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USE OF ANALOG COMPUTERS FOR SIMULATING THE MOVEMENT OF ISOTOPES IN ECOLOGICAL SYSTEMS

R. B. Neel
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R. B. Neel and J. S. Olson

Submitted as a thesis to the Faculty of the Graduate School of Vanderbilt University in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Physics.

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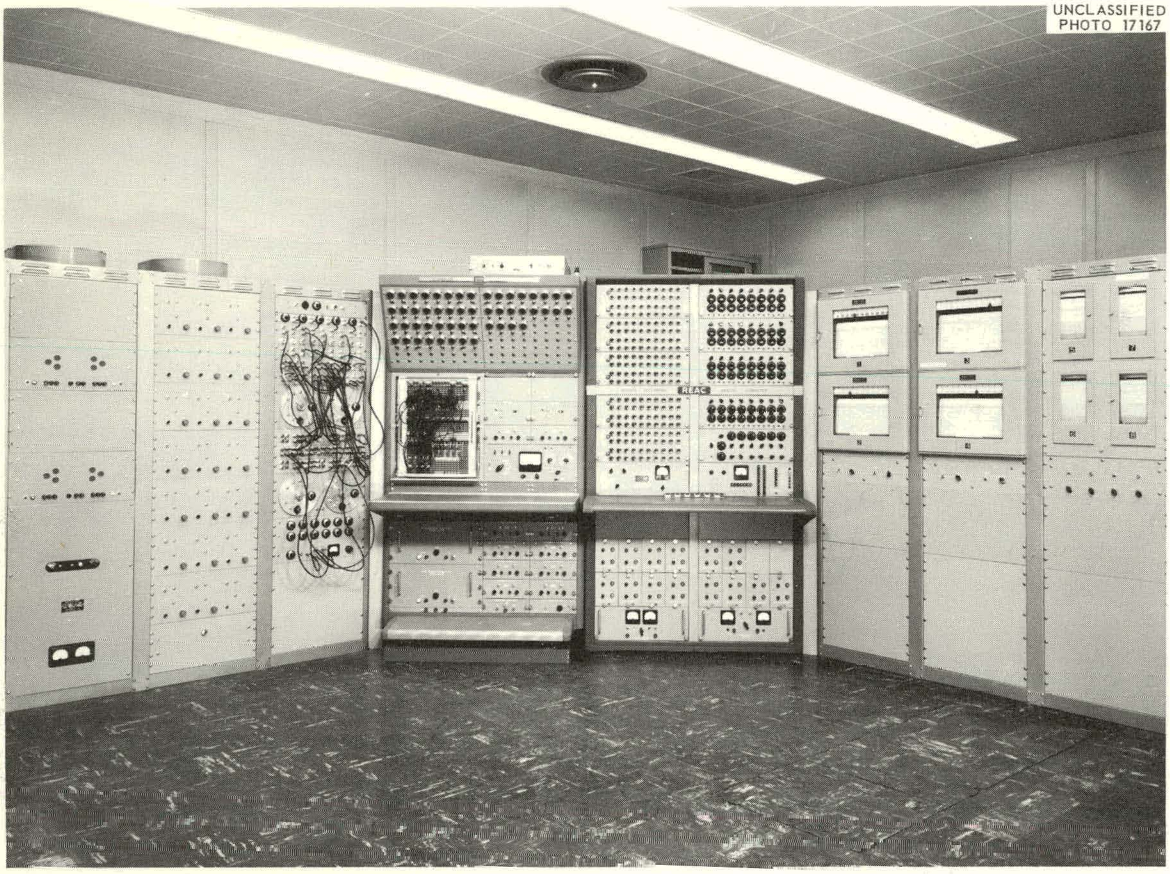

Reactor Controls Analog Computer Facility (RCAF), Oak Ridge National Laboratory

ABSTRACT

Linear differential equations and elementary analog computer techniques were applied to the movement of carbon and C^{14} in simple compartment models for a terrestrial ecological system (including soil, organic litter, plant roots and above-ground vegetation). Extensions of these methods should become helpful in simulating the movement of other elements and radioactive isotopes in the environment.

The parameter k_i controls the rate of loss of material from compartment i; the steady-state level for that compartment and the time required to approach that level are inversely proportional to k_i. "Partial transfer coefficients" ϕ_{ij} describe the fractional allocation of material from compartment i to various other compartments or pathways indexed by j, and hence influence the flux of material into compartments remote from the source. Changes in the concentration per unit area C_j per unit time t are represented by solutions to systems of equations of the form:

$$\frac{dC_j}{dt} = \sum_{i \neq j} \phi_{ij} k_i C_i - k_j C_j \quad \text{where} \quad 0 \leq k \leq 1; \quad 0 \leq \phi \leq 1.$$

Analytical solutions and analog computer chart records for a sequence of compartments were compared. They show a series of linear lags in the approach of each compartment toward a steady-state. An oscillating photosynthetic input (seasonal cycle) imposes an oscillating response, but with decreasing amplitude and shift of phase with each stage. Expontial "transient" terms in the input (representing trend over several years) modify the lags of successive compartments.

A small electronic analog computer (Donner 3400) illustrated effects of varying k_i parameters on the behavior of a small model system. A large computer, the Reactor Controls Analog Computer Facility, was more versatile and offers far more technical possibilities for future ecological studies.

A function generator was used to simulate the expected increase in C^{14} content of the atmosphere as a result of nuclear testing. The transmission of this pulse of C^{14} through the ecological system showed the effects of lag and attenuation in the pulses of C^{14} in each compartment of the system.

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I. INTRODUCTION

Appraisal by the health physicist of the various problems which have their origin in radioactive contamination of the environment involves two objectives. First is to evaluate the long-term effects of chronic low-level radiation. But this requires progress toward the second objective: evaluation of the distribution in the local and global environment of the large quantities of radioactive isotopes which result as by-products of industrial operations, weapons fallout, and research and medical facilities.

Widespread dispersal and dilution of radioactive materials in the various environments of the biosphere have become a source of internal radiation exposure to man. Because food chains of ecological systems, for example, leading from plants to animals to man provide mechanisms by which human populations could be exposed to these radionuclides, the health physicist needs methods for predicting both the present and potential future distributions of radioisotopes in soil, animals, and plants. Such predictions require new information on the biogeochemistry and ecology of the chemical elements, and theoretical models that relate the accumulation and flux of these elements in different parts of an ecological system, or "ecosystem". Such models are also interesting for basic ecological research on the development of ecosystems and the circulation of nutrient elements between organisms and their environment which is necessary to maintain ecosystems in a productive condition.[1,2]

Shepard and Householder,[3] Robertson,[4] Solomon[5] and others[6] have reviewed the rapid development of biophysical theory and physiological experimentation which have been concerned with the movement of substances, particularly radioactive tracers, between different "compartments" (e.g., organs, chemical compounds) of an individual organism. It seems natural to generalize the concepts of compartment models to include whole populations of organisms and masses of environmental materials such as air, water, soils, or organic litter lying over the soil which together constitute the ecosystem covering a specified area of the earth's surface.

The present study illustrates a simple class of ecological models in which the rate of movement of material out of a compartment is

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[1] J. S. Olson, "Exponential Equations Relating Productivity, Decay and Accumulation of Forest Litter", IX International Botanical Congress, Proc. 2, 287. Montreal (1959).

[2] __________ et al., "Forest Studies", Health Physics Ann. Prog. Rept., July 31, 1960, ORNL-2994, Oak Ridge National Laboratory.

[3] C. W. Sheppard and A. S. Householder, "The Mathematical Basis of the Interpretation of Tracer Experiments in Closed Steady-State Systems", Journal of Applied Physics, 22, 510-20 (1951).

[4] J. S. Robertson, "Theory and Use of Tracers in Determining Transfer Rates in Biological Systems", Physiological Reviews 37, 133-54 (1957).

[5] A. K. Solomon, "Compartmental Methods of Kinetic Analysis", Chap. 5 in: Mineral Metabolism: An Advanced Treatise, Vol. I, Part A, C. L. Comar and F. Bronner, Editors. Academic Press, New York (1960).

[6] International Commission on Radiological Protection, "Report of Committee II on Permissible Dose for Internal Radiation (1959)", Health Physics 3, 1-380 (June, 1960). Also published separately as ICRP Publication 2, Pergamon Press, New York.

assumed to be proportional to the quantity of the material in that compartment (Chap. II), so that the behavior of the system can be described by a system of simultaneous linear differential equations. The main objective, however, is to explore the use of analog computer techniques (Chap. III-V) for: (1) facilitating the solution of such equations, (2) simulating the flow of material in the model by the behavior of the computer circuit, used as an analog simulator, and (3) eventually overcoming some limitations inherent in the simple model's assumption of linearity of the differential equations.

Most illustrations concern carbon, a major element of organic materials, whose movements will strongly influence the movement of many other elements that might be considered in later studies. Several possible equations for approximating the photosynthetic input (constant, oscillating, asymptotically rising or falling) are generated (Chap. V) and then fed into a circuit which simulates a hypothetical system consisting of vegetation (tops and roots), dead organic litter, and soil humus (Chap. VI and VII). The implications of a change in C^{14} in such a system are illustrated in Chapter VIII.

II. COMPARTMENT MODELS OF ECOLOGICAL SYSTEMS

A. Major Compartments of Ecological Systems

Due to the mathematical complexity of describing detailed interactions between many organisms and their environment, a first model for simplicity might either consider systems with very few species or deal with groups of species which perform similar functions in nature.[7] Green plants or "producers" are related in their ecological function of producing an annual crop of leaves, roots, stems and other organs. As a group, these plants may be contrasted with a second group--the animals or "consumers", whose food consists of plants or other animals. Some animals and plants, such as fungi and bacteria which decompose and break down dead organic matter, are sometimes separated as a third group and called "reducers". This common usage should not be confused with chemical terminology, for the green plants are those which serve to reduce atmospheric CO_2 to organic carbon by "fixing" solar energy through the process of photosynthesis; this energy is released by oxidation of the organic carbon to CO_2, partly by the green plants themselves and partly by all the other organisms.

Each group may be considered as a compartment of an ecological system, or may be subdivided into sub-compartments of smaller groups

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[7]E. P. Odum, Fundamentals of Ecology, Second Edition (1959).

and sub-groups for more homogeneous groupings which permit simple description of the interactions of natural systems. A compartment might alternatively be divided into sub-compartments according to total mass of the various organs, i.e., foliage, stems, and roots of plants.

The first of several simplified ecological models which will be used to illustrate the mathematical analysis of a few features of a terrestrial ecological system is shown schematically in Fig. 1. Each rectangular block represents a compartment containing organic matter. The lines connecting the three blocks in Fig. 1A represent the main pathway for transfer of carbon. The vegetation group produces living plant matter, e.g., leaves and stems; these fall and constitute dead organic matter or litter. This decays, transferring some organic matter to humus in the mineral soil. Humus in turn decays, releasing CO_2 to the atmosphere. Since the local atmosphere which is a part of the ecosystem is rapidly mixed with the general atmosphere, the system is not closed; but a steady-state balance of income and loss of carbon for the whole system and each of its parts may sometimes be approximated.

Fig. 1B provides a fourth compartment to distinguish organic matter in roots from that above ground, so that the rate of death and decay for roots can be adjusted independently from the rates for dropping of litter on the ground surface and the breakdown of this litter. Animals which feed directly or indirectly on living plants, and various organisms which feed on dead organic litter lying on the

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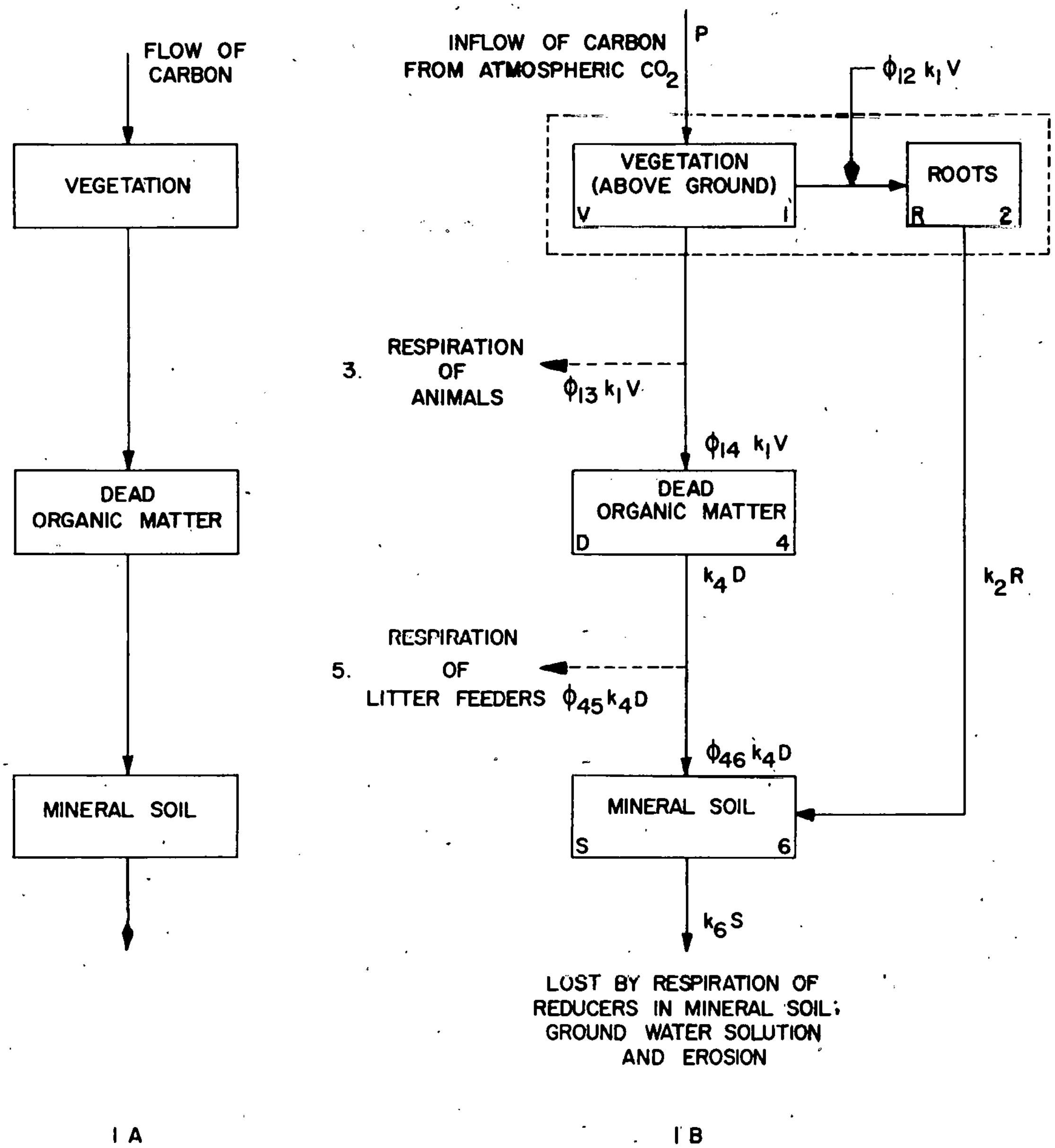

Fig. 1. Simple Compartment Model for an Ecological System.

surface of the ground could be added as separate small compartments, but for immediate purposes it will suffice to recognize that a large fraction of the carbon which they consume is released as CO_2 (arrows pointing left in Fig. 1B), while the remainder is eventually passed to the next compartment.

B. Definitions of Symbols

First, consider the letter symbol in each rectangular block, or compartment, in Fig. 1B to represent a quantity of an element present in that compartment at a given time, t. In addition to this letter designation each compartment is assigned a number to facilitate labelling of pathways of transfer between compartments as shown in Fig. 1B.

Compartment Number (i or j)	Letter	Compartment or Pathway
0	-	Outside (Atmosphere, other systems)
1	V	Vegetation
2	R	Roots
3	-	Animals, or Consumers (Respiration only considered here)
4	D	Dead Organic Matter (Litter mainly on top of soil)
5	-	Microorganisms (Respiration only considered here)
6	S	Mineral Soil

Second, consider that the element moves out of these compartments at some rate which might be described with a first order approximation by the total transfer coefficients, k_i--assuming that loss is directly proportional to the quantity present in compartment i. The total transfer coefficient defines that fraction of the total quantity present in one compartment, i, at any time, t, which is lost per unit time from that compartment by all processes of loss previously described in Section A. Fractions, ϕ_{ij}, are defined to indicate how much of this total carbon lost from the i-th compartment is transferred to the j-th compartment or pathway by each one of the processes of loss for the i-th compartment. These partial transfer coefficients thus describe how the total material lost by one compartment is partitioned between alternate pathways of transfer to adjoining compartments. For example, consider carbon in the vegetation compartment of the ecological model in Fig. 1B. A fraction, k_1, of the carbon in gm of carbon per m^2 of standing vegetation, V, is lost by several processes: (1) one fraction, ϕ_{13}, is lost to the respiration of animals; (2) another fraction, ϕ_{14}, represents primarily the loss by litter fall and secondarily by animal droppings and carcasses added to the dead organic matter compartment. (3) Transfer from tops to roots, ϕ_{12}, will also be considered in Chapter VI. (4) If it were desired to treat plant respiration as a separate loss, this could be represented by ϕ_{10}, but this will not be done in examples of the present report. Similar definitions of transfer coefficients for other compartments are suggested by the discussions in Section A.

Third, the symbol, P, (which might have been written, P_{01}), indicates the rate at which carbon from the atmosphere compartment is incorporated into the vegetation compartment by the process of photosynthesis. With no subscript P will here be considered as some unspecified mathematical function of time, in units of gm carbon assimilated per square meter of the earth's surface per year (g C/m^2 per year). It will here generally be taken as net photosynthesis = gross photosynthesis - plant respiration. When particular mathematical functions are used to approximate the rate of photosynthesis in Chapter V, the following subscripts will be used:

Symbol	Function Describing Photosynthesis
P_1	Constant Rate of Photosynthesis
P_2	Exponentially Decreasing Rate of Photosynthesis
P_3	Exponential, Increasing Rate of Photosynthesis
P_4	Sinusoidal Rate of Photosynthesis
P_5	Sinusoidal Rate of Photosynthesis (Exponentially Decreasing)
P_6	Sinusoidal Rate of Photosynthesis (Exponential, Increasing)

No attempt will be made to relate these rates to the many variables which actually control them in nature. Emphasis is rather on the effects of such patterns of photosynthesis on the transfer of carbon in the other compartments of the model.

C. Differential Equations

With these definitions a mathematical model may be formulated to describe the net accumulation of organic matter (or carbon) in any compartment and also the rates of transfer between compartments as a set of linear differential equations with constant, real, and non-negative coefficients. Consider only the major chain of transfer of carbon in the model Fig. 1B, beginning with the vegetation compartment. The difference between the net rate of influx of carbon from the atmosphere P to the vegetation, V, and the rate of loss of organic carbon each year by all processes, k_1V, gives the net rate of change of carbon, i.e.,

$$\frac{\text{Net Change of Carbon}}{\text{Unit Time}} = \text{Rate of Incorporation of Carbon} - \text{Rate of Loss of Accumulated Carbon}$$

$$\frac{dV}{dt} = P - k_1 V \qquad (1)$$

An equation for the net accumulation of C in dead organic matter, D, is obtained with eq. 2, which describes the difference between the influx from the vegetation compartment and the loss of dead organic matter by decay.

$$\frac{dD}{dt} = \phi_{14} k_1 V - k_4 D \qquad (2)$$

Finally, eq. 3 may be formulated to describe the balance of organic matter remaining in mineral soil after the annual processes of leaf fall and decay, described by equations 1 and 2, have occurred.

$$\frac{dS}{dt} = \phi_{46} k_4 D - k_6 S \qquad (3)$$

In order to develop a generalized linear differential equation for an ecological model of n compartments, consider the symbol, C_i, instead of the letters V, D, R, S..... to represent a quantity of an element present in the i-th compartment. Then the generalized equation for the net rate of change in the concentration of matter in the j-th compartment, C_j, which receives an influx of matter from a number of compartments,

C_i, may be described by the sum of gains from all other compartments ($i \neq j$) minus the loss from compartment j:

$$\frac{dC_j}{dt} = \sum_{i \neq j} \phi_{ij} k_i C_i - k_j C_j \quad \text{where,} \quad 0 \leq k \leq 1;\ 0 \leq \phi \leq 1 \qquad (4)$$

and, $\phi_{qj} = 0$ for all C_q presenting no input to C_j.

Transmission of current or changes of potential through electrical elements may follow similar equations. These quantities lend themselves readily to theoretical investigations of complex systems because simple combinations of electrical components may be designed to act in a manner analogous to the operations of a more complex system. The next chapter will illustrate the concepts of simulation of natural systems by electrical analogs and briefly compare the merits of the electrical network and electronic analogs. After further discussion of analog computer methods, we shall return in Chapters 7 and 8 to consider the solution of equations like (1)-(4) and the behavior of the systems they represent.

III. PREVIOUS USES OF ELECTRICAL NETWORKS AND ELECTRONIC ANALOGS

Two different types of analog computers to be contrasted are: (1) electrical networks in which flow of current is analogous to flow of matter, and (2) electronic analog computers in which propogation of variations in voltage is analogous to the flow of matter. This chapter mentions two previous studies using electrical networks for simulating the flow of carbon, notes some limitations inherent in these networks, and illustrates several applications of electronic analog computers.

A. An Electrical Network Analog for an Ecological System in a Steady-State

An interesting application of an electrical network analog to an ecological system was recently provided by H. T. Odum.[8] The average rates of flow of carbon through an aquatic system were simulated in the electrical network by the flow of current. These were adjusted with variable resistors to be analogous to flow rates estimated from field data. Milliammeters continuously monitored the flow of current, or the flux of matter in the ecological model. A voltmeter was connected across elements of the network to determine the potential differences which "drive" currents through these variable resistors in accordance with Ohm's Law. These potential differences were related to the tendency of

[8] H. T. Odum, Ecological Potential and Analogue Circuits for the Ecosystem, American Scientist 48, 1-8, (March 1960).

the ecological system to maintain a steady-state.

Such a network of resistors may be useful for exploring the effects of differences in one component of the circuit on the responses of the remainder of the circuit in the steady-state. But these networks cannot simulate the time-dependent variations of the system, i.e., transient conditions which are more likely to prevail in nature.

B. Application of an Electrical Analog to the World-wide Movement of Carbon

Transient conditions occurring in an ecosystem may be simulated with circuits similar to that described above by supplementing and/or replacing certain resistor components with capacitors. Such an analog was constructed by H. deVries,[9,10] based on a conceptual model discussed by H. Craig,[11] to simulate the geochemical cycle of C^{14} in a large ecosystem--the whole earth.

