Fundam. appl. Nematol., 1998, **21** (5), 437-458

Forum article

THE SEINHORST RESEARCH PROGRAM

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Accepted for publication 30 January 1998.

Summary – We propose the 'Seinhorst Research Program', derived from Seinhorst's empirical philosophy. All theories of the 'Seinhorst Research Program' are developed by searching for recurring regularities (patterns) in a collection of observations, named 'the empirical base'. To prevent 'ghost theories from sloppy data', all assumptions underlying the empirical base are carefully described in theories with respect to methodology and technology, including statistics. The patterns to be recognised are summarised by mathematical equations, which must be connected with biological processes to bridge the gap between 'normal' language and mathematical language for the description of biological theories. Often, the patterns result from more than one biological process. If so, the basic patterns are disentangled from one another using a method of pattern analysis. The procedure is best carried out when only a limited number of more or less congruent patterns are involved. Therefore, attention must be given to the choice of the hierarchic level and the complexity of the investigated system. Investigations proceed from simple experimental systems to complex natural systems at a hierarchic level that is neither so high that manifesting processes are very dissimilar nor so low that one runs the risk of describing processes irrelevant for the purpose of the investigation. In the 'Seinhorst Research Program', this purpose is finding methods for improvement of financial returns of host crops attacked by plant-parasitic nematodes through calculating risks of nematode population development and subsequent yield reduction. Pattern analysis yields theories about causes of phenomena observed at the investigated hierarchic level and about properties of processes at the nearest lower hierarchic level. Predictions at the next higher hierarchic level are made by synthesising several patterns in (stochastic) simulation models. Synthesis is also applied to compound patterns of processes in simple experimental systems, with the objective of explaining complicated patterns in complex systems. © Orstom/Elsevier, Paris

Résumé – ***Le Programme de Recherche Seinhorstien*** – Nous proposons un " Programme de Recherche Seinhorstien " à partir de la philosophie empirique de Seinhorst. Toutes les théories de ce program sont développées grâce à la recherche de régularités récurrentes (modèles) dans une série d'observations appelée " base empirique ". Pour éviter les " théories fantômes fondées sur des données flasques ", toutes les assertions soutenant cette base empirique sont soigneusement décrites en tant que théories prenant en compte la méthodologie et les techniques, dont les statistiques. Les modèles retenus sont résumés par des équations mathématiques qui doivent être reliées à des processus biologiques afin de combler le fossé entre les théories biologiques exprimées dans les langages " normal " et mathématique. Les modèles se révèlent être souvent le résultat de plus d'un processus biologique. Si c'est le cas, les modèles de base sont démêlés en utilisant une méthode d'analyse des modèles. Cette procédure est accomplie dans les meilleurs conditions si elle ne concerne qu'un nombre limité de modèles plus ou moins congruents. L'attention doit donc être portée sur le choix du niveau hiérarchique et de la complexité du système étudié. Les recherches procèdent à partir de systèmes expérimentaux simples jusqu'à des systèmes naturels complexes et ce à un niveau hiérarchique tel que celui-ci ne soit ni assez élevé pour que les processus révélés ne soient très dissemblables, ni assez bas pour ne pas courir le risque de décrire des processus ne correspondant pas au but de la recherche. Dans le " Programme de Recherche Seinhorstien " ce but est de mettre au point des méthodes permettant une amélioration du rapport financier provenant de plantes hôtes attaquées par des nématodes en calculant les risques concernant l'accroissement des populations de nématodes et de la diminution correspondante des récoltes. L'analyse des modèles conduit à des théories concernant les causes des processus au niveau hiérarchique inférieur le plus proche. Les prédictions concernant le niveau hiérarchique supérieur le plus proche sont réalisées par la synthèse de plusieurs modèles en modèles de simulation stochastique. Cette synthèse est également appliquée aux modèles complexes de processus dans des systèmes expérimentaux simples, et ce dans le but d'expliquer les modèles compliqués existant dans les systèmes complexes. © Orstom/Elsevier, Paris

Keywords: analysis, comprehensive models, empirical base, empirical cycle, empirical philosophy, methodology, nematology, patterns, research program, stochastics, synthesis.

In this paper, we try to describe Seinhorst's empirical philosophy in some detail. He has never put his ideas about this subject into writing, probably because he considered them to be part of a classic philosophy developed and sufficiently described by others. To some extent this may be true but, first, not all interpretations of the classical empirical philosophy are equally satisfactory (Koyré, 1997) and, second, comments of fellow-nematologists on his work suggests that the nature of this philosophy and the way Seinhorst interpreted it in every-day nematological practice might not be quite clear to everybody.

Seinhorst's personal interests (natural sciences, philosophy, modelling) as well as his ideas on what should be the true purpose of science played an important role in his work. These ideas began to take shape in his 'underground period' during the last year of the Second World War, when he was 26 years old and had ample opportunity for reflection and studies in philosophy, natural sciences, theology, and linguistics.

In his personal diary for this period, he formulated his opinions on the ultimate purpose of the (natural) sciences: "Not extended factual knowledge, which can be such a nuisance in ambitious schoolmasters, but the deeper understanding, the possibility of a view over an unknown landscape must be the purpose of all work. Therefore careful examination of the work of the great scientists is also an instigating part of the study" (Personal diary Seinhorst, March 10, 1945; translated from Dutch by the authors). On the role of philosophy in natural sciences he wrote: "I am more interested in natural sciences than in philosophy. But without philosophy understanding is impossible. To me natural sciences and all that consists of separate observations, including art, is a passion. Philosophy is a duty, a necessity and an ambition" (Personal diary Seinhorst, March 12th, 1945).

These considerations, combined with a set of special conditions at the beginning of his career, were to become the backbone of his work.

Conditions

Apart from his personal interests, the research themes and the empirical philosophy which form part and parcel of the 'Seinhorst Research Program' are also logical consequences of a number of circumstances and conditions at the time of the foundation of this program in the early fifties. Many of these conditions are still valid today. They were described by Seinhorst (1996) as follows:

PURPOSE OF RESEARCH - MISSION OF THE IPO

At the time of its foundation in 1949, the mission of the Research Institute for Plant Protection (IPO-DLO), commonly known as IPO, was formulated as "Finding methods, by means of scientific research on pests and diseases in crops, to improve the economic returns of these crops". Seinhorst, responsible for the nematological research at IPO, interpreted the IPO mission for his discipline as follows: providing information to weight the costs of control against its benefits and find the optimal balance in individual cases.

THE TENDER AGE OF NEMATOLOGY AS A QUANTITATIVE NATURAL SCIENCE

When Seinhorst began his research at IPO, almost all scientific tools for accomplishing the IPO mission were lacking. This was even the case for stem, potato cyst, and beet cyst nematodes, that is, for species that were generally considered as harmful ones. There were no quantitative methods for measuring yield reduction by nematode populations in crops. Although the existence of a negative correlation between nematode density at the time of planting of a crop and its expected yield was generally accepted, no mathematical function was available to describe this correlation accurately. Yield reductions by nematodes were prevented by reducing nematode density before planting by means of crop rotation or soil fumigation and by growing resistant varieties, but the true effects of these control measures and the causes of these effects were largely unknown. The lack of knowledge of quantitative relations between nematodes and plants was closely connected to an almost complete lack of reliable methods for quantifying numbers of nematodes in soil samples and in plant parts. Although cysts could be extracted from the soil with Fenwick's (1940) can, no reliable methods were available to estimate numbers of eggs within cysts. Free-living nematodes were separated from soil by Baermann's (1917) funnel, which is only suitable for small soil samples, or by Cobb's (1918) sieving and decanting method, both methods of unknown efficiency and accuracy (Seinhorst, 1988).

PREJUDICES AND FANTASIES

The lack of quantitative knowledge on plant/nematode relations gave ample room for fantasies about causes of yield reduction by nematodes and about nematode control. Even today the situation has not much improved because of the reluctance of most nematologists to be involved in quantitative research.

Reductionism

In The Netherlands, this situation was mainly due to the fact that quantitative nematology was not included in the education of students. Internationally, there is a shift of nematological research to low hierarchic levels (*e.g.*, molecular level) and a tendency to interpret low level results as causes of phenomena at a higher level. The same tendency has been observed in other natural sciences. In physics, it was called 'reductionism' by Lagendijk (1989). Reductionism assumes that all biological processes follow the same laws and that all phenomena can be explained by studying only the building stones at a low hierarchic level. True reductionists consider that the translation of genetic or molecular information to processes in space and time, resulting in an adult organism, is superfluous and they think that theories on nematode/plant interactions and organisation patterns that exist within and between the intermediate hierarchic levels from low (molecular) to high (farmer's field) are irrelevant. However, new concepts became manifest at higher hierarchic levels. These concepts must be consistent with those at the lower hierarchic levels, but they cannot be deduced from them (Kooijman, 1987; Lagendijk, 1989): "More is different" (Anderson *et al.*, 1988). Just as the question of whether or not quarks are locked-in is irrelevant to a brain surgeon (Lagendijk, 1989), the point of protein-based similarity dendrograms for pathogens is irrelevant to breeders and farmers.

Yield reduction

Seinhorst (1986*b*) noted most causes attributed to growth reduction by nematodes in the literature as "myths and fairytales". He mentioned obstruction of plant vessels causing wilting (Oostenbrink, 1950), withdrawal of nutrients, mechanical damage to root tissue resulting in a hampered uptake of water and minerals, and decreased shoot-root ratio causing insufficient mineral uptake (Trudgill *et al.*, 1975*a*,*b*,*c*; Evans *et al.*, 1975; Trudgill, 1980; Trudgill & Cotes, 1983).

