Population dynamics and biological control of red spider mite

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During the last decade, integrated pest control systems have been developed for several crops. The availability of selective pesticides with a low toxicity for natural enemies, and in some cases the utilisation of natural arthropod enemies which possess resistance against these pesticides, made such systems possible (1).

The development of such systems of integrated pest control is mainly empirical. Attempts are made to introduce or to improve the effectiveness of parasites, predators and pathogens, and to adapt cultural measures and spraying programmes until success is achieved and an acceptable degree of control of the pest population is attained. Speculative explanations of the mode of operation of the system are given afterwards, but verification by experiment is often omitted.

One of the main fields of research in integrated control has been the control of orchard pests. The long experience with modified spraying programmes in apple orchards (5, 6), the increasing development of resistance of spider mites to acaricides, and the availability of knowledge on the bionomics of many pest species were major factors promoting the development of integrated pest control systems.

Experiments with predacious mites in commercial apple orchards clearly demonstrated the capacity of these natural enemies to reduce and maintain spider mite populations below the economic threshold level (8). At present, predacious mites are widely utilised to control spider mites in apple orchards and in greenhouse crops (4). However, a quantitative assessment of the changes involved has still not been given, and speculation is rather vain when not supported by knowledge of the underlying ecological processes.

The interactions of spider mite and predacious mite populations with the host plant, the influence of abiotic factors (temperature, relative air humidity, wind and rain) and the effect of cultural measures (including the use of fertilisers as well as insecticides and fungicides) should be known before any conclusions can be drawn about the mechanism of the control. In several countries with a developed agriculture, research has therefore been started on the monitoring of the effect of predators on pest populations. An insight into their ability to control the pests is considered a necessary prerequisite for a stable pest control system. In the Netherlands, RABBINGE and VAN DE VRIE have developed basic models for fruit tree red spider mite (*Panonychus ulmi*) and the native predacious mite, *Amblyseius potentillae* (7).

Dynamic simulation models

Models are constructed according to the state variable approach. This technique is based on the assumption that at any particular time the state of an ecosystem can be expressed quantitatively, and the changes in the system can be described in mathematical terms. State variables characterise and quantify all observed properties of the system, such as biomass, number of animals, amounts of food, stomach content and so on. In mathematical terms, they are quantified by the contents of integrals[1]. The application of the defined state variable approach in ecosystem modelling, and the simulation language being used, Continuous Simulation Modelling Programme (CSMP), are outlined by DE WIT and GOUDRIAAN (9).

The models developed with this technique bridge the gap between biological control with predacious mites in the field and the analytical methods of natural sciences, thus assisting in the introduction and management of biological control agents of the fruit tree red spider mite. These simulation models are based on extensive knowledge of the effect of temperature, humidity, food condition and daylength on prey as well as predator. The predator-prey interaction (predacious mite—fruit tree red spider mite) in these models, which closely approximates the field situation, is based on a detailed analysis of the predation process.

This predator-prey interaction is very complex. Five morphologically distinguishable stages of the prey (larvae, protonymph, deutonymph, adult male and female), and four morphologically distinguishable stages of the predator (protonymph, deutonymph, adult male and female) are involved. The attractiveness of the different stages of the prey varies and depends, among other things, on the stage of the predator. For example, the adult female predator (the most voracious stage) shows a strong preference for the younger stages of the prey but 'hungry' predators are much less selective. The number of prey consumed, therefore, depends on the densities of the different development stages of the prey, on the densities of the predator, and on the state of hunger of the predator.

An explicit definition of the predator's hunger level is difficult, and several workers have attempted to circumvent this problem by estimating the degree of filling of the gut. This is not always acceptable, as the maximum gut content is too variable; moreover, the digestive system may vary widely between species. However, in the case of the predacious mites, the maximum gut content is more or less constant, and the degree of filling correlates with the predatory behaviour expressed as the success ratio (number of successful encounters divided by the total number of encounters). The use of the gut content to estimate the predatory activity is therefore permissible in this case.

