3.4 Population models for fruit-tree red spiter mite and predatory mites

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3.4.1 Introduction

This Section describes a basic model for simulating the population dynamics of the harmful fruit-tree red spider mite, *Panonychus ulmi* (Koch), and one of its natural enemies, the predatory mite *Amblyseius potentillae*. The model, its results and evaluation are briefly presented; a more detailed description of the model, its construction and parameter values, verification and evaluation are given in another monograph in this series (Rabbinge, 1976).

The fruit-tree red spider mite belongs to the family Tetranychidae, a subgroup of the class of Acarina. The members of this vast family are found almost all over the world and cause damage in several types of plants. The fruit-tree red spider mite is one of the most harmful organisms in deciduous orchards, and its control is the major task of the fruit grower. In the last twenty years or so, the mites have become increasingly resistant to the various biocides, so the development of other control techniques has been stimulated. Biological control is an attractive alternative. It is already being practised in several places, and field experiments on the release of predatory mites have proved to be succesful.

3.4.2 Fruit-tree red spiter mite

Figure 37 shows the life cycle of the fruit-tree red spider mite. The mites develop from eggs through several juvenile stages into adults. The female adults deposit their eggs on leaves and a new generation starts; there may be up to six generations a year. Due to a combination of daylength, average daily temperature and food quality, some juveniles may develop into the 'winter form' which oviposit in sheltered places on branches and twigs, but are otherwise indistinguishable from the 'summer form'. (The transition to the winter form, which is partly reversible, is a complicated process and is not discussed here.) Their eggs, winter eggs, have a thicker scale and are redder than the summer eggs. The winter eggs do not hatch until after the winter.

To mimic dispersion in hatching, development classes of the eggs are distinguished. The number of classes and the method of simulation depend on the relative dispersion at different temperatures (see Section 2.2). The start of the hatching process is induced by a combination of external variables: length of cold period, daylength and temperature. Some mites die during the hatching process; their relative mortality rate depends on temperature.

The eggs hatch into juveniles which moult several times during their development into adults. During each juvenile stage, different development classes can

ADULT
FEMALE "SUMMER"

ADULT
MALE "SUMMER"

ADULT
MALE "WINTER"

ADULT
FEMALE "WINTER"

JUVENILES
"SUMMER"
(DEUTONYMPH
TELEIOCHRYSALIS)

JUVENILES
"WINTER"

JUVENILES
LARVA
PROTOCHRYSALIS
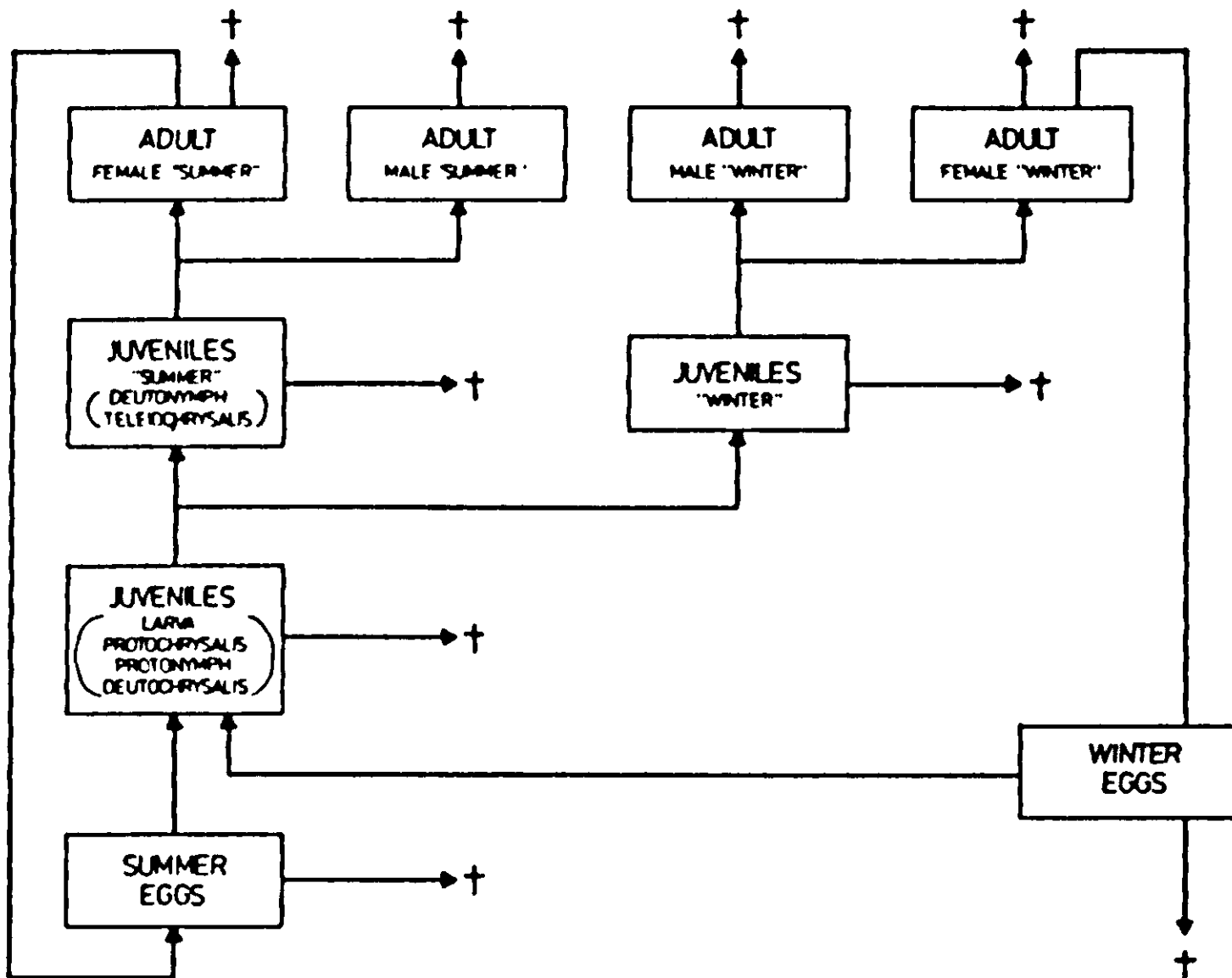PROTONYMPH
DEUTOCHRYSALIS

WINTER
EGGS

SUMMER
EGGS

Figure 37. Life cycle of fruit-tree red spider mite (*Panonychus ulmi* Koch), symbols are not in Forrester notation. (Source: Rabbinge, 1976).

be distinguished. A relational diagram for the development of *P. ulmi* during the juvenile phase from larva to deutonymph is given in Figure 38. This part of the juvenile phase is distinguished, and treated separately because the winter form is induced only in the later juvenile stages. Table 9 gives the length of the development period and its dispersion for the juvenile stages (J and JS) and for winter eggs (EGG), in relation to temperature.