Control measures

Beliefs and ideals on the ultimate solution for nematode problems range from frequent applications of both fumigant and non-fumigant nematicides (Mulder, 1979; Mulder *et al.*, 1979) - which were wrongly supposed to have favourable cost/benefit ratios -, to the use of late-maturing potato cultivars (Trudgill *et al.*, 1990; Haverkort *et al.*, 1992) - which were wrongly presumed to be more tolerant than early cultivars - and to a balanced bio-diverse (agro)-ecosystem - which was supposed to suppress harmful organisms (Sikora, 1992). The true nature - structural or functional - of such an equilibrium, or homeostasis, in which many biologists tend to believe, is still controversial. As 'normal' ecosystems are characterised by large structural fluctuations, there seems to be more reasons to believe in a functional - with respect to food chains - homeostasis (Odum & Biever, 1984) than in a structural one - with respect to numbers of species - (Rosenzweig & McArthur, 1963). However, the hypothesis of homeostasis is basically disputable because reliable quantitative methods, based on identification and distribution patterns of all relevant organisms, to describe 'biodiversity' or 'equilibrated' ecosystems are conspicuous by their absence.

Research themes

Because of these conditions, which to some extent still persist nowadays (especially for *Meloidogyne*, *Pratylenchus*, and *Trichodorus* species), the 'Seinhorst Research Program' on plant-parasitic nematodes consisted of the following four themes (Seinhorst, 1996):

METHODOLOGY

Methods for the estimation of numbers of the various nematode species in plant and soil samples and other experimental methods, with known accuracy, both for research and extension purposes, including:

- Methods for extraction of nematodes from plant and soil samples with known efficiency.
- Identification methods, including fixation techniques and microscopy.
- Nematode distribution patterns at different scales, varying from centimetres to several metres in farmers' fields.
- Methods to identify and quantify sources of variance.

YIELD REDUCTION

General relation between nematode densities at the time of planting and relative yield (yield of plants with nematodes as a proportion of yield in absence of nematodes, all other conditions being identical).

POPULATION DYNAMICS

General relation between nematode densities in soil or plant samples at successive observation dates during the vegetation period of the host plants (for instance at planting and at any time afterwards, such as after ripening of the plants). This relation must take into account the degree of plant growth reduction by the nematodes.

CONTROL MEASURES

Relations between control measures (nematicides, biological control, resistant cultivars, crop rotation) and nematode population dynamics and crop growth.

A proper integration of control measures and farmers' practices requires integration of all relations in an operational model, which implies that they must be available as mathematical equations. The model must predict, within adequate and specified limits, the consequences of control measures against nematodes in an individual field. These control measures must be taken, at the latest, at the time of planting of the host crop to be protected, but generally much earlier. Such a requirement makes inclusion in the model of most external conditions during crop growth useless. Therefore, deterministic models with their high dependence on external conditions can at best predict average effects in large areas. They are unfit to predict nematological phenomena and their consequences on an individual farmer's field. As a consequence, Seinhorst chose to develop stochastic equations with few parameters, the distribution functions of the latter to be estimated by detailed research.

Empirical philosophy

To exclude as far as possible preconceived ideas and biased conclusions on causes of nematological phenomena, both from the literature and from sloppy empirical methods, and to make all nematological equations and theories consistent, including those influencing the empirical base, such as methodology, technology, chemistry, mathematics, and statistics, Seinhorst applied the Newtonian empirical philosophy, excellently described by Cohen and Westfall (1995), in a consistent manner. According to this philosophy, complex natural (here nematological) situations are reduced to mathematical simplicity by studying the properties of a mathematical analogue. The methods of analysis and synthesis are applied in the order described by Newton, the former always preceding the latter, to be sure that relevant principles are assumed. "Analysis proceeds from effects to their causes and from particular causes to more general ones, guided by mathematical properties of recurring regularities (patterns). Synthesis consists in explaining phenomena from their discovered causes, which are then regarded as principles, thus confirming the explanations" (Newton interpreted by Cohen, 1995). The philosophy further includes correspondence rules to link the results of mathematical analysis to nematological theories in 'normal' language. These rules are: *i*) the mathematical analogue should describe biological processes; *ii*) the variables and parameters in the mathematical analogue should have clear nematological interpretations.

We shall use the empirical cycle as a model to clarify each and every step during investigation in the 'Seinhorst Research Program' and to reveal all external theories used. In some respects, the present empirical cycle differs from those described by others, for instance by Zadoks (1978) or by Campbell and Madden (1990). The reasons why will be explained.

To avoid confusion, some terms used in this paper, such as hypothesis, theory, model, accuracy, precision, etc., that do not have an unequivocal meaning for all scientists, are explained in a Glossary.

Glossary

Accuracy	The closeness of a sample estimate to its true value.
Analysis	"... consists in making experiments and observations and in drawing general conclusions from them by induction, and admitting of no objections against conclusions, but such as are taken from experiments and other certain truths. For hypothesis are not to be regarded in experimental philosophy." Analysis enables us to "proceed from effects to their causes" (Newton in Querie 31 of the Opticks, as interpreted by Cohen, 1995).
Anomaly	A manifest phenomenon in a system that is not explained by the theory with respect to that system.
Deduction	Inference - only by logical rules - of hypotheses or new theories from fundamental theories.
Deterministic model	Model in which parameters are considered to be true constants.
Empirical base	Collection of observations that are free from theories, except methodological theories.
Empirical cycle	Reconstruction of working methods in observations and theory building in science.
Empirical philosophy	Philosophy with respect to scientific working methods, especially those with respect to observations and theory building.
Falsification	Elimination of theories or parts of theories that are contradicted by recurring patterns in the empirical base.
Hierarchic levels	Order in the organisation of a system from low (molecule) to high (ecosystem).
Hypothesis	General statement about causes attributed to phenomena, insufficiently supported by a model.

Glossary (cont.)

Induction	Way of reasoning that derives general causes of phenomena from recurring regularities in an empirical base.
Model	Empirical base, pattern, theory, and a set of rules to connect them mutually.
Parameter	Biologically relevant quantity in an equation that determines its outcome over a certain range of values of the independent variable.
Pattern	Regularity, recurring in the empirical base about natural phenomena manifest in a certain system, from which causes are induced by mathematical analysis and predictions about future phenomena in that same system are deduced. Mathematical analogue of a theory.
Philosophy	In this paper philosophy is used as described by Wittgenstein (1918) in his Tractatus 4.112. "The purpose of philosophy is the logic clarification of thoughts. Philosophy is not a science but an occupation. A philosophical work consists basically of elucidations. The results of philosophy do not consist of 'philosophical propositions' but of clarification of propositions. Philosophy should clarify and demarcate thoughts that otherwise would be troubled and vague." (This choice of definition does not imply that in our opinion there is no justification for philosophy as a science. S & B).
Precision	The repeatability or variability of a sample estimate.
Process	Spatial and/or temporal changes in phenomena.
Reductionism	The concept that phenomena at any hierarchic level can be explained by studying the phenomena at the lowest level.
Research program	Lakatos (1978): A set of logical coherent theories named after its founder and used to explain natural phenomena. The theories consist of methodological and fundamental theories and new theories. Falsification of theories in case of anomalies is done only if it brings scientific progress. Apart from the theories, the program also includes: • An empirical philosophy • Methodology (methods and instruments) • Directions for further development of the program. New theories must be logical consistent with the fundamental theories that represent the core of the research program.
Stochastic model	Model in which parameters are considered to vary under influence of changing known and unknown environmental factors.
Synthesis	or 'composition' "*..consists in assuming the causes discovered and established as principles, and by them explaining the phenomena proceeding from them, and proving the explanations.*" (Newton in query 31 of the Optics, as interpreted by Cohen, 1995).
System	Specific surroundings in which observations are made. These surroundings can vary from simple (experimental systems) to complex (natural systems).
Theory	General pronouncements (in 'normal' language) about causes of phenomena in a certain system, sufficiently supported by a model, from which future phenomena in that same system are predicted. Natural analogue of a pattern.

Empirical cycle

The empirical cycle (Fig. 1) is divided into four empirical sub-cycles, covering the following subjects:

- Methodological models.
- Fundamental models.
- Compound models.
- Models of causes.

