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Ecosystem Simulation

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## Introduction

The main object of this paper is to introduce one approach to the subject of ecosystem simulation to people who are interested in ecology but who are unfamiliar with the handling of conceptual ideas. This paper will also serve as a review of project 300 to this date. (Project 300 is entitled "Methods of assessment and computation of ecological models".)

The difference between physiology and biochemistry has been described by the following analogy:- PHYSIOLOGY is like attempting to find out what happens in a laboratory by standing outside and measuring only the chemicals and other materials that enter by the door and pipes and leave by the chimneys and drains and so on. BIOCHEMISTRY, on the other hand, is concerned with the study of each of the different processes that go on inside the laboratory. ECOLOGY might be thought of as the study of the behaviour of a whole research institute from information on the flow in and out of the main gates and other services.

In practice, ecology is not quite so restricted as this analogy implies. It has, for example, quite often detailed but fragmentary information from studies in biochemistry, physiology and traditional ecology. The problem, therefore, is almost literally one of trying to see the wood for the trees!

## An Approach through Traditional Ecology

There are several ways of assembling the parts in a meaningful way and for most practical purposes they all depend on analogue or digital computers. It is, in fact, the advent of these machines which has made it possible to use the classical scientific method in ecology.

At present, there seem to be three main ways of tackling ecosystem simulation. Firstly, purely empirically with little regard for physical reality; secondly, by integration of known or assumed physiological components; and thirdly, by observing the integrated outcome of plant and animal behaviour and fitting reasonable models to the observations.

The choice is governed by the requirements of the simulation. Each of the above methods has strong claims in differing circumstances and in practice all are used, but the last appeals to the traditional ecologist because his qualitative ideas about ecosystems are retained and developed into a quantitative form. It is this third approach which will be described here.

In the introductory account, the deterministic (i.e. without consideration of uncertainty of measurements due to experimental and other sources of error) aspects of the approach will be emphasised. However, it should be appreciated that the main sources of variation can be handled by use of Monte Carlo techniques. Goodall (1967 and in press) has demonstrated this in the simulation of a sheep range ecosystem, and it is worth digressing to give a brief outline of this particular application to illustrate the technique.

He argued that while many features of his model could be treated deterministically, without a severe loss of realism, rainfall over a desert ecosystem must necessarily be treated probabilistically.

Daily rainfall was divided into a number of discrete classes (zero, trace to .1 inch, .11 to .2 inch and so forth), and an empirical distribution was derived from standard meteorological data giving the probability of a particular day falling into each of these classes. One such distribution was derived for days following dry days, another for days following wet days. In this way he was able to simulate a storm pattern. Selection of the rainfall class into which any given day fell was obtained using a random number generator (hence the derivation of the name Monte Carlo). A second selection using the same method was made, this time from a rectangular distribution, to decide the actual precipitation value within the class selected. The procedure effectively introduced an important source of chance variability into the model and its results. Goodall's simulation model is an interesting blend of interacting processes described by deterministic or probabilistic relationships, each based on experience and a careful consideration of their proportionate importance in the whole system. His method is a type of compartment modelling which means that he divided the various components of the system into classes or groupings which could be considered for the purposes in hand to be homogeneous within themselves. The name 'compartment' is, of course, merely a way of emphasising a procedure common throughout science, of delimiting an abstract unit which can be conveniently handled quantitatively.

### Compartment Models I

Growth analysis techniques have been used extensively by plant physiologists and ecologists to obtain quantitative characteristics of species of plants growing in natural and semi-natural environments. One simple model frequently used in these techniques is:-

$$dW/dt = kW \quad (1A)$$

or, in words, the growth rate of a plant or animal is proportional to its weight at any given time. (Blackman, V.H. (1919), Briggs, Kidd and West (1920 A and B), Fisher (1920).)

The value of  $k$  is readily obtained from the slope of  $\log_e W$  against time, i.e.

$$k = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1} \quad (1B)$$

This equation is limited in its application, however, because it does not take account of long periods of growth in which death and decay become important.

Possible alternative models which do make allowance in this way are:-

$$dW/dt = I - kW \quad (2)$$

where the growth rate equals the difference between income and loss; in this case the loss is considered proportional to the weight at any given time.

