SYSTEMS MODELLING: A TOOL FOR ECOLOGISTS

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INTRODUCTION

This paper is designed as an introduction to the two papers that follow. It opens with remarks about the nature of systems ecology before discussing its principal technique, systems modelling. This is followed by two simple agricultural examples and a brief discussion of the potential of systems modelling in ecology. More comprehensive treatments can be found in Walters (1971), Patten (1971), and Jeffers (1972).

SYSTEMS ECOLOGY

Wherever functional relationships between organisms and environment are stressed, systems concepts are implied. S. A. Forbes (1887) had a system in mind when he wrote:

> ". . . that whatever affects any species must have its influence of some sort upon the whole assemblage."

and therefore whoever studied the system would be made to see

> ". . . the necessity of taking a comprehensive survey of the whole as a condition to a satisfactory understanding of any part."

This sort of thinking is fundamental in ecology and pre-dates the foundation of ecology as a separate discipline.

A system can be said to consist of a set of interacting components. The nature of the coupling of components and the organisation which results from the couplings is the essence of the system. A model is an abstraction from the real system and by definition may only represent a subset of the components and variables of the real system. Which components and variables are included will depend on the unique understanding and purposes of the modeller and the resulting model will be only one of a multitude of possible models representing the system.

In practice, systems are modelled in a variety of ways. In models such as those developed by the Odum school, equations represent quantities of energy or materials flowing between compartments which are essentially regarded as black boxes (Van Dyne, 1969; Patten, 1971). In some circumstances it may be more convenient to represent an ecological situation as a series of semi-independent sub-models which can be linked together in various ways as required. In this approach each sub-model can be experimentally investigated independently of other sub-models and biological discontinuities can be easily handled (Holling, 1966; Watt, 1968).

Ecological systems are inherently variable. Thus for any given pattern of input of a system there is a variety of possible patterns to flow through it and a variety of possible outputs from it each with their own probability. For the sake of simplicity in model building it is frequently convenient to ignore such variability and build a deterministic model. By definition such a model does not include the stochasticity (randomness) of real systems and is incapable of producing results in the form of probabilities except in the most limited sense. For greater realism stochastic elements must be included as these profoundly enhance the capacity of models to reflect the variability of real systems.

For other than the simplest models a computer is virtually essential. The capacity of the digital computer to handle complexity and to perform the same task repeatedly and accurately is used interactively with the capacity of the human brain for conceptual thinking. Thus brain and computer form an instrument able to tackle projects that were previously impossibly large or complex.

SYSTEMS MODELLING IN PRACTICE

A model is simply any physical or abstract representation of a real system. Mental, mechanical, graphical, diagrammatic, mathematical and budget models can all be considered. That special type of modelling known as systems modelling has been defined by Walters (1971) as

> ". . . the process of translating physical or biological concepts about any system into a set of mathematical relationships and the manipulation of the mathematical system so derived."

