1.1 Systems, models and simulation

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1.1.1 Introduction

Systems analysis and simulation have been used by engineers for many years and their success with this approach has inspired biologists and agronomists to apply similar techniques in their disciplines. The approach can be 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. Simulation can be defined as the art of building mathematical models and the study of their properties with reference to those of the systems they represent.

1.1.2 Systems

As described elsewhere (de Wit, 1970; 1982), a system is a limited part of reality, so a boundary must be selected. Ideally, this choice should be made so that the system is isolated from its environment, but in most situations this is impossible. In this case, one should select a boundary whereby the environment may influence the system, but where the system affects the environment as little as possible. To achieve this, it may be necessary to choose a system larger than is strictly necessary.

In agricultural systems, for instance, the microclimate is often part of the system, but the influence of the agricultural system on the macroclimate is neglected. However, the assumption that everything is related to everything else would paralyse research. In crop protection agricultural systems are well defined. Thus, four main system types are distinguished here: pathosystems, cropping systems, farming systems and agroecosystems. A pathosystem may include host and parasite populations, and vectors and their mutual interactions. The pathosystem is subject to the effects of climate and man. Pathosystems are parts of cropping systems, which include not only crop protection aspects but also crop agronomic activities. Cropping systems are restricted to one crop and, in principle, deal mainly with crop husbandry and its economics. Farming systems comprise the husbandry and economics of a variety of crops, and the interactions between them. Here, managerial aspects may dominate over the crop agronomic aspects. Farming systems are subsystems of agroecosystems. Agroecosystems are those ecosystems which have been affected or manipulated by man to serve his own needs. Ecosystems have organisms and non-biotic factors as their components, each with its own pattern or distribution in relation to space and

time, and with a recognizable structure consisting of functional relations among these components.

Systems management takes place at all four levels, i.e. pathosystems, cropping systems, farming systems and agroecosystems. The importance of good management of agroecosystems and farming systems is clear, but good management requires considerable ecological and economic information. This book deals with management at both pathosystem and cropping system levels.

Systems may be repeatable, recurring or unique. 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 (peat bogs). However there are also unique ecological systems, or ecological systems with unique aspects. These are systems whose development is not governed by negative feedback (Section 2.1), so their development is unpredictable, even though their initial conditions may be similar. Examples are evolutionary systems and weather systems. Other systems are unique because of their geographical situation, e.g. some estuaries, lakes or islands or, of course, the world as a whole. Models of unique systems cannot be validated experimentally. They can only be verified – more or less – by observing the behaviour of the real system over a period of time. They remain, therefore, speculative models.

It is characteristic of all systems discussed in this book that major elements (e.g. plant biomass) change only gradually with time or location (space), in response to changing external factors, for example weather or fertilization. Such systems are called 'continuous', in contrast to 'discrete' systems (cf. Brockington, 1979), which deal with whole numbers or discontinuities in time. This book introduces systems analysis and simulation of repeatable living systems. The elements of this approach will be introduced in Chapter 2, on systems dynamics.

Throughout the book, CSMP (Continuous System Modeling Program III, IBM, 1975) and FORTRAN are used as computer languages. A brief description of CSMP is given in Appendix 5.

1.1.3 Models

Models may be either static or dynamic. Dynamic models consider changes with time but static models represent relations between variables which do not involve time. An example of a static model is one containing all the calculations necessary to represent the relation between respiration and growth, derived from knowledge of the underlying biochemical processes. Another example is a model used to calculate the light distribution over leaves, based on knowledge of canopy architecture, leaf properties, solar position and so on. Such static models are often components of dynamic models. Dynamic models describe the way in which a system changes over time. An important distinction to be made is that between 'descriptive' and 'explanatory' models.

A file of data on an ecosystem may be called a descriptive model, but it lacks purpose and lucidity. Potential uses of the data may be formulated, and perhaps lucidity can be introduced by mathematical or statistical treatment of the data. This may result in maps that depict characteristics of the ecosystem, or in a summary of the statistical analysis. Such models are called descriptive, because they show only the existence of relations between elements, but do not explain the relations.