The movement of carbon or of C^{14}, produced in the atmosphere by cosmic radiation, was simulated by the current, i, flowing through capacitors whose capacitance was made proportional to the size of the carbon reservoirs in the ecological model. The electrical network of Fig. 2 is a simplified analog of the three compartments (atmosphere,

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[9] H. deVries, Measurement and Use of Natural Radiocarbon, <u>Researches in Geochemistry</u>, John Wiley and Sons, Inc., New York, (1959).

[10] ________, Variation of Concentration of Radiocarbon with Time and Location on Earth, <u>Proc. Koninkl. Ned. Akad. Wetenschap</u>, <u>B61</u>, 94-102 (1958).

[11] H. Craig, The Natural Distribution of Radiocarbon and the Exchange Time of Carbon Dioxide Between Atmosphere and Sea, <u>Tellus</u>, <u>9</u>, 1-17 (1957).

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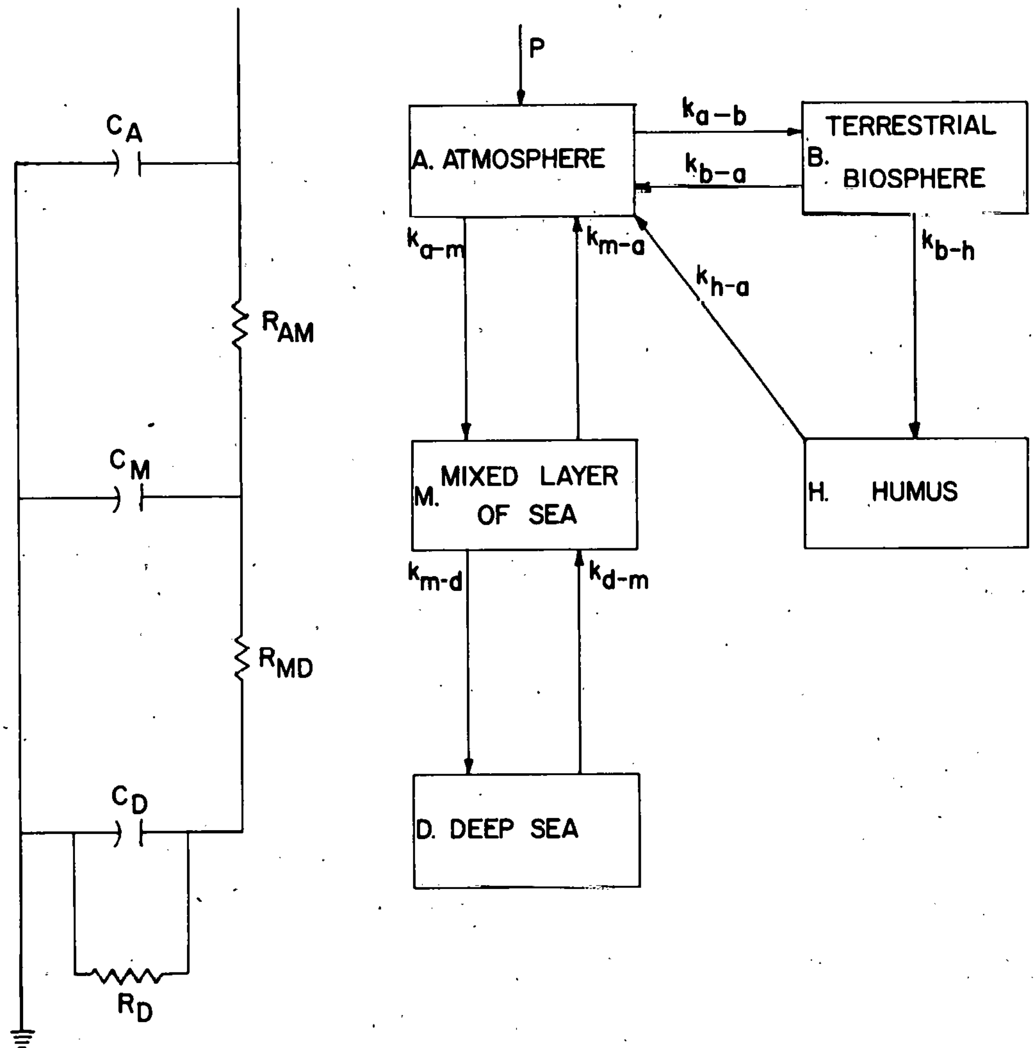

Fig. 2. Geochemical Cycle of C^{14} for the Whole Earth.

mixed layer of oceans, deep ocean waters) which contain over 90% of the C^{14} on the earth, but neglects the terrestrial biosphere and humus compartments which have great ecological interest.

The resistor, R_d, provided a decay path for capacitor, C_d, with a time constant analogous to the radioactive mean life of C^{14} in an isolated reservoir. The resistors, R_{am} and R_{md}, provided a decay path for capacitors C_a and C_m, respectively, such that their time constants are analogous to the exchange rates, k, of C^{14} atoms from atmosphere to the mixed layer of the ocean, and from this to the deep sea. The amount of C^{14} in each reservoir was assumed to be proportional to the potential differences across the corresponding element in the circuit.

Variations in the exchange rates of an atom of C^{14} are simulated by changing resistor-capacitor components to obtain the proper time constants. Although the equations describing this model might have been solved by more conventional mathematical methods, this analog enabled deVries to systematically vary each parameter for a series of values and thus arrive at a large number of solutions rapidly. DeVries concluded that in order to increase the radiocarbon content in the atmosphere by 2 per cent, the rate of production of atmospheric C^{14} must increase by 25 per cent, or the exchange rates must decrease by 50 per cent.

Chapter VIII will return to the problem of the fate of C^{14} produced by nuclear tests, with emphasis on the biosphere and humus components and on the transient conditions which might be significant for biological effects of this contamination. Before this can be considered, however, the remainder of this chapter and several to follow must survey certain basic features of electronic analog computers and their possible ecological applications.

C. Limitations of the Electrical Network Analog as a Simulation Device

The selection of an analog depends upon the approximations and assumptions made in designing the ecological model, the validity of the ecological data, and the desired accuracy of the computer solution for the model. As far as possible, one would desire an analog which has the following characteristics: simplicity in operation and construction, rapid solution of the mathematical equations describing the ecological model, and finally, an analog capable of realistic reproduction of the system under study or at least an instructive approximation of its processes.

The electric network models discussed so far exhibit these characteristics for solution of the steady-state distributions of carbon. However, for many cases these solutions may be obtained with but little more difficulty from the equations describing the ecosystem. Therefore, a major question with regard to the analogs previously discussed would be how well the solutions to the transient phases of their problems conform to the criteria above. Unfortunately, the transient electric network analog solutions are subject to three major sources of systematic error: (1) errors introduced by the electrical components themselves, (2) "counter-emf" errors produced by capacitor components, and (3) errors in measurement of the problem solutions introduced by the charge-voltage monitoring devices.

Electrical components, in particular resistors and capacitors, are never "pure", but contain inductances and stray capacitances. The accuracy of any computer solution, especially an electrical network analog solution, is dependent upon the "purity" of the components in the circuit. All capacitances contain some finite resistance leak and some insulation leak or slow drain of current. Analysis shows that this leak is equivalent to a modification of the effective output voltage of the other components in the circuit. The electric network is so designed that a small change in one component may introduce large errors of interaction and loading into all the other components. To describe these errors quantitatively would require formulation of mesh equations describing the electrical network. These equations become so complicated in the case of multi-compartment systems that electronic analog computers were in part designed to solve them.

In addition to the capacitor loading and leakage error, and more important, is the manner in which a capacitor opposes the charging voltage. As the capacitors are charged to higher potentials, that charge which is accumulated upon the capacitor determines a potential of its own, opposite in polarity to the voltage increase, and effectively creates a counter-electromotive-force. The effect of this opposing potential is to reduce the "true" potential to an effective potential somewhat less in magnitude.

The third source of error is again common to all analog devices, but once more assumes greater importance in the case of electrical network analog. The measuring device, i.e., the recorder to monitor voltage or current changes in electrical circuits, reduces the "true" potential differences across the components in a manner similar to that of the "impurities" of the components and may affect the time constants of the chosen circuit. A well regulated high impedance power supply with some type of null-recording device will reduce the error significantly.

From the operational standpoint the electric network has some additional disadvantages. To vary the exchange rates between compartments, i.e., to change the value of the fixed resistances or capacitances requires manual replacement of one resistance with another resistor from a stock of components. Unless variable resistors and capacitors are available, a series of separate, fixed value components must be in stock for each value of time constant or exchange time desired. Variable components will reduce the inventory required, but on the other hand will introduce additional error with extended usage and wear.

D. Some Previous Applications of Electronic Analog Computers

The electronic analog computer not only conforms well to the criteria of Section C, but also reduces the limitations of the electric network analogs to negligible proportions, as discussed in Chapter IV. For this reason electronic analog computers have recently found a wide range of application in diverse fields of study, ranging from human physiology to weapons fallout.

A typical biological investigation is that of A. K. Solomon and

G. L. Gold.[12] These investigators attempted to describe the experimental data for the evidence of potassium transport in the human erythrocyte with a mathematical model of the unconstrained three compartment type. An electronic analog was constructed to fit the particular mathematical model and the circuit parameters of the analog were modified until the graphical results obtained from the electronic system were in agreement with those found from experimental diffusion studies. In this study a complete, but not unique, description of potassium transport was obtained, i.e., the experimental evidence was completely explained with this one model, but could also be explained with several others.

Fish[13] applied analog computing techniques to analysis of distribution and excretion of intraveneously injected uranium between blood, bone, kidney and urine. His computer simulation of this system indicated that a four compartment linear model was sufficient to account for the experimental data obtained from male rats and from data for humans in the low-dose level.

J. H. Wright[14] et al., described a very high-speed analog com-

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[12] A. K. Solomon and G. L. Gold, "Potassium Transport in Human Erythrocytes: Evidence for a Three Compartment System", J. Gen. Physiol., 38, 371-88 (1955). See also A. K. Solomon op cit.

[13] B. R. Fish, "Applications of an Analog Computer to Analysis of Distribution and Excretion Data", Health Physics, 1, 276-281 (1958).

[14] J. H. Wright, L. Taback, and H. K. Skramstad, "Fallout Patterns", J. Res. Nat. Bur. Stan., 58, 101-109 (1957).

puter consisting primarily of function generators and scanning voltages for predicting geographic patterns of radioactive fallout which occur following a nuclear-weapon explosion. All output data were presented on a cathode-ray tube, the luminance at any point on the screen representing the intensity of fallout accumulated at that point. From a given geometrical distribution of the weapon cloud and known activity of the particles suspended in the cloud, the effects of wind variation on the fallout pattern might be incorporated into the analog and results obtained in from 4 to 7 minutes. In similar manner the other parameters of the fallout pattern might be changed rapidly and approximate solutions easily obtained.

IV. DESCRIPTION AND OPERATION OF ELECTRONIC ANALOG COMPUTERS

Sections A and B of this chapter describe the elementary components of an electronic analog computer and the simple combinations needed to describe the balance of gains and losses of material from a single compartment of an ecosystem. Sections C and D show how these basic circuits readily may be combined to simulate chains of several compartments like those outlined in Chapter II, and more realistic ecological models included later in this report. Section E and Chapter V cover additional methods for adapting the computer to a better approximation of special mathematical functions.

A. Description of the Operational Amplifier and the Coefficient Potentiometer

The practical differences between analog computers are in the types of operations that they can perform and in the methods by which they perform them. The count rate circuit of a radiation survey meter and the slide rule which are simple analog computers, perform limited tasks. The electronic analog computer,[15] on the other hand, is capable of many operations including:

(1) Addition and subtraction

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[15] Many details and principles can be found in textbooks, such as: G. A. Korn and T. M. Korn, Electronic Analog Computers. McGraw-Hill Book Co., New York (1952).

(2) Sign and phase inversion

(3) Integration and differentiation

(4) Multiplication and division

(5) Representation of discontinuities

(6) Generation of arbitrary functions

To perform these functions special "chopper stabilized" DC electronic amplifiers are required and because they operate on simulated mathematical functions they are generally referred to as "operational amplifiers". Figure 3A is a symbolic representation of the operational amplifier and other components to be discussed. Of the six operations listed above, the operational amplifier is capable of the first three.

If a number of signals at arbitrary potentials are applied to the control grid through the input resistors to the operational amplifier, the output signal will then be the algebraic sum of these potentials. Thus the operational amplifier provides a simple method for adding or subtracting potentials, or input voltages, referred to the ground potential of the operational amplifier. The magnitude of the output may be equal to, greater, or less than the input signal depending upon the gain of the amplifier. A complete description of a typical chopper stabilized DC electronic amplifier is provided by computer manuals.[16]

Sign and phase inversion occurs inevitably in each electronic amplifier. Hence a second amplifier may be used as an "inverter" to

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[16] F. P. Green, Reactor Controls Analog Facility Operations Manual, ORNL-2405, (1958).

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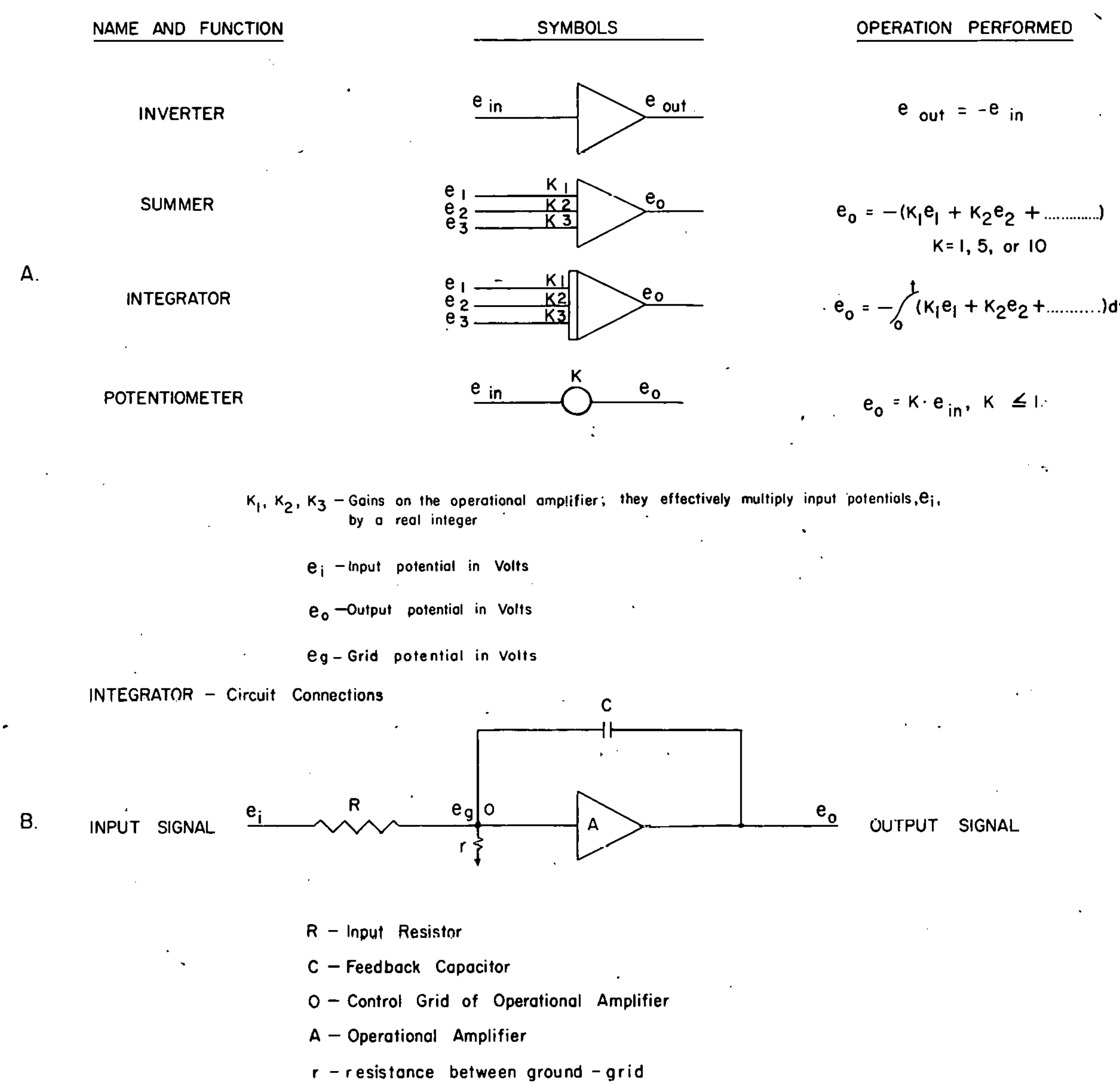

Fig. 3. Symbolic Representation of Analog Computer Components.

restore the signal to its original sign and phase.

The symbols in Fig. 3 labeled integrator represent a special type of integrating circuit. The capacitor of this integrating circuit connects both the input and the output signal points of the operational amplifier in such a manner that the output potential varies as the time integral of the input potential (Fig. 4). As in the case of the inverter above, a number of signals may be applied to the input control grid and the output signal will then be equal to the integral of the sum of these potentials, but of the opposite polarity. The integrator is therefore generally referred to as a summer-integrator. Differentiation is possible, but not advisable, since non-linear distortions are introduced and accentuated through the amplifier.

The potential of the control grid, point O of Fig. 3B, remains near ground potential. Since the operational amplifier acts as an "isolating" amplifier between resistor-capacitor networks a series of input signals connected to the control grid through input resistors do not introduce errors due to interaction of the electrical components as in the case of the electrical network analog.

The active network of the summer-integrator approximates the true integral of a quantity by several orders of magnitude better than the passive electrical network. (See Appendix A). The essential difference between the two is that the control grid potential of the operational amplifier is essentially ground and no "opposing" potentials develop across the feedback capacitor to reduce the desired value of the input potentials through the input resistors. (The effect of this opposing potential, as would be the case for the electrical network RC circuits, is to reduce the value of the true integral.) Appendix A includes a more complete discussion of the theory of the operational amplifier.

Rather than keep a large inventory of precision resistor-capacitor components to simulate varying capacities and exchange rates, the electronic analog computer utilizes the properties of ten-turn voltage dividers, generally referred to as potentiometers or pots. Figure 3A illustrates a pot which selects any desired fraction of the input potential across its terminals. Pots are contained in a metal cylindrical housing with a graduated dial face enabling the operator to note the pot setting for future replications of a given experiment.

To avoid correction terms to the potentiometer arm potentials, servo-voltmeters or null voltmeters are used to select the desired potential while the load resistance is connected to the potentiometer arm. (See Appendix A for details of potentiometer corrections due to circuit loading.)

B. Simple Combinations of the Components of the Analog Computer

The components previously described, the operational amplifier and the potentiometer, may be interconnected in a manner so as to describe the balance between a certain rate of input, P, and a certain rate of loss, k_1V. The numerical values of these rates may be related to input, e_i, and output potentials, e_o, of an operational amplifier with constants of proportionality known as "scaling factors". The magnitude of the difference at any time between these rates is described by a differential equation such as eq. 1 of Chapter II, which is repeated below. In the following equations, each rate of the ecological equation is therefore proportional, or analogous, to a corresponding electrical quantity.

$$\frac{dV}{dt} = P - k_1 V \qquad \frac{de_o}{dt} = e_i - k_1 e_o$$

Since the integrator and potentiometer of Fig. 4A are connected to simulate the solution of the "electrical" equation above, the output potential, e_o, must be proportional to its analog, V. Through relationships like these, the analog computer may be used to solve equations which are formulated for ecological systems.

With the commonly available commercial operational amplifiers, it is necessary to restrict the output voltage to the linear portion of the operating plate-grid voltage curve so that undesirable non-linear distortion will not be introduced into the output signal. Practically, this means that all computing operations must be designed so as to restrict the output potentials of the operational amplifier to an effective full scale range of $\pm$ 100 V. For this reason it is also necessary to use appropriate scaling factors when relating machine voltages to problem variables. Within the linear portion of the operating curve an input signal will be reproduced faithfully at the output of the operational amplifier. That is to say, a sinusoidal signal applied as an input will be converted into a sinusoidal signal as an output, having the same frequency as that of the input signal, but of the opposite polarity and phase.

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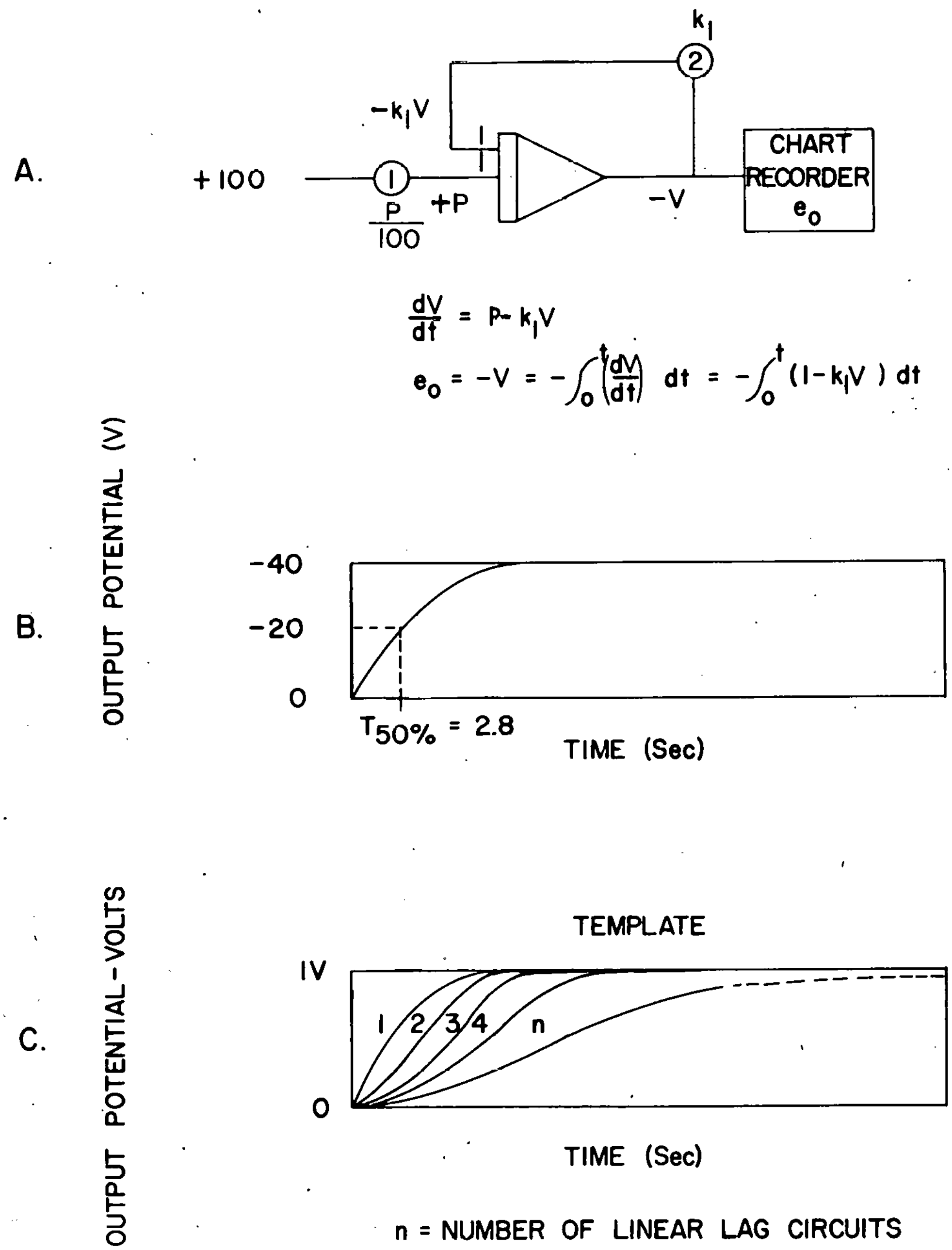

Fig. 4. Simple Combination of Two Potentiometers and Integrator to Solve a First Order Differential Equation.

