

Predator-prey Systems with Mites¹⁾

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ABSTRACT

Population models of fruit tree red spider mite and predatory mites are given, which are used to explain the regulation of spider mites by predatory mites and may be used to manage spider mite systems in apple orchards.

The models are based on extensive experimental knowledge of the bionomics of prey and predator. A detailed analysis of the prey-predator relations on the individual level paved the way for the development of prey-predator models on the population level. These models, based on the state variable approach, simulate the population fluctuations of prey and predator in dependence of the changing abiotic factors during the season using time steps of a quarter of an hour and trace all state variables, as the number of eggs, larvae, adult females and gut content of the adult female predator. Verification of the models at different levels of integration showed good agreement between model output and the results of independent experiments, and this enabled a sensitivity analysis with the model. This sensitivity analysis showed the relative importance of different factors, so that management strategies to achieve tolerable prey-predator levels throughout the year may be developed.

Introduction

During the last 10 years, integrated pest control systems have been developed for several crops. The increasing availability of selective pesticides with a low toxicity for natural enemies and the use of natural enemies, in some cases even possessing resistance to a wide variety of pesticides, has made these pest control systems possible.

The development of these systems is purely empirical. Attempts are made to release parasites and predators, often coming from abroad, and cultural measures and spraying schemes are adapted until an economically acceptable level of control is reached. Explanations of the mechanisms of operation are often given afterwards by speculation and remain rather vague, since the hypotheses are rarely verified experimentally. However, a stable control system requires insight into the mode of operation of the system and knowledge of the relevant processes.

One of the main fields of research in integrated pest control is the apple orchard. The increased development of acaricide resistance in spider mites and the availability of knowledge on the bionomics of many pests has made the development of non-chemical pest control systems necessary and possible. Experiments with predatory mites have shown the possibilities of these natural enemies in controlling the fruit tree red spider mite. However, insight into the regulation mechanism is lacking, so that it has been difficult to give advice to the fruit grower. This paper is based on a detailed study (RABBINGE, 1976) that fills this gap by means of simulation.

1) Paper presented at the Joint EPP0/IOBC Conference on Systems Modelling in Modern Crop Protection, Paris, 12-14 October, 1976.

Simulation Models

Simulation models of fruit tree red spider mite (*Panonychus ulmi* [Koch]) and predatory mites were developed to bridge the gap between basic knowledge of the bionomics of spider mite and predatory mites and the experience with biological control in the field. These models are based on detailed knowledge of the effect of temperature, humidity, day length and food quality and quantity, on both predator and prey. The predator-prey interactions in the models are based on a detailed analysis of the predation process. All models in this study are constructed according to the state variable approach. State variables characterize and quantify characteristics such as biomass, number of animals, quantity of food, gut content, etc. In mathematical terms, they are expressed in integrals. Their rates of change are given in mathematical terms, as functions of the state of the system. The state variable approach is introduced by DE WIT and RABBINGE (1979). A more detailed description of the technique and its use in ecological problems is given by DE WIT and GOUDRIAAN (1974).

Models for Fruit Tree Red Spider Mite and the Predatory Mites

In figure 1, a simplified relational diagram of the life cycle of fruit tree red spider mite is given in Forrester notation. In the development from egg to adult, six stages are morphologically distinguishable; larva, protochrysalis, protonymph, deutochrysalis, deutonymph and teleiochrysalis. In the relational diagram, each of the rectangles expresses the number of animals in that particular stage. The rate of change is determined by the actual number of individuals and a relative rate, often affected by temperature. During development, some animals die, the rate of mortality being determined by the amount of animals within the state variable and the relative rate of mortality; the latter is again a temperature-dependent function. The females oviposit at a rate that depends on the number of females and a temperature-dependent relative reproduction rate. The newly-laid eggs hatch and give rise to a new generation of mites. In this way, 4-6 generations of mites may appear during the season. Overwintering takes place as winter eggs, laid by females induced to lay at the deutonymph stage in sheltered places. The flow of individuals to this winter females stage is also given in figure 1.

