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APPLICATION OF SIMULATION MODELS IN THE EPIDEMIOLOGY OF
PESTS AND DISEASES; AN INTRODUCTORY REVIEW

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1. Introduction

Watt (1961a, b, 1963, 1964) was one of the first people to realise the full potential of agricultural pest modelling. Watt's main interest was to use models to evaluate different control strategies, and he was able to show theoretically that pest populations could reach higher levels after the application of a pesticide than in its absence (Watt, 1961a). Watt (1961b) was also concerned with modelling field populations and later extended his ideas to resource management (Watt, 1968).

Conway (1973, 1977) criticised many of the existing mathematical pest models for being too general (producing only obvious or trivial results), for ignoring the economic aspects of control, for failing to initiate the interaction between modelling and experimentation and for their irrelevance to pest management systems. The first criticism is now less important as systems teams start to tackle specific problems with specific objectives. The analytical approach however is still interested in general models e. g. to account for the searching strategies of predators and parasitoids. The second point is a reflection of two considerations; most modellers are trained in one subject, in this case biology, and know little of economics and the economic aspects of crop protection have not often been calculated. These considerations are changing as entomologists and phytopathologists realise the importance of damage levels, economic thresholds and action levels. The third criticism is possibly unjustified. Model builders quickly realise what experimental work needs to be done to provide the missing data for their models. Very often however with an analytical approach the importance of directly unmeasurable variables and parameters are stressed, e. g. the mutual interference constant of predators. These values are usually calculated from graphs and are very often an incorporation of many biological processes into one variable or parameter. Thus they are purely descriptive with little explanatory value. Analytical models are, because of their abstract character, usually difficult to validate in the real world. Very often the author gives examples where his model fits observations in the field but this does not answer the question as to whether his theoretical considerations are valid. This makes the value

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of these analytical models for interpretation of a specific field situation limited, and conclusions on the mode of action of a system speculative and dangerous. Finally, models are now being employed in pest management systems.

2. Types of models

Mathematical models can be classified into three partially overlapping types; analytical, statistical and simulation. The analytical models mentioned in the introduction are of interest in theoretical considerations of ecological concepts but quickly become too complex if applied to field populations. In many cases knowledge and insight of the ecological processes are lacking or are of a rudimentary nature. Statistical models, usually regression type, are purely empirical not relying on causal relationships and hence describe rather than explain processes. They are rarely consistent in the long term and when they do fail, the model itself cannot be used for explanation. They are therefore of limited use in plant protection. Simulation models are dynamic and can either be deterministic (based on mean values) or stochastic (based on probability distributions). The majority of pest simulation models are deterministic, as the use of stochastic models is very expensive in computing time and often unnecessary. Fransz (1974) discusses stochastic processes in relation to his work on the predatory behaviour of mites. He gives a number of ways that stochastic variables can be simulated either with single or population processes. He concludes that when some characters of the animals with stochastic variation have curvilinear relations with other variables (i.e. rate variables) the outcome of a deterministic model in which averages are used may deviate from the expectation value of a stochastic model. Thus, generally there are two reasons to use stochastic models: 1) when a reliable estimate of the expectation value is desired and curvilinear relationships between a stochastic characteristic and one of the state variables are present, 2) when interest lies in the variance of model output. Unfortunately many biological properties show curvilinear relationships and the high variation in these characteristics often necessitates the use of stochastic models. Since these models are very time consuming and therefore expensive to run, several techniques have been developed to prevent the use of expensive, and often inappropriate, Monte Carlo methods. Fransz (1974) developed 'compound simulation', which is the application of deterministic simulation models to classes of individuals. Within each class the relation is assumed to be linear. The number of classes depends on the required balance between accuracy and computer time. The calculation of each class of individuals is made at each time step of integration, after which the contents of the classes are updated and another computation starts. In this way only one simulation needs to be carried out for each set of conditions, instead of 1000 times in Monte Carlo methods. Sabelis (1981) describes the application of Fransz's methods, Monte Carlo techniques and queuing techniques, to the predation process of mites. The latter method is an especially powerful approach that requires only a limited amount of computer time. Basically, this method may be compared with calculating the waiting

time of a client in the waiting room of a dentist. The client may enter the waiting-room (gut) at a certain rate in expectance of the service (digestion). An evaluation of the mentioned models, i. e. deterministic, stochastic compound or queuing is done in an acarine system by Sabelis (1981). He shows that the deterministic model gives erroneous results and that the outcomes of the three other models fall within the confidence intervals of the measurements, the latter with the least computing time.

