COST 819

BIOTECHNOLOGY

Ecology and transmission strategies
of entomopathogenic nematodes

Edited by

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CONCEPTS AND PROSPECTS FOR MODELLING THE EFFICACY AND ECOLOGY OF ENTOMOPATHOGENIC NEMATODES

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SUMMARY

Simulation models can improve insight in the ecology of entomopathogenic nematodes (EPNs) and their potential as biocontrol agents of soil pests. Models that include environmental and behavioural factors that are critical for the efficacy of an inundative release, may be used for guiding application strategies, EPN biocontrol-product formulation and genetic engineering of EPNs. Multi-generation population dynamical model provide a tool for estimating persistence, thus allowing assessment of risks associated with releasing genetically modified EPNs into the environment. Constructing a simulation model for one or more species of entomopathogenic nematode requires the retrieval and integration of existing knowledge of the quantitative ecology and behaviour of EPNs. Additional process-oriented research must be carried out to fill gaps in the available knowledge. The validation of simulation models will involve experiments under field conditions.

INTRODUCTION: MODELLING APPROACHES IN ECOLOGY AND CROP PROTECTION

A model is a simplified representation of a system and a system is a limited part of reality. Mathematical models represent numerical relationships between elements of a system. There are many different types of mathematical models and many criteria to classify them, e.g. process-based *versus* statistical, dynamic *versus* static, deterministic *versus* stochastic, and spatially explicit *versus* temporal (Peters, 1991; De Wit, 1993; Hurd & Kaneene, 1993). The character of a model depends foremost on its purpose. In crop protection ecology, three categories of models are prevalent: analytical models, simulation models, and descriptive models. These models differ in many aspects, including the level of aggregation and simplification, structure, purpose, methodology and data requirements (Table 1). These three modelling approaches could be characterized as speculative, mechanistic and correlative.

Table 1: Characterization of analytical models, simulation models and descriptive models in crop protection ecology

	Analytical models	Simulation models	Descriptive models
Characteristic	dynamic one to few equations	dynamic many equations	seldom dynamic one to few equations
Level of aggregation and simplification	high	low elaborate biological detail hierarchical: two levels, system & process level	high or intermediate
Purpose	abstraction generalization insight in principles	relationship processes <-> system influence environment insight in specifics	prediction
Examples	exponential & logistic growth predator-prey models Janssen & Sabelis (1992)	SeMNPV (see text); Nachman (1991) van den Bos & Rabbinge (1976); van der Werf et al. (1989)	Yellowing viruses, cereal diseases (see text)
Methodology	mathematical analysis: analytical integration stability analysis of equilibria	simulation of dynamics numerical integration sensitivity analysis simplification into decision rules	statistical regression
Required skills	mathematics	experimentation & programming	data survey and statistics
Data requirements	often loose relationship to data	detailed knowledge of life cycle (process level) data for model validation (system level)	elaborate data set
Disadvantages	oversimplification, irrealistic difficult to understand for biologists	lacking data laborious to verify code lengthy documentation difficult to keep overview	little or no insight little generality

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Analytical models summarize the main components of dynamic biological systems in a few equations that characterize the rates of change of the state variables. The foremost aim of analytical models is to study general principles underlying dynamic systems behaviour. Analytical models characterize a whole class of systems and their predictions, formulated as general insights, have wide validity. Such predictions may be difficult to operationalize in a specific system. An example of an analytical model of interacting pest and enemy populations is the system of differential equations

$$
\begin{cases}
\dfrac{dx}{dt} = \alpha\, x - \beta\, y \\
\dfrac{dy}{dt} = \gamma\, y
\end{cases}
$$

where x is the state variable prey density and dx/dt is its rate of change
y is predator density
α is the relative growth rate of the prey population (assuming unlimited resources)
β is the prey consumption rate per predator (assumed to be independent of prey density)
γ is the relative growth rate of the predator population (assuming unlimited food)

This simple set of equations characterizes some fundamental aspects of the interaction between spider mites and predatory mites in local patches (Janssen & Sabelis, 1992). Analytical integration of the differential equations yields general and testable predictions about the future course of the dynamics of the system. For example, it can be shown that the prey will finally be eradicated if the initial predator/prey ratio is greater than

$$
\frac{\alpha - \gamma}{\beta}
$$

The equation shows how the critical initial predator/prey ratio is affected by the relative growth rates of the prey and predator populations and by the feeding rate of the predator. These parameters are - of course - dependent upon conditions, such as temperature and host plant quality. This model serves the purpose of providing insight quite well.

