0 0 0 0 4 2 0 2 9 1 6

RECEIVED
LAWRENCE
BERKELEY LABORATORY

AUG 20 1975

LIBRARY AND
DOCUMENTS SECTION

LBL-3264
UC-11
TID-4500-R62

STABILITY INDICATORS FOR NUTRIENT CYCLES IN ECOSYSTEMS

Michael Dudzik, John Harte, Donald Levy, and James Sandusky

June 1975

Prepared for the U. S. Energy Research and
Development Administration under Contract W-7405-ENG-48

For Reference

Not to be taken from this room

LBL-3264
c.1

DISCLAIMER

This document was prepared as an account of work sponsored by the United States Government. While this document is believed to contain correct information, neither the United States Government nor any agency thereof, nor the Regents of the University of California, nor any of their employees, makes any warranty, express or implied, or assumes any legal responsibility for the accuracy, completeness, or usefulness of any information, apparatus, product, or process disclosed, or represents that its use would not infringe privately owned rights. Reference herein to any specific commercial product, process, or service by its trade name, trademark, manufacturer, or otherwise, does not necessarily constitute or imply its endorsement, recommendation, or favoring by the United States Government or any agency thereof, or the Regents of the University of California. The views and opinions of authors expressed herein do not necessarily state or reflect those of the United States Government or any agency thereof or the Regents of the University of California.

0 0 0 0 4 2 0 2 9 1 7

LBL-3264

STABILITY INDICATORS FOR NUTRIENT CYCLES IN ECOSYSTEMS

BY

Michael Dudzik
John Harte
Donald Levy
James Sandusky

Lawrence Berkeley Laboratory
Energy and Environment Division
University of California
Berkeley, California 94720

June 1975

0 0 0 0 4 2 0 2 9 1 8

ABSTRACT

A variety of models for nutrient cycling in ecosystems are examined, both numerically and analytically, to determine ecosystem responses to perturbations. The structure of the decomposer-detritus dynamics is found to play a governing role in the stability of the ecosystem. Stability indicators are shown to exist and may potentially be evaluated in real systems from measurements of decomposer population dynamics parameters. The especial sensitivity of ecosystems to perturbations in the amount of organic litter is demonstrated, and highly subsidized ecosystems are shown to possess greater stability than low-subsidy (closed-loop) systems. These conclusions, it is argued, are likely to be generally true in any model which captures certain minimal aspects of the decomposer-detritus dynamics which are necessary for a realistic description of nutrient flow.

0 0 0 0 4 2 0 2 9 1 9

I. INTRODUCTION

This paper is concerned with the search for useful stability indicators for ecosystems. It explores two related problems; the first is that of determining what kinds of perturbations can most dramatically disrupt ecosystems, and the second is that of determining what combinations of ecosystem parameters are reliable indicators capable of predicting whether an ecosystem will collapse or significantly change when perturbed.

Because ecosystems are extremely complex, a nearly exact characterization of even a simple ecosystem would involve the detailed knowledge of a vast quantity of physical, chemical, and biological information. Instead of trying to model ecosystems in great detail, we have used simplified models which we feel are realistic enough to allow us to draw some important conclusions about real ecosystems. Out of the multitude of quantities which describe an ecosystem we have isolated a small number of potentially measurable factors which are important for the understanding of the system's stability. One of these factors is a stability indicator and is related to the carrying capacity for <u>decomposers</u> in the ecosystem. Another critical factor is the size of the initial disturbance to the <u>organic litter</u> pool in the ecosystem. This pool appears to represent a sensitive "weak link" in many ecosystems, in the sense that a given per cent change in the organic litter pool is likely to induce a more significant alteration in the future time development of the system than would a similar per cent change

in other compartments in the system such as the inorganic nutrient pool, the plants, the herbivores, or the carnivores. A third property of ecosystems which we show to be critical to stability is the degree to which the nutrients (nitrogen, phosphorous, etc.) in the system flow in closed loops.

These and other results described below were first suggested from studies made using the Liapunov technique for stability analysis.[1] The great advantage of this technique is that it can be used to assess finite, and therefore realistic, perturbations. This is in contrast to the most common tool used to analyze stability properties, the community matrix, which can only be used to assess the stability properties of an ecosystem perturbed by environmentally unrealistic infinitesimal perturbations.[2] Another advantage of the Liapunov method is that it allows analysis of the stability properties of a complicated set of coupled nonlinear differential equations without the necessity of explicitly solving the equations.

A detailed description of our use of the Liapunov technique has appeared elsewhere.[1] The primary focus of this paper is on numerical simulation of model ecosystems. We emphasize that the analytic Liapunov technique and the numerical computer techniques are complementary. Without the analytic work, use of computer simulation would be unlikely to lead to identification of stability indicators because of the great difficulty of probing the multitude of possibly significant combinations of parameters. On the other hand hand, the computer simulations are needed to probe the finite regions

of stability, because our techniques for using the Liapunov method do not guarantee that we have found the largest finite domain of stability (See Appendix B). Furthermore, the computer simulations allow us to determine the explicit time-evolution of a perturbed ecosystem.

One realistic and important feature of the models discussed here is that they include cyclic feedback loops. Much of the past empirical analysis of environmental disturbances of ecosystems has focused upon the effects of pollution or of other habitat changes upon the higher organisms (e.g., birds, fish, mammals, trees,). In parallel with this, theoretical studies[2] have emphasized the predator-prey dynamics of ecosystems to the near exclusion of the feedback dynamics of the decomposer-detritus link. These studies of the upper stages of the trophic web have attempted to explore the role of diversity in ecosystems, but the contradictory nature of the evidence for any clear positive or negative correlation between diversity and stability has diminished the practical utility of such efforts. Our work suggests that the inclusion of the decomposing-bacteria and fungi, ignored in most previous studies[3], is crucial to understanding stability properties of ecosystems. Knowledge of the population dynamics of the decomposers in the unperturbed system, knowledge of the manner in which the disturbance to the system affects organic litter, and knowledge of the fraction of nutrient flow which is processed by decomposers in the system appear to be of great importance. We suspect that by the time "interesting", organisms are

disturbed, it is often too late or too difficult, to prevent significant alteration or collapse of the system.

This paper is organized as follows: in Section 2 we discuss the salient features of nutrient flow in ecosystems and describe the general properties of model equations used for their description. Section 3 contains a detailed description of several models for nutrient flow in two systems - a grasslands biome and a shallow mesotrophic freshwater lake. In Section 4 we discuss the results of computer simulations of these models. Evidence for the importance of certain stability indicators is presented. There are two appendices. Appendix A contains the equations we use to describe our model ecosystems. Appendix B can be skipped by readers not interested in mathematical methods; it is a review of the Liapunov stability method, an explanation of its applicability to ecological models, and a summary of how the results obtained in Section 4 were first suggested by analytic methods.

II. NUTRIENT FLOW IN ECOSYSTEMS

The flow of basic elements through the pathways within and linking the biosphere, the geosphere, and the atmosphere is crucial to the functioning of ecosystems. We do not attempt here to add any new insight into the nature of the mechanisms involved in this flow. Rather, our purpose is to show that the stability of ecosystems is intimately linked to certain qualitative properties of the flow mechanism and of the population dynamics of the microbial organisms responsible for maintaining nutrient levels and cyclic nutrient flow patterns. In this section we set forth what we consider to be the salient aspects of nutrient flow in ecosystems and describe simple minimal criteria for their adequate mathematical description.

There is a major difference between the flow of nutrients such as carbon, nitrogen, or phosphorus, and the flow of energy in an ecosystem. Whereas the energy supply to the primary producers is almost entirely obtained from the sun and not cycled, many of the basic nutrients that nourish an ecosystem flow in a cycle, at least to the extent that the forces of wind, erosion, human intervention, etc. permit. The biological cycling of these nutrients is, in large part, brought about by the activity of a special group of organisms, the decomposers. Since these decomposers are, themselves, a living component of the ecosystem, internal feedback dynamics must be considered.

The simplest pattern of single nutrient flow in an ecosystem is shown in Fig. 1. Organic materials are converted into usable inorganic nutrient by the decomposers.[4] This usable nutrient is then assimilated by the primary producers for their growth.[5] Nutrient is then returned to the organic litter pool in the form of dead primary producers. In more complex systems, some nutrient (see Fig. 2) flow continues to herbivores, carnivores, etc. Then via the excrement and carcasses of all these organisms, the nutrient is returned to the organic litter pool, completing the cycle. The cycling is never closed in any circumscribed ecosystem because nutrient can leave or enter the organic and inorganic reservoirs by a variety of mechanisms such as erosion or the application of fertilizer. It can also enter or leave the system via the mobility of living organisms. We speak of systems with external inputs and outputs as "subsidized" systems. If the rate of nutrient input originating from external sources is large (small) compared to the net primary productivity rate, then the system is a high (low) - subsidy system.

A sensible mathematical description of the complex processes involved in nutrient flow must involve a tradeoff between mathematical tractability and ecological realism. To keep the mathematics manageable, many exquisite biological nuances, some of which may be crucial to the existence of a particular species in the ecosystem must be ignored. The general structure of such a mathematical

model must be in conformity with the laws of physics and chemistry, and must include a reasonable description of the mechanisms responsible for nutrient flow.

To begin, we must select the variables of the model. If we are interested in a particular cycle such as the nitrogen cycle, then it is most convenient to choose as variables the nitrogen content of the various compartments of the system. A minimal choice of compartments is that shown in Fig. 1. It is possible, of course, to add to or subdivide the compartments in the figure and for certain applications this is necessary (see Fig.2). For example, in studying the nitrogen cycle in a lake, a detailed model would include the fact that grazing zooplankton exhibit different preferences for various kinds of algae. In some cases, a selective distaste for blue-green algae can hasten the onset of the visible effects of eutrophication. To include this effect, the compartments for primary producers and for zooplankton would need to be subdivided. A further subdivision of the primary producers compartment could be made between nitrogen fixers and non-fixers, and between phytoplankton which can utilize organic litter directly and those which can utilize only inorganic forms of nutrient.

In most terristrial systems, the excrement and carcasses of the various organisms must be chewed and broken up by worms, insects and other animals in order to process the organic litter for the

decomposers. In order to include the important functional role in nutrient cycling which these organisms play, we would need to introduce a new compartment for them and an additional compartment for "processed" organic litter. In addition to the trophic complexities described above, other effects sometimes need to be considered when attempting to model nutrient flow in detail. Some of these are time-lags, age distribution, geographical mobility, spatial heterogeneity, temperature dependence, and daily or yearly cycles. In some cases these effects can be included by judicious use of compartmental structure. For example, age distribution or generation effects may be crudely incorporated into models by placing, say, larvae and adults into separate compartments. Certain spatial mobility effects can be included by use of additional compartments. For example, in a deep lake a given compartment of organisms could be subdivided into surface and benthic compartments. In certain other situations, spatial heterogeneity can be approximated by making use of a horizontal grid of distinct compartments.

Because of the complexity of interrelationships among various organisms and nutrients in an ecosystem, a detailed description of such a system sometimes requires that a model incorporate the flow of several nutrients simultaneously. If it were true that a single limiting factor really determined an ecosystem's behavior, then a model describing flow of a single nutrient could

0 0 0 0 4 2 0 2 9 2 3

yield accurate detailed information. But, in fact, empirical research[6] on lakes has given strong support for the necessity of a multi-variabled approach to nutrient flow. These studies show, for instance, that fertilization of a lake with nitrogen and phosphorous leads to increased algal growth, but that this growth is also dependent upon the assimilation of dissolved inorganic carbon into the lake from the atmosphere. Thus, a realistic model may need to include simultaneously separate variables of the important nutrients in an ecosystem. In living organisms, the values these variables take on are constrained to approximately fixed ratios determined by biochemistry, but the magnitudes of the various nutrients in the inorganic nutrient pool compartments must be allowed to vary independently.

Given a set of compartments and variables, formulation of a mathematical model still requires knowledge of functional relationships. We will adopt here the choice of coupled, non-lienar, first order differential equations (i.e., involving first time derivatives only), which relate the time rate of change of the system's variables to the values of the variables and to other parameters in the system. These equations then have the general form:

$$\frac{dX_i}{dt} = F_i\ (X_1, \text{---}\ X_N;\ w_1, \text{---}\ , w_m) \qquad (1)$$

$$(i = 1, \text{---}\ , N)$$

where the X_i are the system's variables, the w_i are parameters such as rate constants, carrying capacities, Michaelis-Menten coefficients, etc., and the F_i are functions to be specified. More complicated systems of integro-differential equations can be constructed, but such models usually involve the introduction of quantities which are extraordinarily difficult to measure and thus have very little practical utility.

The variables in our nutrient models can be conveniently grouped into three categories; those that describe living organisms, those that describe the organic litter, and those that describe the inorganic nutrient. There are two important differences between the form of the rate equations which describe living organisms and the form of the rate equations which describe the organic litter and inorganic nutrient pools.