At the beginning of a new investigation, when hardly any quantitative information is available, the sequence indicated above is followed, the development of methodological theories with respect to

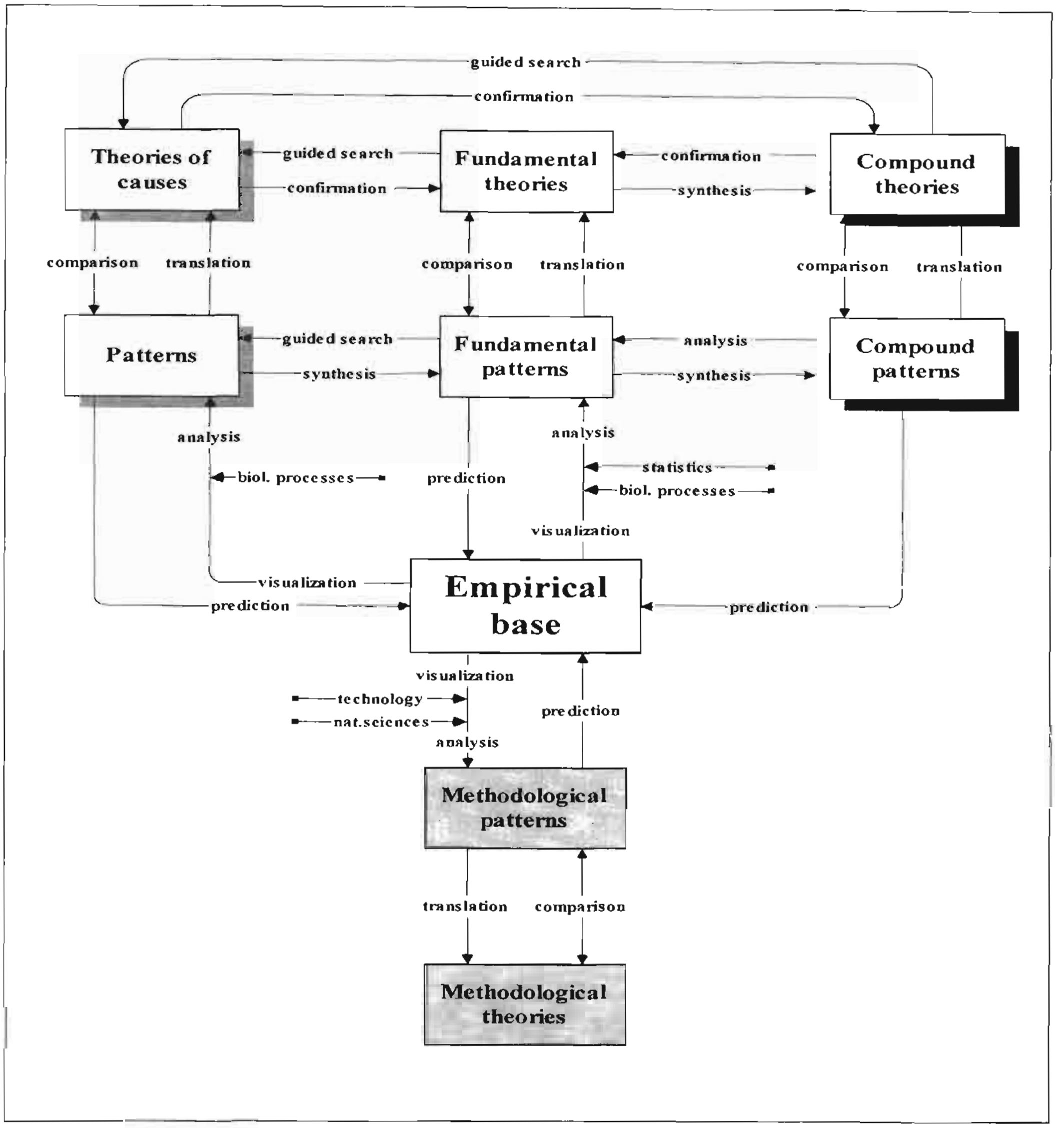

Fig. 1. *Model of the empirical cycle of the 'Seinhorst Research Program', divided in four empirical sub-cycles. Patterns and theories are placed in different box types for each sub-cycle, as indicated below.*
Grey rectangle: Methodological models; White rectangle: Fundamental nematological models; White and black rectangles superposed: Compound nematological models; White and grey rectangle superposed: Models of causes; Empirical base: All sub-cycles originate from and return to the empirical base. ■→ *Imported external information (statistics, biological processes etc.);* → *Processes leading from one (intermediate) result to another (analysis, synthesis, etc.)*

nematological observations preceding that of fundamental nematological theories and theories deduced from these fundamental theories. Later on, the theories in the cycles are considered as jigsaw puzzles. Whenever a piece becomes available, often because of research-questions on agricultural problems, sometimes by coincidence, it is fitted in. When a pattern appears in the puzzle, it can be used in three ways, first to improve calculations on risks of unwanted phenomena in farmers' fields, second to discover the causes (at a lower hierarchic level) to these phenomena, guided by the newly discovered properties of these causes, and third to develop new ways of control (prevention or counteraction) based on these causes, for instance by manipulating plant properties through biotechnology programs.

New nematological theories can only be derived from fundamental nematological theories and their mathematical analogues. In all sub-cycles, the following steps are taken from observation to theory and back.

EMPIRICAL BASE (OBSERVATIONS)

Assumptions

All empirical knowledge goes ultimately back to an empirical base, with records of details of experiments and observations. As this base serves as an impartial arbiter in accepting or rejecting theories, it should be independent of these theories. The requirement of independence also applies to the observation language. Thus, replacement of one theory by another would be of no consequence for the observation terminology or the truth of the basic conclusions (Koningsveld, 1976). It may be feasible to make observations not loaded with nematological theories, but it is impossible to perform theory-free observations when theories from other disciplines are needed to do any observations at all. Examples are physical or statistical theories needed if microscopy or counting problems play a role in the observations and in the basic conclusions drawn from them. Generally speaking, all methods and measuring instruments used to obtain the facts on which theories are to be based contain their own theories and assumptions that will influence the conclusions from observations if these theories should be changed (Popper, 1968). To handle these biases as carefully as possible, all necessary 'external' theories are formulated in a separate methodological empirical sub-cycle (Fig. 1) and are carefully checked for their consistency with fundamental nematological theories during the progress of the research process. Observations from the literature, either on methodology or nematology, are handled in the same way. Nematological observations are added to the empirical base only when the theories underlying the methods are recognised as fundamental in their own disciplines and are consistent with the fundamental nematological theories. If not, the observations cannot be used in the research program discussed here.

The requirement of 'theory-free' observations does not mean that nematological theories cannot be used to decide which observations are relevant and which are not (Koningsveld, 1976). For instance, when nematode/plant relations are studied, one can decide to make observations at a specific range of nematode densities because one knows from the theories that these are relevant to the pattern. In such a case, a nematological theory is used to do observations that will remain valid if the nematological theory should be changed.

Systems studied

In the 'Seinhorst Research Program', the investigations proceed, in general, from simple experimental systems (pot experiments) to complex natural systems (farmer's fields) so that all fundamental processes can be identified without being masked by each other or by secondary effects. Patterns found in simplified experimental systems are compared with those in natural systems (individual farmers' fields) to find out whether the experimental system has the necessary level of complexity to attribute causes, judged as sufficient and true to explain effects in the experimental system, to effects in the natural system. The hierarchic level at which the investigations begin is chosen so that all manifest processes at that level are relevant to predictions at the chosen explanatory level (farmers' fields), without ignoring essential patterns in the relations between the hierarchic levels. The investigations proceed from higher to lower hierarchic levels to answer further questions with respect to the causes of phenomena that appear at the explanatory level. Example 1 illustrates this procedure for Seinhorst's theory on growth reduction by nematodes.

PATTERNS

Sawyer (1955) defines patterns as any kind of regularities that can be recognised by the mind. Sawyer's thesis "A recurring pattern is significant" is adopted in the 'Seinhorst Research Program'. It is therefore assumed that a repeatedly manifesting pattern always has a (here biological) meaning which should be investigated. The significance of the pattern needs no other proof than its recurrence and its biological meaning. The ultimate aim of pattern analysis is twofold:

- Recognition and identification of the biological process(es) that belong to the pattern(s) found. The number of biological processes is higher than the number of patterns. So, the same pattern can be attributed to several biological processes. Therefore,

Example 1. "Growth reduction"

Yield reductions at small and medium nematode densities are caused by a constant reduction of plant growth, desynchronising plants with and without nematodes (Seinhorst, 1986*b*). From Seinhorst's fundamental theory it can be deduced that this phenomenon can be involved only if nematodes affect growth for a short period (at most 24 hours). Questions about the physiological or biochemical mechanisms involved must be investigated at a lower hierarchic level.

the connection of a biological process with a pattern is also dictated by the nature of the investigated subject.

- Mathematical description of the pattern with minimum differences between observation and theory, in such a manner that variables and parameters have clear biological interpretations.

Visualisation

To trace and recognise regularities in the empirical base in the form of mathematical patterns, the results of observations are visualised graphically, mostly in two-dimensional graphs, but sometimes in three-dimensional graphs when patterns behind patterns are important to attribute causes to phenomena. For instance, this was the case in Seinhorst's relation between relative yield and pre-plant nematode density P (Example 2).

Recurring aberrations from the expected pattern in an empirical base, for instance non-monotonic change in the pattern for population dynamics (Example 3; Fig. 3) or in dose-response relations (Example 7; Fig. 5), or discontinuities often indicate that more than one process became manifest.

Biological processes

In the 'Seinhorst Research Program', patterns are condensed into one or more mathematical equations describing biological processes. The equation parameters must have clear biological meanings so that theory building (transfer of mathematical properties to nematological theories formulated in normal language and vice versa) is possible. The number of parameters in these equations is as small as possible but sufficient to explain the effects of the full range of the independent variable under investigation. "As a rule, no more causes of effects are admitted than is sufficient for their explanation and the same causes are assigned, as far as possible, to the same effects" (Newton interpreted by Cohen, 1995).

To recognise and describe patterns in the empirical base under investigation, one must be familiar with the mathematical patterns belonging to the biological processes discovered up to now and with all underlying assumptions. Pattern analysis opens the possibility to trace biological processes that have not yet been described.