3. Strategy in model building

Ruesink (1976) has listed some of the agricultural pest models. He proposes that the frontiers of model building lie not with the production of more models, these can be turned out by anyone familiar with the techniques, but with the production of improved submodels for important processes. This is a view shared by some phytopathologists (Rijsdijk & Zadoks, pers. comm.). Ruesink (1976) has produced a methodology for developing models which needs further refinement and extension. The first step should be to define the objective of the system analysis before the objects within the system, and hence the boundary of the system, are defined. The modeller usually then produces flow- or relational diagrams prior to formulating equations. This latter procedure is usually carried out section by section, i. e. submodels, so that each part can be checked for accuracy (validated) independent of all other parts. There is also at this time a two-way interaction between model building and experimentation. Output from the submodels indicates the importance of each process so that experimental effort can be concentrated on relations that primarily determine the behaviour of the system. Once all the submodels have been coupled to produce a first generation model it has to be verified. Verification means testing to see that the computer program in fact operates on input data in the intended way (Loomis et al., 1979). Thus the production of negative numbers of animals indicates that the model is not working correctly but unfortunately not all errors are so easy to spot! Verification is a step which is often left out (see Jeger, this volume). Next the model has to be validated as it has to be accurate and reliable if prediction is the aim. Teng et al. (1980) describe some of the procedures they have used in validating their model, BARSIM-I, a simulator of barley leaf rust epidemics. The most simple test is a subjective comparison of model output with field results; preferably from a number of different sites over a number of years so that environmental circumstances may vary considerably. Not only should the model predict accurately the timing and size of the peak population density but the growth curve should be of the same type as observed in the field. By plotting a scatter diagram of field observations against model predictions a further impression of the accuracy of the model can be made. Regression analysis on these data should yield a regression coefficient (b) not significantly different from 1, an intercept (a) close to 0, and a correlation coefficient which approaches 1 so that a high percentage of the observations is being 'explained' in statistical terms. Sensitivity analysis can be carried out once the reliability of the model has been proven. This is the process of changing the values of rates, variables, parameters and initial conditions in the model to determine their

importance. This again leads to feedback with experimentation so that model building is an ongoing process. There is some danger in this approach as differences between model calculations and experimental outcomes at the system level may lead to adaptation of the input relations which are not in agreement with the results of experiments at the process level. In this way, the process of model building is losing its meaning as simulation has degenerated into a sophisticated way of curve fitting. Deviations between model results and experiments at the system level should lead to a reorientation of the conceptualisation and implicit hypotheses in the model.

A good, validated and reliable model may be used in sensitivity analysis to test the relative importance of different input relations and to pin-point the deficiencies in our knowledge. After this process of sensitivity analysis, simplification is usually possible and may lead to summary models which are used in decision making to predict the population dynamics of pests and diseases in a crop protection management system.

A very fundamental question in all types of simulation models which use numerical integration methods concerns the choice of the time interval of integration. An appropriate time interval is necessary as too small time intervals will lead to an overuse of computing time, and too big time intervals will lead to erroneous results and in extreme cases to oscillations. The time interval is dictated by the time coefficient (De Wit & Goudriaan, 1978). It characterises the rate of change of the system and is best defined as the inverse of the relative rates (De Wit & Goudriaan, 1978). The smallest time coefficient is found by writing all rate equations explicitly. If an appropriate time interval of integration is used, errors due to the method of integration are negligible. However, modellers do not always realise the danger of using inappropriate time intervals of integration, and their time step is dictated by observation frequencies of the driving variables. This may lead to considerable calculation errors and even induce oscillations with increasing amplitude when the time step of integration exceeds twice the time coefficient (Ferrari, 1978).