The time constant of the circuit of Fig. 4A or its analog, the unit of time required for growth or decay of some variable in the ecological system, may be adjusted to a desired value by proper choice of the feedback capacitor and the input resistor to the integrator. If, for example, the value of the input resistor to the integrator is assigned a value of 1 megohm and the value of the feedback capacitor is 1 microfarad, the time constant of the circuit would be 1 second. (See Fig. 3B) With a time constant of 1 second, a constant input potential, P, of 10 V, and a decay parameter, k_1, of 0.25, the solution to the ecological equation will be given by the analog computer as shown in Fig. 4B.

Combinations of the operational amplifiers and other computer components are simply made with special insert plugs, jacks, and jumper cords. A large array of operational amplifiers, with feedback capacitor and resistors available, is contained in commercially designed cabinets with input and output jacks conveniently located on patch panels. Using jumper cords, similar to telephone switchboard cables, these jacks may be interconnected in any desired manner on the patch panel. Figure 5 is a photograph of the Donner Model 3400 electronic analog computer and illustrates the components above as well as units to be described later. At the top of the computer cabinet is the function generator containing 24 diodes. The chart recorder, of the null balance type, has controls for selection of full scale value directly below. The control board is located at center with outlets from the regulated power supply located at the

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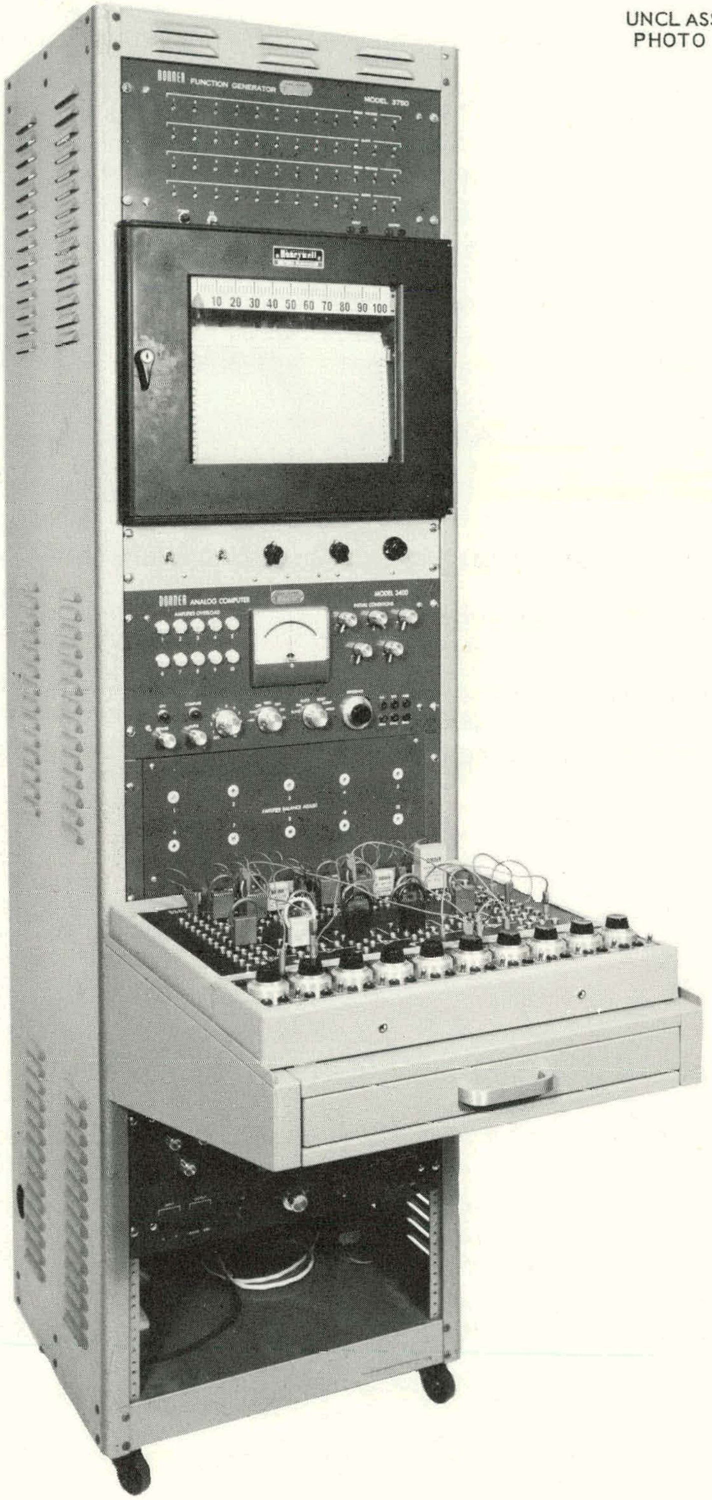

Fig. 5. Photograph of the Donner Model 3400 Electronic Analog Computer.

bottom right. The ten operational amplifiers are housed behind the panel directly beneath the control board. The patch panel containing resistor-capacitor components is orientated horizontally under the amplifier cabinet. A row of potentiometers is located directly in front of the control board while the function multiplier unit is partially visible beneath the patch panel.

The Reactor Controls Analog Computer Facility of the Oak Ridge National Laboratory has a larger number of recorders (frontispiece, right), and potentiometers and amplifier controls (center) which enable it to simulate more compartments. Connections are made on a removable wiring board (left center) so that the setting up of some problems can proceed while the computer is being used for other problems. Also included are several auxiliary devices discussed below which enhance the versatility of the computer.

C. Relation of an Analog Computer Circuit to an Ecological Model

One summer-integrator provides the solution to one differential equation which describes the change in one compartment of an ecological model. For example, solutions to the series of differential equations, equations 1 to 3 in Chapter II, provide a description of the changing distribution of organic carbon between the series of compartments and may be obtained from combinations of summer-integrators as shown in Fig. 6. The input voltage to integrator No. 1 might be considered analogous to the input matter to the vegetation compartment. A certain number of volts input is related to a quantity of input

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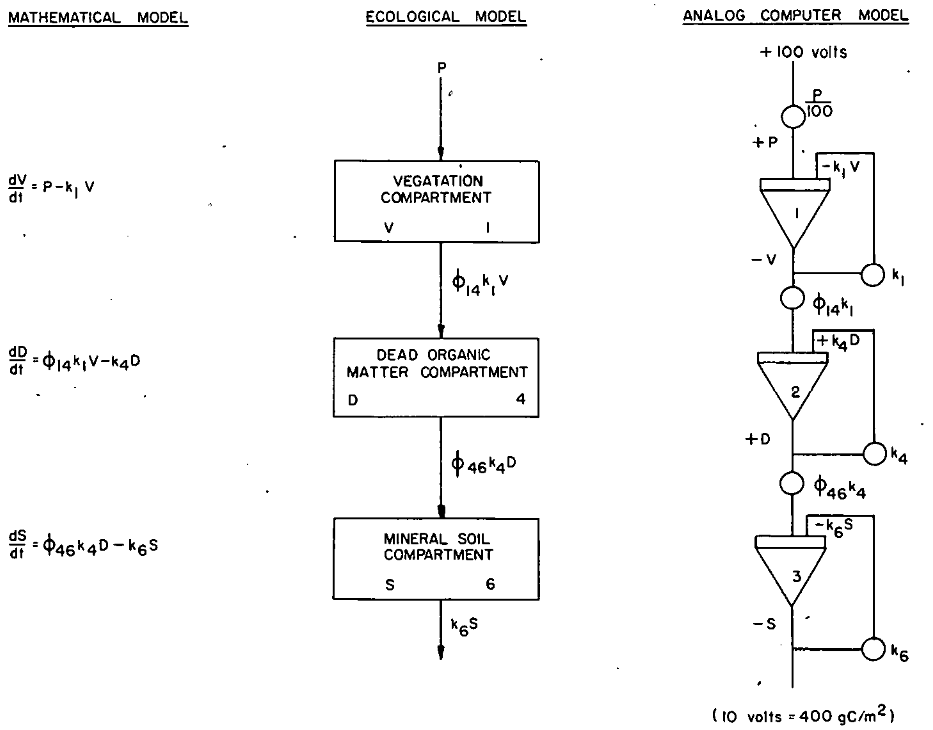

Fig. 6. Linear Lag Circuit and Relation to the Main Pathway of Carbon in an Ecological Model.

matter with an appropriate scaling factor, e.g.,

10 volts per second equivalent to 400 grams/square meter of organic carbon

Then the accumulation of organic matter in each separate compartment of the model will be described by the increase of output potential on its analog, a summer-integrator. Settings on the feedback potentiometers are analogs of the decay parameters of each compartment, k_i, and the potentiometers connecting integrators are analogs of partial transfer coefficients, $\phi_{ij}k_i$.

D. Discussion of the Linear Lag and Relation to Ecological Models

The circuit described in Fig. 4A and discussed in Section C is more generally referred to as a linear lag circuit for it provides the solution to linear differential equations such as eq. 5 below,

$$\frac{dV}{dt} = k_2P - k_1V \qquad \text{or} \qquad \frac{de_o}{dt} = k_2\, e_i - k_1 e_o \tag{5}$$

Which reduces to these equations in the steady-state (when $\frac{dV}{dt} = 0$) ,

$$\frac{V_{ss}}{P} = \frac{k_2}{k_1} \qquad \text{or} \qquad \frac{e_o}{e_i} = \frac{k_2}{k_1} \tag{6}$$

The potentiometer, k_2, couples groups of linear lag circuits such as those shown in Fig. 6. To focus attention on the lag feature of this circuit, consider the gains on the summer-integrator of Fig. 4A to be unity and the potentiometers set such that k_1 equals k_2. If a step function of 10 V is now introduced into the summer-integrator through the potentiometer k_2, the output voltage will ultimately attain the equilibrium value of 10 V. However, the rapidity of the response of the output potential, i.e., the time required to attain the equilibrium value of 10 V, is entirely a function of the parameter k_1. This delay in response of the output potential may be described in terms of the time for half-response, more commonly called the half-time, which is given by the relation:

$$\text{Half-time} = 0.693/k_1$$

The ratio of output to input potential, described by eq. 6, is called the amplifier gain and will be considered analogous to the corresponding ecological ratio of steady-state accumulation of matter to the flux of matter into the compartment. It is evident that the quantity of matter accumulated in a given compartment, as well as the rate of accumulation, is a function of two parameters, k_1 and k_2. The parameter, k_2, corresponds to the partial transfer coefficients described in Chapter II, $\phi_{ij}k_i$; while the parameter, k_1, corresponds to the decay parameter also defined therein.

Combinations of several linear lag circuits in series, such as in Fig. 6, with the value of the input pot set equal to that of the feedback pot, would produce correspondingly greater lags in the response of the machine as shown diagrammatically in Fig. 4C. However, for this more complex arrangement, no simple mathematical combination of the parameters, k_i ($i = 1,2,3.....n$), will adequately describe the time for half-response (as was the case for the single linear lag circuit) because each additional lag will be contingent upon the preceding lag in a rather complex manner. Solutions of the mathematical equations which describe the system will permit calculation of each point on a curve such as one of those in Fig. 4C, however the analog computer will plot a continuous sequence of points much more rapidly and is recommended to solve ecological models characterized by sets of decay parameters. Once these solutions are recorded, they then could be used as templates to describe the various ways in which certain type of ecological systems, characterized by the parameters chosen, would change.

From the standpoint of ecological models we may summarize the foregoing theory of the linear lag circuit in the following manner. Each ecological compartment of a series connected chainwise, e.g., the producer-litter-soil compartments of Fig. 1, will exhibit a delay in the accumulation of organic carbon in the transient state which might be described in terms of the half-time response of the analog computer or as in the model template of Fig. 4C. The steady-state level of carbon accumulation will be described in terms of the decay parameters of each compartment and the transfer parameter of the succeeding compartment analogous to eq. 6 above. Effects of variable decay parameters on the growth of the transient phase and the steady-state accumulations of carbon will be discussed in Chapter VII.

E. Equations with Variable Coefficients; Use of the Function Multiplier

The models of sections C and D do not provide for the possibility that the transfer coefficients k may vary. For example, the vegetation V instead of depending only on the input from photosynthesis and on some constant fraction k_1 of the vegetation being lost per unit time (eq. 1), may depend on a k which is either, a) an arbitrary function of time, or b) a function of the amount of material in one of the compartments. Equation 7 represents the class of linear differential equations with variable coefficients, where $K_1(t)$ is specified by some function of t (e.g., representing an oscillation with time, which might simulate an annual cycle in the fall of litter). Equation 8 represents a non-linear differential equation in which the coefficient (here distinguished as the upper case K_1) is a function of the variable representing a compartment in the system.

$$\frac{dV}{dt} = P - k_1 V \quad \text{Linear equation, constant coefficient} \qquad (1)$$

$$\frac{dV}{dt} = P - K_1(t)V \quad \text{Linear equation, variable coefficients} \qquad (7)$$

$$\frac{dV}{dt} = P - K_1(V)V \quad \text{Non-linear differential equation} \qquad (8)$$

In a whole system of equations like (4), it is possible that coefficients governing the loss for certain compartments might vary as a function of some other compartments in the system. For example, if there were compartments for various animal species, the K_1 for vegetation might change along with the population of certain defoliating insects.

This non-linear condition may be programmed on the analog computer with an additional electronic device generally referred to as the function multiplier. When two distinct voltage signals are introduced into the function multiplier the resultant output signal of the multiplier is proportional to the product of the two input voltages. The analog computer circuits of Fig. 7 contrast the computer models necessary to describe equations 1, 7 and 8. The significant difference between the two circuits is the replacement of the potentiometer, necessary to simulate the constant decay parameter, k_1, with a function multiplier which permits incorporation of the variable decay rate parameter, K_1, into the negative feedback circuit of the integrator. Two amplifiers with gains of 10 compensate for voltage reduction by 1/100 by the function multiplier to avoid overloading of the integrator.

F. The Function Generator

The function generator,[17] (Fig. 5) an auxiliary electronic device to the analog computer, is used to generate arbitrary functions of time and other variables which can be introduced into function multipliers (as above), or into integrators to simulate variations in nature. The function generator is calibrated in such a manner that when X volts, the driving voltage, is the input function to the generator, the output potential may be adjusted to a value proportional to F (X). If the input signal to the function generator changes at a rate $\frac{dX}{dt}$ volts/second, the output potential changes at a rate proportional to $\frac{dF(X)}{dX}$ volts per volt input, where $\frac{dF(X)}{dX}$ is the slope of the curve as described by the function generator. The shape of the generated function may be described as a function of

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[17] C. L. Johnson, Analog Computer Techniques, McGraw-Hill Book Co., Inc. 136-165 (1956).

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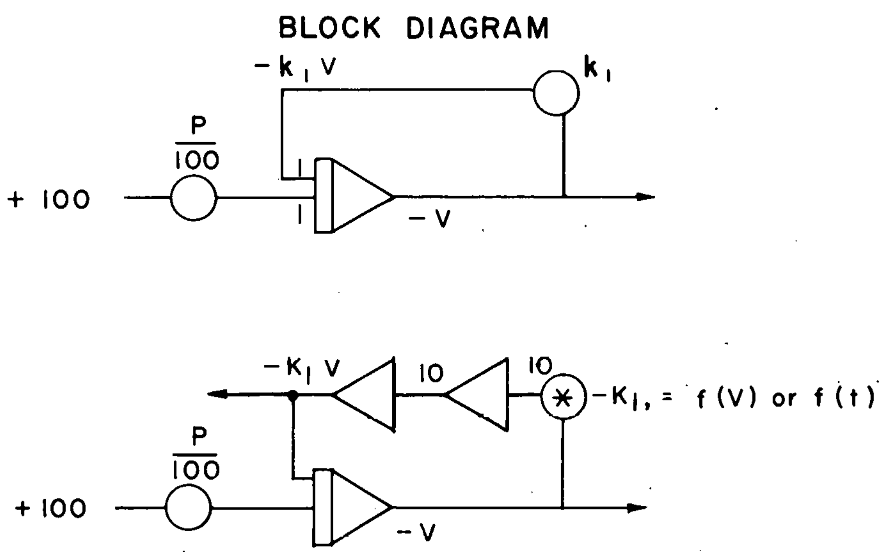

* FUNCTION MULTIPLIER

Fig. 7. Use of the Function Multiplier to Solve Non-linear Equations.

time for,

$$\frac{dF(X)}{dt} = \frac{dF(X)}{dX} \cdot \frac{dX}{dt}$$

Most arbitrary F(x,t) may be generated subject to two restrictions: (1) the driving voltage to the function generator must be such that it never exceeds linear operating range of the operational amplifiers housed with the function generator circuit. (2) The function which is to be simulated is approximated by straight line segments whose slopes are given by:

$$\frac{F(X_2) - F(X_1)}{X_2 - X_1} = \frac{2 \text{ volts}}{1 \text{ volt}} \qquad X_i = f(\text{time or other variables}) \quad i = 1,2,\ldots.n$$

The maximum tolerable slope is generally of the order of 2:1. Hence the accuracy of approximation of the function of time generated is related to the complexity of the curve to be simulated. Because the function generator has a lag of its own, which rounds off the corners separating linear segments, this restriction is not so serious as might first appear (Fig. 8). An example of the use of the function generator to describe an arbitrary function of time, not easily simulated with the two components above, will be included in Chapter VIII.

Instead of using the function generator, it frequently will be possible to approximate fairly arbitrary functions by certain combinations of trigonometric and exponential functions which can be generated by certain sub-circuits of the computer itself. The next chapter will illustrate this procedure in general terms, using examples of input functions which will be utilized in the chapters to follow.

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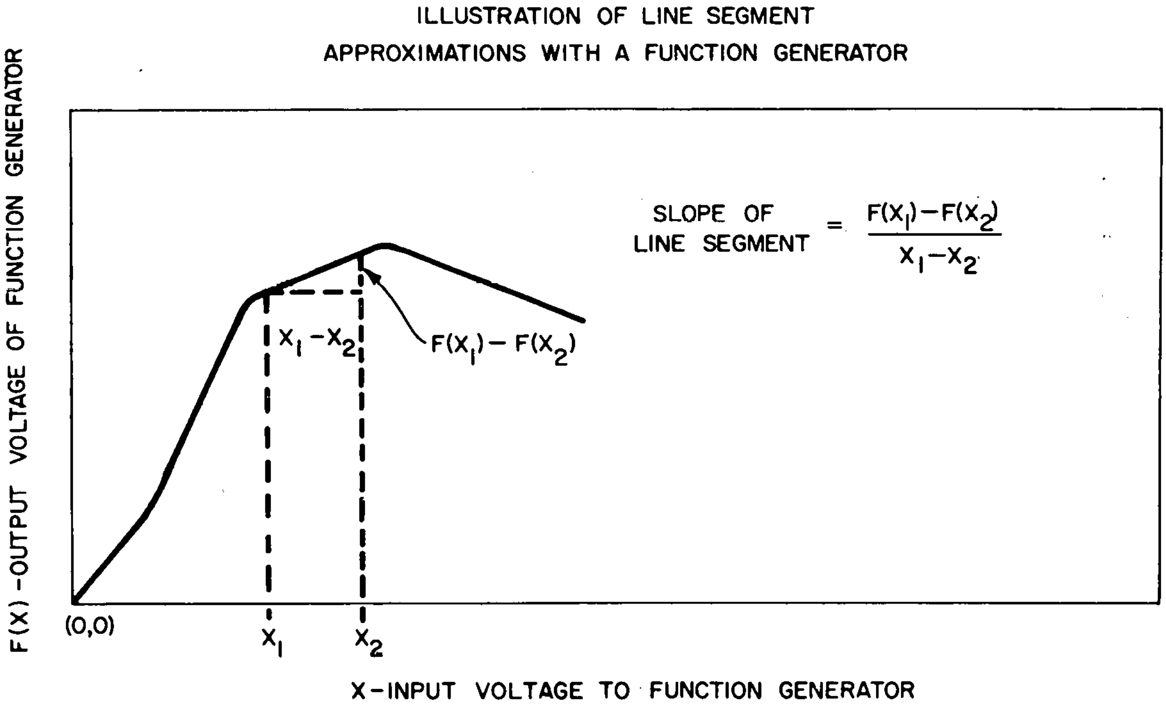

Fig. 8. Illustration of the Principle of the Function Generator.

V. COMPUTER INPUTS: ALTERNATIVE MODELS FOR ASSIMILATION OF CARBON

For the sake of simplicity, a constant input, P, was assumed in the examples of Chapters II and IV. Implications of this hypothetical model will be made explicit in sections A and B of the present chapter and will continue to be used for mathematical convenience in examples of some later chapters. The remaining sections of this chapter show several different ways by which the computer can simulate more complicated and realistic conditions whenever this is desired.

One obvious method of obtaining the non-uniform input for the ecological analog model is simply to precede it by a circuit with operational amplifiers connected in the manner of the last chapter. In section B this device allows consideration of transient conditions, i.e., inputs which are initially either higher or lower than the final steady value, but which approach the final value asymptotically. In section C, amplifiers are combined in such a way as to provide a sinusoidal oscillation, which potentially can be adapted to simulate a wide variety of seasonal oscillations in productivity. Both transient and oscillatory features are combined by means of a servomultiplier in section D. Finally, section E notes the wide range of possibilities by which real field data or arbitrary hypotheses can be approximated by the function generator if all the preceding methods are inadequate.