A simplified relational diagram for the predatory mite, *Amblyseius potentillae* (Garman), is given in figure 2. The life cycle of these mites is similar to that of the red spider mite, except that overwintering takes place in the adult female stage. Again, the rates are state- and relative rate-dependent and the growth and development of the predatory mites can thus be simulated in the same way as for the fruit tree red spider mite.

In figures 1 and 2, the interactions of prey and predator are expressed by broken lines. Larvae, protonymphae, deutonymphae, adult females and males of the prey are eaten by protonymphae, deutonymphae, adult females and males of the predator, each combination with its own preference, depending, to a large extent, on the state of the predator expressed in its gut content. To quantify all these relations, a detailed analysis on the individual level is required.

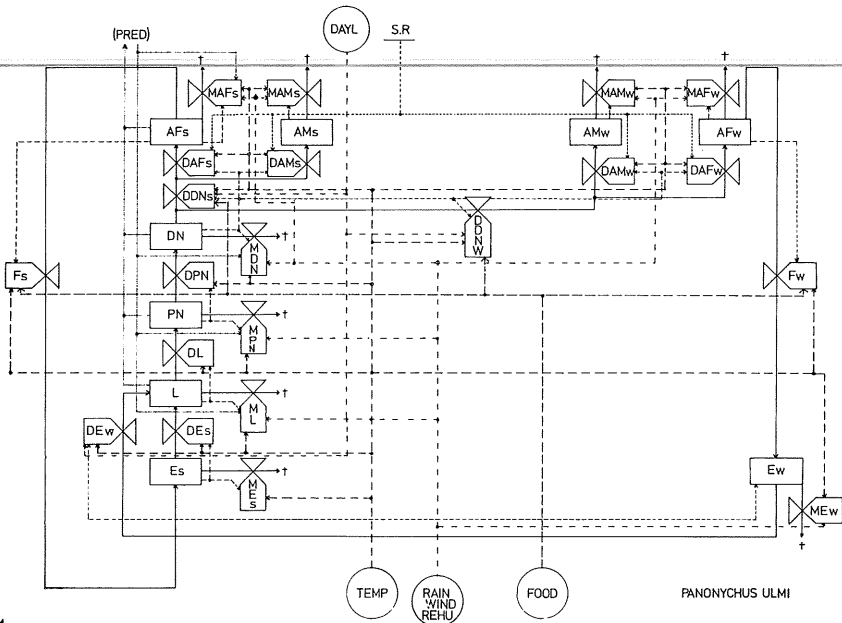


Fig. 1
Simplified relational diagram of the life cycle of fruit tree red spider mite (Es = summer eggs, L = larvae, PN = protonymphs, DN = deutonymphs, AFs = adult females laying summer eggs, AMs = adult males, AFw = adult females laying winter eggs, AMw = adult males, AFw = rate of ovipositing winter eggs, Fw = rate of ovipositing winter eggs).