Exercise 47
Calculate the number of classes required to mimic the dispersion of stages EGG, J and JS using a boxcar train with constant relative dispersion (see Section 2.2). Why can this method be used only when the temperature is constant? Which method must be used when the temperature varies? Write a simulation program for the hatching process of winter eggs, assuming an initial quantity of 1000 and a daily sinusoidal temperature fluctuation between 15°C and 30°C. Mortality during this development process may be neglected. Calculate the relative rate of mortality in the juvenile stage for a constant temperature of 30°C, if the experimental results on mortality show that at this temperature, 50% of the juveniles die during their development from egg to deutonymph.
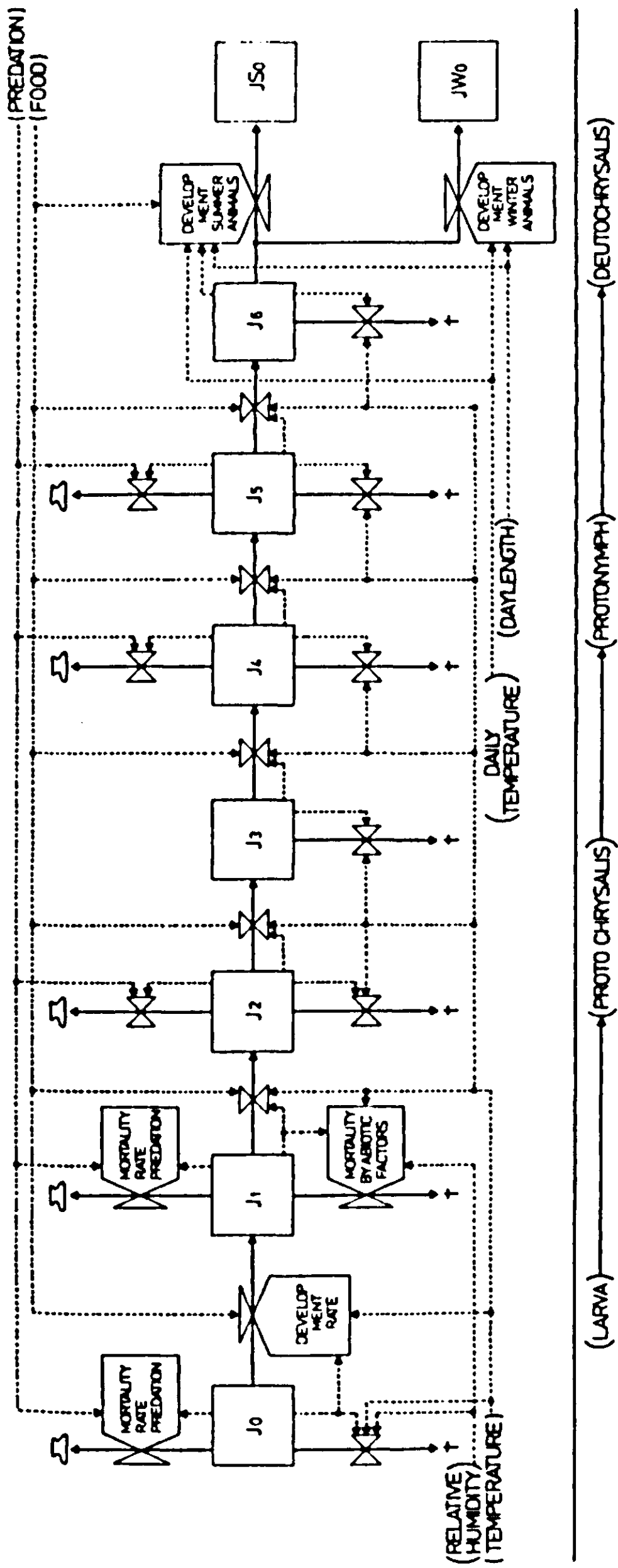
Figure 38. Growth and development of the juvenile stages of the fruit-tree red spider mite *P. ulmi* (larva, protochrysalis, protonymph, deutochrysalis). (Source: Rabbinge, 1976).

Table 9. Duration (x) of different development stages of fruit-tree red spider mite in days at various temperatures with standard deviation (s(x)).

| | Temperature | | | | | | | |
| | 15°C | | 18°C | | 25°C | | 30°C | |
	x	s(x)	x	s(x)	x	s(x)	x	s(x)
Egg	18.0	3.0	10.0	1.6	6.3	1.06	5.0	1.25
J	10.1	2.0	6.5	1.3	4.0	0.8	2.5	0.62 ♂
JS	5.5	1.1	4.3	0.85	2.4	0.6	2.0	0.5

J = Juveniles insensitive to diapause-inducing conditions (larva, protochrysales, proto-nymph, deutochrysales).

JS = Juveniles Sensitive to diapause-inducing conditions (deutonymph, teleiochrysales).

Development of both eggs and juveniles is simulated by the BOXCAR subroutine developed by Goudriaan & van Roermund (Section 2.2). This subroutine is added at the end of a program and then called upon in the program by inserting the statement:

A0,A,ATOT,MORFL,OUTFL,GAMMA,GCYCL = ...
BOXCAR(1,AI,DEVR,RD,RMR,INFL,N,DELT,TIME)

In this statement the variables A0 to GCYCL express the output of the subroutine, OUTFL is the rate of outflow of the last integral of the train and ATOT the sum of the contents of the integrals in the train with initial value AI. The variable RD (relative dispersion) is the standard deviation divided by the total residence time (development period) and RMR is the relative rate of mortality during this development period. INFL is the rate of flow into the first boxcar and N the number of boxcars in the train.

Exercise 48
Write a simulation program for the development of fruit-tree red spider mite into adults using the data of Table 9. Use the subroutine BOXCAR. Temperature is the only changing external variable.

Females and males emerge from the last juvenile stage in equal proportions. After copulation, the fertile females mature during a temperature-dependent pre-oviposition period and then start laying eggs. The oviposition rate and

ageing rate of the females depend directly on temperature (Table 10). The oviposition rate also depends on temperature, indirectly through the physiological age of the females.

This age-dependence normally means that the oviposition rate of young females is above average, while that of old females is much less than the mean. When calculations are performed using the average oviposition rate during the whole life span of a female, the simulated total number of produced eggs may be correct, but the course of the cumulative egg production curve is wrong. At the beginning, egg production per day is underestimated, and at the end it is overestimated.

Exercise 49
Explain why the subroutine BOXCAR cannot be used to mimic the ageing process when oviposition rate is dependent on physiological age.

Ageing of the reproducing female is simulated using the basic method described in Section 2.2, taking into account temperature-dependent and age-dependent relative mortality rates. These relative mortality rates are calculated as follows.

The maximum life span is arbitrarily defined as the mean life span plus three standard deviations. The residence time in a single class is the maximum period, just defined, divided by the number of classes N. The percentages of animals alive at the end of each age class are now read from the cumulative frequency distribution drawn on probability paper. This is done by dividing the total

Table 10. The oviposition rate (x) and its standard deviation (s(x)) in eggs per day for each age class, and the total oviposition period in days of *P. ulmi*, as a function of temperature.