First, at low population levels the growth term in the rate equations for living organisms is proportional to the value of the variable which describes the living organism (and also, of course, to its food supply). On the other hand the growth (gain) rates in the rate equations which describe the organic litter and inorganic nutrient pools are not proportional to, or even directly dependent on, the variable which describes them. The gain rate of inorganic nutrient is dependent, instead, upon the amount of decomposers and the amount of organic litter, while the gain rate of organic nutrient is dependent upon the death rate of organisms

0 0 0 0 4 2 0 2 9 2 4

and the rate of excretion of organisms throughout the trophic web. Secondly, for high values of the variable which describes a living organism, its loss or death rate is non-linear (and very roughly quadratic) in that variable due to a carrying capacity or resource saturation effect.[7] On the other hand, for large values of the variables which describe the organic litter and inorganic nutrient pool, the loss rate for each pool is at most linear in their respective variables.

It is this distinction in the general form of the rate equations for the three categories of variables, the relatively large size of the organic litter pool, and the special role that decomposers play in effecting the conversion of organic to inorganic litter, which we believe determine the primary stability properties of nutrient cycles. In the following section several explicit examples of model equations are presented. Although they do not include all of the specialized phenomena shown in Fig. 2 and discussed above they do incorporate general properties of nutrient flow, and they respect the above-noted distinctions among the three categories of variables.

III. MODEL GRASSLAND AND AQUATIC ECOSYSTEMS

This section describes nutrient flow models for two ecosystems. In order to emphasize the quite general nature of our stability results, we have purposely chosen two quite different systems: a grasslands biome and a shallow mesotrophic freshwater lake. The two models differ considerably in complexity of structure and, of course, in the values of their rate parameters. Where possible, reliable field data is used to determine rate parameters in the models. The grasslands model for nitrogen flow is unrealistically simple, yet it contains the basic minimal features discussed in the previous section. The lake models, one involving nitrogen flow alone, and one combining nitrogen and oxygen flow, include more structure. Although the models considered here are quite simple, they have in common the basic feedback structure described in the previous section. We re-emphasize that the purpose of this modeling effort is not to simulate or predict the detailed behavior of ecosystems but to learn about the stability implications of gross structural properties of nutrient flow.

In Fig. 1, the nitrogen cycle in a simple grasslands ecosystem (e.g. shortgrass prairie) is depicted. The four compartments, correspond to plants such as western wheatgrass, inorganic nutrient such as NO_3^-, decomposers (bacteria and fungi), and organic litter. Here, we envision the nitrogen cycle in the following way. As the decomposers feed and grow, they transform the nitrogen content of the organic litter into inorganic nutrient (NO_3^- primarily) for the plants,

0 0 0 0 4 2 0 2 9 2 5

while their excrement and carcasses add to the organic litter pool. The plants absorb the inorganic nutrient for their growth; when they die, their nitrogen content adds to the organic litter pool. In addition, there can be external inputs to and outputs from the inorganic litter pools (e.g. fertilizer, washout). Our system is thus an open one with feedback and cycling.

Our nitrogen cycle equations for the grasslands biome are:

$$\frac{dX_P}{dt} = \underbrace{-\alpha_P X_P - \gamma_P X_P^2}_{1} + \underbrace{\beta_{PI} X_P X_I}_{2} \qquad \text{(Plants)}$$

$$\frac{dX_I}{dt} = \underbrace{\Omega_I}_{3} - \underbrace{\alpha_I X_I}_{4} - \underbrace{\beta_{IP} X_I X_P}_{5} + \underbrace{\sigma_{DL} X_D X_L}_{6} \qquad \text{(Inorganic nutrient)}$$

$$\frac{dX_D}{dt} = \underbrace{-\alpha_D X_D - \gamma_D X_D^2}_{7} + \underbrace{\beta_{DL} X_D X_L}_{8} \qquad \text{(Decomposers)} \qquad (2)$$

$$\frac{dX_L}{dt} = \underbrace{\Omega_L}_{9} - \underbrace{\alpha_L X_L}_{10} - \underbrace{\beta_{LD} X_L X_D}_{11} + \Gamma(\underbrace{\alpha_D X_D + \gamma_D X_D^2 + \alpha_P X_P + \gamma_P X_P^2}_{12}) \qquad \text{(Organic litter)}$$

where the X_i represent the nitrogen content of the compartments.[8]

The numbered terms are:

(1) Plant death rate including resource scarcity term ($\gamma_P X_P^2$).

(2) Plant growth due to uptake of inorganic nutrient.

(3) Addition of inorganic nutrient (e.g. fertilizer).

(4) Washout of inorganic nutrient.

(5) Decrease of inorganic nutrient due to uptake by plants.

(6) Production of inorganic nutrient by decomposer action on litter.

(7) Decomposer death rate including resource scarcity term ($\gamma_D X_D^2$).

(8) Decomposer growth due to feeding on litter.

(9) Addition to organic litter (e.g. sewage dumping).

(10) Washout of litter.

(11) Litter decrease due to decomposer action.

(12) Litter increase due to carcasses of organisms, (Γ is an efficiency factor).

In these equations the relationship $\beta_{LD} \geq \beta_{DL} + \sigma_{DL}$ must hold true.

The interaction terms (β_{ij}, σ_{DL}) in equations 2 have the general Michaelis-Menten dependence on the X_i, or

$$\beta_{ij} = \bar{\beta}_{ij} \;/\; (1 + c^{ij}X_i + d^{ij}X_j) \qquad (3)$$

where $\bar{\beta}_{ij}$ is assumed to be constant. In our numerical work we have examined cases in which the c^{ij} and the d^{ij} are both equal to and unequal to zero. All other parameters in our equations are constants.

Experimental work [9,10] has verified that the Michaelis-Menten form is a reasonable one to describe the zooplankton-phytoplankton interaction. For the grassland biome and the aquatic system, the precise

0 0 0 0 4 2 0 2 9 2 6

forms of the interaction terms have not been determined. Our results, however, do not depend crucially upon the specific form of these terms. For example, it will be important in what follows that there be a contribution to the loss rate of decomposers which arises from crowding or resource scarcity. We have written this term as $-\gamma_D X_D^2$, but all that is really important to our conclusions is that this term grows faster than linearly in X_D as X_D grows large.

Typical perturbations to such a grassland ecosystem, which we will simulate in our analysis, are a decrease or increase of its organic litter, depletion or increase of its inorganic nutrients (by runoff or fertilization), and addition of toxic chemicals which alter plant and decomposer growth rates, death rates, and levels.

The aquatic ecosystem we consider is a simple version of a shallow freshwater mesotrophic lake. In such a lake, several species of phytoplankton can exist which differ from one another in their relationship to the nitrogen cycle. Many blue-green algae are nitrogen fixers under certain conditions;[11] in addition, some species of blue green algae may be able to utilize the nitrogen content of organic litter directly.[12] Most phytoplankton need to absorb the nitrogen in the form of inorganic nutrient (e.g. NO_3^-).[13] In our model, we have taken account of these distinctions by dividing the phytoplankton into three compartments: 1) phytoplankton which absorb nitrogen from organic litter directly (phyto-ℓ), 2) phytoplankton which are nitrogen fixers (phyto-f), and 3) phytoplankton which need to absorb nitrogen in the form of inorganic nutrients (phyto-i).

In Fig. 3, our seven compartment model for the nitrogen cycle in a shallow mesotrophic lake is schematically given. The compartments are zooplankton (X_Z), phyto-i (X_{P_i}), phyto-f (X_{P_f}), phyto-ℓ (X_{P_ℓ}), inorganic nutrient pool (X_I), decomposers (X_D) and organic litter pool (X_L). We can envision this nitrogen cycle in the following way. As the decomposers grow, they transform the nitrogen content of the organic litter pool into inorganic nutrient, while their excrement and corpses add to the organic litter. The phyto-i absorb the inorganic nutrient as they grow, while their corpses add to the organic litter pool. The phyto-ℓ uptake nutrient from organic litter directly as they grow, while their corpses add to the organic litter pool. The phyto-f fix nitrogen from the effectively unlimited pool of the atmosphere and their corpses also add to the organic litter pool. The zooplankton graze on all three types of phytoplankton and their excrement and corpses adds to the organic litter pool. External inputs to and/or outputs from the inorganic nutrient and organic litter pools can also occur.

The equations which we take to describe this seven level aquatic system are given in Appendix A, Eqs. A-1. Their structure is similar to that of the four level grassland biome and the same comments concerning the Michaelis-Menten form of the interactions apply. Typical perturbations of such an aquatic system can be thermal pollution altering rate constants, chemical pollution toxic to living organisms, and excess sewage inflow.

Eutrophication, a fundamental problem for freshwater ecosystems

0 0 0 0 4 2 0 2 9 2 7

is often accompanied by an algal bloom. In order to understand such a bloom, the phosphorous, oxygen and trace element cycles temperature dependence of rate constants, and energy flow through the system, must be considered together with the nitrogen cycle. To incorporate some of this complexity, we made several simulations with a seven compartment aquatic model which simultaneously describes the flow of nitrogen and dissolved oxygen. The defining equations are listed in Appendix A (Eqs. A-2). The additional compartment, Y, represents dissolved oxygen. There are two kinds of processes which contribute to its rate of change. First there are physical mechanisms such as the transport of oxygen either by stream flow or by movement across the lake-atmosphere interface. Second, there are biological mechanisms including the photosynthetic production of oxygen by phytoplankton and the uptake of oxygen by zooplankton and decomposers. The dependence of zooplankton and decomposer metabolic activity upon oxygen is also crudely taken into account. (See Fig. 4)

Obtaining experimental (field) values for many of the nitrogen content quantities (X_i) and parameters (β_{ij}, σ_{DL}, etc.) in our equations is difficult and many of them are not well determined. For example, reliable estimates of the decomposer dry biomass (or nitrogen content) do not exist for aquatic ecosystems. Grazing rates for some, but not all, important species of zooplankton have been measured.[14,15] Even the general trophic structure of many aquatic ecosystems is in doubt. There is very little qualitative or quantitative information on the ability of certain phytoplankton to directly absorb organic nutrient.[13] On the other hand chlorophyll concentrations (which are proportional to

phytoplankton biomass) and inorganic nutrient concentrations are somewhat better determined.[16]

In general, the situation is slightly better for grasslands ecosystems. Here crude order of magnitude determinations of decomposer dry biomass or nitrogen content have been made.[17,18] In addition, steady state (unperturbed) amounts of organic litter and inorganic nutrient are crudely known for some grassland biomes, while the amount and growth rate of plant material (or nitrogen content therein) are quite well known.[17]

In both grasslands and aquatic systems, in-situ decomposer metabolism rates are very poorly known. These rates are difficult to measure in-situ since, to a large degree, their measurement depends on a knowledge of another poorly determined quantity - the biomass of decomposers present.

In tables 1, 2, and 3, we list the values of the various parameters and the equilibrium values of nitrogen content of the various compartments ($\bar{X}_i$), which were used in our computer work. In many cases, the entries in the tables were obtained by arbitrarily choosing a numerical value falling within a broad range of experimental values.

The number of compartments in these models is truncated in order to keep initial analytic and numerical work manageable. Many trophic links, such as the grazing of zooplankton on bacteria and the grazing of carnivores upon zooplankton and each other are ignored. In addition, the models assume spatial homogeneity, ignore age distribution effects, and take the basic rate parameters to be time independent. Further studies which treat several important nutrients simultaneously

0 0 0 0 4 2 0 2 9 2 8

and which are more generous with regard to the number of compartments are in progress; what our initial studies indicate is that the results obtained below are relatively independent of such complexities provided the general properties described here are respected.

Another important feature of natural systems which we ignore in our models is diurnal and annual variation. We are not concerned here with the effects of such driving forces as temperature or rainfall or insolation variation. Although model equations with Michaelis-Menten factors are known to possess limit cycle solutions for certain ranges of the parameters,[10] we take the unperturbed (equilibrium) state of our model equations to be the static solution ($X_i = \bar{X}_i$) obtained by setting $dX_i/dt = 0$. In all our models, the static solution has at least some domain of stability (the eigenvalues of the community matrix have negative real parts). In a future publication, we will describe the results of stability studies for systems with time-varying unperturbed states.

Although the systems we study here are locally stable, the domain of stability is usually finite. Thus while an infinitesimal perturbation only slightly and temporarily alters the system, a large enough distrubance can cause significant damage and even total collapse of the system. It is these finite perturbations which we study by simulation in the following section.

Our concept of stability is utilitarian. We perturb the system and determine whether the response is gentle or violent - a

distinction which will be clear in the figures illustrating numerical simulation of our systems. Traditional definitions of stability distinguish between a perturbed state which returns to equilibrium and one which does not. This is of relatively little concern to us, since a system which is sufficiently, even though temporarily dislodged from equilibrium, would probably be perceived as dangerously vulnerable to change. Furthermore, in such a case, it is unlikely that the original dynamical equations could be trusted far from equilibrium, so even if they predicted in a strict mathematical sense that the system would eventually return to its original state, it would often be prudent to consider such a system as if it were unstable. The term resilience is sometimes used to denote the decay constant characterizing how rapidly a perturbed state returns to equilibrium. Our concept of stability is concerned with the magnitude as well as the duration of the deviation of the perturbed state from equilibrium, and is therefore not the same as the concept of resilience. A quantitative measure of our notion of instability can be obtained by taking the ratio of the integral over time of the sum of the squares of the deviations between the perturbed and equilibrium state variables to the integral over time of the sum of the squares of the equilibrium state variables.