However in biology, it is possible to construct models to explain systems, since, as in many other natural sciences, various levels of organization can be distinguished. These different levels of organization may be classified, according to the size of the system, for example, molecules, cell structures, cells, tissues, organs, individuals, populations and ecosystems. Models developed for the purpose of explanation are bridges between levels of organization; they allow the understanding of systems on a higher level of organization through knowledge gained by experiments on a lower level. In this way, for example, the properties of membranes may be understood better by studying molecules, and the properties of ecosystems by studying species. In this book, such explanatory simulation models of pathosystems and cropping systems are introduced. The construction of these models and the study of their behaviour in comparison with the performance of the real systems is termed simulation. Simulation may aid the understanding of important aspects of complex systems in such a way that their behaviour is understood and a guide to their management obtained. But solutions are acceptable only if they can be verified or their usefulness proved. There are models that can be validated in this way, but only models of repeatable or recurring systems. Many agricultural systems are represented by repeatable systems. A growing crop or a population of a pest or a disease organism that develops, can be repeated under various conditions and at different times.

Recurring ecological systems appear to the observer in different places at the same time in different stages. A good field ecologist is able to interpret as a time series what is observed in different places at the same time. Repeatable systems can always be analysed by experiment, but recurring systems, only sometimes, by observation. Today, there is a strong emphasis on the experimental analysis of recurring ecological systems. This experimentation does not cause irreversible effects if the disturbances to the system are damped. Also, if there are many of these systems even destruction of the system during experimentation may be acceptable.

1.1.4 Explanatory models

If the knowledge on the level which is used to explain the system is sufficiently detailed and complete, a model of the system whose behaviour has to be explained can be designed. If all of the elements composing the model are well understood 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 as a test of the model. Explanatory models in biology are so rudimentary, however, that proof of their usefulness is necessary. Good agreement between predictions and observations is still more the exception than the rule, and even when there is good agreement, there is room for doubt.

If there are discrepancies between the model and the real system, the model may be adjusted by tuning variables to obtain better agreement. Then, something that started as an explanatory model degenerates progressively into a cumbersome descriptive model. By which time it may be much more satisfying to use statistically efficient models designed for this purpose, such as the multivariate regression models used by Thompson (1969), Pitter (1977) and Bridge (1976) to describe cropping systems.

The appropriate approach in explanatory modelling is heuristic, by way of gradual improvement. If unacceptable discrepancies between model and system are observed, it may be possible to judge which aspects are then to be studied experimentally on the level used for explanation. On the basis of this renewed study, elements of the model may be replaced and a renewed confrontation between the results of the model and the real system may again be useful. This way of working is widely used to gain insight into the functioning of repeatable and recurring systems and has proved to be very productive.

1.1.5 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 can be quantified at any moment, 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 such as biomass, number of individuals of a species, the amount of nitrogen in the soil, plant or animal and the water content of the soil.

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.

Each state variable is associated with rate variables that characterize its rate of change at a certain instant, as a result of specific processes. These variables represent flows of material between state variables; for example, between vegetative biomass and grazing animals. Their values are calculated from the state and driving variables according to rules based on knowledge of the physical, chemical and biological processes involved.

After calculating the values of all rate variables, they are then used to calculate the state variables according to the scheme: state variable at time

t + Δt equals state variable at time t plus the rate at time t multiplied by Δt. This procedure, called numerical integration, gives the new values of the state variables, from which the calculation of rate variables is repeated. The time interval Δt must be small enough, so that the rates do not change materially within this period to avoid instabilities. This is generally the case when the time interval of integration is smaller than one-tenth of the 'time coefficient' or 'response time'. This characteristic time of a system is equal to the inverse 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 the 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. The concept is illustrated in the following example. It is clear that the growth rate 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 non-structural reserves, and this amount is one of the states that determine the rate of growth. At the onset of darkness photosynthesis stops, but growth proceeds until the non-structural reserves are depleted.