Age class	Temperature									
	10°C		15°C		20°C		25°C		30°C	
	x	s(x)	x	s(x)	x	s(x)	x	s(x)	x	s(x)
1	0.6	0.15	1.2	0.2	1.9	0.7	3.1	0.8	4.2	1.1
2	0.5	0.1	1.2	0.2	2.2	0.7	3.7	0.8	5.5	1.2
3	0.5	0.1	1.1	0.2	1.8	0.6	3.1	0.6	3.8	1.1
4	0.4	0.08	1.0	0.2	1.4	0.4	2.0	0.4	1.4	0.4
5	0.2	0.05	0.8	0.15	0.8	0.2	1.0	0.2	0.8	0.1
Oviposition period	24	14.5	25	12	13	5.0	9.0	3.7	7.5	2.4

residence time in, for example, five equal classes and interpolating the line that describes the relation between residence time and frequency. At the ordinate, the percentage that survives in each class can now be derived. The relative mortality rate per age class is calculated with the formula used in Exercise 47. This yields the results given in Table 11.

The only function of the males is to copulate, for which task their number is not limiting; more than one copulation being possible. For this aspect, they can be disregarded. However, they act as a source of food for predators, so they cannot be omitted from the simulation. The ageing process of the males is described by inserting the statement:

M0,M,MTOT,MORFLM,OUTFLM,GAMMAM,GCYCLM = ...
    BOXCAR(5, MI, DEVRM, RDM, RMRM, INFLOM, NM, ...
    DELT, TIME)

The females lay either winter eggs, that overwinter on twigs or branches, or summer eggs that give rise to a new generation of mites during that summer. The hatching process of summer eggs is again mimicked by a boxcar train.

Exercise 50
Extend the simulation program of Exercise 48 to include oviposition and ageing of females, using the data of Tables 10 and 11.

3.4.3   Predatory mite, Amblyseius potentillae

The life cycle of the predatory mite is very similar to that of the fruit-tree red spider mite (Figure 37). The only difference is that it overwinters as a mated adult female and not as an egg. The sensitive period for induction of either summer or

Table 11. Relative mortality rate (day^{-1}) of female *P. ulmi* per age class in dependence of temperature.

Age class	Temperature				
	10°C	15°C	20°C	25°C	30°C
1	0.011	0.011	0.005	0.005	0.003
2	0.033	0.031	0.049	0.050	0.027
3	0.088	0.089	0.061	0.245	0.273
4	0.15	0.138	0.360	0.504	0.709
5	0.2	0.15	0.4	0.6	0.8

winter adults is the same: the older juvenile stage. Therefore, the structure of the program is also almost the same, and need not be given here.

3.4.4 Relations between predator and prey

The food source does not affect reproduction and development of the fruit-tree red spider mite, as long as crop functions are optimal and densities so low that interference between individuals is absent. For the predatory mite, however, food supply is restricted. The availability of prey affects development rate, reproduction rate and fecundity (total number of eggs produced during the life of a female) of the predator. When prey is scarce, the relative mortality rates of the predators in the different stages may increase.

The motivation state of the predatory mite is characterized by its gut content (Figure 39) which determines the relative predation rate and prey utilization by the predator. The relative predation rate is the absolute predation rate per unit area divided by prey density; this variable has the dimension $time^{-1}$. Hungry predators have a high relative predation rate, activity increases with decreasing gut content, their encounters with prey are nearly always successful (fatal for the prey), and the dead prey is completely consumed. Well-fed predators, on the other hand, are less active, have a low success ratio (successful encounters divided by total number of encounters) and only partly consume the prey that are killed. A predator kept at a constant prey density, rapidly reaches a steady state (Fransz, 1974; Section 3.3) in which a unique relation exists between gut content and temperature on the one hand, and the relative predation rate and prey utilization on the other, provided that prey stage and prey composition are fixed. The stochastic models of Section 3.3 can, therefore, be omitted in this situation.
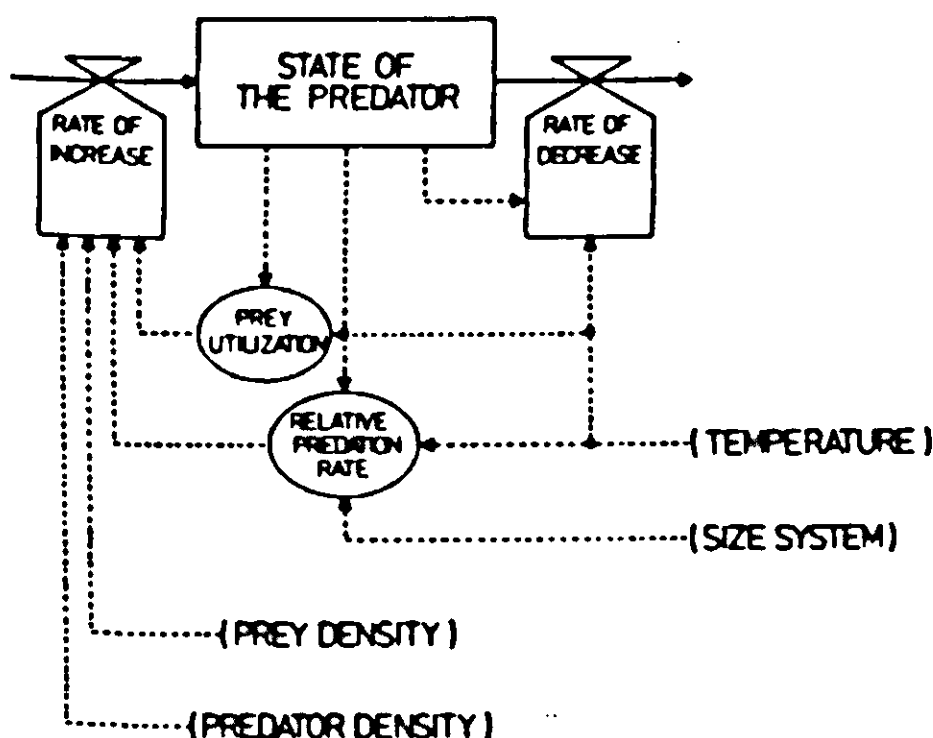

Figure 39. A predator-prey system, one predator versus a fixed number of prey of one stage. (Source: Rabbinge, 1976).

Old adult female predators eat all stages of prey except eggs, and show a clear preference for the younger stages, especially at higher gut contents. Young predator juveniles can kill only larvae and young prey juveniles, because the older prey stages are too vigorous. The gut contents are digested at a rate proportional to the content; there is thus a relative rate of digestion which depends only on temperature.

Exercise 51
Write a simulation model for the state (gut content) of a predator based on the relations presented above. Assume that temperature and densities of prey and predators are constant. You can fill in the required data yourself. Give the dimensions of all parameters and variables.

3.4.5 Preference as a competitive process

So far, preference of the predator for some types of prey has been treated as a difference in relative predation rate. At higher gut contents, relative predation rate of an unattractive prey type drops to zero. This relative predation rate is introduced into the simulation model as a variable, dependent on temperature and gut content. The relative predation rate is easily determined from the functional response curve (predation rate as a function of prey density (Figure 40)). Each prey density corresponds to a well-determined level of gut content of the predator, so the relative rates of predation on different prey types can be related through this gut content. Thus, the response to various prey species may be different but they are all related to the same state variable 'gut content'. This approach is straightforward and its validity can be tested in experiments using replacement series of two prey types (Rabbinge, 1976). The results support the assumption that the density of one prey type can affect the predation rate on another, only through the gut content of the predator.

