ECOLOGICAL STABILITY: A SYSTEMS THEORY VIEWPOINT

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ECOLOGICAL STABILITY: A SYSTEMS THEORY VIEWPOINT

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CHAPTER I

INTRODUCTION

Systems ecologists seek to gain a more thorough understanding of ecosystems through the application of systems theory concepts. Systems analysis provides a formal framework for understanding and quantifying the interactions of a complex system such as an ecosystem. The use of the formal mathematical tools of systems theory necessitates a continual quantification of ecological concepts in order for their importance to be realized in the systems ecology area.

The primary goal of this research effort is the quantification of ecological stability. The name ecological stability has been used to represent several different ecosystem properties (2, 3, 11, 12, 15, 22). Ecological stability here will refer to the ability of an ecosystem to resist changes in the presence of perturbations. The responses of the individual components to perturbation give an indication of the ecosystem's resistance to change. Ecosystems with larger individual component responses are less stable than other ecosystems with smaller responses (2, 11, 12, 18). Ecological stability, then, is a sensitivity concept since the response of the individual components is also an indication of the sensitivity of the ecosystem to perturbation. High sensitivity to perturbation implies large individual component responses and low stability, while low sensitivity implies high stability. Another major objective of this research effort is to develop a total ecosystem sensitivity measure and find its relationship to the ecological stability measure.

The importance of ecological stability can be seen during the process of succession. Succession is a process of self-organization with the ecosystem passing through different states and immediately assuming any state which is more resistant to further change (12). The strategy of succession is increased homeostasis with the physical environment in the sense of achieving maximum protection from its perturbations (18). The process of succession is obviously closely tied to the concept of stability. Selecting a state more resistant to further alteration and achieving maximum protection from environmental perturbations imply that increased stability is selected for during succession. So a measure of stability could be useful in one of two ways. First, long-term changes in a stability measure would indicate the direction of succession. Also, a measure of stability could be used as an objective function for a control problem.

The development of an ecological stability measure leads to consideration of relationships among stability, diversity, and complexity. Diversity indices measure the variety and evenness in the apportionment of individuals, biomass, or energy content among the species within an ecosystem. Although ecological stability tends to increase during succession, diversity sometimes increases and then decreases (12). Thus, the cause-and-effect relationship between diversity and stability is not clear (18). Complexity of the food web structure, or connectivity, refers to the degree and pattern of component interdependence in an ecosystem (21). Ecosystems become more organized and, hence, more complex during succession suggesting that a relationship exists between stability and complexity. A properly chosen measure of ecological stability should maintain the proper relationships to diversity and complexity.

CHAPTER II

REVIEW OF RELATED LITERATURE

Introduction

Ecological stability has been used to represent several different properties of the ecosystem by different authors. The ecosystem property which MacArthur (11), Odum (18), Margalef (12), and Conrad (2) call ecological stability is a sensitivity concept. The magnitudes of the responses of the individual components of the ecosystem in the presence of perturbation are taken as an indication of the stability of the ecosystem. Larger individual component responses by definition mean that the ecosystem is more sensitive to environmental perturbations and, consequently, would be judged to be less stable than other ecosystems with smaller individual component responses. Preston (3) and Margalef (3) equate ecological stability to persistance over time. The ecosystem or population which has persisted over many years would be considered more stable than shorter lived ones. Still others such as Lewontin (3) and May (14) define ecological stability in terms of recovery from perturbation. If an ecosystem returns to its equilibrium state after being perturbed away, it is said to be stable regardless of the magnitude of the fluctuation. This type of stability is equivalent to asymptotic stability of a dynamic mathematical model.

Stability Measures

MacArthur (11) was the first to propose an ecological stability index. This index is based on choice of pathways for energy flow which was suggested by Odum (20). MacArthur's index is best presented by an example. The q's between the compartments of Figure 1 represent the likelihood that the lower compartment is an energy source of the upper compartment. The index is computed using the formula

$$S = \sum_{i=1}^{n} p_i \log p_i, \qquad (2.1)$$

where the p_i's are the products of the q's along each path of the food web. For example, path ABDA yields $p_1 = q_1 \cdot q_3 \cdot q_7$, path ACFA yields $p_2 = q_2 \cdot q_5 \cdot q_{11}$, and so on.

Choice of pathways for energy flow may be interpreted two ways: choice of paths along the entire length of the food chain, which is MacArthur's interpretation, or the choice of paths between individual compartments. The second interpretation resembles more closely what actually occurs in an ecosystem. The flow of energy which occurs based on a choice made in nature spans only one link in the food web. At any instant of time the choice of pathways for energy flow in the total ecosystem is a function of all the choices which result in a flow of energy along one link in the food web.

Other stability measures not based on choice have been proposed by Patten (22) and Margalef (3). Patten's measure is given by

$$S = M^{-1} \sum_{j=1}^{M} \det P_j, \qquad (2.2)$$

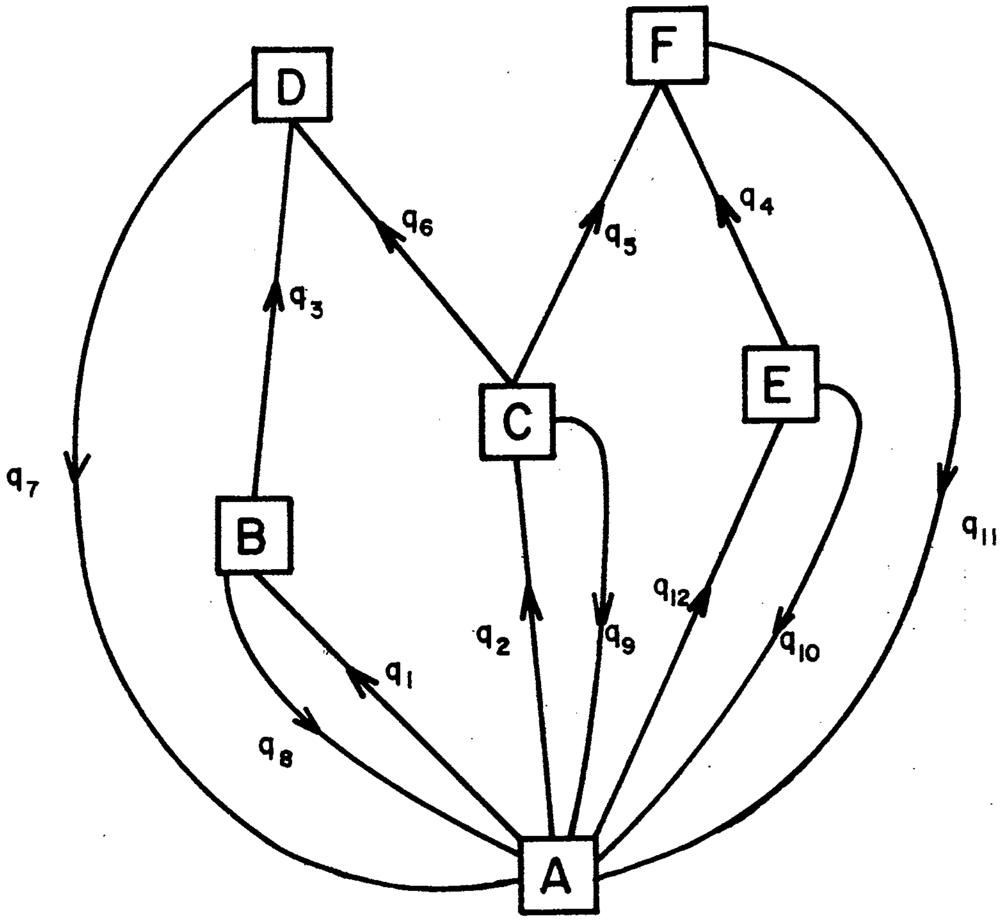

Figure 1. Hypothetical Food Web

where P_j is the matrix of transition probabilities for the j^{th} of M variables,

$$P_j = \begin{bmatrix} P_{id} & P_{ii} \\ P_{dd} & P_{di} \end{bmatrix} . \qquad (2.3)$$

P_{id} is the probability for decrease in the value of the variable following an increase, P_{ii} for an increase following an increase, etc. The obvious shortcoming of this measure lies in its consistency. No method is given for computing or estimating the transition probabilities leaving them open to interpretation and inconsistent.

Margalef defines ecological stability in terms of persistance over time. The stability measure is given by

$$S = (1/C_1) \sum_{i=1}^{n} b_i t_i, \qquad (2.4)$$

where b_i is the fraction that any species, i, is of the total biomass and t_i is the time measure for the biomass to be reduced to 50%. The time measure, t_i, is closely related to the turnover time of a compartment. Consider a general n^{th} order compartment model assuming linear, donor-controlled energy flows (Appendix A).

The i^{th} member of the set of n equations is given by

$$\dot{X}_i = \sum_{j=1}^{n} a_{ji} X_j - \sum_{i=1}^{n} a_{ik} X_i . \qquad (2.5)$$

Turnover is defined as the ratio of throughput (Y_i) to content (X_i) of the i^{th} compartment,

$$T_i = Y_i / X_i \tag{2.6}$$

For the linear, donor-controlled energy flow assumption,

$$Y_i = \sum_{k=1}^{n} a_{ik} X_i . \tag{2.7}$$

So,

$$T_i = \frac{\sum_{k=1}^{n} a_{ik} X_i}{X_i} = \sum_{k=1}^{n} a_{ik} . \tag{2.8}$$

The turnover time, τ_i, is the reciprocal of the turnover, so equation (2.5) becomes

$$\dot{X}_i = \sum_{j=1}^{n} a_{ji} X_j - \frac{1}{\tau_i} X_i . \tag{2.9}$$

If the inputs to the i^{th} compartment are removed, then

$$\dot{X}_i = - \frac{1}{\tau_i} X_i . \tag{2.10}$$

Equation (2.10) has the solution

$$X_i = X_o \cdot e^{-t/\tau_i} \tag{2.11}$$

where X_o is the initial condition and t is time. For this case the turnover time, τ_i, is the time constant, or the time required for a 62% reduction from the initial condition. Thus, the stability measure proposed by Margalef, summing a time measure, t (time required for a 50% reduction) weighted by percent biomass, is closely tied to summing turnover times weighted by percent biomass.

May (15) discusses the relationship between complexity of the food web and the mathematical stability of generalized Volterra-Lotka equations:

$$\dot{N}_i = N_i \left(a_i - \sum_{j=1}^{m} b_{ij} N_j\right). \tag{2.12}$$

May's conclusion is that the model (m equations of the form of (2.12)) provides a specific counterexample to any universal use of trophic link counting as a measure of stability. While May has shown that increased complexity of the food web sometimes leads to instability of the generalized Volterra-Lotka ecosystem model, a question arises as to the biological significance of this result. Is the model instability a result of ecosystem interactions or simply a modeling insufficiency? The latter conclusion seems the more plausible. Ecosystem models are typically constructed to predict or reproduce measurements of the number of individuals, energy, or biomass content of functional classes of individuals. The number of individuals, biomass, or energy content of these functional classifications is determined by many factors such as competition, predation, or tolerance to environmental changes. In the absence of fundamental physical laws to describe these factors they must be described in the context of a particular ecosystem. When fundamental physical laws are used to construct a model, then the behavior of the model can be used to infer system properties. For instance, a mathematical model of electrical network can be used to determine the component values to assure stable behavior of the network. But due to the methods of constructing and identifying the generalized Volterra-Lotka model, it seems unlikely that any ecosystem properties cause the instability of the model reported by May.

Complexity Measures

Complexity and connectivity refer to the degree and pattern of component interaction. These ecological variables depend upon the number and relative importance of the energy pathways in an ecosystem. The only complexity measure appearing in the literature concerns itself with the number of energy pathways and ignores the relative importance of each pathway (21). If the relative importance component of complexity is ignored, a food web may appear to be quite complex when actually because of the small amounts of energy which pass through most of the pathways, it is quite simple and for all practical purposes a linear food chain. A more advanced approach would be to determine directly the diversity of links or pathways in the network pattern (18).

Diversity Measures

Diversity measures give an indication of the variety and evenness in the apportionment of individuals, biomass, or energy content among the species of an ecosystem. Diversity indices should be dimensionless, reasonably independent of sample size, and express the relative importance of each species. Many indices have been proposed (5, 13, 14, 16, 23), but most fail to satisfy one or more of the above properties. The most widely used formula is given by (25),

$$\overline{D} = \sum_{i=1}^{n} p_i \log p_i \qquad (2.13)$$

where p_i is the probability of selecting an individual from the i^{th} species. This probability, p_i, is commonly estimated from sampled values (n_i/n) where n_i is the number of individuals, biomass, or energy content of the i^{th} species and n is the total individuals, biomass, or energy content in the sample. This index has the desired properties and is now used commonly as a measure of diversity.

CHAPTER III

QUANTIFICATION OF ECOLOGICAL STABILITY

Introduction

Ecological stability refers to the ability of an ecosystem to resist changes in the presence of perturbations. Ecological stability has been related to choice of pathways for energy flow (20). Choice depends on the degree and pattern of component interdependence which defines the complexity of food web structure. Increased choice results from a larger and more complex organic structure which mitigates perturbations of the physical environment (18). Choice may be increased in two ways, either of which may or may not be accompanied by increased diversity; increased numbers of possible alternatives as energy sources and consumers, or by a more uniform interdependence among the existing energy sources and consumers. But, a more diverse ecosystem has the potential of becoming more complex and possessing more choice than a less diverse one.

In this chapter a measure of ecological stability is developed using choice, presented from an information theory viewpoint, as an index. Relationships among ecological stability, diversity, and complexity consistent with observed behavior arise naturally within this development. The usefulness of the resulting ecological stability measure is examined with the aid of dynamic mathematical models of two actual ecosystems.

The Meaning of Choice

The concept of choice is a fundamental consideration in information theory, a mathematical theory developed in the 1940's by C. E. Shannon for dealing with communications systems (6). The most simple communication system consists of a source, channel, and a receiver (Figure 2). The source output of Figure 2 might represent a set of sensors, a voice waveform, or a sequence of binary digits from a magnetic tape. Information from the source is transmitted through the channel which may be as simple as the distance between two people, one speaking to the other, or as complex as a high frequency satellite communication link. Due to the presence of noise, many communication situations can be represented by probabilistic models. One probabilistic model may be visualized as an experiment with outcomes chosen from a set of possible alternatives with a probability measure on the alternatives. The set of possible alternatives is called the sample space, each alternative being an element of the sample space. A sample space and its probability measure is called an ensemble. In this development the source ensemble will be denoted by X and the probability that the outcome x will be a particular element a_k of the sample space will be denoted by $P_X(a_k)$. Similarly, the received ensemble at the destination in Figure 2 will be denoted by Y, and the probability that the outcome y will be a particular element b_j of the sample space will be denoted by $P_Y(b_j)$.

If the source is assumed to consist of K arbitrary events and the k^{th} event has probability $P_X(a_k)$, then its self-information is defined as (6).