Simulation models are often depicted by relational diagrams, according to the method 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 of these flows is represented by the valve symbol. Constants, driving variables or forcing functions are placed in parenthesis. The dotted arrows indicate the flows of information that are considered. Relational diagrams contain no 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, containing one state variable whose change is given by a rate variable which depends on information flowing from the state variable to the rate variable. In many cases more complicated relational diagrams are needed to represent living systems, and another type of variable, e.g. an auxiliary variable, is needed (Section 2.1).

1.1.6 Defining the boundaries

The number of state variables that may be distinguished 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 are the weight and surface area of the leaves of importance but also their nitrogen and mineral contents, their enzymes and other biochemical characteristics. One could continue in this way *ad in-*

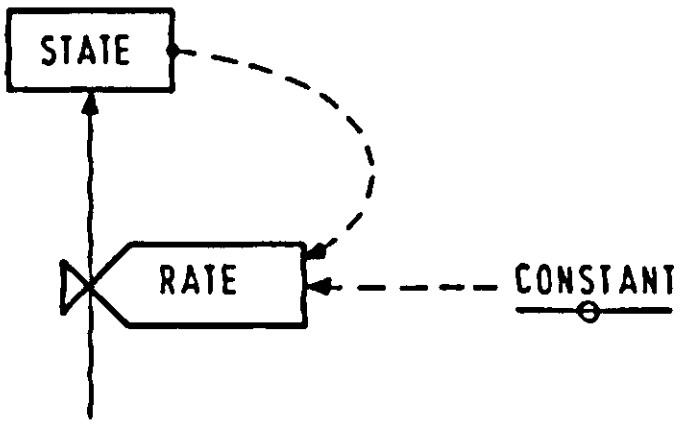

Figure 1. A relational diagram of exponential growth, drawn to the conventions of Forrester (1961).

finitum, so it is obviously not feasible to construct a model based on full knowledge of all biological, physical and chemical phenomena. Models are simplified representations of systems, and this simplification manifests itself in the limited number of state variables that are considered.

The number of state variables can be reduced considerably by limiting the boundaries of the model and by focussing only on important aspects. The number of state variables that can be considered in any model is limited, not so much by the size of the computer, or the cost of computer time, as by the research effort that can be invested in any one problem.

For each purpose there is an optimal number of state variables that should be considered. At first the applicability of the model to the real world increases with the number of state variables, but eventually the addition of new state variables diverts attention from more important state variables already present in the model. The heuristic process of obtaining a set of state variables in order of importance takes time, and many modelling efforts in ecology are explicitly, or more often implicitly, directed towards this goal.

1.1.7 Steps in model building

We may distinguish three types of models, expressing different levels, or phases of development, knowledge and insight. At the frontiers of knowledge, preliminary or conceptual models are very common. These are useful in the quantification and evaluation of hypotheses but are seldom of lasting value. Many different hypotheses may be expressed quantitatively in these models, and their consequences may be calculated and used for an evaluation. These models may help as guidelines in experimental research. Comprehensive models may be developed from these preliminary models as a result of scientific progress: more knowledge and insight become available and may clarify the processes in the system studied.

To evaluate the relative importance of the various parameters and relations and the structure, these models are subjected to a numerical sensitivity test, by changing parameter and input values, and to a structural sensitivity test, by altering the structure of the model. After these sensitivity tests, summary models

may be developed by simplifying the structure of the model. These summary models serve as vehicles for communication, instruction and may sometimes be used for management purposes. Since summary models are derived from comprehensive models, different forms may be constructed depending on the objective and interest of the user.

Various steps in model building may thus be distinguished: (a) the conceptual phase or model, (b) the comprehensive model and (c) the summary model. Within the conceptual phase, the following steps may be distinguished:

1. Formulation of objectives;
2. Definition of the limits of the system;
3. Conceptualization of the system (states, rates, auxiliary variables, forcing variables, etc.).