The assumption of a constant consumption rate, independent of prey density, is only tenable if prey density is high enough. Inclusion of a curvilinear relationship between prey density and predator feeding rate would make the model more truthful. If that is done, analytical solution of the rate equations is no longer possible and the dynamics must be investigated by simulation. By making more realistic assumptions about the system, the model gradually develops into a simulation model.

Analytical models are criticized - and often rightly so - by biologists for being oversimplified, which makes their results less credible. Moreover, the mathematics involved in many papers on analytical models deters interest by biologists, especially if the results of mathematical analysis are not confronted with biologically interesting questions. Nevertheless, analytical models are a powerful tool for analysing and

demonstrating general principles in biological systems. Hudson & Norman (this volume) give an example of the application of analytical modelling to EPNs.

Simulation models are complementary to analytical models. They are much less aggregated than analytical models. This means that details of the life cycle, such as stage structure and spatial processes, are often explicitly represented in computer code. The model integrates the processes into a 'grand picture' of the whole system. Such models enable the study of the relationship between individual traits, environmental factors and the behaviour of the system. Simulation models are system specific. Predictions of the model, which are mostly formulated quantitatively, are therefore not of general validity.

An example of such a simulation model is the model for the epidemiology of the *Spodoptera exigua* nuclear polyhedrosis virus (SeMNPV) in a population of beet armyworm (*Spodoptera exigua*) in glasshouse chrysanthemums (de Moed *et al.*, 1990; van der Werf *et al.*, 1991). The model is constructed according to the state variable approach (Leffelaar, 1993).

In the model there is a bookkeeping of the initiation, development and demise of insect-infested crop patches. These patches are classified according to time of initiation and the presence or absence of virus. State variables that characterize patches include the numbers of caterpillars in each stage, the leaf area index of the crop and the density profile of virus over the height of the canopy. Processes within a patch that are modeled include the decay of virus, caterpillar infection by sprayed virus, insect feeding, spatial dispersal of caterpillars within and between plants, encounters between healthy caterpillars and virus-contaminated leaves, the development of caterpillars from one stage to the next, and the development of disease in infected specimens. The insect life-cycle is closed when eggs are laid by adult moths that emerge from the patches, starting a new generation of patches. Depending upon processes within the patch, and subject to stochastic influences, newly laid eggs may be infected or not. Infected eggs close the life-cycle of virus.

An important limitation to simulation models, based on state variables, is the often lengthy code and the difficulty of maintaining a firm conceptual hold of the interrelationships between parts and the whole. Good programming practice is an important tool to secure such overview and to ensure computational correctness, as is mathematical analysis of simplified model versions and limiting cases. Because simulation models incorporate biological details, they invite permanent updating as new insights and data become available. Such updating may or may not be appropriate, depending upon the model's objectives (which is seldom completeness) and the consequences of new insights and data for model behaviour. When making a simulation model it often becomes obvious that data, that are crucial to the model building, are unavailable. Such identification of knowledge gaps is useful for the progress of research and prioritization of research efforts, but the lacks of knowledge may frustrate the timely development and fruitful use of simulation models.

Three phases may be distinguished during the construction of a simulation model and within those phases there are several steps (Rabbinge & de Wit, 1989).

First, there is the *conceptual phase*. It includes at least three steps:
1. Formulation of the objectives
2. Definition of the limits of the system
3. Conceptualization of the system; determining the level of aggregation, simplification and detail, choice of state variables, relationships and external influences.