A. Constant Rate of Producer Assimilation

A constant rate of assimilation of atmospheric CO_2 by plants implies a hypothetical ecological condition in which the standing vegetation produces the same quantity of organic carbon from season to season and year to year. To simulate a constant rate of photosynthesis, P_1, on the analog computer it is necessary only to adjust the input signal to a summer-integrator such that it is unvarying with time. If the voltage is obtained from the reference power supply through a potentiometer set to some desired value, e.g., 10 V, and introduced into a summer-integrator with a time constant of one second, the rate of increase of potential on the feedback capacitor will be 10 V per second. This constant rate of increase of potential on the capacitor is related to the constant rate of increase of producer assimilation with appropriate scaling factors, e.g.,

$$\frac{10\ \text{V}}{\text{sec.}} = \frac{400\ \text{g carbon/m}^2}{\text{year}} \quad \begin{array}{l}\text{1 second computer time} = \\ \text{1 year ecosystem time}\end{array} \tag{9}$$

We may then represent the constant rate of photosynthesis as a straight line, i.e., in Fig. 9 this is an extension of the asymptote back to the ordinate, 400 grams of carbon/square meter per year. The ordinates of this graph are labelled both in input potential per second, volts, and rate of photosynthesis, in grams of carbon/square meter per year to show their relationship as defined by eq. 9. Likewise, the abscissa is labelled in units of time which refer to the computer time constant, seconds, and also in units of time which refer to the ecological model time, years.

The computer methods which are described here could be used to simulate either the net or gross rate of photosynthesis.

For the vegetation compartment described in Chapter II and simulated on the electronic analog computer in Chapter IV, one decay parameter, k_1, was considered to represent the total loss of the growing vegetation both by seasonal leaf fall to produce litter, and by losses to the consumers whose food consisted of living plants. For this type model, to be used throughout this study, the assimilation by producer plants would correspond to the <u>net</u> rate of photosynthesis because no provision was made for losses of standing vegetation by the processes of plant respiration. The net rate of photosynthesis is described in terms of the conversion of the quantity of carbon dioxide of the atmosphere, as grams of carbon per square meter of vegetation per year, into organic carbon of the vegetation expressed in the same units. The equation describing the growth of vegetation with a constant net rate of photosyntheses and constant rate of loss of material has been given:

$$\frac{dV}{dt} = P_1 - k_1 V \tag{10}$$

where the symbol, P_1, represents the producer assimilation in grams of carbon/meter^2 per year.

With a slight modification, eq. 10 might describe the <u>gross</u> rate of photosynthesis, i.e., considering losses to plant respiration as well as the losses described above.

$$\frac{dV}{dt} = P_1 - k_1 V - rV = P_1 - (k_1 + r)V \tag{11}$$

In eq. 11 the symbol, r, corresponds to the annual fractional loss of the organic matter comprising vegetation to the atmosphere as respired CO_2. For this one modification of the mathematical model, the corresponding adaptation of the analog computer circuit described up to this point could assume two forms. Introduction of one additional negative feedback pathway between the output and input points of the summer-integrator through a potentiometer set equal to the value of the respiration parameter, r, will simulate the additional loss. Alternatively, a single feedback potentiometer could be scaled to correspond with the combined losses (k_1+r) instead of k_1.

B. Exponential Trends of Producer Assimilation

Ecological systems are known to undergo gradual changes in average productivity over periods of several years. Ecologically speaking, the model of the exponentially decreasing rate of photosynthesis might correspond to a decrease in the gross production of the vegetation during each seasonal cycle until some equilibrium condition has been attained. For example, this decrease might result due to the depletion by leaching or erosion of certain minerals necessary for plant growth and hence for carbon assimilation. The model for increasing photosynthetic rates, or average annual increases in the vegetation productivity, conversely might correspond to gradual invasion of plants on a bare area or to accumulation in the soil of nutrients such as nitrogen which might influence the potential and actual photosynthesis rates.

Mathematical models of both these types might be described in terms of equations resembling 12 and 13:

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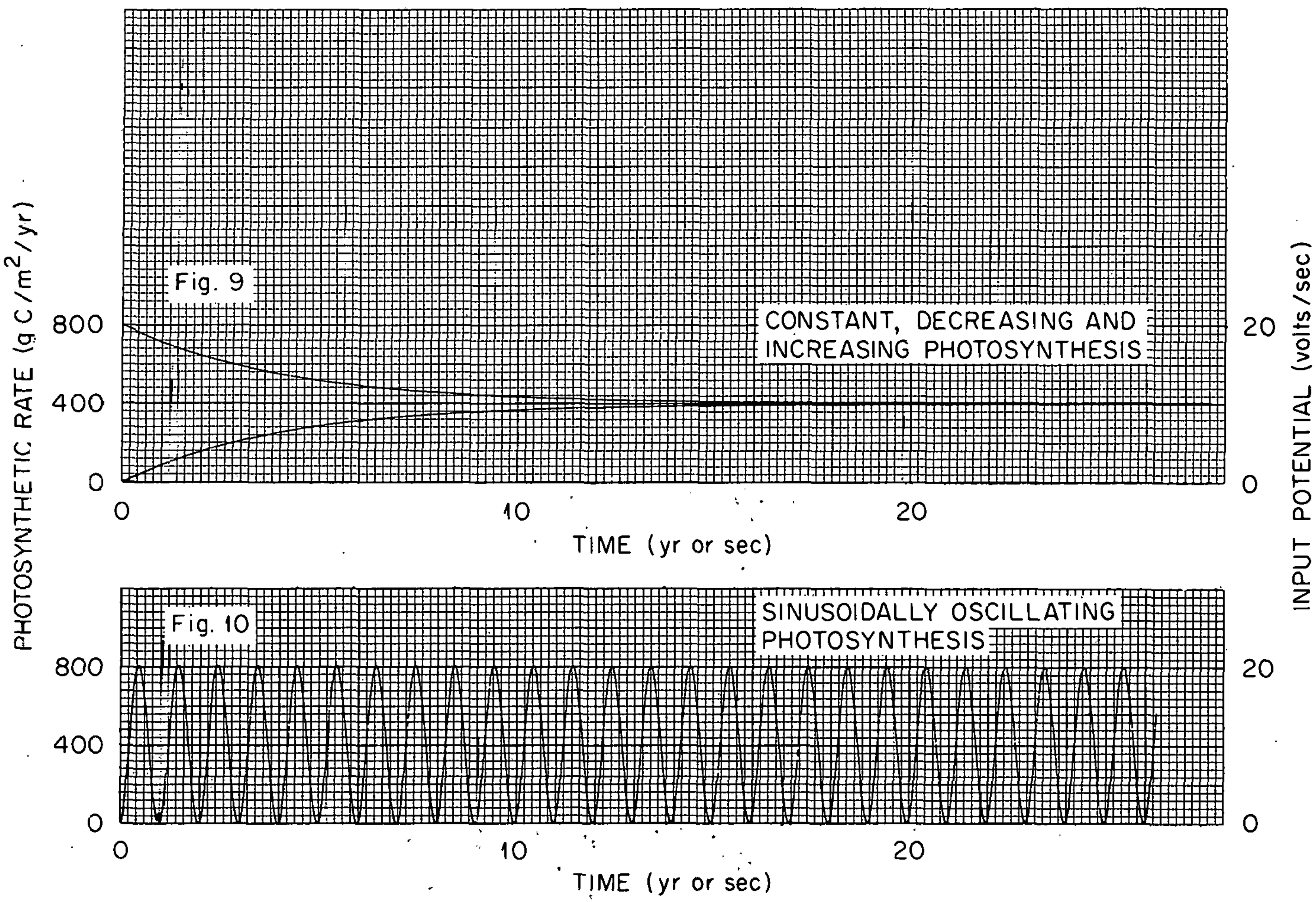

Fig. 9. Simulation of Uniform and Gradually Changing Rates of Photosynthesis on X-Y Plotter.

Fig. 10. Simulation of Simple Sinusoidal Oscillation of Photosynthesis.

$$P_2 = a \quad (1 + e^{-kt}) \qquad \text{Exponentially decreasing rate} \qquad (12)$$

$$P_3 = a \quad (1 - e^{-kt}) \qquad \text{Exponentially increasing rate} \qquad (13)$$

Graphical examples of these equations are shown in Fig. 9, the upper curve corresponding to eq. 12, the lower curve to eq. 13. Both equations were programmed on the analog computer (Fig. 11B) using the linear lag circuit described in Chapter IV. The decay parameter, k, was arbitrarily set at 1/4 for illustrative purposes. The input voltage, a, was adjusted with the input potentiometer to 10 V; the initial condition voltages on the feedback capacitor, $Ba=BP_f$, were fixed at 20 V and 0 V in order to simulate equations 12 and 13, respectively.

The general form of the mathematical equation described by the analog computer circuit of Fig. 11 may be written:

$$P = a\ (1 - e^{-kt}) + P_o e^{-kt} \qquad P_o = BP_f = Ba \qquad (14)$$

The symbol, P_o, represents the initial rate of photosynthesis or the value of the rate at time zero. It is convenient to consider the initial rate of photosynthesis, P_o, in terms of the final rate of photosynthesis, P_f, and therefore P_o has been related to a by the constant, B. Equations 12 and 13 consider extreme cases in which the ratio of the initial to final rate of photosynthesis, B, is respectively, 2:1 and 0. Substitution of these values of B into eq. 14 gives both equations 12 and 13. The time required to either decrease or increase the rate of photosynthesis by one-half its initial rate, the half-time, is found from Fig. 9 to be 2.8 years for both cases. This would be expected from the exponential type mathematical equation which this computer circuit simulates.

C. Sinusoidal Approximations to Producer Assimilation

Most vegetation exhibits fluctuations in photosynthesis which reflect variations in the annual seasons and variations in the inherent rhythmic nature of growth.

A simple approximation to a natural cycle might be a mathematical equation of a sinusoidal type such as:

$$P_4 = A\omega - A\omega \cos \omega t \qquad (15)$$

where,
- A - an arbitrary constant which determines the amplitude of the sinusoid, so $A\omega = 10$ volts $= 400$ gC/m^2.
- ω - angular velocity of sinusoid $= 2\pi f = 2\pi = 6.28$ sec^{-1}
- f - frequency of oscillation, one cycle per year
- t - time in years

The analog computer generated the curve shown in Fig. 10, from the mathematical form above, and future use of this form will occur throughout this chapter with symbols so defined. Note that the annual fluctuations[18] are between 0 gC/m^2 and 800 gC/m^2. These amplitudes have been adopted for Fig. 10 so that the variable quantity of atmospheric CO_2

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[18]The recorders used in this study were of the servo-mechanism type. Pulses from the panels in Fig. 11 modulate the amplifiers of the recorder servo-mechanism which activates the recording pen arm on the chart paper. The frequency response of the servo-device is inadequate to record frequencies greater than 1 radian per second, and will not faithfully reproduce frequencies smaller than this if these are of large amplitude. The operational amplifier "sees" voltage pulses of the order described by the mathematical models, however the recorders will not reproduce these pulses faithfully, but will attenuate them slightly depending upon both frequency and amplitude of the pulse. This kind of limitation on the normal and even the fast-response strip chart recorder was overcome by the use of a Varian X-Y plotter with the Reactor Controls Computer for illustrations.

(carbon) assimilated by producers over one annual cycle, P_4, is equivalent to that quantity of CO_2 which would be assimilated annually with a constant rate of producer assimilation P_1:

Over n annual cycles, the

Constant Rate of Photosynthesis	=	Sinusoidal Rate of Photosynthesis

$$\int_o^{t_n} P_1(t)\ dt = \int_o^{t_n} P_4(t)\ dt \qquad (16)$$

where, P_1 = a constant rate of producer assimilation = 400 $gC/m^2/yr$

P_4 = a sinusoidal rate of producer assimilation of eq. 15

t_n = an integral number of annual cycles (years)

Therefore,

$$\int_o^{t_n} 400\ dt = \int_o^{t_n} A\omega(1 - \cos\ \omega t)\ dt$$

Solving for the mean amplitude of the sinusoid over one annual cycle, t = 1, and

$$A\omega = 400 - \frac{\sin\ \omega t}{\omega t} = 400 - \frac{\sin 2\pi}{2\pi} = 400\ gC/m^2$$

Therefore the analog computer will simulate the desired function, in both amplitude and frequency, if a scaling factor of

$$\frac{10\ V}{sec.} = \frac{400\ gC/m^2}{year} \quad \text{is used.}$$

Eq. 15 was programmed on the analog computer from the circuit of Fig. 11A; one branch producing the cosine function, $A\omega \cos \omega t$, the other, the quantity, $-A\omega$. When voltage analogs of these quantities are combined through the summer-inverter, the desired voltage variations are produced at the output of the inverter corresponding to eq. 15. The potentio-

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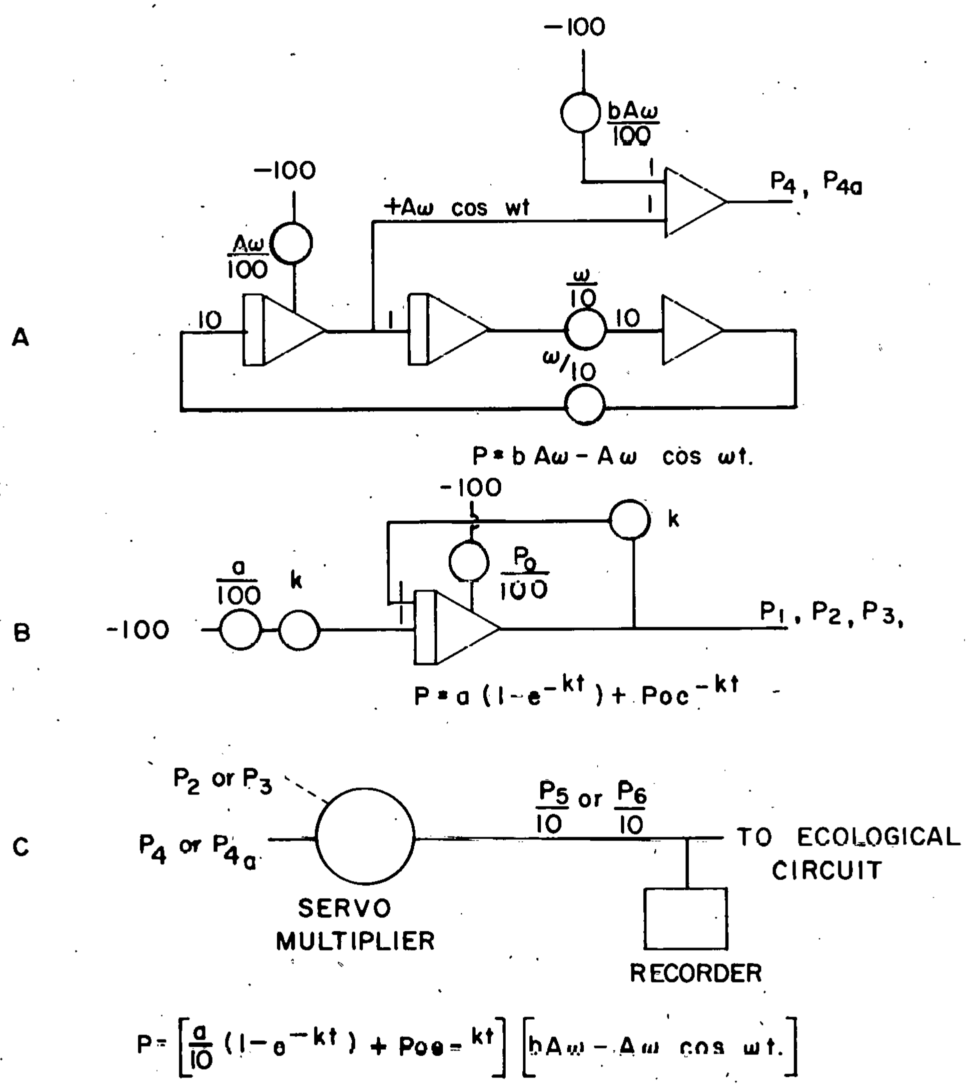

Fig. 11. Analog Computer Circuits Used to Generate Time-varying Rates of Photosynthesis.

meter settings $\omega/10 = 0.628$, in conjunction with gain settings of 10 on two amplifiers, determine the frequency of the sinusoidal output (6.28 radians per second or 1 cycle per second = 1 year). On the left of Fig. 11A, the potentiometer setting of $A\omega/100$ determines the fraction of -100 volts ($-A\omega$) which becomes inverted to $+A\omega$ as the initial condition on the sinusoidal branch of the circuit, since cos $\omega t = 1$ at $t = 0$. When $b = 1$, the initial condition setting $bA\omega/100$ leads to a constant voltage of $-A\omega$ on the non-sinusoidal branch. These two terms are summed and inverted in the summer-integrator to give P_4, or eq. 15.

Letting b take values other than 1 permits the representation of other seasonal cycles shown in Fig. 12. Let eq. 17 define a periodic function p which is equal to P_{4a} for positive values of p, but let P_{4a} be zero for negative values of p.

$$P_{4a} = p = bA\omega - A\omega \cos \omega t = A\omega\,(b - \cos \omega t) \quad \text{when } p > 0 \qquad (17)$$

$$P_{4a} = 0 \qquad \text{when } p \leq 0$$

When $b = 1$ we have the twelve month cycle of production alternating between 0 and $2A\omega$, already illustrated in Fig. 10. $b > 1$ represents a 12-month cycle of production which never falls below $A\omega(b - 1)$ and never rises to $A\omega(b + 1)$; $b = 0$ represents the case where production is negligible through half the year, and rises to $A\omega$ during the other half (a half-wave rectification); values of b between -1 and 0 correspond with producing seasons of less than 6 months. The case where $b < 0$ might similate the conditions of the growing vegetation in

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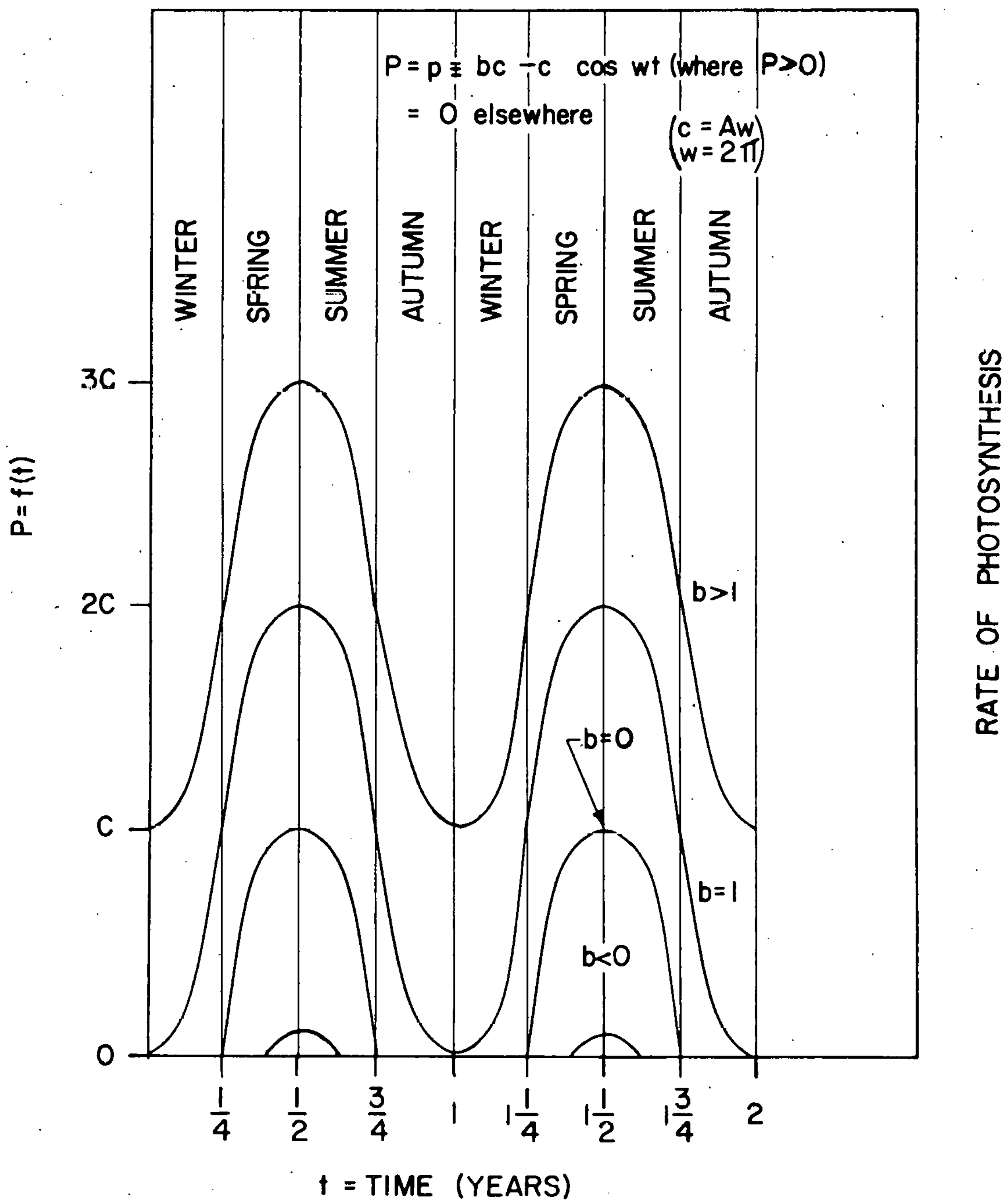

Fig. 12. Simulation of Seasonally Fluctuating Rates of Photosynthesis.

arctic regions of the earth; $b = 0$ to 1, many temperate conditions; and $b > 1$ some temperate to tropical conditions in which production is significant even in the coldest (or driest) season. (Still further refinements in the periodic input are possible through the use of Fourier series noted in section E).

In case $b < 1$, the condition of preventing the input from falling below zero can be attained by connecting a limiting diode to the amplifier leading to P_4 in Fig. 11A.

D. Exponential Trends Superimposed on Oscillating Producer Assimilation; an Example of the Use of a Function Multiplier

In addition to the simple sinusoidal approximation to the rates of producer assimilation, consideration might also be given to the sinusoidal analogs of the exponentially changing rates of photosynthesis. These might be described by the mathematical equations:

$$P_5 = (1 + e^{-kt})(A\omega - A\omega \cos \omega t) \tag{18}$$

$$P_6 = (1 - e^{-kt})(A\omega - A\omega \cos \omega t) \tag{19}$$

Figures 13 and 14 are plots of equations 18 and 19, respectively, and were generated by the analog computer by means of a function multiplier such as that discussed in Chapter IV. Because the servomultiplier automatically divides the product by 100 to prevent possible overloading of amplifiers (10 volts x 10 volts/100 = 1 volt the steady-state average output from the servomultiplier in Fig. 11C), multiplication by a gain of 10 is needed to get the final output of P_5 or P_6 approaching the same 10 volt average value as P_1 to P_4.