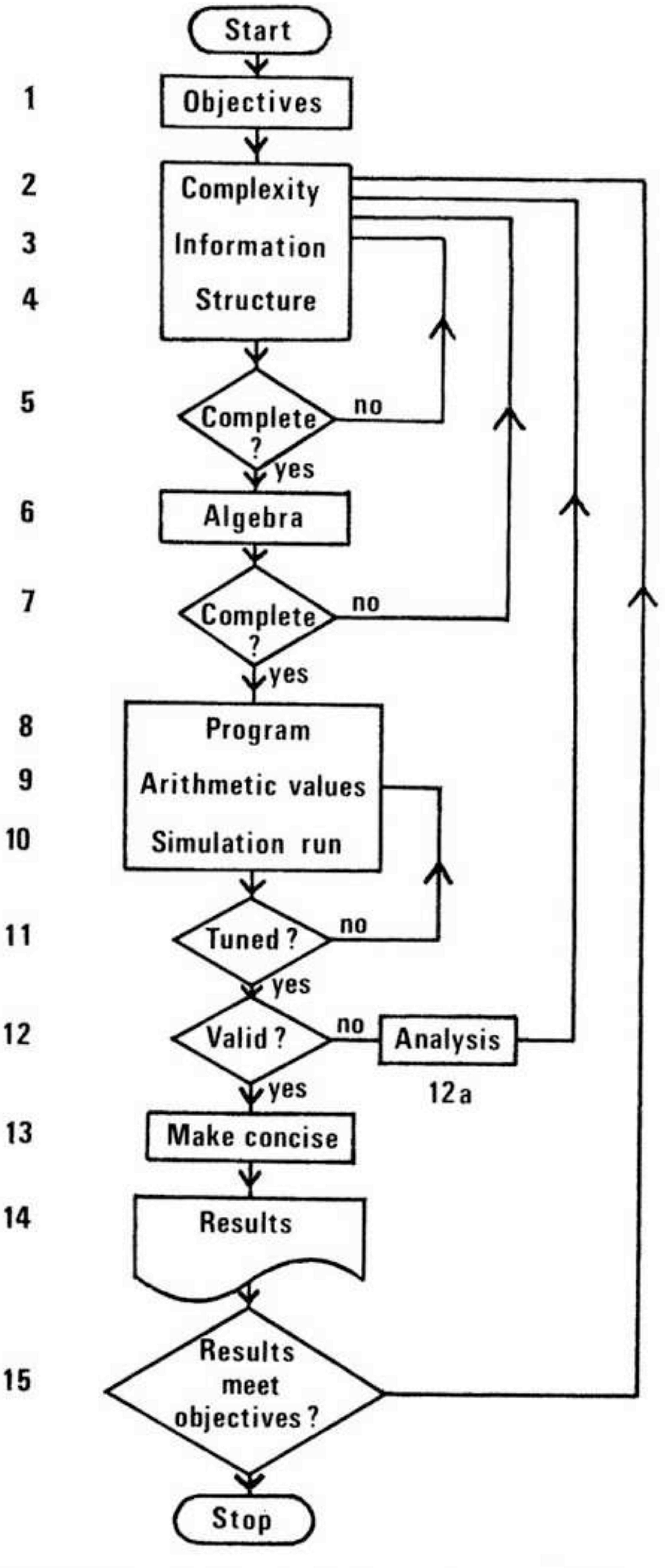

FIGURE 1. *A flowchart for systems modelling. Numbers refer to text.*

The digital computer relies on repeated calculations which are computed at intervals which are usually predetermined and fixed, to update the state of the system. For convenience components are assumed not to influence each other over the short increments of time between calculations and the next state of any component is considered to depend only on the state of all components at the previous instant. As time increments lengthen so does the error. Therefore the state of all components is usually calculated over a sequence of very short increments, an ideal task for a digital computer.

This approach immensely simplifies the mathematical part of model building because it is only necessary to write a single set of equations that relate components to each other, to specify initial values for each component and thirdly to set criteria for determining the lengths of the time increments such that mathematical error is kept within acceptable bounds.

Figure 1 is simply one of many possible flow charts to show how a model could be developed. It serves to emphasise that systems modelling is only a tool and, if used, should be an integral part of the normal research process.

Certain features of this chart require amplification. Numbers in the text refer to numbers in Figure 1.

Objectives (1) include: *investigation* of internal characteristics of the system, *description* of the system (usually for the sake of improving understanding of the interactions within it), and *prediction* of the likely behaviour of the system in conditions or stages of development not yet encountered in reality.

To meet the pre-determined objectives it is necessary to consider the complexity (2) at which the model will be built. De Wit (1971) describes seven levels of biology from the molecule to the ecosystem and points out that, because of relaxation time, it is technically infeasible to link more than two or at most three of these in any one study. Too much detail may be an encumberance. Walters (1971) adopts three criteria for determining the necessary complexity of a study. He describes *realism* as the degree to which the mathematical statements of the model correspond to the biological concepts they represent. A model requires a certain *precision* (a certain degree of complexity is needed to give acceptable accuracy). Thirdly, *generality* is linked to complexity. Simple models can often be made to mimic highly particular situations but they may be of little utility when applied to other combinations of circumstances.

All relevant information is gathered from the literature, by observation, or experiment (3), and the internal structure of the model is specified (4). The latter process is essentially the setting up of an hypothesis and an attempt to bring together on paper an overview of how the system is thought to function. There are many ways in which this can be done (for examples of different styles see numerous articles in Jeffers, 1972; Patten, 1971; Reichle, 1970 and this paper). If it is to be complete this process must involve formal identification and definition of the system components, a statement of the directions of interaction (regulation) between components, an indication of forcing factors (which affect the system but are not affected by it) and outputs. Thus all facts and assumptions about the system are represented. The formal consideration of these aspects aids the achievement of internal consistency and logical completeness of the model, which is usually also aided by the prior construction of an interaction matrix wherein the factors affecting each component are listed.

Much of the original thinking for the model has been done by this stage. It is not often reached easily and the model will still require constant modification as work progresses (5).

To translate a structural statement into an algebraic statement or mathematical model (6), each component and interaction is replaced by its equivalent equation or decision function. Each component (either quantity or rate) is included as a system variable and interactions are represented as transfer functions. These may have associated parameters (or constants of equations). At this stage the initial conditions of system variables are symbolically represented.

In translation to a mathematical model further conceptual deficiencies are usually found. These may either be corrected at once or further experiments may be carried out (7). If there is no way round the problem assumptions may have to be made. Unrecognised assumptions are a major source of confusion in model building. Minor alterations may in turn alter the whole model so that it may be necessary to reappraise the earlier stages of the model building process.

The model is next translated into a computer programme (8); real or test arithmetic values for initial conditions and parameters are supplied in place of the symbols (9) and a simulation run is carried out (10). It is unlikely that the output from this run will accurately mimic the real situation. By successively adjusting the arithmetic values through a cycle or runs (11) the model is brought to mimic the real situation as closely as it is able. This tuning procedure can be utilised as a process of active experimentation on the computer (see Figure 4). If subsequent real experiments show that parameter values obtained by tuning are correct within experimental error then this may represent a partial validation of the model.

Validation (12) is the testing of the model to determine whether within its inherent limitations, its behaviour is in sufficiently close agreement with the behaviour of the real system.

Validation procedures for small models come closest to statistical methods developed for small scale experimentation in that the model is validated against data sets of the whole system independent of those used in the model's construction. However it is difficult to obtain reliably independent data sets in ecological situations. Independence in time, place and pattern of component values need to be ensured. For instance, independence of data between seasons is frequently assumed. Such data is independent in time, but degrees of difference in weather and soil factors, etc. may be impossible to define. When construction and test data sets are similar the model may appear valid. A common reason for this is that models, by their nature, normally obscure undetected non-linear relationships which show up under the influence of variable data. Thus varied data sets are the most informative and frequently point to the need for experimentation and model modification. In general, the greater number of data sets accommodated by a model, the more reliable it becomes.