This type of equation is particularly appropriate for application to the change in weight of litter on a forest floor, for example Jenney, Gessel and Bingham (1949) and Olson (1963), assuming as it does a constant input I. A similar model, known as the Pearl - Verhulst Law of Population growth is:-

$$dW/dt = k_1 W - K_2 W^2 \quad (3A)$$

Another way of expressing this equation is:-

$$dW/dt = \sqrt{k_1} - (k_1/K) W \sqrt{W} \quad (3B)$$

where  $k_1/K$  is  $k_2$  of the previous equation. In this latter form it will be recognised that this is a modification of equation (1A) in which  $k$  is made variable instead of constant and is dependent on  $W$ . In some circumstances  $K$  can be regarded as a particular value of  $W$  equivalent to the carrying capacity or saturation level of the environment (Slobodkin, 1953).

Equation (3A) may also be solved analytically:-

$$W = \frac{A}{1 + B e^{-C(t - D)}}$$

where  $A = k_1/k_2$ ,  $C = k_1$ ,  $D = t_0$  and  $B = \sqrt{(k_1/k_2 w_0)} - 1$  and  $t_0$  and  $w_0$  are the initial time and weight values. In this case it may be necessary to find the values of  $k_1$  and  $k_2$  by successive approximations.

Equations (2) and (3A) make specific allowance for limitations of the environment by including a loss term dependent on the size of the organism (or population) itself. Each produces a steady state in which gains in weight are balanced by losses. They still only represent physiological facets of ecosystems, however, in the sense I referred to earlier. They might be thought of as describing one compartment of an ecosystem such as one species of plant or animal.

An ecosystem, however, is an assemblage of different species of plants, animals and microbes interacting with each other and their environment. A possible first abstraction is to pool the organisms with common functional characteristics. This has been done in the hypothetical case (Patten, 1966) illustrated in Figure 1, where all the green plants are represented by box  $B_1$ , all herbivores by box  $B_2$ , all carnivores by box  $B_3$  and all decomposers by box  $B_4$ . The arrows represent flow pathways along which it is known that such materials as carbon and/or mineral nutrients pass. Such arrows imply a coupling process which can be achieved mathematically by the system of equations (4).

$$\begin{aligned} dB_1/dt &= \tau_{01} B_0 - \tau_{12} B_1 - \rho_{14} B_1 - \rho_{10} B_1 \\ dB_2/dt &= \tau_{12} B_1 + \tau_{42} B_4 - \tau_{23} B_2 - \rho_{20} B_2 - \mu_{24} B_2 \\ dB_3/dt &= \tau_{23} B_2 - \rho_{30} B_3 - \mu_{34} B_3 \\ dB_4/dt &= \mu_{14} B_1 + \mu_{24} B_2 + \mu_{34} B_3 - \tau_{42} B_4 - \rho_{40} B_4 \end{aligned} \quad (4)$$

This set of equations may be solved by analogue or by digital computer after suitably chosen values have been inserted for the starting or initial conditions of the masses within the 'boxes' and for the parameters  $\tau$ ,  $\rho$  and  $\mu$ . In an analogue simulation, the masses are represented by voltages and years of real time by seconds or multiples of seconds of computing time. The parameters are fractions of the masses transferred to and from different compartments at each time step  $dt$ . Solution by analogue computer has the advantage of giving rather direct acquaintance with the characteristics of the model because of the ease with which initial conditions and parameter values can be modified. This facility, now considerably enhanced by the availability of oscilloscope displays, gives a ready appreciation of the consequence of changes. Analogue computers do have limitations of scaling and accuracy, however. Neel and Olson (1962) have explored many of the theoretical and practical problems associated with the application of analogue methods to ecosystem studies, and have pointed out that the limitations are not insuperable. Newer versions of analogue computers certainly have considerably increased flexibility.

Digital computers now exist which have none of the disadvantages of analogue computers, having been equipped with programs which are based on analogue circuit concepts, e.g. the I.B.M./C.S.M.P. (Continuous Systems Modelling Package). However, many digital computers take longer to learn to use in this respect and an introduction to the concepts via the more readily understood analogue computer can be very valuable. Apart from this teaching and introductory role of analogue computers, they can provide a very useful first-approximation tool in the initial study of a system for which equations have been proposed. The two types of computer are complementary and the increasing popularity of hybrid computers which incorporate both analogue and digital features can be appreciated.