Note that the amplitude of the oscillations of these functions in the

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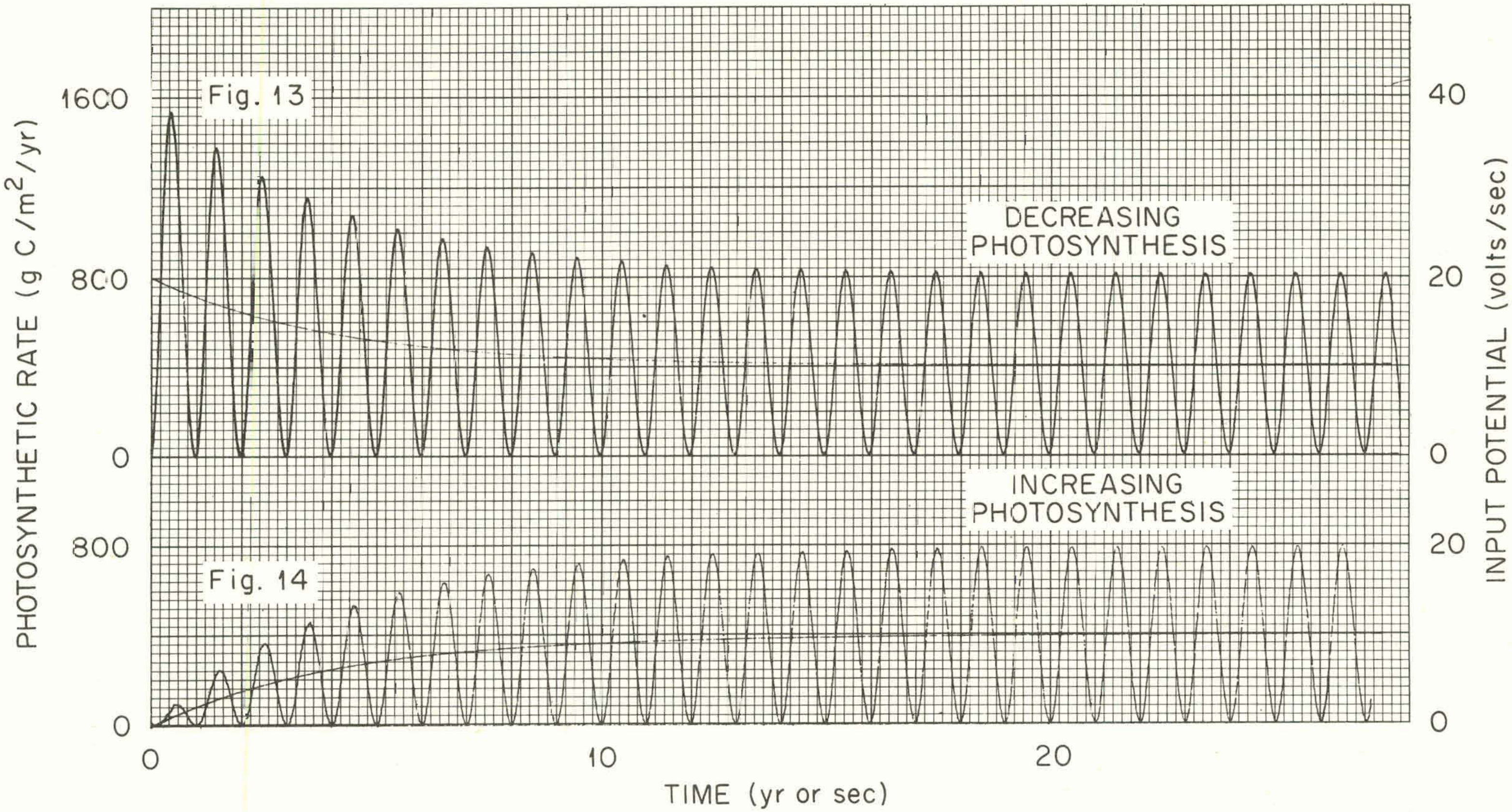

Fig. 13. Decreasing Sinusoidal Rate of Photosynthesis.
Fig. 14. Increasing Sinusoidal Rate of Photosynthesis.

steady-state are equivalent in magnitude to those of the simple sinusoid of Fig. 10. The maximum and minimum values of the rates, expressed on an annual basis, may be obtained from the solution of time-integral equations in the manner of Part C. Since the rate of producer assimilation is expressed on an annual basis the instantaneous productivity rate reaches a maximum value of 1600 gC/m^2 per year for the decreasing sinusoid and up to 800 g/m^2 per year for the increasing sinusoid. As might be expected from the mathematical equation, the time for the rate to change to one-half its initial value is given in terms of the parameter, k, the exponential function in equations 18 and 19. The measured values of the half-time of growth or decay are 2.8 years for both Figures 13 and 14. Naturally these curves generated by the analog computer are typical of the infinite number which might be produced with this limited amount of equipment by varying the parameters in either the mathematical equations or on their analogs (Fig. 11).

To obtain these plots, transient voltage fluctuations of the circuit of Fig. 11C were allowed to attain the steady-state, and then the output potentiometer of the servo-multiplier was adjusted so that the steady-state output voltage oscillations were of mean amplitude 10 V. In this manner the scaling factor equation,

$$\frac{10\ V}{sec} = \frac{400\ gC/m^2}{year}$$ was maintained.

E. Additional Approximations to Producer Assimilation Using Fourier Series and A Diode Function Generator

For rates of photosynthesis which are not described by simple mathematical models, two methods of approximation are available: (1) representation of the form of the time function by a sum of series of trignometric terms with subsequent computer programming; (2) direct approximation of the function with the function generator described in Chapter IV. Each method may offer the better approximation to a particular curve depending upon the nature of the function itself.

The function generator is well-adapted to single-valued functions which contain few maxima and minima. The shape of the curve is approximated by straight line segments with a technique similar to that for the method of finite differences (see Chap. IV). Since the number of diodes is limited, and each straight line requires two diodes for generation, a complicated curve could be approximated only with a large number of diodes. In addition, the more rapidly the slope of the function changes, the more diodes are required to approximate this slope. Fig. 8, Chapter IV, represents the approximation to the curve of arbitrary shape by the function generator. A better fit might have been obtained in this case if the trace were compared directly to the original curve and corrections made to the straight line approximations of thé diodes. In general, for curves of simple form, the approximation of the diode function generator might be made as close as the available time and the number of available diodes permits.

The general equation of the Fourier Series, with coefficients subject to Dirichlet conditions, is:

$$f(x) = \frac{a_o}{2} + \sum_{n=1}^{\infty} (a_n \cos nx + b_n \sin nx) \tag{20}$$

The coefficients are defined over an interval of 2π and $f(x)$ is considered to be periodic, i.e.,

$$F(x) = f(x + 2\pi) \tag{21}$$

The Fourier Series approximations in contrast to the function generator approximations are well-adapted to description of functions with a finite number of maxima and minima per cycle. Hence, this type of mathematical model would be most appropriate for approximation of a curve of complex shape, i.e., one with rapidly varying slopes. From the computer circuit of Fig. 11A, both the cosine and sine functions of identical frequencies may be obtained. A series of these circuits might be combined in a summer-inverter to generate a series of cosine-sine functions, each set with a frequency determined by the potentiometer setting, ω, with a circuit similar to A. The output of the summer-inverter then corresponds to the function described by eq. 20, the Fourier Series. In this manner, approximations to a large number of functions might be made.

Much of the literature of ecology contains data from conditions which do not conform precisely to the simple approximations described earlier in this chapter, but as these analyses have demonstrated, the function generator and/or Fourier series provide powerful tools with which to handle information from ecological systems as found in nature.

VI. COMPARISON OF CHANGES IN ORGANIC CARBON IN A FOUR COMPARTMENT ECOLOGICAL MODEL FOR CERTAIN TYPES OF PRODUCER ASSIMILATION

This chapter analyzes the transfer of the assimilated organic carbon through four compartments of a simple ecological model (Section A) and shows how this transfer is affected by steady or oscillating production (Sections B and C).

A. Description of the Four Compartment Model

The ecological model illustrated in Fig. 15 is equivalent to that first described in Chapter II, except that it omits the small total loss of carbon as CO_2 by animal respiration, i.e., ϕ_{13}, is zero; also, a certain constant fraction, $\phi_{12}k_1$, of the organic carbon accumulated by the vegetation above ground is distinguished as input to roots. The root compartment is assumed to transfer a constant fraction, k_2, of the carbon to the mineral soil because of death and decay of parts of the root system itself. As in Chapter II, another fraction, $\phi_{14}k_1$, of the organic carbon accumulated by the producers is lost as dying or falling litter. This litter layer loses a constant fraction, $\phi_{46}k_4$, to the mineral soil mainly by activity of "reducers". The mineral soil, which accumulates organic carbon from both sources, the litter and roots, in turn loses a constant fraction, k_6, of its accumulated carbon mainly by the biological activity of the soil organisms, and partly by solution in percolating ground water or soil erosion. The numerical values of the parameters, k and ϕ, are kept uniform in this chapter in order to

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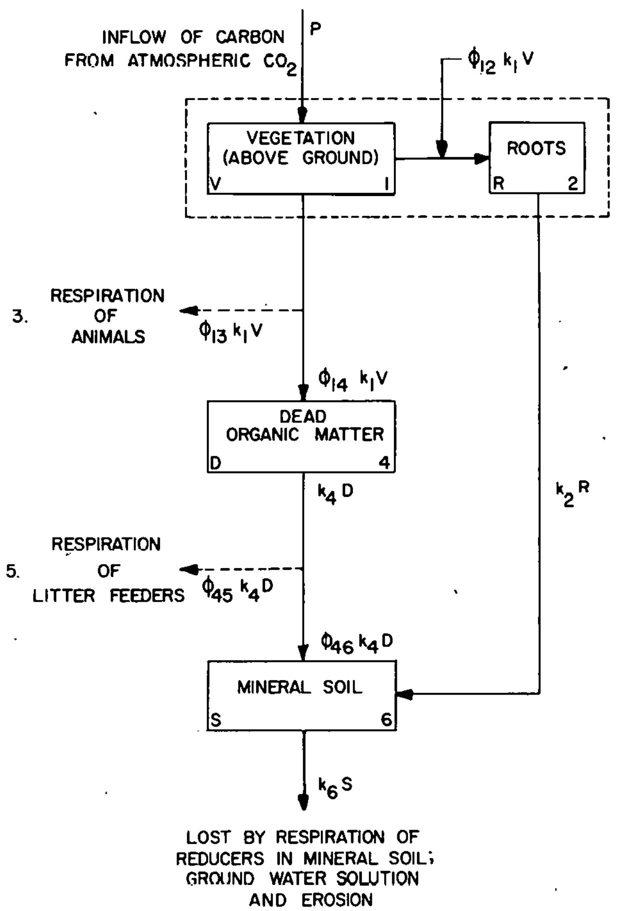

PARTIAL TRANSFER COEFFICIENTS		DECAY PARAMETERS	
ϕ_{12}	0.20	k_1	0.25
ϕ_{13}	0.00	k_2	0.25
ϕ_{14}	0.80	k_4	0.693
ϕ_{45}	0.50	k_6	0.0156
ϕ_{46}	0.50		

Fig. 15. Four Compartment Ecological Model.

illustrate the contrasting distributions of carbon for different types of producer assimilation.

The graphs of this chapter were produced by introducing the output voltages of the analog computer circuits of Chapter V (Figs. 9, 10, 13, 14) as inputs P into the first summer-integrator of Fig. 16 which simulates the producer compartment, V. Losses from each compartment are controlled by potentiometers on the feedback pathways which subtract a certain fraction of the output from the input of each summer-integrator (Chapter IV). The curves of potential versus time illustrated in this chapter were obtained by monitoring the output potentials of the summer-integrators of Fig. 16 at the points marked, X, with a strip chart recorder or an X-Y plotter whose independent variable (here time) is driven by the voltage on an integrator which increases uniformly with time. Figs. 17 to 20 are arranged such that the curve for the vegetation compartment, V, is oriented above the curves for the roots, R, dead organic matter or litter compartment, D, and the mineral soil compartment, S, respectively.

B. Changes of Organic Carbon in the Ecological Model When the Rate of Producer Assimilation is Constant

The changes of the quantities of organic carbon throughout the ecological model were simulated on the analog computer and are illustrated in Fig. 17. A constant voltage of 10 V, which simulates a constant productivity of 400 gC/m^2 per year, was introduced into the first integrator of Fig. 16. Initial voltages of zero on the integrators simulating vegetation and dead organic matter compartments, $V_o = 0$,

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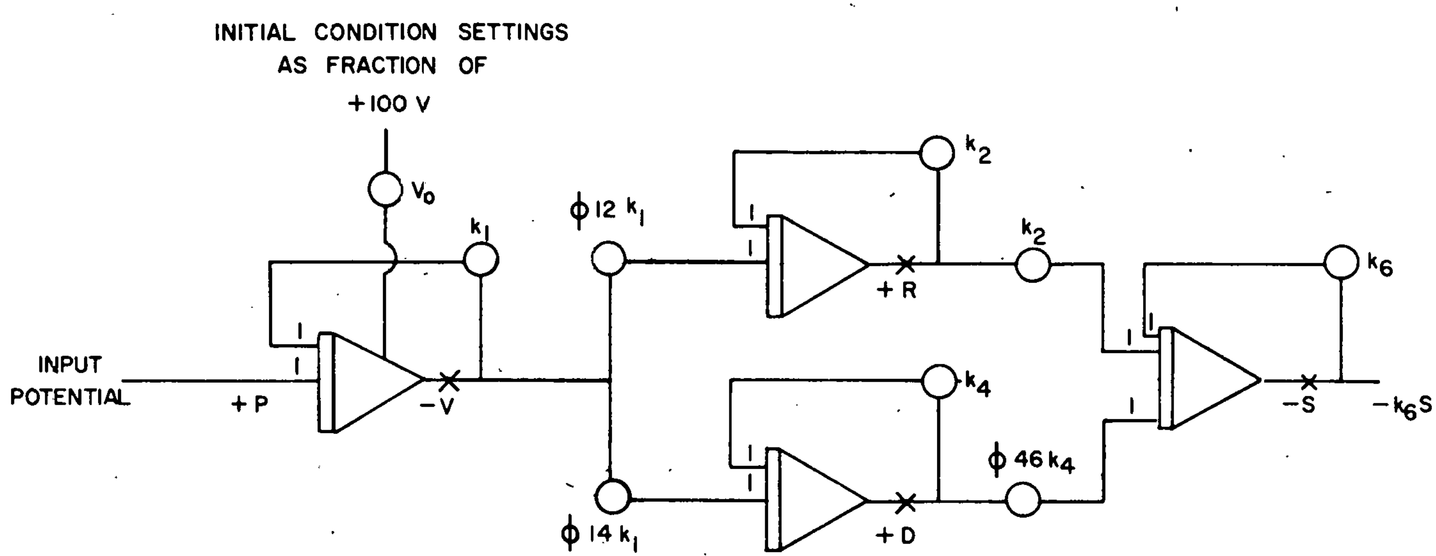

X-POINTS OF ANALOG COMPUTER CIRCUIT CONTINUOUSLY MONITORED BY VOLTAGE CHART RECORDERS

Fig. 16. Analog Computer Circuit for Simulation of a Four Compartment Ecological Model.

and $D_o = 0$, respectively, correspond to common ecological situations of plant invasion on bare areas such as abandoned agricultural fields or freshly exposed lake or river sediments. Such parent materials for soil would not necessarily contain negligible carbon content, but it is easiest to consider this extreme case where $S_o = 0$, for the sake of comparison with the compartments of vegetation and dead organic matter.

The final levels of organic carbon, which approach asymptotes (p. 72, Table 1, Column 1), are determined by the condition at which input is balanced by loss for each compartment, i.e., when the differential changes in that compartment approach zero. This condition is described mathematically by setting the differential equations formulated for the ecological model to zero and solving for the final level, V, or steady-state value V_f, D_f, S_f, R_f.

Differential Equation of Compartment	Steady-State Solution	
$\frac{dV}{dt} = P_1 - k_1V$	$V_f = P_1/k_1$	(22)
$\frac{dD}{dt} = \phi_{14}k_1V - k_4D$	$D_f = \phi_{14}k_1V_f/k_4$	(23)
$\frac{dS}{dt} = \phi_{46}k_4D - k_6S + k_2R$	$S_f = (\phi_{46}k_4D_f + k_2R_f)/k_6$	(24)
$\frac{dR}{dt} = \phi_{12}k_1V - k_2R$	$R_f = \phi_{12}k_1V_f/k_2$	(25)

The value chosen for the fraction, $k_1 = 1/4$, of the vegetation compartment V being lost each year as leaf litter and dead branches, etc., represents a case intermediate between two extremes: For herbaceous growth, all above-ground material dies down at the end of the growing season; large forests accumulate material in tree holes for many years before the larger trees mature and die. Perhaps the present case approximates k_1 for certain shrubby or scrub-forest growth. The value of k_2 used here is also 1/4. The arbitrary choice of $k_4 = 0.693$ and $k_6 = 0.0156 = 1/64$ will be compared with other values for these parameters in Chapter VII.

Mathematical methods available for the solution of equations of the type 22 to 25 are discussed in Appendix B. Using these methods, the general solutions to eqs. 22 and 23, which describe the changes in the vegetation and dead organic matter compartments of the ecological model of Fig. 15 are:[19]

$$\frac{dV}{dt} = P_1 - k_1 V$$

$$\text{Solution:} \quad V = \frac{P_1}{k_1}(1 - e^{-k_1 t}) + V_o e^{-k_1 t} \qquad (26)$$

$$\frac{dD}{dt} = \phi_{14} k_1 V - k_4 D$$

$$\text{Solution:} \quad D = \frac{P_1}{k_4}(1 - e^{-k_4 t}) + \frac{k_1(P_o - P_1)}{k_4 - k_1}(e^{-k_1 t} - e^{-k_4 t}) + D_o e^{-k_4 t} \qquad (27)$$

[19]Note that the subscripts of zero on the letters, V, D, and P above here indicate an initial condition of the given compartment and have no relation to the compartment designated as zero (outside, atmosphere) as defined in Chapter II.

The linear lags described earlier in Chapter IV are determined by the number of exponential terms involving the decay parameters, k_1, and no simple combination of these terms will uniquely describe the delay phenomenon encountered in these ecological models. Data in column 1 of Table 1 give the measured delay times for each compartment; i.e., the time required to reach 50% and 95% of the steady-state quantity of organic matter as determined from computer plots.

In many cases, the values for k_6 will be so much smaller than those for other compartments that the lag in equilibration is far greater than that of preceding compartments. Furthermore, the equilibrium level of carbon in humus in S that is approached during this long period of time is high in spite of the fact that a significant fraction ϕ_{40} of the carbon in D is released to the atmosphere in the process of decay. To illustrate these slow changes in the same figures as the more rapid ones, the time scaling factor (eq. 9) in the computer was changed so that each second of machine time = 10 years of ecosystem time. In addition the X-Y plotter abscissa value was changed so that 40 years corresponds with 1" of chart paper, 1 cm. in the reduced illustrations (Figs. 17 to 20); the X-Y plotter ordinate value was changed so that 10 volts machine potential corresponds to 1600 gC/m^2 of accumulated carbon.

C. Comparison of Constant and Sinusoidal Assimilation

Figures 18, 19, and 20 illustrate the effects on the accumulation of carbon in the ecosystem model, Fig. 15, produced by the variable rates of photosynthesis described in Chapter V by equations 15, 19, and 18, respectively.

The circuits of Fig. 11C were electrically coupled with the circuit, Fig. 16.

In order to contrast certain features in the development of the simulated ecosystem of Fig. 15, page 68 summarizes the general solutions to the differential equations which describe the effects of a constant rate and variable rates of photosynthesis on the growth of the vegetation compartment. The phenomena illustrated by this compartment will be shown by other compartments for this model. (See Appendix B for method of solution.)

The following equivalence was defined for the constants in the input equations, 15, 19, 18, and 22:

$$P_1 = A\omega = \frac{A\omega a}{k_1} = \frac{10\ V}{sec} = \frac{400 gC/m^2}{year}$$

The general solutions in equations 26, 32, 33, and 34 reduce either to eq. 35 for the constant rate of photosynthesis or to eq. 36 for the sinusoidal rates when the system attains equilibrium, i.e., when the term $e^{-k_1 t}$ approaches zero.