De Wit (1971) adopts a validation technique similar to that used in the development of the American space programme, an outstanding example of a predictive modelling project involving human safety and for which neither construction nor test data on whole system functioning could be obtained in advance. His models are built and the parts are severally tested at a more detailed level of understanding than the level which is to be modelled. For example physiological experiments may be used to build a model of crop growth. Data is obtained independently of the whole system, the system need not be manipulated and prior knowledge of whole system functioning may not be essential. This approach suits certain types of ecological study.

As Nelder (1972) points out, modelling is a pattern matching activity. It is therefore necessary to know when patterns match. Greater emphasis on stochastic models and the more widespread use of validation methods involving likelihood functions are needed. To the extent that stochastic models can offer predictions in the form of alternative probabilities they are more realistic and offer the environmental decision-maker a more reliable base for decisions.

Should the model prove invalid it becomes necessary to analyse its properties (12a). In sensitivity analysis the forcing functions, internal relationships, and other parameters are varied through their maximum range to elucidate their effect and importance to the model so as to determine which aspects of the real system need further investigation.

Even after validation a model is likely to include much redundancy so that its mathematical simplicity and therefore its ability to be understood is obscured. Sensitivity analysis can be used to detect redundancy and so assist in reduction of the model to a concise statement (13). Once unnecessary material has been pruned it can be further simplified mathematically.

At this stage the model should be capable, hopefully, or providing answers to the questions originally posed (14). The values of the system variables of the tuned model or the structures of the model may themselves constitute the required result. If the model is to be used predictively a sequence of hypothetical data sets is manipulated so that over a sequence of runs the expected pattern of possible results is determined. Usually in the development of a predictive model it is necessary to pass through investigative and descriptive stages. The failure of a model to adequately describe or predict a system may itself be useful as a pointer to the need for further investigation.

Finally an evaluation is carried out (15). If the original objectives are not met the model building process can be repeated in cyclic fashion until adequate match between simulated and real results is obtained. This is essentially tuning on a larger scale.

EXAMPLES

Example 1: A student wheat growth model

Each year a class of third year undergraduates at Massey University is given six weeks to build a systems model to describe and then to predict the early growth of wheat in a partly controlled set of environmental conditions. It is suggested that they approach the problem by first isolating the effects of those environmental factors that they perceive to be of major importance and then progressively investigate other factors until their model simulates measured growth within experimental error. A greenhouse, weather data, advice, some plants at various stages of growth and the usual laboratory facilities are provided. Plants are provided with optimal water and mineral requirement except for nitrogen. Different batches of plants are grown in different nitrogen conditions. Apart from these limitations the entire development of the model is up to the students.

This example is based on the efforts of students carrying out this project over the last three years. Figure 2 illustrates a typical model produced by students in the initial design stage prior to any experimentation. It represents their attempt to reconcile prior theoretical understanding with practical model building technique and experiment. It is based on simple measurements of seed weight, the proportion by weight of green tissue in 3 week old plants, information from the literature on photosynthesis and respiration rates and day-length. The algebra for this model is extremely simple, the output of each equation simply being the product of the inputs, whole plant weight change is the algebric sum of equation simply being the product of the inputs. The results are clearly inadequate (Figure 4).

