value.

The goal of this study has been to develop a model which predicts the population growth over 1 generation well, in order to evaluate the effectiveness of parasitoic wasps for biological control of leafminers. It can be concluded that during the generations early in the season it seems possible to make a reliable estimation of the numbers of leafminers. Applying the model later in the season is still unreliable. Relations between temperature and life history variables are rather clear. Temperature is probably not the only important forcing variable, however. Data are needed on the influence of leaf nitrogen content on L.bryoniae's life history variables. The possible role of other forcing variables has to be studied, e.g. tomatine content of the leaves or day-length.

In its present shape the parasitoid part of the model is not useful for practical applications. A lot of essential relations between host and parasitoid are unknown yet. It may not be necessary, however, to strive for a model which can simulate the development of the populations for a longer period. A model which simulates the first generations after introduction well may be used to predict optimal introduction time and numbers of parasitoids needed to control leafminer numbers. The present model may predict the initial phase well enough for these purposes. A good validation is lacking, however. If mortality due to parasitoids is high enough, growers will not be interested in intricate relationships which may become important after the initial relative simple phase, as long as the pest is kept under the economic threshold.

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Appendix 1a: Listing of the model.

```
TITLE MINPOP
*** A PARASITOID-HOST MODEL OF THE LEAFMINERS L. BRYONIAE AND L.
*** TRIFOLII AND THE PARASITOID D. ISAEA.
************************************************************
INITIAL
************************************************************

HISTORY CALCRM(20)

STORAGE Y(250)
STORAGE AFI(10),HI(10)
STORAGE AF(10),NTFL(10),REP(10),NTFLP(10),H(10)
STORAGE RENC(10),RRE(10),PRM(10)
STORAGE RMA(10),RDR(10)
STORAGE MORTA(10),MORTP(10),CUMPA(10),CUMPP(10)
STORAGE NTREP(10),NTPAR(10)
STORAGE AIRTMP(2400)

*** INITIAL CONSTANTS, TABLES AND PARAMETERS OF THE LEAFMINER
*** MODEL.

INCON STINTA=0.
INCON NOMIN=0.
INCON EGGI=0.,LAR1I=0.,LAR2I=0.,LAR3I=40.,PUPI=0.
INCON AFI0=0.

TABLE AFI(1-10)=10*0.

FIXED N1,N2,INDEX,I,II
FIXED K,M

* NUMBER OF CLASSES IN LEAFMINER DEVELOPMENT BOXCARS.

FIXED N1,N2,N3,N4,N5
PARAM N1=10
PARAM N2=5
PARAM N3=6
PARAM N4=7
PARAM N5=10

*** INITIAL CONSTANTS,TABLES AND PARAMETERS OF THE PARASITOID
*** MODEL.

INCON START=61.
INCON    LPARI=0.,HI0=0.

TABLE HI(1-10)=10*0.

PARAM INWASP=200.,NOPLA=390.,SR=0.5,B=1.

* FRACTION PARASITATION OF ENCOUNTERED LARVAE (PREFPR)

PARAM PREFPR=0.65
```

```
*** INCORPORATION OF TEMPERATURE FILE IN THE MODEL.
NOSORT
    CALL READ(AIRTMP)
SORT

TIMER FINTIM=147.,PRDEL=1.,DELT=0.1,OUTDEL=2.
METHOD RECT

**********************************************************************
DYNAMIC
**********************************************************************
* INDEX IS USED IN THE BOXCAR SUBROUTINE.

INDEX=0

*** THE ACTUAL TEMPERATURE IN TIME STEP DELT IS CALCULATED.

NOSORT
      M=TIME
      KL=TIME-M
      IF(TIME.GT.47.)THEN
          K=(TIME-47.)*24.
          TMP=AIRTMP(K)+((TIME-47.)*24.-K)*(AIRTMP(K+1.)-AIRTMP(K))
          TEMP=TMP/10.
      ELSE
          TEMP=AFGEN(TEMPT,KL)
      ENDIF
      GTMP=AMIN1(TEMP+0.9,40.)
SORT

*** THE LEAF NITROGEN LEVEL (%) IS CALCULATED.

NPERC=AFGEN(NPERCT,TIME)

*** DEVELOPMENT OF LEAFMINERS
**********************************************************************

OUTE,EGG=BOXCAR(EGGI,RESE,SDE,RME,OVIP,N1,STINTA)
OUT1,LAR1=BOXCAR(LAR1I,RES1,SD1,TRM1,OUTE,N2,STINTA)
OUT2,LAR2=BOXCAR(LAR2I,RES2,SD2,TRM2,OUT1,N3,STINTA)
OUT3,LAR3=BOXCAR(LAR3I,RES3,SD3,TRM3,OUT2,N4,STINTA)
OUTP,PUP =BOXCAR(PUPI ,RESP,SDP,RMP ,OUT3,N5,STINTA)

DVRE=AFGEN(DVRET,TEMP)
DVR1=AFGEN(DVR1T,TEMP)
DVR2=AFGEN(DVR2T,TEMP)
DVR3=AFGEN(DVR3T,TEMP)
DVRP=AFGEN(DVRPT,GTMP)
```

```
* THE RESEDENCE TIME IS CALCULATED AS THE INVERSE OF THE
* DEVELOPMENT RATE.