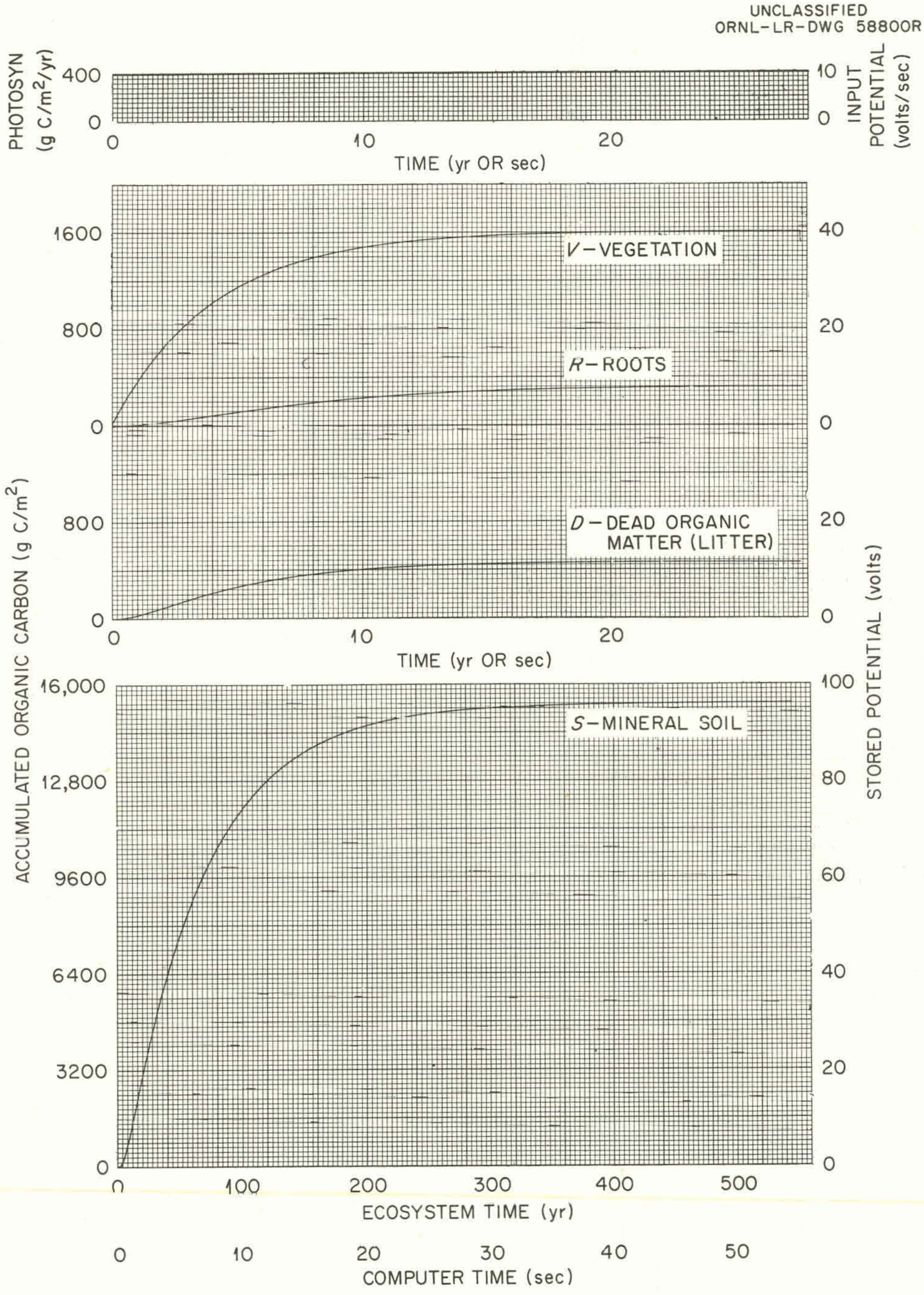

Fig. 17. Accumulation of Carbon in a Four-compartment Model with a Constant Rate of Photosynthesis.

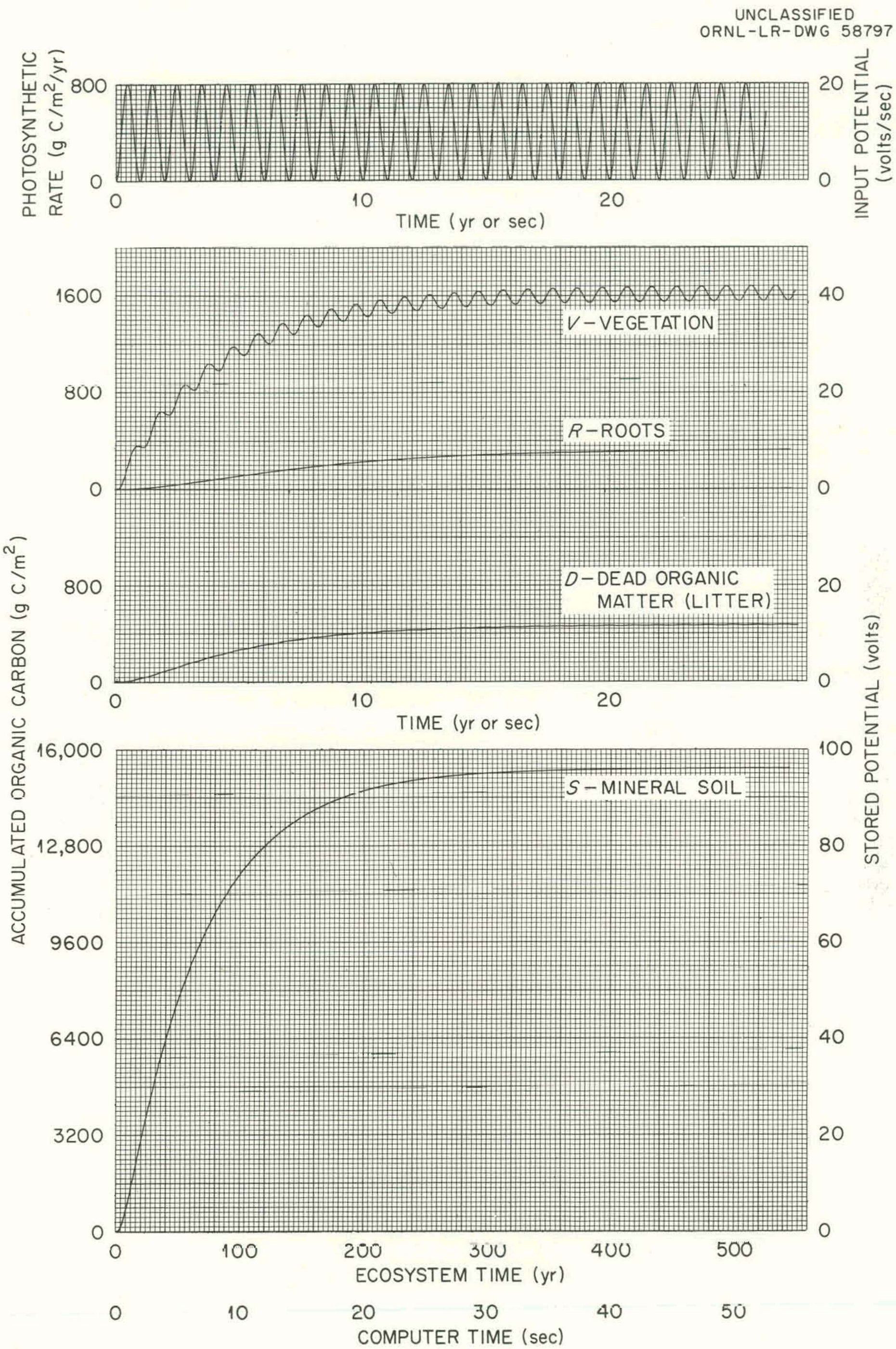

Fig. 18. Accumulation of Carbon in a Four-compartment Model with a Simple Sinusoidal Rate of Photosynthesis.

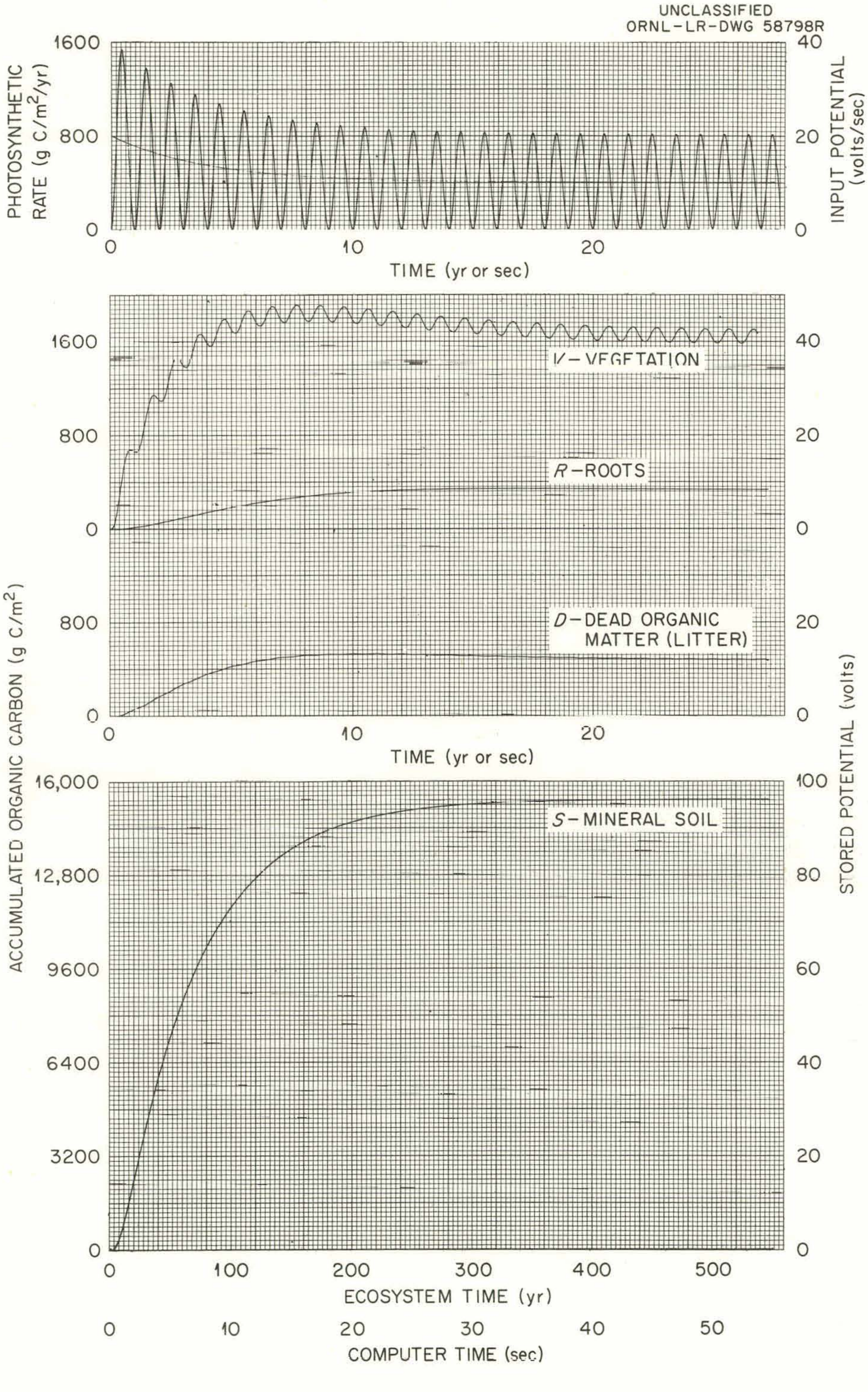

Fig. 19. Accumulation of Carbon in a Four-compartment Model with a Decreasing Sinusoidal Rate of Photosynthesis.

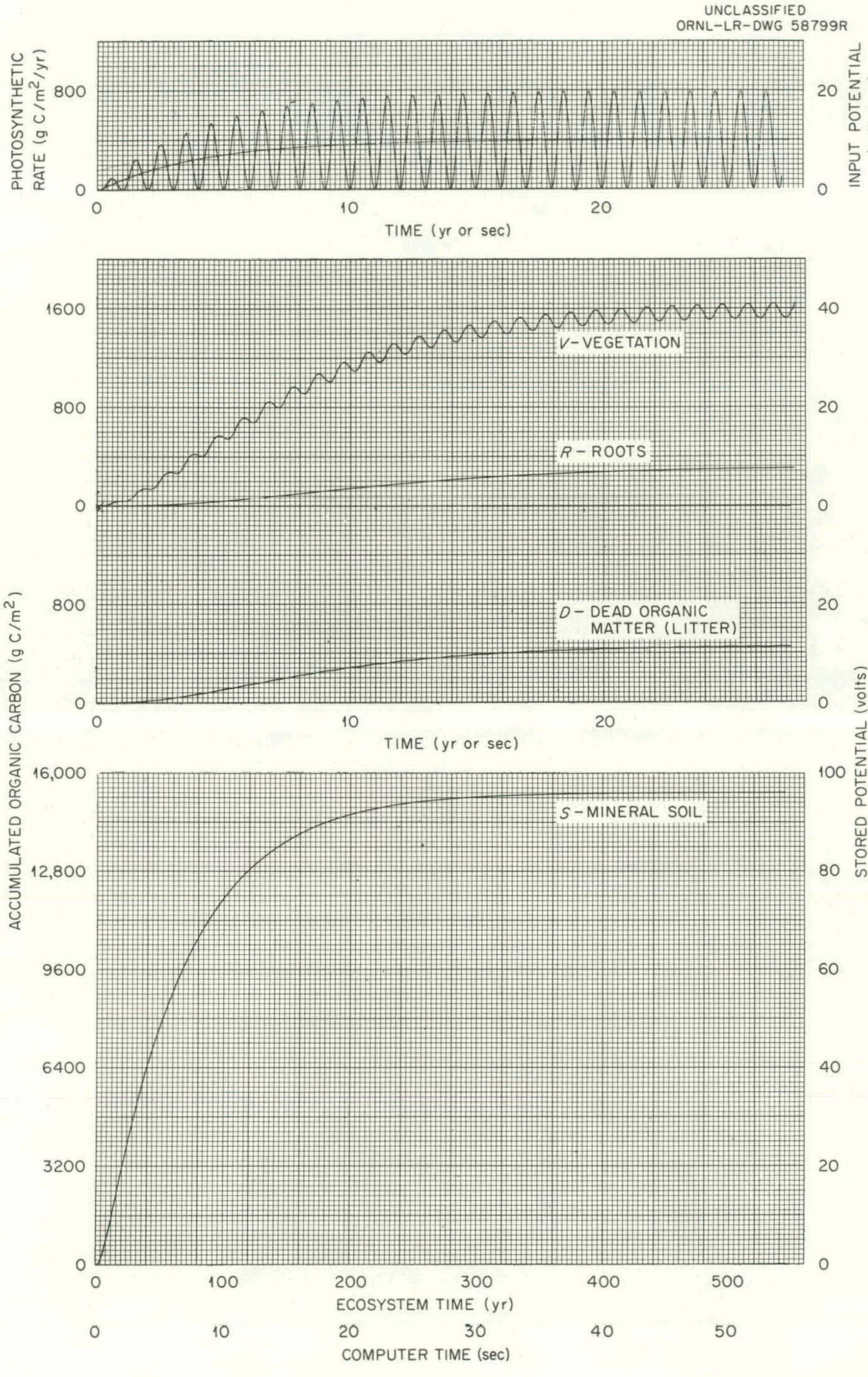

Fig. 20. Accumulation of Carbon in a Four-compartment Model with an Increasing Sinusoidal Rate of Photosynthesis.

Input Rate of Photosynthesis		Differential Equations of Growth for Vegetation Compartment	
$P_1 = 400$		$\frac{dV}{dt} = 400 - k_1V$	
$P_4 = 400\ (1 - \cos \omega t)$	(15)	$\frac{dV}{dt} = P_4 - k_1V$	(29)
$P_5 = (1 + e^{-kt})(P_4)$	(18)	$\frac{dV}{dt} = P_5 - k_1V$	(30)
$P_6 = (1 - e^{-kt})(P_4)$	(19)	$\frac{dV}{dt} = P_6 - k_1V$	(31)

General Solutions to Equations of Growth for the Vegetation Compartment

$$V = \frac{400}{k_1}(1-e^{-k_1t}) - V_oe^{-k_1t} \tag{26}$$

$$V = \frac{400}{k_1}(1-e^{-k_1t}) + V_oe^{-k_1t} + \frac{400\ k_1e^{-k_1t}}{(\omega^2 + k_1^2)} - \frac{400}{\sqrt{\omega^2 + k_1^2}}\cos(\omega t-\delta) \tag{32}$$

$$V = \frac{400}{k_1}(1-e^{-k_1t}) + V_oe^{-k_1t} + \frac{400\ k_1e^{-k_1t}}{(\omega^2 + k_1^2)} - \frac{400}{\sqrt{\omega^2 + k_1^2}}\cos(\omega t-\delta) \tag{33}$$

$$- \frac{400}{k_1-k}(e^{-k_1t}-e^{-kt}) + \frac{400\ e^{-k_1t}}{\omega^2-(k_1-k)^2}(k_1-k) - \frac{400\ e^{-kt}}{\sqrt{\omega^2-(k_1-k)^2}}\cos(\omega t-\alpha)$$

$$V = \frac{400}{k_1}(1-e^{-k_1t}) + V_oe^{-k_1t} + \frac{400\ k_1e^{-k_1t}}{(\omega^2 + k_1^2)} - \frac{400}{\sqrt{\omega^2 + k_1^2}}\cos(\omega t-\delta) \tag{34}$$

$$+ \frac{400}{k_1-k}(e^{-k_1t}-e^{-kt}) - \frac{400\ e^{-k_1t}}{\omega^2-(k_1-k)^2}(k_1-k) + \frac{400\ e^{-kt}}{\sqrt{\omega^2-(k_1-k)^2}}\cos(\omega t-\alpha)$$

$$V_{\text{equilibrium}} = \frac{400}{k_1} \tag{35}$$

$$V_{\text{equilibrium}} = \frac{400}{k_1} - \frac{400}{\sqrt{\omega^2 + k_1^{\;2}}} \cos(\omega t - \delta); \quad \delta = \tan^{-} \frac{\omega}{k_1} \tag{36}$$

If the frequency f of each input sinusoid is 1 cycle per second computer time, or 1 cycle per year ecosystem time, then the angular frequency

$\omega = 2\pi f = 2\pi(1) = 2\pi$ radians/year.

The mean steady-state quantity of accumulated organic matter for the sinusoidal rates of photosynthesis is equivalent to that for the constant rate of photosynthesis in the vegetation compartment and also for the other ecological compartments. The significant difference between the effects of these different rates of photosynthesis on the equilibrium level of vegetation are: (1) Fluctuations of input of a given frequency produce fluctuations of the same frequency in the quantities of accumulated matter, (2) The amplitude of the fluctuation around the mean equilibrium level of accumulated matter are reduced by an "attenuation factor" of $1/(\omega^2 + k_1^{\;2})^{1/2}$ from the input fluctuation for that compartment:

$$\text{Mean Input Pulse Amplitude} \times \frac{1}{(\omega^2 + k_1^{\;2})^{1/2}} = \text{Fluctuation of amplitude around mean equilibrium level} \tag{37}$$

(3) A change of the phase of the fluctuations occurs depending upon the frequency of the input fluctuation and the decay parameter of the compartment. This is equivalent to a delay in the growth response of the producer system to the input fluctuations.

When the decay parameters, k, are small fractions, k^2 may be neglected in comparison to the value of the angular frequency squared, ω^2, and then the attenuation factor approximates $1/\omega = 1/2\pi = 0.159$, which compares closely with observed values of 0.15 on Figs. 18-20. The attenuation of the input pulses is therefore inversely proportional to the angular frequency of the pulses--the decay or transfer rate having negligible effect until it exceeds 1. Neglecting the transient phase of the build-up for a moment, a similar attenuation phenomenon might, in general, be observed for each of the compartments of Fig. 15, each compartment reducing the value of its respective input pulse by the factor, $1/\omega$.

For example, the fluctuations in the accumulation of dead organic matter in the litter layer are further reduced compared with those of the vegetation compartment in this model. Since the input pulse amplitude to the root compartment is here assumed to be only 1/4 of that to the litter compartment, the fluctuations in the root compartment are proportionally reduced (eq. 37). The soil compartment, which introduces still another linear lag, shows negligible fluctuations.

Attenuation might be less drastic than would be expected in special situations in which there were parallel pathways of transfer converging finally into one compartment with phase lags that made the oscillations from each pathway additive. Such a phenomenon would be analogous to natural resonance in physical systems.

D. Effects of Changing Average Rates of Photosynthesis on the Transient Phase of Growth of an Ecosystem

The effects of different rates of photosynthesis on the transient phase of growth of the ecosystem are adequately described only by direct inspection of the analog computer recorder traces (Figs. 18, 19, 20). Notice that in the limit, as time increases without bound and e^{-kt} as well as $e^{-k_1 t}$ approaches 0, equations 33 and 34 reduce to the steady-state solutions.

A comparison of the transient phases of growth for the simple sinusoid and the constant rates of photosynthesis illustrate a significant difference between fluctuating and steady inputs. Eq. 32 describes the quantity of organic matter accumulated in the vegetation compartment at any time, t, for the simple sinusoid input of Fig. 10, Chapter V, and is equivalent to eq. 26 for the constant rate, except for the additional sinusoidal and exponential terms. Since the third exponential term of eq. 32 is negligible, no significant difference may be observed between the data for levels of accumulation and response time for the cases of the simple sinusoid and the constant rates of photosynthesis (except for fluctuations around the mean equilibrium level). On the other hand, the transient growth phases of the complex sinusoids of Figs. 19 and 20 differ in the times required to attain equilibrium precisely because the additional transient terms with e^{-kt} in eq. 33 and 34 are not negligible.

Table 1. Accumulation of Organic Carbon in a Model Ecosystem, and Times T_{50} and T_{95} Required to Attain 50% and 95% of these Values.

Compartment		Type of Input (Rate of Photosynthesis)			
		Constant P_1 Fig. 9	Oscillating P_4 Fig. 10	Decreasing P_5 Fig. 13	Increasing P_6 Fig. 14
		Change of Organic Carbon in an Ecological Model			
		Fig. 17	Fig. 18	Fig. 19	Fig. 20
		(1)	(2)	(3)	(4)
Final Levels for Accumulation of Organic Carbon--gCarbon/meter^2					
V_f		1600	1600 ∓ 52[a]	1600 ∓ 52[a]	1600 ∓ 52[a]
R_f		320	320	320	320
D_f		460	460	460	460
S_f		15,360	15,360	15,360	15,360
Response Time Parameters--years					
V:	T_{50}	2.8	2.8	--	7.0
	T_{95}	11.8	11.4	--	19.2
R:	T_{50}	6.8	7.0	4.5	11.0
	T_{95}	17.0	19.8	9.2	24.0
D:	T_{50}	4.4	4.4	2.6	8.4
	T_{95}	12.2	12.0	5.2	19.2
S:	T_{50}	50.0	50.0	46.0	52.0
	T_{95}	200.0	196.0	188.0	200.0

[a]Mean values of accumulation of carbon for sinusoidal types of input.

Linear lags introduced by k are accompanied by phase lags introduced by δ and α, and the final term in equations 33 and 34 produce additional damped oscillations. Close comparison of Figs. 19 and 20 shows such effects in the amplitude and timing of the annual oscillations.

Effects of the terms in k on the delay in build-up of carbon, which was discussed in Chapter V, are also demonstrated by the data of Table 1, columns 2 to 4. As compared with uniform average photosynthesis, delay in attainment of the maximum rate of photosynthesis means a longer delay before the ecosystem attains its equilibrium level of accumulated organic carbon (col. 4), but for an initially high and decreasing rate of photosynthesis, the system attains equilibrium more rapidly (col. 3). In each case, the delay or response time for the vegetation compartment is less than that for the dead organic matter and soil compartments. The response of the root compartment is somewhere between that of the vegetation and dead organic matter compartments, as would be expected from considerations of lags and of the decay parameters.