4. Examples of models

4.1 Insect models

Most insect pests have more than one generation in a season and very often the generations overlap, thus preventing the use of key factor analyses (Morris, 1959; Varley, Gradwell & Hassell, 1973). These, basically graphical, methods are intended to indicate the major regulating factor of an insect population. Hughes (1962, 1963) proposed an analytical approach, based on the time-specific life table method, to study aphid populations. The basic assumption of this method is that the population has developed a stable age distribution. Carter et al. (1978) were able to show, with the aid of a computer model, that this did not occur in the field. The simulation approach appears to be a better way to investigate the population dynamics of aphids and many other pests.

Although Watt proposed the use of the models in 1961, it was not until 1968 that Hughes and Gilbert published a paper concerned with modelling a specific species, the cabbage aphid Brevicoryne brassicae L., its predators, parasitoids and hyperparasitoids. One important concept that Hughes & Gilbert (1968) introduced into modelling was the use of a physiological time scale. This allows the modeller to neglect the daily vagaries of temperature. Instead 'time' is measured in day degrees; the cumulative total of temperature (above a certain threshold temperature) x time (in days). Four assumptions are made when dealing with this time scale; i) aphid development is primarily dependent on temperature, this is probably reasonable although Hughes (1963) did remark on the effect of different host plants and different physiological conditions of the same host plant on aphid development. These effects could be introduced in the model explicitly when their effects are known. ii) Development rate is linear with regard to temperature over the normal range of temperatures which is true for most aphid species studied (Hughes, 1963), iii) there is a constant threshold temperature below which development is zero, this temperature is only theoretical as development is non-linear at lower temperatures and it probably varies for different strains of the same species (Carter et al., 1980), and iv) fluctuating temperatures have the same effect as a constant temperature. This last assumption means that the aphid response to changing temperature is instantaneous. There is little information available on this but the evidence collected so far indicates that this assumption is justifiable (Rabbinge et al., 1979). In mites this hypothesis has been verified experimentally (Rabbinge, 1976; Sabelis, 1981, 1983) and is valid. However in other development processes, e.g. germination of seeds, it is not the case (Jansen, 1974). Gutierrez et al. (1976) emphasise the importance of the non-linear relationship between development and temperature at the extremes of the temperature range. Sharpe & DeMichele (1976) have produced a stochastic model which explains development processes on an enzyme kinetics basis. How important this will turn out to be for pest modelling remains to be seen.

Hughes and Gilbert's model is deterministic and employs no direct interaction between the different mortality factors. The model uses discrete time steps to simulate continuous processes and Hughes and Gilbert ran the model with different time steps to discover an accurate but efficient one. The result was a time step one quarter of an instar period (the physiological time for any of the first three instars). Thus the time interval of integration was determined by trial and error. This is the most appropriate way in large simulation models as direct determination of the time coefficient is only possible in small models.

Gutierrez et al. (1976) have attempted a truly systems approach to pest management on cotton. They started with analytical models to clarify what information would be required for ecosystem models. Next the team built a model for plant growth (Wang et al., 1977) which can be coupled to a number of pest models. These pests are either defoliators or they attack the fruits. This represents one of the first

attempts to explain the effects of pests on their host plant and hence the final yield. Attempts have been made to add a further level to insect models, where the insects are vectors of disease (Gutierrez *et al.*, 1974). Obviously this further complication increases the problems involved; the results and conclusions have not been very important, so far, in controlling diseases transmitted by insects.

The increasing economic importance of cereal aphids in Western Europe during the last decade has stimulated the development of models on the population dynamics of these insects. Carter (1978) and Rabbinge *et al.* (1979) developed such models; a detailed description of these models being given elsewhere (Carter, Dixon & Rabbinge, 1982). With these models, the population development of cereal aphids during a season may be simulated. An explanation for the population dynamics of cereal aphids can be given on the basis of insight gained by this modelling effort. It has been demonstrated that wing formation induced by a shift in assimilate composition during the medium milky ripe crop development stage is important in determining peak density. The decline in aphid population density induced by emigrating alatae is amplified by natural enemies; parasites, predators and *Entomophthora* spp. The simulation studies shows also that immigration is relatively unimportant after flowering, and that the potential of biological control of cereal aphids with presently available natural enemies is limited.