Another approach, in which simulation is not needed and which allows us to bypass the gut content of the predator, is to consider predation and preference as competitive processes. Prey 'compete' for space in the gut of the predator, so it should be possible to derive the predation rates in mixed prey populations from the predation rates in pure populations (monocultures, see also Section 4.2). The predation rate (PR) as a function of prey density (Figure 40) is described by

$$PR = \frac{B \cdot D}{B \cdot D + 1} \cdot PRM \qquad \text{Equation 60}$$

where D is prey density, PRM the maximum predation rate and B an apparent area per prey. PRM and B are determined for each combination of prey type and predator type from the functional response curve. Inversion of Equation 60 gives:
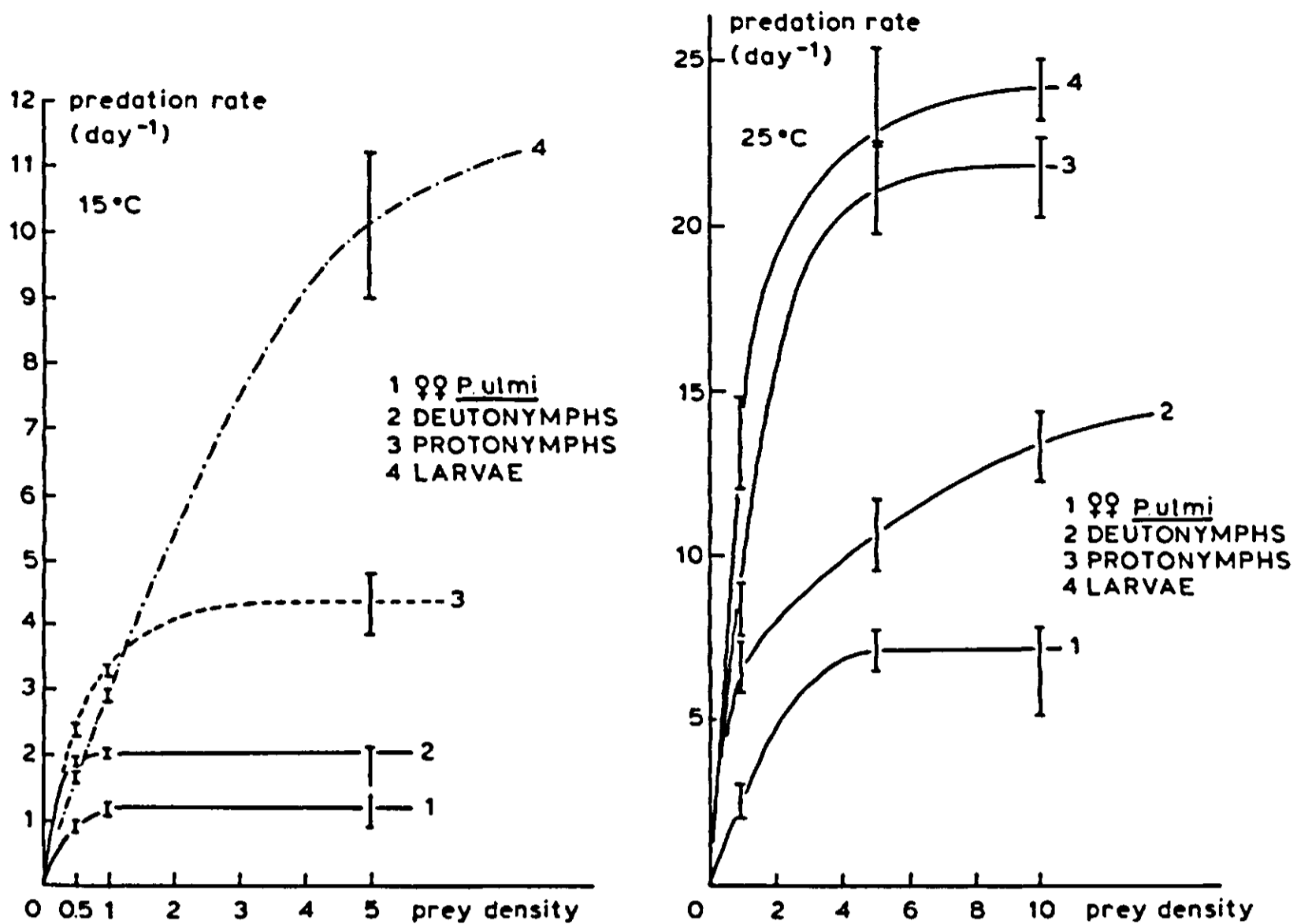
Figure 40. Functional response curves of the adult female stage of the predatory mite *Amblyseius potentillae* feeding on the fruit-tree red spider mite *P. ulmi* at 15°C and 25°C. (Source: Rabbinge, 1976).

$$\frac{1}{PR} = \frac{B \cdot D + 1}{B \cdot D} \cdot \frac{1}{PRM} = \frac{1}{PRM} + \frac{1}{B \cdot D} \cdot \frac{1}{PRM}$$

The corresponding graphical representation of $1/PR$ versus $1/D$ is a straight line that crosses the ordinate at $1/PRM$ and has a slope of $1/(B \cdot PRM)$. Maximum predation rate and apparent area per prey can be derived directly from the lines produced. An analogy to the competition of cereal-weed mixtures can be shown (Section 4.2). It is tempting, therefore, to describe predation on a mixture of prey with the same equations used to compute yield of one of the species in a cereal-weed mixture