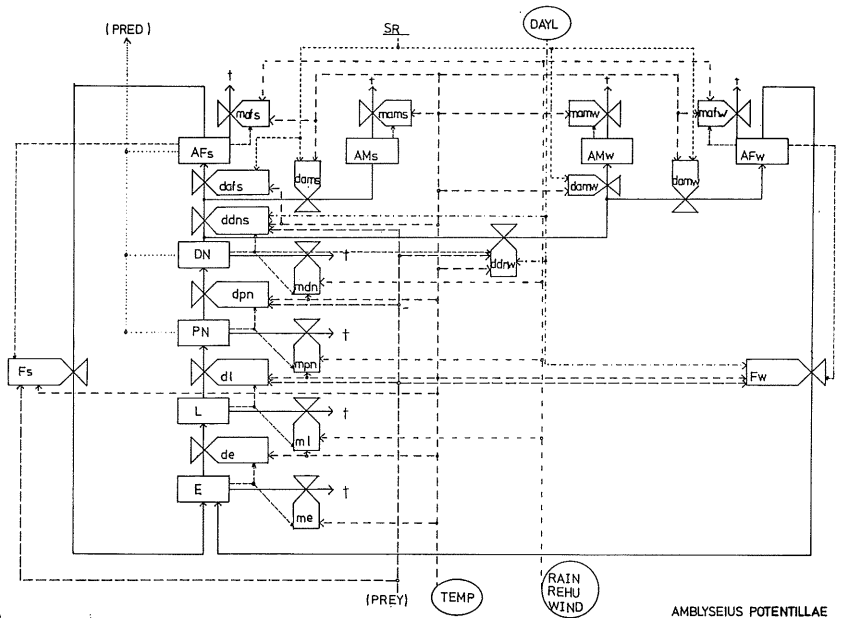


Fig. 2
Simplified relational diagram of the life cycle of the predatory mite *Amblyseius potentillae* (E = eggs, L = larvae, PN = protonymphs, DN = deutonymphs, AFs = adult females not overwintering, AMs = adult males not overwintering, AFw = adult females overwintering, AMw = adult males overwintering, only females overwinter, Fw = oviposition rate of winter females).

Prey-predator Interactions on the Individual Level

Detailed analysis of predator-prey systems on the individual level are given by several authors. HOLLING (1966) gave a general description of the predation process and developed a mathematical model which provides an explanation of the three fundamental types of functional response curves he distinguished. In these models, searching periods of the predator are calculated as a function of the state variables at the beginning of searching, such as the gut content of the predator. However, these variables change during searching and so do the searching periods. Computations of the values of the state variables at the beginning of the searching periods are therefore not sufficient to simulate the results of the predation process and the general applicability of Holling's analytical models is accordingly questionable.

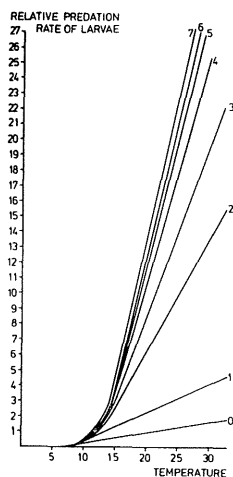


Fig. 3
Relative predation rate of larvae per day against temperature at various steady gut contents of the adult female predator (0-7).

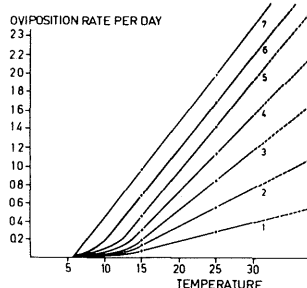


Fig. 4
Oviposition rate of *Amblyseius potentillae* in eggs per day against temperature at various steady gut contents (1-7) of the adult female predator.

On the basis of a detailed experimental analysis of the predation process, FRANSZ (1974) succeeded in constructing models that keep trace of all state variables and their change during the searching periods, taking into consideration the stochastic character of the predation process. Calculations with these models made clear that a system of one predator with a constant number of prey reaches an equilibrium within a few hours, the gut content of the predator oscillating with a small amplitude

on a level that depends on predator and prey density and the temperature of the system. Thus only three parameters characterize the steady gut content of the predator at a certain prey density: relative predation rate, prey utilization and the relative rate of decrease of the gut content of the predator.

To quantify the interactions between the fruit tree red spider mite and the predatory mites, these three parameters should be determined at different steady gut contents and at various temperatures. Determination of the gut content of the predatory mite is in this case rather simple, since well-fed predatory mites possess a red colour, whereas hungry predators are whitish or transparent. A colour scale was developed, relating the colour of the predatory mite to the amount of pigment in the animal. Relative predation rate in relation to temperature is given in figure 3 for adult females of the predator feeding on larvae of the prey. The decreased development rate and the diminished reproduction rate of the predator at low gut-content levels were also determined at various temperatures (fig. 4).

Verification of the Simulation Models

Verification of the output of the simulation models is done at several levels of integration. A rather simple situation is the simulation of the growth of fruit tree red spider mite and predatory mite populations in small ecosystems under the controlled conditions of growth chambers or glasshouses. In figure 5, the results of these simulations are given for different morphological stages of prey and predator. The models trace all stages and the results are in good correspondence with the results of the independent experiments presented in the same figures as confidence intervals.