VII. EFFECTS OF DECAY PARAMETERS ON THE DISTRIBUTION OF ORGANIC CARBON IN A FOUR COMPARTMENT MODEL

While Chapter VI considered the effects of continually varying rates of photosynthesis on an ecological model with fixed decay and transfer parameters, this chapter will consider the effects of systematically changing the values of the k_i parameters. Within each trial it is still assumed that the k_i's are constant rather than variable through time. A steady rate of photosynthesis is assumed, to simplify comparison between trials; as shown in Chapter VI, the equilibrium levels of carbon in the compartments of the ecological model will be similar to the average values for models with oscillating types of photosynthesis. Curves of voltage versus time (Fig. 21) show details of the transient phase accumulation.

A. Effects of Litter Decay Parameters on Litter Accumulation

As a further simplification, vegetation is assumed to have reached the steady state and hence the input to compartment 4, $\phi_{14}k_1V$, is a fixed value for all values of the litter decay parameter, k_4 (Table 2, column 1). This assumption is made so that simple calculations of the expected values can easily be compared with computer traces. Initial conditions D_o and S_o on the computer are again assumed to be 0 for simplicity of illustration. A natural approximation to these boundary conditions might occasionally be found where new litter and soil humus begin accumulating on fresh flood deposits that partially buried a pre-existing stand of vegetation, without destroying the vegetation or its productivity.

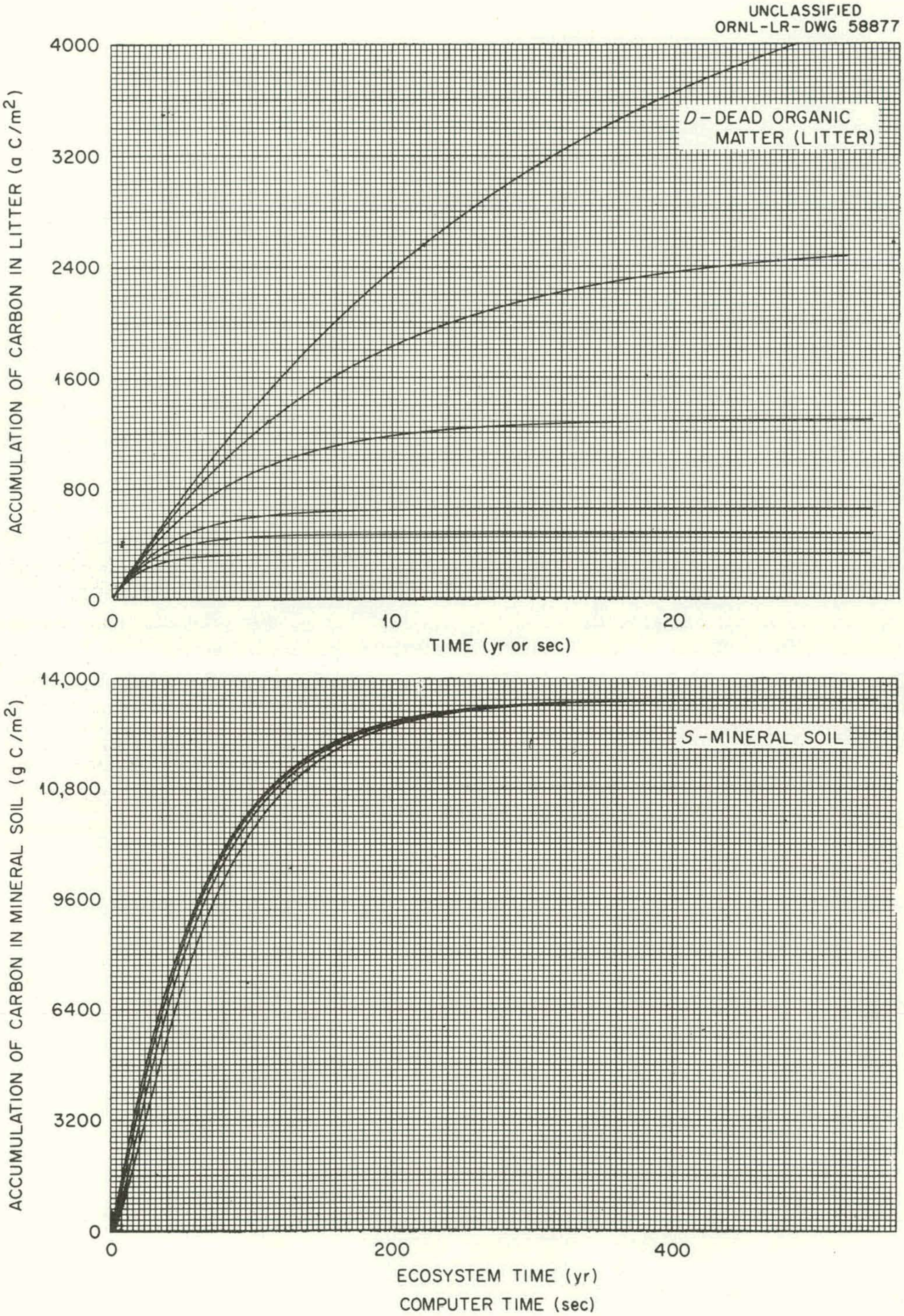

Fig. 21. Effects of Variation of Decay Parameters on Accumulation of Litter and Soil.

Table 2. Comparison of Estimated and Calculated Levels and Rates of Accumulation of Organic Litter.

k_4	Final levels (g C/m^2)	T_{50}	T_{95}
(1)	(2)	(3)	(4)
	Values estimated from charts		
0.625	--	11.1	--
0.125	2580	5.6	23.7
0.25	1290	2.8	11.9
0.50	650	1.4	6.0
0.693	470	1.0	4.1
1.000	325	0.7	3.0
	Values calculated from formulas	$0.693/k_4$	$3/k_4$
0.0625	5120	11.09	48.0
0.125	2560	5.54	24.0
0.25	1280	2.77	12.0
0.50	640	1.39	6.0
0.693	464	1.00	4.3
1.000	320	.69	3.0

The equilibrium level of accumulated organic carbon and the time required to attain any fraction of this equilibrium level are inversely proportional to k_4. This is illustrated by analog computer traces for litter accumulation as a function of time, as in Fig. 21A, which were used to estimate values in the upper part of Table 2.

The equilibrium levels of accumulated organic carbon in the lower part of Table 2 were calculated from eq. 23 of Chapter VI by setting the rate of change equal to 0:

$$\frac{dD}{dt} = \phi_{14} k_1 V - k_4 D \qquad D_f = \phi_{14} k_1 V_f / k_4 \tag{23}$$

Columns 3 and 4 show how the time required for the accumulation of a fraction (0.5 or 0.95) of each equilibrium level is inversely related to the rates of transfer of carbon from the litter compartment, k_4. For the present case, the time required to attain 95% of the equilibrium level is approximately $3/k_4$. The time required to attain 50% of the equilibrium level should be $0.693/k_4$. The analog computer trace data agree with calculated values with sufficient accuracy to take the place of exact computations in cases where the computations would be much more difficult.

The quantity of organic carbon in the root compartment grows to the identical equilibrium level, 320 gC/m^2, at the same rate for each set of decay parameters discussed, and is not listed in Table 2.

B. Effects of Variation of Litter and Mineral Soil Parameters on the Accumulation of Organic Carbon in the Mineral Soil

The accumulation of organic carbon in the mineral soil, tabulated in Table 3, and illustrated in Fig. 21B, is a function of the three factors given by eq. 24, Chapter VI.

$$\frac{dS}{dt} = \phi_{46}k_4D + k_2R - k_6S \qquad S_f = (\phi_{46}k_4D + k_2R)/k_6 \qquad (24)$$

The first term, $\phi_{46}k_4D$, is the quantity of carbon transferred from the dead organic matter compartment by infiltration or physical incorporation; the second term, k_2R, refers to the transfer from death or exudates of root systems spread throughout the mineral soil; and the last, k_6S, is the rate at which carbon moves out of the soil system by decay of humus, ground water solution, and perhaps soil erosion. The values of the parameters, k_4 and k_6 are given in Table 3. Other parameters are the same as given in Fig. 15.

For a fixed value of the soil decay parameter, (e.g., $k_6 = 1/64$ in Fig. 21), extreme variations of the decay parameters of the litter layer produce no significant differences in the quantity of organic carbon accumulated at equilibrium in the mineral soil. In two other soils, with greater hypothetical rates of loss ($k_6 = 1/16$ or $1/4$), the expected equilibrium accumulation of carbon and time required to approach this level would be less, just as in the case relating D and k_4 (Table 2, column 5). The data from Table 3, columns 3 and 4, illustrate the overall decrease in the times required to attain a specified fraction of the equilibrium accumulations of organic carbon in the mineral soil of

Table 3. Effects of Decay Parameters for Soil Compartment and Litter Compartment on Soil Organic Carbon.

k_4 (yr^{-1})	Final Levels ($g\ C/m^2$) Expected values = observed values	Delay-Time (years) T_{50}	T_{95}
(1)	(2)	(3)	(4)
	Soil Compartment, very rapid loss (k_6=0.25=1/4)		
0.0625	960	12.6	48
0.250	960	7.5	22
0.693	960	5.6	16.5
	Soil Compartment, rapid loss (k_6=0.0625=1/16)		
0.0625	3840	24	65
0.250	3840	11	49
0.693	3840	14	48
	Soil Compartment, medium loss (k_6=0.0125=1/64)		
0.0625	15,360	46	198
0.25	15,360	39	191
0.693	15,360	36	186

Fig. 23 as the rate of transfer from litter decay, $\phi_{46}k_4$, increases, but the lag due to k_4 has no effect on the eventual level of S.

VIII. MOVEMENT OF CARBON-14 THROUGH AN ECOLOGICAL SYSTEM

The isotope, C^{14}, was selected to illustrate the application of the methods of the analog computer to radioisotopes because of its association with the major element of organic matter. In general, the radioactive decay of an isotope would be accounted for by an increase in the decay constant k for each compartment of the model, and a corresponding increase in the negative feedback potentiometer for each integrator of the analog computer circuit. Because the radioactive half-life of C^{14} is of the order of 5500 years, radioactive decay is very small for the relatively short periods of time considered in this report.

A. Potential Hazards of C^{14}

Relatively slight changes in the concentration of atmospheric C^{14} ($< 1\%$) are believed to occur as a result of corresponding changes in the cosmic ray flux impinging on the earth's atmosphere. Broecker and Olson[20] recently have estimated that nuclear weapons tests have increased this overall natural equilibrium concentration of C^{14} in the earth's atmosphere by approximately 5% per year during the years 1956 to 1960, with smaller increases dating from 1953.

Totter et al.[21] estimate that this bomb-produced C^{14} will ulti-

[20] W. S. Broecker and E. A. Olson, Radiocarbon from Nuclear Tests, II, Science, 130, 712-721 (1960).

[21] J. R. Totter, M. R. Zelle, and H. Hollister, Hazard to Man of Carbon-14, Science, 128, 1490 (1958).

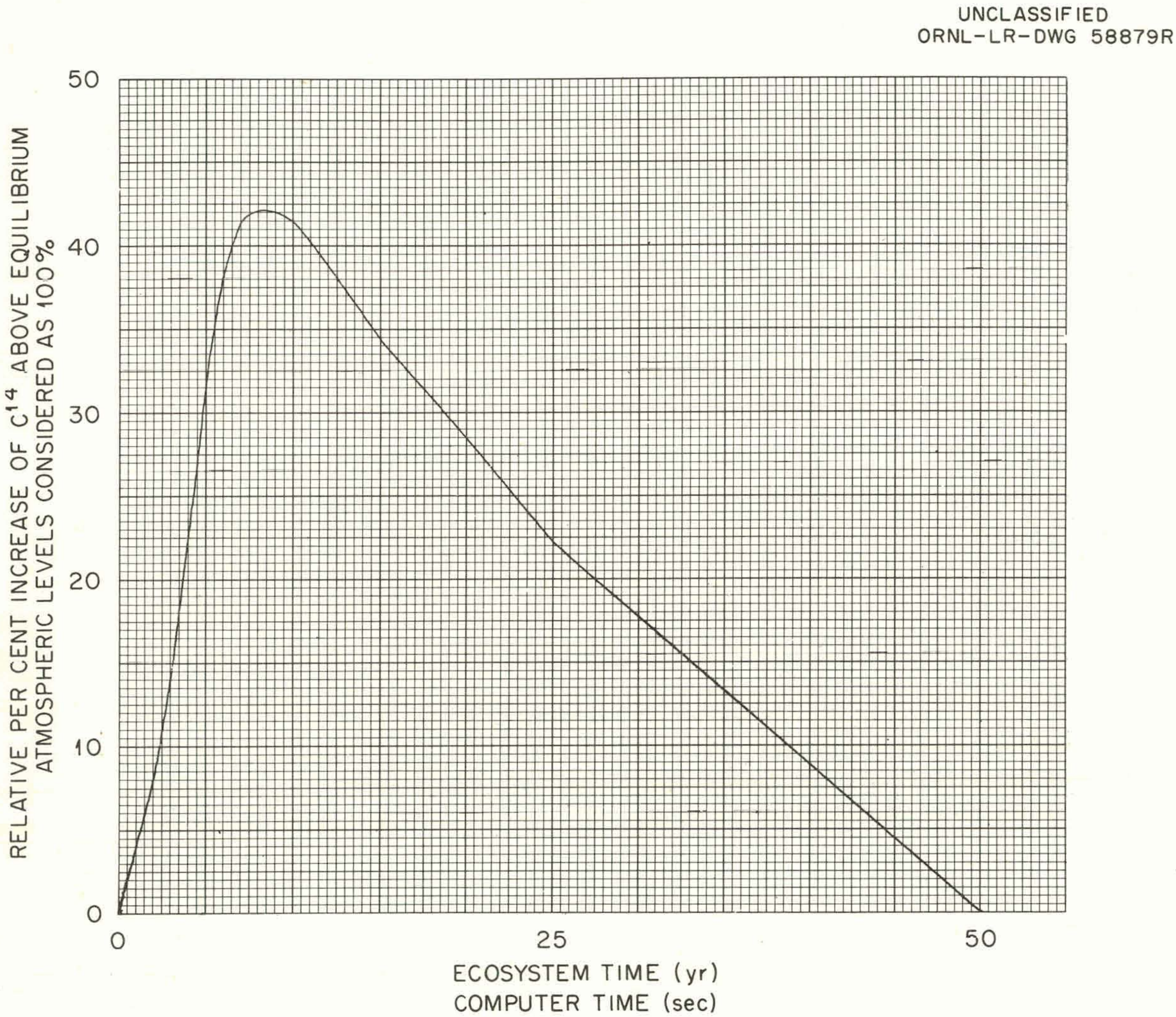

Fig. 22. Application of the Function Generator to Describe the Estimated Change of Carbon-14 in the Atmosphere.

mately result in a 0.5% increase in the dose rate of this isotope above the natural background C^{14} dose. Incorporation of this radionuclide through the food chain in a manner similar to the stable isotopes might lead to mutation effects produced both by transmutation of the cellular carbon by beta decay to nitrogen and by the energetic effects of beta radiation itself upon tissue. They conclude that the immediate effects of this increase are negligible, but that the long-term effects in terms of mutations or other abnormalities on a fixed population might not be considered negligible if emphasis is placed on the total number of people affected rather than the very small percentage of the population likely to be affected by the slight addition to natural radiation background.

B. Analog Computer Methods for Examining the Lag in Build-up of $Carbon^{14}$ in an Ecosystem

Atmospheric CO_2 is composed of three isotopes: C^{12}, 98.9%; C^{13}, 1.1%; and C^{14}, 10^{-10}%. With a few reservations concerning fractionation of isotopes by weight[22], the distributions of the heavier isotopes of carbon will parallel those to the light isotope, C^{12}. Therefore, the probable effects of an influx of extra C^{14} into the atmosphere will be to produce increases in the natural concentrations of C^{14} in each part of the ecosystem, moving in proportion to the quantities of the stable

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[22] Craig (op. cit)

isotope, C^{12}. The rates and magnitude of these increases are determined by the decay and transfer parameters characteristic of the local ecosystem itself.

The curve in Fig. 22 is an approximation by the function generator of the projections of Fig. 4 of Broecker _et al._[23] which assumed a peak increase to 142% of the natural equilibrium levels of C^{14}. Losses from the atmosphere to the ocean and storage in the deep sea reservoir, discussed in Chapter III, lead one to expect a gradual decline, to be practically completed in 50 years, barring further atmospheric tests. The shape of this curve might be altered to conform to many other hypotheses of C^{14} growth by simply adjusting the function generator output potentials.

The ordinate on the left of Fig. 22 describes the relative per cent increase of the rate of incorporation of C^{14}, compared with the natural equilibrium rate, considered as 100%. Therefore a 10% increase in the C^{14} concentration is equivalent to its analog, a change of 1 V in the input potential in the computer model. As in Chapter VI, a steady voltage, 10 V = P_1, was applied to the first integrator of Fig. 16 as an analog to one unit of normal annual incorporation of C^{14} in terrestrial plants. After the steady-state condition was attained, the computer was stopped in the "hold" condition, and a single-pole, double-throw switch permitted addition of the output potential of the function

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[23] W. S. Broecker and E. A. Olson (_op. cit._)

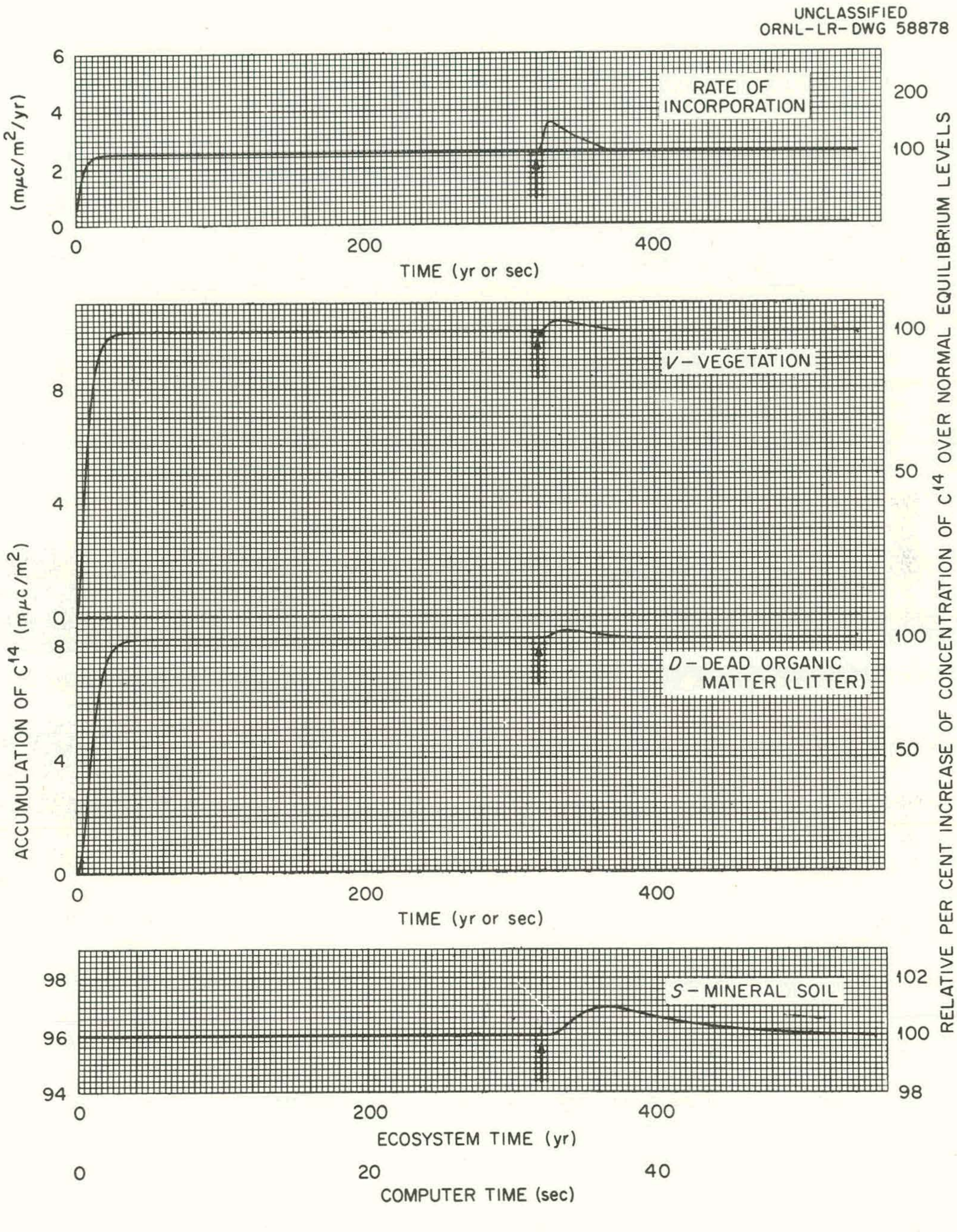

Fig. 23. Effects of a Change in the Concentration of Carbon-14 in the Atmosphere on Changes in the Accumulations of Carbon in a Four-compartment Ecological Model.

generator to simulate the per cent increase over the natural equilibrium level of C^{14} shown in the top of Fig. 23.

The resultant changes in the distribution of C^{14} in the ecological model of Chapter VI (Fig. 15) are illustrated in Fig. 23. The values of k and ϕ_{ij} are numerically the same as in Chapter VI. Prior to nuclear testing, Fig. 23 shows that the general build-up of C^{14} in the ecological model parallels that of the stable isotope of carbon, C^{12}. Here 1 volt is assumed equivalent to 1 mμc of C^{14}, originally present in each 160 gm C. The equilibrium quantity of C^{14} is assumed to be present in the soil compartment at the outset--about 96 mμc/m^2. Continuation of equilibrium levels would have been maintained if no increase in atmospheric C^{14} had occurred. Vertical arrows indicate when C^{14} increased in the atmosphere as a result of nuclear weapons testing; i.e., the point at which the curve of Fig. 22 was switched into the analog computer circuit with the function generator. The subsequently rising curve shows the predicted per cent increase of the concentration of C^{14} in each compartment above the reference level labeled as 100%.

The general trends which these functions of time might exhibit in ecological models may be estimated from the principles described in earlier chapters. Considerations of linear lag effects indicate that the lag in the build-up of the input pulse of Fig. 22 in each later compartment of the ecological model will be identical to those lags in the accumulation for each compartment with a steady input, P_1. Study of Fig. 23, especially the dead organic matter compartment, will show that the greater the lag to reach the equilibrium condition for each compartment, the greater the lag for the build-up of concentration of C^{14}. The greater the decay parameter for any compartment, the greater is the delay in readjusting to the change of input.