Figure 2 illustrates the type of output which is obtained from an analogue computer solution or simulation of the set of equations (4) given above for the five compartment model of Patten (loc. cit.) shown in Figure 1. The initial masses have been made to coincide, for purposes of clear illustration, at a point equivalent to five volts. The scaling factors ( $10B_2$ ), ( $100B_3$ ) etc. were made to correspond with the expected relations of biomasses of the different compartments, the plants being the largest, the carnivores being  $1/100$  part of the plant mass, with the herbivores and decomposers in an intermediate position. In this hypothetical case the starting point might be visualised as corresponding to a sudden increase of herbivores and possibly carnivores, which led to the observed disturbance and subsequent establishment of new equilibria.

Thus, analogue computers solve (integrate) differential equations efficiently provided the physical limitations of the electronic amplifiers are not exceeded. It is this physical limitation which renders it necessary to pay particular regard to matters of scaling.

#### "Solution" of the System of Equations

In the context of the approach described here initial conditions and of parameter values are of primary consideration. The initial conditions are usually known but the parameter values are being sought in much the same way as the relative growth constant  $k$  is sought for the relationship given in equation (1A).

Use of an analogue computer facilitates rapid modification of parameter values until a satisfactory fit is obtained. Iterative least square techniques are now being developed, however, to do the same task using a digital computer. As far as error is concerned, systematic variation of parameter values obtained in the above ways can provide an estimate of the range of variation in parameter values which produces errors in the variables of similar order to those observed.

### Compartment Models II

In the above example, and in the work reported by Gore and Olson (1967), there was a strict application of the concept of flows, transfers of a single material were considered and these transfers depended solely on the amounts of material in compartments from which the material originated.

This concept of a rate of change of a compartment being proportional to the size of the compartment itself is too restricting for much realistic simulation and Bledsoe and Van Dyne (1969) have used similar methods to include indirect effects on rates of change. These workers have simulated the qualitative results of Billings (1958) on the mechanisms of change from a grass-forb stage through a short leaf pine stage and finally to a deciduous forest.

In order to illustrate the idea of indirect effects, a simplified preliminary stage is shown in Figure 3. The solid arrows represent a direct transfer of the compartment contents as implied above, the dotted arrows indicate an indirect effect of one compartment by modification of some parameter of another compartment.

In words, Figure 3 represents the pioneer growth of Andropogon virginicus (1) which is succeeded by Viburnum, Aster and Plantago (2). These two compartments both contributed to the accumulation of organic matter in the soil (3) and one of them (2) forms "shade" (4) which affects the Andropogon compartment. The relevant equations:-

$$dV_1/dt = f_{11} V_1 - C_{11} V_1^2$$

which describes the growth rate of A. virginicus,  $f_{11}$  and  $C_{11}$  being empirically defined in the sense already mentioned (cf. equation (3A)). Compartment 2 has a similar equation describing the growth of Plantago, etc.

The change of shading effect with time is given by:-

$$dV_4/dt = f_{24} V_2 + f_{44} V_4$$

where  $f_{24} = +1.0$  and  $f_{44} = -1.0$ . The inclusion of this shading effect on compartment  $V_1$  was achieved by replacing  $f_{11}$  by  $f_{11}^*$  where:-

$$f_{11}^* = \frac{f_{11} (D_1 - V_4)}{D_1}$$

Where  $D_1$  is some empirically defined positive constant, this will force  $V_1$  down as  $V_4$  increases; when  $V_4$  is near zero with  $f_{11}^*$  negative, the quadratic term may be ignored and  $V_1$  will tend to zero; this agrees with Billings' data which shows that many woody shrubs persist much longer than broomsedge (A. virginicus).

Figure 4 illustrates the full successional model with all the direct and indirect effects considered. One of these latter of particular interest, is the build-up of soil organic matter and its beneficial effect, at first, on the germination and establishment of pine seedlings and then its later deleterious effect on them as they fail to compete with the older trees for water.

$$dV_5/dt = f_{55}^* V_5 - C_{55} V_5^2$$

$$f_{55}^* = \begin{cases} f_{55} & \text{if } D_2 \leq V_3 < D_3 \\ 0. & \text{otherwise} \end{cases}$$

will allow for this, even if in a somewhat abrupt way,  $D_2$  and  $D_3$  being lower and upper threshold values respectively.

Finally, the oak seedlings become established as soon as sufficient litter has developed to prevent dehydration of the acorns and the soil compaction has been reduced by accumulation of organic matter. The root morphology of the oaks is such that the seedlings are able to extract water from beneath the zone of intense root competition, i.e. the top 6" layer of the soil.