Verification under field conditions is also done. The results of these simulations for prey and predator are compared with the averaged results of accurate population surveys in several orchards during a complete season (fig. 6). The correspondence in model output and the results of the independent verification experiments validates the model and makes it suitable for sensitivity analysis. This sensitivity analysis is done to evaluate the structure of the system and the relative importance of different parameters, and to improve insight into the management of the system.

Sensitivity Analysis and Application

Sensitivity analysis is done by changing structural elements in the model or by changing rates, some results being given in figure 7. The predation activity of the younger stages and the adult male predatory mite is relatively unimportant. The female predator is the important regulator, due to its high predation activity, its long life-span and an increase in rate of oviposition until the predator is well fed. The system is rather sensitive to length of the prey's juvenile period, relative predation rate and oviposition rate of the adult female predator and the delay in development of the predator due to insufficient food.

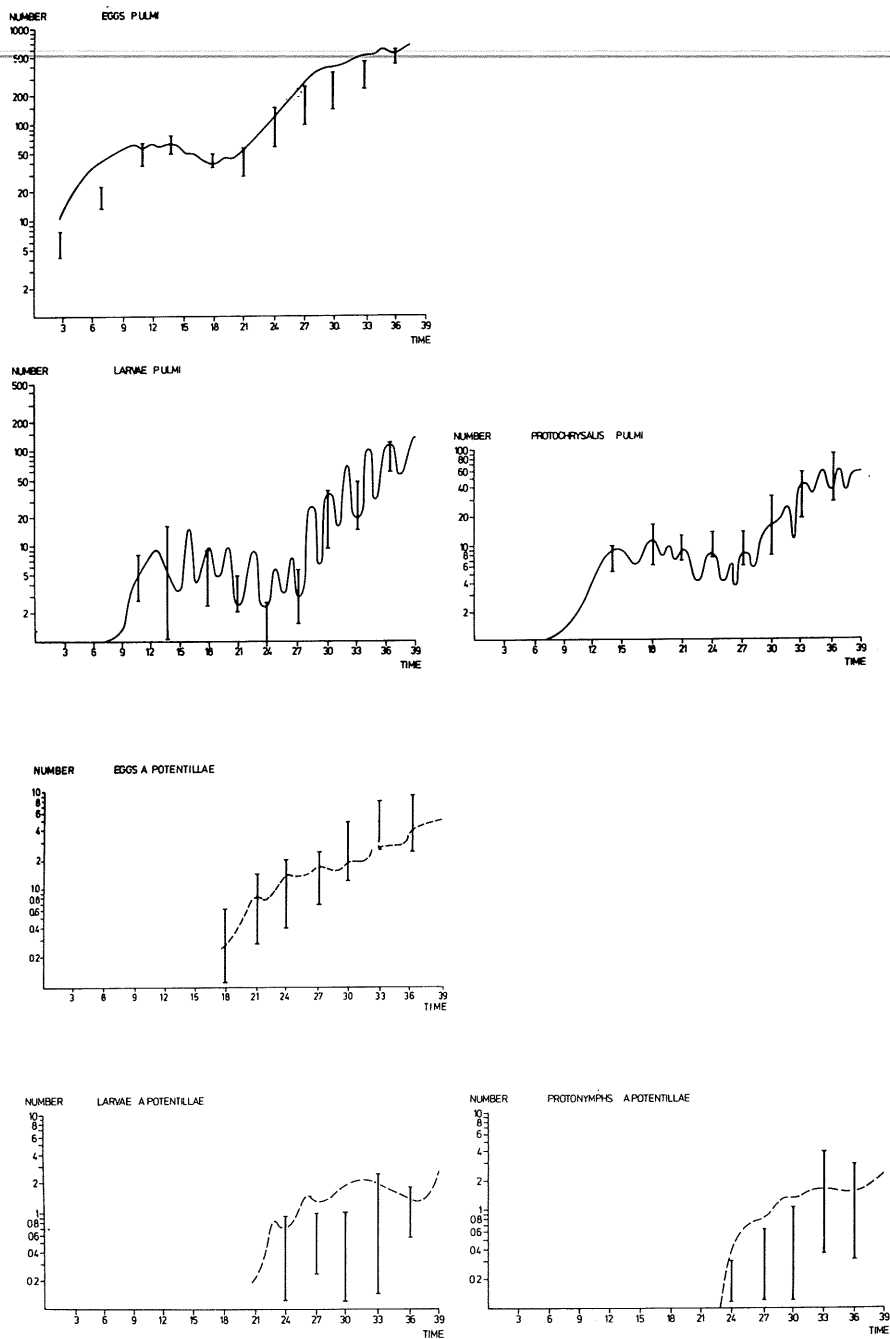