IV. NUMERICAL RESULTS FOR PERTURBED MODEL SYSTEMS

Here we describe the results of our computer simulation work. The non-linear differential equations which describe our models for the grassland and aquatic ecosystems were solved using a computer. A variety of perturbations were introduced and the subsequent evolution with time of the perturbed system was studied. We explored a range of rate parameters in our grassland and aquatic systems and generated over 500 simulations.

We have identified from our theoretical work a stability indicator. It is a dimensionless ratio formed from the terms in the rate equation for the decomposers (see Eqs. 2,A-1,A-2). This ratio is labeled K_D and is given by

$$K_D = \frac{\alpha_D}{\gamma_D \bar{X}_D} \quad . \tag{4}$$

K_D is the ratio of the linear death rate of the decomposers to the quadratic resource scarcity loss rate. Note that it is defined at $X_D = \bar{X}_D$, the unperturbed value of the decomposer level. It is intuitively reasonable that large values of K_D might result in systems which are less stable than those with small values, because the coefficient γ_D is a damping term preventing rapid change in the population. But the same comment could be made concerning $K_P = \alpha_P/\gamma_P\bar{X}_P$ or $K_Z = \alpha_Z/\gamma_Z\bar{X}_Z$ and yet we shall see that these ratios are less critical to stability. We shall speak of systems for which $K_D >> 1$ as having decomposers which are "lifespan limited" (the linear death rate exceeds

the quadratic carrying capacity, or resource saturation, death rate) while systems with $K_D << 1$ have decomposers which we shall call "resource limited" (the resource saturation loss rate exceeds the linear death rate).

The ecosystem stability properties, which are derived from our analytic work and are further explored in the following computer simulations, can be summarized as:

1) The more an ecosystem's decomposers are lifespan limited ($K_D >> 1$), the more unstable the ecosystem is. (see Figs. 5, 8)

2) Perturbations in the organic litter pool can lead to more severe disturbances of the ecosystem, than the same-sized perturbations in the other compartments. (See Fig. 6)

3) Low subsidy systems are more unstable than high subsidy ones. (See Fig. 7)

The computer simulation runs involved different perturbations of the X_i's as well as alterations of the rate parameters. For each type of perturbation or alteration, different values of K_D and K_P between 0.1 and 10.0, were considered. First consider the shortgrass prairie or grassland ecosystem. For our computer work, we considered two grassland systems. One is a low subsidy system with 2 lbs. (N)/acre. year of inorganic nutrient being added to system; while the other is moderately subsidized system with 10 lbs. (N)/acre. year of inorganic nutrient being added.

In the low subsidy system, the unperturbed value for the nitrogen content of the standing crop was taken to be 25 lbs. (N) acre.

year. Here the decomposers are taken (at equilibrium) to produce 33 lbs.(N)/acre.year of inorganic nutrients. The unperturbed or equilibrium value for the nitrogen content of the decomposers is taken to be 1.5 lbs.(N)/acre (which implies that they can double about every 20 days). This corresponds to about 2×10^{18} bacteria per acre. The unperturbed value of the nitrogen content of organic litter is taken to be 1000 lbs.(N)/acre and of inorganic nutrient 25 lbs.(N)/acre.

The second grassland system we consider is a more highly subsidized one, with 10 lbs./acre.year of inorganic nutrient in the form of nitrogen being added to the system and organic litter being washed out. The decomposers are taken to be slightly less efficient than in the first grassland system and produce 25 lbs./acre. year of inorganic nutrient. Otherwise, almost all the parameters and the values of the nitrogen content of the four compartments are the same as in the first (low subsidy) grassland system. In table 1 the parameters and equilibrium values for the nitrogen content of each compartment in the low and high subsidy system are given.

For both grassland systems, the time, but not the magnitude, of initial response, and the later time evolution of the variables following the initial disturbance were similar. Given an initial perturbation, the systems respond fairly dramatically over a 2-4 year period and

then evolve very slowly, if at all, over the next 16 years (see Figs. 4, 5, 6). Of course, there were some exceptions to this general behavior. For example, for perturbations which involved only the increase or decrease of the decomposers and nothing else, both grassland systems were quite resilient, returning to their original equilibrium states within a few years. This occurs because as long as there is sufficient organic litter for the bacteria to feed upon, their rapid doubling rate provides a mechanism for rapid recovery of the system.

We now list several specific results obtained from computer calculations for our grasslands ecosystems.

1) Systems whose decomposers are lifespan limited (K_D large) undergo far greater change when perturbed than do systems whose decomposers are resource limited (K_D small). Stability of the system is far less sensitive to the value of K_P (see Fig. 5).

2) Small (10%) decreases in organic litter can lead to major alterations in the system (see Fig. 6), if K_D is large and the system has a nearly closed (low external subsidy) nitrogen cycle. In this case, plant cover diminishes by 50% and the decomposers decrease until they are nearly extinct. Total extinction, while a mathematical possibility for larger reductions in the litter, is not usually a biological one, except in extremely pathological situations. Nonetheless, greatly reduced decomposer levels could occur in systems in which the organic litter is only moderately reduced. The system does not show a similar sensitivity to an initial disturbance of any of the other compartments.

3) A highly subsidized system is more stable than a low-subsidy system subjected to the same perturbation. (see Fig. 7)

4) After a large decrease or increase in decomposers the system returns to equilibrium within a few months. (see Fig. 6)

5) Following a decrease in organic litter, and allowing 20 years to elapse during which time the system exists in a state of partial collapse, new organic litter is added. The additional litter, instantaneously applied, raises the litter level up to 1100 lbs./acre or 10% above thr original unperturbed level. The plant cover then rebounds and after 5 years reaches a value 30% above its original unperturbed level. This could be considered a healthy instability.

In several of the computer simulations, the full Michaelis-Menten form (c^{ij}, $d^{ij} \neq 0$ in Eq. 3) of the uptake terms was included. This inclusion made no substantive differences in our computer results, even in the cases of decreases in organic litter where the decomposers were life-span limited.

We now consider our computer results for our model of a shallow freshwater mesotrophic lake. For this seven compartment model, we take the nitrogen content of the zooplankton as .08 mg (N)/liter or $.25 \times 10^4$ zooplankton/liter. Their total grazing rate on all three types of phytoplankton is taken to be .01 mg (N)/liter.day. The total nitrogen content of the phytoplankton (equally divided between the three types P_ℓ, P_i, P_f,) is .21 mg (N)/liter or $\sim .4 \times 10^6$ cells/liter and their total nitrogen uptake was .014 mg (N)/liter.day. The nitrogen content of the decomposers is taken as .002 mg (N)/liter or about

.6 x 10^8 bac/liter. Their growth rate due to uptake of organic nutrient was .002 mg (N)/liter day, which implies that they can double about once a day. The equilibrium value of the organic litter pool is taken as .5 mg (N)/liter and of inorganic nubrient as .15 mg (N) liter. Much uncertainty exists concerning the roles of dissolved and particulate organic litter as a food supply for the decomposers. In our computer simulations, the numbers used represent an amalgam of experimental data on this point as well as a crude lumping of these two states of organic litter into one compartment.

In table 2, a complete tabulation of parameters and equilibrium values of the nitrogen content of the seven compartments is given.

Our computer simulation runs for the aquatic system evaluated the effect of perturbed nitrogen content values and rate parameters. For each run different values of the ratios of the linear death rate to the quadratic resource scarcity reduction rate were considered for decomposers (K_D), phyto-ℓ (K_ℓ), and phyto-f (K_f). In most cases, the initial and most dramatic response of the aquatic ecosystem to an initial perturbation, occurred over a 10 day period. This was followed over the next 50 days by gradual or unnoticeable changes in the state of the systems.

Below, we describe some computer results which are specific to this system. (Our general comments such as the fact that large values for K_D lead to instability, that the system is most vulnerable to changes in the organic litter pool, and that low subsidy systems are more vulnerable than high subsidy systems, apply here as they

did in the grassland system.)

1) A decrease in organic litter generally leads to a decrease in phyto-ℓ and phyto-i and an increase in phyto-f.

2) An increase in organic litter leads to a small phyto-ℓ bloom small phyto-i oscillations, and a decrease in phyto-f over a 2 day period.

3) A decrease in zooplankton gives a small three way bloom of phyto-ℓ, i, and f with an eventual return to equilibrium conditions. The system is quite resilient to this perturbation.

4) After a decrease in decomposers, the system rapidly returns to equilibrium due to the short doubling time of the decomposers.

5) A parameter change where the external organic litter input (Ω_L) rate is increased, leads to an increase of organic litter, inorganic nutrient, and phyto-ℓ while phyto-f decreases.

6) An increase in growth rates with no initial changes in the X_i, leads to a sizable algal bloom if K_D is large.

Of course, some of these specific results (e.g. the phyto-f decrease following organic litter reduction) are likely to be simply features of this model and will not be generally true in nature. We re-emphasize that a detailed predictive capability is not a goal of these studies.

Next, we performed computer simulations using the combined nitrogen-oxygen aquatic model. The stability results were similar to those of the previous nitrogen models. For example, the importance

of K_D as a stability indicator is illustrated in Fig. 8. The following additional conclusions were also drawn from the combined nitrogen-oxygen model.

i) Systems in which the physical rate of oxygen flow (corresponding to external subsidy of oxygen from wind mixing and stream flow) is large compared to the biological production rate of oxygen (from phytoplankton photosynthesis) are more resilient to perturbation than systems with little subsidized input. This is consistent with the results of the previous two models concerning subsidization and stability.

ii) If the litter or inorganic nutrient levels are increased sufficiently above equilibrium, or if oxygen uptake rates by zooplankton are moderately increased (corresponding to spring conditions), then anoxic conditions result along with a decline in herbivore numbers and an algal bloom.

In the models treated above, the process of decomposition is oversimplified. The decomposing agents were assumed to be bacteria (or fungi) which eat organic litter and convert it into organic nutrient. In reality a variety of insects and other animals chew up raw organic litter and process portions of it before bacterial decomposition takes place. Moreover, bacterial processing of chewed litter is multifaceted. Bacteria can feed directly on chewed litter, making it digestible for worms and other animals inhabitating the soil. In addition, the feces of these animals constitute the humus particles upon which decomposing-bacteria also feast. It is at this latter stage that most inorganic nutrients are finally made available.

In order to partially take into account this complexity, we have examined a six-level grassland system which included the original four levels plus a compartment of litter chewers and a compartment of chewed litter processed for subsequent bacterial decomposition. This pathway and compartment structure is included in the bottom of Fig. 2. The mathematical description of the litter chewing process is taken to be analogous to the description of the decomposition process; only the rate parameters and the sizes of the two compartments were chosen to distinguish the two stages of the process of converting organic litter to inorganic nutrient. We then sought to determine whether the quantity K_D is still the most appropriate stability indicator or whether the corresponding K for the litter chewers is a better indicator. Using values for the litter process rates and the sizes of the litter compartments which are within the broad ranges of existing crude field data,[19] we found that the most reliable stability indicator for effects persisting over the first half-dozen years following a disturbance was again K_D, although K for the litter chewers was a more significant indicator than the analogous factor for plants (K_P) and was increasingly important for predicting long term effects.

The continued importance of K_D as a stability indicator appears to depend upon two factors. One is the rapid turnover of nitrogen in the decomposer compartment, and the second is the large ratio of the nitrogen content in the food supply of the decomposers (processed litter) to the nitrogen content of the inorganic nutrient pool. We also found that the system was most

sensitive to perturbations in the processed litter pool and second-most sensitive to perturbations in the raw litter pool. By varying the size of the raw and processed litter pools, relative to the size of the plant compartment, we were able to gain some insight into the conditions under which organic litter of either form is the sensitive, or weak, link in the systems. For example, we simulated a "jungle" biome in which the standing crop of plant material was considerably greater than the standing crop of raw or processed litter and found that in this case the system was most sensitive to fixed-percentage perturbations in the plant variable. It is evident that experimental studies, both under controlled laboratory conditions with microcosms and in the field, are needed to further explore the issues we have raised.

V. CONCLUSION

We have examined the stability properties of a variety of models for cyclic nutrient flow in ecosystems. The models differed considerably in mathematical form, in their numerical values of rate parameters, and in their trophic complexity, but all contained, in common, a decomposer-detritus nutrient recycle mechanism. Three stability properties were found to be shared by all models considered These stability results are: i) A quantity, K_D (Eq. 4), is a reliable stability indicator-this quantity is determined from the rate parameters describing the population dynamics of the decomposers in the ecosystem; ii) The systems are more vulnerable to perturbations in the organic litter than to perturbations in their other compartments; iii) Low subsidy systems are more fragile than high subsidy systems.

These results were obtained originally for a simple model by using analytic Liapunov techniques to analyze stability. They are confirmed here in a variety of models by computer simulation. If these results are verified in field and in controlled laboratory experiments, we believe that they can be of practical use in building a capability for identifying fragile ecosystems and for <u>anticipating</u> ecologically deleterious impacts of human activity.