Blodsoe and Van Dync, therefore, let  $V_6$  be the oak-hickory variable

$$dV_6/dt = f_{66} V_6 - C_{66}^* V_6^2$$

where

$$C_{66}^* = \begin{cases} 1.0 / (D_5 \cdot V_4) & \text{if } V_3 > D_4 \text{ and } \text{MAX}(V_2, V_5, V_6, V_7) \neq V_6 \\ C_{66} & \text{if } \text{MAX}(V_2, V_6, V_7) = V_6 \\ 0. & \text{otherwise} \end{cases}$$

where  $D_4$  is the appropriate organic matter threshold,  $D_5$  is empirically defined and  $C_{66}$  also. The MAX function ensures that  $V_6$  is shaded by all species other than by itself.

A similar model form was employed for the maple compartment allowing for the known higher growth rate (in open, unrestricted growth)  $f_{77}$  of the species, and allowing  $C_{77} > C_{66}$ . Figure 5 illustrates the simulation of compartments 5, 6, and 7 of the model.

A computer model experiment, Figure 6, to remove the pine at an early stage illustrates Billings' expectations that the maple assumed dominance before the oak had had time to gain the ascendancy. A pine resurgence was noted due presumably to the litter compartment state at the time of cutting. Failure of oak to regain a belated dominance in the "experiment" was attributed to the need for closer adjustment of the empirically defined parameters. Reference to further field observation or experiment would provide a clearer idea of the mechanisms involved and hence a better model representation. Other improvements in this preliminary model are suggested, for example, failure to reproduce on the part of the pine suggests that provision of a root density compartment in the top six inches would provide such closer control of root interactions.



### Conclusions

The last example has been selected because it is particularly relevant to woodland studies but more importantly illustrates the technique and its flexibility. I am indebted to Drs. Bledsoe and Van Dyne for permitting me to use it in its formative stage.

It can be seen that the method is essentially similar to approach in so called "growth analysis" studies but instead of confining attention to single parameter values like the relative growth rate ( $k$  of equation (1A)) a whole set of empirically defined parameters is sought from coupled equations representing ecological processes. Of course, the more parameters that are capable of assessment independently of the coupled model the better.

The process has the advantage of initial recognisability in terms of classical ecology, together with the capacity for constant improvement on a modular basis to the point of satisfaction for the purposes in hand.