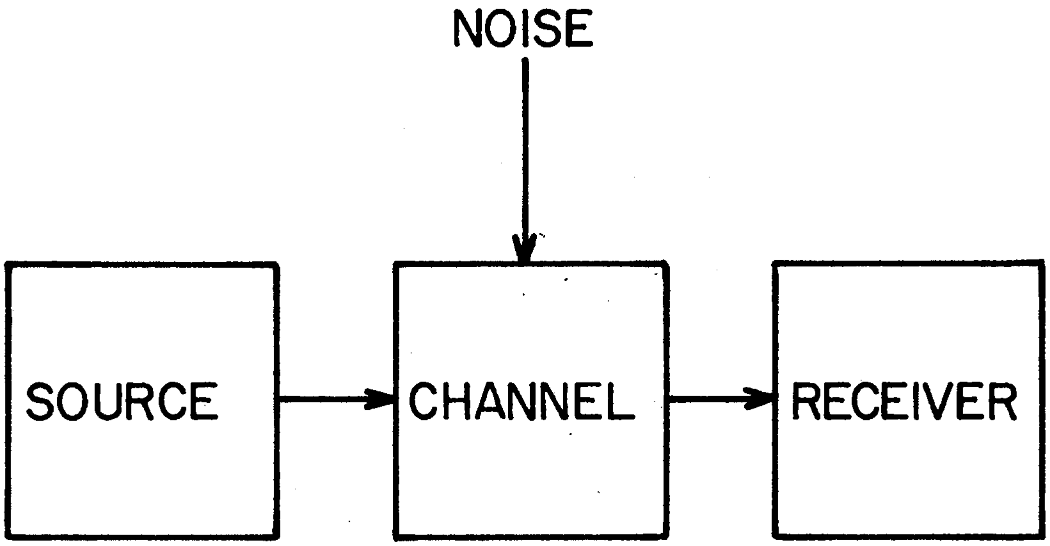

Figure 2. Block Diagram of a Simple Communication System

$$I_X(a_k) = - \log P_X(a_k). \tag{3.1}$$

This definition provides a measure of information associated with each of the K arbitrary events of the source. The unexpectedness at the occurrence of an event is measured rather than its particular interest or meaning, i.e. $P_X(a_k) = 1$ yields $I_X(a_k) = 0$, or no information conveyed. The average value of self-information over all the arbitrary events is the uncertainty associated with the selection of an event and is known as the entropy of the ensemble. It is given by (6),

$$H(X) = - \sum_{k=1}^{K} P_X(a_k) \log P_X(a_k). \tag{3.2}$$

Mutual information is defined as the information provided about the event $x = a_k$ by the occurrence of the event $y = b_j$. A quantitative measure of mutual information should measure how much information the occurrence of a particular alternative, b_j, in the Y ensemble provides about the occurrence of some alternative, a_k, in the X ensemble. The probability, $P_X(a_k)$, is an <u>a priori</u> probability concerning the occurrence of the alternative a_k. The occurrence of outcome $y = b_j$ changes this <u>a priori</u> probability to the <u>a posteriori</u> probability $P_{X/Y}(a_k/b_j)$, which is the probability that $x = a_k$ has occurred conditioned on the occurrence of the event $y = b_j$. A widely used quantitative measure of mutual information is the logarithm of the ratio of <u>a posteriori</u> to <u>a priori</u> probability given by the formula (6),

$$I(a_k;b_j) = \log \frac{P_{X/Y}(a_k/b_j)}{P_X(a_k)} \quad . \tag{3.3}$$

The expected value, which is called the average mutual information, is given by (6),

$$I(X;Y) = \sum_{k=1}^{K} \sum_{j=1}^{J} P_{XY}(a_k;b_j) \log \frac{P_{X/Y}(a_k/b_j)}{P_X(a_k)} \; , \tag{3.4}$$

where $P_{XY}(a_k;b_j)$ is the joint probability that $y = b_j$ and $x = a_k$ have occurred.

Conditional self-information can be interpreted as the information that must be supplied to an observer to specify $x = a_k$ after the observer has observed the occurrence of $y = b_j$. The conditional self-information of an event $x = a_k$, given the occurrence of $y = b_j$, is defined as (6),

$$I_{X/Y}(a_k/b_j) = - \log P_{X/Y}(a_k/b_j) . \tag{3.5}$$

The average value of conditional self-information is given by (6),

$$H(X/Y) = \sum_{k=1}^{K} \sum_{j=1}^{J} P_{XY}(a_k;b_j) \log P_{X/Y}(a_k/b_j), \tag{3.6}$$

and can be interpreted as the average information required to specify x after y is known.

Combining definitions (3.1), (3.3), and (3.5) the following relationship results,

$$I_{XY}(a_k;b_j) = I_X(a_k) - I_{X/Y}(a_k/b_j). \qquad (3.7)$$

Rearranging and averaging over the XY ensemble this relationship becomes

$$H(X/Y) = H(X) - I(X;Y) \qquad (3.8)$$

where H(X) can be interpreted as the average uncertainty in X before observation of Y, I(X;Y) as the average amount of uncertainty in X resolved by the observation of the outcome in the Y ensemble, and H(X/Y) as the average remaining uncertainty in X after the observation. The entropy, H(X), is a function only of the source, while I(X;Y) and H(X/Y), for a given H(X), are functions of the channel each with a maximum value of H(X) and a minimum value of zero. The average remaining uncertainty as measured by H(X/Y) can be interpreted as the effective freedom to exercise choice in a system. No uncertainty remaining in X, after observation of Y, would imply resolved uncertainty, I(X;Y), is equivalent to initial average uncertainty, H(X), and the effective freedom of choice is zero. Similarly, remaining average uncertainty equal to H(X) implies no resolved uncertainty (I(X;Y)=0) and freedom of choice is maximum for the given X ensemble. The relationship between remaining average uncertainty and choice is illustrated in Figure 3.

Because of the many types of communication systems, the channel as shown in Figure 2 may take many forms. The channel might represent a telephone line, a storage medium, a radio link, or a biological

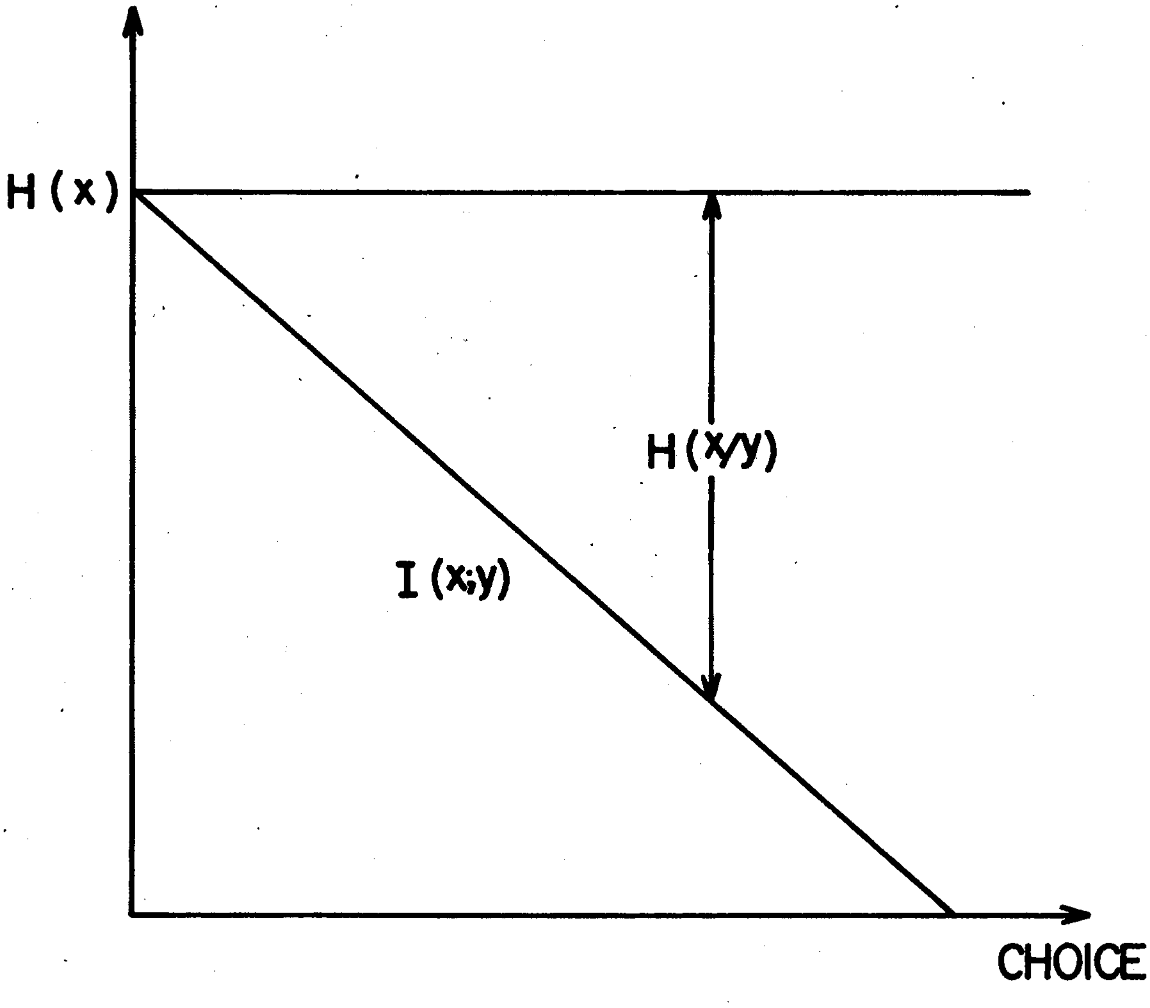

Figure 3. Relationships Among Entropy, H(X), Average Mutual Information, I(X;Y), Conditional Entropy, H(X/Y), and Choice

organism. Since the channel is usually subject to noise, it is usually specified in terms of the set of inputs available at the input terminal, the set of outputs available at the output terminal, and for each input the probability measure on the output events conditioned on that input. In the present study, a discrete memoryless channel will be considered. For this channel, the input and output are each sequences from finite sets of arbitrary events and for which the output at a given time depends statistically only on the corresponding input. The channel is specified by the transition probability assignment $P_{Y/X}(j/k)$, given $1\leq j\leq J$ and $1\leq k\leq K$. By definition $P_{Y/X}(j/k)$ is the probability that arbitrary event $y = b_j$ will be received given that arbitrary event $x = a_k$ is the input. Of particular interest later is the form of equation (3.8) for the discrete memoryless channel which becomes,

$$H(X/Y) = -\sum_{k=1}^{K} P_X(a_k)\log P_X(a_k) - \sum_{k=1}^{K}\sum_{j=1}^{J} P_X(a_k)P_{Y/X}(j/k)\log\frac{P_{Y/X}(j/k)}{P_Y(b_j)} \qquad (3.9)$$

Choice in an Ecological Context

Ecological stability is a dynamic characteristic of an ecosystem. Although the conventional compartment model diagram has an implicit dependence on time, a modified compartment model diagram is now introduced which explicitly shows this dependence. Consider such a compartment diagram as given in Figure 4. In this diagram, the n compartments, denoted by $X_1, X_2, \ldots, X_n$ are represented at two arbitrary times t_1 and t_2. The other terms of Figure 4 are defined as follows:

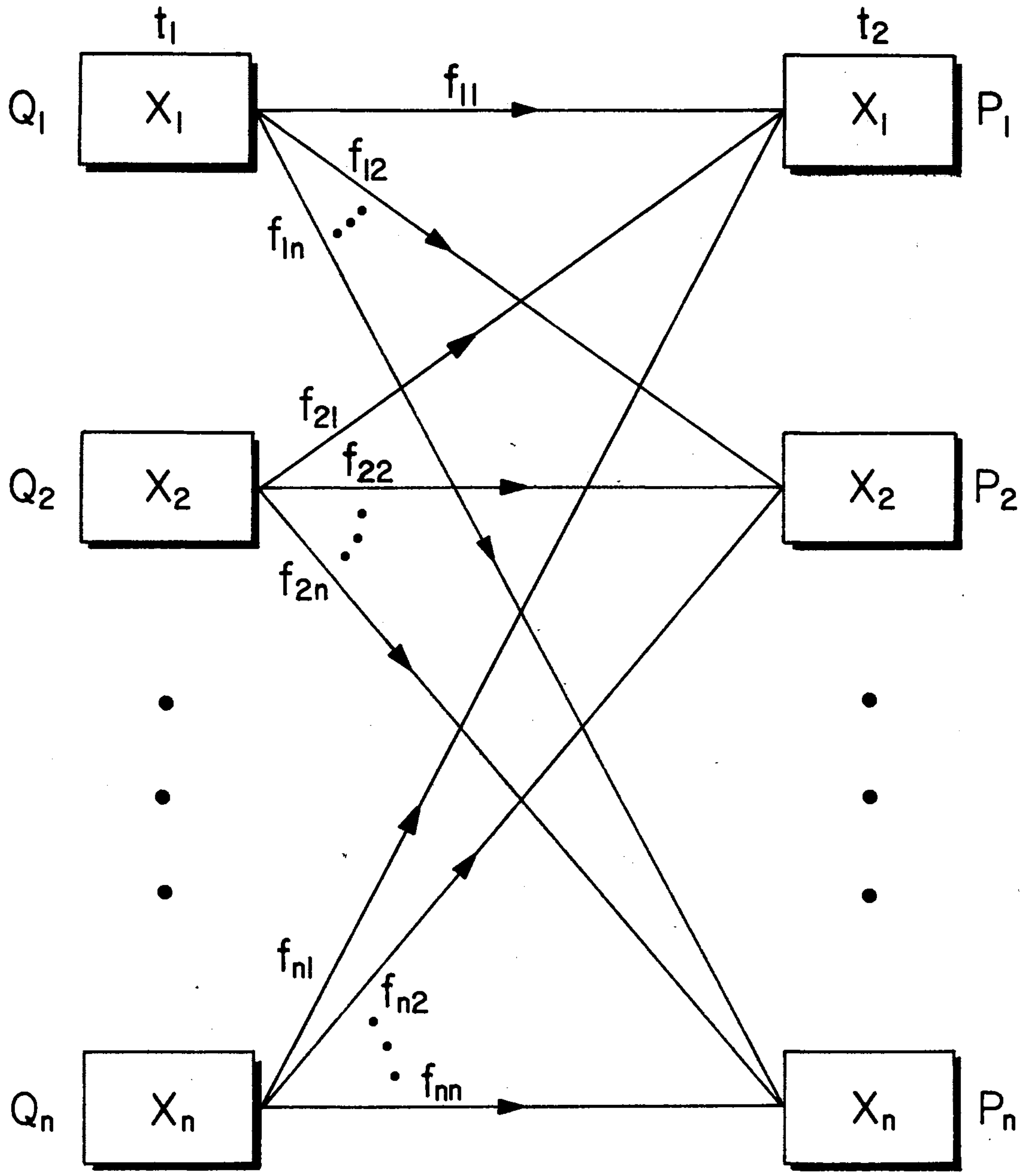

Figure 4. Modified Compartment Diagram

Q_i - percentage of the total energy flow through the ecosystem at time t_1 which passes through the i^{th} compartment.

P_j - percentage of the total energy flow through the ecosystem at time t_2 which passes through the j^{th} compartment.

f_{ij} - percentage of the total energy flow through the i^{th} compartment that passes to the j^{th} compartment between times t_1 and t_2.

The percentages Q_i and P_i refer to compartment X_i considered at different times with any difference in these variables accounted for by f_{ij}. The relationships between these variables is provided by the equation,

$$P_j = \sum_{i=1}^{n} f_{ij} Q_i. \qquad (3.10)$$

Diversity and the complexity of food web structure, or connectivity, are central to the development of an ecological stability measure. Diversity indices usually measure the variety and evenness in the apportionment of individuals, biomass, or energy content among the species within an ecosystem; but since choice of pathways for energy flow is being used as an index, diversity will refer to the throughput of energy of the ecosystem. Throughput is related to content by,

$$\text{throughput} = \text{content x turnover} \qquad (3.11)$$

where turnover is the reciprocal of the time a specific increment of energy remains in a compartment. Included in the diversity of the throughput of energy are the flows which represent energy used and respired by the ecosystem resulting in additional environmental compartments to represent these variables. These additional environmental compartments were also used by MacArthur (11) in a similar study.