$$PR_1 = \frac{B_1 \cdot D_1}{B_1 \cdot D_1 + B_2 \cdot D_2 + 1} \cdot PRM_1$$

and, similarly, for the rate of predation on prey type 2. Comparison of experimental and simulation results with the computations for mixtures, show that the various approaches give satisfactory results (Figure 41). Of course, the validity of the computation can be confirmed only with the restriction that the gut content of the predator must be in equilibrium with the available density and composition of prey.
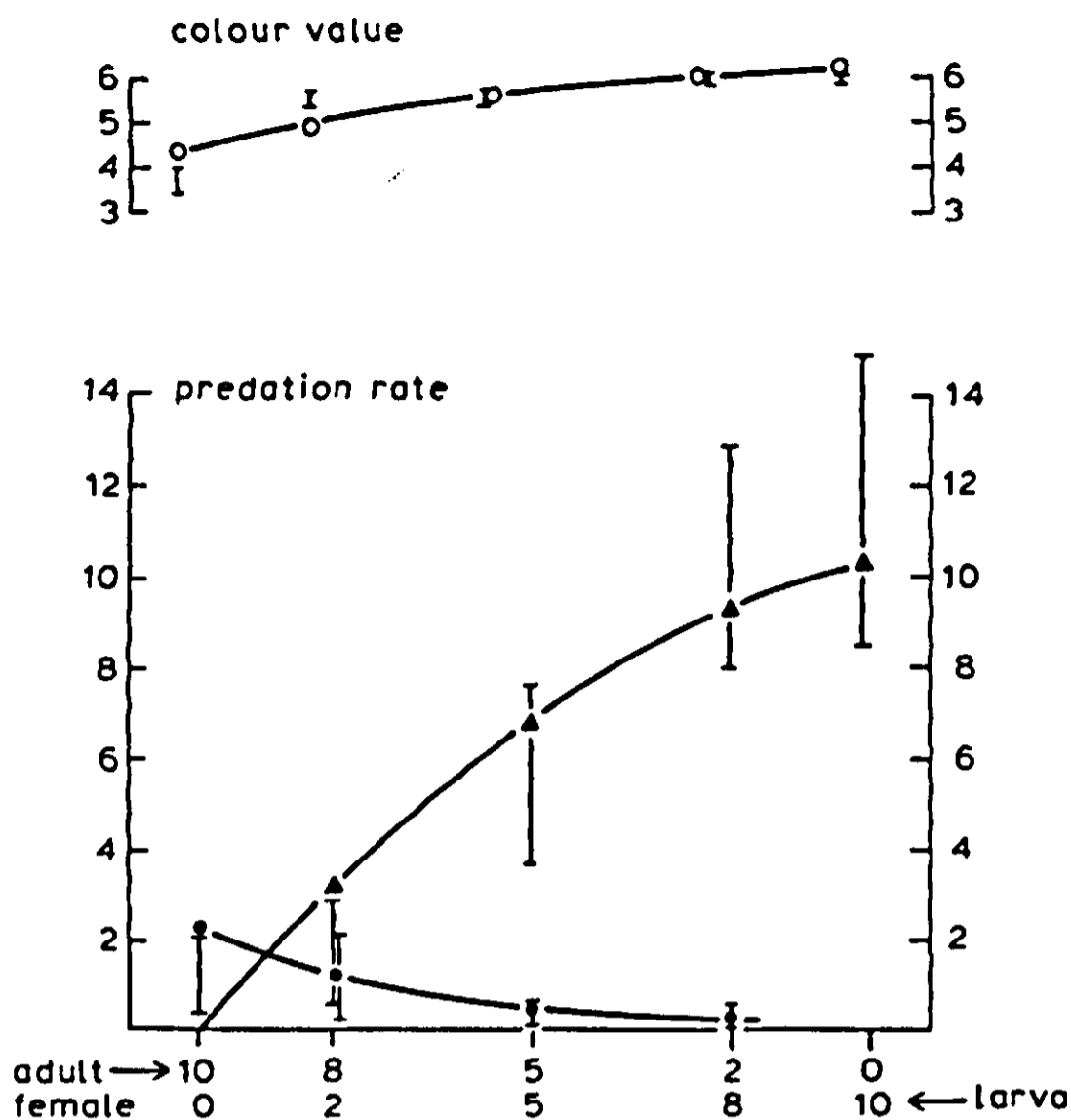
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Figure 41. Simulated and experimental results of a replacement series of larvae and adult females of *Panonychus ulmi*, with one adult female of *Amblyseius potentillae* at 15°C. Simulated results (———), and experimental results (I bar with 95% confidence intervals). (Source: Rabbinge, 1976).

3.4.6 Model testing

Model building is a futile exercise unless the model output is compared with the results of independent experiments. Such tests are preferably done at different levels. One such level is mixed prey predation, as derived from predation on single prey types. This can be used to test the assumption about the interaction between different prey types as discussed in Subsection 3.4.4.