RESE=1./DVRE
RES1=FRES/DVR1
RES2=FRES/DVR2
RES3=FRES/DVR3
RESP=1./DVRP

FRES=AFGEN(FREST,NPERC)

SDE=AFGEN(SDET,TEMP)
SD1=AFGEN(SD1T,TEMP)
SD2=AFGEN(SD2T,TEMP)
SD3=AFGEN(SD3T,TEMP)
SDP=AFGEN(SDPT,GTMP)

RME=AFGEN(RMET,TEMP)
NIRM1=AFGEN(RM1T,TEMP)
RM1=NIRM1*FRM
NIRM2=AFGEN(RM2T,TEMP)
RM2=NIRM2*FRM
NIRM3=AFGEN(RM3T,TEMP)
RM3=NIRM3*FRM
RMP=AFGEN(RMPT,GTMP)

FRM=AFGEN(FRMT,NPERC)
* THE RELATIVE MORTALITIES DUE TO HOST FEEDING AND PARASITATION
* (RMHFL AND RMPAR) ARE CALCULATED IN A DIFFERENT SECTION.

TRM1 = AMIN1(RM1+RMHFL1,1./DELT)
TRM2 = AMIN1(RM2+RMHFL2+RMPAR2,1./DELT)
TRM3 = AMIN1(RM3+RMHFL3+RMPAR3,1./DELT)

*** SENESCENCE OF LEAFMINERS.
*****************************************************************
*** SENESCENCE OF LEAFMINERS IS SIMULATED BY A BOXCAR TRAIN
*** WITHOUT DISPERSION.

* MORTALITY IN EVERY CLASS OF FLIES.

FAVL=AFGEN(FAVLT,NPERC)
RMA,MORTA,CUMPA,NILONG=CALCRM(TEMP,CUMPT,AVLT,SIGMT,FAVL)
NOSORT
DO 50 I=1,10
    IF (RMA(I).GT.1./DELT) THEN
        RMA(I)=1./DELT
    ENDIF
50 CONTINUE
SORT
```

```
* NUMBER OF FLIES IN THE PRECLASS.

AF0=INTGRL(AFI0,FLOW0-FLOW1)
SEXR=0.5
FLOW0=OUTP*SEXR
FLOW1=AF0*AMIN1(2./(NILONG*1./10.),1./DELT)

* DEVELOPMENT IN THE CLASSES.

PUSHA=INSW(SEN-1./10.,0.,1./DELT)
RSEN=1./NILONG
SEN=INTGRL(0.,RSEN-PUSHA/10.)

* NUMBER OF FLIES IN THE CLASSES AND TOTAL NUMBER OF FLIES.

NOSORT

NTFL,FLOW11=NETFLW(AFI,FLOW1,PUSHA,AF,RMA,DELT)
AF,DUM=ARRINT(10,AFI,NTFL,DELT,TIME,STINTA)
TAF,DUM=SUMA(AF,10)


*** REPRODUCTION OF LEAFMINERS.
**********************************************************************
*** REPRODUCTION DEPENDS ON AGE AND TEMPERATURE.
* RELATIVE REPRODUCTION IN EVERY CLASS.

RRE(1)=AFGEN(RRT1,TEMP)
RRE(2)=AFGEN(RRT2,TEMP)
RRE(3)=AFGEN(RRT3,TEMP)
RRE(4)=AFGEN(RRT4,TEMP)
RRE(5)=AFGEN(RRT5,TEMP)
RRE(6)=AFGEN(RRT6,TEMP)
RRE(7)=AFGEN(RRT7,TEMP)
RRE(8)=AFGEN(RRT8,TEMP)
RRE(9)=AFGEN(RRT9,TEMP)
RRE(10)=AFGEN(RRT10,TEMP)

* REPRODUCTION IN EVERY CLASS.

FCAP=AFGEN(FCAPT,NPERC)
DO 10 I=1,10
    REP(I)=RRE(I)*AF(I)*FCAP
10 CONTINUE

SORT

* TOTAL REPRODUCTION. THE TOTAL REPRODUCTION OVER 1 DAY (OVIP)
* IS PUSHED ONCE A DAY IN STATE VARIABLE EGG.

TREP,DUM=SUMA(REP,10)
REPBUF=INTGRL(0.,TREP-OVIP)
OVIP=PUSHOV*(REPBUF/DELT +TREP)
PUSHOV=IMPULS(0.35,1.)
```

```
************************************************************
*** POPULATION DYNAMICS OF THE PARASITOID
************************************************************
NOSORT

IF (TIME.GE.START-DELT/2..AND.INWASP.GT.0.) THEN

*** DEVELOPMENT OF D.ISAEA TO THE ADULT STAGE.
************************************************************

DVRPAR = AFGEN(DVRPRT,TEMP)
RMLP = AFGEN(RMLPT,TEMP)
SDPAR = AFGEN(SDPART,TEMP)
RESLP = 1/DVRPAR
OUTPAR,LPAR=BOXCAR(LPARI,RESLP,SDPAR,RMLP,REPPAR,10,START)

*** SENESCENCE OF D.ISAEA.
************************************************************
* MORTALITY IN EVERY CLASS OF PARASITOIDS.
* NITROGEN CONTENT DOESN'T INFLUENCE D.ISAEA, FAVL = 1.)

FAVL=1.
RDR,MORTP,CUMPP,REST=CALCRM(TEMP,CUMPT,AVLTP,SIGMTP,FAVL)

* NUMBER OF PARASITOIDS IN THE PRECLASS.