Although diversity is an important ecological concept, measures of diversity do not provide an adequate expression of component interdependence but merely the potential for the existence of such interdependences (12, 18). Diversity does not completely characterize the choice of pathways for energy flow and, as has been demonstrated experimentally (7), cannot be used exclusively as a measure of ecological stability. The choice of pathways for energy flow and ecological stability depend also on the degree and pattern of component interdependence which is defined as complexity of the food web structure, or connectivity.

At time t_1, before knowledge about the food web is introduced, the diversity of the ecosystem in terms of its throughput as measured by

$$\overline{D}_T = - \sum_{i=1}^{n} Q_i \log Q_i, \tag{3.12}$$

can be thought of as a measure of the uncertainty about how energy from specific sources is distributed among the compartments. The probability, $P_X(x_i)$ that a particular compartment will be selected as an energy source is approximated by the sampled percentage, Q_i, as defined previously.

The food web structure determines the pathways for energy through the ecosystem. This structure prescribes the destinations and relative amounts to each of those destinations of the energy throughput of each compartment. The distribution of energy flow in an ecosystem can be appropriately represented using probabilistic models. For every increment of energy passing through a compartment, a probability assignment can be made as to its ultimate destination. More formally, given that a specific increment of energy has passed through the k^{th} compartment, $P_{Y/X}(j/k)$ is the probability that the specific increment of energy will be taken up by the j^{th} compartment. This probability assignment specifies the channel for the 'transmission' of energy through an ecosystem. The channel probability assignment can be approximated with sampled percentages as with the diversity measure. The probability $P_{Y/X}(j/k)$ can be approximated by the sampled percentage f_{jk} which has been previously defined.

The flow of energy through an ecosystem as defined in Figure 4 specifies a discrete memoryless channel. The average uncertainty resolved about the source of an increment of energy by its uptake can be approximated using sampled percentages by,

$$I = \sum_{k=1}^{n} \sum_{j=1}^{n} Q_i f_{ij} \log \frac{f_{ij}}{P_j}. \tag{3.13}$$

The average remaining uncertainty as measured by equation (3.8) can be approximated by,

$$S = \overline{D}_T - I. \tag{3.14}$$

The average remaining uncertainty is equivalent to effective choice of pathways for energy flow. So, equation (3.14) is also a measure of choice of pathways for energy flow and, therefore, is a useful index of ecological stability.

Complexity refers to the degree and pattern of component interdependence and reflects the opportunities for choice of path. So, a measure of choice can also be used as an index of complexity of food web structure.

The proposed ecological stability measure, (3.14), is a function of the time period,

$$\Delta t = t_2 - t_1. \tag{3.15}$$

If the time period is chosen to be the same length as the period of any of the major driving functions, such as sunlight and temperature, then only successional changes will be seen. But, smaller time period selections will produce seasonal dynamics. The smallest time period which may be chosen depends on the source of the necessary energy flow data. When actual data are being used, the primary consideration is the discovery of all energy pathways in the ecosystem. A minimum time period bound, greater than the longest time between feedings of all the species of organisms within an ecosystem, must be established. When a continuous mathematical model generates the data, the discrete energy flows are modeled by equivalent continuous energy flows. Thus, the food web structure is known at all times and no minimum time period bound is necessary.

The quantitative definition of ecological stability, S, is consistent with statements and observations made by ecologists about stability. Margalef (12) observed that, in some ecosystems, diversity increases then decreases during succession. This behavior can be explained within the context of equation (3.14). If the species within an ecosystem become more interdependent, the resolved uncertainty, I, decreases. If the decrease in I is greater than the corresponding decrease in $\overline{D}_T$,as observed by Margalef, then the stability as measured by equation (3.14) may still increase. Hutchison (9) states ". . . complex trophic organization of a community is more stable than a simple one, . . ." This statement is totally consistent with both the rationale used in developing the stability measure as well as its quantitative behavior.

Stream Ecosystem Example

The objective of this experiment is to determine the usefulness of the stability measure as an objective function for a control problem. A model is constructed using data from a study of the effects of an energy subsidy on a stream community (27). Using the model to simulate the ecosystem, the control problem is to determine the level of energy subsidy which maximizes the stability measure at the end of one year.

From 1960 through 1963, Warren et al. (27) studied production, food habits, and food consumption of coastal cutthroat trout in sucrose-enriched and in unenriched sections of Berry Creek, a small woodland stream in the Willamette River Basin of Oregon. These experiments were part of a general study of the trophic pathways through which energy from light, organic debris, and dissolved organic matter enters into the production of fish and other organisms. The water in two sections of the stream was continuously enriched by introducing sucrose to maintain a 4.0 mg/l concentration, while two other stream sections were maintained in their natural state. The trophic structure of the woodland stream is typical of most ecosystems with primary producers, herbivores, carnivores, and top carnivores (Figure 5). From the data contained in Riffle A and several general references (1, 10, 18, 27, 28, 29, 30), a compartment diagram was constructed (Figure 6). The energy flows and contents indicated on the diagram are mean values on a per month basis. From the data in Figure 6, a linear, donor-controlled model was developed. The model includes the effects of light, temperature, and terrestrial import and is time varying. The simulation period is one year with the mean value of the energy contents of the compartments over the simulation period being equal to the standing crops reported by Warren, et al. in Figure 6. Although the model was constructed using data from unenriched sections of the stream, terms were included which caused the energy contents of the compartments to change to those of the enriched sections, Riffle B in Figure 5, when the sucrose concentration is increased from 0.0 to 4.0 mg/l. Thus, the sucrose concentration may be adjusted to any desired intermediate value. Since the energy contents generated by the model closely approximated those reported by Warren, et al. (28) for 0.0 and 4.0 mg/l sucrose concentrations, it seems reasonable that for intermediate sucrose concentrations the model will also generate energy contents closely resembling those which might be found experimentally.

To determine the sucrose concentration which maximizes the stability index at the end of one year, a fine control grid was established with 0.4 mg/l increments between 0.0 and 4.0 mg/l. Beginning with the initial conditions of the unenriched sections, simulations were performed at each of these grid points (Figure 7). Since the model is linear and the solutions well behaved, the optimization method

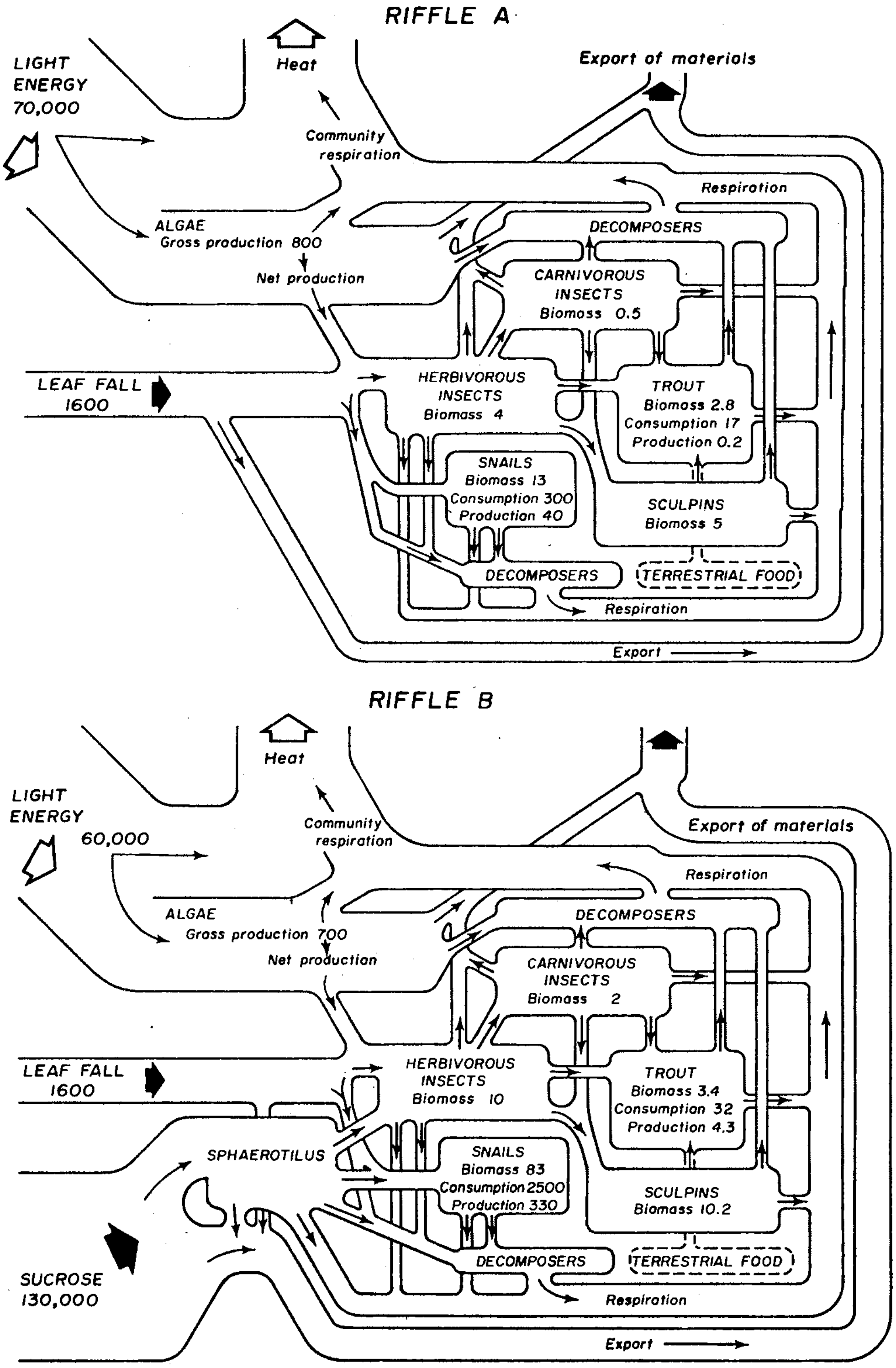

Figure 5. Energy Flow Diagram of Berry Creek After Warren 1971 - All Values in Kilocalories per Square Meter per Year

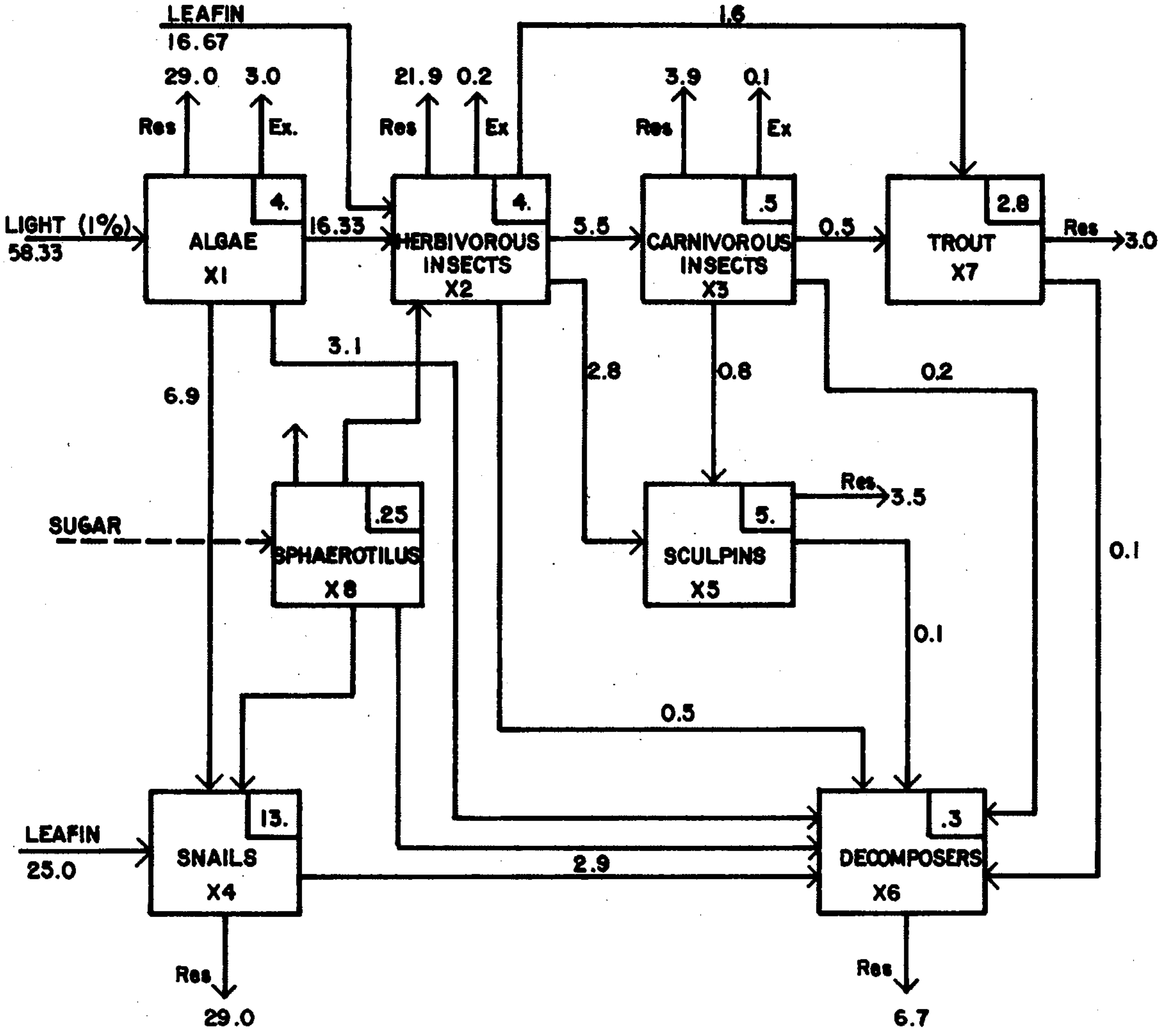

Figure 6. Energy Flow Diagram of Berry Creek - All Values in Kilocalories per Square Meter per Month

described above proved sufficient for the present study. A sucrose concentration of 2.0 mg/l produced the maximum value of the stability index at the end of one year. This result is consistent with the rationale on which the stability index is based. An additional source of energy is provided which creates additional energy pathways in the ecosystem (Figure 5). The additional energy pathways increase the choice of pathways for energy flow. For a sucrose concentration of 2.0 mg/l effective choice is maximum indicating this concentration would produce maximum stability. The stability index thus appears to be a viable objective function for this particular ecosystem and perhaps other ecosystems where the effect of a particular action on the total ecosystem is desired.

The time period, equation (3.15), chosen for computing the stability index was one month. Because the data are generated from a continuous mathematical model, no minimum time period bound exists. So, the time period was chosen small enough to produce dynamic behavior of the stability index over the simulation period. Several of the stability index trajectories are shown in Figure 8. The dynamic behavior of the trajectories is caused by a changing organization of the ecosystem, reflected in changes in the degree and pattern of energy flow. Ecosystems are exposed to reoccurring environmental changes (4, 19) such as seasonal sunlight, moisture, and temperature variations. During ecological succession, organisms develop adaptive mechanisms in response to environmental changes and adaptive changes made by other interdependent organisms resulting in a changing organization of the ecosystem. This adaptive process also causes organizational changes in response to reoccurring environmental changes such as yearly rhythms.