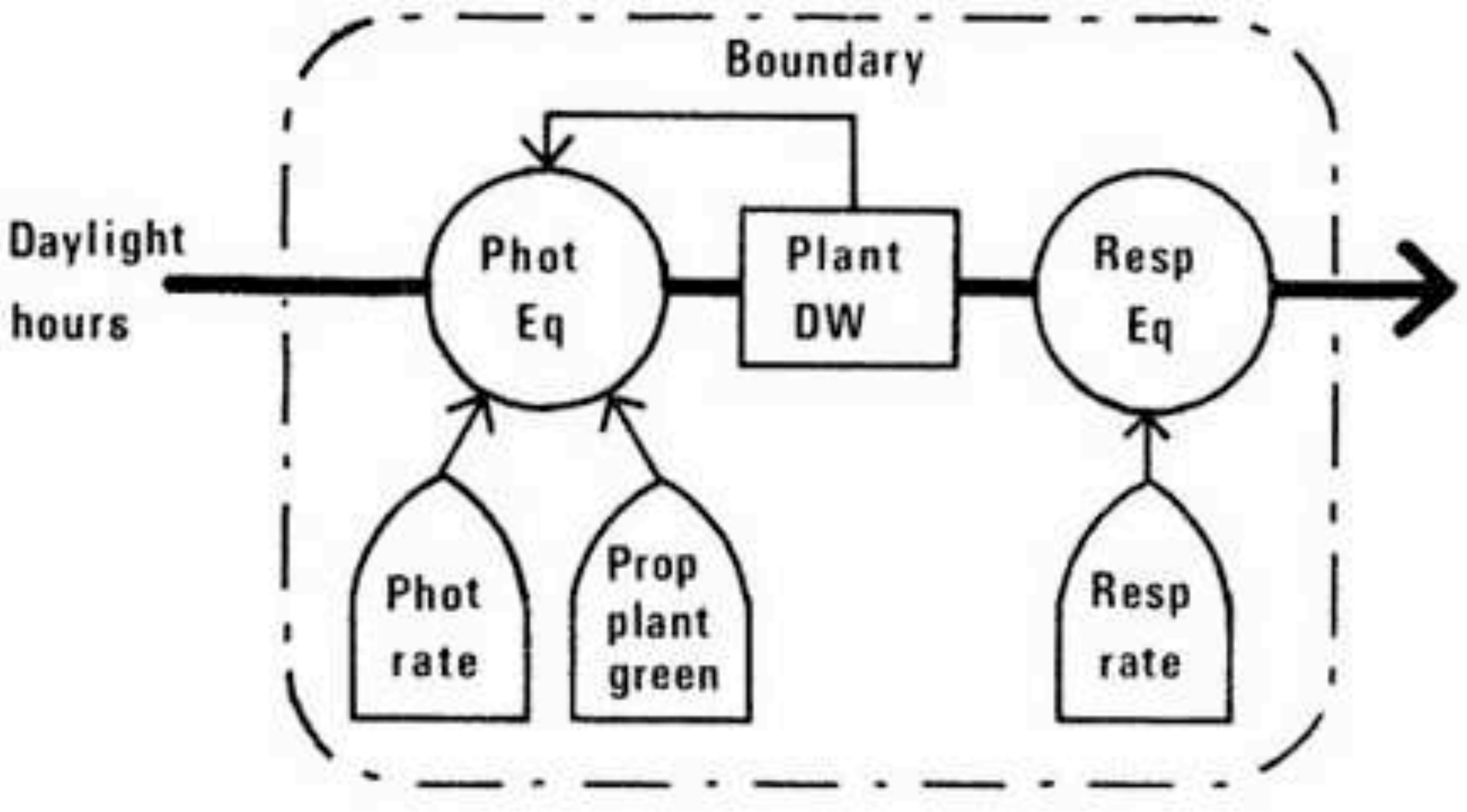

FIGURE 2. *Initial student diagram for the early growth of wheat. Rectangles*—components. *Circles*—equations. *Bullet shapes*—information from lower level experiments. *Fine arrows*—information flow. *Bold arrows*—flow of energy or materials. Terms defined as in Figure 3.

Figure 3 is typical of a final structural diagram produced after five weeks work. The number of components is increased to four and except in one case all interaction equations are complex non-linear structures and some involve state transitions. For instance, during the cycles of modelling and experiment it emerged that respiratory rate is initially high but settles down at a fairly constant value after twelve days. A rectangular hyperbola is fitted to simulate this. Similarly the photosynthesis equation is complex. It involves a change of state in that prior to four days of age the plants have no green tissue and their dry weight falls due to respiratory losses. After four days the organism is photosynthetic and the principal factor controlling photosynthesis is the proportion of green tissue. This increases rapidly at