Statistics

In the 'Seinhorst Research Program' statistical methods are developed with the same caution as nematological theories, but nematological theories always come first, before statistics. Statistical theories hardly ever used during pattern analysis as they usually demand drastic additional assumptions, which, later, when more data are available, are often found to be conflicting with the observations. Moreover, information from the usual regression analysis, such as the amount of variance explained or the confidence intervals of parameters, is irrelevant for the explanation of biological patterns.

The aims for pattern analysis in the 'Seinhorst Research Program' do not comply with the common practice of many biologists and nematologists who only try to find the best fitting equation by assuming that the higher the value for R^2, the better the equation describes the relationship. Some nematologists, *e.g.*, Elston *et al.* (1991) and Mulder (1994), even apply this procedure without any restriction to field data on relationships between nematode density P and yield obtained with unknown, but non-constant (as sample sizes were small and not adjusted to nematode density) estimation errors on both the abscissa and the ordinate, with no observations at $P = 0$, and with variables other than nematode density determining yield. Such use degenerates statistics into a ritual (Slob, 1986) instead of a purposeful occupation to develop theories about sources of variation that are consistent with the other (biological and methodological) theories. These statistical theories are mostly developed at the later stages of theory building, when the empirical base is sufficient to determine the distributions' functions of variables and parameters for both the experimental and the natural systems. A recent statistical theory, consistent with nematological theory, is that for infestation foci (Schomaker & Been, unpubl.).

The following quotations of Seinhorst in 'Comments to comments of referees' or in letters to colleagues illustrate the misunderstandings occurring between nematologists with very different opinions on

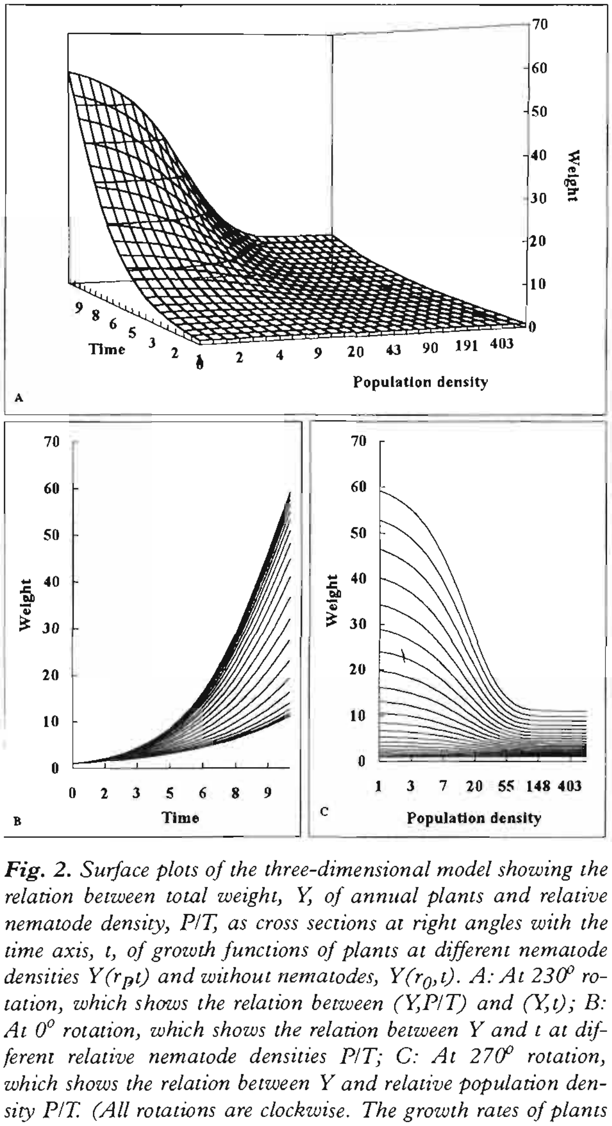

Fig. 2. *Surface plots of the three-dimensional model showing the relation between total weight, Y, of annual plants and relative nematode density, P/T, as cross sections at right angles with the time axis, t, of growth functions of plants at different nematode densities* $Y(r_P t)$ *and without nematodes,* $Y(r_0,t)$*. A: At* 230^0 *rotation, which shows the relation between (Y,P/T) and (Y,t); B: At* 0^0 *rotation, which shows the relation between Y and t at different relative nematode densities P/T; C: At* 270^0 *rotation, which shows the relation between Y and relative population density P/T. (All rotations are clockwise. The growth rates of plants of the same weight without nematodes* (r_0) *and at nematode densities P* (r_P) *are related by Equation 3.* $r_P/r_0 = k + (1-k).z^{P-T}$ *for* $P > T$*).*

the purpose of statistics: "Models cannot be derived from the data with the help of statistical methods. A straightforward multiple linear regression analysis would almost certainly have led us astray by finding a chaotic set of slopes and would at best tell us that the treatments had one or perhaps two ... effects, which of course is apparent without formal statistical analysis" and "If science would have proceeded as he [the referee, taking pattern analysis for speculation. S & B] seems to suggest it should, it would have stopped developing before Newton. If anything is 'speculative' the 'Principia' is, deriving the weight of the sun, the moon and the planets from what can be seen by simply looking at the sky at night, a simple hypothesis, based on nothing and a lot of mathematics."

Most patterns in biology, including nematology, are non-linear, as dictated by the nature of the investigated subject. Best fits are found by least square calculations of all observations, using numerical trial and error, which is most easily - but not necessarily - done by computer, especially when compound effects are involved. Commercial computer programs for numerical analysis must be regarded with some mistrust because of their ability to produce nonsense estimates in the case of wrong starting values, unsuitable step values, a too small number of iterations or wrong additional assumptions, for instance about the nature and the constancy of variance.

In Example 4, the mathematical analogue of Seinhorst's theory on growth reduction of plants attacked by small and medium densities of nematodes is summarised. The theory is more fully described by Seinhorst (1986*b*) and Schomaker *et al.* (1995). It can be transcribed in 'normal' language because the correspondence rules required in the 'Seinhorst Research Program' are obeyed.

COMPOUNDS PATTERNS

Often, a pattern cannot be explained by a single process but only by a combination of two or more processes. In such a case, analysis of the pattern makes it possible to split it into separate patterns, each belonging to separate biological processes. Then, patterns are regrouped by synthesis and compared with patterns from new observations. The choice of the hierarchical level at which observations are made is crucial for the success of this procedure of alternate analysis and synthesis. It should not be too high, because manifest but overlapping processes would become too numerous and too different from each other to be separated. Nor should it be too low, as then one is at risk to describe biological processes that are irrelevant for the purpose of the investigation. The analysis and synthesis of compound comprehensive models on population dynamics, hatching processes, and dose-response relations into separate processes is illustrated in Examples 5, 6, and 7. Full descriptions of these models are given by Seinhorst (1993), Schomaker and Been (1998), and Been and Schomaker (unpubl.).

In the methodological empirical sub-cycle, alternate analysis and synthesis are also applied to compound variance from different sources to make more efficient experimental schemes or practical tests for resistance and tolerance (getting more information from less work) or to choose tests with an optimal cost/uncertainty ratio for extension purposes. In the latter case,

Example 2. "Growth reduction"

Seinhorst (1998) gives the relations in pot and micro-plot experiments between P/T of various nematode species and $y' = (y-m)/(1-m)$ where y and m are the relative dry weights of different hosts at $P/T > 1$ and $P/T = \infty$, respectively, several months after planting. T is the highest density that causes no noticeable yield reduction. The relation between P/T and y' is in close accordance with

$$y' = 0.95^{P/T-1} \tag{1}$$

in all 36 experiments but this equation does not describe an underlying process. The cause of reduction in plant weights by nematodes - a constant growth retardation ("the same happens later", Seinhorst 1986*b*) - is revealed only when these relations are represented as cross sections at right angles with the time axis of growth functions of plants at different nematode densities P (Fig. 2).

Example 3. "Population dynamics"

The pattern belonging to Seinhorst's extended population dynamic model for nematodes with one generation per vegetation period (P_f) is visualised in Fig. 3. The non-monotonic change in its pattern indicates that we are dealing with a compound pattern, the result of two or more underlying patterns. The relevant questions at this stage are: "How many patterns can be distinguished?" and "To which processes are they referring?" These questions can only be answered properly by a mathematical analysis of the pattern.

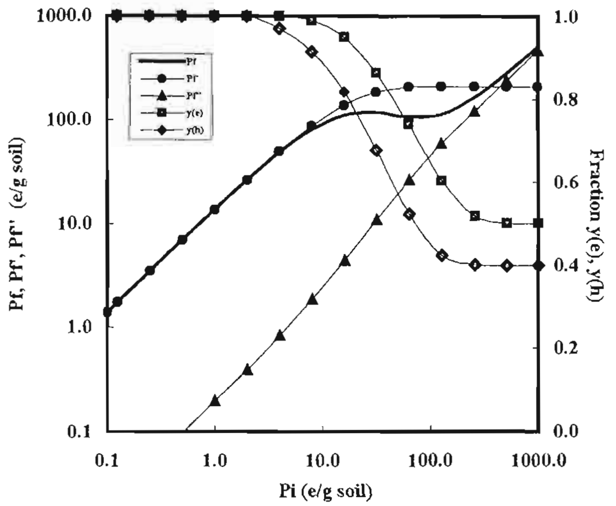

Fig. 3. *The compound model Pf, represented by the heavy line, for population dynamics of tylenchid nematodes with one generation per growing season. It consists of four non-linear equations. Three of them,* ●*Pf',* ◇y_h *and* □y_e*, are multiplicative and one,* ▲*Pf'', is additive.* ◇y_h *and* □y_e *represent fractions;* ●*Pf' and* ▲*Pf'' eggs per gram of soil (e/g).*

the financial consequences of the uncertainty in predictions by a test, due to a certain amount of variance, are weighted against the costs of the test to find the optimum.