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Figure 1

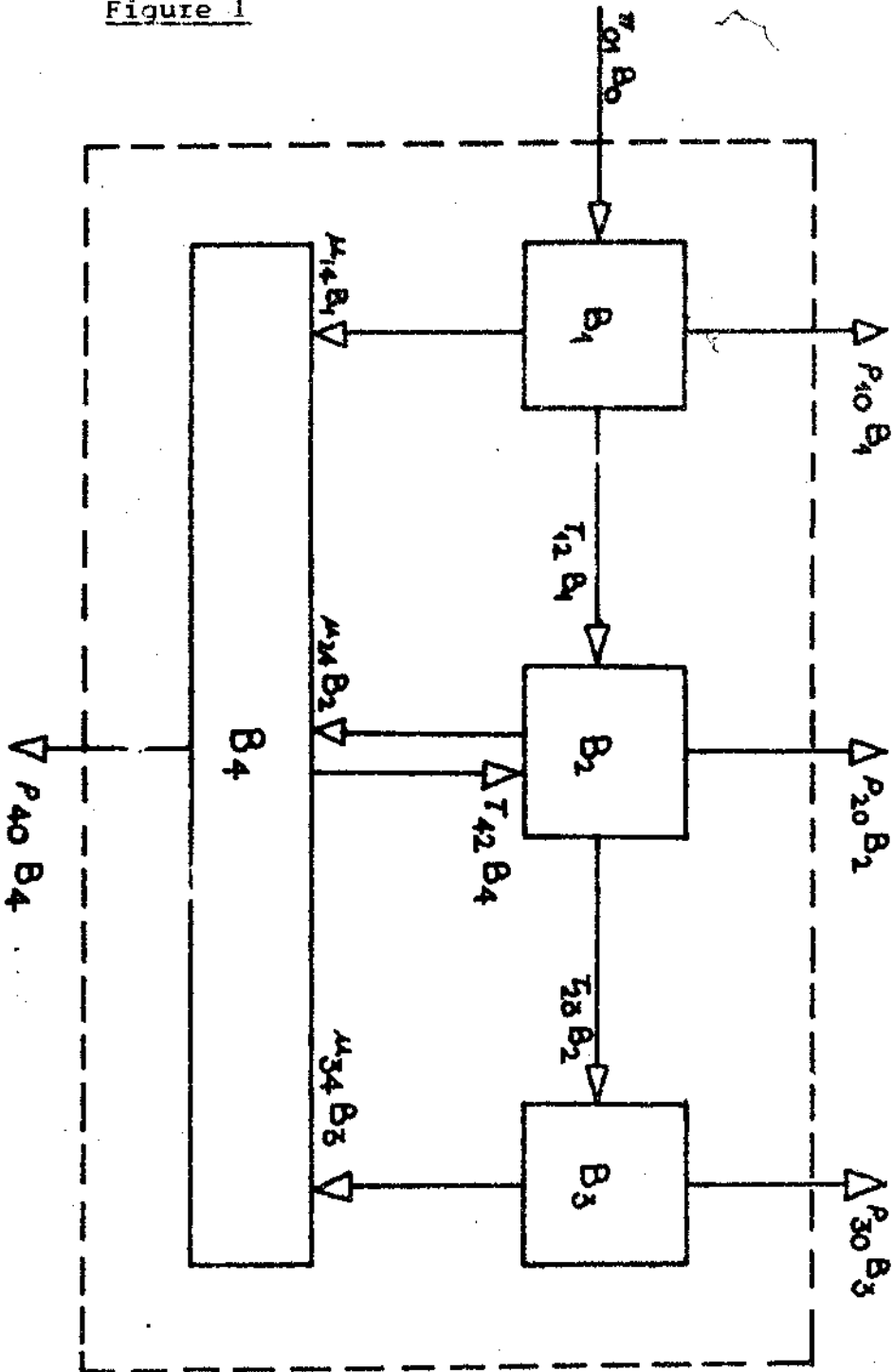


FIGURE 2

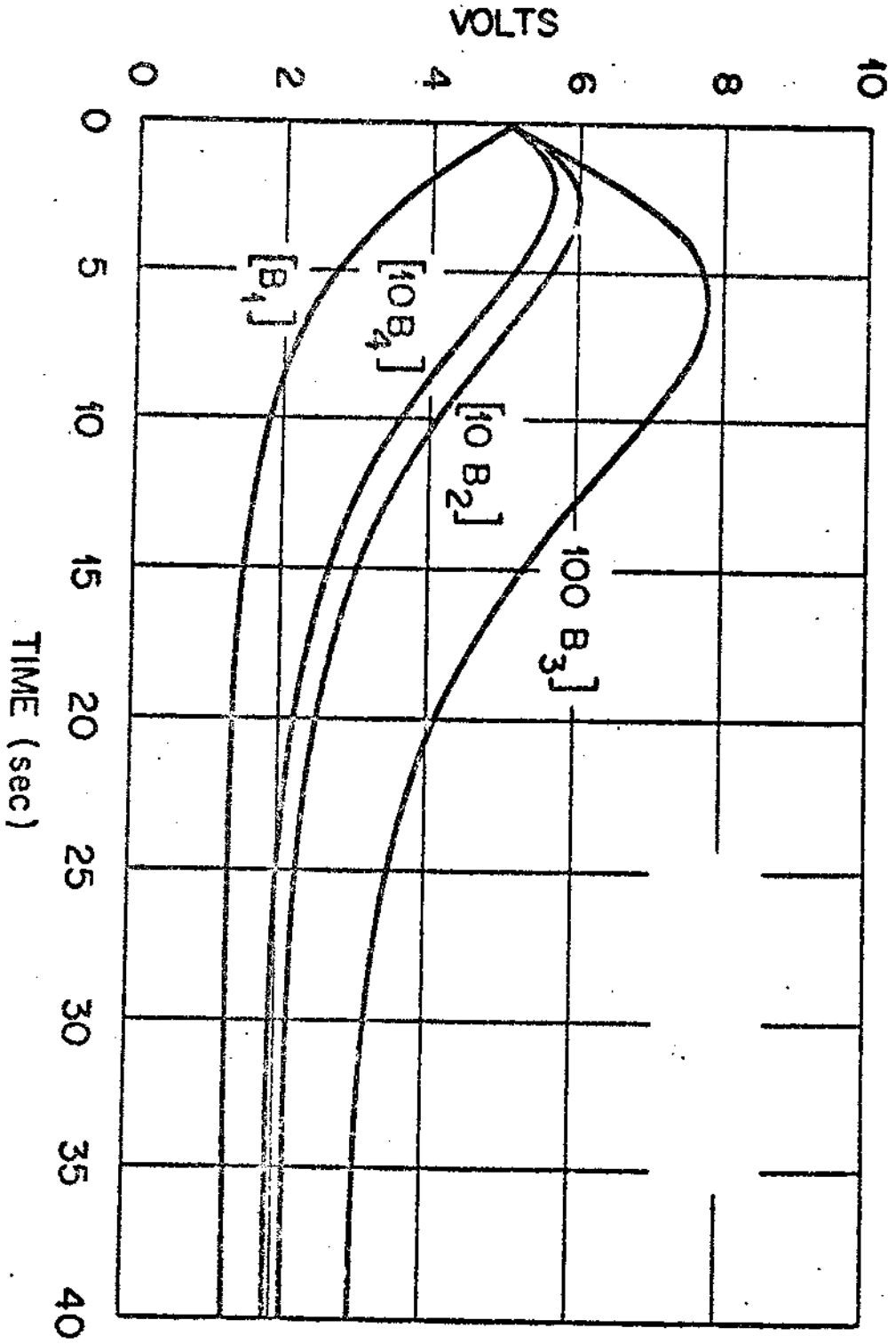