FLP0  =OUTPAR*SR
    IF (TIME.GT.START-DELT/2..AND.TIME.LT.START+DELT/2.) THEN
        FLP1=INWASP/DELT
        H0=0.
    ELSE
        FLP1=H0*AMIN1(2./(REST*1./10.),1./DELT)
        H0=INTGRL(HI0,FLP0-FLP1)
    ENDIF

* DEVELOPMENT IN THE CLASSES.

RSENP   =1./REST
PUSHP   =INSW(SENP-1./10.,0.,1./DELT)
SENP    =INTGRL(0.,RSENP-PUSHP/10.)

* NUMBER OF PARSITOIDS IN EVERY CLASS AND THE TOTAL NUMBER
* OF PARASITOIDS.

NTFLP,FLWP11=NETFLW(HI,FLP1,PUSHP,H,RDR,DELT)
STINTH=START
H,DUM=ARRINT(10,HI,NTFLP,DELT,TIME,STINTH)
SUMH,DUM=SUMA(H,10)

*** PARASITATION AND HOST-FEEDING BY D.ISAEA.
************************************************************
* THE RATE OF ENCOUNTERS IS CALCULATED FOR EVERY CLASS ACCORDING
* TO A 'TYPE 2' FUNCTIONAL RESPONS.
```

```
A = AFGEN(AT,TEMP)
NOLARP=LAR1/8.+LAR2+LAR3
DENS=NOLARP/NOPLA

PRM(1)=AFGEN(PRMT1,TEMP)
PRM(2)=AFGEN(PRMT2,TEMP)
PRM(3)=AFGEN(PRMT3,TEMP)
PRM(4)=AFGEN(PRMT4,TEMP)
PRM(5)=AFGEN(PRMT5,TEMP)
PRM(6)=AFGEN(PRMT6,TEMP)
PRM(7)=AFGEN(PRMT7,TEMP)
PRM(8)=AFGEN(PRMT8,TEMP)
PRM(9)=AFGEN(PRMT9,TEMP)
PRM(10)=AFGEN(PRMT10,TEMP)

RENC,DUM=ENCOUN(PRM,A,DENS,H)

* TOTAL RATE OF ENCOUNTERS. IN THE NEXT PART OF THE MODEL THIS
* RATE WILL BE DISTRIBUTED OVER HOST FEEDING AND PARASITISM.

TRENC,DUM=SUMA(RENC,10)

* CALCULATION OF MORTALITY FACTOR OF LAR1 DUE TO PARASITOIDS.

    IF (LAR1.GT.1.) THEN
        RMHFL1=TRENC/(8*NOLARP)
    ELSE
        RMHFL1=0.
    ENDIF

* CALCULATION OF THE FRACTION OF ENCOUNTERS WITH LAR2,3 WHICH
* RESULT IN PARASITATION.

F1=PREFPR*(LAR1/8+LAR2+LAR3)/(LAR2+LAR3+0.1)

    IF (F1.GT.1.) THEN
        FACT=1.
    ELSE
        FACT=F1
    ENDIF

* CALCULATION OF MORTALITY FACTORS OF LAR2 DUE TO PARASITOIDS.

    IF (LAR2.GT.1.) THEN
        RMHFL2=(1-FACT)*TRENC/NOLARP
        RMPAR2=FACT*TRENC/NOLARP
    ELSE
        RMPAR2=0.
        RMHFL2=0.
    ENDIF
```

```
* CALCULATION OF MORTALITY FACTORS OF LAR3 DUE TO PARASITOIDS

    IF (LAR3.GT.1.) THEN
        RMHFL3=(1-FACT)*TRENC/NOLARP
        RMPAR3=FACT*TRENC/NOLARP
    ELSE
        RMHFL3=0.
        RMPAR3=0.
    ENDIF



* TOTAL RATES OF PARASITATION AND HOSTFEEDING.

TRHF=RMHFL1*LAR1+RMHFL2*LAR2+RMHFL3*LAR3
TRPAR=RMPAR2*LAR2+RMPAR3*LAR3
REPPAR=TRPAR*B

THF=INTGRL(0.,TRHF)
TPR=INTGRL(0.,TRPAR)
ENDIF

***********************************************************************
*** OUTPUT FACILITIES.
***********************************************************************
* NUMBER OF PUPATIONS A DAY.

    IF ((KL.GT.DELT/2.).AND.(KL.LT.3.*DELT/2.)) THEN
        NOPUPI=OUT3*DELT
        NOPUP=0.
    ELSE
        NOPUP=INTGRL(NOPUPI,OUT3)
    ENDIF

* TOTAL NUMBER OF MINES.

NOMIN=INTGRL(NOMINI,OUTE)

* LOGARITHMIC VALUES OF INTERESTING PARAMETERS ARE CALCULATED.

LOGMIN=ALOG10(NOMIN+1.)
LGNPUP=ALOG10(NOPUP+1.)
LOGEGG=ALOG10(EGG+1.)
LOGPUP=ALOG10(PUP+1.)
LOGPAR=ALOG10(SUMH+1.)
LOGTHF=ALOG10(THF+1.)
LOGTPR=ALOG10(TPR+1.)
LOGL1=ALOG10(LAR1+1.)
LOGL2=ALOG10(LAR2+1.)