Examples of the use of compound pattern analysis to identify and quantify sources of variance using parametric statistics (not to be confused with ANOVA or Multivariate Analysis) are presented in a posthumous paper by Seinhorst *et al.* (unpubl.) on tests for partial resistance to potato cultivars for potato cyst nematodes and in a paper by Been and Schomaker (unpubl.) on effects of pesticides on hatching behaviour of potato cyst nematodes.

Another possible use of compound patterns (and theories) are simulation models that synthesize several fundamental (simplified) patterns at a given hierarchic level into a comprehensive model generating predictions and new theories about relevant nematological scenarios at the same and higher hierarchic levels. An instance of a stochastic simulation model for advisory purposes is described in Example 8.

PATTERNS TO CAUSES

Fundamental nematological patterns make it possible to derive the properties of processes at a lower hierarchic level. These properties can be used to trace these processes and the patterns belonging to them. This type of research has never been done at IPO, but we are planning to change that. Elsewhere in this paper, under 'Causes at low hierarchic levels' in

Example 4. "Growth reduction"

The mathematical analogue of Seinhorst's theory on growth of plants affected by small and medium nematode densities (Seinhorst, 1986*b*; Schomaker *et al.*, 1995) shows that:

$$\begin{array}{lll}
r_p/r_0 & = t_0/t_p & \text{for } Y_0 = Y_p \qquad (2)\\
 & = k + (1-k).z^{P-T} & \text{for } P > T \qquad (3)\\
 & = 1 & \text{for } P \leq T \text{ and}\\
 & = k & \text{for } P \to \infty\\
z^T & = 0.95 & \qquad (4)
\end{array}$$

As a consequence

$$\begin{array}{lll}
y & = m + (1-m).0.95^{P/T-1} & \text{for } P > T \qquad (5)\\
 & = 1 & \text{for } P \leq T \text{ and}\\
 & = m & \text{for } P \to \infty
\end{array}$$

The parameters *m, k, T,* r_P, r_P and *z* have a clear biological meaning.

Y_0	g	weight of whole plants or parts of plants without nematodes.
Yp	g	weight of whole plants or parts of plants at nematode density *P*
y	-	relative plant weight Y_P/Y_0
t_0; t_p	day	time needed for plants respectively without and with nematodes to reach the same weight *Y.*
r_p/r_0	-	relative growth rate
m	-	minimum relative plant weight.
k	-	minimum relative growth rate.
T	e/g	largest nematode density not affecting the relative growth rate and relative plant weight
r_P	g/day	growth rate of plants at nematode density *P*
r_0	g/day	growth rate of plants without nematodes
z	-	the degree to which plants can prevent growth and weight reduction by nematodes.

Equation (3) describes the relevant nematological process at play when nematodes compete for effect on plant growth.

'Future Research' and in Examples 1 and 9, suggestions are given about research proposals to this effect.

THEORIES

Pattern translation

In many biological studies, the stage of theory building is never reached because the conditions (see PATTERNS) enabling translation of the mathematical equations into a theory in 'normal language' are not fulfilled. General conclusions from the observations are then reduced to reports of alternative 'facts' that usually are evaluated statistically in H_0 *vs* H_1 tests (Zadoks, 1978). Campbell and Madden (1990) call these types of models 'correlative models' which, contrary to 'explanatory models', give no information on the causes of phenomena (Fig. 6). In explanatory models, the phenomena are deduced from a theory or concept, which appears out of nowhere or comes - in an unspecified manner - from the descriptive model. The main objection against the working method proposed by Campbell and Madden (1990) is that it

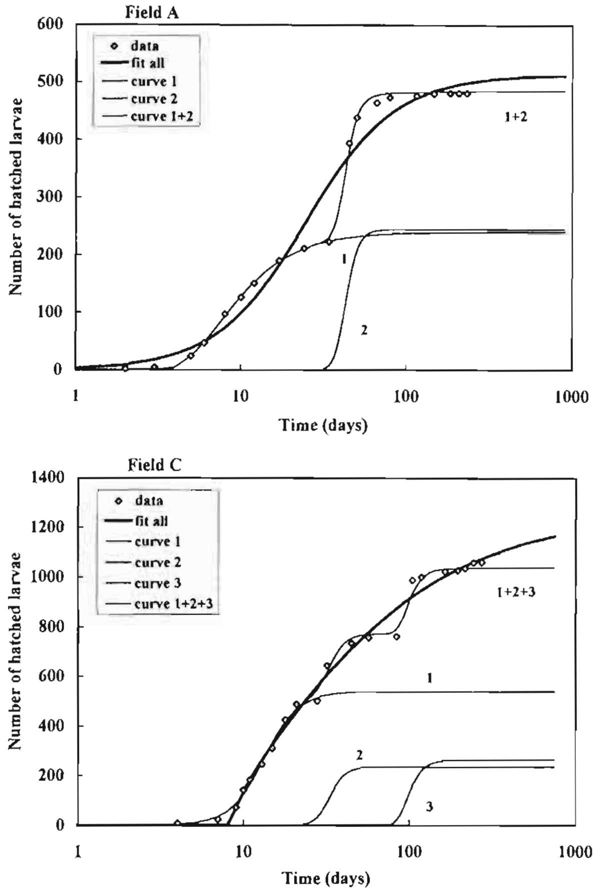

Fig. 4. *Compound hatching curves of field populations of nematodes, consisting of two (field A) and three (field C) superimposed hatching curves. Original data (◇), overall fit to a log-logistic equation using all data, fit of separate curves and a compound fit using two and three log-logistic equations, respectively.*

leaves too much room for preconceived ideas, which, if the model contains many parameters, can explain observation satisfactorily in hindsight (by adjusting the parameters), but need not be true and sufficient causes of the phenomena. Descriptive models have the disadvantage that - although some facts may become plausible - they hardly contribute to theory building as causes of the observed phenomena are not revealed. Unfortunately they have found a widespread use in the 'Deterministic Dynamic Simulation Models', at the cost of theory-building. Seinhorst wrote about this subject: "They confuse dynamic models with *ad hoc* equations for statistical operations, thus reducing scientific work to plain fact reporting, not understanding that 'a fact without a theory is a ship without a sail' ".

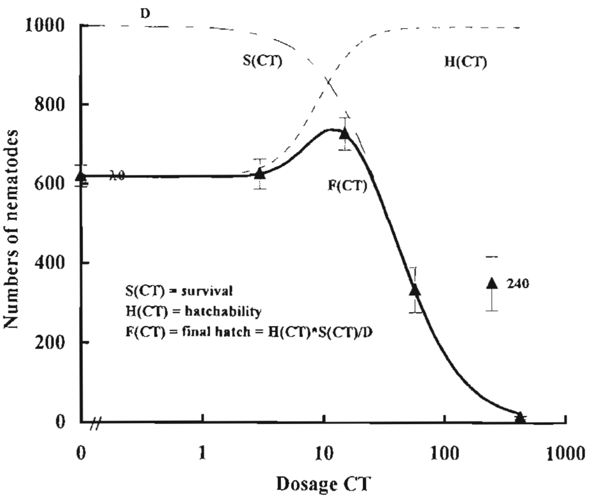

Fig. 5. *Dosage/response relations for the (z)-isomer of 1,3-dichloropropene, expressed in numbers of nematodes. The number of hatched nematodes F(CT) is explained as a product of hatchable nematodes H(CT) and surviving nematodes S(CT), both dependent on dosage CT. There were 1000 (D) nematodes per hatching cup in the test. The symbols (▲) with bars indicate the averages of five × five observations (except for CT = 0 with ten × five replications) with standard errors.*

The correspondence rules in the 'Seinhorst Research Program' make it possible to transfer the conclusions from the mathematical analogue to the corresponding 'natural' analogue in 'normal' language. Here, 'normal' means that the language is understandable and useful for those who are not involved in the 'Seinhorst Research Program'. Therefore, jargon and technical terms are avoided as much as possible. If technical terms are inevitable, they are explained in 'normal' language.

In Examples 9 and 10, Seinhorst's theories on growth reduction of annual crops attacked by nematodes and on population dynamics of nematodes with one generation per year (for instance *Globodera rostochiensis*, *G. pallida*, *Heterodera avenae*, *H. schachtii*, *Meloidogyne naasi*) are summarised. For more details, the reader is referred to Seinhorst (1986*a*, *b*, 1993, 1998) and Schomaker *et al.* (1995).

Comparison

The correspondence rules in the 'Seinhorst Research Program' make it possible to compare new and current theories. Patterns from simple experimental systems are compared with patterns from more complex systems, and the theories on causes of effects are compared in both systems.