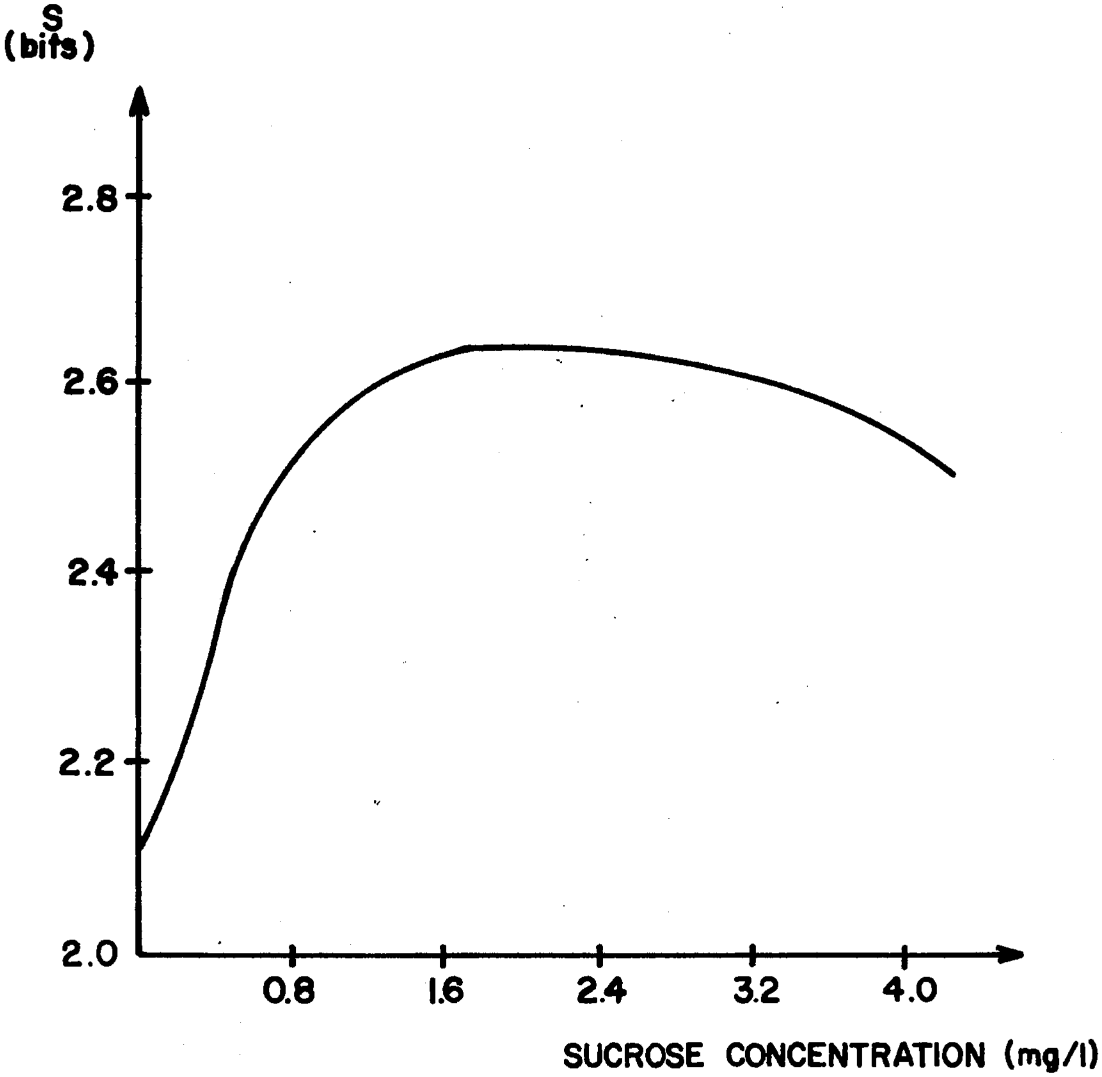

Figure 7. Stability Index - Sucrose Concentration Plot

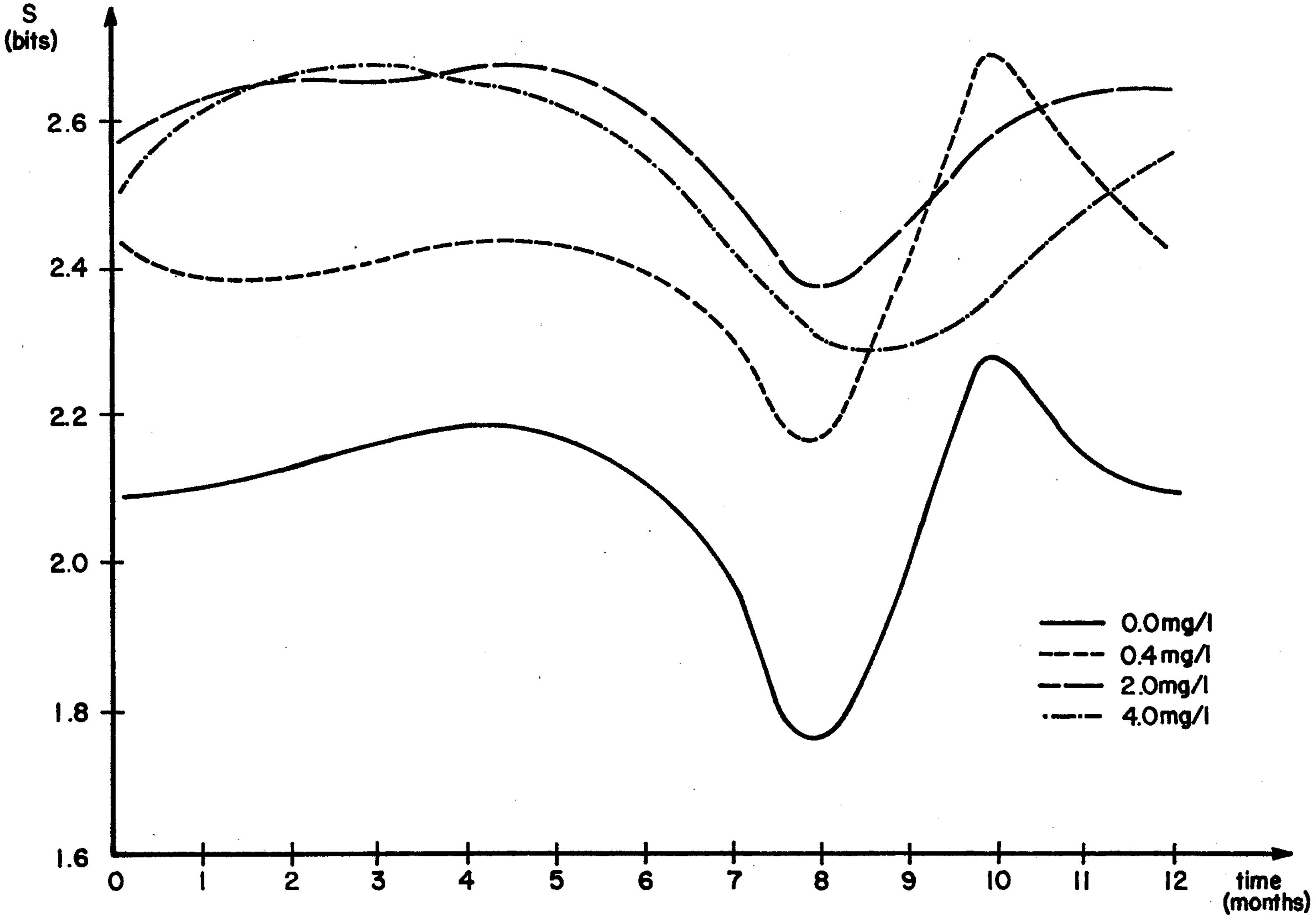

Figure 8. Stability Index Trajectories - Sucrose Concentration Plot

Seasonal succession and other periodicities often follow the same pattern as ecological succession, namely, an early seasonal bloom characterized by rapid growth of a few dominate species followed later in the season by increased diversity, high B/P ratios, and a relatively steady state in terms of P and R (18). In ecological succession these three late season characteristics imply increased stability (18). The stability index trajectory for the unenriched stream section shows that for seasonal succession they also imply increased stability (Figure 8). A definite and pronounced maximum occurs in late January and early February.

The response of a species to changes in an environmental factor is shown in Figure 9. Typically, there exists an optimum range of an environmental factor with respect to a particular species (26). Deviations of the factor within the optimum range have little or no effect on the population density of that species. But, deviations from the optimum range decrease the population density until it becomes zero when the minimum or maximum tolerance is reached. Also, an interaction between factors occurs causing the effect of one factor not to be the same at all levels of another factor. This factor interaction may be either positively or negatively correlated. For instance, maximum temperature and light intensity and minimum oxygen concentration in the stream typically occur at the same time. As environmental conditions deviate from their optimum ranges the environment becomes more harsh with the most harsh conditions occurring when the total deviation is greatest. Environmental factors are closer on the average to the minimum or maximum tolerance levels under most harsh conditions than at any other time. So, perturbation is more likely

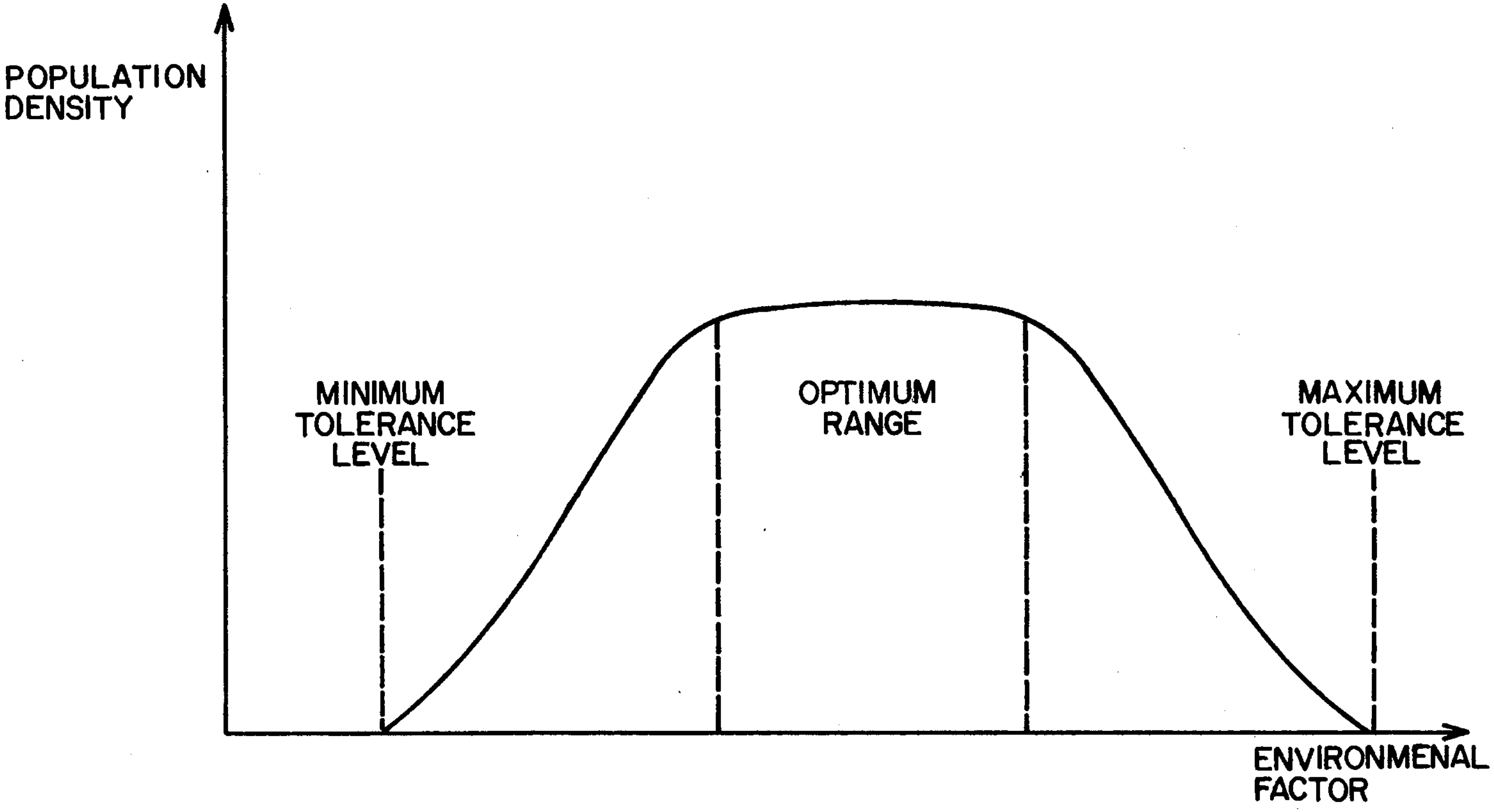

Figure 9. Population Density - Environmental Factor Plot

to cause a minimum or maximum tolerance level to be reached resulting in the local extinction of a particular species. Perhaps, those organizations which possess higher stability (resistance to change) when environmental conditions are most harsh are selected for during succession.

As the sucrose concentration is increased, the form of the stability index trajectory is changed (Figure 8). The stream community has evolved such that it possesses specific organizations in response to environmental changes. The addition of sucrose caused this response to be altered. This behavior suggests that if a specific sucrose concentration is maintained, as it would be with some pollutants (28), additional long-term community changes could be expected.

Shortgrass Prairie Ecosystem Example

The objective of this experiment is to determine the usefulness of the stability index as an indicator of the effect of environmental stress. A mathematical model is used to simulate a shortgrass prairie over a 20 year period for normal and reduced moisture conditions. The behavior of the stability index is examined to determine the effects of the reduced moisture conditions.

The shortgrass prairie ecosystem to be considered is part of the Pawnee National Grassland in northeastern Colorado. The shortgrass prairie ecosystem can be divided into four sections: abiotic, producer, consumer, and decomposer. The abiotic section consists of the system driving functions such as light intensity, temperature, moisture, and nutrients. The producer section contains warm season and cool season grasses, forbs, cacti, below-ground plant parts, plants standing dead, and plant litter. The consumer section consists of wild and domestic herbivores, carnivores, birds, and insects. The decomposer section consists of 28 compartments. These compartments can be divided into five sectors: root, soil, litter, and carrion organisms, and a nitrogen pool subsystem. The function of the decomposer section is to decay organic matter from producers and consumers and to generate a pool of inorganic soil nitrogen which then regulates plant primary production.

The model to be used in the present study was produced as a systems ecology class exercise under the direction of Patten (24) and is an outgrowth of one developed by the Grassland Biome Study Group of the United States International Biological Program. The model is a piecewise linear, donor-controlled compartment model (Appendix B). The principal variables of the model are biomass (total dry weight of organisms in gm^{-2}) and total inorganic nitrogen (gNm^{-2}). The model is piecewise due to the method used to regulate plant net production based on the availability of soil nitrogen. Potential net photosynthesis of the four compartments for plants living above ground, VA(I), I = 1, . . . , 4, was formulated from the driving variables of the abiotic section:

$$\text{PHOTO(I)} = \text{SUN} * \text{TEMP} * \text{MOIST} * \text{EFF(I)} \qquad (3.16)$$

where EFF(I) represents constant efficiency coefficients for each of the four plant compartments. The system driving functions, sunlight, air temperature, and soil moisture were represented by the following functions:

$$\text{SUN} = 200. * \text{SIN}(.12093 * t) + 400. \tag{3.17}$$

$$\text{TEMP} = (9.0 + 11.0 * \text{SIN}(.1293 * t - .3424)) * 0.061 \tag{3.18}$$

$$\text{MOIST} = 2.0 - 0.07692 * t \tag{3.19}$$

where t represents time in weeks. MOIST is assumed to be zero after the initial growing season of 23 weeks.

Availability of soil nitrogen to each plant compartment was taken as proportioned to the nitrogen pool Q9:

$$\text{ANI(I)} = \text{FNI(I)} * \text{Q9} \tag{3.20}$$

where ANI(I) is nitrogen available to VA(I) and FNI(I) are constant coefficients. A nonlinear switch was introduced in the formulation of actual net production:

$$\text{FORCE(I)} = \begin{cases} \text{PHOTO(I)} & \text{PHOTO(I)} \leq \text{ANI(I)} \\ \text{ANI(I)} & \text{OTHERWISE} \end{cases} \tag{3.21}$$

This equation sets actual net production of VA(I) equal to potential net production PHOTO(I) if nitrogen ANI(I) is not limiting, or to an amount of photosynthesis equal (in biomass units) to available nitrogen when the latter is limiting.