A second level of testing involves population experiments with prey and predator in a larger system with well-defined boundaries, under controlled conditions; e.g. a small apple tree in a greenhouse. The comparison of such measurements with simulated results indicates a reasonable correspondence (Figure 42), so a third phase of validation is justified: the apple orchard. Some results of simulations for orchards, together with experimental results, are given in Figure 43. The reasonable agreement increases confidence in the model. Validation at different levels can pinpoint errors in model structure or parameter values. Another important tool in error-spotting is sensitivity analysis, which shows which parameters have the greatest influence and might thus be responsible for deviations between measure-ments and results. The results of a sensitivity analysis can also help in deciding research priorities. For instance, sensitivity
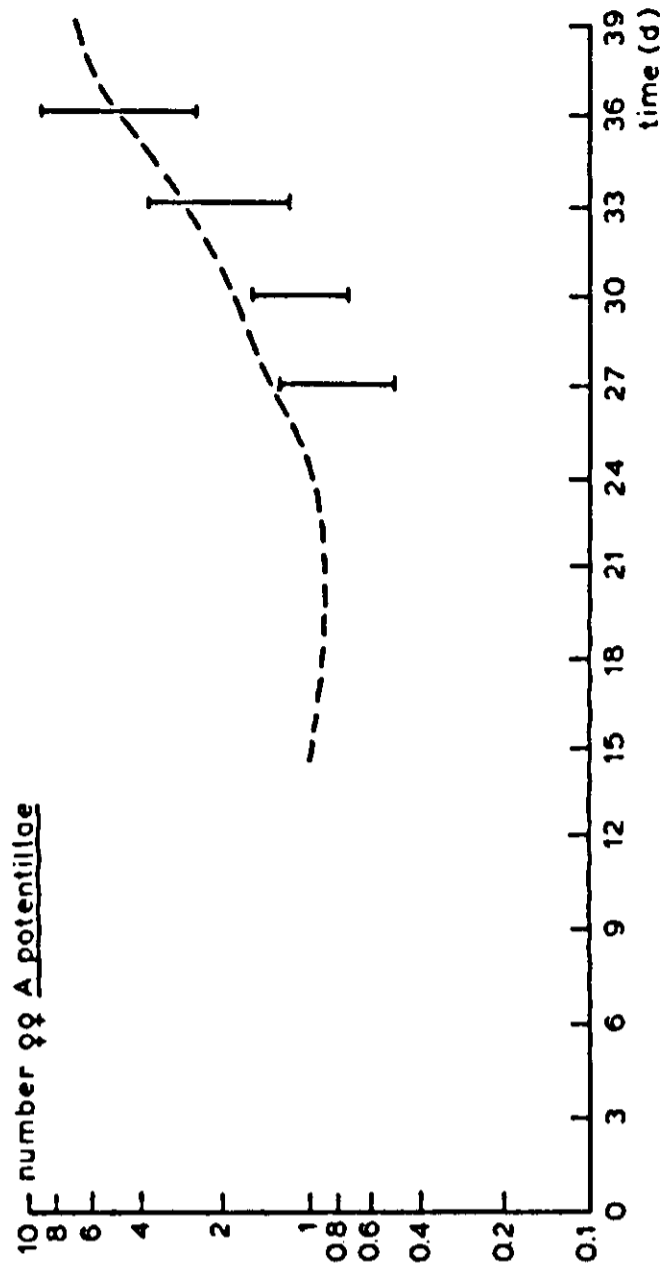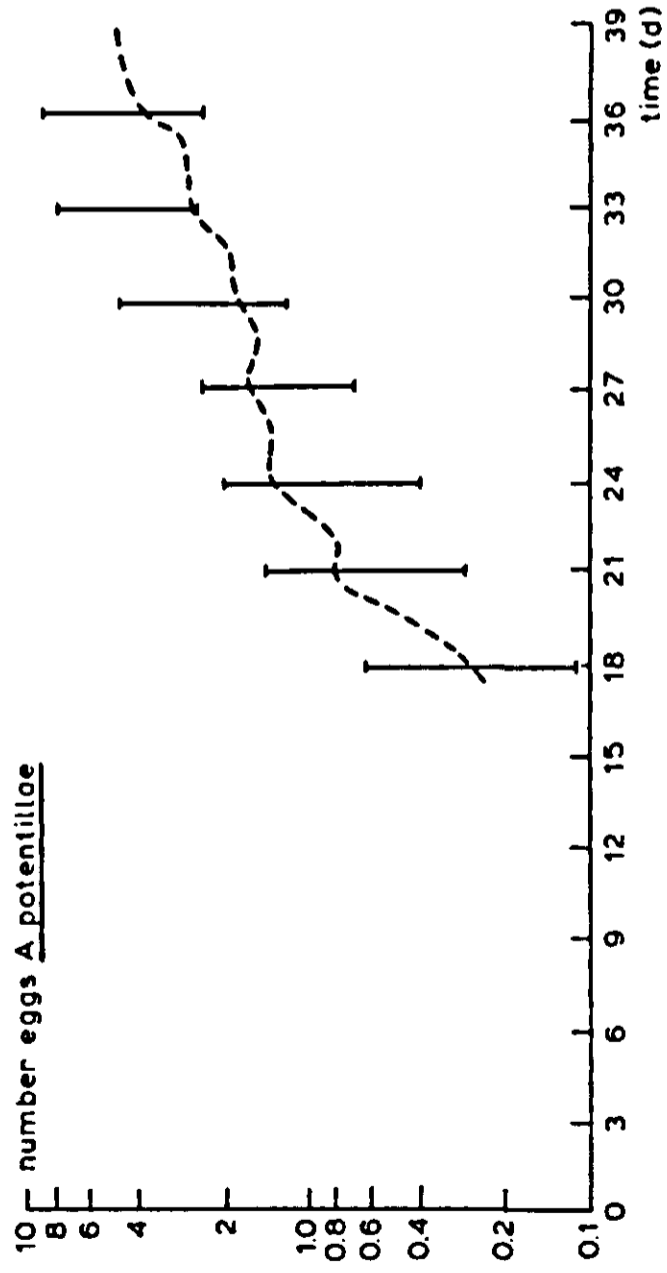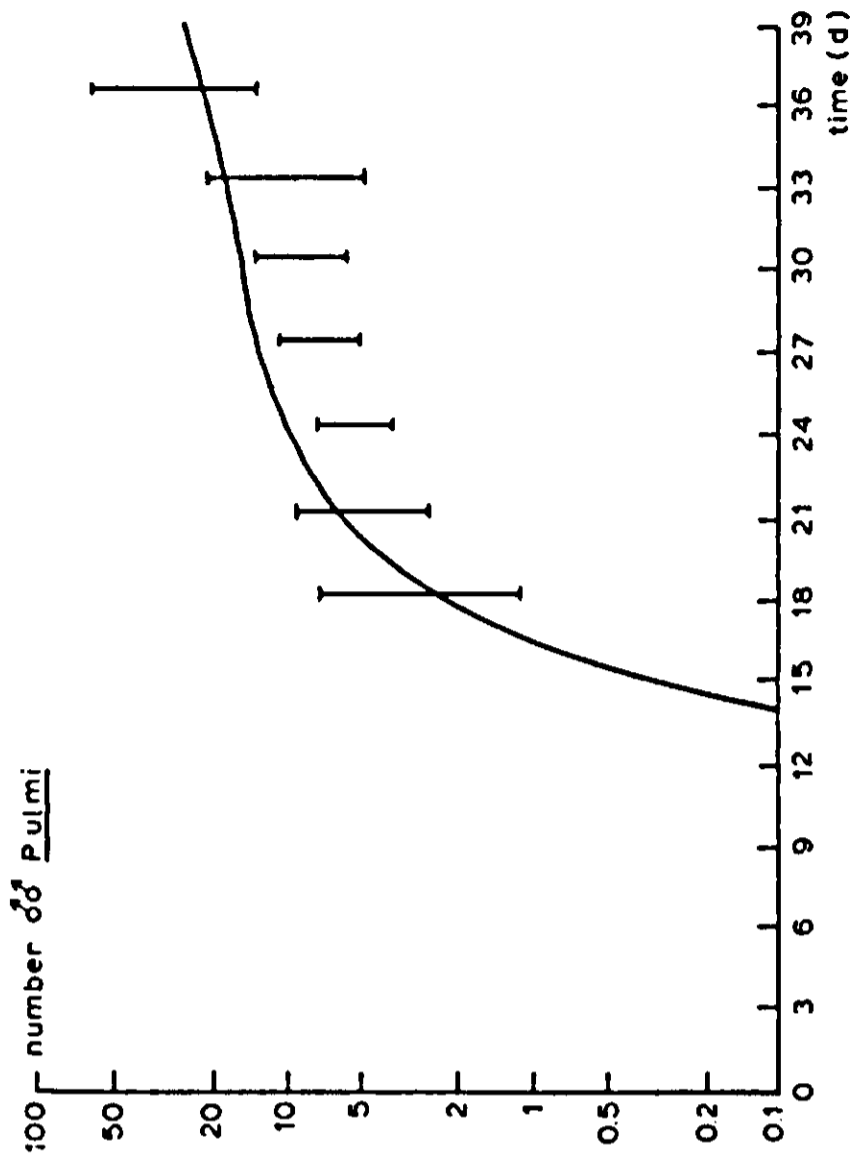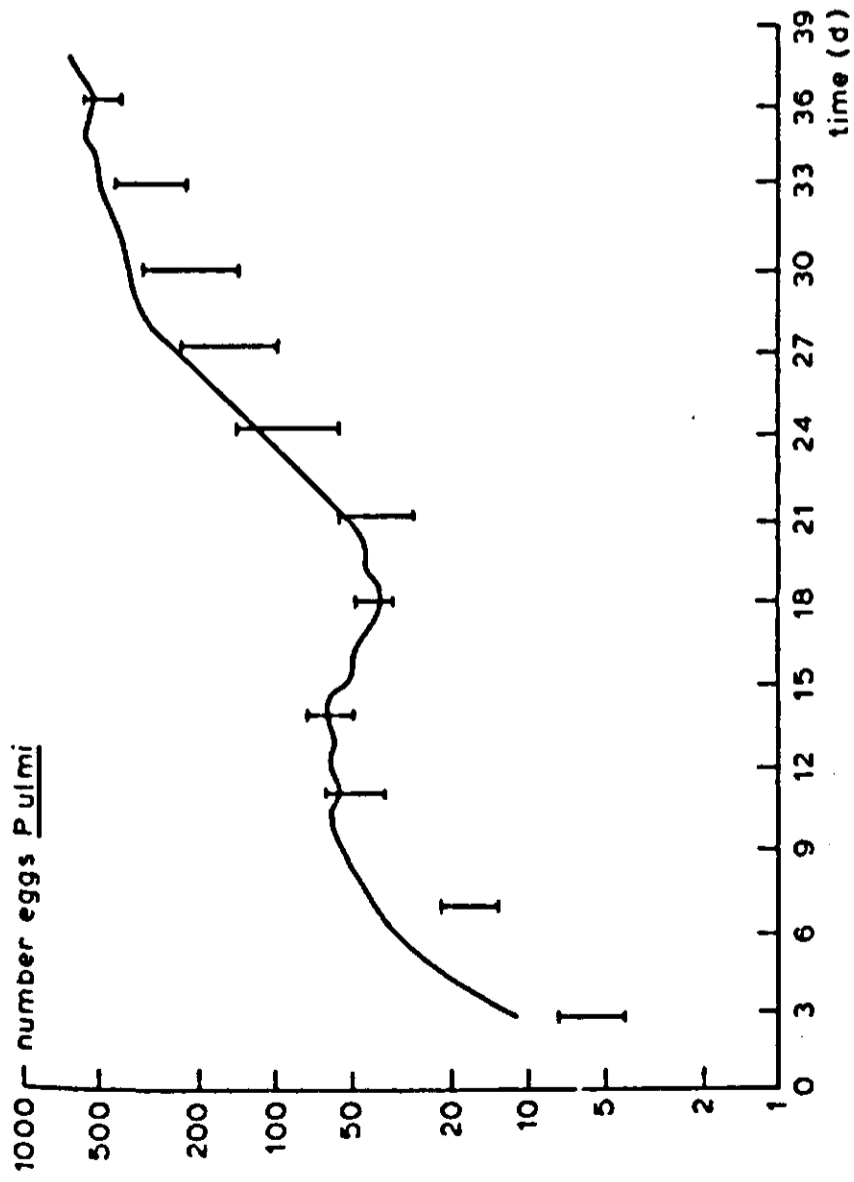
Figure. 42. Simulated and experimental results of a population experiment of *P. ulmi* and *A. potentillae* in a greenhouse; simulated number of *P. ulmi* (———), simulated number of *A. potentillae* (----), and experimental results (I bar with 95% confidence intervals). (Source: Rabbinge, 1976).
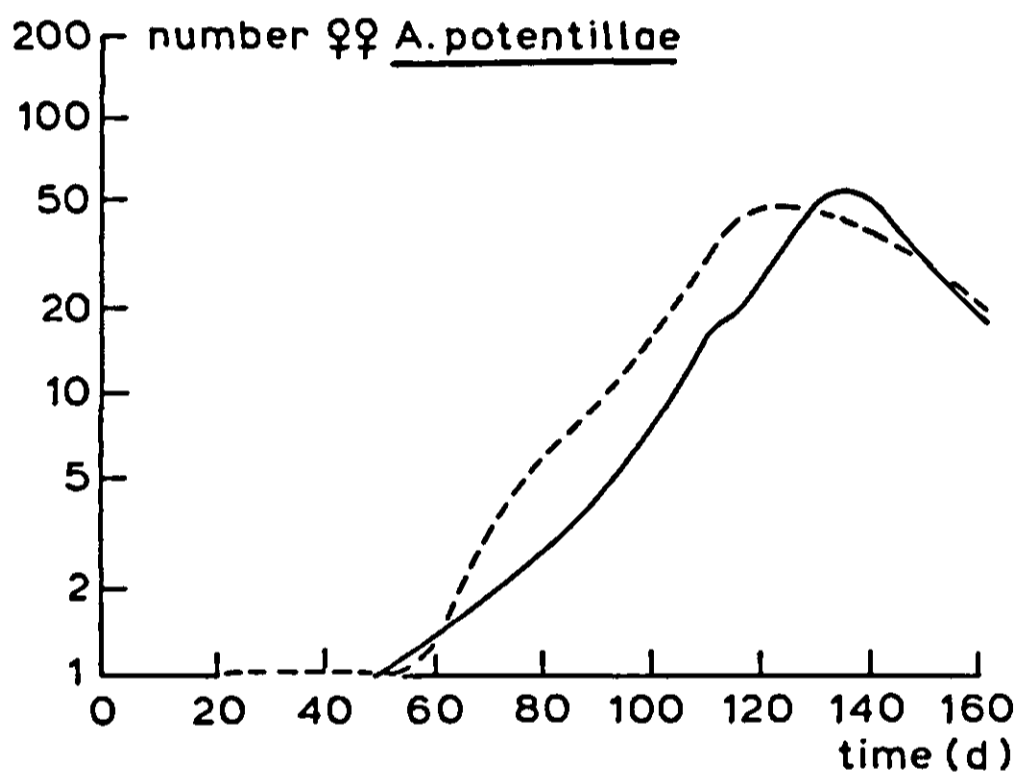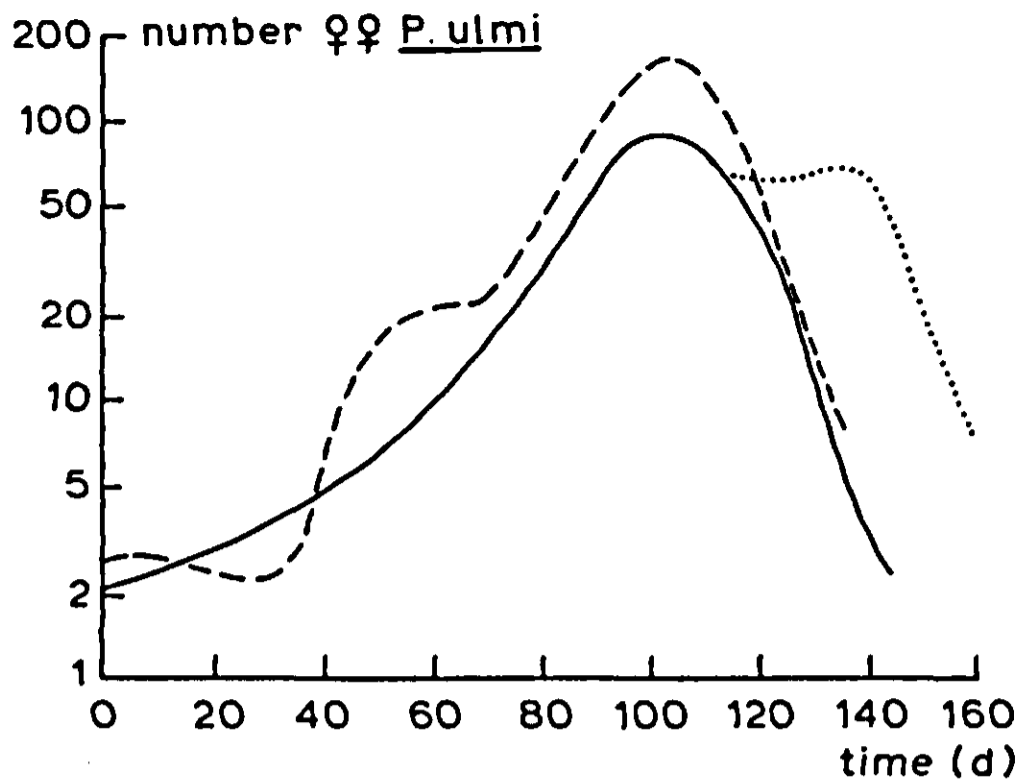
Figure 43. Simulated (----) and experimental (——) results of *P. ulmi* and *A. potentillae* in an orchard. The experimental results are the means for several orchards. (Source: Rabbinge, 1976).