In the comprehensive modelling phase, steps 4 to 6 may be distinguished:

4. Quantification through literature, process experiment or estimation of the relations between rate and forcing variables, state or auxiliary variables;
5. Model construction (definition of the computer algorithm);
6. Verification of the model, i.e. testing the intended behaviour of the model.

Finally, the model is used to set research priorities and to develop management tools:

7. Validation, i.e. testing the model in parts or as a whole, using independent experiments on system level;
8. Sensitivity analysis, numerical or structural;
9. Simplification, development of a summary model;
10. Formulation of decision rules or forecasting models to be used in management.

These ten steps may be seen in any modelling effort, although very often incomplete or not exactly in this order. In steps 1 to 3 there is a clear emphasis on conceptualization, steps 4 to 6 stress explanation and should therefore be considered as scientific effort, whereas the management or instructive aspects are merely seen in steps 7 to 10.

In many cases it is possible to work at the same time with comprehensive explanatory models and simple universal summary models which are used to derive management methods. Mutual interaction may improve the quality of both. This iterative improvement of both types of models may improve insight and stimulate better management schedules.

1.2 Crop growth under optimal and suboptimal conditions

The factors that influence crop production may be divided into three broad categories: (1) factors that determine potential yields, such as light, temperature and the main crop physiological properties, (2) factors that limit yields such as the availability of water and nutrients and (3) factors that reduce yields such as weeds, pests and diseases, hail and other disasters. To study the effects of yield-determining and yield-limiting factors, and their interactions, different

production situations are distinguished, whereas the effect of the yield-reducing factors are superimposed on these factors (de Wit & Penning de Vries, 1982).

1.2.1 Production situations

In many studies it suffices to distinguish the following four production situations:

- **Production Situation 1**
  This is the potential production situation reached in conditions with ample plant nutrients and soil water throughout growth. The growth rate of the crop in these conditions is determined by weather conditions, and in terms of dry matter amounts to 150-350 kg ha^{-1} d^{-1} when the canopy fully covers the soil. In these conditions the absorbed radiation is often the factor limiting growth rate during the growing season. Major state variables are the dry weight of leaves, stems, reproductive or storage organs and roots, and the surfaces of photosynthesizing tissues; major processes are CO_2 assimilation, maintenance and growth, assimilate distribution and leaf area development. This production situation can be created in field and laboratory experiments, and is approached in practice in glasshouses and in the intensive production of sugar beet, potato and wheat on some Western European farms and on some sugar cane plantations in South America.

- **Production Situation 2**
  Growth is limited by water shortage for at least part of the time, but when sufficient water is available the growth rate increases up to the maximum rate set by the weather. Such situations can be created experimentally by fertilization in temperate climates and in semi-arid zones. They are approached in practice in non-irrigated but intensively fertilized fields, such as many Dutch pastures. Additional state variables are the water balances of the plant and soil; crucial processes are transpiration and its coupling to CO_2 assimilation, and the loss or gain of water by the soil through evaporation, drainage and run-off. The heat balance of the canopy needs detailed consideration in this production situation because of its relation to the water balance.

- **Production Situation 3**
  Growth is limited by shortage of nitrogen (N) for at least part of the time, and by water or weather conditions for the remainder of the growth period. Minerals are well supplied. This is quite a common situation in agricultural systems even with ample fertilization, N shortage commonly develops in crops at the end of the growing season. Important elements in these systems are the various forms of N in both soil and plant; important processes are the transformations of nitrogenous compounds in the soil to forms which are available to plants, leaching, denitrification, N absorption by roots, uptake

and redistribution of N within the plant from old organs to growing ones and its growth response.

- **Production Situation 4**
  Growth is also limited by the low availability of phosphorus (P) or by other minerals such as potassium (K) for at least part of the time. Growth rates are typically only 10-15 kg ha^{-1} d^{-1} of dry matter. This situation often occurs in heavily exploited areas where no fertilizer is used, such as in the poorest parts of the world. Important elements of this class of system are mineral contents of the soils and plants; important processes are their transformation into organic and inorganic forms of differing availabilities, absorption of minerals by roots, and the response of plant growth to their supply. The availability of P relative to that of N is of special interest.