Falsification

These comparisons usually give rise to extensions and/or modifications of the original theory. Not every

Example 5. "Population dynamics"

The pattern for population dynamics of potato cyst nematodes in a complex system (the field) is a compound one. It could be disentengled into four non-linear patterns only after three of these patterns were identified separately in simple experimental systems (plastic containers where plant roots were allowed to occupy the same space as under field conditions). This was done by repeated comparisons of the population dynamic patterns in complex and simple systems. These four patterns are:

1. The relation between P_i, the density of potato cyst nematodes at planting, and P'_f at harvest, (the number of cysts produced per unit haulm weight times the maximum number of eggs per cyst). It describes the way nematodes compete for a feeding site in the roots.

$$P'_f \quad = \quad M\times(1 - e^{-\alpha}) \qquad (6)$$

$$\alpha \quad = \quad a\times P_i / M$$

a - maximum multiplication rate
M - maximum number of eggs per gram of soil

2. The relation between P_i and the relative number of eggs per cyst (y_e), describing the way the feeding cells are damaged by the penetration of large numbers of nematodes.

$$y_e \quad = \quad m_e + (1-m_e)\times 0.9^{\gamma} \qquad \text{for } P_i > T_e \qquad (7)$$

$$\gamma \quad = \quad P_i //T_e - 1$$

$$y_e \quad = \quad 1 \qquad \text{for } P_i \leq T_e$$

m_e - relative minimum number of eggs per cyst
T_e - largest nematode density P_i at which the number of eggs per cyst is not reduced

3. The relation between P_i and relative haulm dry weight (y_h), describing the competition between nematodes for effect on size of the total food source (the latter estimated by haulm dry weight).

$$y_h \quad = \quad m_h + (1-m_h)\times 0.9^{\lambda} \qquad \text{for } P_i > T_h \qquad (8)$$

λ - $P_i / T_h - 1$
y_h - 1 for $P_i \leq T_h$
m_h - minimum relative haulm weight
T_h - largest nematode density *Pi* that does not reduce haulm weight

4. The relation between P''_f and P_i in the part of the tilth where no roots are present, which depends on 'normal' root growth, the reduction of root growth by the nematodes, and the fraction of nematode eggs that do not hatch in spring.

$$P''_f \qquad b_1\times(1-s\times y_h)\times P_i \qquad (9)$$

b - fraction of unhatched eggs
s - proportion of soil with roots present in the tilth

The four patterns compound the extended population dynamic pattern of original Fig. 11.2:

$$P_f \qquad s\times y_h\times y_e\times P'_f + P''_f \qquad (10)$$

$y_h\times y_e\times M$ is also called M' or hybrid M, for instance in a paper about the partial resistance of eleven potato cultivars (Seinhorst *et al.* 1995).

Example 6. "Hatching curves"

Compound hatching curves of nematodes from farmer's fields (Been & Schomaker, unpub.) are shown in Fig. 4. They indicate that the population consists of three sub-populations with different hatching properties, caused by nematicide treatments in previous years.

Example 7. "Dose-response relations"

Compound response curves of nematodes to doses of nematicides (Schomaker & Been, 1998) are shown in Fig. 5. They indicate two stimulating and one reducing effects at different ranges of doses of a nematicide, the reducing effect and at least one of the stimulating effects being independent, meaning that they act on different nematode receptors.

aberrant pattern leads to changes in the theory. Four conditions must be satisfied before a theory is replaced by another:

- The aberrant pattern must come from observations based on sound methodological theories described in the methodological empirical cycle.
- The aberrant pattern must be a recurring one.
- The aberrant pattern must reveal new processes or clarify already known processes.
- The new theory connected with the aberrant pattern must be consistent with the fundamental theories in the 'Seinhorst Research Program'.

All conditions for falsification, except perhaps the second condition cited, agree well with those described by Lakatos (1978). An 'old' theory is only replaced by a 'new' one if it brings scientific progress. The 'new' theory must be able to explain and predict all phenomena that were satisfactorily explained and predicted by the 'old' theory and it must also explain and predict new phenomena.

Confirmation

Comparisons between new and old patterns from observations and the theories connected to these patterns are repeated whenever additions to the empirical base give cause. If the same process is involved, combining a large number of observations enables an improved separation between 'signal' and 'noise' and results in a more complete and clear emergence of the patterns, thus confirming the theories on the causes of the manifesting phenomena. Example 11 illustrates this for the pattern of equation (1): $y' = 0.95^{\alpha}$.

The fundamental theories are also confirmed if new theories from compound fundamental patterns, or 'theories of causes' derived from the properties indicated by the 'fundamental theories', in turn successfully predict observations in the empirical base.

Working thus from high hierarchic levels to lower ones, applied, fundamental physiological, and molecular biological research can meet and formulate together coherent, consistent theories. This approach has the advantage that every new theory at a low hierarchic level that is relevant to the explanatory level can be directly implemented.

Deduction

When theory building has progressed so far that the theory on the explanatory system agrees satisfactorily with the patterns derived from the observations of simple and more complex systems, unobserved effects of nematodes in host plants can be deduced from the general causes in the theory, which now are considered as principles. For instance general relationships of non-studied or newly discovered nematode species, such as *Meloidogyne chitwoodi* or *M. fallax,* can be predicted from relationships known from fifteen experiments with other *Meloidogyne* species and their hosts (Example 12. Growth reduction).

Future research

In the very near future, the authors and some of their Dutch colleagues will be involved in a research program (not in the sense proposed by Lakatos, 1978), financed by the Dutch government, on population dynamics and distribution patterns of *Pratylenchus penetrans, Meloidogyne chitwoodi,* and *Trichodorus* spp. and growth reduction caused by these species in some relevant host plants. An attempt will be made to describe distribution patterns of viruses transmitted by trichodorid nematodes. This approach could later be used with other plant viruses. The part of this program under our responsibility will be done as described in this paper and summarised in Fig. 1. Methodological theories will be developed before nematological theories, all theories will be derived from mathematical properties of patterns describing biological processes. Analysis will always come first, then alternate with synthesis. We will also apply Seinhorst's empirical philosophy to integrate our know-

Example 8. "A stochastic simulation model"

A stochastic dynamic simulation model for potato cyst nematodes was compounded from theories about growth reduction and population dynamics in partially resistant and non-host crops to serve as the basis for an advisory system, enabling farmers to choose agricultural scenarios with maximum financial returns (Been *et al.*, 1995). The extended equation on population dynamics contains ten parameters; too many to be useful in an advisory system. For those values of P_i where potatoes can be grown with acceptable yield reductions ($P_i /T < 100$), the relation between P_i and P_f can be simplified to:

$$P_f = \varphi \times M'(1 - e^{-\alpha}) \qquad (11)$$

in which

$$a = a \times P_i / M'$$

φ - degree of susceptibility of the potato cultivar for the nematode population

a - maximum multiplication rate

M' - hybrid maximum population density ($y_h \times y_e \times M$, see Example 5) which does not differ much from M under the given constraints ($P_i /T < 100$)

M - maximum egg density per gram of soil.

The population dynamics under non-hosts is given by

$$Pf'' = P_i \times (b_1) \times (b_2)^{n-1} \qquad (12)$$

b_1 - fraction of unhatched nematodes during the first year of a non-host crop.

b_2 - fraction of unhatched nematodes during the second and next years of a non-host crop

n - number of years with a non-host crop

The fraction b_1 in the first year of cultivation of a non-host crop is smaller than the fraction b_2 in the following years. Schomaker and Been (unpubl.) found on twenty experimental fields an average fraction of 30-40% unhatched nematodes in the first year after a potato crop and of 65% in the second year.

The value of the maximum multiplication rate, a, varies strongly from year to year and from field to field, while the variation of M is more limited as M is closely connected with the size of the food source (estimated by dry haulm weight). The large variation of the maximum multiplication rate, a, makes the population dynamics and subsequent yield losses in susceptible potato crops too unpredictable to recommend a fixed rotation, with or without chemical control. Control measures must then be based on nematode numbers in samples using methods with known accuracy and precision. However, the probabilities of densities P_f and their subsequent yield reductions in years following partially resistant potato crops can be predicated from equations (5), (11), and (12) and the probabilities of all possible combination of a and M, based on their distribution functions.

ledge and that of colleagues from various research stations in The Netherlands into a limited number of consistent theories and hypotheses. Later in the program, our attention will turn to the subjects discussed below.

CONNECTION WITH OTHER RESEARCH PROGRAMS

In 'Deterministic Dynamic Simulation Models', applied to potato cyst nematodes in potatoes by several authors (Ward *et al.*, 1985; Schans, 1993; Van Oijen *et al.*, 1995*a*, *b*) and to *Tylenchorhynchus dubius* in *Lolium perenne* by Den Toom (1989, 1990), the approach is the opposite of Seinhorst's. Synthesis goes before analysis, which undermines and questions the relevance, truth, and sufficiency of the assumed principles (biological processes, equations describing these processes, and external conditions influencing them) to explain the nematological phenomena and their consequences in farmers' fields. The situation is exacerbated as these models represent not just one mathematical equation but numerous equations with dozens of parameters. Both the equations and the parameters can be adjusted flexibly to the observations. Consequently, these deterministic simulation

Example 9. "Growth reduction"

Relevant small and medium ($P/T < 100$) nematode densities cause growth retardation of their host plants, resulting in a decrease in weight of whole plants and plant parts. At any time during the growing period, the growth rate r_P of plants at a certain nematode density P is always the same percentage of the growth rate r_0 of (younger) plants with the same weight but without nematodes. Understanding the system demands a comparison between plants of the same weight, but of different age (Seinhorst, 1979, 1986*a*, *b*; Schomaker *et al.*, 1995). A value of k larger than zero - k is seldom smaller than 0.5 - implies that the mechanism causing growth reduction at small and medium densities is unable to stop growth completely (this remains true at large and very large nematode densities). T is the maximum density up to which growth reduction is prevented or counteracted by a yet unknown mechanism. The factor z^x implies that nematodes are randomly distributed over the surface of root tips and that, if areas where nematodes directly exert their effects overlap, the total effect in the overlapping area is the same as the effect exerted by one nematode ($1 + 1 = 1$). It also implies that the average number of nematodes penetrating the roots per unit of time and per unit of volume of soil is constant. The small scale distribution of nematodes through the soil is regular enough to make this plausible. The total growth reducing effect of all nematodes at a certain density is proportional to the total volume of these area's. Host plants of any species of tylenchid nematodes are able to prevent growth reduction by these nematodes to the same degree z^T (= 0.95), which indicates that properties of a large group of nematodes and plants vary little in this respect. The growth reduction by one nematode, one day after its penetration of the root, is negligible. Investigation at a lower hierarchic level into the fundamental cause of growth reduction by tylenchid nematodes - guided by the properties described in the theory - can lead to new control approaches. Theories about these fundamental causes must be consistent with the other theories to be accepted in the 'Seinhorst Research Program'.