LOGL3=ALOG10(LAR3+1.)
LOGLPR=ALOG10(LPAR+1.)
SORT
```

```
*****************************************************************
*** FUNCTION STATEMENTS.
*****************************************************************
* FUNCTION STATEMENTS CONCERNING L. BRYONIAE.

FUNCTION DVRET=5.,0.01, 6.5,0.01,40.,0.64
FUNCTION DVR1T=5.,0.01,11.6,0.01,40.,1.49
FUNCTION DVR2T=5.,0.01, 6.7,0.01,40.,1.00
FUNCTION DVR3T=5.,0.01, 7.0,0.01,40.,0.92
FUNCTION DVRPT=4.,0.01,5.,0.01, 8.2,0.01,40.,.202

FUNCTION SDET=5.,2.,15.,0.48,20.,.17,25.,.28,40.,.1
FUNCTION SD1T=5.,2.,15.,1.02,20.,.39,25.,.19,40.,.1
FUNCTION SD2T=5.,2.,15.,0.68,20.,.43,25.,.20,40.,.1
FUNCTION SD3T=5.,2.,15.,0.76,20.,.44,25.,.20,40.,.1
FUNCTION SDPT=4.,2.,5.,2.,15.,0.66,20.,.41,25.,.40,40.,.1

FUNCTION RMET=5.,0.,40.,0.
FUNCTION RM1T=5.,0.5,15.,.202,20.,.009,25.,.020,40.,.10
FUNCTION RM2T=5.,0.3,15.,.060,20.,.012,25.,.081,40.,.40
FUNCTION RM3T=5.,.05,15.,.009,20.,.012,25.,.028,40.,.15
FUNCTION RMPT=4.,.02,5.,.02,15.,.017,20.,.021,25.,.020,40.,.02

FUNCTION AVLT=5.,20.,10.,20.,15.,16.8,20.,9.1,25.,7.3,30.,2.,40.,0.1
FUNCTION SIGMT=5.,7.,15.,6.7,20.,6.2,25.,3.5,30.,1.,40.,0.05


FUNCTION RRT1= 0.,0.,8.,0.,15., 1.8,20., 3.3,25.,20.3,30., 0.0,50., 0.0
FUNCTION RRT2= 0.,0.,8.,0.,15.,13.0,20.,24.5,25.,35.9,30.,13.8,50.,13.8
FUNCTION RRT3= 0.,0.,8.,0.,15.,11.8,20.,26.5,25.,41.0,30.,27.1,50.,27.1
FUNCTION RRT4= 0.,0.,8.,0.,15., 6.1,20.,18.7,25.,33.3,30.,40.0,50.,40.0
FUNCTION RRT5= 0.,0.,8.,0.,15., 4.0,20.,14.0,25.,24.8,30.,46.9,50.,46.9
FUNCTION RRT6= 0.,0.,8.,0.,15., 3.0,20.,10.4,25.,18.3,30.,48.3,50.,48.3
FUNCTION RRT7= 0.,0.,8.,0.,15., 1.8,20., 6.5,25.,12.4,30.,44.9,50.,44.9
FUNCTION RRT8= 0.,0.,8.,0.,15., 0.5,20., 3.4,25., 6.3,30.,37.1,50.,37.1
FUNCTION RRT9= 0.,0.,8.,0.,15., 0.0,20., 1.0,25., 1.4,30.,33.1,50.,33.1
FUNCTION RRT10=0.,0.,8.,0.,15., 0.0,20., 0.0,25., 0.0,30.,31.8,50.,31.8

* INTRODUCED FACTORS BY BUILDING LEAF NITROGEN IN THE MODEL
* AS A FORCING VARIABLE.

FUNCTION FREST=2.,1.24,3.,1.23,4.,1.2,5.,1.09,6.,1.,8.,0.89
FUNCTION FRMT=2.,3.05,3.4,2.75,5.2,1.,8.,1.
FUNCTION FAVLT=2.,.27,5.7,1.,8.,1.
FUNCTION FCAPT=2.,0.5,6.,1.,8.,1.

* GENERAL FUNCTION STATEMENTS.

FUNCTION TEMPT=0.0,15.7,0.30,15.7,0.55,22.7,0.70,15.7,1.0,15.7
*FUNCTION TEMPT=0.,20.,0.1,5.,0.2,35.,.3,40.,.4,10.
FUNCTION NPERCT=0.,6.,75.,6.,75.1,4.,150.,4.
```

```
FUNCTION CUMPT=-9999., 1.,   -3.5,.9998,  -2.3,.99,  -1.88,.97,...
               -1.65,.05,  -1.28,.9   , -1.04,.85,  -0.84,.8 ,...
               -0.67,.75,  -0.52,.7   , -0.39,.65,  -0.25,.6 ,...
               -0.13,.55,    0.,.5    ,  0.13,.45,   0.25,.4 ,...
                0.39,.35,   0.52,.3   ,  0.67,.25,   0.84,.2 ,...
                1.04,.15,   1.28,.1   ,  1.65,.05,   1.88,.03,...
                2.30,.01,   3.50,.0002, 9999.,0.

* FUNCTION STATEMENTS CONCERNING PARASITOIDS.