APPENDIX A

Aquatic Ecosystem Nutrient Cycle Models

Here we give the equations for the seven level aquatic nitrogen cycle and the seven level aquatic nitrogen-oxygen cycle in a shallow freshwater mesotrophic lake. The nitrogen cycle model described qualitatively in Section 3 contained seven compartments: zooplankton (X_Z), phyto-ℓ (X_{P_ℓ}), phyto-i (X_{P_i}), phyto-f (X_{P_f}), inorganic nutrient (X_I), decomposers (X_D), and organic litter (X_L). The equations for this model are:

$$\frac{dX_Z}{dt} = \underbrace{-\alpha_Z X_Z - \gamma_Z X_Z^2}_{1} + \underbrace{\beta_{ZP_\ell} X_Z X_{P_\ell} + \beta_{ZP_i} X_Z X_{P_i} + \beta_{ZP_f} X_Z X_{P_f}}_{2}$$

$$\frac{X_{P_\ell}}{dt} = \underbrace{-\alpha_{P_\ell} X_{P_\ell} - \gamma_{P_\ell} X_{P_\ell}^2}_{3} \underbrace{-\beta_{P_\ell Z} X_{P_\ell} X_Z}_{4} + \underbrace{\beta_{P_\ell L} X_{P_\ell} X_L}_{5}$$

$$\frac{dX_{P_i}}{dt} = \underbrace{-\alpha_{P_i} X_{P_i} - \gamma_{P_i} X_{P_i}^2}_{6} \underbrace{- \beta_{P_i Z} X_{P_i} X_Z}_{7} + \underbrace{\beta_{P_i I} X_{P_i} X_I}_{8} \qquad \text{(A-1)}$$

$$\frac{dX_{P_f}}{dt} = \underbrace{-\alpha_{P_f} X_{P_f} - \gamma_{P_f} X_{P_f}^2}_{9} \underbrace{-\beta_{P_f Z} X_{P_f} X_Z}_{10} + \underbrace{r X_{P_f}}_{11}$$

$$\frac{dX_I}{dt} = \underbrace{\Omega_I}_{12} - \underbrace{\alpha_I X_I}_{13} - \underbrace{\beta_{IP_i} X_I X_{P_i}}_{14} + \underbrace{\sigma_{DL} X_D X_L}_{15}$$

$$\frac{dX_D}{dt} = \underbrace{-\alpha_D X_D - \gamma_D X_D^2}_{16} + \underbrace{\beta_{DL} X_D X_L}_{17}$$

$$\frac{dX_L}{dt} = \underbrace{\Omega_L}_{18} - \underbrace{\alpha_L X_L}_{19} - \underbrace{\beta_{LP_\ell} X_L X_{P_\ell}}_{20} - \underbrace{\beta_{LD} X_L X_D}_{21}$$

$$\underbrace{+\Gamma\{\alpha_Z X_Z + \gamma_Z X_Z^2 + \alpha_{P_\ell} X_{P_\ell} + \gamma_{P_\ell} X_{P_\ell}^2}$$

$$\underbrace{+ \alpha_{P_i} X_{P_i} + \gamma_{P_i} X_{P_i}^2 + \alpha_{P_f} X_{P_f} + \gamma_{P_f} X_{P_f}^2 + \alpha_D X_D + \gamma_D X_D^2\}}_{22}$$

$$\underbrace{+\Gamma\{(\beta_{P_\ell Z} - \beta_{ZP_\ell}) X_{P_\ell} X_Z + (\beta_{P_i Z} - \beta_{ZP_i}) X_{P_i} X_Z + (\beta_{P_f Z} - \beta_{ZP_f}) X_{P_f} X_Z\}}_{23}$$

The numbered terms are:

(1) Zooplankton death rate including resource scarcity term $(\gamma_Z X_Z^2)$.

(2) Zooplankton growth rate as a result of grazing on all three types of phytoplankton.

(3) Phyto-ℓ death rate including resource scarcity term $(\gamma_{P_\ell} X_{P_\ell}^2)$.

(4) Phyto-ℓ reduction rate due to zooplankton grazing.

(5) Phyto-ℓ growth rate due to uptake of organic litter.

(6) Phyto-i death rate including resource scarcity term $(\gamma_{P_i} X_{P_i}^2)$.

(7) Phyto-i reduction rate due to zooplankton grazing.

(8) Phyto-i growth rate due to uptake of inorganic nutrient.

(9) Phyto-f death rate including resource scarcity term $(\gamma_{P_f} X_{P_f}^2)$.

(10) Phyto-f reduction rate due to zooplankton grazing.

(11) Phyto-f growth rate from nitrogen fixation.

(12) External input to inorganic nutrient pool.

(13) Washout of inorganic nutrient.

(14) Decrease of inorganic nutrient by uptake of phyto-i.

(15) Production rate of inorganic nutrient by decomposer action on organic litter.

(16) Decomposer loss rate including resource scarcity term $(\gamma_D X_D^2)$.

(17) Decomposer growth rate due to uptake of organic litter.

(18) External input rate to organic litter pool.

(19) Washout of organic litter.

(20) Reduction rate of organic litter due to uptake by phyto-ℓ.

(21) Reduction rate of organic litter due to decomposer action.

(22) Gain rate of organic litter pool from carcasses.

(23) Gain rate of organic litter pool from excrement (Γ is an efficiency factor).

Here the interaction terms (β_{ij}, σ_{DL}) have the general Michaelis-Menten form

$$\beta_{ij} = \frac{\bar{\beta}_{ij}}{1 + c^{ij}X_i + d^{ij}X_j} .$$

Equilibrium values for the nitrogen content quantities ($\bar{X}_i$) and the rate parameters are given in table 2.

The model for the nitrogen-oxygen cycle is a modification of the nitrogen cycle model. The number of nitrogen content compartments is reduced by one with the removal of the phyto-ℓ while a compartment for the concentration of dissolved oxygen (Y) in the water is added. In addition, the uptake, death, growth, and production rate terms in the equations for the nitrogen content quantities are modified by factors which depend on the concentration of dissolved oxygen.

The gain and loss rate terms in the equation for the time rate of change of the concentration of dissolved oxygen are of two types. There are terms describing oxygen transfer resulting from biological activity and a term describing the physical transfer of oxygen between the atmosphere and the water. The size of this last term is strongly effected by wind conditions. Incorporating the above features, our equations for the nitrogen-oxygen cycle become,

$$\frac{dX_Z}{dt} = \frac{-\alpha_Z X_Z - \gamma_Z X_Z^2}{\lambda_{\bar{Z}}} + \{\beta_{ZP_i} X_Z X_{P_i} + \beta_{ZP_f} X_Z X_{P_f}\} \lambda_Z$$

$$\frac{dX_{P_i}}{dt} = -\alpha_{P_i} X_{P_i} - \gamma_{P_i} X_{P_i}^2 - \beta_{P_i Z} X_{P_i} X_Z \lambda_{P_i} + \beta_{P_i I} X_{P_i} X_I$$

$$\frac{dX_{P_f}}{dt} = -\alpha_{P_f} X_{P_f} - \gamma_{P_f} X_{P_f}^2 - \beta_{P_f Z} X_{P_f} X_Z \lambda_{P_f} + r X_{P_f} \qquad \text{(A-2)}$$

$$\frac{dX_I}{dt} = \Omega_I - \alpha_I X_I - \beta_{IP_i} X_I X_{P_i} + \sigma_{DL} X_D X_L \lambda_D$$

$$\frac{dX_D}{dt} = \frac{-\alpha_D X_D - \gamma_D X_D^{\,2}}{\lambda_{\bar{D}}} + \beta_{DL} X_D X_L \lambda_D$$

$$\frac{dX_L}{dt} = \Omega_L - \alpha_L X_L - \beta_{LD} X_D X_L \lambda_D$$

$$+\Gamma\cdot\{\frac{\alpha_Z X_Z + \gamma_Z X_Z^2}{\lambda_{\bar{Z}}} + \alpha_{P_i} X_{P_i} + \gamma_{P_i} X_{P_i}^{\,2}$$

$$+ \alpha_{P_f} X_{P_f} + \gamma_{P_f} X_{P_f}^{\,2} + \frac{\alpha_D X_D + \gamma_D X_D^2}{\lambda_{\bar{D}}}\}$$

$$+\Gamma\cdot\{(\beta_{P_i Z}\lambda_{P_i} - \beta_{ZP_i}\lambda_Z)\ X_{P_i} X_Z + (\beta_{P_f Z}\lambda_{P_f} - \beta_{ZP_f}\lambda_Z)\ X_{P_f} X_Z\}$$

$$\frac{dY}{dt} = \underbrace{-\alpha_o (Y - \bar{Y})}_{1} - \underbrace{20C\ X_D X_L \lambda_D}_{2}$$

$$\underbrace{-20(.8)(\beta_{P_i Z} X_{P_i} + \beta_{P_f Z} X_{P_f} - \beta_{ZP_i} X_{P_i} - \beta_{ZP_f} X_{P_f}) X_Z \lambda_Z}_{3}$$

$$+ \underbrace{20\ \beta_{P_i I} X_{P_i} X_I + 20\ r X_{P_f}}_{4}$$

$$\text{where } \lambda_j = \frac{Y(\bar{Y} + M_j)}{\bar{Y}(Y+M_j)},\quad j = Z,\ \bar{Z},\ P_f,\ P_i,\ D,\ \bar{D}$$

All the X's denote the nitrogen concentration of their respective compartments and Y denotes the concentration of dissolved oxygen in the water. The λ_j's depend on the concentration of dissolved oxygen and modify the uptake, death, metabolic, and grazing rates in the time rate of change equations for the nitrogen

content in the six nitrogen compartments. For example, λ_Z modifies the zooplankton grazing rate in such a way that a decrease (increase) in the concentration of dissolved oxygen decreases (increases) the grazing rate of zooplankton. The M_i are simply constants in the λ_i peculiar to each organism. In the case of bacteria, λ_D modifies the bacterial growth term and metabolic production rate of inorganic nutrient such that an increase(decrease) in the concentration of dissolved oxygen increases (decreases) both these rates.

In the equation for the time rate of change of the concentration of dissolved oxygen, the number 20 in the equation is a crude conversion factor which is necessary to relate the amount of oxygen to the amount of nitrogen needed in the various growth, death, metabolic, and production processes. It is obtained by multiplying the C/N ratio in typical aquatic organic material by a factor of $\frac{32}{12}$ which is the O/C ratio in CO_2. Although oversimplified, this is accurate enough for our purposes. The numbered terms in the equation for oxygen transfer are:

1) A transfer rate of oxygen to/from the lake.[20,21] This transfer could be a result of inflow/outflow of water into the system, or a result of wind conditions, with a high wind increasing the oxygen transfer rate between the atmosphere and the water. Here $\bar{Y}$ is the saturation concentration of oxygen in the water which is also taken to be the equilibrium concentration.

2) Uptake rate of oxygen from the water due to decomposer metabolism.

3) Uptake rate of oxygen from the water due to zooplankton growth and grazing.

4) Oxygen input to the water due to phytoplankton photosynthesis.

APPENDIX B

An Analytic Rationale

The results of our numerical analysis of ecosystem models might appear to the reader to be specific to the models and to the detailed numbers used in the models chosen for numerical analysis. The reader might also be somewhat puzzled as to how we arrived at the choices of parameters we varied from among the myriad of quantities that could potentially be of relevance to the stability of systems. To provide an analytic rationale, we describe here the results of a Liapunov stability analysis[22] of ecosystem models. The use of Liapunov techniques allows us to demonstrate the generalizability of the results of Section IV; chronologically it is the first approach we used to study ecosystem stability and led us to the choices made of quantities to vary in the numerical analysis. The details of our method of application of the Liapunov technique for stability analysis have been published elsewhere.[1] What follows is a brief description of this technique and of our results.

The Liapunov direct method has the advantage that it can be used to investigate stability properties of the solutions of complex sets of equations, even though the explicit solutions are not known. In addition, it allows us to handle finite (realistic) perturbations as opposed to infinitesimal ones. Application of the method proceeds as follows. The first step is to construct a function (called a Liapunov function) of the variables $\Delta X_i = X_i - \bar{X}_i$

which are the deviations of the system variables from their unperturbed values. This function must vanish when the ΔX_i all vanish and it must increase from zero as any or all of the ΔX_i become non-zero. That is, the function must be cup-shaped in some domain about $\Delta X_i = 0$. This first step is easy; many functions, the simplest of which is $L = \Delta X_1^2 + \Delta X_2^2 + \ldots + \Delta X_N^2$, will satisfy the conditions. The next step is to evaluate the time rate of change of the function, or dL/dt. This is to be done using the equations of motion for the dX_i/dt ($=d\Delta X_i/dt$ if the unperturbed state is static), and the rule:

$$\frac{dL}{dt} = \Sigma \frac{\partial L}{\partial \Delta X_i} \frac{d \Delta X_i}{dt} \qquad \text{(B-1)}$$

The last step is to examine the sign of dL/dt. If dL/dt is zero, the solutions are neutrally stable- i.e., if displaced from equilibrium, the system will neither return to its unperturbed value, nor will it wander far from it; it will simply remain in a displaced orbit. If dL/dt is negative in some domain about $\Delta X_i = 0$, then displacements of the system which are initially confined to within that domain will damp out and the system will return to its unperturbed value. Such a system is called "asymptotically stable" and the range of perturbations which damp out is called the "domain of asymptotic stability". If dL/dt is positive, then the perturbations will grow in time and the system is unstable.