The conceptual phase results in a conceptual model and work plan for collecting the required process data and working out the model in computer code. The second phase includes at least three steps:
4. Quantification of relationships in the model using literature data and new experiments at the process level
5. Writing the computer code; documentation of the model
6. Testing the components of the model, verification of the code and checking that the performance of the simulation program is in agreement with the input data

The second phase results in a functioning computer program that is in accordance with the knowledge about the system and that is usable for the original (or adapted) objectives. During the second phase a technical documentation of the model and its inputs and outputs must be written. The third phase focuses on further analysis, application and (where possible) simplification of the model.
7. Validation of the model and parts of it, using independent experiments on the system level.
8. Structural and numerical sensitivity analysis
9. Simplification; development of a summary model; scenario studies with the model
10. Formulation of decision rules or forecasting tools to be used in management.

The SeNPV model was conceptualized by the use of state variables which quantify the number or density of individuals or 'amounts' in a certain category. An alternative approach in population models is to represent the individuals themselves and build an individual-based model (IBM; de Angelis & Gross, 1992; van der Werf *et al.*, 1989). This approach is especially appropriate for systems with small numbers of moving individuals in which spatial interactions and chance processes (encounters) are of prime importance.

Individual-based models hold promise for investigating host finding behaviour and movement of EPNs in the soil. The result of an individual based model can be summarized in a functional response formula (Fransz, 1974; Mols, 1993; van Roermund & van Lenteren, 1993), which, in its turn, can be implemented in a simulation model that is based on state variables. When simulating the whole soil-plant-insect-EPN system, computer-time of an IBM is likely to become limiting as EPNs are sprayed in high densities, up to 10^9 individuals m^{-2}.

Descriptive models are calculation tools, that are based on a statistical analysis of data, without an attempt to unravel the underlying mechanisms. They are complementary to analytical and simulation models. Their purpose is to predict an 'output' variable on the basis of knowledge of one or more 'input' variables.

Most descriptive models are static. Examples of this are regression equations that predict disease intensity on a regional scale, based on preceding weather. To predict

mildew severity in winter wheat in the Netherlands, Daamen *et al.* (1992) give the equation

$$y = -132 + 12\,x_1 + 10\,x_2$$

Here, *y* is predicted percentage of mildew-infested fields, x_1 is the average temperature in the preceding month of October (°C) and x_2 is the average temperature over the period december-March.

To predict the severity of sugarbeet yellows disease in the eastern beet growing area of England, Harrington *et al.* (1989) give the equation

$$y = 111 + 0.20\,x_1 - 68\,x_2$$

Here, *y* is predicted percentage of virus-infected plants in August, x_1 is virus incidence in the preceding year, and x_2 is the logarithm of the number of days with ground frost in January and February. In the equation, arcsine-transformed virus incidences are used (Snedecor & Cochran, 1989). Shortly before crop emergence, when the virus transmitting aphids *Myzus persicae* have begun to fly, the equation is modified into

$$y = 306 + 0.37\,x_1 - 26\,x_2 - 3.1\,x_3 + 0.0092\,x_3{}^2$$

Here, x_3 is the day (counting from 1 January as day 1) when the first *M. persicae* are caught in a suction trap for aphids in the centre of the eastern sugar beet growing area, near Bury St Edmunds.

The above static regression models are based on biological and empirical insight in what are the key factors in the system and on a thorough statistical analysis of the data set.

Berryman (1991) advocates the use of delayed discrete logistic equations to describe time-series of forest insects. These equations can be used to forecast outbreak years of these insects. Here again, the approach is correlative, but the model is dynamic.

Cellular automata models A class of models that are highly abstract and simplified representations of reality (like the analytical models) are the so-called cellular automata models (Sigmund, 1993). Here, individuals move and perform life functions on a chequerboard, representing the living space. Interactions occur between individuals in adjacent or nearby cells. Offspring is often produced into neighbouring cells. The rules regulating individual behaviour are generally stochastic (involving chance) rather than deterministic. Cellular automata models provide a useful vehicle for exploring the behaviour of spatially distributed population systems (insight function). They lack the specificity and biological realism required for prediction in practical situations. Their role in research is exploratory, like analytical models.

