1.1 Simulation of living systems

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1.1.1 Systems, models and simulation

System analysis and simulation has been used by engineers for more than 30 years. Their successes inspired biologists and agronomists to apply similar techniques in their disciplines. The approach is characterized by the terms: systems, models and simulation. A system is a limited part of reality that contains interrelated elements, a model is a simplified representation of a system and simulation may be defined as the art of building mathematical models and the study of their properties in reference to those of the systems.

Although any model should have definite goals, be lucid and achieve its objective, in practice it seems that goals are too often described in such broad terms that sufficient lucidity is reached only for the initiated, and that the models achieve less than expected by the biologist. For these reasons the word 'art' rather than 'science' is used in the definition of simulation.

It follows from the definition that a model is a system, but the reverse may also be true. A work of art is a simplified representation or a model of the vision of the artist. A machine is a model of the conception of the engineer and it certainly performs worse than anticipated. And when an engineer applies simulation, he develops simulation models that lie in between his conception and reality. The ultimate machine is in fact a model of his simulation model, which in its turn is a simplified representation of his mental conception.

Although some wish it otherwise, biological systems are not simplified representations of the conception of the biologist, and the interchange of the terms models and systems does not make any sense. Therefore, it may be that the approach that has been so successful in engineering is not as useful in biology. Fools rush in where wise men fear to tread. Much of this rushing in simulation in biology is done by agronomists, perhaps because they are fools, but maybe because they deal with systems in which the technical aspects overrule more and more the biological aspects.

As has been said, a system is a limited part of reality, so that a border has to be chosen. It is wise to make this choice so that the system is isolated from its environment. This is almost always impossible, but then it should be attempted to choose a border so that the environment may influence the system, but the system affects the environment as little as possible. To achieve this, it may be necessary to choose a system that is larger than necessary for the original purpose.

In agricultural systems, for instance, the microclimate is often part of the system, but everybody happily neglects the influence of the agricultural system on the macroclimate, even though this is not correct. However, the assumption that everything is related to everything is sure to kill all research.

1.1.2 Explanatory models

A file with data on an ecosystem may be called a model, but it is a model without purpose and lucidity. Potential uses of the data may be formulated and then lucidity may be introduced by a treatment of the data. This may result in maps that represent aspects of the ecosystem, or in statistical analyses, which summarize some of the interrelations. Dynamic models are obtained if the time dimension is introduced during the collection and treatment of the data. But those models remain descriptive, showing the existence of relations between elements without any explanation, but, of course, this was not their purpose to begin with.

However, models that have the purpose of explaining systems are possible in biology because various levels of organization are distinguished in this science, as many other natural sciences. These different levels of organization may be classified, according to the size of the system, as those of molecules, cell structures, cells, tissues, organs, individuals, populations and ecosystems. Models that are made with the objective of explaining are bridges between levels of organization; they allow the understanding of larger systems on the basis of the knowledge gained by experimentation on smaller systems. In this way the properties of membranes may be understood better by studying molecules and the properties of ecosystems by studying species.

If the knowledge on the level which is used for explanation is sufficiently detailed and complete, and on the basis of this a model of the system which behaviour has to be explained is designed, it may not be necessary to evaluate the model by comparing its results with those of the real system. For example, models for space travel are so good that the 'proof of the pudding' – the journey itself – is unnecessary. But explanatory models in biology are so rudimentary that proof of their usefulness is necessary. And even when there is good agreement, there is room for doubt. However, good agreement is still more the exception than the rule.

If there are discrepancies between model and real system, the model may be adjusted to obtain better agreement. Then, something that started as an explanatory model degenerates progressively into a descriptive model. The term 'degeneration' in this context does not mean that descriptive models are inferior to explanatory models. It is used here to emphasize that in this way inscrutable models are obtained with an unjustified pretention to explain something. It is for this reason that many models are still doing more harm than good.

The proper way of working is heuristic, by the road of gradual improvement. If unacceptable discrepancies between model and system are observed it may be possible to judge which aspects of the model should be treated with suspicion, by experimenting with both. These aspects are then studied on the level that is used for explanation. On basis of this renewed study, elements of the model may be replaced by others and then a renewed confrontation between the results of the model and the real system may be again useful.

Explanatory models may be of the static or dynamic kind. An example of a static model is a model that contains all the necessary calculations to achieve the relation between respiration and growth on basis of the knowledge of the underlying biochemical processes. Another example is a model that is used to calculate the light distribution over leaves based on canopy architecture, leaf properties, solar position and so on. Such static models form often a part of dynamic models.