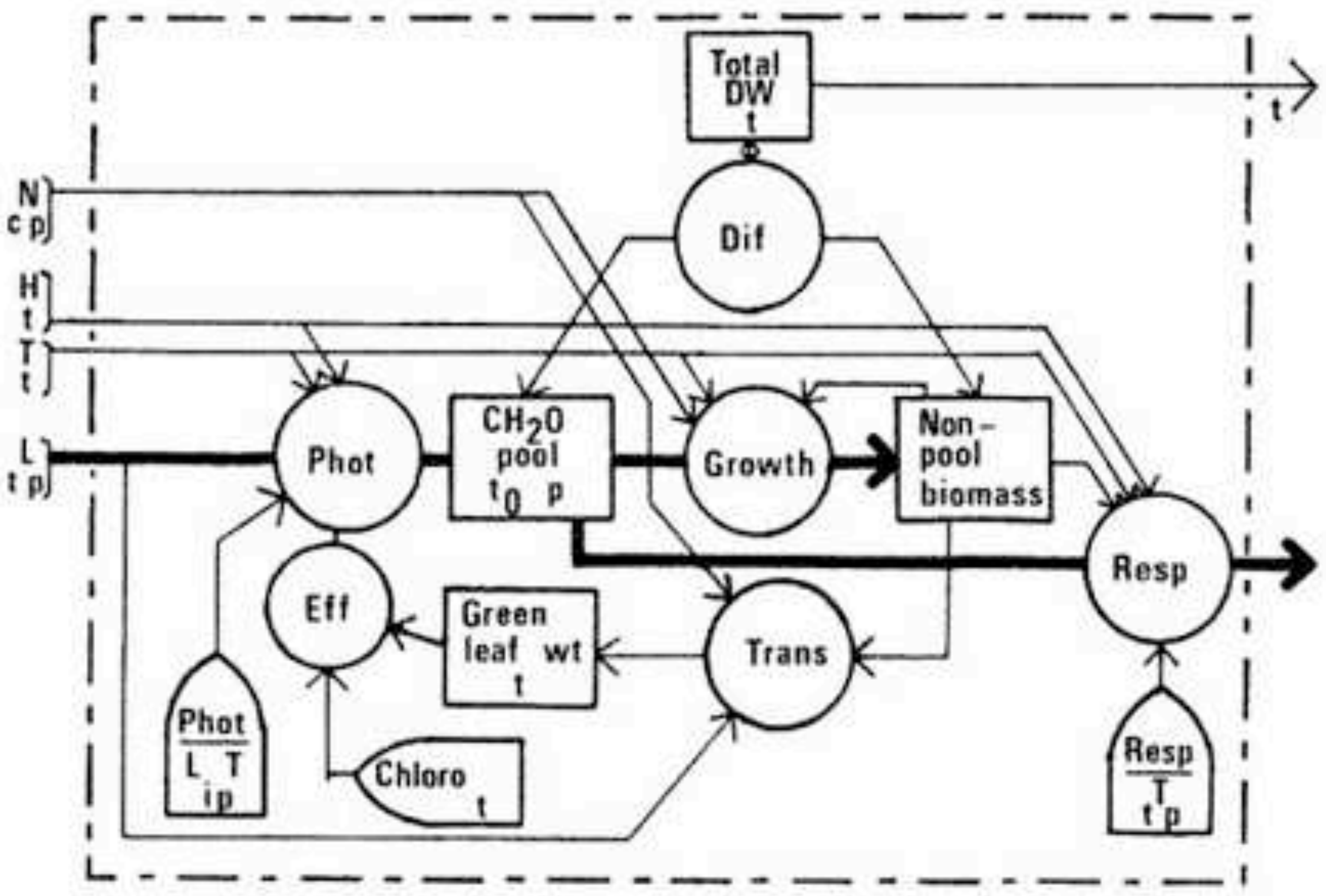

FIGURE 3. *Final student diagram for the early growth of wheat. Phot*—photosynthesis. *Resp*—respiration. *Chloro*—chlorophyll per unit leaf. *Dif*—difference equation. *Eff*—efficiency equation. *Trans*—transfer equation. *N*—nitrogen. *H*—humidity. *T*—temperature. *L*—light. *c*—measured constant. *t*—measured over time. *i*—measured independently of time. t_0—measured at time zero. *p*—utilised in prediction phase. *DW*—dry weight. *Other symbols as in Figure 4.*

first, but then gradually reaches an assymptote after 30 days at about 0.61 plant dry weight in greenhouse conditions of full light and nitrogen. As expected a reduced supply of nitrogen reduces overall growth but increases the proportion of root, while reduced light reduces overall growth but increases the proportion of leaf.

Perhaps one of the most spectacular aspects of systems modelling is that it offers a dynamic description of the real system under study. This is dramatically exemplified for students in the difficulties they have in handling one extremely variable forcing factor—light energy. Daylight or sunshine hours are quickly shown to be hopelessly inadequate as a measure of light energy input and daily total incident radiant energy readings are substituted. For programming reasons these are first averaged over several days. The length of these periods and position of the cut-off points makes a tremendous difference to the accuracy with which the model mimics real growth.

A characteristic of systems modelling is that so called "emergent properties" of the real system are discovered. In one case much time was spent trying to elucidate the reason for a significant increase in real photosynthetic output during the third and fourth weeks of growth. This could be allowed for in the model by an artificial efficiency equation. Although many reasons were proposed and some, for instance the changing chlorophyll content of leaves, were investigated experimentally no satisfactory explanation was found.