Fig. 5 Simulated and experimental numbers of *Panonychus ulmi* and *Amblyseius potentillae* in a population experiment in a glasshouse. The experimental results are given in terms of confidence intervals for eggs, larvae and protochrysalis of the prey and for eggs, larvae and protonymphs of the predator. The solid line represents the simulated numbers.

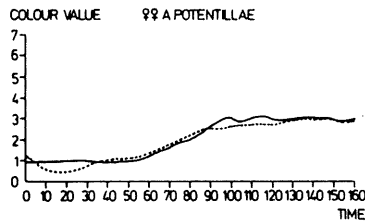
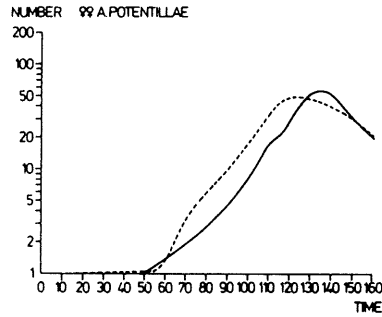
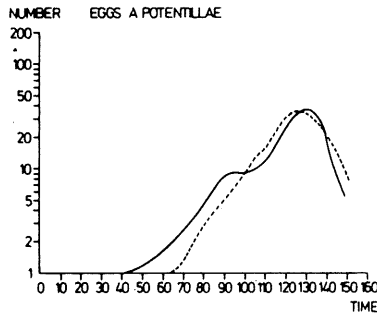
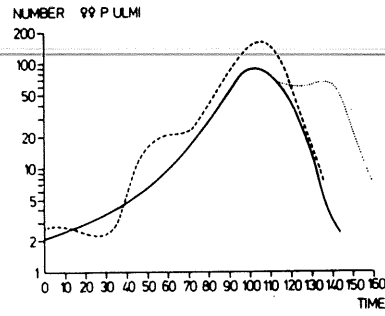
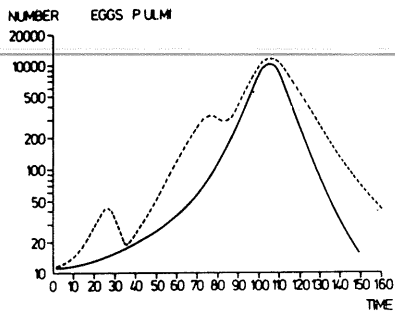


Fig. 6
 Simulated and averaged experimental density curve during the season 1974 for adult females and eggs of *Panonychus ulmi* and *Amblyseius potentillae*, simulated and average experimental colour value for adult female predators. The broken line represents the simulated numbers ; only summer females are given.

It also appeared possible to calculate in spring the number of predators needed at a certain prey density to avoid damage levels later in the season, and this for various climate situations. Year-to-year weather differences may be large enough to influence population growth of prey and predator, so that it may be useful to monitor this development with models based on actual weather data.