Figure 3

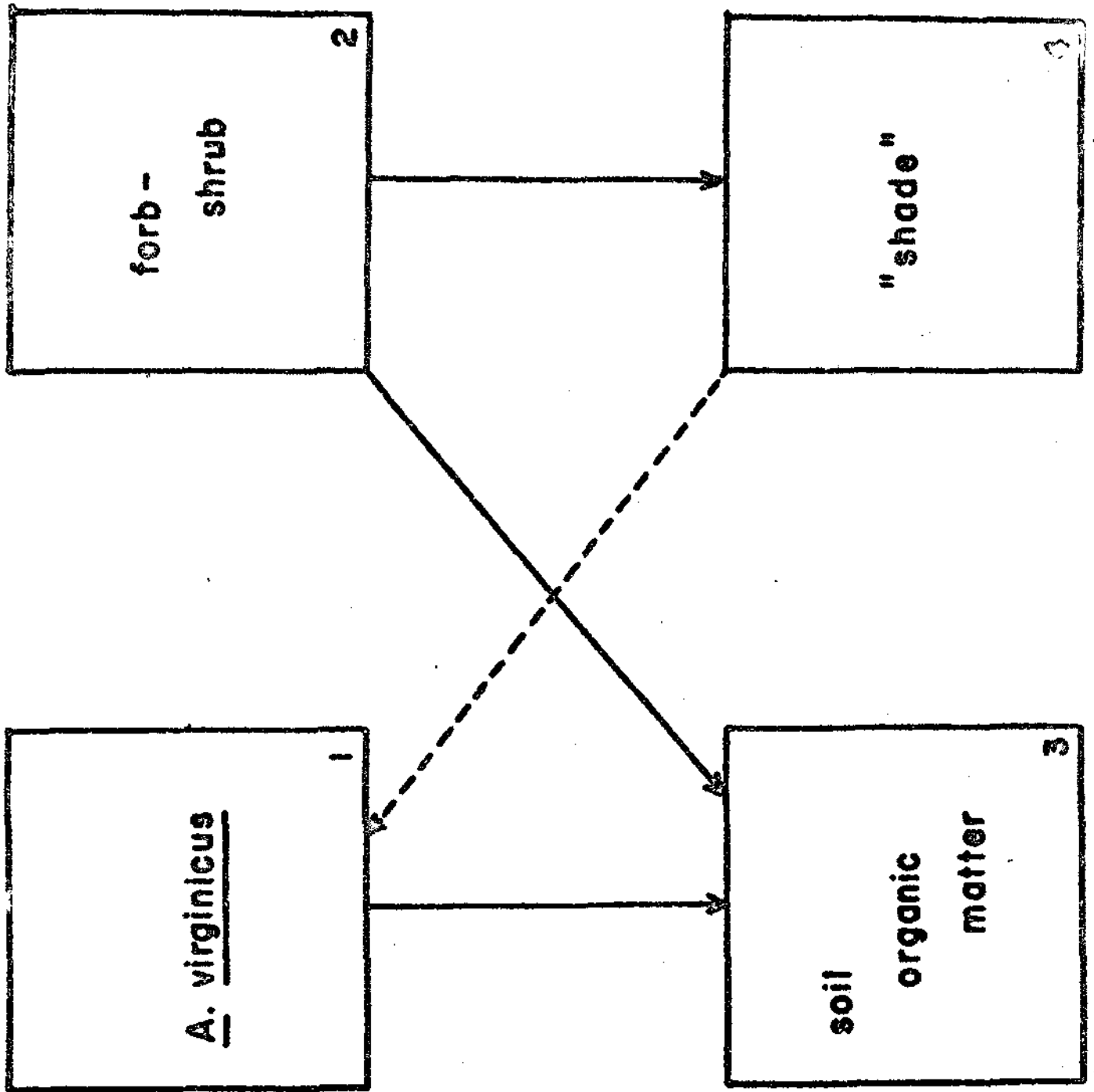


Figure 4

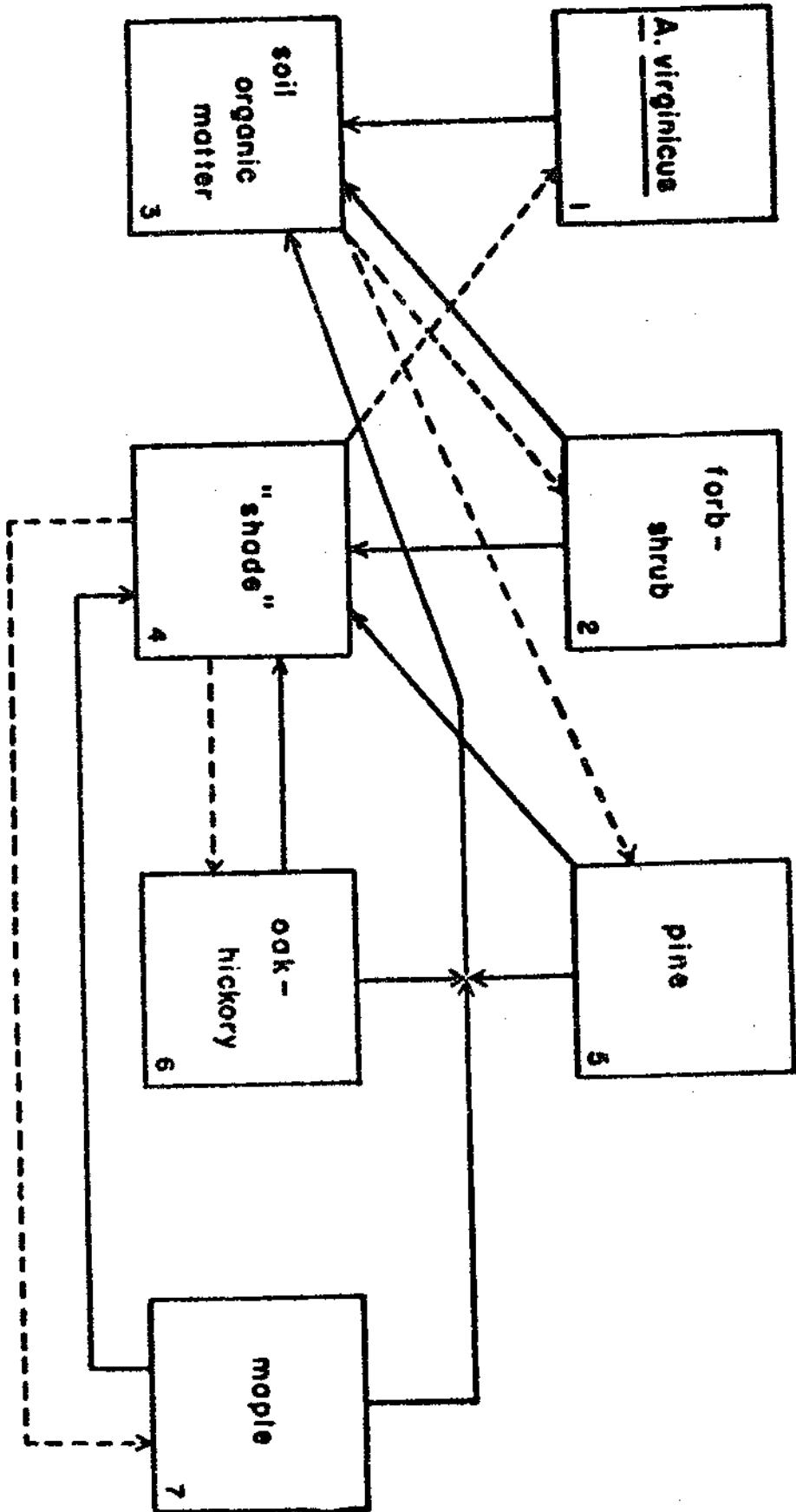