To evaluate the stability index all the flows from one compartment to another must be known. In some instances in the model formulation the biomass flow from a compartment was said to go to a section or sector of the ecosystem rather than to particular compartments (24). For example, a biomass flow from the carnivores, C3, went to the carrion sector of the decomposer section. In these instances it was assumed that the flow to each compartment in the section or sector was linearly proportioned to the percent biomass that particular compartment was of the total biomass of the section or sector.

The soil moisture driving function, equation (3.19), represents soil moisture storage over a normal 23 week growing season beginning on March 20. To moisture stress the model of the shortgrass prairie the soil moisture storage was reduced by 20% over the entire growing season resulting in the following equation for MOIST:

$$MOIST = 1.6 - 0.06154 * t. \qquad (3.22)$$

This moisture level is within the normal operating experience of the shortgrass prairie ecosystem (24). The model was moisture stressed in a similar manner by Patten (24) with the following results.

> While aboveground biomass of vegetation declined in proportion to the loss of soil water, roots, VB, were conserved (only 3% reduction). This is consistent with the known ecology of root systems, which tend to be highly resistant to perturbing influences. Soil nitrogen, Q9, increased slightly; nitrogen never became limiting in this experiment due to the reduced values of PHOTO(I). Carrion AD increased slightly, but fecal material SH more than doubled. Unusual accumulations of feces are symptomatic to range managers that something is out of balance in the ecosystem. The simulation appears to have captured this characteristic quite well.

A 20 year simulation with normal moisture conditions showed that the shortgrass prairie was in steady state (24).

In the present study the shortgrass prairie ecosystem was simulated over a 20 year period for both normal and reduced moisture conditions and the stability measure observed over time. The time period chosen for computation of the stability measure is one week due to the piecewise nature of the model. The results of the experiments appear in

Figures 10, 11, 12, and 13. Stability index trajectories for the first and twentieth years for normal moisture conditions (Figure 10) showed the ecosystem to be in steady state as reported by Patten (24). Except for the first ten weeks of the growing season, the difference between the trajectories is less than 2%. The twentieth year trajectory is greater than the first year trajectory for 39 weeks of the year. Stability index trajectories for the first and twentieth years for reduced moisture conditions (Figure 11) indicated that succession had been reversed. The twentieth year trajectory was lower than the first year trajectory for 48 weeks of the year. Continued exposure to reduced moisture conditions would be expected to lead to a less complex and, therefore, less stable ecosystem.

The shortgrass prairie ecosystem is primarily determined by moisture conditions (24). Sufficient reduction in moisture leads to desert conditions and, thus, represents one of the major threats to the continued existence of the ecosystem. The reduced moisture conditions are encountered on a reoccurring basis (24). The components of the ecosystem could be expected to have adapted during succession to this reoccurring environmental change. During the first year of the simulation, the reduced moisture trajectories are greater (Figure 12). These results indicate that the xeric prairie ecosystem has evolved such that it possesses a greater resistance to change for reduced moisture conditions. These results are consistent with the behavior observed in the previous example where maximum stability occurred seasonally when environmental conditions were most harsh. Continued exposure to reduced moisture resulted in changes in the ecosystem (24) which led to a gradual reduction of the stability index trajectory.

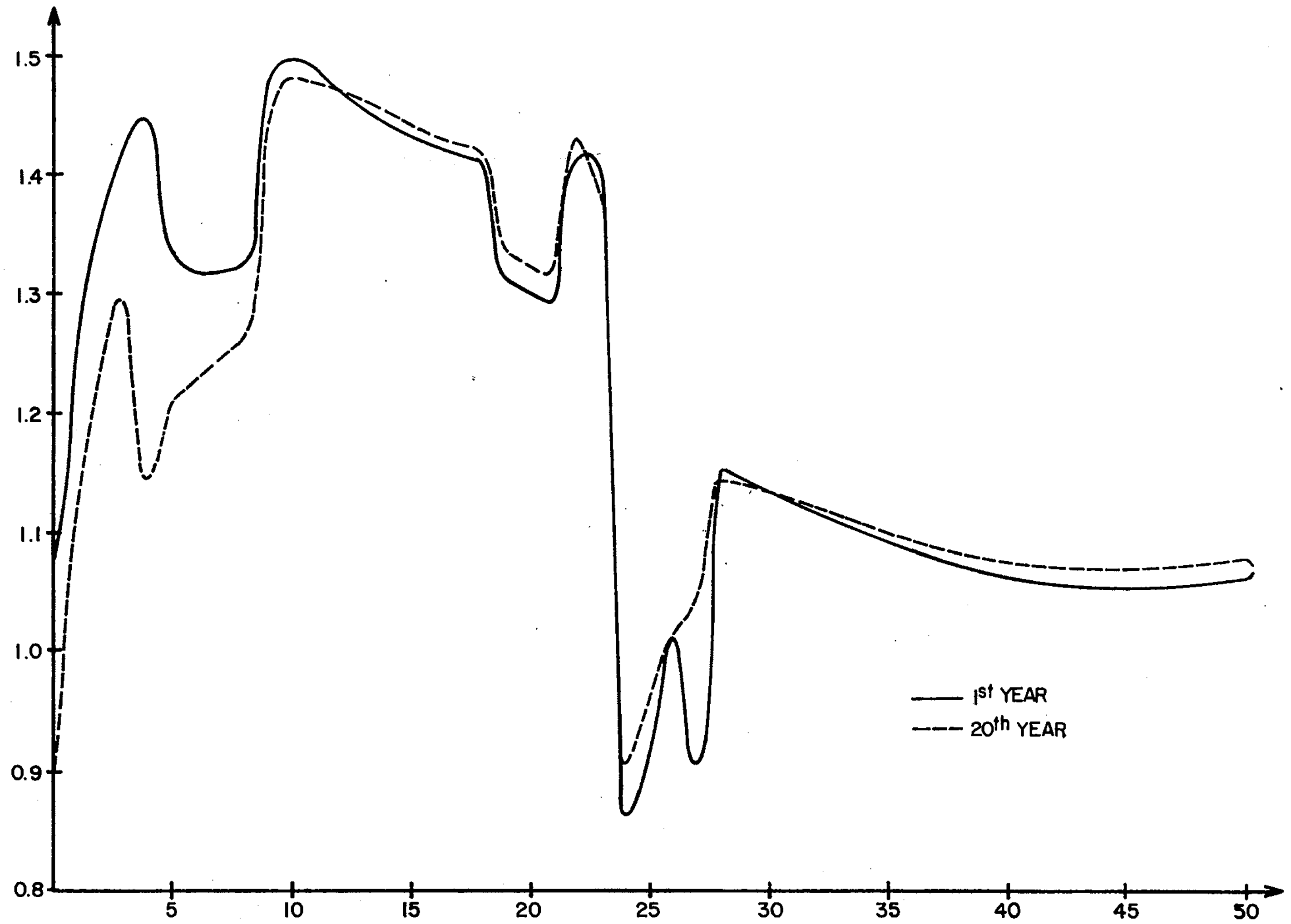

Figure 10. Plot of Normal Moisture Stability Index Trajectories for the First and Twentieth Years

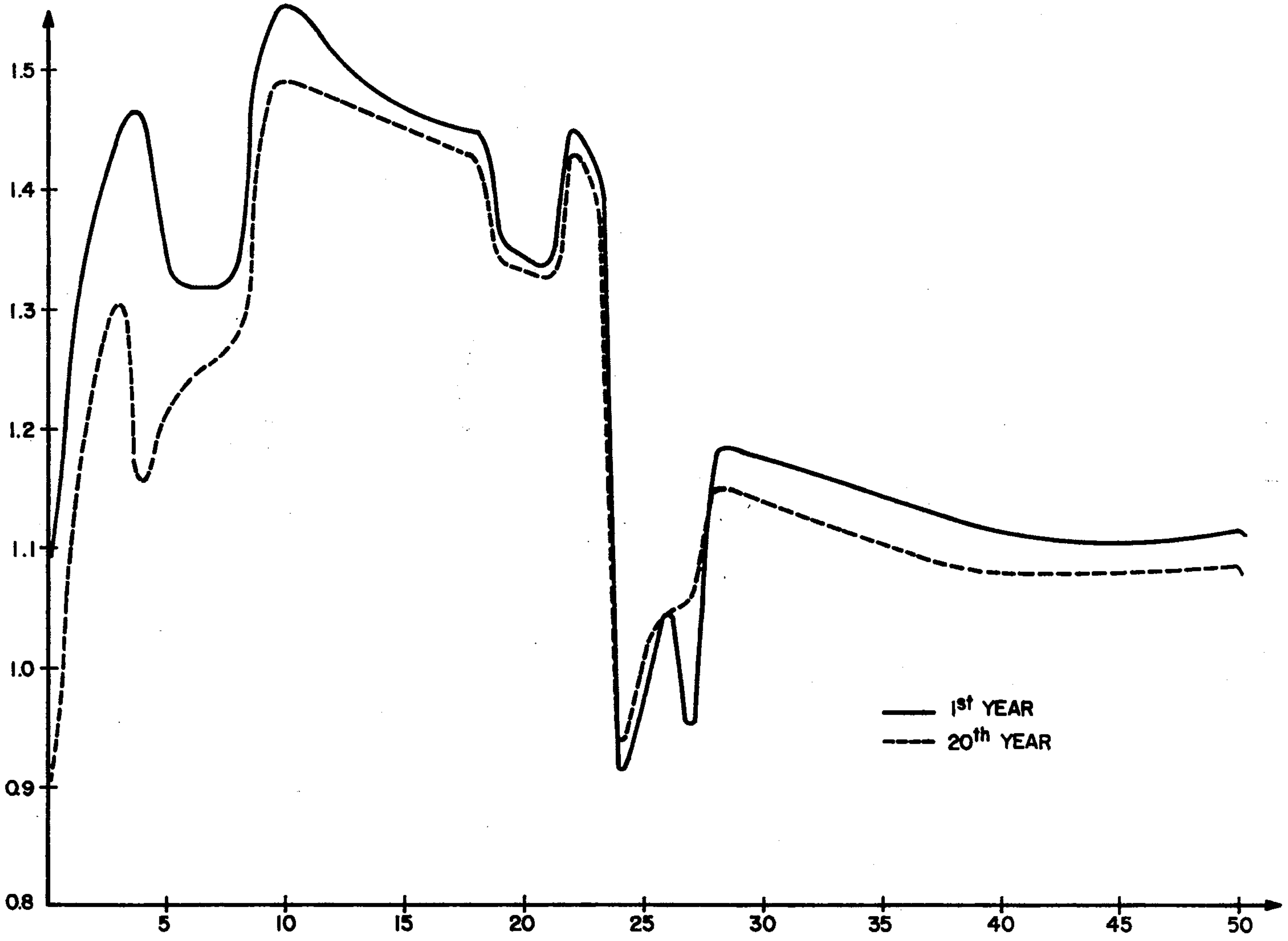

Figure 11. Plot of Low Moisture Stability Index Trajectories for the First and Twentieth Years

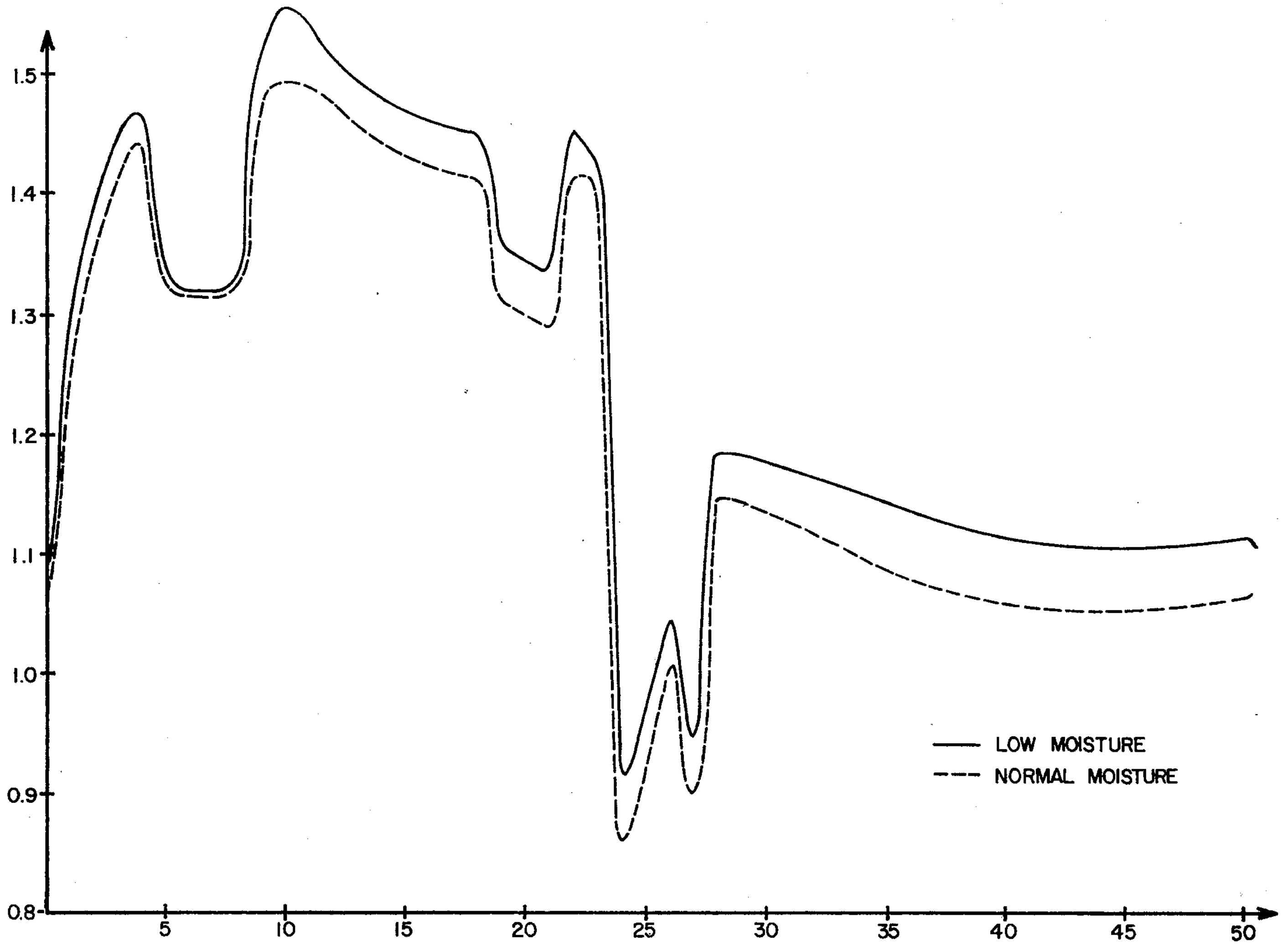

Figure 12. Plot of Low and Normal Moisture Stability Index Trajectories for the First Year