FUNCTION DVRPRT=5.,0.001,8.9,0.001,40.,0.179

FUNCTION SDPART=5.,2.3,10.,2.3,15.,1.4,20.,0.60,25.,0.74,40.,0.7

FUNCTION RMLPT=5.,0.04,15.,0.03,20.,0.012,25.,0.025,40.,0.05

FUNCTION AVLTP= 5.,2.,15.,23.7,20.,35.9,25.,9.5,35.,1.,40.,1.
FUNCTION SIGMTP=5.,1.,15.,11.2,20., 7.3,25.,8.4,35.,.5,40.,.5

FUNCTION AT =0.,0.2,100.,0.2

FUNCTION PRMT1 =0.,0.,8.,0.,10.,1.2,15., 2.0, 20., 2.0,...
               25., 4.1,30., 4.1,40., 4.1
FUNCTION PRMT2 =0.,0.,8.,0.,10.,6.4,15.,15.0, 20.,15.0,...
               25.,24.6,30.,25.7,50.,25.7
FUNCTION PRMT3 =0.,0.,8.,0.,10.,8.2,15.,19.6, 20.,20.2,...
               25.,32.0,30.,34.9,50.,34.9
FUNCTION PRMT4 =0.,0.,8.,0.,10.,5.6,15.,14.6, 20.,15.7,...
               25.,27.9,30.,30.7,50.,30.7
FUNCTION PRMT5 =0.,0.,8.,0.,10.,3.2,15., 9.6, 20.,10.6,...
               25.,23.2,30.,26.0,50.,26.0
FUNCTION PRMT6 =0.,0.,8.,0.,10.,1.6,15., 5.7, 20., 6.5,...
               25.,18.7,30.,21.3,50.,21.3
FUNCTION PRMT7 =0.,0.,8.,0.,10.,0.6,15., 2.8, 20., 4.2,...
               25.,14.5,30.,16.6,50.,16.6
FUNCTION PRMT8 =0.,0.,8.,0.,10.,0.1,15., 0.6, 20.,3.0,...
               25.,10.2,30.,11.9,40.,11.9
FUNCTION PRMT9 =0.,0.,8.,0.,10.,0.0,15., 0.0, 20., 2.0,...
               25., 6.0,30., 7.2,50., 7.2
FUNCTION PRMT10=0.,0.,8.,0.,10.,0.0,15., 0.0, 20., 1.3,...
               25., 2.0,30., 2.8,50., 2.8


*****************************************************************
OUTPUT ...
PRINT ...
*****************************************************************

END
STOP
```

```
C*****************************************************************
C SUBROUTINE READ
C*****************************************************************
      SUBROUTINE READ(AIRTMP)
      IMPLICIT REAL(A-Z)
      INTEGER I
      DIMENSION  AIRTMP(2400)

      OPEN (UNIT=21,FILE='AIRTMP.DAT')

      I=0
10    FORMAT(4F)
5     READ(21,*,END=20) X1,X2,X3,X4
      AIRTMP(I)=X4
      I=I+1
      GOTO 5

20    CONTINUE
      CLOSE(UNIT=21)
      RETURN
      END

C*****************************************************************
C SUBROUTINE BOXCAR; BOXCAR, A SUBROUTINE TO SIMULATE DISPERSION,
C WAS DEVELOPED BY DE WIT AND GOUDRIAAN (1978).
C*****************************************************************
      SUBROUTINE BOXCAR(TOTALI,RT,SD,RM,RIN,N,STARTB,OUT,TOTAL)
COMMON

C     INITIALISATION
      IF (TIME.GT.STARTB+DELT/2.) GO TO 1

C     DEVELOPMENT STAGE
      Y(INDEX+1)=0.5

C     PRECLASS
      Y(INDEX+2)=TOTALI
C     N CLASSES
      DO 2 II=1,N
    2 Y(II+INDEX+2)=0.

    1 INDEX=INDEX+1
      PUSH =1.
C     TEST FOR DEVELOPMENT STAGE
      IF (Y(INDEX).LT.1.) PUSH=0.
      F    =1.-N*(SD/RT)**2.
      IF(F.GT.N*DELT/RT) GO TO 5
      WRITE(6,800)
  800 FORMAT(' NUMBER OF CLASSES TOO LARGE: F TOO SMALL OR NEGATIVE')
      CALL EXIT
    5 CONTINUE
C     INTEGRATION OF RATE OF DEVELOPMENT
      Y(INDEX)=Y(INDEX)+N*DELT/(RT*F)-PUSH
      INDEX=INDEX+1
      TOTAL=Y(INDEX)
```

```
      FL =2.*TOTAL*(1.-RM*DELT)*N/(RT*F)
C     INTEGRATION OF PRECLASS
      Y(INDEX)=TOTAL+(RIN-TOTAL*RM-FL)*DELT
      IF (Y(INDEX).GE.0.) GO TO 3
      FL =FL+Y(INDEX)/DELT
      Y(INDEX)=0.
    3 PUSH =PUSH*(1./DELT-RM)*F
        DO 4 II=1,N
        INDEX=INDEX+1
        OUT  =Y(INDEX)*PUSH
        TOTAL=TOTAL+Y(INDEX)
        FLN   =FL-Y(INDEX)*RM-OUT
        IF (ABS(FLN).LT.1.E-35) GO TO 4
C     INTEGRATION OF CLASS
        Y(INDEX)=Y(INDEX)+FLN*DELT
    4   FL =OUT
      RETURN
      END

C*************************************************************
C SUBROUTINE NETFLOW; NETFLOW CALCULATES THE RATE OF CHANGE
C BETWEEN CLASSES OF LEAFMINER AND PARASITOID ADULTS.