It is rare to find cases that fit exactly into one of these four production situations, but it is a useful simplification to reduce specific cases to one of them. It focusses attention on the dynamics of the principal environmental factor and on the plant's response. Other factors can be neglected, because they do not determine the growth rate; or rather, it is the growth rate that sets the rate of absorption or efficiency of utilization of the non-limiting factor.

If, for example, plant growth is limited by the availability of N, there is little use in studying CO_2 assimilation or transpiration to understand the current growth rate. All emphasis should then be on N availability, the N balance and the response of the plants to N.

1.2.2 Yield-reducing factors

Pests and diseases are the main yield-reducing factors considered in this book. They may affect the growth of a crop in all production situations. However, the nature of the relation between crop and pest or disease organism may be considerably different and crop losses, both qualitative and quantitative, depend on the way crop growth is affected.

Many diseases and pests work in a complicated way through shifts in carboxylation resistances, e.g. mildew (Rabbinge et al., 1985), phloem blockage (e.g. mites), shifts in N balances (e.g. aphids), or injection of hormones or viruses (e.g. aphids and white flies). The simulation of these processes may help to formulate specific damage relations for the various yield situations that are distinguished.

In a detailed study on crop losses due to cereal aphids, Rabbinge et al. (1983) demonstrated that the effect of a constant aphid load on the wheat plant differs considerably among the different production situations. Yield loss (kernels in kg ha^{-1}) is correlated with the maximum aphid density per kernel, typically reached when crops have milk-ripe seeds. At a wheat production level of about 5000 kg ha^{-1}, a maximum aphid density of 15 $tiller^{-1}$ caused yield depression of about 250 kg ha^{-1}; whereas the same population density at a yield level of 7500 kg ha^{-1}

caused a yield loss of 700 kg ha^{-1}. In the analysis of this damage relation, it was demonstrated that the major reason for the progressive damage relation was the importance of indirect effects on yield loss, such as honeydew on the leaves.

Comparison of leaf damage by mutilation and by the formation of necrotic tissue provides another example. In the case of mutilation, the light that passes through is not lost but intercepted by lower leaves, provided that the canopy is well developed and closed. Only in situations where production is already low, is the light likely to be lost. However, light that falls on a necrotic area is always lost, irrespective of whether the canopy is closed or not.

These examples demonstrate the importance of defining the yield or production situation at which the crop-pathogen relation is studied.

1.3 Systems management

The main processes and phenomena involved in crop growth and pest and disease development are schematically presented in Figure 2. They all centre around the plant-pathogen interaction but are, nevertheless, related to various fields of knowledge that have developed rather independently of each other: plant physiology, biochemistry, meteorology, plant pathology, entomology, plant ecology and weed science. The integration of knowledge from these different fields is done by the comprehensive models which may, depending on the focus of interest, be worked out in more detail in various parts. Submodels have been developed for various processes, and can be combined to study the interaction of various aspects. This hierarchical modelling (de Wit, 1982) permits linkage of