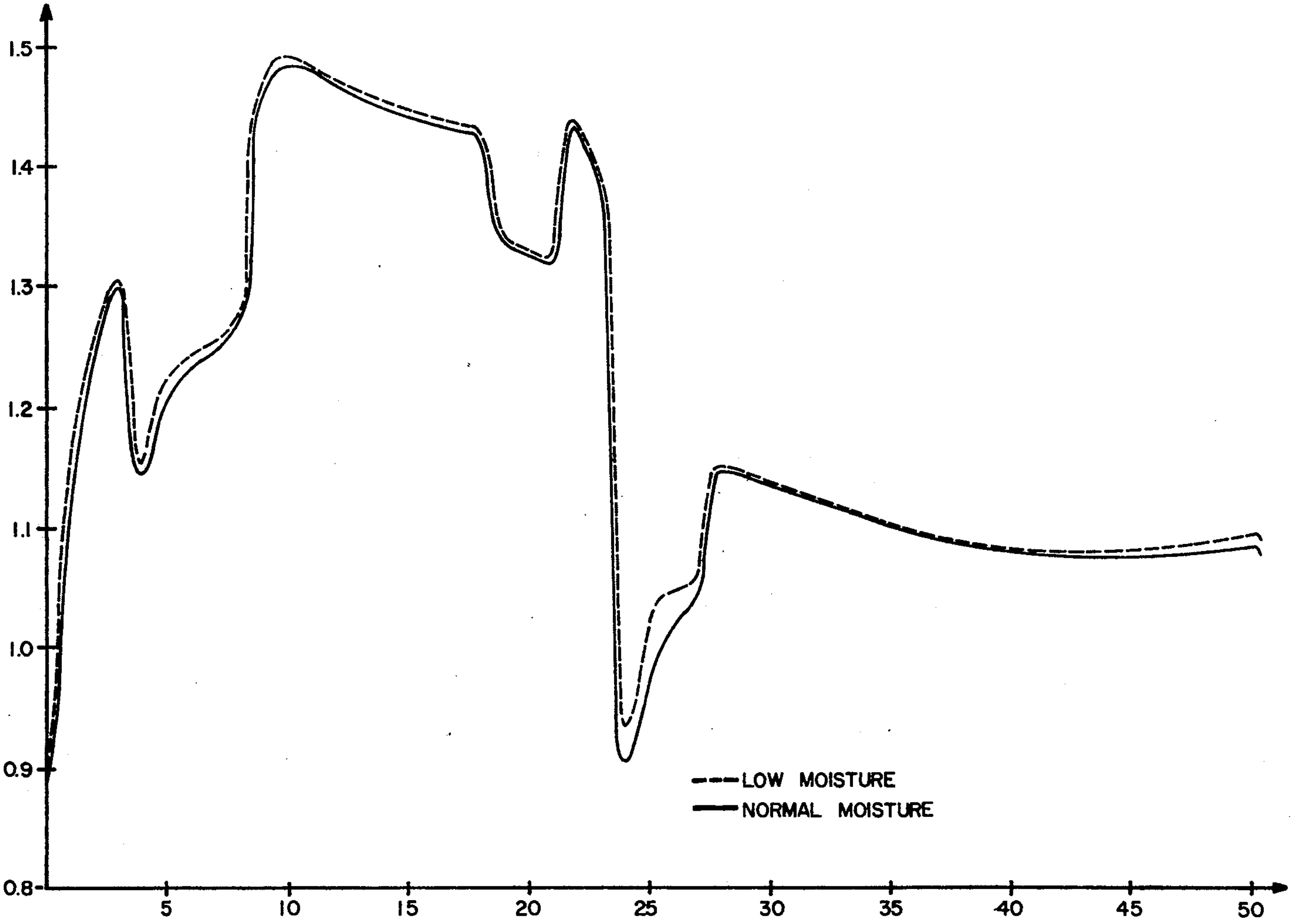

Figure 13. Plot of Low and Normal Moisture Stability Index Trajectories for the Twentieth Year

During the twentieth year, the stability index trajectories differed by less than 1% (Figure 13) as opposed to approximately 6% differences during 30 weeks of the first year.

The model did not predict maximum stability when environmental conditions were most harsh during the year due to emigration. During the final 29 weeks of the simulation year, no soil moisture was available for primary production resulting in an emigration of herbivores and carnivores out of the ecosystem. The ecosystem is less complex during the time of the year when the environment is most harsh, resulting in smaller values of the stability index.

Summary

A measure of ecological stability has been developed based on choice of pathways for energy flow. The concept of choice is developed from a quantitative concept from information theory. Relationships among ecological stability, diversity, and complexity consistent with observed behavior during succession arise naturally in the development of the stability index. Stability and complexity increase during succession, but diversity may increase during initial stages but decrease during final stages of succession. This behavior can be explained within the context of the stability measure development.

Two ecosystems were chosen to test the validity of the stability measure: a stream community and a xeric prairie. A model of the stream community was used to test the validity of the stability index as an objective function with positive results. The stream community experiment led to consideration of annual changes in stability, a subject which has received little or no previous consideration. Experimental results indicated that the stability index was maximum when environmental conditions were most harsh. The same results were obtained from analysis of the shortgrass prairie model. The shortgrass prairie is subjected to reoccurring low moisture conditions which represent the greatest threat to its continued existence and, hence, could be considered harsh environmental conditions. Consistent with the stream community results, the model predicted maximum stability for the most harsh environmental conditions.

CHAPTER IV

SENSITIVITY ANALYSIS

Introduction

The response of an ecosystem to a perturbation is an indication of its sensitivity to that perturbation with larger fluctuation implying greater sensitivity. Environmental perturbation results in ecosystem fluctuation by causing variations in energy flows in the ecosystem. In this chapter a total ecosystem sensitivity measure will be developed for a linear, donor-controlled model. This total measure will be constructed by summing modified sensitivity measures of each ecosystem component to a perturbed energy flow. Each individual sensitivity measure will be modified by weighting functions which reflect the relative importance of a perturbed energy flow to a particular component and the intrinsic characteristics of that component.

Ecological stability is also based on ecosystem response to perturbation. A less responsive ecosystem is said to be more stable than a more responsive one (3, 11, 12, 18). The development of a total ecosystem sensitivity measure allows the relationship to ecological stability to be quantified.

A Total Ecosystem Sensitivity Measure

A quantitative analysis of sensitivity usually consists of taking partial derivatives of the functional relationships between the variables of interest and requires a mathematical model of the particular system under consideration (17). The model to be considered in the development of a total ecosystem sensitivity index is the so-called linear, donor-controlled (LDC) compartment model (Appendix A). The individuals within an ecosystem are grouped into functional classes called compartments. The time rate of change of the energy content of the j^{th} compartment is given by,

$$\dot{X}_j = \sum(\text{FLOWS IN}) - \sum(\text{FLOWS OUT}). \tag{4.1}$$

Assuming that the energy flow from one compartment to another depends linearly on the donor compartment, equation (4.1) becomes

$$\dot{X}_j = F_{oj} + \sum_{i=1}^{n} a_{ij} X_i - \sum_{i=1}^{n} a_{ji} X_j , \tag{4.2}$$

where a_{ij} is a constant satisfying the equation,

$$F_{ij} = a_{ij} X_i, \tag{4.3}$$

and F_{ij} is the energy flow from the i^{th} to the j^{th} compartment. The flow F_{oj} represents environmental inputs for an open system. If the environment is modeled as a compartment, then the system is closed and F_{oj} is equivalent to zero. The total ecosystem model, then, consists of n first order differential equations where n is the number of compartments and equation (4.2) is the j^{th} member of these equations.

Elton (4) observes that the "chief cause of fluctuations in animal numbers is the instability of the environment." Environmental perturbations cause fluctuations in the ecosystem by first causing variations in energy flows in the ecosystem. These variations in energy flows then propogate through the ecosystem along the food web interconnection. From equation (4.1) it is apparent that energy flow variations cause perturbations in the rate of change of the energy content of the compartments which are affected by this flow. Perturbations in the rate of change of energy content, in turn, causes perturbations in the energy content, which then causes perturbations in the energy flows to other compartments. A partial derivative which reflects this phenomenon is,

$$s_{ij} = \frac{\partial \dot{X}_j}{\partial X_i} , \tag{4.4}$$

where X_i and X_j represent the energy content of the i^{th} and j^{th} compartments of the ecosystem, respectively. This sensitivity measure is an indication of the effect that a perturbed state, X_i, has on the rate of change of another state, X_j. For the (LDC) model, as described by equation (4.2), s_{ij} becomes,

$$s_{ij} = \begin{cases} a_{ij} & i \neq j \qquad (4.5.1) \\ \sum_{\substack{i=1 \\ i \neq j}}^{n} a_{ij} & i = j \qquad (4.5.2) \end{cases} .$$

Odum (20) defines turnover as the ratio of throughput to content or,

$$T_i = \frac{\sum_{j=1}^{n} F_{ij}}{X_i} . \tag{4.6}$$

For the linear, donor-controlled assumption equation (4.6) becomes

$$T_i = \frac{\sum_{j=1}^{n} a_{ij} X_i}{X_i} = \sum_{j=1}^{n} a_{ij}. \tag{4.7}$$

The self-sensitivity measure equation (4.5.2), then, is

$$s_{ii} = -T_i. \tag{4.8}$$

Since this measure is negatively correlated to the other sensitivity measures it is a measure of a compartment's reaction to being perturbed. A larger turnover implies that the recovery time from a perturbation will be smaller when compared to a smaller turnover. This effect will be considered later in the development.

A total ecosystem sensitivity measure could be constructed by simply summing the individual sensitivity measures of equation (4.5.1):

$$S_T = \sum_{i=1}^{n} \sum_{j=1}^{n} s_{ij}. \tag{4.9}$$

But, summing in this manner assumes that all energy flows are of equal importance to the ecosystem and all compartments have an equal ability to recover from or resist perturbations. These assumptions are not realistic. Weighting functions are needed for each of the individual sensitivity measures reflecting the relative importance of that particular energy flow to the total ecosystem and taking into account the intrinsic characteristics of the compartments involved.

The perturbation of state X_i causes a variation in the energy flow, F_{ij}, from the i^{th} to the j^{th} compartment. The impact of the energy flow variation on the j^{th} compartment depends on the degree to which the j^{th} compartment relies on this energy flow to fulfill its energy requirement. A measure of this dependence is the percentage of the energy consumed by the j^{th} compartment which is provided by the i^{th} compartment,

$$W^1_{ij} = \frac{F_{ij}}{\sum\limits_{i=1}^{n} F_{ij}} , \tag{4.10}$$

where F_{ij} is the energy provided by the i^{th} compartment to the j^{th} compartment and $\sum\limits_{i=1}^{n} F_{ij}$ is the total energy consumed by the j^{th} compartment during some arbitrary time period. Substituting equation (4.3) into equation (4.10) gives

$$W^1_{ij} = \frac{a_{ij}\ X_i}{\sum\limits_{i=1}^{n} a_{ij}\ X_i} . \tag{4.11}$$

Rearranging and multiplying by,

$$\frac{T_i}{T_i} \cdot \frac{\sum\limits_{k=1}^{n} X_k\ T_k}{\sum\limits_{k=1}^{n} X_k\ T_k} , \tag{4.12}$$

this weighting function becomes,

$$W^1_{ij} = \frac{a_{ij}}{T_i} \cdot \frac{(X_i\ T_i\ )}{(\sum\limits_{k=1}^{n} X_k\ T_k)} \cdot \frac{(\sum\limits_{k=1}^{n} X_k\ T_k\ )}{(\sum\limits_{i=1}^{n} a_{ij}\ X_i)} . \tag{4.13}$$

In the development of the stability measure in Chapter III certain percentages were defined, namely,

Q_i - percentage of the total energy flow through the ecosystem at time t_1 which passes through the i^{th} compartment,

P_j - percentage of the total energy flow through the ecosystem at time t_2 which passes through the j^{th} compartment, and

f_{ij} - percentage of the total energy flow through the i^{th} compartment that passes to the j^{th} compartment between times t_1 and t_2.

Assume that Y_i and X_i represent the total throughput and content of the i^{th} compartment, respectively. These variables are related through equation (3.10), so

$$Y_i = T_i \, X_i \; , \tag{4.14}$$

where T_i is the turnover of the i^{th} compartment. The percentage, Q_i, is given by

$$Q_i = \frac{Y_i}{\sum_{k=1}^{n} Y_k} \tag{4.15}$$

But, in terms of the energy contents, X_i, equation (4.15) becomes

$$Q_i = \frac{X_i \, T_i}{\sum_{k=1}^{n} X_k \, T_k} \; . \tag{4.16}$$

The percentage, P_j, is given by

$$P_j = \sum_{i=1}^{n} f_{ij} Q_i \tag{4.17}$$

where

$$f_{ij} = \frac{a_{ij}}{\sum_{j=1}^{n} a_{ij}} = \frac{a_{ij}}{T_i} . \tag{4.18}$$

Substituting equations (4.18) and (4.16) into equation (4.17) this percentage becomes

$$P_j = \sum_{i=1}^{n} \frac{a_{ij}}{T_i} \frac{X_i T_i}{\sum_{k=1}^{n} X_k T_k} \tag{4.19}$$

or, simplifying,

$$P_j = \frac{\sum_{i=1}^{n} a_{ij} X_i}{\sum_{k=1}^{n} X_k T_k} . \tag{4.20}$$

Using equations (4.16) and (4.20) the weighting function defined by equation (4.13) becomes

$$W_{ij}^{1} = \frac{a_{ij}}{T_i} \cdot Q_i \cdot \frac{1}{P_j} . \tag{4.21}$$

Another important consideration in determining the effect of a perturbed flow on the total ecosystem is the intrinsic characteristics of the compartments involved. A basic characteristic which is usually well known and to a large extent determines a compartment's response or recovery time from a perturbation is the turnover time. Turnover time is the reciprocal of turnover as defined in equation (4.7). A donor compartment with a shorter turnover time implies a more rapid recovery from perturbations than a donor compartment with a longer turnover time, thus, the effect of a perturbed energy flow on the total ecosystem will be less if the energy flow originates from a compartment with a smaller turnover time. A second weighting function, then, is

$$W_{ij}^{2} = \frac{1}{T_i} . \tag{4.22}$$

By considering the turnover time of the donor compartment as weighting functions, all of the turnover times will be considered as the individual sensitivity terms are summed.

The individual sensitivity measure multiplied by the two weighting functions is

$$s_{ij}^{w} = a_{ij} \; \frac{a_{ij}}{T_i} \cdot Q_i \cdot \frac{1}{T_i} . \tag{4.23}$$

Rearranging and summing over all possible energy flows, the total measure becomes

$$S^{w} = \sum_{i=1}^{n} \sum_{j=1}^{n} \frac{Q_i \, a_{ij}}{T_i} \; \frac{a_{ij}}{T_i \, P_j} . \tag{4.24}$$

The ordering of all possible values of equation (4.24) on the real line will not be changed if the following logarithmic mapping is used:

$$S^{1} = \sum_{i=1}^{n} \sum_{j=1}^{n} \frac{Q_i \, a_{ij}}{T_i} \log \frac{a_{ij}}{T_i \, P_j} . \tag{4.25}$$

A sensitivity measure constructed in this manner measures the potential for change if all energy flows are perturbed. But, typically all energy flows are not perturbed simultaneously and a larger number of unperturbed energy flows decreases the sensitivity of the ecosystem to perturbation. A consumer is less sensitive to perturbations of a source if the consumer depends on several sources rather than only upon the perturbed source. Similarly, a source is less sensitive to perturbations of a consumer if the source is used by several consumers rather than by only the perturbed consumer. A method of taking this effect into account would be by subtracting equation (4.25) from an index of the potential number of pathways. One index would be a measure of the diversity of the throughput of energy. The sensitivity measure now becomes,

$$S^N = \bar{D}_T - S^1 , \tag{4.26}$$

where $\bar{D}_T$ is defined by equation (3.12). <u>This sensitivity measure produces higher values for less sensitive ecosystems and vice versa.</u> Substituting equation (4.18) into equation (4.25) the total sensitivity measure becomes,

$$S^N = -\sum_{i=1}^{n} Q_i \log Q_i - \sum_{i=1}^{n} \sum_{j=1}^{n} Q_i f_{ij} \log \frac{f_{ij}}{P_j} . \tag{4.27}$$

This sensitivity measure is identical to the ecological stability measure developed in Chapter III. It is apparent from its definition and statements and discussions by ecologists that ecological stability is a sensitivity concept. The relationship between the stability and sensitivity measures provides strong analytical evidence that the apparent qualitative relationship is true.