General Applicability of the Method

RABBINGE (1976) used the state variable throughout. This approach, given form with the simulation language CSMP, enables the biologist or agronomist to handle all aspects of modelling, while keeping fully in touch with the experimental

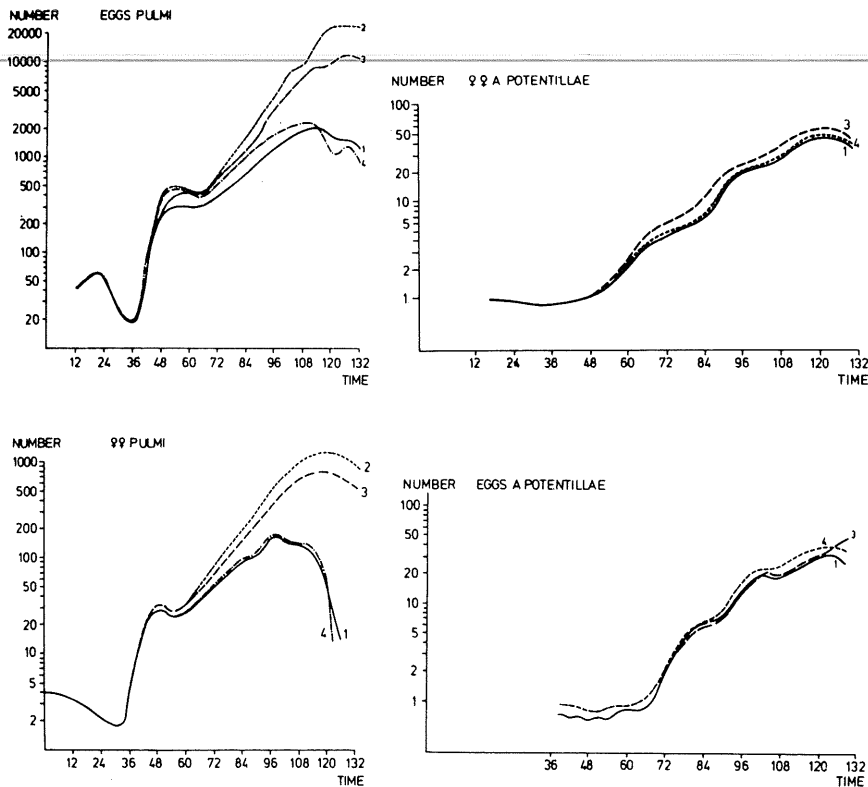


Fig. 7
Simulation results for the numbers of adult females and eggs of *Panonychus ulmi* and *Amblyseius potentillae*. 1) reference model; 2) without any predation; 3) without predation by adult female predators; 4) without predation by juvenile and adult male predators.

situation. It prevents communication errors between modeller and experimenter and makes the models readable and usable for outsiders. For instance, the technique applied for simulating development and ageing is generally applicable. It is used for simulating flow of water, transport of solutes and heat in soils, germination and development of plants and fungi, and for biochemical processes.

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RESUME

Systèmes proie-prédateur chez les acariens

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Des modèles de populations de l'acarien rouge et d'acariens prédateurs permettent d'expliquer les effets qu'exercent les prédateurs sur leurs proies et d'introduire des systèmes de management pour contenir ces acariens phytophages dans les vergers.

Les modèles reposent sur une connaissance expérimentale approfondie de la bionomie de la proie et du prédateur. Une analyse détaillée des relations proie-prédateur étudiées sur des spécimens isolés a permis d'établir des modèles au niveau de la population. Ces modèles, basés sur le principe des variables conditionnant l'état, simulent les fluctuations de populations de la proie et du prédateur en fonction de la variation des facteurs abiotiques au cours de la période de végétation, à intervalles d'un quart d'heure. Ils suivent la progression de toutes les variables d'état, telles que le nombre d'œufs, de larves et de femelles adultes ainsi que le contenu intestinal des femelles adultes du prédateur. Les modèles ont été vérifiés à différents niveaux d'intégration et révèlent une bonne concordance entre les données du modèle et les résultats d'expérience. Ceci a permis de réaliser une analyse de la fiabilité du modèle, qui montre l'importance relative des différents facteurs, ce qui a permis de développer des stratégies de management où le niveau des proies par rapport aux prédateurs est optimisé tout au cours de l'année.

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