analysis shows that in this model the abiotic mortality of prey and predator are of minor importance. The most important factors are the oviposition rate, the predation rate of the adult female predator and the length of the juvenile period of the prey. The gut content, especially when it is low, also has quite an important effect on the predator's rates of development and reproduction. Experimental data on these relations are scarce and inaccurate, so more research in this direction is required.

The model described here has also been used for the development of a practical pest management method. When, rather arbitrarily, an economic injury level of 3 mites per leaf is assumed (Rabbinge, 1985), model computations demonstrate that predator-prey ratios may vary from 3 to 0.3 without leading to a risk of local extinction of the predator or of very high prey densities (Rabbinge, 1976). The

preset damage threshold can be tested by the use of combination models (as described in Section 4.3) in which crop growth models are combined with population models of phytophagous and predatory arthropods. After quantification of the relation between the host plant and the phytophagous pest, these combined models may be used to calculate reduction in yield. With a preset limit for acceptable yield reduction, threshold levels for the density of the pest can then be determined, and can replace the arbitrary threshold values currently used to decide whether the introduction of control of predatory mites should be recommended.

3.4.7 Stiff equations

In the case of the predatory mites, the physiological state of an individual predatory mite approaches equilibrium with a very small time coefficient in minutes, while the time coefficient for the changes in the prey population is many orders of magnitude greater, in days. This is called a model with 'stiff equations'. Such a population model, which includes a dynamic model of the individual predator's gut contents would, therefore, require a very short time step of integration, and a large amount of computing time. The assumption of physiological equilibrium thus reduces the cost of a simulation run by an order of magnitude of 100, but need not involve any important loss of accuracy.

Two other approaches can be used to deal with models with stiff equations. First, if the period over which the system is to be simulated is short, relative to the time coefficient of the slow process, then this process can be omitted or simplified (i.e. input as parameters or calculated only once). This method, however, can be used only if the simulation's timescale was initially overestimated (Goudriaan, 1977).

A more generally method is to calculate the effects of the slow process less frequently than those of the rapid process. Thus, for example, the spatial distribution of the cereal aphids and parasitoids modelled in Subsection 3.2.4 is calculated once every 50 time steps (Rabbinge et al., 1984a).

Figure 44 shows a scheme for combining the two main methods of reducing the computation time needed to simulate systems involving processes with very different time coefficients.

Clearly, the use of short cuts of this type introduces some inaccuracy into the model. As pointed out by Goudriaan (1977), however, errors in the data used in agricultural models mean that extremely precise integration methods may be an expensive luxury. Short cuts, therefore, can yield dramatic reductions in computation time without resulting in significant errors in the model's results.
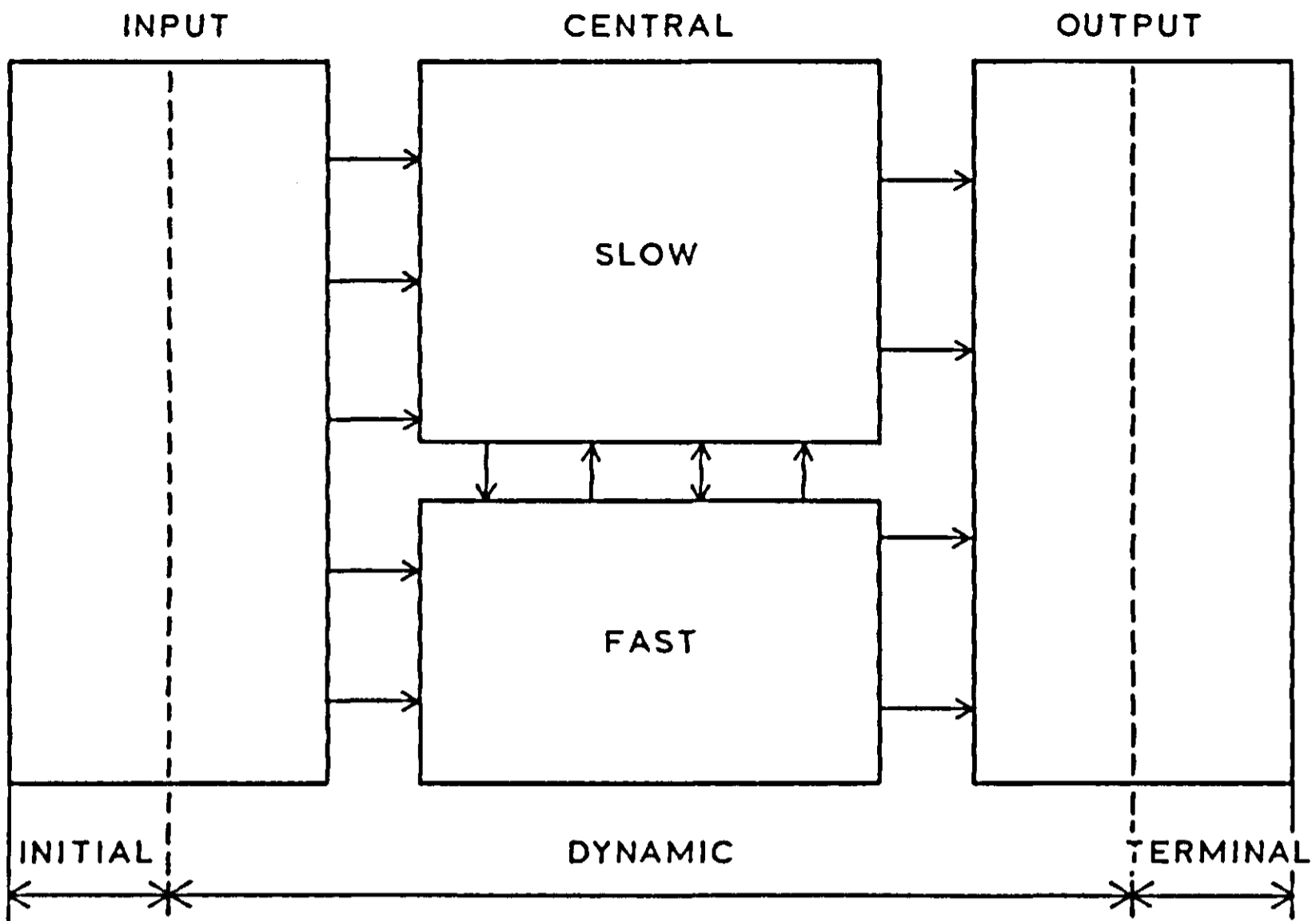
Figure 44. The main parts of a dynamic simulation model. The words 'INITIAL', 'DYNAMIC' and 'TERMINAL' refer to the CSMP terms that are used to indicate the segments of a simulation model. The input part contains those calculations connected with initial values and forcing functions, in as far as they are not subject to a feedback from state variables of the model. The output part contains those calculations connected with output variables, from the point where they no longer influence state variables. (Source: Goudriaan, 1973).