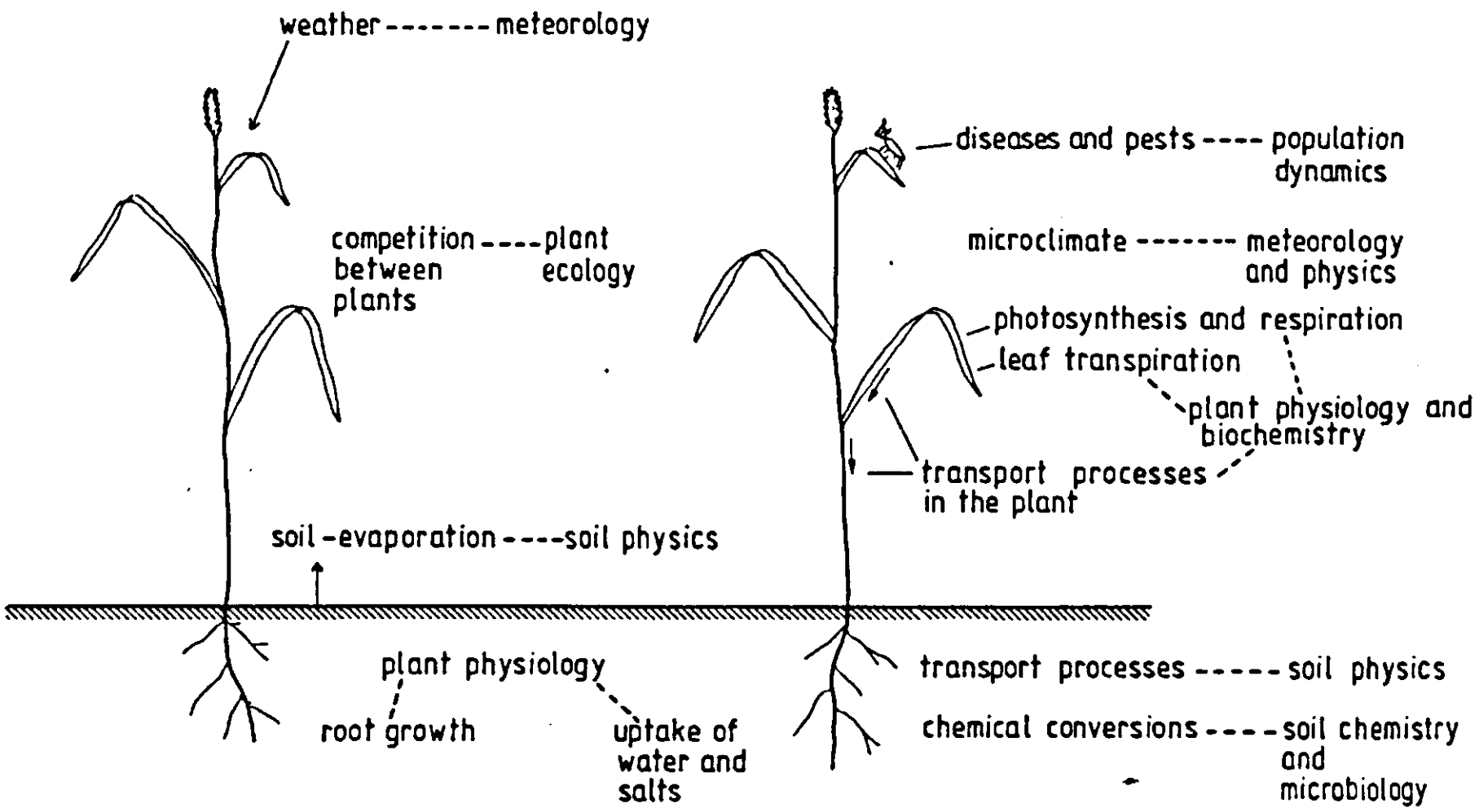

Figure 2. Fields of knowledge that need consideration in a study of plant growth. (Source: de Wit, 1982).

models at different organizational levels. Linkage of models at a similar level of organization but with different points of focus is also possible. This linkage between organization levels and between fields of interest is the task of combination models of pests and diseases and crop growth.

For example, submodels can be produced for the uptake, distribution and redistribution of nitrogen in a wheat plant after flowering. The consequences of an extra N drain, for example, due to aphids can be evaluated by these submodels in terms of assimilation rate reduction or shortening of leaf area duration. This information is then used in crop growth models as an input relation.

Pest, disease and weed management (pathosystem management) form part of all systems. It incorporates knowledge of crop growth, pathogen dynamics and economy of the production process in programs that help to maintain pest populations below economic damage thresholds.