Several years ago HOLLING (3) gave a general description of the predation process, and developed a mathematical model to provide an explanation of the three fundamental types of functional response curves which he distinguished. (Here, functional response means an increased predation with an increasing prey density up to a certain level when the predator is satiated.)

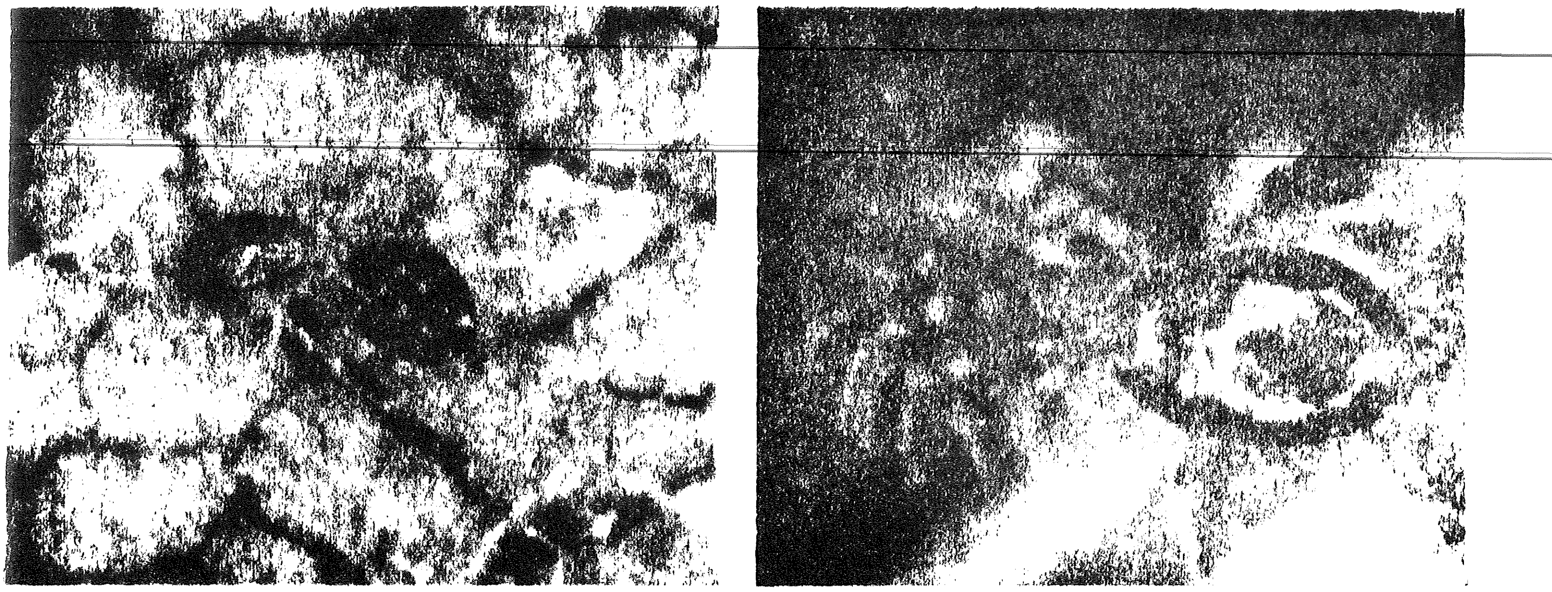
In these models, searching periods of the predator are calculated as a function of the variables at the start of searching, such as the degree of filling of the predator's gut. However, as mentioned above, the gut content of the predator changes during searching; therefore, computations of the values of the variables at the beginning of the searching periods are not sufficient to describe the predation process correctly. FRANSZ (2) used more flexible numerical integration methods by applying CSMP, and could include these effects. He succeeded in constructing explanatory simulation models for the predation process based on detailed analysis of the two-spotted spider mite (*Tetranychus urticae*)—predacious mite system.