This deceptively simple analytic method has one difficulty. Often a trial Liapunov function does not have a time derivative, $\frac{dL}{dt}$,

with a single sign in some domain about $\Delta X_i = 0$ rather it will be positive in some directions and negative in others. In this case, no conclusions can be reached and a new Liapunov function is needed. Nonetheless, there is a theorem which guarantess that for a system with well defined stability properties, a Laipunov function, L, must exist. Unfortunately, for general systems, no algorithm exists for finding it. For conservative or dissipative mechanical systems, the Hamiltonian with the damping term neglected is often the appropriate stability indicator; for the equations of chemical kinetics, the Gibbs free energy often works; and in ecology, the Liapunov function described below appears to be of practical use.

For any ecosystem model of the general form of Eq.1, (Sec. II) the function

$$L = \sum_i C_i \; (\bar{X}_1, \ldots, \bar{X}_N; w_1, \ldots, w_m) \; [X_i - \bar{X}_i - \bar{X}_i \; \ln \left(\frac{X_i}{\bar{X}_i}\right)] \qquad \text{(B-2)}$$

is a Liapunov function provided the functions C_i are positive definite. However, the time derivative, dL/dt, is not always of positive sign only or of negative sign only in some neighborhood of $X_i = \bar{X}_i$. What we have shown is that if the C_i $(\bar{X}_1, \ldots, \bar{X}_N; w_1, \ldots, w_m)$ are carefully chosen, then in a large class of models for which nutrient cycling via decomposer-detritus feedback loops is included, there is a range of parameters in the model (e.g. carrying capacities, rate coefficients, Michaelis-Menten factors, etc.) for which dL/dt is negative and thus the system is stable in a finite domain about $X_i = \bar{X}_i$.

To see how the Liapunov Direct Method works in practice, consider the simple grassland model (Eq. 2, Sec. II). Here, we determined the C_i's by trying to maximize the size of the domain of stability where $\frac{dL}{dt} < 0$. In doing this, we derived a number of algebraic constraints on our variables (X_i and the rate parameters).

One such constraint is

$$\frac{R\ \sigma_{DL}^2\ (X_L + \bar{X}_L)^2 X_I}{16\ \gamma_D\ (\Omega_I + \sigma_{DL} X_D X_L)\bar{X}_I} < 1 \qquad \text{(B-3)}$$

where R is a numerical factor of order unity. From this inequality we can learn that if Ω_I is small and the perturbation of the organic litter, ΔX_L $(= X_L - \bar{X}_L)$, is sufficiently big, then the inequality will no longer be satisfied and the stability of the system is no longer guarnateed. Furthermore, the significance of the parameter $K_D = \alpha_D/\gamma_D\bar{X}_D$ is apparent from this equation because if K_D becomes too large then the inequality is again no longer satisfied.

The complete evaluation of dL/dt leads to a number of constraints of which Eq. B-3 is simply one. Detailed analysis of these constraints leads to our prediction of the three stability criteria: i. K_D is a stability indicator, ii. Systems are most sensitive to litter perturbations, and iii. Low subsidy systems are especially vulnerable to perturbations. We believe it is the decomposer-litter link in the flow cycle of our systems which is responsible for the significance of these criteria. This belief is enhanced by the fact that these results follow from examination of a variety of models,

analyzed by both Liapunov and numerical techniques, which contain this critical link.

It should be pointed out, however, that for ecological systems the Liapunov function we discuss here may not be the optimal one. For open systems with nutrient cycling, our function indicates asymptotic stability only if the magnitude of the initial perturbation is not too large. A better function might indicate stability in a large domain. We urge interested readers to search for Liapunov functions for their favorite models. Trial and error techniques will be required at first, but we suspect that intuition and insight will be acquired in the process.

FIGURE AND TABLE CAPTIONS

Figure 1 Nutrient flow in a simple four-level system. The wiggly lines correspond to external inputs and outputs of nutrient.

Figure 2. Nutrient flow in a more realistic ecosystem.

Figure 3. Nitrogen flow in a simple aquatic ecosystem. The phyto-i are phytoplankton which uptake nitrogen from inorganic litter; the phyto-ℓ are phytoplankton which uptake nitrogen from organic litter; the phyto-f are phytoplankton which uptake nitrogen from the atmosphere by nitrogen fixation.

Figure 4. Nitrogen and oxygen flow in a simple aquatic ecosystem. The dashed lines correspond to oxygen flow and the solid lines correspond to nitrogen flow.

Figure 5. Computer simulation of the effect of an initial disturbance to the four-level grasslands ecosystem. The perturbation was chosen to be a 10% reduction in the organic litter. The three cases shown here correspond to a high subsidy system with three combinations of values for K_P and K_D (see Table 1). Note that instability is correlated with large values of K_D and is relatively insensitive to K_P.

Figure 6. Computer simulation of the effect of three different initial disturbances to the four-level grasslands ecosystem. The three cases shown all correspond to a low subsidy system with $K_P = 0.1$ and $K_D = 10.0$ (see Table 1). Note that the litter perturbation has more effect on the system than the other perturbations do.

Figure 7. Computer simulation of the effect of an initial 10% decrease in organic litter in two systems - one with high subsidy and one with low subsidy. The two systems each have $K_P = 0.1$ and $K_D = 10.0$ (see Table 1). Note that the low subsidy system is more sensitive to perturbations than is the high subsidy system.

Figure 8. Computer simulation of the effect of an initial 50% increase in the organic litter in a combined nitrogen-oxygen model of a shallow freshwater mesotrophic lake. The two cases correspond to $K_D = 0.1$ and 10.0. Note that a large value of K_D again indicates instability.

Table 1. Equilibrium nitrogen levels and rate parameters for four-level nitrogen cycle model of low and high subsidy grasslands ecosystem.

Table 2. Equilibrium nitrogen levels and rate parameters for seven-level aquatic nitrogen cycle model.

Table 3. Equilibrium nitrogen and oxygen levels and rate parameters for seven-level aquatic nitrogen-oxygen cycle model.

Table 1

SYMBOL	DESCRIPTION	VALUE (units) (lbs N acre^{-1}) Low Subsidy	High Subsidy
Standing Crops:			
$\overline{X}_L$	Organic Litter [a]	1000	1000
$\overline{X}_P$	Plants [a]	25	25
$\overline{X}_I$	Inorganic Nutrient [a]	25	25
$\overline{X}_D$	Decomposer [a,b]	1.5	1.5
Flow Rates:		(lbs. N acre^{-1} year^{-1}) Low	High
$\alpha_P\overline{X}_P+\gamma_P\overline{X}_P^2$	Plant death rate [a]	35	35
$\beta_{PI}\ \overline{X}_P\ \overline{X}_I$	Plant increase due to uptake of inorganic nutrients [a]	35	35
$\beta_{IP}\ \overline{X}_P\ \overline{X}_I$	Inorganic nutrient loss due to plant uptake [a]	35	35
$\alpha_D\overline{X}_D+\gamma_D\overline{X}_D^2$	Decomposer death rate [a,b]	33	25
$\beta_{DL}\ \overline{X}_D\ \overline{X}_L$	Decomposer growth due to uptake of organic litter [a,b]	33	25
$\beta_{LD}\ \overline{X}_D\ \overline{X}_L$	Loss of organic litter due to decomposer action [a,b]	66	50
$\sigma_{DL}\ \overline{X}_D\ \overline{X}_L$	Inorganic nutrient produced be decomposer metabolism [a,b]	33	25
$\alpha_I\ \overline{X}_I$	Inorganic nutrient washout	0	0
Ω_I	Inorganic nutrient subsidy	2	10
$\alpha_L\ \overline{X}_L$	Organic litter washout	2	2
Ω_L	Organic litter subsidy	0	2
Dimensionless Parameter :		Low	High
Γ	Cycling Efficiency	1	.83

a) See Ref. 17
b) See Ref. 18

Table 2

SYMBOL	DESCRIPTION	VALUE (units)
Standing Crops:		(mg N liter^{-1})
$\bar{X}_Z$	Zooplankton [a,b,c]	.08
$\bar{X}_{P_\ell}$	Phyto-ℓ [b,c,e]	.007
$\bar{X}_{P_i}$	Phyto-i [b,c,e]	.007
$\bar{X}_{P_f}$	Phyto-f [b,c,d,e]	.007
$\bar{X}_I$	Inorganic Nutrient [b,c,e]	.15
$\bar{X}_D$	Decomposer [b]	.002
$\bar{X}_L$	Organic Litter [c,e]	.5
Flow Rates:		(mg N liter^{-1} day^{-1})
$\alpha_Z\bar{X}_Z+\gamma_Z\bar{X}_Z^2$	Zooplankton death rate [a,b]	.005
$\beta_{ZP_\ell}\bar{X}_Z\bar{X}_{P_\ell}$	Zooplankton gain from grazing on Phyto-ℓ [a,b]	.002
$\alpha_{P_\ell}\bar{X}_{P_\ell}+\gamma_{P_\ell}\bar{X}_{P_\ell}^2$	Phyto-ℓ death rate [a,b]	.004
$\beta_{ZP_i}\bar{X}_Z\bar{X}_{P_i}$	Zooplankton gain from grazing on Phyto-i [a,b]	.0015
$\alpha_{P_i}\bar{X}_{P_i}+\gamma_{P_i}\bar{X}_{P_i}^2$	Phyto-i death rate [a,b]	.003
$\beta_{P_iZ}\bar{X}_Z\bar{X}_{P_i}$	Phyto-i loss from grazing [a,b]	.003
$\beta_{ZP_f}\bar{X}_Z\bar{X}_{P_f}$	Zooplankton gain from grazing on Phyto-f [a,b]	.0015
$\alpha_{P_f}\bar{X}_{P_f}+\gamma_{P_f}\bar{X}_{P_f}^2$	Phyto-f death rate [a,b]	.003
$\beta_{P_fZ}\bar{X}_Z\bar{X}_{P_f}$	Phyto-f loss from grazing [a,b]	.003
$\beta_{P_\ell L}\bar{X}_{P_\ell}\bar{X}_L$	Consumption of litter by Phyto-ℓ [a,b]	.008
$\beta_{LP_\ell}\bar{X}_{P_\ell}\bar{X}_L$	Loss of litter due to Phyto-ℓ uptake [a,b]	.008
$\beta_{P_iI}\bar{X}_{P_i}\bar{X}_I$	Phyto-i growth due to uptake of inorganic nutrient [a,b]	.006
$\alpha_D\bar{X}_D+\gamma_D\bar{X}_D^2$	Decomposer death rate [b,c]	.002

$\beta_{IP_i} \overline{X}_I \overline{X}_{P_i}$	Phyto-i uptake of inorganic nutrient [a,b]	.006
$\beta_{DL} \overline{X}_D \overline{X}_L$	Decomposer growth due to uptake of organic litter [b,c]	.002
$\beta_{LD} \overline{X}_D \overline{X}_L$	Loss of organic litter due to decomposer uptake [b,c]	.004
$\sigma_{DL} \overline{X}_D \overline{X}_L$	Inorganic nutrient produced by decomposer metabolism [b,c]	.002
$r \overline{X}_{P_f}$	N fixation by Phyto-f [d]	.006
$\alpha_I \overline{X}_I$	Inorganic nutrient washout	0
Ω_I	Inorganic nutrient subsidy	.004
$\alpha_L \overline{X}_L$	Organic litter washout	.01
Ω_L	Organic litter subsidy	0

Dimensionless Parameter

Γ	Cycling efficiency	1

a) See Ref. 14

b) See Ref. 15

c) See Ref. 16

d) See Ref. 11

e) See Ref. 21

Table 3[a]

SYMBOL	DESCRIPTION	VALUE (Units)
Standing Crop:		(mg N liter^{-1})
$\bar{X}_Z$	Zooplankton	.080
$\bar{X}_{P_i}$	Phytoplankton-i	.014
$\bar{X}_{P_f}$	Phytoplankton-f	.007
$\bar{X}_D$	Decomposer	.002
$\bar{X}_L$	Organic litter	.500
$\bar{X}_I$	Inorganic nutient	.150
Nitrogen Flow Rates:		(mg N liter^{-1} day^{-1})
$\alpha_Z\bar{X}_Z+\gamma_Z\bar{X}_Z^2$	Zooplankton death rate	.005
$\beta_{ZP_i}\bar{X}_Z\bar{X}_{P_i}$	Zooplankton gain from grazing on Phyto-i	.0035
$\alpha_{P_i}\bar{X}_{P_i}+\gamma_{P_i}\bar{X}_{P_i}^2$	Phyto-i death rate	.007
$\beta_{P_iZ}\bar{X}_{P_i}\bar{X}_Z$	Phyto-i loss from grazing	.007
$\beta_{ZP_f}\bar{X}_Z\bar{X}_{P_f}$	Zooplankton gain from grazing on Phyto-f	.0015
$\alpha_{P_f}\bar{X}_{P_f}+\gamma_{P_f}\bar{X}_{P_f}^2$	Phyto-f death rate	.003
$\beta_{P_fZ}\bar{X}_{P_f}\bar{X}_Z$	Phyto-f loss from grazing	.003
$\beta_{IP_i}\bar{X}_I\bar{X}_{P_i}$	Phyto-i uptake of inorganic nutrient	.014
$\beta_{P_iI}\bar{X}_{P_i}\bar{X}_I$	Loss of inorganic nutrient due to Phyto-i uptake	.014
$r\bar{X}_{P_f}$	N_2 fixation by phyto-f	.006
$\alpha_D\bar{X}_D+\gamma_D\bar{X}_D^2$	Decomposer death rate	.005
$\beta_{DL}\bar{X}_D\bar{X}_L$	Decomposer increase from organic litter	.005
$\sigma_{DL}\bar{X}_D\bar{X}_L$	Inorganic nutrient produced by decomposer metabolism	.010
$\beta_{LD}\bar{X}_L\bar{X}_D$	Loss of organic litter from decomposer metabolism	.015
Ω_I	Inorganic nutrient subsidy	.004
Ω_L	Organic litter subsidy	0.0