Summary

A total ecosystem sensitivity measure, equation (4.27), has been developed for the linear, donor-controlled class of models. A measure of the sensitivity of each state to flow variations, equation (4.5.1), was computed. Weighting functions, equations (4.21) and (4.22), based on reasonable assumptions, were introduced which modify each of the individual sensitivity measures. These weighting functions measure the relative importance of an energy flow to a particular compartment and take into account the intrinsic characteristics of the components involved. Summing over all possible energy flows, assuming a logarithmic mapping, and subtracting from an index of the potential number of energy pathways result in a total ecosystem sensitivity measure. This measure is identical to the ecological stability measure developed in Chapter III which is based on choice of pathways for energy flow. Thus, strong analytical evidence has been provided that ecological stability is a sensitivity concept.

CHAPTER V

DYNAMIC BEHAVIOR OF THE ECOLOGICAL STABILITY MEASURE

Introduction

The ecological stability index depends on the degree and pattern of component interdependence. The changing degree and pattern of component interdependence results in dynamic behavior of the stability index when the time period is small. This chapter will consider the case where the energy flows are assumed to be linearly proportionate to the energy contents of donor compartments. For this case the stability index is not only a function of time period but also an implicit function of time since it depends on the energy contents of the compartments which are functions of time. The linear, donor-controlled flow assumption prescribes the flow distribution from each of the compartments, defined by the f_{ij}'s, to be the same throughout the year. The stability index then can be written as a function only of the energy contents of the compartments. Since, for the linear, donor-controlled energy flow assumption, the derivatives of the energy contents with respect to time are known, the derivative of the stability index with respect to time can be computed using the chain rule for differentation. The computation of the derivative of the stability index will allow upper and lower bounds on the rate of change of the index to be established.

Computation of the Derivative of the Stability Measure

The ecological stability index is given by

$$S = -\sum_i Q_i \log Q_i - \sum_i \sum_j Q_i f_{ij} \log \frac{f_{ij}}{P_j} . \qquad (5.1)$$

If the energy flows are assumed linearly proportionate to the donor compartment, the percentage f_{ij} becomes

$$f_{ij} = \frac{a_{ij} X_i}{\sum_j a_{ij} X_i} , \qquad (5.2)$$

or,

$$f_{ij} = \frac{a_{ij}}{\sum_j a_{ij}} , \qquad (5.3)$$

where a_{ij} is a constant for $i=1, 2, \ldots, n$, $j=1, 2, \ldots, n$ (Appendix A). So the percentage f_{ij} is a constant when the energy flows are assumed linearly proportionate to the donor comparment. Substituting equations (4.16) and (4.20) into equation (5.1) the stability index becomes

$$S = -\sum_i \frac{X_i T_i}{\sum_k X_k T_k} \log \frac{X_i T_i}{\sum_k X_k T_k} - \sum_i \sum_j \frac{X_i T_i}{\sum_k X_k T_k} f_{ij} \log \frac{f_{ij} {}_{k} X_k T_k}{\sum_m a_{mj} X_m} \qquad (5.4)$$

An expression for the rate of change of the stability index may be found by taking the total derivative of the stability index, S, with respect to time. The total derivative can be computed using the composite function rule or chain rule. The stability index defined by equation (5.4) is a function of the energy contents

$$S = f(X_1, X_2, \ldots, X_n), \tag{5.5}$$

where the energy contents are functions of time,

$$X_i = g_i(t). \tag{5.6}$$

The chain rule (8) prescribes that

$$\dot{S} = \frac{dS}{dt} = \sum_{i=1}^{n} \frac{\partial S}{\partial X_i} \cdot \frac{dX_i}{dt}. \tag{5.7}$$

To demonstrate the method used to compute $\dot{S}$ for a general n^{th} order model, a third order example will be considered. For a third order example equation (5.7) becomes

$$\dot{S} = \frac{\partial S}{\partial X_1} \cdot \dot{X}_1 + \frac{\partial S}{\partial X_2} \cdot \dot{X}_2 + \frac{\partial S}{\partial X_3} \cdot \dot{X}_3 \quad . \tag{5.8}$$

Expressions for the time rate of change of the energy contents are given by,

$$\dot{X}_i = \sum_{j=1}^{3} a_{ji} X_j - \sum_{i=1}^{3} a_{ij} X_i \quad , \tag{5.9}$$

for i=1, 2, 3. The only unknowns in equation (5.8) are the partial derivatives, $\frac{\partial S}{\partial X_i}$, i=1, 2, 3. Since the stability index is composed of two terms, these partials will be computed in two parts. The first term of equation (5.4) will be denoted by H and the second by I. The total derivative now becomes

$$\dot{S} = \sum_{i=1}^{3} \left(\frac{\partial H}{\partial X_i} - \frac{\partial I}{\partial X_i}\right) \frac{dX_i}{dt} . \tag{5.10}$$

The first term, H, of the stability index can be written as

$$H = -\frac{X_1T_1}{\sum\limits_k X_kT_k} \log \frac{X_1T_1}{\sum\limits_k X_kT_k} - \frac{X_2T_2}{\sum\limits_k X_kT_k} \log \frac{X_2T_2}{\sum\limits_k X_kT_k} - \frac{X_3T_3}{\sum\limits_k X_kT_k} \log \frac{X_3T_3}{\sum\limits_k X_kT_k} . \tag{5.11}$$

The partial of H with respect to X_1 is

$$\frac{\partial H}{\partial X_1} = \frac{-(X_2T_2+X_3T_3)T_1}{(\sum\limits_k X_kT_k)^2} \left(1 + \log \frac{X_1T_1}{\sum\limits_k X_kT_k}\right) + \frac{X_2T_2T_1}{(\sum\limits_k X_kT_k)^2} \left(1 + \log \frac{X_2T_2}{\sum\limits_k X_kT_k}\right)$$

$$+ \frac{X_3T_3T_1}{(\sum\limits_k X_kT_k)^2} \left(1 + \log \frac{X_3T_3}{\sum\limits_k X_kT_k}\right) . \tag{5.12}$$

Simplifying, equation (5.12) becomes

$$\frac{\partial H}{\partial X_1} = \frac{X_2T_2T_1}{(\sum\limits_k X_kT_k)^2} \log \frac{X_2T_2}{X_1T_1} + \frac{X_3T_3T_1}{(\sum\limits_k X_kT_k)^2} \log \frac{X_3T_3}{X_1T_1} . \tag{5.13}$$

Similarly, the partials of H with respect to X_2 and X_3 are

$$\frac{\partial H}{\partial X_2} = \frac{X_1T_1T_2}{(\sum\limits_k X_kT_k)^2} \log \frac{X_1T_1}{X_2T_2} + \frac{X_3T_3T_2}{(\sum\limits_k X_kT_k)^2} \log \frac{X_3T_3}{X_2T_2} , \tag{5.14}$$

and

$$\frac{\partial H}{\partial X_3} = \frac{X_1T_1T_3}{(\sum_k X_kT_k)^2} \log \frac{X_1T_1}{X_3T_3} + \frac{X_2T_2T_3}{(\sum_k X_kT_k)^2} \log \frac{X_2T_2}{X_3T_3} . \tag{5.15}$$

In a similar manner the partials for the n^{th} order can be computed and a general formula derived:

$$\frac{\partial H}{\partial X_i} = \sum_{\substack{j \\ j \neq i}} \frac{X_jT_jT_i}{(\sum_k X_kT_k)^2} \log \frac{X_jT_j}{X_iT_i} . \tag{5.16}$$

The second term of the stability index, I, consists of nine terms:

$$I_1 = \frac{X_1a_{11}}{X_1T_1+X_2T_2+X_3T_3} \log \frac{a_{11}(X_1T_1+X_2T_2+X_3T_3)}{T_1(X_1a_{11}+X_2a_{21}+X_3a_{31})} \tag{5.17}$$

$$I_2 = \frac{X_1a_{12}}{X_1T_1+X_2T_2+X_3T_3} \log \frac{a_{12}(X_1T_1+X_2T_2+X_3T_3)}{T_1(X_1a_{12}+X_2a_{22}+X_3a_{32})} \tag{5.18}$$

$$I_3 = \frac{X_1a_{13}}{X_1T_1+X_2T_2+X_3T_3} \log \frac{a_{13}(X_1T_1+X_2T_2+X_3T_3)}{T_1(X_1a_{13}+X_2a_{23}+X_3a_{33})} \tag{5.19}$$

$$I_4 = \frac{X_2a_{21}}{X_1T_1+X_2T_2+X_3T_3} \log \frac{a_{21}(X_1T_1+X_2T_2+X_3T_3)}{T_2(X_1a_{11}+X_2a_{21}+X_3a_{31})} \tag{5.20}$$

$$I_5 = \frac{X_2a_{22}}{X_1T_1+X_2T_2+X_3T_3} \log \frac{a_{22}(X_1T_1+X_2T_2+X_3T_3)}{T_2(X_1a_{12}+X_2a_{22}+X_3a_{32})} \tag{5.21}$$

$$I_6 = \frac{X_2a_{23}}{X_1T_1+X_2T_2+X_3T_3} \log \frac{a_{23}(X_1T_1+X_2T_2+X_3T_3)}{T_2(X_1a_{13}+X_2a_{23}+X_3a_{33})} \tag{5.22}$$

$$I_7 = \frac{X_3a_{31}}{X_1T_1+X_2T_2+X_3T_3} \log \frac{a_{31}(X_1T_1+X_2T_2+X_3T_3)}{T_3(X_1a_{11}+X_2a_{21}+X_3a_{31})} \qquad (5.23)$$

$$I_8 = \frac{X_3a_{32}}{X_1T_1+X_2T_2+X_3T_3} \log \frac{a_{32}(X_1T_1+X_2T_2+X_3T_3)}{T_3(X_1a_{12}+X_2a_{22}+X_3a_{32})} \qquad (5.24)$$

$$I_9 = \frac{X_3a_{33}}{X_1T_1+X_2T_2+X_3T_3} \log \frac{a_{33}(X_1T_1+X_2T_2+X_3T_3)}{T_3(X_1a_{13}+X_2a_{23}+X_3a_{33})} \qquad (5.25)$$

The partials of these nine terms with respect to X_1 appear below:

$$\frac{\partial I_1}{\partial X_1} = \frac{a_{11}(X_2T_2+X_3T_3)}{(\sum_k X_kT_k)^2} \log \frac{a_{11}(\sum_k X_kT_k)}{T_1(X_1a_{11}+X_2a_{21}+X_3a_{31})} \qquad (5.26)$$

$$\frac{\partial I_2}{\partial X_1} = \frac{a_{12}(X_2T_2+X_3T_3)}{(\sum_k X_kT_k)^2} \log \frac{a_{12}(\sum_k X_kT_k)}{T_1(X_1a_{12}+X_2a_{22}+X_3a_{32})} \qquad (5.27)$$

$$\frac{\partial I_3}{\partial X_1} = \frac{a_{13}(X_2T_2+X_3T_3)}{(\sum_k X_kT_k)^2} \log \frac{a_{13}(\sum_k X_kT_k)}{T_1(X_1a_{13}+X_2a_{23}+X_3a_{33})} \qquad (5.28)$$

$$\frac{\partial I_4}{\partial X_1} = \frac{-X_2a_{21}T_1}{(\sum_k X_kT_k)^2} \log \frac{a_{21}(\sum_k X_kT_k)}{T_2(X_1a_{11}+X_2a_{21}+X_3a_{31})} \qquad (5.29)$$

$$\frac{\partial I_5}{\partial X_1} = \frac{-X_2a_{22}T_1}{(\sum_k X_kT_k)^2} \log \frac{a_{22}(\sum_k X_kT_k)}{T_2(X_1a_{12}+X_2a_{22}+X_3a_{32})} \qquad (5.30)$$

$$\frac{\partial I_6}{\partial X_1} = \frac{-X_2 a_{23} T_1}{(\sum_k X_k T_k)^2} \log \frac{a_{23}(\sum_k X_k T_k)}{T_2(X_1 a_{13} + X_2 a_{23} + X_3 a_{33})} \qquad (5.31)$$

$$\frac{\partial I_7}{\partial X_1} = \frac{-X_3 a_{31} T_1}{(\sum_k X_k T_k)^2} \log \frac{a_{31}(\sum_k X_k T_k)}{T_3(X_1 a_{11} + X_2 a_{21} + X_3 a_{31})} \qquad (5.32)$$

$$\frac{\partial I_8}{\partial X_1} = \frac{-X_3 a_{32} T_1}{(\sum_k X_k T_k)^2} \log \frac{a_{32}(\sum_k X_k T_k)}{T_3(X_1 a_{12} + X_2 a_{22} + X_3 a_{32})} \qquad (5.33)$$

$$\frac{\partial I_9}{\partial X_1} = \frac{-X_3 a_{33} T_1}{(\sum_k X_k T_k)^2} \log \frac{a_{33}(\sum_k X_k T_k)}{T_3(X_1 a_{13} + X_2 a_{23} + X_3 a_{33})} \qquad (5.34)$$

The nonlogarithm terms which result from the differentiation all sum to zero. The general term for $\frac{\partial I}{\partial X_i}$ is

$$\frac{\partial I}{\partial X_i} = \sum_j \frac{a_{ij}(\sum_{\substack{k \\ k \neq i}} X_k T_k)}{(\sum_k X_k T_k)^2} \log \frac{a_{ij}}{T_i P_j} - \sum_{\substack{k \\ k \neq i}} \sum_j \frac{X_k a_{kj} T_i}{(\sum_m X_m T_m)^2} \log \frac{a_{kj}}{T_k P_j} . \qquad (5.35)$$

The total derivative of the stability index with respect to time is

$$\dot{S} = \sum_i \left(\frac{\partial H}{\partial X_i} - \frac{\partial I}{\partial X_i}\right) \dot{X}_i , \qquad (5.36)$$

where $\frac{\partial H}{\partial X_i}$ and $\frac{\partial I}{\partial X_i}$ are given by equations (5.16) and (5.35), respectively. Since S is dimensionless, this derivative has the same units as turnover, namely, inverse time.

Upper and Lower Bounds

The derivative of the stability measure consists of three terms, one from equation (5.16) and two from equation (5.35) each multiplied by $\dot{X}_i$ and summed over i, which will be denoted by S_1, S_2, and S_3, respectively. Since all the variables in these terms are always positive except the $\dot{X}_i$'s, the relationship between the signs of S_1, S_2, and S_3 and the signs of the $\dot{X}_i$'s must be determined to establish upper and lower bounds.