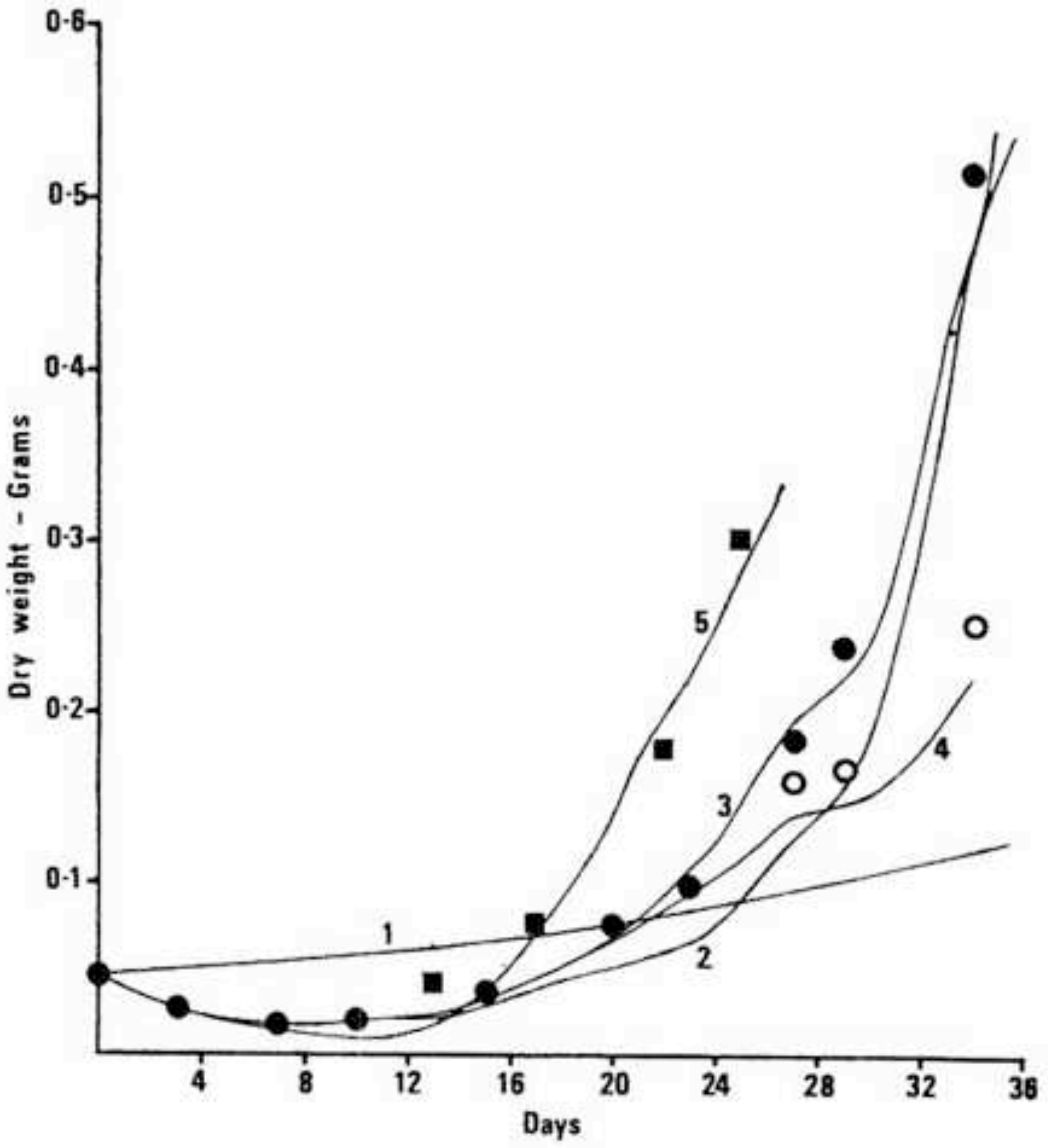

FIGURE 4. *Developmental stages of student model of early growth of wheat. Solid circles*—measured growth, full nitrogen. *Open circles*—measured growth, half nitrogen. *Squares*—measured growth, validation curve, full nitrogen. *Curve 1*—results of initial model, full nitrogen. *Curve 2*—results of model prior to incorporation of photosynthesis "bulge", full nitrogen. *Curve 3*—results of model incorporating photosynthesis "bulge", full nitrogen. *Curve 4*—results of model as in curve 3, half nitrogen. *Curve 5*—validation curve for final model, full nitrogen, plants grown in longer days. *Curves only indicated where they diverge from previous curves.*

Attempts to validate models against sets of data independent in time usually fail at first. In the case illustrated analysis showed that photosynthetic output was unrealistic for the pattern of light input in test data. In the original model the proportion of green tissue had been related to the age of the plant rather than to its stage of development. Development depends, of course, on the amount of photosynthate available for growth and therefore on the light regime. The problem was solved by modifying the model to calculate the proportion of green tissue on the basis of plant weight instead of age.

Depending on how the model has been constructed sensitivity analysis usually shows that certain factors can be eliminated so making it more concise. In this case the amount of chlorophyll per unit leaf was eliminated (see Figure 3). In addition, recognising that this model only be used to predict greenhouse growth, factors of temperature and humidity were also eliminated since these were reasonably constant in the semi-controlled greenhouse conditions.

The purpose of presenting this example of a student project is mainly to demonstrate the facility with which modelling can be carried out. Few of the values or hypotheses used would bear examination. In any case time always runs out long before results are suitable for a proper evaluation. The fact that the models are trivial is of no consequence. All projects can look trivial with the wisdom of hindsight and greater experience. An initial concern that these biology students would not be able to handle the programming aspects of model building was unfounded. It takes students only a few hours to learn the basics of programming in 1130 CSMP.

Example 2: A dairy farm model

A dairy farm is an example of a community level ecosystem of considerable complexity. Figure 5 is an extremely simplified version of the whole system. For clarity the boundaries of the whole system and of the decomposer unit have been omitted, while water balance and the only nutrient considered, nitrogen, have been included with the primary producer unit.