$\alpha_I \bar{X}_I$	Inorganic nutrient washout	0.0
$\alpha_L \bar{X}_L$	Organic litter washout	.010
Dimensionless Parameter:		
Γ	Cycling efficiency	1.0
Oxygen Level and Parameters:		(mg O liter^{-1})
$\bar{Y}$	Equilibrium oxygen level	9.0
M_Z	Zooplankton uptake Michaelis coefficient [b]	3.5
$M_{\bar{Z}}$	Zooplankton death Michaelis coefficient [b]	2.0
M_{P_f}	Phyto-f grazing Michaelis coefficient [b]	2.0
M_{P_i}	Phyto-i grazing Michaelis coefficient [b]	2.0
M_D	Decomposer uptake Michaelis coefficient [b]	2.0
$M_{\bar{D}}$	Decomposer death Michaelis coefficient [b]	0.1
Oxygen Flow Rate:		(mg O liter^{-1}day^{-1})
$\alpha_o \bar{Y}$	Wind mixing of oxygen into lake [c]	0.9, 1.8
$CX_D X_L$	O loss from decomposer activity	.016

a) Where not otherwise noted, references are same as in Table 2

b) See Ref. 23

c) See Ref. 20, 21

Footnotes and References

1. Harte, J. and D. Levy., "On the Vulnerability of Ecosystems Disturbed by Man", LBL report 3214, to be published in Unifying Concepts in Ecology, Proceedings of the First International Congress of Ecology, The Hague, Netherlands.

2. For a review of the community matrix approach to stability, see May, R. Stability and Complexity in Model Ecosystems, Princeton University Press, (1973).

3. Notable exceptions are the collection of papers in Modeling the Eutrophication Process, edited by Middlebrooks, E.J., Falkenborg, D.H. and Maloney, T.E., Ann Arbor Science, Ann Arbor, Michigan, (1974); Detritus and Its Role in Aquatic Ecosystem, Proceedings of an IBP-UNESCO Symposium, edited by U. Melchiorri-Santolini and Jack W. Hopton, (1972); Lassiter, R., Modeling Dynamics of Biological and Chemical Components of Aquatic Ecosystems, EPA-660 (1975).

4. There are, of course, exceptions to this. Among the best known is the carbon cycle wherein a small percentage of the flow of carbon to the inorganic atmospheric pool of CO_2 is returned by breathing animals without the necessity of direct decomposer action.

5. In the case of the carbon cycle this occurs in green plants by photosynthesis. Nitrogen uptake, in the form of nitrates, can occur through the roots of plants or, more rarely, by nitrogen fixation from atmospheric nitrogen.

6. See, e.g., Schindler, D.W., Journal of the Fisheries Research Board of Canada, Vol. 30, P. 1415, (1972) and Vol. 30, p. 1501 (1972).

7. A number of papers discuss non-linear resource scarity effects. See, for example, Gilpin, M.E. and Ayalo, F.J., Proc. Nat. Acad. Sci. USA, Vol. 70, No. 12, Part I pp. 3590 (1973); or Ecology, Ricklefs, R.E., Chapter 36, (1973).

8. Note that these equations are not of the Lotka-Volterra form. In particular, there are terms in the rate equations for two of the variables which are not proportional to the variables themselves.

9. Salt, G.W., "Predation in an Experimental Protozoan Population (Woodruffia-Paramecium)", Ecol. Monogr. 37: 113-144 (1967); Salt, G.W., "Predator and Prey Densities as Controls of the rate of capture by the Predator Didinium nasutum", Salt, G.W., Ecology 55: 434-439, (1974).

10. DeAngelis, D.L., R.A. Goldstein., and R.V. O'Neill., "A Model for Trophic Interaction," ORNL #675, (To be published).

11. Dugdale, V.A., and R.C. Dugdale, "Nitrogen Metabolism in Lakes: II Role of Nitrogen Fixation in Sanctuary Lake, Pennsylvania." Limnol Oceanogr. 7, 170-177 (1962); A.J. Horne and C.R. Goldman, Nitrogen Fixation in Clearlake, CA, Limnology and Oceanography, 17, 678 (1972).

12. Edmondson, W.T., 'Lake Washington', in Environmental Quality and Data Development, W.H. Freeman Co., (ed.) C.R. Goldman, J. McEroy III, P.J. Richerson, pp. 281-298 (1973).

13. Dugdale, V.A. and R.C. Dugdale, Nitrogen Metabolism in Lakes: III Tracer Studies of the Assimilation of Inorganic Nitrogen. Limnology and Oceanography, 10, 53-57, (1965).

14. Thomann, R.V., D.J. O'Conner and D.M. DiToro, Modelling of the Nitrogen and Algal Cycles in Estuaries, 5th Intern. Water Pollution Research Conference, San Francisco, CA, July, 1970: DiToro, D.M. et.al., "A Dynamic Model of the Phytoplankton Population in the Sacramento San Joaquin Delta," in Non-equilibrium Systems in Natural Water Chemistry, (131-180), 1971.

15. Eutrophication: Causes , Consequences, Correctives. Proceedings of International Symposium, University of Wisconsin, National Academy Of Sciences, 1969.

16. Martin, D.M. and D.R. Goff, The Role of Nitrogen in the Aquatic Environment. Contributions from the Dept. of Limnology-Academy of Natural Sciences of Philadelphia, 1972; D.R. Keeney, The Fate of Nitrogen in Aquatic Ecosystems. University of Wisconsin, Water Resources Program, 1972.

17. Brock, T.D., Principles of Microbial Ecology, 1966; M. Alexander, Soil Microbiology, 1962.

18. Hattori, T., Microbial Life in the Soil, 1973; A. McLaren, Soil Bio chemistry, 1967; T.R.G. Gray and D. Parkinson, the Ecology of Soil Bacteria - An International Symposium (Liverpool, U.K.), 1968.

19. See, for example, Schaller, F., Soil Animals, The University of Michigan Press, Ann Arbor, Michigan, 1968.

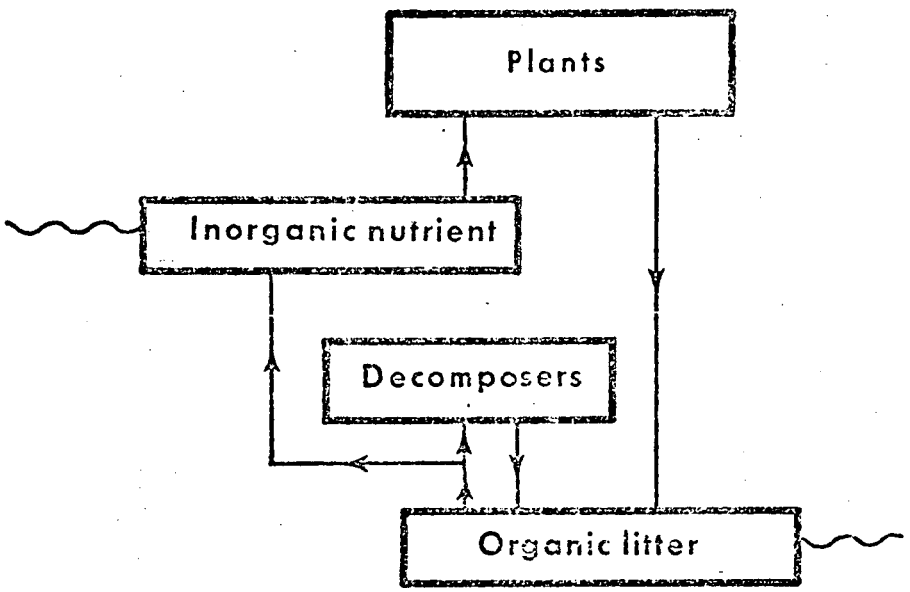
20. Hutchinson, G.E., A Treatise on Limnology, Vol. II: Introduction to lake biology and limnoplankton, John Wiley and Sons, (1967).

21. Redfield, A.C., The Exchange of Oxygen Across the Sea, Jour. Mar. Res., 7, 347-361 (1949).

22. Lasalle, J. and S. Lefshetz, Stability by Liapunov's Direct Method, Academic Press (1961).

23. Macam, T.T., Freshwater Ecology, John Wiley & Sons (1974); T.R. Parsons and M. Takahaski, Biological Oceanographic Processes, Pergamon Press (1973).

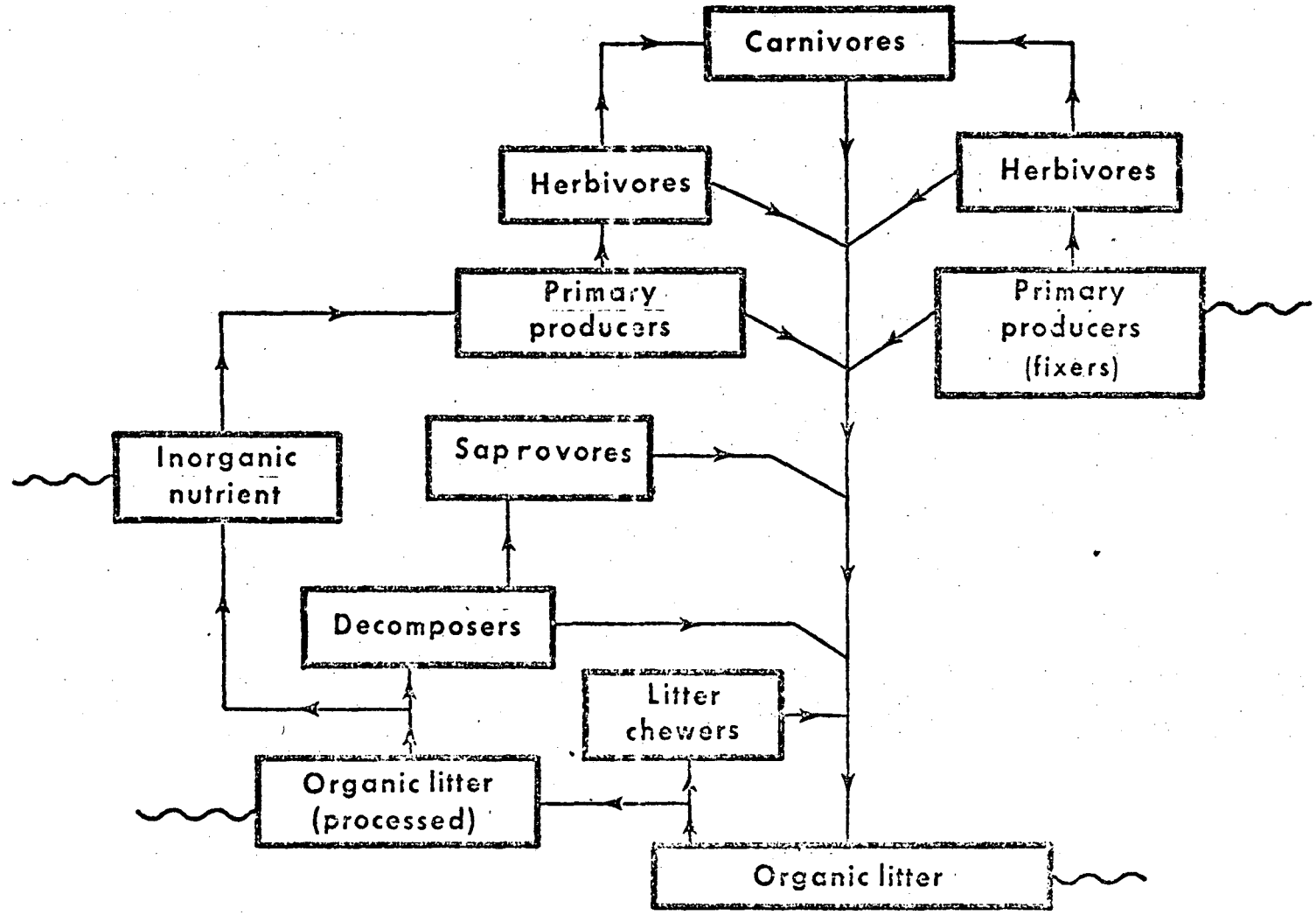
24. We thank the United States Energy Research and Development Administration for their support of this research.