Figure 5

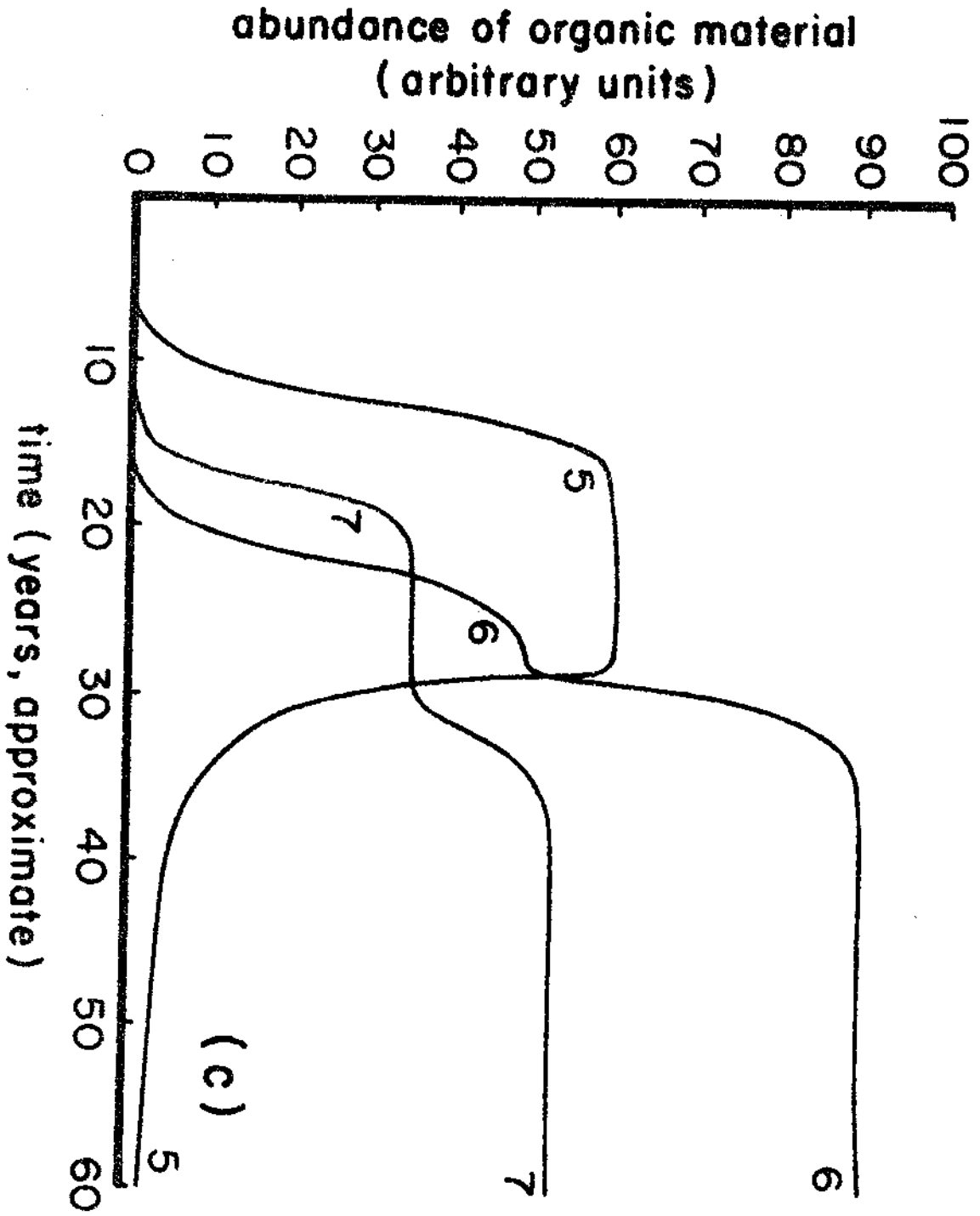


Figure 6