C*************************************************************
      SUBROUTINE NETFLW(AFI,FLOW1,PUSHA,AF,RMA,DELT,NTFL,FLOW11)
      IMPLICIT REAL (A-Z)
      INTEGER I
      DIMENSION AFI(10),AF(10),RMA(10),NTFL(10),FLOW(11)

      DO 10 I=1,10
          FLOW(1)=FLOW1
          FLOW(I+1)=PUSHA*(AF(I)-RMA(I)*AF(I)*DELT)
          NTFL(I)=FLOW(I)-FLOW(I+1)-AF(I)*RMA(I)
10    CONTINUE
      FLOW11=FLOW(11)
      RETURN
      END

C*************************************************************
C SUBROUTINE CALCRM; CALCRM CALCULATES THE RELATIVE MORTALITIES
C PER CLASS OF LEAFMINER AND PARASITOID ADULTS.
C*************************************************************
      SUBROUTINE CALCRM(NLOC,TEMP,CUMPT,AVLT,SIGMT,FAVL,RMA,
     $MORT,CUMP,NILONG)
      IMPLICIT REAL (A-Z)
      INTEGER NLOC,I
      DIMENSION RMA(10),MORT(10),A(10),Q(10),CUMP(10)

      NIAVL=AFGEN(NLOC,AVLT,TEMP)
      AVL=NIAVL*FAVL
      NISIGM=AFGEN(NLOC+5,SIGMT,TEMP)
      NILONG=NIAVL+3.*NISIGM

      SIGMA=NISIGM*FAVL
```

```
      MU=AVL/NILONG
      SIGML=SIGMA/NILONG

      DO 100 I=1,10

          A(I)=((2.*3.1416)**-.5)/SIGMA
          MORT(I)=A(I)*EXP(-.5*(((I-0.5)/10.-MU)/SIGML)**2.)

          Q(I)=((I-0.5)/10.-MU)/SIGML

          CUMP(I)=AFGEN(NLOC+15,CUMPT,Q(I))

          RMA(I)=MORT(I)/CUMP(I)
100   CONTINUE

      RETURN
      END


C*****************************************************************
C SUBROUTINE ENCOUN; ENCOUN CALCULATES THE ENCOUNTER RATE
C PER CLASS OF PARASITOID ADULTS.
C*****************************************************************
      SUBROUTINE ENCOUN(PRM,A,DENS,H,RENC,DUM)
      IMPLICIT REAL (A-Z)
      INTEGER I
      DIMENSION PRM(10),RER(10),RENC(10)
      DIMENSION H(10)

      DO 10 I=1,10
          IF (PRM(I).LT.0.1) THEN
              RENC(I)=0.
          ELSE

              RER(I)=((A*DENS*PRM(I)*5/4)/(A*DENS+PRM(I)*5/4))
              RENC(I)=RER(I)*H(I)

          ENDIF
10    CONTINUE

      RETURN
      END

C*****************************************************************
C SUBROUTINE SUMA; SUMA SUMMARATES ARRAY ELEMENTS.
C*****************************************************************
      SUBROUTINE SUMA(ARR,N,SUM,DUM)

      IMPLICIT REAL (A-Z)
      INTEGER I,N
      DIMENSION ARR(N)

      SUM=0.
```

```
      DO 10 I=1,N
          SUM=SUM+ARR(I)
10    CONTINUE
      RETURN
      END

C*************************************************************
C SUBROUTINE ARRINT;ARRINT INTEGRATES THE ARRAY:
C Y(I)=INTGRL(YI(I),X(I)) WITH METHOD RECT.
C*************************************************************
      SUBROUTINE ARRINT(N,YI,X,DELT,TIME,STINT,Y,DUM)
      IMPLICIT REAL (A-Z)
      INTEGER N
      DIMENSION Y(N),YI(N),X(N)

      DO 10 I=1,N
          IF (TIME.EQ.STINT) THEN
              Y(I)=YI(I) + X(I)*DELT
          END IF
          IF (TIME.GT.STINT) THEN
               Y(I)=Y(I)+X(I)*DELT
          END IF
10    CONTINUE
      RETURN
      END


ENDJOB
```

Appendix 1b: Listing of L. trifolii specific function statements.

```
FUNCTION DVRET=5.,0.01,5.7,0.01,50.,1.01
FUNCTION DVR1T=5.,0.01,9.2,0.01,50.,2.25
FUNCTION DVR2T=5.,0.01,8.8,0.01,50.,2.10
FUNCTION DVR3T=4.,0.01,4.8,0.01,50.,1.39
FUNCTION DVRPT=5.,0.01,9.5,0.01,50.,0.37

FUNCTION SDET=5.,0.5,15.,0.2,20.,0.1,25.,0.1,40.,0.1
FUNCTION SD1T=5.,0.9,15.,0.6,20.,0.5,25.,0.2,40.,0.1
FUNCTION SD2T=5.,1.2,15.,0.9,20.,0.4,25.,0.3,40.,0.2
FUNCTION SD3T=5.,0.9,15.,0.5,20.,0.6,25.,0.6,40.,0.3
FUNCTION SDPT=5.,1.2,15.,0.9,20.,0.8,25.,0.4,40.,0.2

FUNCTION RMET=5.,0.00,15.,0.00,20.,0.00,25.,0.00,40.,0.00
FUNCTION RM1T=5.,0.30,15.,0.18,20.,0.09,25.,0.14,40.,0.24
FUNCTION RM2T=5.,0.18,15.,0.09,20.,0.05,25.,0.15,40.,0.28
FUNCTION RM3T=5.,0.11,15.,0.00,20.,0.00,25.,0.05,40.,0.12
FUNCTION RMPT=5.,0.05,15.,0.00,20.,0.01,25.,0.02,40.,0.07

FUNCTION AVLT= 5.,2.,10.,2.,15.,5.5,20.,13.6,25.,4.8,30.,2.,40.,0.1
FUNCTION SIGMT=5.,1.,10.,1.,15.,2.5,20., 8.3,25.,3.4,30.,1.,40.,0.05

FUNCTION FREST=2.,1.24,3.,1.23,4.,1.2,5.,1.09,6.,1.,8.,1.