XBL755-2890 A

Fig. 1

0 0 0 0 4 2 0 2 9 4 3



XBL755-2889A

Fig. 2

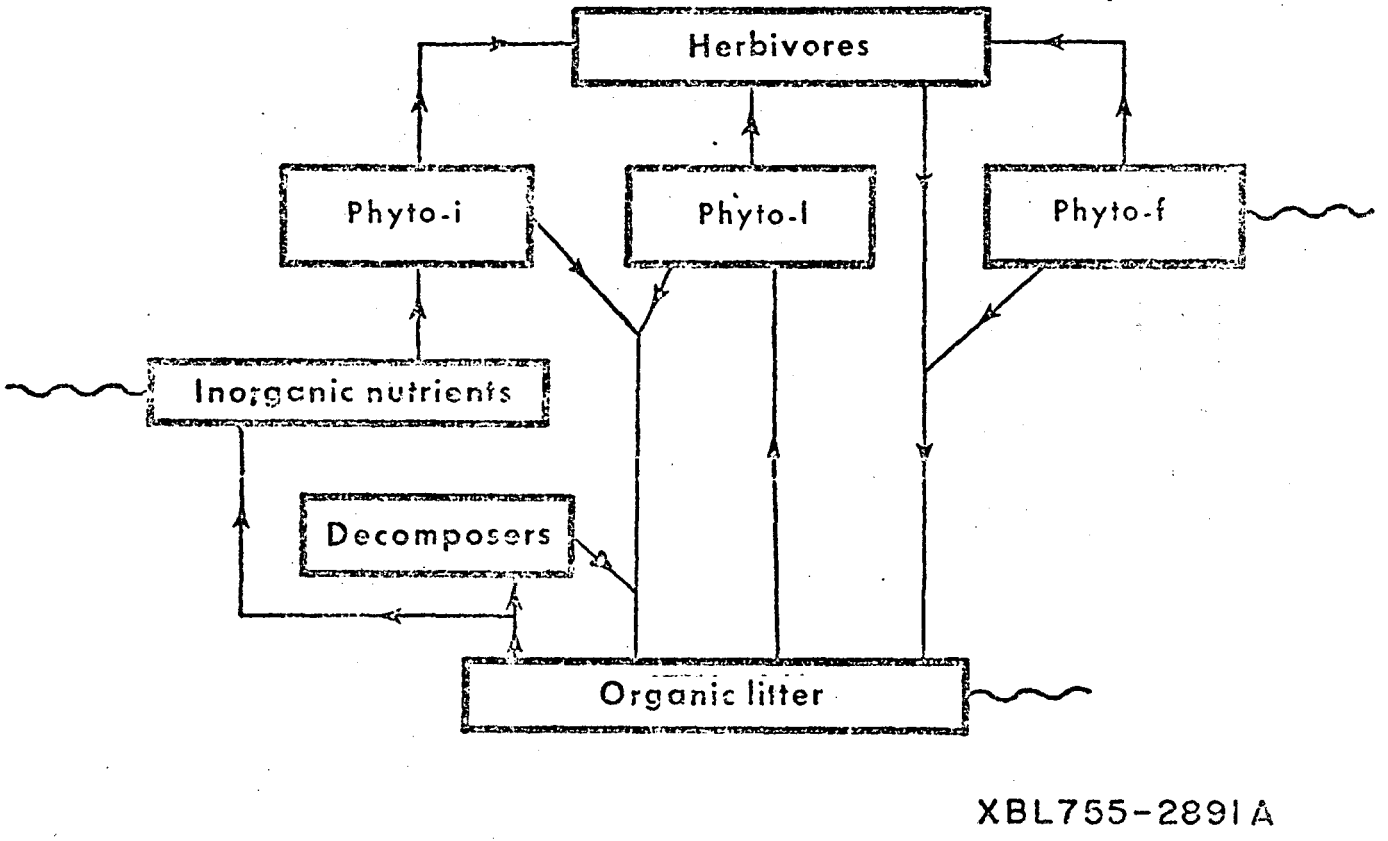
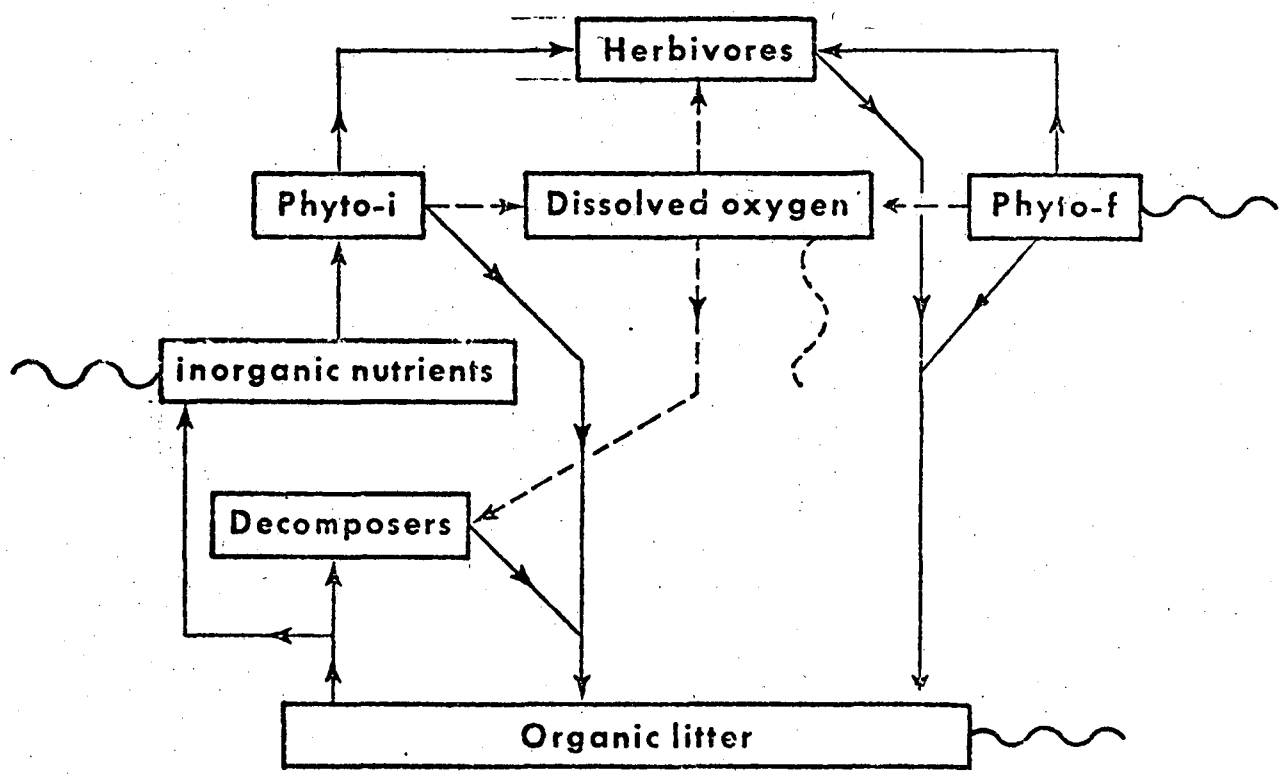
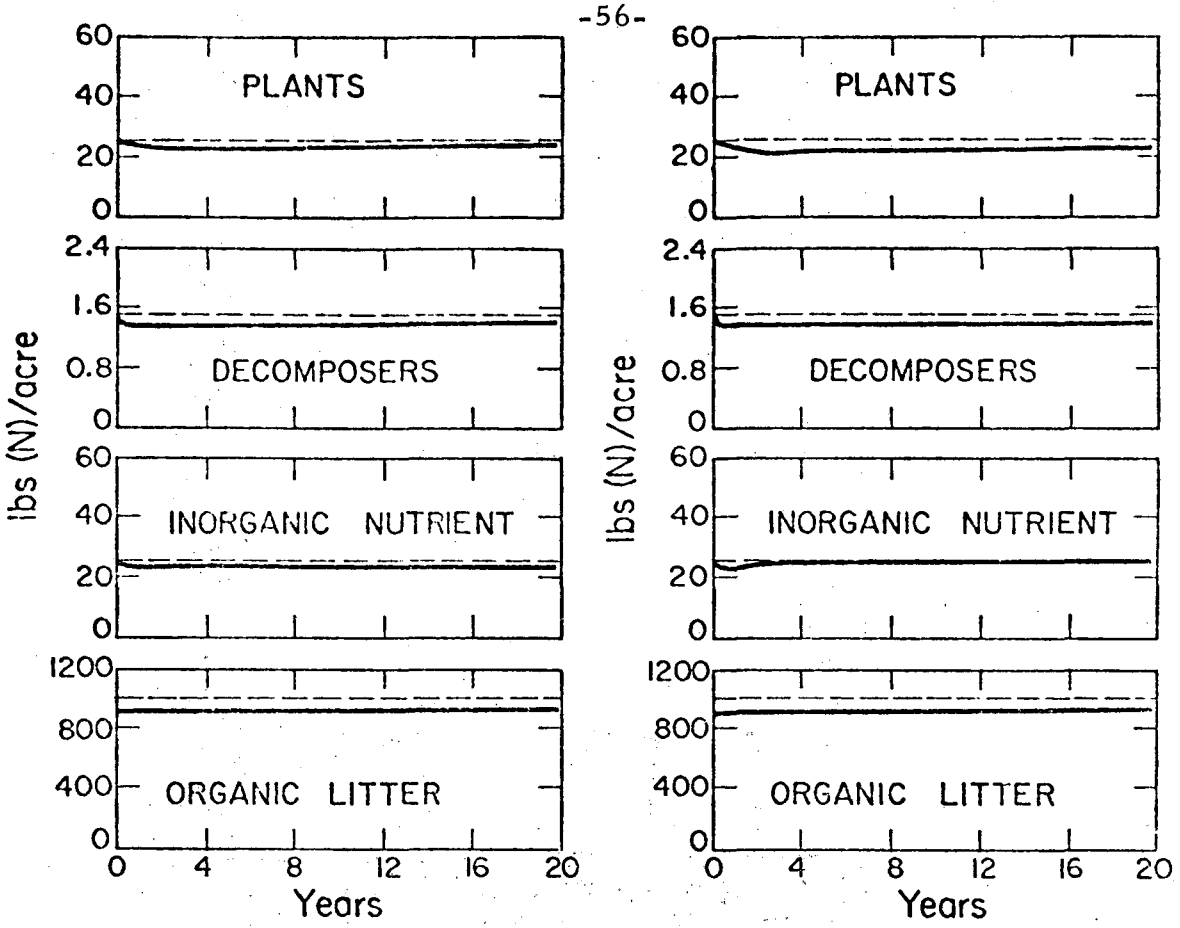

Herbivores
Phyto-i
Phyto-l
Phyto-f
Inorganic nutrients
Decomposers
Organic litter
XBL755-2891A