It is characteristic for all systems discussed in this book that major elements (like plant biomass) change only gradually in amount with time or in space in response to changing external factors such as weather or fertilization. Such systems are called 'continuous', in contrast to 'discrete' systems (cf. Brockington, 1979), which deal with numbers and discontinuities in time.

1.1.3 The state-variable approach

For dynamic models that claim to be of the explanatory type, the state-variable approach is gaining wide acceptance. These models are based on the assumption that the state of each system at any moment can be quantified, and that changes in the state can be described by mathematical equations. This leads to models in which state, rate, and driving variables are distinguished.

State variables are quantities like biomass, number for a species, the amount of nitrogen in soil, plant or animal, the water content of the soil. Roughly, those variables that can still be measured when time stands still as in the fairy world of the Sleeping Beauty, are state variables.

Driving variables, or forcing functions, characterize the effect of the environment on the system at its boundaries, and their value must be monitored continuously. Examples are macrometeorological variables like rain, wind, temperature and irradiation, but also the food supply or migration of animals over the boundaries of the system. It depends on the position of these boundaries whether the same variables are driving, state or rate variables. For instance, the heat stored within a vegetation canopy is a state variable when the system includes micrometeorological aspects, but a driving variable that has to be measured when the micrometeorological aspects are excluded from the system.

Each state variable is associated with rate variables that characterize their rate of change at a certain instant as a result of specific processes. These variables represent flows of material or energy between state variables, for example, between vegetative biomass and grazing animals. Their values depend on the state and driving variables according to rules that are based on knowledge of the physical, chemical and biological processes that take place, and not on a statistical analysis of the behaviour of the system that is being studied. This is the most important distinction between models that describe and models that attempt to explain.

After the calculation of the values of all rate variables, these are used to calculate the state variables according to the scheme: state variable at time $t + \Delta t$ equals state variable at time t plus the rate at time t multiplied by Δt. This procedure, called integration, gives the new values of the state variables, by means of which the calculation of rate variables is repeated. The time interval Δt has to be chosen so small that the rates do not change materially within this period. To avoid instabilities, the time interval of integration has also to be smaller than one-third of the time coefficient or response time. This characteristic time of a system is equal to the reverse of the fastest relative rate of change of one of its state variables. The smaller the time coefficient, the smaller the time interval of integration.

Rates are not dependent on each other in these state determined systems. Each rate depends at each moment on state and forcing variables only and is therefore computed independently of any other rate. Hence it is never necessary to solve n equations with n unknowns. An example may be needed. It is clear that the rate of growth of a plant, as measured by the increase in weight of its structural tissues, is closely related to the rate of photosynthesis of the leaves. In a state variable model, this dependency is a result of the simultaneous operation of two independent processes. Photosynthesis contributes to the amount of reserves and this amount is one of the states that determine the rate of growth. At the onset of darkness, photosynthesis stops immediately, but growth proceeds until the reserves are depleted, or even longer, but then at the expense of existing tissue.

Especially for the uninitiated, attempts are made to depict simulation models by relational diagrams, often according to a method that was developed by Forrester (1961) to represent models of industrial systems. Examples of such relational diagrams may be found throughout this book. The state variables are represented by rectangles and the flow of material (water, carbon, nutrients) by solid arrows. The rate control of these flows is presented by the valve symbol. Constants, driving variables or forcing functions are often placed between parentheses. The dotted lines indicate the flows of information that are considered. Relational diagrams do not contain any quantitative information. Such a diagram of the simplest dynamic system is given in Figure 1. If the rate is mathematically described as RATE = CONSTANT • STATE it depicts exponential growth. It is the most simple information feedback loop, which must always contain one state variable whose change is controlled by a rate and a flow of information from state to rate.

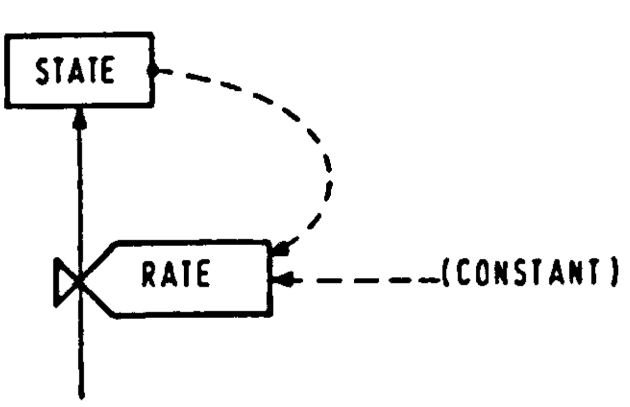

Figure 1. A relational diagram of exponential growth, drawn according to the conventions of Forrester (1961).