CONCEPTUAL STRUCTURE OF A SIMULATION MODEL FOR ENTOMOPATHOGENIC NEMATODES

Simulation models offer great potential for answering two critical questions with regard to entomopathogenic nematodes. 1. What are the critical factors determining the biological control success of applied entomopathogenic nematodes and how can the BC success be raised by more appropriate application techniques, formulation, environmental circumstances or genetic modification of EPNs?' 2. Will genetically-modified EPNs persist in the environment and how quickly will they or their genes disperse or disappear?

The first question can be answered with a monocyclic model, spanning a single life-cycle of the EPN. The investigation of EPN persistence in a given system requires insight into a series of such lifecycles. This requires a polycyclic model.

In the following a preliminary conceptual model, which is suitable for addressing the first question, is outlined. It bears resemblance to an existing model for plant pathogenic nematodes (van der Werf *et al.*, 1986). The system is a column of soil, surface area 1 m^2, containing spatially distributed insect hosts. The column is subdivided in layers to keep track of vertical redistribution of nematodes (Fig. 1). Vertical redistribution encompasses three processes: 1. mass movement with water fluxes, 2. random movement (diffusion), and 3. directed movement to hosts. No horizontal distribution of nematodes or hosts is taken into account. The frequency of encounters between nematodes and hosts is determined by 1. densities, 2. activity, 3. detection distance, 4. spatial clumping, 5. movement pattern of nematodes.
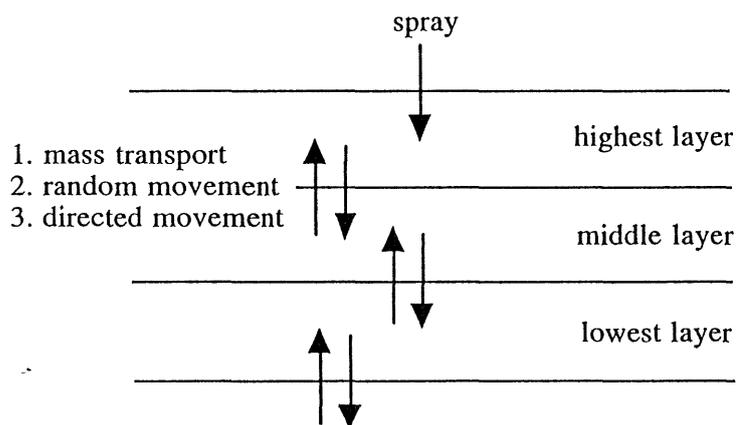
Fig. 1. Vertical movements of nematodes in a layered soil system, to be taken into account in a mono-cyclic model simulating biocontrol by applied EPNs

Studies on insect host finding behaviour provide good examples of how the encounter process may be modeled (Sabelis, 1981; Mols, 1993). Nematodes are subject to mortality and loss of vitality (quality), due to aging and biotic factors (Fig. 2). Infection success depends on vitality. Infected hosts produce a new generation of infective