FUNCTION FRMT =2.0,2.3,3.4,1.93,4.1,1.,5.2,.116,8.0,.116
FUNCTION FCAPT=2.,.5,6.,1.,8.,1.
FUNCTION FAVLT=2.,.27,5.7,1.,8.,1.

FUNCTION  RRT1=5.,0.,13.,0.,15.,0.1,20., 5.8,25., 0.7,30., 0.0,40., 0.0
FUNCTION  RRT2=5.,0.,13.,0.,15.,0.7,20.,10.2,25., 9.3,30., 0.6,40., 0.6
FUNCTION  RRT3=5.,0.,13.,0.,15.,1.1,20., 7.3,25.,14.0,30., 4.1,40., 4.1
FUNCTION  RRT4=5.,0.,13.,0.,15.,1.2,20., 5.0,25.,14.4,30., 6.9,40., 6.9
FUNCTION  RRT5=5.,0.,13.,0.,15.,1.1,20., 3.0,25., 9.6,30.,10.6,40.,10.6
FUNCTION  RRT6=5.,0.,13.,0.,15.,0.8,20., 1.1,25., 8.6,30.,12.3,40.,12.3
FUNCTION  RRT7=5.,0.,13.,0.,15.,0.6,20., 0.0,25., 7.3,30.,13.9,40.,13.9
FUNCTION  RRT8=5.,0.,13.,0.,15.,0.4,20., 0.0,25., 6.4,30.,14.7,40.,14.7
FUNCTION  RRT9=5.,0.,13.,0.,15.,0.2,20., 0.0,25., 5.5,30.,16.4,40.,16.4
FUNCTION RRT10=5.,0.,13.,0.,15.,0.1,20., 0.0,25., 4.7,30.,16.4,40.,16.4
```

Appendix 2: Listing of variables.

Variable		Dimension
AF	: Number of adult flies per class (array)	flies
AF0	: Number of adult flies in the preclass	flies
AFI	: Initial AF (array)	flies
AFI0	: Initial AF0	flies
AIRTMP	: Air temperature (array)	°C*10
ARR	: Array (array); From subroutine SUMA	
ARRINT	: Subroutine for integration of arrays	
AT	: Tabulated searching efficiency, dependent on temperature	plant/day
AVL	: Average longevity; From subroutine CALCRM	days
AVLT	: Tabulated AVL of flies, dependent on temperature	days
AVLTP	: Tabulated AVL of wasps, dependent on temperature	days
BOXCAR	: Subroutine for simulating dispersion	
CALCRM	: Subroutine for calculating relative mortalities per class	
CLWDTH	: Class width	days
CUMP	: Cumulative mortality per class (array); From subroutine CALCRM	(-)
CUMPA	: Cumulative fly mortality per class (array)	(-)
CUMPP	: Cumulative wasp mortality per class (array)	(-)
CUMPT	: Tabulated CUMP, dependent on Q	(-)
DELT	: Time step of integration	days
DENS	: Density of leafminer larvae suitable for wasps	larvae /plant
DUM	: Dummy variable	
DVR1	: Development rate of LAR1	1/day
DVR1T	: Tabulated DVR1, dependent on temperature	1/day
DVR2	: Development of LAR2	1/day
DVR2T	: Tabulated DVR2, dependent on temperature	1/day
DVR3	: Development rate of LAR3	1/day
DVR3T	: Tabulated DVR3, dependent on temperature	1/day
DVRE	: Development rate of EGG	1/day
DVRET	: Tabulated DVRE, dependent on temperature	1/day
DVRP	: Development rate of PUP	1/day
DVRPAR	: Development rate of LPAR	1/day
DVRPRT	: Tabulated DVRPAR, dependent on temperature	1/day
DVRPT	: Tabulated DVRP, dependent on temperature	1/day
EGG	: Number of leafminer eggs	eggs
EGGI	: Initial EGG	eggs
ENCOUN	: Subroutine for calculation of the rate of encounters	
F1	: Helper variable for calculating FACT	(-)
FACT	: Preferred fraction of parasitation	(-)
FAVL	: Factor to adjust average longevity	(-)
FAVLT	: Tabulated FAVL, dependent on leaf nitrogen	(-)
FCAP	: Factor to adjust reproduction	(-)
FCAPT	: Tabulated FCAP, dependent on leaf nitrogen	(-)
FL	: Variable from BOXCAR	

FLN	: Variable from BOXCAR	
FLOW	: Flow between classes; From NETFLW (array)	number/day
FLOW0	: Flow into the preclass for flies	flies/day
FLOW1	: Flow into the first class of flies	flies/day
FLOW11	: Flow out of the last class of flies	flies/day
FLP0	: Flow into the preclass for wasps	wasps/day
FLP1	: Flow into the first class of wasps	wasps/day
FLWP11	: Flow out of the last class of wasps	wasps/day
FRES	: Factor to adjust residence time in leafminer larval stages	(-)
FREST	: Tabulated FRES, dependent on leaf nitrogen	(-)
FRM	: Factor to adjust relative mortality in leafminer larval stages	(-)
FRMT	: Tabulated FRMT, dependent on leaf nitrogen	(-)