Options for production may be designed and offered to the farmer through various combinations of yield-limiting and yield-reducing factors. Depending on the farmers objectives different combinations are optimal. Some farmers like to gamble and do not care much about a high chance of loss, provided it is compensated by high returns in case the gamble pays off. Others are extremely averse to taking risks, and are willing to pay a high premium to reduce the chances of substantial loss.

Pathosystem management may be applied for one single pest or disease, but is of little use, since the farmer is concerned about all pests, diseases and weeds in a specific crop, and about their interaction. Control of various combinations of diseases and pests requires different control strategies to minimize damage. Zadoks & Schein (1979) expressed the possible control strategies for plant diseases in a simple diagram (Figure 3). It shows how a disease may be delayed or set back by (a) sanitation, (b) change in planting time, (c) partial resistance, (d) treatment with eradicant fungicide, (e) treatment with protective fungicide, or (f) residual adult plant resistance or repeated fungicide treatment. The same diagram holds for insect pests if biological control measures with natural enemies like bacteria or fungi is applied. In cases of biological control with parasites or predators the aim is not completely to eradicate the disease organism or the prey, but to maintain it at a low level that is acceptable to both farmer and natural enemy.

In the summarizing diagram of Zadoks & Schein (1979) the concept of damage threshold or economic injury level is incorporated. This is the lowest population density that causes economic damage and justifies the cost of control measures. When the damage threshold is known and the disease or pest is present the farmer must know how and when to act. For this purpose it is necessary to define an action threshold, which is reached earlier than the damage threshold. Both damage threshold and action threshold depend on the pathosystem's reaction to environmental conditions such as temperature, humidity and irradiation and the crop production situation. In most cases, the damage threshold is not constant but depends very much on time, growing conditions and expected yield. It is often