An attenuation of the pulse of C^{14} is shown, as expected for compartments which are remote from the source. The soil compartment shows the greatest delay and the greatest attenuation in percentage increase of C^{14}, considering the large total reservoir of C^{14} already present in this compartment. But the slow decay parameter for this compartment also results in a larger increase in total C^{14} than for the litter compartment. Furthermore, the soil compartment still retains its excess C^{14} long after the pulse in other compartments has come and gone.

IX. EXTENSIONS OF ANALOG COMPUTER APPLICATIONS IN ECOLOGY AND HEALTH PHYSICS

All chemical elements exhibit movement between compartments of an ecological system. An important contrast with the carbon cycle is provided by the cycles of some of the mineral nutrient elements and hazardous radioisotopes such as Sr^{90} and Cs^{137}. In these cases, major pathways of movement are from soil-to-roots-to-above-ground vegetation and back to litter and soil (Fig. 24). Modified circuit connections would thus be needed to connect the integrators already included in the present study. Additional integrators would be needed for additional compartments.

While strontium and cesium follow similar pathways, they differ in values for the parameters describing the amount and direction of movement, k and ϕ. Certain types of mineral soil selectively adsorb cesium and exhibit low uptake to plants compared with quantities of strontium taken up by vegetation[24]. For a given level of plant contamination, some animals (e.g., insects) eliminate strontium more rapidly than cesium so that the final levels of Cs^{137} are considerably higher (relative to intake) than are the levels of Sr^{90}.[25] Mammals, having a calcareous skeleton tend to accumulate relatively more Sr^{90}.

Analog computer circuits for the ecological movements of the

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[24] Lars Fredriksson et al, "Uptake of Fission Products by Soils, Plants and Animals", Proc. Second UN Intern. Conf. Peaceful Uses of Atomic Energy, 18:449-70. (1958)

[25] D. A. Crossley, Jr. and H. F. Howden, "Insect-vegetation Relationships in an Area Contaminated by Radioactive Wastes", Ecology 42, 302-317 (April 1961).

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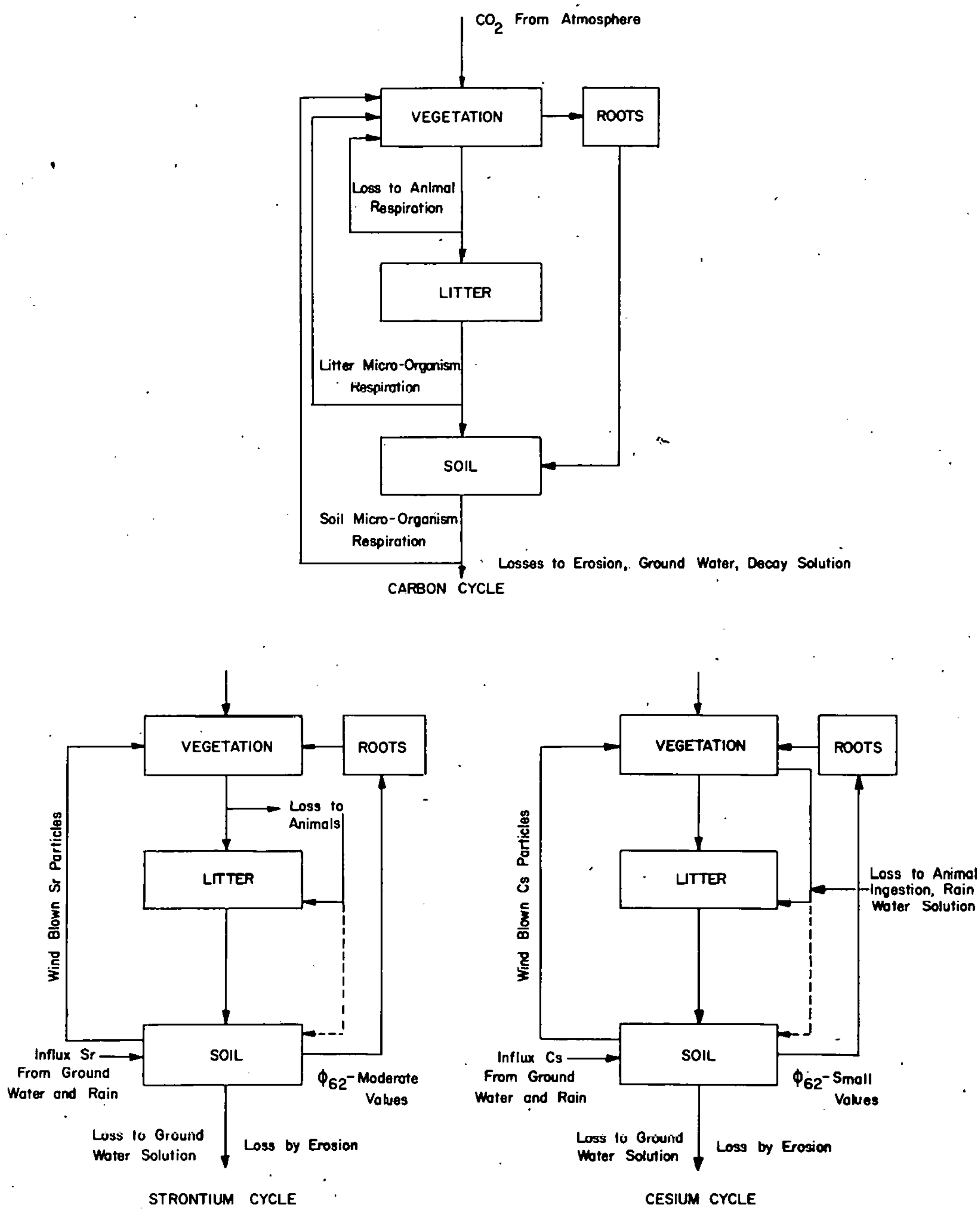

Fig. 24. General Contrast of the Carbon Cycle (Assuming Some Fraction Recycling) with the Cycles of Strontium and Cesium.

element carbon may be modified to apply to the movements of isotopes by using methods illustrated in this report and certain additional features not fully exploited in this study. The possibility of recycling of a certain percentage of the locally respired CO_2 into the local vegetation could be considered.

Most of the present study restricted attention to three or four compartments to illustrate principles on a small computer, the Donner Model 3400 which has only five integrators; more complicated ecological models with many more compartments could be simulated on a large computer such as the RCAF, Reactor Controls Analog Facility, which has forty or more integrators.

In order to take advantage of various changes of input, such as exponential trends, seasonal oscillations, and more complicated functions produced by Fourier series, the many additional integrators of the large computer offer a wide range of possibilities. The function generator can be utilized in many cases where these methods are not sufficiently flexible to simulate arbitrary functions.

Many refinements are possible by subdividing one compartment into subcompartments representing different states of an element. For example, cesium in soil could include: (1) a fraction which is fixed by clay mineral structure and has very low transfer parameters to any other compartment, (2) a fraction which is subject to normal ion exchange, and (3) a soluble fraction. Independent adjustment could be made for parameters connecting each sub-compartment to the others; sub-compartments (2) and (3) would have higher parameters for transfer to organisms than would (1).

Certain limits could be imposed on the amount of material in a compartment by adjusting the voltage of a limiting diode circuit.

X. SUMMARY AND CONCLUSIONS

Compartment models relate the flow of materials between parts of a system to the amounts of materials in each part of the system. Such models are already widely used in chemical, physiological and biophysical studies of elements or isotopes in organisms. This approach can be extended to ecological systems (ecosystems) consisting of populations of organisms and components of their environment. Analog computer methods illustrated in this report should be helpful in making this extension.

Simplified assumptions were made here to illustrate basic principles. However, many possibilities were suggested for later removing oversimplifications in order to provide more realistic ecological models. 1) Only four compartments of a simple terrestrial system were included (soil, overlying dead organic matter, and vegetation, including tops and roots), but additional compartments for individual plant organs, for various species of plants and animals, and for different kinds of material in the environment could be added. 2) Relatively simple functions were assumed for the photosynthetic input to the system (constant, sinusoidal, and exponential terms), but many other functions can be used in the same way as was done here. 3) Present applications were limited to differential equations with constant coefficients, but analog computer methods should be particularly helpful in solving linear differential equations with variable coefficients, and non-linear systems of equations.

The analog computer not only helps solve equations that have already been formulated in explicit mathematical form, but it can be used for direct simulation of the behavior of the model system without necessarily requiring explicit formulation of all the equations. The electronic computers used here simulated the accumulation of carbon in each ecological compartment by the change in electric potential on a corresponding integrator. Such computers simulated the transfer of material between compartments by transmission of electrical potential, rather than by the flow of electric current. Many technical advantages of an electronic computer over an electric network become particularly important during consideration of oscillating or transient conditions, which were illustrated in this report. Experience suggests that the chief limitations in accuracy are related to the graphical recording and reading of data, and these difficulties can be minimized with the aid of a fast-response X-Y plotter and judicious scaling of the parameters of the plotter and the problem variable.

The accumulation of carbon in an ecological system on a bare area was simulated by introducing an assumed input function, representing rate of photosynthesis, into the ecological circuit. Each compartment was represented by an integrator whose potential changed at a rate controlled by the algebraic sum of gains and losses (negative feedback) for that compartment. The feedback time constant was inversely proportional to the equilibrium level for potential (or carbon content) that is approached as losses approximately balance the gains. It was also inversely proportional to the time required for attaining a specified fraction of this equilibrium level. A sequence of several compartments in series or parallel (vegetation tops, to both roots and dead organic litter, from both of these to soil) results in a series of linear lags which make the behavior of later compartments depend on the preceding ones as well as on their own parameters.

The addition of oscillating or exponential transient terms in the input function results in corresponding terms in the response of the system. However, the oscillations are abruptly damped (usually by a factor of $1/2\pi$, or less) with each transfer, and can often be neglected in later compartments.

After input for the system and the initial conditions for each compartment are specified, it was simple to trace the response of a given compartment for many possible values of the parameters which control it. For example, the level of soil carbon eventually attained during soil formation was controlled by the loss parameter of the soil compartment and by all the parameters which control the input of organic matter to the soil. For the normal case in which the loss parameter for soil was much slower than other time constants in the system, it controlled the speed of approaching equilibrium and the other time constants had only a minor modifying influence.

The parameters which controlled the amount and speed of total carbon accumulation in the system also control the future ecological distribution of C^{14} from nuclear testing. A pulse potential was introduced in a manner simulating the estimated changes in atmospheric $C^{14}O_2$ over a 50-year period. Vegetation showed a prompt increase, followed by a fairly prompt decrease to normal levels. Soil showed a prolonged delay and relatively smaller percentage increase because of the lags in the circuit and the slow time constant of the soil compartment. But these influences led to a persistence of excess C^{14} in the soil long after the other compartments had returned to normal.

Similar influences could affect the rate and amount of accumulation of other elements and other radioactive isotopes, including the hazardous fission products that are released to the environment from fallout and through radioactive waste disposal. Additional complications will be involved in the ecological analysis for the inorganic elements, because of the feedback from soils to vegetation. But the computer techniques which were illustrated in this report promise to be helpful in predicting the fate of these materials when the necessary ecological information can be organized in terms of a compartment model.

APPENDIX A

SIMPLIFIED TREATMENT OF THE THEORY OF THE ANALOG COMPUTER

The manner in which electronic components contained within an operational amplifier simulate the operations of summation and integration may be clarified by applying Kirchoff's Law to circuit B., Figure 3, Chapter IV. Consider the operational amplifier as a "black box" with a voltage gain or amplification factor, G. At point 'O', the sum of currents is zero by Kirchoff's Law. Thus....

$$\frac{e_i - e_g}{R} \quad \frac{-e_g}{r} - C\frac{d}{dt}\left(e_g - e_o\right) = 0 \qquad (38)$$

Symbols are defined above as in Chapter IV. The amplification factor, G, is defined as the ratio of output to input potential so that,

$$G = \frac{e_o}{e_g} \quad \text{or} \quad e_g = \frac{e_o}{G} \qquad (39)$$

If we substitute eq. 39 into eq. 38 above we obtain,

$$\frac{e_i - \frac{e_o}{G}}{R} - \frac{e_o}{Gr} - C\frac{d}{dt}\left(\frac{e_o}{G} - e_o\right) = 0 \qquad (40)$$

The operational amplifier is designed so that the amplification factor, G, approximates an infinitely large positive number in comparison to the other terms in eq. 40 above. Thus, we may consider eq. 40 to reduce to...

$$C \frac{de_o}{dt} = \frac{e_i}{R} + \epsilon (G) \qquad (41)$$

The last term of eq. 41 represents the error introduced into the integral solution which may be made small by designing the amplifier with as large an amplification factor, G, as desired. For the Reactor Controls Facility, G is of the order of 10^7-- 10^8, while G is not quite that large for the Donner Computer; thus integral solutions on the RCAF should have somewhat more precision than those of the Donner equipment.

This error term is a function of time only because G may vary with time due to statistical drift currents in the resistor and vacuum tube components. Only because of this variation in G can the length of time in integration affect the accuracy of the operation. Assuming that the error term of eq. 41 is negligible to the input term we may solve to obtain,

$$e_o = \int_o^t de_o = \frac{-1}{RC} \int_o^t e_i \; dt$$

Hence, the output potential, e_o, of the operational amplifier varies as the negative time integral of the input potential. A general equation for n input potentials presented through n input resistors may be derived in like manner to show that the output potential of the integrator will be the integral of the sum of the input potentials:

$$e_o = \frac{-1}{RC} \int_o^t (e_1 + e_2 + \; . \; . \; . \; . \; . \; . \; e_n) dt \qquad n = 1, 2. \; . \; . \; .$$

The term RC in the denominator of these equations is the familiar time constant. Adjustment of the values of the resistor and the capacitor allow what has been referred to in Chapter VII as time scaling, i.e., adjustment of the circuit parameters to give the desired integral in a desired period of time.

Replacing the capacitor in Fig. 3B, Chapter IV, with a feedback resistor, converts the operational amplifier from an integrator to an inverter. With Kirchoff's Law, the variation of the output potential of the summer inverter may be described as:

$$i_R + i_{R_{fb}} = 0 \qquad \Sigma i = 0$$

$$\frac{e_i}{R} + \frac{e_o}{R_{fb}} \cong 0 \qquad \begin{array}{l} R = \text{input resistor} \\ R_{fb} = \text{feedback resistor} \end{array}$$

therefore: $$e_o = -\frac{R_{fb}}{R} \cdot e_i$$

Note that the output potential of an inverter is of the opposite sign to that of the input. The characteristics of the control grid are such as to reverse the polarity of the output signal also. Solution to Kirchoff's equation for a number of inputs leads to an equation describing the output potential of the inverter as the sum of the input potentials:

$$e_o = -R_{fb}\left(\frac{e_1}{R_1} + \frac{e_2}{R_2} \;\ldots\ldots\; \frac{e_n}{R_n}\right)$$

Adjusting the values of the input resistors, R_n, effectively multiplies the input by a number determined by the ratio R_n/R feedback, and is generally referred to operational amplifier gain.

In comparison to the electric network[26], the electronic analog computer generates solutions which correspond much more closely to those which would be obtained from mathematical integration. Equations 42, 43, and 44 compare the transfer function, or ratio of output to input, for mathematical integration, electric network integrating RC circuit, and the electronic analog computer integrator, respectively.

"True" Integration $$\frac{e_o}{e_i} = \frac{1}{RCP} \qquad (42)$$

Electric Network Integrating Circuit $$\frac{e_o}{e_i} = \frac{1}{g\ RCP + \sim 1/g} \qquad (43)$$

Summer-Integrator of Electronic Analog Computer $$\frac{e_o}{e_i} = \frac{G}{(1-G)}\ \frac{1}{RCP + 1} \qquad (44)$$

$$\lim_{G \to \infty} \frac{e_o}{e_i} = -\frac{1}{RCP}$$

e_o = output voltage

e_i = input voltage

R = input resistor

R_L = load resistor

C = capacitor

G = operational amplifier forward gain

$g = \frac{R_L}{R + R_L}$ = resistance factor

$\frac{1}{P} = \int dt$ = integral operator

The electric RC network, equation 43, approximates "true" integration only with large values of resistance and capacitance, with correspondingly

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[26] G. A. Korn and T. M. Korn, Electronic Analog Computers, McGraw-Hill Book Co., Inc. 116-157, (1952).

longer solution times, to reduce the effects of leakage and loading, R_L. The output potential, e_o, built up on the capacitor of the RC integrating network will tend to oppose the input charging potential, e_i, in addition to leakage and loading of components and may thus make accurate integration impossible.

A voltage divider, or potentiometer, connects circuits such as those above. These are resistance slidewires with a potential difference across their terminals, with provision to select a fraction, k, of this potential difference on a sliding contact, generally referred to as the "arm". (This arm corresponds to the connecting wire of potential, e_o, in the potentiometer of Fig. 3A, Chapter IV.) When the potentiometer is connected between operational amplifiers, the input resistors, R, to the amplifiers are in parallel with the resistance of the connecting wire. This coupling tends to reduce the effective fraction of the potential difference between the arm and the ground potential, i.e., it changes the value of potentiometer setting, k, from the desired setting. Correcting this condition normally involves calibration with some type of null-voltmeter while the circuit components are connected as in the working problem.

The overall accuracy of the analog computer solutions to a given series of equations is determined by the manner of connection of the computer components, the skill of computer operator, and the nature of the problem. The investigator should not require the accuracy of solution which only exact solution or digital computer approximations can offer. Such analog computers are particularly useful at the present stage because they not only permit the exploration of alternate values for certain imperfectly known parameters but they also may help determine whether uncertainties in some inputs or decay parameters lead to large or small effects on the rest of the system.

APPENDIX B

COMMENT ON ANALYTICAL SOLUTIONS TO ECOLOGICAL MODEL EQUATIONS

Solution of the differential equations which serve as mathematical models for the proposed ecosystem models were derived from a general integral solution form discussed in any text on differential equations. Consider the general equation for the net rate of change of the quantity of organic carbon in the vegetation compartment with an input rate of photosynthesis, P, which is a function of time only.

$$\frac{dV}{dt} = P(t) - k_1V$$

Where, k =constant, real, non-negative
P(t)=any arbitrary function of time
C =any arbitrary constant

$$V = Ce^{-k_1t} + e^{-k_1t}\int e^{k_1t}\, P(t)\, dt \qquad (45)$$

The function, P, may be considered for the purposes of this study, to be represented by the special input rates of photosynthesis $P_1, \ldots P_6$ summarized on page 68. The differential equation for the case of constant input P_1 has a solution (eq. 26) which follows directly from the general form of eq. 45 above, under the boundary conditions that $V = V_o$ when $t = 0$. Using this solution for V, then $\phi_{14}k_1V$ can be similarly inserted in a differential equation for D:

$$\frac{dD}{dt} = \phi_{14}k_1V - k_4D \qquad (4)$$

which has the general solution

$$D = Ce^{-k_4t} + e^{-k_4t}\int e^{k_4t}\, \phi_{14}k_1V(t)dt. \qquad (46)$$

Equation 27 follows from 39 after introduction of the boundary conditions $D = D_o$ when $t = 0$. This general form equation might be extended by the process of iteration to include solutions to the differential equations describing each compartment of the ecological models included in this study.

One can similarly obtain general solutions (eq. 32, 33 and 34) for the vegetation compartment from eq. 45, with P(t) defined as $P_4 \ldots P_6$, or from other standard methods such as the use of differential operators. Integration of the several terms resulting from the differential equation with input P_6 results in:

$$V = \frac{400}{k_1}(1-e^{-k_1 t})+V_o e^{-k_1 t}+\frac{400}{k_1-k}(e^{-k_1 t}-e^{-kt}) \tag{47}$$

$$+\frac{400}{(\omega^2+k_1^2)}\left[k_1 e^{-k_1 t}-\omega \sin \omega t-k_1 \cos \omega t\right]$$

$$+\frac{400}{\omega^2-(k_1-k)^2}\left[(k-k_1)e^{-k_1 t}+e^{-kt}(\omega \sin \omega t+(k_1-k) \cos \omega t\right]$$

Using the trigonometric relation

$$k_1 \cos \omega t + \omega \sin \omega t = \sqrt{w^2 + k_1^2} \cos (\omega t - \delta), \text{ where } \delta = \tan^{-1}\frac{\omega}{k_1},$$

this long formula reduces to the form of eq. 34 (or 33, with reversal of appropriate signs). A lag in phase due to k_1 is represented by δ. Similarly a lag in phase α in equations 33 and 34 is influenced by the combination of k_1 and k:

$$\alpha = \tan^{-1}\frac{\omega}{k_1-k}$$

While equations 33, 34, and 47 cover the general case in which $k_1 \neq k$, a special solution is needed in the special case when $k_1 = k$. In the term

$$\frac{400}{k_1-k}\left(e^{-k_1t}-e^{-kt}\right)$$

the limit as k_1 approaches k is 0/0. From L'Hospital's rule, the limit of the ratio of the functions is the limit of the ratio of the derivatives of the functions, or $-400t\ e^{-k_1t}$. This simplification and the equality of k and k_1 reduce equation 47 to the following form:

$$V = \frac{400}{k_1}\left(1-e^{-kt}\right) + V_o e^{-kt} - 400t\ e^{-k_1t} \qquad (48)$$

$$+ \frac{400}{\omega^2+k_1{}^2}\ k_1 e^{-k_1t} - \frac{400}{\sqrt{\omega^2+k_1{}^2}}\ \cos\ (\omega t - \delta) + \frac{400}{\omega}\ e^{-kt}\ \sin\ \omega t.$$

Turning to the more flexible cases of input P represented by equations 14 and 17, the solutions and boundary conditions become more awkward. The analog computer becomes increasingly helpful because it provides direct solutions from a given input function and any boundary conditions.

Unwieldy solutions to the equations for early compartments become compounded in tedious analytical solutions for later compartments. The analog computer essentially substitutes a few electronic operations for a long sequence of numerical operations.

The solution for the general equation to a system of multi-compartments when connected chain-wise, as well as those for cyclic systems, has been thoroughly discussed by Sheppard and Householder[27] and Robertson[28]. In general, the complexity of these solutions makes indispensable the use of modes of representation such as matrices and determinants for systems containing more than three compartments.

Solutions to linear differential equations with variable coefficients may be obtained from a solution in series or a numerical solution. In each case, the desired solution is an approximation dependent upon the number of terms considered. Except for those equations which can be reduced to those with constant coefficients by a change of variable, there are no general methods for solving linear differential equations with variable coefficients with an order higher than one. No general rules can be given for solving non-linear differential equations and this task must be left to the skill and ingenuity of the investigator.

For these latter types of equations, an excellent alternate method of solution may be offered by the analog computer. The computer solutions will also be approximations to the "true" solutions, although their reliability with respect to the mathematical approximations must also be determined for each separate case.

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[27] Op cit.

[28] Op cit.

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