4.2 Non-insect invertebrate models

Most of these models are concerned with the population dynamics of mites, which are probably the most important invertebrate pests after insects. However, the first model discussed concerns nematodes which have special features making them, perhaps, easier for study.

Jones & Perry (1978) have produced a model to describe the population build-up of cyst-nematodes within and between years. Cyst nematodes are relatively immobile, which makes experimentation and modelling easier than with insects and fungi. In northern Europe these species only pass through one or possibly two generations per year and the observed maximum annual multiplication rate is less than 100-fold. Problems are encountered in sampling the nematode populations as they are aggregated around the roots and are difficult to extract and count. Also, eggs may remain unhatched for several years, thus complicating predications of population increase from year to year. However, this carry over proportion is density-independent and remains virtually constant from year to year.

Jones & Perry (1978) fitted a logistic-type equation for population growth within a year. The major density-dependent factor in these species is intra-specific competition (delays in growth rate due to their struggle for limited resources) and also, possibly, more males than females being produced as the density increases. They then constructed a model to predict yearly population changes under different rotation systems. The input of the model consisted of information about the population processes of the nematode and the crop rotation policies.

Thus the model can be used to decide on the optimum management practices to adopt to regulate the nematode population. The model was further modified to include the effects of nematicides on population increase.

In a detailed study, Rabbinge (1976) presented an explanatory model of the population dynamics of the fruit tree red spider mite (Panonychus ulmi Koch) and one of its natural enemies, the predatory mite Amblyseius potentillae. Predatory mites are now widely used as biological control agents in glasshouse vegetable crops and in fruit orchards (Gruys and Minks, 1980). The simulation study was undertaken to explain the regulatory potential of predatory mites and to derive guidelines for management. In these models of acarine systems, the gut content of the predatory mite plays an important role in governing the predation behaviour of the predatory mite. Special sub-models have been developed to deal with the dynamics of gut content and the corresponding predatory behaviour. These submodels are based on detailed models in which searching behaviour of individual predators is included. This searching behaviour is largely affected by motivational state. On the basis of the simulation studies a ranking of phytoseiid mites with regard to their prospective use in biological control is possible.

Another important phenomenon introduced in models of acarine systems (Sabelis, 1981, 1983) is the distribution of prey mites in space and the effect of clustering in webs. These phenomena are introduced in the models and their effect on biological control is evaluated. Some phytoseiids (e. g. Phytoseiculus persimilis) prefer to search in webbed areas whereas other predatory mites (e. g. Amblyseius potentillae) are hampered in their monitoring activity due to the presence of webs.

4.3 Models of plant diseases

An early entire plant disease epidemic simulator was that of Waggoner & Horsfall (1969). Their simulator, EPIDEM, employed a number of weather factors; temperature, relative humidity, windspeed, sunniness and wetness. Thus the system is more complex than invertebrate models where temperature is usually regarded as the main driving variable and the effects of other factors, usually known to play some role in the system, are not quantified. EPIDEM is updated every 3 hours and simulates many of the processes occurring in a disease epidemic. Although Waggoner and Horsfall found that much of the relevant data was already available from the literature, several important components had not been measured before. These included: the speed with which a germinated spore penetrates the leaf, the washing-off of spores by rain, and the fertility of the spore-bearing conidiophores. Hence, the simulation model helped direct experimental research along certain lines.

The disease they were concerned with, early blight of tomato and potato caused by Alternaria solani, is rather a complex disease with different optimum weather conditions throughout its life history.

Although the correspondence between model output and field results was not complete they were sufficient to demonstrate clearly the relationship between the weather conditions and the different life history stages. Waggoner and Horsfall also performed sensitivity analysis which indicated that the fertility of the conidiophores was very important to the final outcome of the simulation. They hoped that their model could form a basis for other diseases with similar life histories to A. solani.