The special case of spider mites and predacious mites

In the most elementary situation one predator and a constant number of prey is continuously watched. The number of captures per unit time (predation rate) depends on the number of encounters per unit time (encountering rate) and the success ratio. The success ratio is influenced by the hunger level of the predator and the frequency of encounters which may induce a lessening of the response termed by HOLLING, 'inhibition by prey'. The gut content of the predator is affected by the predation rate, the prey utilisation and the digestion. Both increase and decrease of hunger level are influenced by temperature.

The rate of decrease of gut content can be assumed to be exponential, being expressed as the gut content multiplied by the temperature-dependent, relative digestion rate. The ingestion rate of the predator depends on the state of the predator, whether it is handling or searching for prey, whether it actually feeds on the prey, and on the edible volume of the prey. The

[1] The content of an integral is the sum of the rates of change during a given period.



Left. *An adult female predacious mite feeding on an adult female prey (colour scale 5).* Right. *An adult female predator still feeding on the adult female of the prey, showing a dark reddish colour, indicating that she is nearly satiated (colour scale 6).*

nutritive values of different prey are assumed to be equal. The ingestion rate is assumed to vary according to the difference between the actual gut content and the maximum gut content.

Within the predation process, composed of searching, encountering, killing the prey, feeding, abandoning the prey, resting, and again searching, stochastic elements are present. The handling and abandoning of the prey are random processes; irrespective of handling and feeding time the number of prey caught in a short period Δt has a Poisson probability distribution with the average value $SE\Delta t$, S being the success ratio and E the average number of encounters per unit time.

Simulation models of the process described above may help in interpreting this process and promoting the understanding of the functional response curves, found experimentally, on the basis of the underlying ethological and physiological processes. At the same time, these models provide a basis for the incorporation of the predation process into higher order population models.

Calculations with models of the predation process made clear that the simple system reaches an equilibrium within a few hours, which means that the degree of filling of the gut of the predator oscillates with a small amplitude, at a level depending on predator and prey density and on the temperature of the system. This simplifies the incorporation of the complex predation process into higher ordered population models. It works adequately if the values of 'prey risk' and 'prey value' are simply expressed as a function of the variable most related to the predatory activity. Prey risk expresses the chance of each individual prey being caught. Prey value, for instance in units of gut content per killed prey, expresses the extent to which a prey is eaten and the predator's preference for a certain type of prey.

Quantification of the variable which expresses 'hunger' level in predacious mites can be effected colorimetrically, because well fed predators show a dark reddish colour, while hungry predators are whitish and transparent. A colour scale has been developed which relates the behaviour of the predator expressed in success ratio to the quantity of leaf and animal pigments in the predator, which together constitutes its colour. The rate of decrease of the colour, which is supposed to equal the digestion rate, is temperature-dependent, and this can be quantified in temperature controlled experiments. The ingestion rate of the predator and the rate of increase of the condition variable depend on the density of the prey and the predator.

From the experimentally found relations, 'predatory rate to prey density' and the 'predator state to prey density', the relations 'prey risk to predator state' and 'prey value to predator state' are found by calculation. All these relations are determined at different temperatures. The numerical response of the predator (an increased fecundity and/or a faster development from egg to adult as food is unlimited) depends also on its state and on temperature.

The switching of the predator from less preferred food to well accepted food, when available, has some ecological meaning. The predator thereby possesses the possibility of surviving long periods of absence of prey by switching to other, less attractive food such as honey, honeydew and pollen. *Amblysius potentillae* and the other predacious mites, *Amblyseius finlandicus* and *Typhlodromus pyri*, often found in Dutch apple orchards, have this ability. The presence of harmless, unattractive prey or food such as Eryophidae, pollen, honey and honeydew in Dutch orchards may stabilise the predator—prey system in such a way that, notwithstanding the absence of the prey, the predator still reaches a degree of nutrition which allows it to develop and lay eggs, although at a much diminished rate.

Considerations such as those given above may pave the way for a better understanding of regulation mechanisms in biological control. Man's interference with pest populations in terms of technical control should be based on this understanding. The final aim must be to guarantee the grower a more stable pest control system.

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