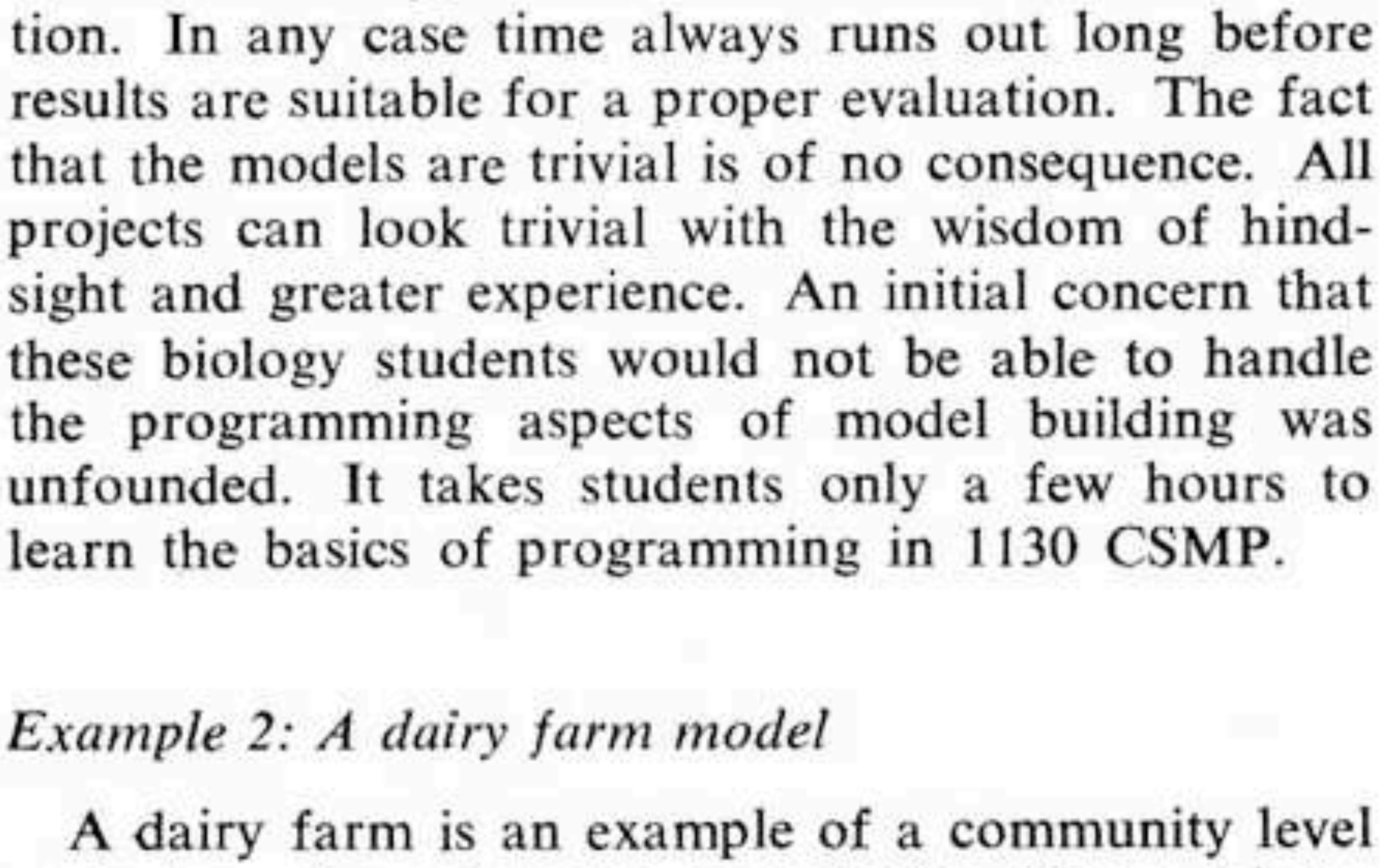

FIGURE 5. *The dairy farm—a community management problem. Bold arrows*—energy flow. *Interrupted bold arrows*—nitrogen flow. *Fine arrows*—information flow. *Interrupted fine arrows*—water flow. *Closed X symbol*—control valve.

Models are frequently criticised for lack of realism on the grounds that they are concerned with only one type of throughput, usually energy. Pleas have been made for broader based studies particularly for the inclusion of nutrient flows in productivity studies (Bourliere and Hadley, 1970).

In this model three types of flow are considered within the context of a single system. Energy enters as light, flows from producers to consumers through various routes in vegetable feed, and leaves the system through respiration or other losses and as milk or meat. Energy is stored naturally as a standing crop and in animal tissue, or artificially as silage or hay. Thus the rate of flow of energy is controlled by both natural and man-made feedback systems and can be extremely variable. Deficiency in energy from primary production can be rectified by the import of supplements.

The cycling of nitrogen differs from that in many natural systems principally in the greater importance of imports and exports while the flow of water is considered only as far as it directly affects plant growth.

This model also illustrates the fact that any component can be regarded as a system at a lower level. Thus an understanding of the complex relationships within the primary production unit is required if its equivalent component in the model is to give sensible outputs. The model therefore links three levels of biological complexity which is about as much as any model can do with current technology and understanding.

The model for the growth of green feed in any one paddock of the primary production unit is not unlike the wheat growth model above. However whole unit production is not as simple at this. The herd is shifted progressively round the farm in grazing rotation. Thus, while the stage of growth is synchronous in any one paddock, the feed on hand overall, particularly potential feed on hand, is a quite complex sum involving management decisions and knowledge of average weather conditions from previous years.

Similarly the primary consumption unit is complex even if there is only one class of animal in the herd at any one time since any normal seasonal dairy herd goes through several transitions over a period of time. The key to these transitions is conception dates which become important parameters in the model. A cow "changes state" depending on whether it is young, a non-reproductive adult, gestating, and/or lactating.

Finally the biological management unit represents that part of the system in which man attempts to control the way in which the basic biological components are allowed to interact. The farmer attempts to channel all the outputs of the system through components he can use. The first way he does this is to eliminate most unwanted species from the system and modify the species he retains. In the short term however his immediate problem is to maintain stability in his highly artificial ecosystem by forward feed budgeting procedures of considerable complexity. Not only must he feed his cattle now but he must also retain enough feed to form the basis for future growth. He must know when or how much silage or hay to make or fertiliser to spread. He has in fact to replace natural controls by a highly sophisticated human feedback system.

The influence a farmer has on his farm system is so great that in fact he virtually synthesizes a new system. Thus, in attempting to model a dairy farm, probably the greatest problem is to recognise and define the management practices and strategies, which, so far as the ordinary farmer is concerned, are part of his inherited tradition.

THE POTENTIAL OF SYSTEMS MODELLING IN ECOLOGY

Like statistics, systems modelling is a tool for ecologists. Much more than statistics, systems modelling is concerned with the matching of continuously changing patterns, possibly this is its most important single characteristic. It adds a new technique to the rather limited range of *dynamic* descriptive tools in ecology.