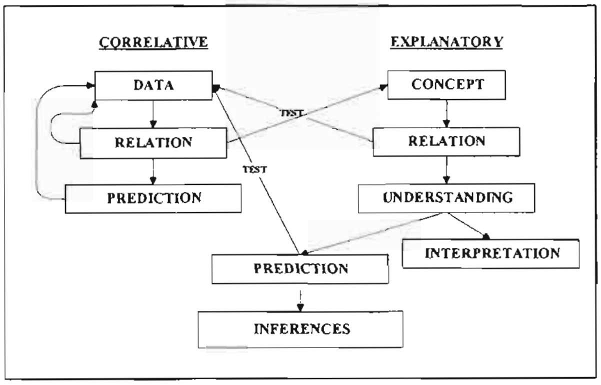

Fig. 6. The empirical cycle according to Campbell & Madden (1990). This figure discriminates in some respects between empirical or correlative models and explanatory or mechanistic models. Concepts for explanatory models are derived from descriptive ones, but the correspondence rules are absent.

models can predict almost any phenomenon, albeit only *after the fact*. Therefore, and because the mathematical equations are often purely descriptive (see also Example 13), the 'Deterministic Dynamic Simulation Models' in their present quality do not contribute much to theory building.

The assumptions leading to the 'Dynamic Energy Budget' (DEB) model, which tries to "capture the diversity of the energetics of the different species into one model with different parameter values and to build theories for the parameter values" (Kooijman, 1993), interpreted for potato cyst nematodes by Van Haren *et al.* (1993), proved not to be sufficient and true causes of population dynamics of these nematodes at the explanatory level. The causes are insufficient as they ignore the 'all or nothing' principle in population dynamics of potato cyst nematodes. The causes are non-true causes because they attribute differences in relative susceptibility only to differences in egg numbers produced per female and ascribe decrease in plant weight to withdrawal of food by the nematodes (Seinhorst, 1986*a*, *b*, 1993).

The 'Deterministic Dynamic Simulation Models' as interpreted and applied by various authors (Ward *et al.*, 1985; Den Toom, 1989, 1990; Schans, 1993; Van Oijen *et al.*, 1995*a*, *b*) and the 'Dynamic Energy Budget Model' as interpreted and applied by Van Haren *et al.* (1993) are trying to deduce effects from assumed causes, but these causes are derived from a jumble of loose facts reported in the literature, many of them questionable with respect to their relevance and validity.

Example 10. "Population dynamics"

Equation (6)

$$P'_f = M(1 - e^{-a})$$

The occurrence of discrete, random events in space and/or time, such as the random encounters of nematodes and plant roots, are described by the Poisson distribution. The first term in this distribution function, the likelihood for a plant root to escape nematode attack (zero encounters), is given by e^{α}. The probability of one or more encounters is given by 1- e^{α}. In its strictest interpretation, the presence of the factor 1-e^{α} suggests that plant roots can be imagined as a cylindrical surface divided into equal compartments, that are per cross section randomly penetrated by juvenile nematodes, the cross sections moving up along the cylinder as time goes on. The juveniles can settle in only one compartment at the same time. If they could settle in more than one compartment, this would result in overlapping territories and a decrease in eggs per settled nematode which is in contradiction with the observed patterns. Only one juvenile per compartment can survive. The size of the compartments depends on the place of the root in the root system and the growing conditions of the plant, but not on the density of the surviving juveniles. Juveniles trying to settle in an engaged compartment will remain unsuccessful and eventually die from starvation. In other words, juveniles that successfully enter a root possess a territory that is inaccessible to others. This mechanism prevents females from decreasing in size because of competition for food and, at high densities or in case of coincidental clustering, remain too small to become adults and reproduce.

Equation (7)

$$y_e = m_e + (1-m_e)\times 0.9^{\gamma} \qquad \text{for } P_i > T_e$$

At higher densities P_i, the numbers of eggs per cyst are decreasing, but not because of competition for space between the growing females. The appropriateness and the form of Equation (7) suggest that the quality of the territory degenerates because of random overlapping areas of damaged root tissue, from which these territories are to be developed. (see also Example 8 'growth reduction'). The factor 0.9^{γ} implies that the territories can still reach their maximum quality by using undamaged root cells if they are less than 10% damaged.

Equation (8)

$$y_h = m_h + (1-m_h)\times 0.95^{\gamma} \qquad \text{for } P_i > T_h$$

This equation describes the relative size of the food source, estimated by relative haulm dry weight. Its theory is described under Example 8 'growth reduction'.

Equation (9)

$$P''_f = b_2\times (1-s\times y_h)\times P_i$$

In case of cyst nematodes, the theory must be extended by a term for the number of nematodes per unit of soil that did not hatch spontaneously or under influence of the root system. This number of nematodes is determined by:

- The proportion, s, of soil with roots at nematode densities smaller than T_h. The proportion of nematodes stimulated to hatch in the presence of plant roots is proportional to the relative size of the root system.
- The relative size of the root system at nematode density P_i, described by y_h (Equation 8). The nematode density per unit root weight does not change because of this reduction.
- The fraction b of unhatched nematodes.

Van Oijen *et al.* (1995*a*) carry off the palm as they managed to incorporate only wrong assumptions on plant-nematode relations into the LINTUL crop growth model (Spitters & Schapendonk, 1990) and still obtained, in hindsight and thanks to a convenient number of adjustable parameters and - because of their arbitrariness - adjustable mathematical equations describing nematode-plant relations, some resemblance between simulations and observations in one experiment. Their approach is described in Example 13 as an illustration of 'incomprehensive' and incomprehensible modelling.

The drawbacks of the 'Deterministic Dynamic Simulation Models' could be eliminated if these

Example 11. "Growth reduction"

The existence of a tolerance limit *T* and its constancy for a given nematode/plant combination under almost all conditions (except short days conditions combined with high light intensity) is often met with doubts or even disbelief. However, Seinhorst did not start his modelling of yield reductions with the concept of a tolerance limit (the fewer parameters the better) but was forced to add this parameter because it gave a better description of the patterns found. The analysis of 29 nematode/plant combinations in Seinhorst's (1998) paper, elsewhere in this edition, is bound to end all doubts. The combination of such a large number of observations reduced variance and clarified the pattern to such an extent that the existence and constancy of *T* ($z^T = 0.95$) for all nematode/plant combinations) becomes abundantly clear.

Example 12. "Growth reduction"

Seinhorst (1998) proved that the relation between P/T and y', based on his theory about growth reduction by nematodes, closely agree with $y' = z^{P-T}$ (Eq. 1), with $z^T = 0.95$ for all investigated 29 combinations of nematodes and plants. From his theory, growth reduction can be deduced for host plants and tylenchid nematode species other than those investigated, for instance, growth reduction of host plants of the newly discovered nematode species *Meloidogyne chitwoodi* and *M. fallax*.

Example 13. "Growth reduction"

The assumptions on plant growth reducing effects of potato cyst nematodes, conveniently chosen by Van Oijen *et al.* (1995*a*) from a multitude of reports in the literature, are:
1. Accelerated leaf senescence
2. Root death
3. Allocation of assimilates in favour of roots
4. Decreased Light Use Efficiency

but all are demonstrably untrue for (economically important) small and medium nematode densities (Been & Schomaker, 1986; Seinhorst, 1986*b*; Schomaker *et al.*, 1995).

The validity of the model and its predictive ability at the explanatory level (farmer's field) was checked by comparing simulated results with observations in a field experiment (without control) with two cultivars on fumigated and non-fumigated plots. The same observations (biased by questionable methodological methods, especially with respect to the estimation of nematode densities) were used to describe the nematode-plant relations and to estimate the parameters in the model. Aberrant observations in a second field experiment (Van Oijen *et al.*, 1995*b*) were ignored. Differences in growth between the two cultivars could not be explained by the model as it attributes one (linear) mechanism of growth reduction to all nematode densities. Seinhorst's theory on growth reduction by nematodes, confirmed for 29 different nematode/plant combinations in 36 experiments, explain the observations in both experiments well as it discriminates between two mechanism of growth reduction: one operating at small and medium nematode densities ($P/T < 100$) and one at large ($P/T > 100$) nematode densities.

models paid more attention to empirical methodology and if synthesis alternated with pattern analysis of phenomena at the explanatory level to trace and describe processes and causes of relevant processes. Arbitrary equations must be replaced by comprehensive equations describing biological processes. Neither the 'Deterministic Dynamic Simulation Models' nor the 'Dynamic Energy Budget Model' are necessarily incompatible with Seinhorst's models. It is obvious that models inducing causes from their effects, guided by (mathematical) properties of the latter, are useful to models deducing effects from principles and *vice versa*. The two types of models could meet half-way on the hierarchic ladder if the 'believers' in the various models (including the authors of this paper) were able to overcome their inclination to worship the one and only true 'model' and to strive for more consistency of experimental methods and biological theories between different schools of thought.