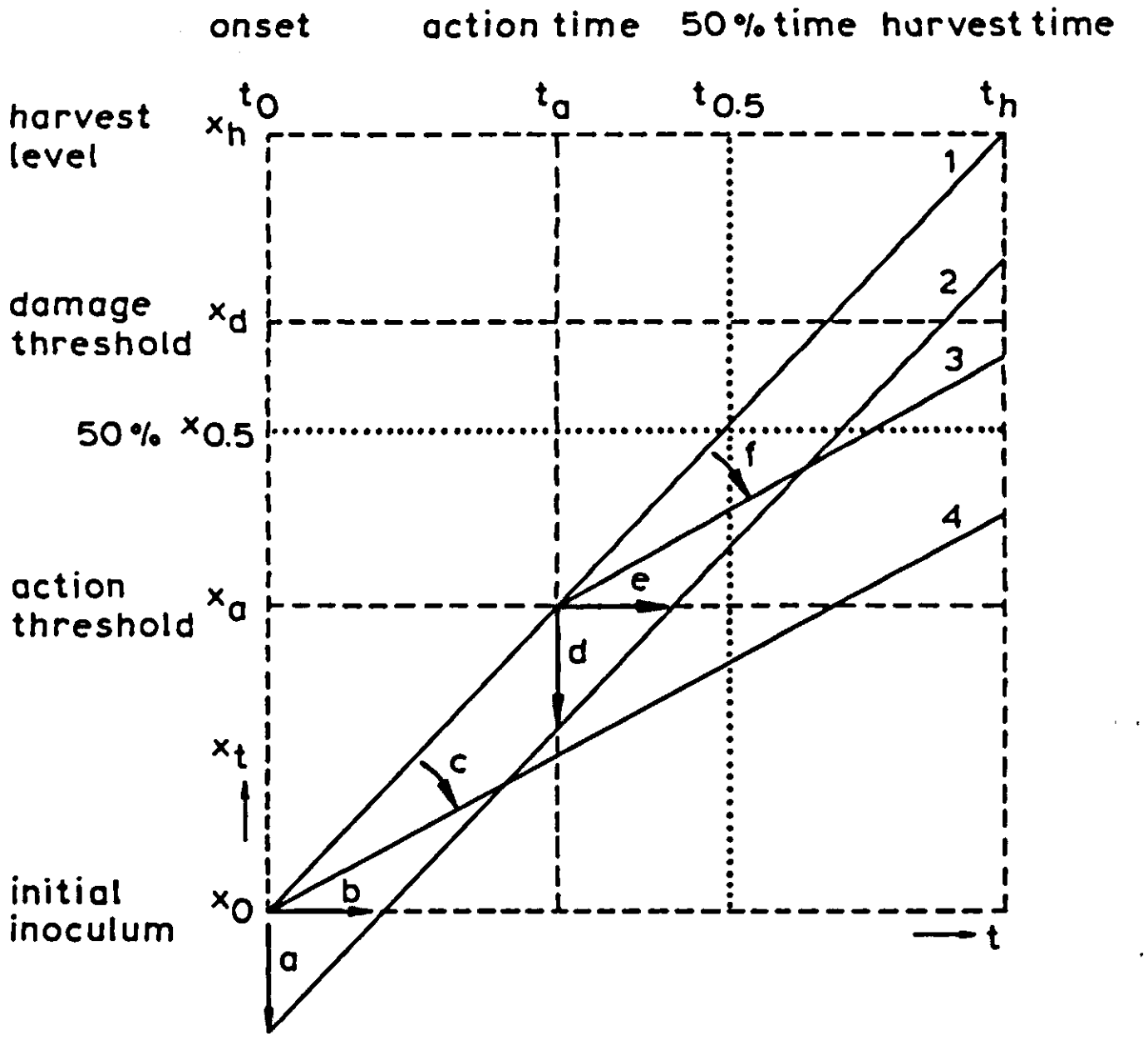

Figure 3. A model demonstrating the effects of various control actions in terms of the equivalence theorum, reduction of r, the slope, and x_0 or x_t. Relation between time (t) and disease severity (x_t). Entries: (1) original disease progress curve, (2) same after reduction of x_0 or x_t (actions a and d) or delay of the epidemic (actions b and c), curves 1 and 2 have the same r value, (3) r changed after action f taken at action time, (4) r changed from the beginning of the season by action c. Actions (examples only); a: sanitation, b: change of planting time, c: partial resistance, d: treatment with eradicant fungicide, e: treatment with protective fungicide, f: residual resistance in the adult stage, or regular treatments with fungicides. (Source: Zadoks & Schein, 1979).

very loosely quantified and therefore difficult to incorporate in crop management. Decision making thus becomes a complicated affair in which intuition generally plays an important role. The value of good intuition and experience in farm management is considerable and determines in many cases whether a farmer has 'green fingers' or not. However, such characteristics are non-transferable, and can be explained only with hindsight.

As decision making is such a complicated affair, information processing equipment may help in handling the relevant data, simulating and/or predicting population dynamics and estimating damage or yield loss (Section 5.1). To optimize decisions and to determine appropriate damage thresholds for various objectives, e.g. profit maximization, pesticide minimization or yield maximization, dynamic optimization techniques are also developed (Section 5.1).

These techniques should enable the farmer or his adviser to improve decision making. However, it should be kept in mind that the quality of the decision is in general not limited by such technical constraints but by the availability of basic biological knowledge. In crop protection, this concerns information on the population dynamics of the pests and diseases and their interactions with the host crop, and with each other.

Population models used for these purposes are discussed in Chapter 3. These models have proved to be reliable predictors of pest or disease development but their value as quantitative predictors of injury to the crop is limited. For that purpose, combination models of the population dynamics of the pest or disease organism and of the growing crop are needed. Such combined models have been developed for situations in specific crops, such as cotton, alfalfa, apple and wheat (Gutierrez et al., 1975; Gutierrez et al., 1976; Rabbinge, 1976; Rabbinge et al., 1981; Section 4.3). In some cases, these comprehensive simulation models have led to simplified models that contain sufficient economic elements to form a management instrument for decision making about sprayings. However, they require considerable input information on various processes and a great deal of parameterization to be more reliable than the simpler approaches.