The two examples given earlier illustrate a naive and a complex model, but both are naive in concept. This is easy to see if one has even a rudimentary knowledge of plant physiology or dairy farming. Critics of systems modelling point out that one's mental model of any ecological system is more sensitive and responsive than any computer model and that consequently such models are not able to further understanding.

However the human mind works by handling a few variables at a time and it cannot handle numerical complexity. It is liable both to qualitative inconsistency and quantitative error. Computer assisted systems modelling can progressively uncover unrecognised inconsistency and provide the numerical backup required in complex models. Even naive models can aid in the development of understanding of interaction patterns as the first example above attempts to show.

Further to this, it is relatively easy to convey to others the understanding that results from analytic experimentation on some part of the system. It is much harder to convey one's mental synthesis of the whole system. Systems modelling can assist in making the mental model of the experienced scientist available to others. It can be argued that any such overview would inevitably be hypothetical, but surely there is no danger in this provided that this is made clear.

Another advantage of systems modelling is its usefulness in guiding research. For the individual or group it can save time in determining priorities and help in avoidance of unfruitful or redundant lines. For the group it can assist communications and bring unity to the project particularly so that the whole project moves in step. Thus, at least in theory, a project can reach its conclusion at some feasible level of sophistication for which the results are rigorous, precise and complete.

It is this "keeping in step" which is the essence of what has been called "systems orientation". While its advantage to the administrator are obvious it is perhaps the Achilles' heel of the method so far as the ordinary scientist is concerned. There is inevitably some restrictiveness involved, which is contrary to the common scientific style of the pursuit of selected leads individually to exhaustion. Depth of study in some areas may be traded for a synthetic understanding of the whole. However it is logically impossible for any description ever to be complete, there will always be something more particular to describe. Any model will inevitably look inadequate when viewed from a more detailed level of understanding. This in no way invalidates the use of models for making broader but less detailed syntheses which are so useful in ecology.

THE FUTURE

Systems modelling in ecology still has deficiences of under-development and it can be expected that some of these will be rectified by technical advance over the next few years.

For instance adequate data on capriciously variable microclimate forcing factors is difficult to obtain at present. The development of small, cheap electronic microclimate recorders for field use is urgently necessary if many ecological models are to be developed successfully.

A more direct need is for further development of computer languages for modelling. We need to get beyond the stage where simple models are programmed in modelling languages whereas more complex models revert to Fortran. We need higher-level languages good enough for all modelling. Relative to machine language Fortran is a high level sophisticated language. Its development made the computer accessible to biological scientists by the simplification of the logic required and by the use of meaningful symbols or mnemonics. Just as Fortran is a high level language enabling the programmer not to have to work at the machine or assembly language level so there are today even higher level modelling languages (some of which are based on Fortran) which further simplify the programming and mathematical competence and effort required of the user.

As Fortran took time to develop, so these higher level languages are taking their time in turn. CSMP (Continuous Systems Modelling Programme) is a good example. 1130 CSMP (Brennan, 1966), uses a functional block approach. It is extremely easy to use but is severely limited in its capability to handle capriciously variable input data such as weather data. It does not have logarithmic or trigonometric functions, the size of the programme that can be written is limited and it is slow. For all that it can be most useful especially for small quick problems and for teaching. In 1967 Brennan brought out 360 CSMP, a much improved and more versatile programme for which either an equation or a block approach can be adopted. A version available in New Zealand is CSMP73 (Fugasi, 1973). 360 CSMP has a whole variety of available functions and capability for large programmes including unlimited lists of varying data. It also has a "macro" capability, that is, units within the programme can be linked to give an even higher level unit. It also has some deficiences, for instance the inputting of lists is clumsy. Also one might wish it had a function for day-length and radiant energy input based on parameters for latitude, starting date, etc. but this latter type of difficulty is easily overcome since it is fully compatible with Fortran.

As well as CSMP, there are other higher level language series such as Dynamo which have undergone similar evolution. Dynamo was initiated by Pugh (1962) and is particularly used in management problems for which it was originally developed.

Another area where improvement could take place is in validation techniques. There is little excuse for improperly validated models if a hard logical line is taken from the start. Some of the difficulties of this have been discussed above. However there is the need for the development of new statistical procedures based on the matching of continuously changing patterns and any methods that are developed need to be easy to apply.

These deficiencies only serve to show up what is probably the major deficiency of all, that of training. All ecology graduates need training in modelling just as they need training in statistics. This is brought up wherever modelling is discussed (e.g. Jeffers, 1972; Drummond and Wright, 1975). It is especially important to allay doubts based on misunderstanding of this new technique and to get it into general use. This is best done by training at all levels.

Finally it would seem that several uses for systems modelling in ecology are becoming differentiated. Despite its simplicity relative to the average community ecosystem the dairy farm can only be satisfactorily represented by a complex model. As pointed out by Maynard Smith (1974)—

> "Whereas a good simulation should include as much detail as possible, a good model should include as little as possible".

He is making the distinction, not made earlier in this paper, between "simulation" which is aimed at specific project solution, such as the description of the behaviour of a whole ecosystem, and "modelling" by which he means analytical abstraction of general laws which can be applied to any system. He may use the techniques referred to earlier as systems modelling in this process of abstraction but it is clear that his aims are general and theoretical, not specific. The underlying theme of this statement and of this paper alike is that systems modelling is a tool to be used, when appropriate, for many purposes. The variety of these purposes and the limits of usefulness of the technique are now being defined.

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