CAUSES AT LOW HIERARCHICAL LEVELS

Patterns and theories in the 'Seinhorst Research Program' indicate properties of nematological processes at lower hierarchic levels. In Example 1, the causes at a lower hierarchic level of the 'first mechanism of growth reduction' at small and medium nematode densities are biochemical or physiological processes and their properties are indicated by the theory that an individual nematode affects plant growth only during a limited period. From Seinhorst's (1998) data, it is confirmed that this 'first mechanism' applies to many - if not all - plant-parasitic nematodes and their hosts. To find new, broadly applicable, nematological control strategies, these processes should be investigated under the guidance of their properties derived from the mathematical patterns. Other processes considered suitable for investigation in Seinhorst's theory on growth reduction at small and medium nematode densities are the mechanism that neutralises or inhibits the effects of small nematode densities and the mechanism inducing differences in plant growth reducing effects between the first and the second generation (Seinhorst 1986*b*, 1995, 1998). The causes of the 'second mechanism of growth reduction', which becomes noticeable at $P/T > 100$ (Seinhorst, 1998) and is accompanied by diagnostic characteristics (Seinhorst, 1986*b*), and the relation of this mechanism with plant age should be investigated as well.

In population dynamics, much work at molecular and genetic level has already been done, but unfortunately it is not or little (only by establishing a multiplication factor) related to quantitative nematological work at higher hierarchic levels. Therefore, this research cannot be used to make predictions on population dynamics and noxiousness of nematode populations, nor to establish similarities in relevant agricultural properties between nematode populations. For the sake of consistency in theory building, the relationship between the research at higher and lower hierarchic levels must be established in the years to come.

CAUSES OF DISTRIBUTION PATTERNS

A new simulation model would be that of distribution patterns of sedentary nematodes, based on distribution patterns of potato cyst nematodes. The small and medium scale distribution patterns of potato cyst nematodes have been extensively described (Seinhorst, 1988; Been & Schomaker, 1996; Schomaker & Been, unpubl.). The small scale distribution of these and other nematodes was well described by the 'Negative Binomial Distribution' (Seinhorst, 1988). For potato cyst nematodes, the dispersing forces causing small and medium scale patterns proved to be constant and independent of time, place (external conditions), and population density (Schomaker & Been, unpubl.). As the mobility of potato cyst nematodes is only a few centimetres per year - which is negligible - their distribution patterns depend on their population dynamics and on the activities of farmers, who disperse cysts within and between fields and horizontally and vertically through the soil with their machinery - including soil fumigation equipment. It would be relatively simple to use vector analysis of the dispersal forces to explain the distribution patterns of these nematodes. More complex distribution patterns of other nematodes could then be deduced by means of simulation models of the vectors using sub-models of the population dynamics and mobility of these nematodes. The relevant external conditions for mobility should not be suggested by preconceived ideas, *e.g.*, on effects of organic matter or biodiversity, but by mathematical properties of distribution patterns of nematodes under natural conditions, following the empirical cycle (Fig. 1) in a consequent manner. If the presence or absence of micro-organisms and their metabolic products are critical for nematode mobility then the distribution patterns of these micro-organisms must be studied too, for instance by DNA extraction from soils (Van Elsas *et al.*, 1997), and related to that of the nematode species under study and to (small and medium scale) geographic patterns.

GROWTH REDUCTION BY ROOT NEMATODES IN PERENNIAL PLANTS

During the first year after planting, effects of nematode attack on perennial plants can be investigated in the same way as on annual plants. We cannot yet answer the question of whether a reduction in growth and productivity should be expected in the second and following years, depending on nematode densities at planting, especially at low densities. It is known from studies on *Radopholus similis* on citrus that nematodes spread from older to new roots at the periphery, thus rapidly increasing in numbers. The same tendency to rapidly increase in numbers and to migrate is observed for stem nematodes in red clover and lucerne - here via moist surfaces of plant leaves. We know that nematodes do not generally cause specific disease symptoms (see Examples 1, 2, 4, 9, 11, and 12 on growth reduction) and that annuals are more tolerant to second and later generations of nematodes than to the first generation present at planting (Seinhorst, 1995). Therefore, it is by no means certain that the presence of large nematode numbers in old orchards will cause substantial reductions in productivity. An increase in productivity, in some but not all cases, after treatment with non-fumigant nematicides is not proof of nematode damage if the effect of these chemicals on the yield of trees without nematodes under the same conditions is not known.

To investigate growth reduction of perennial plants by increasingly large nematode populations, patterns of weight of the whole plant and its fruits must be studied at a sufficiently wide range of nematode densities and at regular time intervals. To produce a clear pattern, a simple system with external conditions as constant as possible must be studied first. Later, more complex systems can be studied and their patterns compared with the patterns from the simple system.

FUNGI AND INSECTS

Extension of the 'Research Program' with research on infestation focus development and distribution patterns of fungi and insects living in the soil is worth consideration. The model for foci developed by Van den Bosch (1990) has similarities with our model. It contains a gamma density function for the relative number of biological entities produced per time unit and an exponential function for the spatial distribution. For nematodes, the spatial distribution function is the same as in the model of Van den Bosch (1990). The parameters of the function must be estimated for each separate species. For nematodes, we are planning (see Future Research) to deduce a comprehensive temporal model from nematode dispersal forces and population dynamics. We might do the same for other organisms.

POTATO CYST NEMATODES

Of all plant-parasitic nematodes, the methodological and nematological theories in the 'Seinhorst Research Program' are the most advanced for potato cyst nematodes. The reason is that potato cyst nematodes are economically important and relatively simple research objects because they have only one generation per year and they are easily manageable. Seinhorst (1998) has demonstrated that many causes of phenomena at the explanatory level, especially those with respect to growth reduction, apply to all nematodes. Therefore, we want to choose potato cyst nematodes and their hosts as model organisms to induce theories on the causes of different aspects of growth reduction, distribution patterns, and molecular aspects of population dynamics. From these theories and supplementary observations, similar theories can be deduced for other nematodes.

Final considerations

Seinhorst and the authors of this paper worked together in close collaboration for almost thirteen years. To us, his pupils, Seinhorst's approach to science is a sensible one, adopted naturally. We cannot imagine working in a different manner. During these years of co-operation, the research program was developed further and our influence gradually increased. At the present stage, it is difficult to discriminate between Seinhorst's and our own contribution in the development of the research program during the last decade. Either contribution is reflected in both Seinhorst's and our publications, but we always discussed and criticised each others' work and we wrote some papers together. Our contribution consists mainly in the development of computer programs for analyses and in the synthesis or composition part of the program. This synthesis resulted in simulation models for both distribution patterns of nematodes in farmers' fields (from which sampling methods can be developed) and expert systems for potato cyst nematodes (from which control scenarios can be chosen). Much time and energy were invested in the implementation of scientific results in agricultural practice, *e.g.*, Seinhorst's concept of partial resistance of potato cultivars to pathotypes of *Globodera pallida,* and in the introduction of new sampling methods for the detection of small foci in fields of ware and seed potatoes. This made it possible to reduce nematicide use and improve financial returns.

During the period of our co-operation with Seinhorst, we had many discussions on methods, theories, and philosophy, not because we disagreed but because a relatively small 'Research Program' is 'subject to offence' (Lakatos, 1978) and must develop strategies for its defence. We feel we succeeded in establishing and defending the 'Seinhorst Research Program' so that, in our opinion, it has a fair position and good prospects in comparison with other 'Research Programs'. If the foregoing paragraphs gave the impression that we reject all concepts on which other 'Research Programs' are based, then this image wants nuance. We mainly object against the way these concepts were interpreted and applied for nematode/plant relations, but we know from experience that any 'Research Program' can be put in an unfavourable light if amateurs tamper with its models (Anon., 1991). Therefore, we will not hesitate to adopt approaches or theories from other 'Research Programs' if patterns from observations should guide us in that direction.

Many foreign colleagues co-operated with Seinhorst for long periods. Without suggesting to be complete, we want to mention here our Scandinavian colleagues who appointed Seinhorst as an Honorary Doctor at the Agricultural University of Uppsala and our Italian colleagues from the Istituto di Nematologia Agraria in Bari, where Seinhorst was a consultant for many years, who made a large contribution to the confirmation of Seinhorst's theories (Seinhorst, 1998). They all greatly influenced the course the 'Seinhorst Research Program' has taken in the past, and we hope that they and other colleagues will continue to do so in the future.

Acknowledgements

We are indebted to the late Dr J.W. Seinhorst for the valuable discussions on his theories and their philosophical background and to his family for making available after his death his unpublished scientific manuscripts, published and unpublished data sets, correspondence with referees, colleagues and editors, scientific books, and personal diaries. We thank Prof. J.C. Zadoks and Dr T. Gremmen (Department of Applied

Philosophy of the Wageningen Agricultural University) for critically reading the manuscript and clarifying discussions.

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