Fig. 3

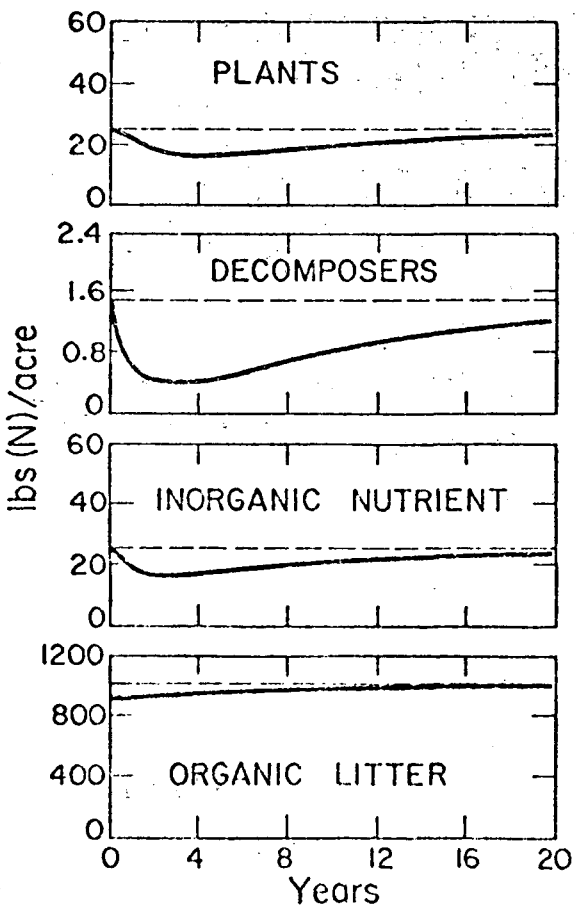


XBL 757-3345

Fig. 4



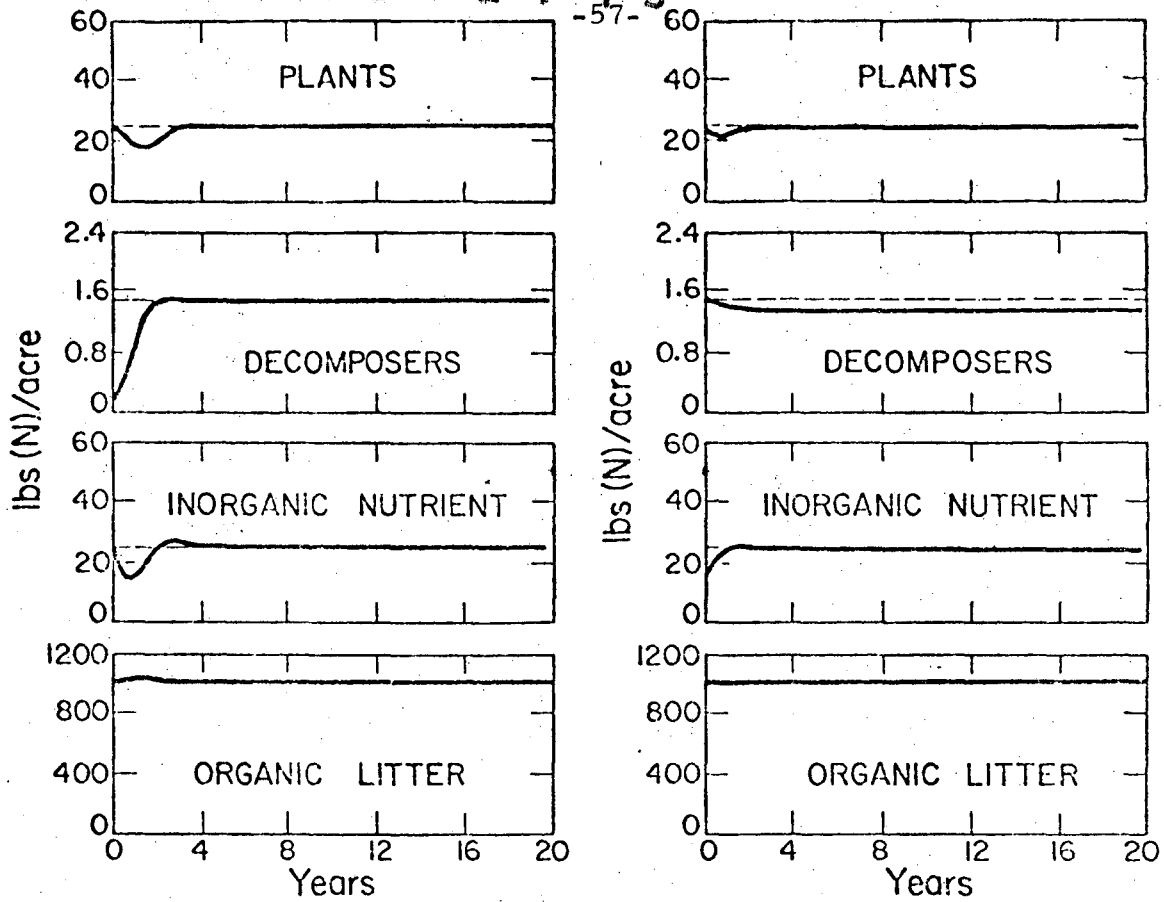
$K_P = 0.1$, $K_D = 0.1$ $K_P = 10$, $K_D = 0.1$



$K_P = 0.1$, $K_D = 10$

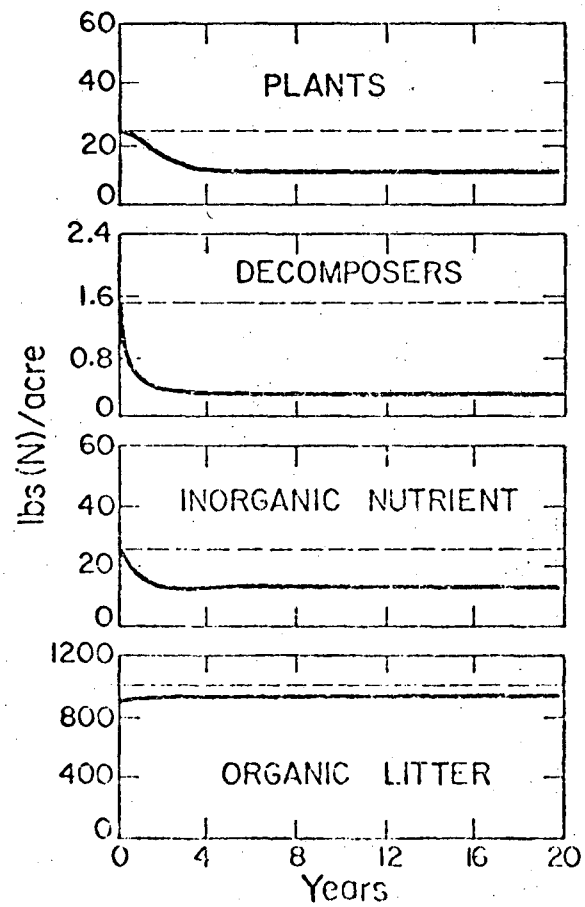
Fig. 5

XBL 755-2993



90% DECREASE OF DECOMPOSERS

40% DECREASE OF INORGANIC NUTRIENT



10% DECREASE OF ORGANIC LITTER

XBL 755-2994

Fig. 6

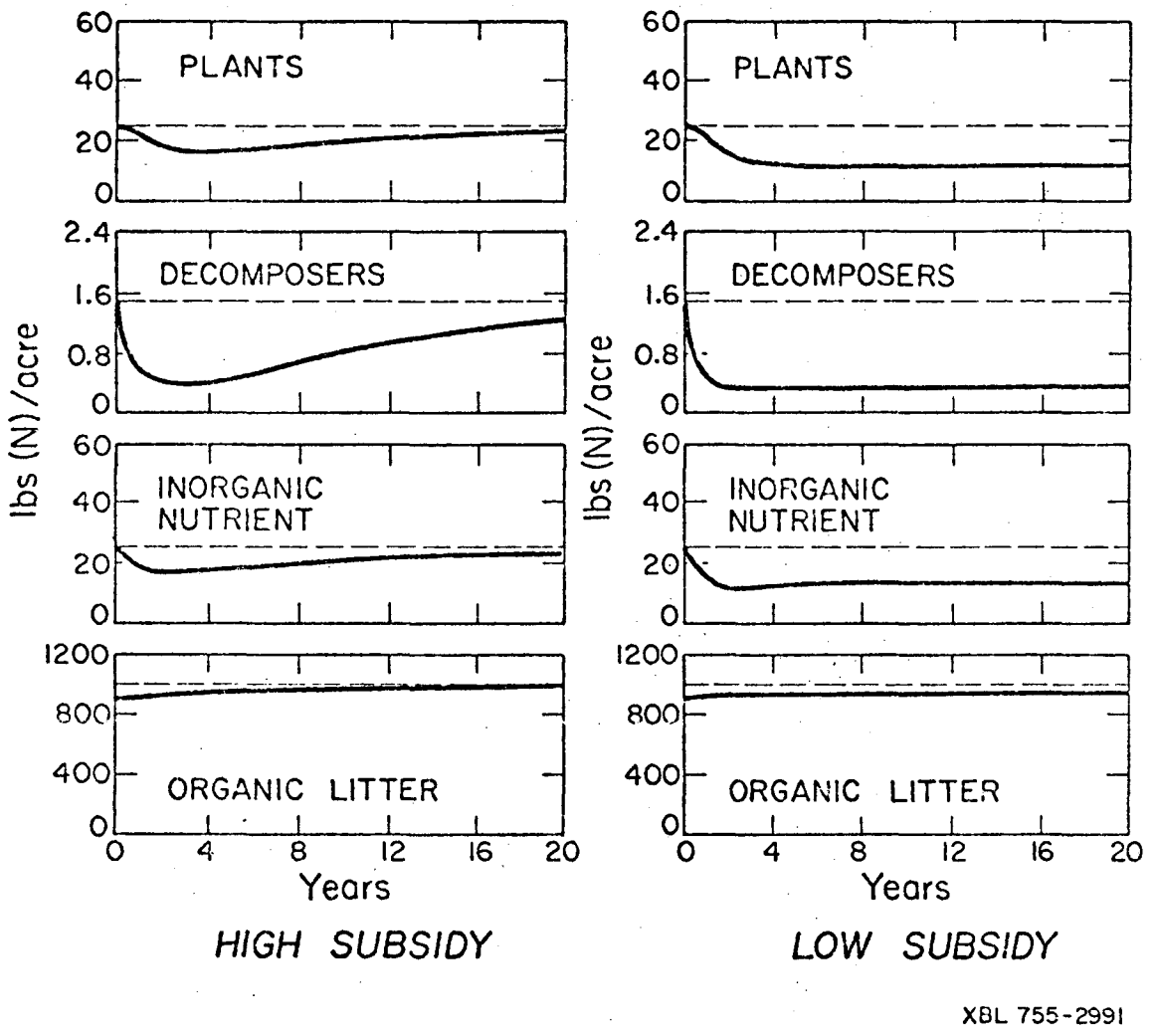
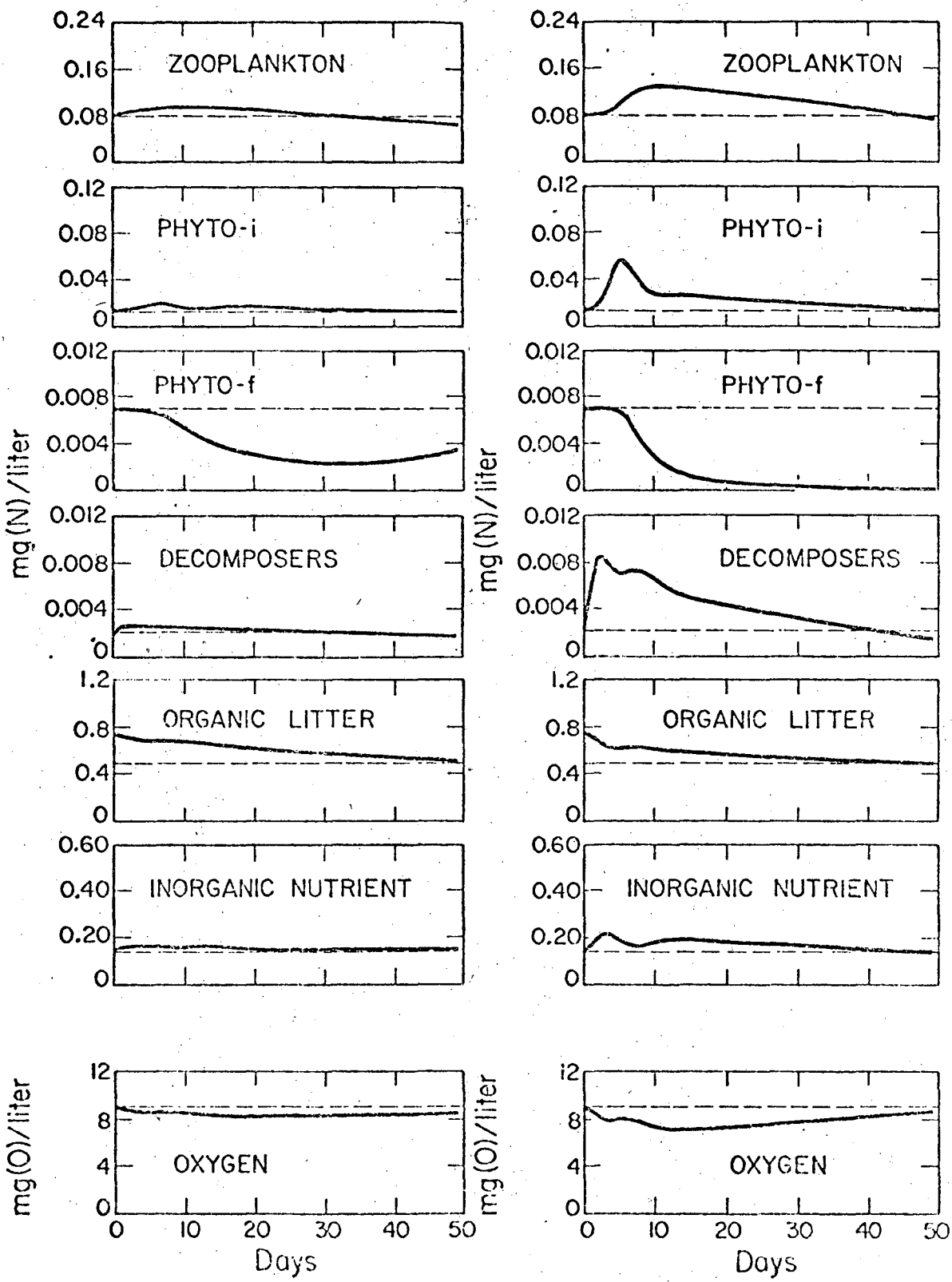

PLANTS
DECOMPOSERS
INORGANIC NUTRIENT
ORGANIC LITTER
lbs (N)/acre
Years
HIGH SUBSIDY
LOW SUBSIDY
XBL 755-2991

Fig. 7



$K_P = 10.0$, $K_D = 0.1$

$K_P = 10.0$, $K_D = 10.0$

XBL 755-2992

Fig. 8

0 0 0 0 4 2 0 2 9 4 7

LEGAL NOTICE

This report was prepared as an account of work sponsored by the United States Government. Neither the United States nor the United States Energy Research and Development Administration, nor any of their employees, nor any of their contractors, subcontractors, or their employees, makes any warranty, express or implied, or assumes any legal liability or responsibility for the accuracy, completeness or usefulness of any information, apparatus, product or process disclosed, or represents that its use would not infringe privately owned rights.

TECHNICAL INFORMATION DIVISION
LAWRENCE BERKELEY LABORATORY
UNIVERSITY OF CALIFORNIA
BERKELEY, CALIFORNIA 94720