GTMP	: Soil temperature	°C
H	: Number of wasps per class (array)	wasps
H0	: Number of wasps in the preclass	wasps
HI	: Initial H	wasps
HI0	: Initial H0	wasps
II	: Variable from BOXCAR	
INDEX	: Helper variable for BOXCAR	(-)
INWASP	: Number of introduced wasps	wasps
KL	: Decimal part of time	days
LAR1	: Number of L1 larvae	larvae
LAR1I	: Initial LAR1	larvae
LAR2	: Number of L2 larvae	larvae
LAR2I	: Initial LAR2	larvae
LAR3	: Number of L3 larvae	larvae
LAR3I	: Initial LAR3	larvae
LGNPUP	: Logarithm of NOPUP	log(pupae)
LOGEGG	: Logarithm of EGG	log(eggs)
LOGMIN	: Logarithm of NOMIN	log(mines)
LOGPAR	: Logarithm of SUMH	log(wasps)
LOGPUP	: Logarithm of PUP	log(pupae)
LPAR	: Number of undeveloped wasps	und. wasps
LPARI	: Initial number of LPAR	und. wasps
M	: Integer part of time	days
MORT	: Mortality rate; From CALCRM (array)	number/day
MORTA	: Mortality rate of flies per class (array)	flies/day
MORTP	: Mortality rate of wasps per class (array)	wasps/day
MU	: Variable from CALCRM	phys. time
N1-5	: Number of classes	(-)
NETFLW	: Subroutine to calculate flow rates between classes	
NIAVL	: AVL when N=6%	days
NILONG	: Longevity when N=6%	days
NIRM1	: RM1 when N=6%	1/day
NIRM2	: RM2 when N=6%	1/day
NIRM3	: RM3 when N=6%	1/day
NISIGM	: SIGMA when N=6%	days
NLOC	: Helper variable when AFGEN statement is used in subroutines	(-)
NOLARP	: Cumulative number of undeveloped wasps	und. wasps
NOMIN	: Cumulative number of mines	mines
NOMINI	: Initial NOMIN	mines

NOPLA	: Number of plants	plants
NOPUP	: Cumulative number of pupae	pupae
NOPUPI	: Initial NOPUP	pupae
NPERC	: Leaf nitrogen content %	(-)
NPERCT	: Tabulated NPERC, dependent on time	(-)
NTFL	: Netto flow into classes of flies (array)	flies/day
NTFLP	: Netto flow into classes of wasps (array)	wasps/day
NTREP	: Netto reproduction per class (array)	eggs /female
OUT	: Variable from BOXCAR	
OUT1	: Flow out of LAR1	larvae/day
OUT2	: Flow out of LAR2	larvae/day
OUT3	: Flow out of LAR3	pupae/day
OUTE	: Flow out of EGG	larvae/day
OUTP	: Flow out of PUP	flies/day
OUTPAR	: Flow out of LPAR	wasps/day
OVIP	: Flow into EGG	eggs
PREFPR	: Fraction of encounters used for parasitation	(-)
PRM	: Maximum parasitation rate (array)	larvae /day*wasp
PRMT	: Tabulated PRM, dependent on temperature	larvae /day*wasp
PUP	: Number of pupae	pupae
PUPI	: Initial PUP	pupae
PUSHA	: Variable to push flies to the next class	(-)
PUSHOV	: Variable to push reproduction in EGG	(-)
PUSHP	: Variable to push wasps to the next class	(-)
RDR	: Relative death rate of wasps per class (array)	1/day
READ	: Subroutine to read temperature file	
RENC	: Rate of successful encounters per class (array)	larvae/day
REP	: Reproduction rate per class (array)	eggs/day
REPBUF	: Helper variable summarising reproduction per day	eggs
REPPAR	: Reproduction of wasps	und. wasps /day
RER	: Relative rate of encounters per class (array)	larvae /day*wasp
RES1	: Residence time in LAR1	days
RES2	: Residence time in LAR2	days
RES3	: Residence time in LAR3	days
RESE	: Residence time in EGG	days
RESLP	: Residence time in LPAR	days
RESP	: Residence time in PUP	days
REST	: Longevity of wasps	days
RIN	: Variable from BOXCAR	
RM	: Variable from BOXCAR	
RM1	: Relative mortality of L1	1/day
RM1T	: Tabulated RM1, dependent on temperature	1/day
RM2	: Relative mortality of L2	1/day
RM2T	: Tabulated RM2, dependent on temperature	1/day
RM3	: Relative mortality of L3	1/day
RM3T	: Tabulated RM3, dependent on temperature	1/day
RMA	: Relative mortality of flies per class (array)	1/day
RME	: Relative mortality of eggs	1/day
RMET	: Tabulated RME, dependent on temperature	1/day