1.1.4 A practical problem

The number of state variables that may be distinguished in a living organism or in an ecosystem is depressingly large. They concern not only primary producers, consumers and decomposers, but also the various species, their number, size, age, sex, stage of development, etc. For plants, not only the weight and surface area of the leaves are of importance but also their nitrogen and mineral content, their enzymes and other biochemical characteristics. One can continue in this way and therefore a model that is based on full knowledge of all biological, physical and chemical phenomena that occur is never realised. Models are simplified representations of systems, and the simplification manifests itself by the limited number of state variables that are considered.

Analogous with other approaches, it is assumed that considerable reduction of the number of state variables may be obtained by limiting the boundaries of the model and by focussing on those aspects of interest for which understanding is most wanted. Then processes can be ordered by their importance and only processes within the limited focus need to be handled in detail.

The number of state variables that can be considered in any model is limited, not so much because of the size of the computer or the cost of computer time, but because the research effort that can be invested in any one problem is limited. Models that contain about a hundred state variables are for this reason already very large, but at the same time they may be small compared with the complexity of the systems that are considered.

For each purpose there is somewhere an optimum in the number of state variables that should be considered. At first the applicability of the model to the real world problem increases with increasing number of state variables, but then it decreases again as the addition of new state variables diverts attention from state variables introduced earlier because they were considered more important. The heuristic process of obtaining a set of state variables in order of their importance takes much time, and many modelling efforts in ecology are sometimes explicitly, but mostly implicitly, geared towards this goal.

1.1.5 A validation problem

Simulation may aid the understanding of important aspects of complex systems in such a way that their behaviour is visualized and a guide to their management is obtained. But solutions are only accepted as such if methods to falsify them are available or, to express it more positively, if they can be verified or their usefulness can be proven. Are there models that can be validated? Yes, but only models of systems that are repeatable or recur. Only then may the model be derived from the analyses of some systems and validated on others. Examples of repeatable systems are found in microbiology (manufacture of vinegar), agriculture (growth of maize) or industry (manufacture of cars). Examples of recurring systems are stars, individuals of a species and ecological systems with so much resilience that after disturbance the original course of development is restored in due course (peat bogs). These recurring ecological systems appear to the observer at different places at the same time in different stages. The strength of the field ecologist lies in his ability to interpret as a time series in one place what is observed in different places at one moment. Repeatable systems can always be analysed by experimentation, but recurring systems sometimes only by observation. There is at present a strong emphasis on the experimental analysis of recurring ecological systems and this is justified because disturbances are damped and destruction of the system during experimentation may be acceptable because there are many of them.

But there are also unique ecological systems or ecological systems with unique aspects. These are systems in which development is not governed by negative feedback, so that their development is diverse, although the origin may be the same. Other systems are unique because of the geographical situation, like some estuaries, lakes, islands and of course the world as a whole. Models of unique systems are concepts that cannot be validated experimentally but only more or less verified by observation of the behaviour of the real system over time. They remain therefore speculative models. The faith in speculative models is strengthened if similar methods of systems analysis, applied to repeatable or recurring systems, lead to validated models that cannot be falsified. Such models of physical systems exist: speculative models that predict the chances of flooding on the basis of an analysis of the physical processes are trusted, although sufficient floods for verification never occur within a life span. But whatever the model predicts, the dykes are strengthened as soon as one flood takes place and this proves that trust in models of this kind has its limits. Speculative models of ecological systems cannot be trusted as yet, because few models that are properly validated exist and the principles of modelling in ecology are still being developed. This certainly holds for 'world models' unless their results are so obvious that the proper conclusion may be drawn without sophisticated techniques.

But if a speculative model of a unique system is sufficiently trusted, can it be used? For this purpose it is at least necessary to initialize the model so that the values of all the state variables have to be determined within such a short time span that they do not change materially. And this should be done without disturbing the unique system to such an extent that its course of development is affected. This is impossible. Therefore, in the final analysis it may appear that the ecologist is in the same position as the outmoded physicist, who claims that it is only necessary to determine at the same time the position, mass and velocity of all gas atoms in his room to predict their future. He may be in an even worse position because he has to live with or even within his unique system as one of its elements and cannot escape the problem by using the law of averages.