Waggoner, Horsfall & Lukens (1972) produced a simulator EPIMAY for southern corn leaf blight caused by Helminthosporium maydis a fungal disease which caused much yield loss in the U. S. A. in 1970. Their approach to the problem was almost identical to that which they had employed for EPIDEM. The step length employed (3 hours) is the same as used in EPIDEM. Much of the similarity between the two models is due to the similarity between the life histories of the two fungal species. Again, when they tested their model they did not compare output directly with field results. One reason for this is the lack of detailed field observations especially at the start of the epidemic which is needed for input to the model. They do indicate however that their model was used in 1971 as an aid for forecasting corn leaf blight.

Shrum (1975) has developed a model (EPIDEMIC) to simulate the growth of stripe rust caused by Puccinia striiformis, West. on wheat. The model is hierarchal and comprises three layers, (cellular-organismal-population). This, Shrum claims, is an attempt to produce a flexible simulator which can be used for other plant diseases. It will be some time, however, before this statement is accepted by other disease modellers. He claims to have entered all important factors, but by introducing so much detail in one single model there is a danger of number-grinding rather than correct simulation. He goes on to list the uses of the model if developed further; i. e. prediction, estimation of effects of partial resistance, and the effects of fungicide on an epidemic. It would be unwise, however, to use an unvalidated model for management and this should always be avoided.

Kampmeijer & Zadoks (1977) and Zadoks & Kampmeijer (1977) have developed a model, EPIMUL, to determine the effect of crop populations on the course of an epidemic. This is a theoretical attempt to model disease epidemics on a time and space scale. It is, therefore, a general model and is used to study the properties of a disease. The model (written in FORTRAN) has a time step of one day compared to the 3 h of the models of Waggoner and Horsfall. This is an arbitrary choice but acceptable as the model is meant, not for actual disease situations, but purely as an academic exercise. It should however be realised that since van der Plank's equation (a logistic growth formula with a latent period delay and a finite infectious period) is applied for the different compartments, the relative growth rate of this equation dictates the time coefficient. Therefore, the time step should be adapted if another relative growth rate is applied. To introduce the spatial component, a large square (a field, a country, a continent) is divided into a number of smaller square compartments. Basically the model applies the same logistic growth equation with time delay to all

compartments and used a Gaussian distribution curve to spread the spores over the different compartments. The dispersion of spores is assumed to take place according to this function. The model thus presumes a certain nature of dispersion rather than calculating it on basis of the geometrical and physical characteristics of canopy, spores and their interrelations.

Effects of host development are neglected in this model since the size of the model in space ($20 \times 20 = 400$ compartments) limits the dynamics of the model in time. Nevertheless the model throws some light on the effects of spore dispersal. It indicates that the focus of a disease expands radially at a constant speed, and that the daily multiplication rate has little effect on the rate of displacement of the disease front. Also, the model indicates the importance of the initial spore pattern in determining the speed an epidemic moves through a crop. They warn however that the validation of the model is purely qualitative due to the artificial nature of the model and the inadequacy of published data.

5. Discussion

Although the models in the examples mentioned have been developed independently they are, in general, remarkably similar. This is a reflection of the similarity of the biological processes in populations of pest and disease organisms and also the shared aims of builders in trying to produce a model for prediction purposes. The most important aspect of this is the accuracy of the model, but as we have seen most models are poorly validated. Modellers compare their model output with field results and usually comment that the agreement between the two is reasonable. No effort is made to use stringent quantitative statistical tests and so the accuracy of the models is difficult to determine. Thus their reliability is uncertain and, as Way (1973) has pointed out, their impact in pest control has been limited. Some of the distrust that the field worker has against the modeller is the lack of the latter's practical experience. This is being remedied in studies in England (Carter *et al.*, 1982), the Netherlands (Zadoks *et al.*, in press; Rabbinge *et al.*, 1979; Sabelis, 1983) and New Zealand (Teng *et al.*, 1980). Detailed field experiments are performed to test the model outcome by comparison with the results of independent experiments. This test phase has been completed by several pest and disease models, so that the next step to simplified and summary models is being made. These summary models form the backbone of the pest and disease management system EPIPRED implemented in intensive wheat cultivation in the Netherlands. Pesticide usage in agriculture seems high and more supervised systems of pest and disease control should be developed in the near future in order to develop sound agricultural methods.

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