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juveniles. Rates of movement, loss of vitality and infection are dependent on environmental factors, primarily temperature and water availability. Soil texture and structure affects the relationship between water content and suction force (pF). Water relationships affect nematode movement and oxygen availability (Wallace, 1963). The modelling concept is straightforward. Critical steps include the choice of the level of detail which should be both feasible and relevant. The quantification of rates, environmental influences and interrelationships in the system will be a challenge.
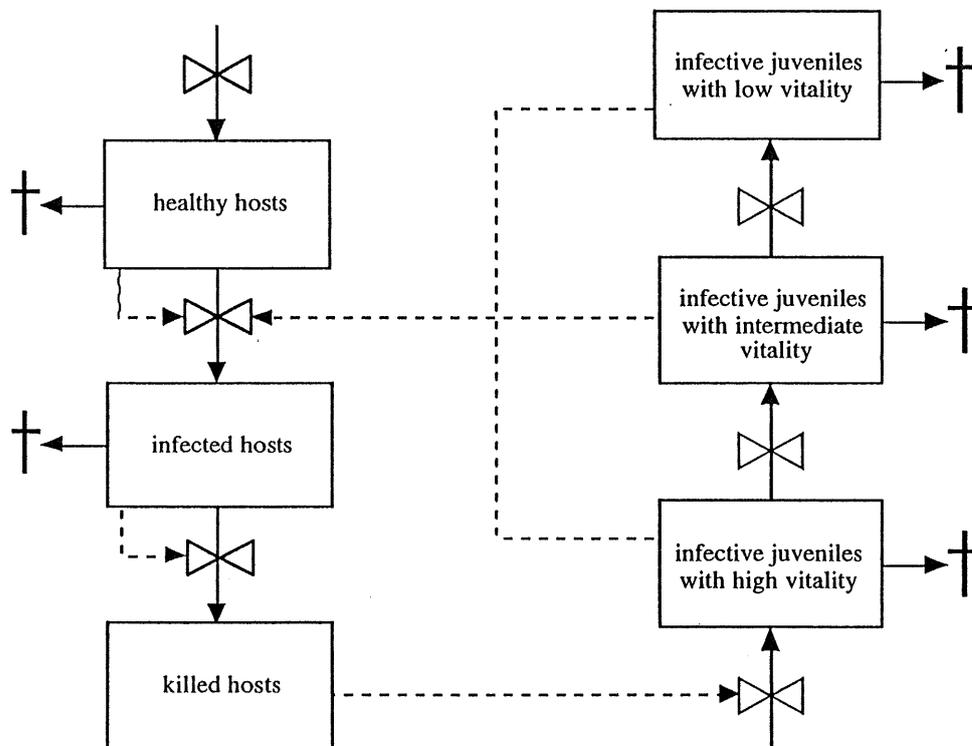
Fig. 2. Relational diagram illustrating the infection process (healthy insect hosts becoming infected and dying subsequently) and the gradual loss of infectivity of EPNs with age. Boxes are state variables. Drawn arrows + valves (-⋈►) represent rates of change of state variables. Hatched arrows indicate that the state variable at the origin of the arrow influences the rate(s) of change of (an)other state variable(s).

PROSPECTS

There is a wealth of information about temperature requirements and optima, survival rates and dose-mortality relationships for a range of hosts for several *Steinernema* and *Heterorhabditis* species, especially *S. carpocapsae* and *H. bacteriophora*. Although not all of the available information is optimally suited for parameterizing a model, there is at least sufficient information available to construct a preliminary model. Despite the knowledge of survival under standardized laboratory conditions, it

is still an unresolved puzzle by which process and in which quantities EPNs are 'lost' in the soil system after spraying. Recoveries directly after spray are seldom higher than 50% and often much lower.

There is little knowledge about the quantitative aspects of movement of EPNs in soil. Different EPNs have different host finding strategies; some are of the lying-in-wait type, others can be characterized as search-and-destroy strategists. The model building will require a quantitative concretization of these behaviours under a range of abiotic conditions, host distribution and quality, and the internal condition of the nematode. Modelling the foraging behaviour will help elucidate what strategies are viable from the nematode perspective and which strategies will enhance biological control under different conditions.

The influence of season on life-history parameters and behaviour is yet unknown as are interactions between EPNs and other soil biota (plant roots, competitors, predators, synergists)

Modelling the ecology and efficacy of EPNs is a challenging task. A full and detailed parameterization of the system will be impossible because it would require decades of work to quantify all the relevant relationships for the whole range of environmental conditions, even for a single nematode-host interaction. Research priorities must be set. This can be done with the aid of a preliminary model. Building such a model with literature data will help in structuring the information available and locating essential knowledge gaps. Sensitivity analysis of such a model will demonstrate which of the processes and parameters have the greatest influence on nematode ecology and efficacy and deserve therefore research priority. Modelling and systems analysis thus help to define spear points and allocate tasks in a network of research groups and industries interested in the development of EPNs as biocontrol agents. Models as the intermediate and end-products of systems analysis will provide unique tools for pinpointing critical factors for biological control success, for designing effective application strategies, and for analyzing the risks of persistence and spread of genetically-modified EPNs in the environment.

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