The sign of the first term, equation (5.16) multiplied by $\dot{X}_i$ and summed over i, may be either positive or negative independent of the signs of the X_i's. The second term, S_2, is given by the first term of equation (5.35) multiplied by $\dot{X}_i$ and summed over i. Since

$$\sum_j a_{ij} \log \frac{a_{ij}}{T_i P_j} \geq 0.0, \qquad (5.37)$$

the sign of S_2 is determined by the signs of the $\dot{X}_i$'s. The maximum value of this term occurs when the $\dot{X}_i$'s are equal to their maximum positive values. Similarly, the minimum value occurs when the $\dot{X}_i$'s are equal to their maximum negative values. The third term, S_3, is given by the second term of equation (5.35) multiplied by $\dot{X}_i$ and summed over i. From inequality (5.37) it follows that the sign of S_3 is also determined by the signs of the $\dot{X}_i$'s. So, the maximum and minimum values of S_3 occur when the $\dot{X}_i$'s are equal to their maximum positive and negative values, respectively. From equation (4.2), the maximum positive and negative values of $\dot{X}_i$ are:

$$-T_iX_i \leq \dot{X}_i \leq \sum_k a_{ki}X_k. \tag{5.38}$$

To establish upper and lower bounds for $\dot{S}$ the inequality,

$$\log Z \leq Z - 1, \tag{5.39}$$

will be used. If all the $\dot{X}_i$'s are equal to their maximum positive values then,

$$-\sum_i T_i \leq S_1 \leq \sum_i T_i \tag{5.40}$$

$$S_3 \leq I \sum_i T_i, \tag{5.41}$$

and

$$S_2 \geq -\bar{D}_T \sum_i T_i. \tag{5.42}$$

If all the $\dot{X}_i$'s are equal to their maximum negative values then,

$$-\sum_i T_i \leq S_1 \leq \sum_i T_i \tag{5.43}$$

$$S_3 \geq I\sum_i T_i, \tag{5.44}$$

and

$$S_2 \leq \bar{D}_T \sum_i T_i. \tag{5.45}$$

Since,

$$\dot{S} = S_1 - S_2 + S_3, \tag{5.46}$$

an upper bound of $\mathring{S}$ is

$$UB = MAX\ ((1+I) \sum_i T_i, (1+\bar{D}_T) \sum_i T_i). \tag{5.47}$$

Similarly a lower bound is

$$LB = MIN\ (-(1+I) \sum_i T_i, -(1+\bar{D}_T) \sum_i T_i). \tag{5.48}$$

But,

$$S = \bar{D}_T - I, \tag{5.49}$$

and,

$$S \geq 0.0. \tag{5.50}$$

So,

$$|\dot{S}| \leq (1+\bar{D}_T) \sum_i T_i. \tag{5.51}$$

The rate of change of major structural and functional characteristics of an ecosystem becomes smaller during succession (18). The stability measure is a function of the metabolic structure and function of an ecosystem and should, therefore, exhibit a decreasing rate of change during succession. Although diversity increases during succession, Margalef (12) has observed that diversity often decreases during the latter stages of succession. Turnovers, T_i, which are the reciprocal of the turnover times, become smaller during succession (18). So, during the latter stages of succession, the bound on the magnitude of the rate of change of the stability measure, equation (5.51), becomes smaller. This suggests that a smaller rate of change of the stability measure could be expected during the latter stages of succession.

Summary

An analytical expression of the time rate of change of the stability measure has been computed for the linear, donor-controlled class of ecosystem models. Upper and lower bounds on the rate of change of the stability measure were determined. These bounds are functions of the diversity of the throughput of energy and the sum of the turnovers. Since the diversity and the turnovers typically decrease during the latter stages of succession, the rate of change of the stability measure could be expected to also decrease.

CHAPTER VI

RECOMMENDATIONS FOR FURTHER RESEARCH

Odum (18) suggested computing the diversity of pathways. This computation requires knowledge of the energy flow through each pathway. The probability that a given increment of energy passed through a particular path can be approximated by a sample percentage

$$P_k = \frac{F_{ij}}{X_T} , \tag{6.1}$$

where F_{ij} is the total energy which passed through the path from the i^{th} to the j^{th} compartment and X_T is the total energy flow through the ecosystem during some arbitrary time period. The diversity of pathways could then be computed using the formula,

$$\overline{D}_p = - \sum_{k=1}^{N^2} p_k \log p_k \tag{6.2}$$

where N is the number of compartments. The sampled percentages, Q_i and f_{ij} presented in Chapter III, are given by,

$$Q_i = \frac{X_i}{X_T} , \tag{6.3}$$

and

$$f_{ij} = \frac{F_{ij}}{X_i} \tag{6.4}$$

where X_i is the total energy which passed through the i^{th} compartment, F_{ij} is the total energy which passed through the path from the i^{th} to the j^{th} compartment, and X_T is the total energy flow through the ecosystem during some arbitrary time period. So,

$$p_k = Q_i f_{ij} \tag{6.5}$$

where the k^{th} path is defined as the path from the i^{th} to the j^{th} compartment. The diversity of pathways now becomes

$$\overline{D}_p = - \sum_i \sum_j Q_i . f_{ij} \log Q_i . f_{ij} . \tag{6.6}$$

The percentages, Q_i and f_{ij}, are approximations of the probabilities, $P_X(a_i)$ and $P_{Y/X}(b_j/a_i)$. So, the product $Q_i . f_{ij}$ is an approximation of the joint probability $P_{XY}(a_i,b_j)$. Equation (6.6), then, represents an approximation of the joint entropy

$$H(XY) = \sum_i \sum_j P_{XY}(a_i,b_j) \log P_{XY}(a_i b_j) . \tag{6.7}$$

The joint entropy can be written as

$$H(XY) = H(X) + H(Y) - I(X;Y) \tag{6.8}$$

where H(X) is the source entropy, H(Y) is the receiver entropy, and I(X;Y) is the average mutual information. An approximation, S, of the conditional entropy, H(X/Y), is equivalent to choice of pathways for energy flow in an ecosystem and has been proposed as a measure of ecological stability. Conditional entropy is given by

$$H(X/Y) = H(X) - I(X:Y). \tag{6.9}$$

So,

$$H(XY) = H(X/Y) + H(Y). \tag{6.10}$$

But, the receiver entropy, H(Y) can be approximated by

$$\bar{D}_{t_2} = - \sum_j p_j \log p_j \tag{6.11}$$

where p_j is the percentage of energy which passes through the j^{th} compartment at time t_2 (Figure 4). Therefore, the diversity of pathways, equation (6.6), is given by

$$\bar{D}_p = S + \bar{D}_{t_2} \tag{6.12}$$

where S is the stability measure presented in Chapter III. Qualitatively, the diversity of pathways is equivalent to choice of pathways for energy flow plus the diversity of the throughput of energy at time t_2. Although this concise relationship exists, an ecological interpretation is lacking and needs to be considered.

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APPENDIX A

LINEAR, DONOR-CONTROLLED MODEL FORMULATION

The so-called linear, donor-controlled ecosystem model is a particular type of compartment model. Compartment models are based on the assumption that individuals within the ecosystem can be grouped into functional classes called compartments. For a n compartment ecosystem the biomass, or equivalent energy of the individuals of each compartment is lumped and represented by the variables X_1, X_2, . . ., X_n. The possible flow of biomass, or energy, from the i^{th} to the j^{th} compartment is represented by F_{ij} so that the mass balance equation for each compartment is,

$$\dot{X}_i = \frac{dX_i}{d_t} = \sum_{j=0}^{n} F_{ji} - \sum_{j=0}^{n} F_{ij}, \tag{A.1}$$

where the first summation gives the inflow and the second sum the outflow, and F_{oi} and F_{io} represent the interactions with the environment. The assumption that the flows are linearly proportionate to the biomass, or energy, content of the donor compartment requires that,

$$F_{ij} = a_{ij}X_i, \tag{A.2}$$

for all i=0 and j indicated, where a_{ij} is the rate coefficient of the biomass, or energy, transfer from the i^{th} to the j^{th} compartment. The flows F_{oi} are regarded as inputs which drive the ecosystem into steady-state. Thus, equation (A.1) becomes,

$$\dot{X}_i = F_{oi} + \sum_{j=1}^{n} a_{ji}X_j - (a_{io} + \sum_{j=1}^{n} a_{ij})X_i, \tag{A.3}$$

for each i=1, 2, . . ., n. The rate coefficients, a_{ij}, are computed from average flows $\overline{F_{ij}}$ and the average standing crops $\overline{X_i}$ as

$$a_{ij} = \overline{F_{ij}}/\overline{X_i} \ . \tag{A.4}$$

Ecosystems and all of the flows which describe their structure are temperature dependent. The temperature dependence of the interactions between compartments in an ecosystem model is defined through the use of a temperature coefficient which is usually designated by the symbol Q_{10}. This Q_{10} factor describes the ratio of the flow F_{ij} measured at two temperatures differing by 10^{o}C, and has the form:

$$Q_{10} = F_{ij}(T_2)/F_{ij}(T_1) . \tag{A.5}$$

The coefficient which modifies the flow from the i^{th} to the j^{th} compartment to include the effects of temperature is,

$$q_{ij} = Q_{10} \frac{T(t) - T_{AV}}{10} , \tag{A.6}$$

where T(t) is the actual temperature and T_{AV} is the average temperature.

The ecosystem inputs, representing the interaction of the ecosystem with its environment, are dependent upon, for example, temperature, light, nutrients, and so on and are represented by appropriate functions of time.

APPENDIX B

PROGRAM LISTINGS FOR BERRY CREEK AND GRASSLAND MODELS

```
C
C      BERRY CREEK MODEL
C
//     EXEC CSMP360
//CSMP1.SYSIN DD *
INITIAL
STORAGE X(11),Q(11),QB(11),P(11),A(121),F(121)
STCFAGE SUM(11)
       CONSTANT Q101=1.0,Q102=1.0,Q103=1.0,Q104=1.0,Q105=1.0,Q106=1.0,...
       Q107=1.0,Q108=1.0
       CONSTANT ICOUNT = 0
       CONSTANT C01=.01,C10R=7.25,C10E=.75,C12=4.0825,C16=.7750,C14=1.725
       CONSTANT C20R=5.600,C20E=.05,C23=1.375,C25=.700,C26=.125,...
       C27=.40,C02=.1251
       CONSTANT C30R=7.8,C35=1.6,C36=.4,C37=1.,C30E=.2
       CONSTANT C04=.1975,C40=2.231,C46=.2231
       CONSTANT C50=.70,C56=.02
       CONSTANT C60=22.33
       CONSTANT C70=1.25,C76=.03572
       CONSTANT C08=.1,C80R=101.33,C80E=8.,C82=13.33,C84=57.26,C86=.667
       CONSTANT AVG1=5833.3,DEV1=4462.6,AVG2=51.9,DEV2=14.1
       CONSTANT TERR=1.5
       PARAMETER SUGAR = 0.0
FIXED ITIME
FIXED ICCUNT
FIXED I
FIXED J
FIXED JJ
FIXED IJ
DYNAMIC
       LEAFIN = 133.33
     5 LIGHT=AVG1+DEV1*SIN(TIME*6.28/12.+.26)
       X1 = INTGRL(4.7,(-C10R*X1-C10E*X1-C12*X1-C16*X1-C14*X1+C01*...
       LIGHT)*Q101)
       X2=INTGRL(4.238,(-C20R*X2-C20E*X2-C25*X2-C26*X2-C23*X2-C27*...
       X2+C82*X8+C12*X1+C02*LEAFIN)*Q102)
       X3=INTGRL(.474,(-C30R*X3-C30E*X3-C37*X3-C35*X3-C36*X3+1.25*X2...
       )*Q103)
       X4=INTGRL(13.60,(-C40*X4-C46*X4+C84*X8+C14*X1+C04*LEAFIN)*Q104)
       X5=INTGRL(4.2085,(-C50*X5-C56*X5+C25*X2+C35*X3)*Q105)
       X6=INTGRL(.3346,(-C60*X6+C16*X1+C26*X2+C36*X3+C46*X4+C56*X5...
       +C76*X7+C86*X8)*Q106)
       X7=INTGRL(2.633,(-C70*X7-C76*X7+C27*X2+C37*X3+TERR)*Q107)
       X8=0.0
NCSCRT
       ITIME = TIME + .005
       IF(ITIME.EQ.ICOUNT) GO TO 83
       GO TC 82
    83 ICCLNT = ICCUNT + 1
       CO 100 J = 1 , 121
       A(J) = 0.0
   100 F(J) = 0.0
       A(2)= C12
       A(4) = C14
       A(6) = C16
       A(9) = C10R + C10E
       A(14) = C23
       A(16) = C25
       A(17) = C26
```

```
      A(18) = C27
      A(20) = C20R + C20E
      A(27) = C35
      A(28) = C36
      A(29) = C37
      A(31) = C30R + C30E
      A(39) = C46
      A(42) = C40
      A(50) = C56
      A(53) = C50
      A(64) = C60
      A(72) = C76
      A(75) = C70
      A(79) = C82
      A(81) = C84
      A(83) = C86
      A(86) = C80R + C80E
      A(89) = C01
      A(101) = C02
      A(103) = C04
      A(118) = C08
      X(1) = X1
      X(2) = X2
      X(3) = X3
      X(4) = X4
      X(5) = X5
      X(6) = X6
      X(7) = X7
      X(8) = X8
      X(9) = LIGHT
      X(10) = LEAFIN
      X(11) = SUGAR
      DBBAR=0.0
      XBTOT=0.0
      DO 64 J = 1 , 11
   64 XBTOT = XBTOT + X(J)
      DO 65 J = 1 , 11
      QB(J) = X(J)/XBTOT
      IF(QB(J).LE.0.0000001) GO TO 65
      DBBAR = DBBAR - 1.442695 * QB(J) * ALOG(QB(J))
   65 CONTINUE
      IJ = 0
      DO 11 I = 1 , 11
      SUM(I) = 0.0
      DO 10 J = 1 , 11
      JJ = J + IJ
   10 SUM(I) = SUM(I) + A(JJ)
      IJ = 11 * I
   11 SUM(I) = SUM(I) * X(I)
      SUMTOT = 0.0
      DO 12 J = 1 , 11
   12 SUMTOT = SUMTOT + SUM(J)
      DO 13 J = 1 , 11
   13 Q(J) = SUM(J)/SUMTOT
      IJ = 0
      DO 19 I = 1 , 11
      DO 14 J = 1 , 11
      P(J) = 0.0
      JJ = J + IJ
```

```
      IF(SUM(I).EQ.0.0) GO TO 71
   14 F(JJ) = A(JJ) * X(I) / SUM(I)
   71 IJ = 11 * I
   19 CONTINUE
      IJ = 0
      DO 22 I = 1 , 11
      DO 15 J = 1 , 11
      JJ = J + IJ
   15 P(J) = P(J) + Q(I) * F(JJ)
      IJ = 11 * IJ
   22 CONTINUE
      DBAR = 0.0
      DO 16 I = 1 , 11
      IF(Q(I).LE.0.0000001) GO TO 16
      DBAR = DBAR - 1.442695 * Q(I) * ALOG(Q(I))
   16 CONTINUE
      AMI = 0.0
      IJ = 0
      DO 23 I = 1 , 11
      DO 17 J = 1 , 11
      JJ = J + IJ
      IF(F(JJ).EQ.0.0.OR.P(J).EQ.0.0) GO TO 17
      DIV1 = F(JJ)/P(J)
      IF(DIV1.LE.0.0000001) GO TO 17
      AMI = AMI + 1.442695 * Q(I) * F(JJ) * ALOG(DIV1)
   17 CONTINUE
      IJ = 11 * I
   23 CONTINUE
      S = DBAR - AMI
   82 CONTINUE
      PRTPLT S,DBAR,DBBAR,AMI
      TIMER FINTIM=12.0,DELT=.01,OUTDEL=1.0
      PRINT X1,X2,X3,X4,X5,X6,X7,X8
      METHOD RKSFX
END
STOP
ENDJOB
//
```

```
C
C      GRASSLAND MODEL
C
//     EXEC CSMP360
//CSMP1.SYSIN DD *
INITIAL
STORAGE SS(5),ST(5),SB(5)
STORAGE QB(41)
STORAGE EFF(4),FNI(4),PHOTO(4),FORCE(4),ANI(4),DA(4),TB(4),DAI(4),TBI(4)
STORAGE DFORCE(1)
STORAGE X(41),SUM(41),Q(41),P(41),A(1681),F(1681)
TABLE EFF(1)=1.3187,EFF(2)=.13219,EFF(3)=.13219,EFF(4)=.02902,...
       PARAMETER IQ9=8.0,MOINT=1.6,SLOPE=.06154
       FNI(1)=1.2519,FNI(2)=.12549,FNI(3)=.12549,FNI(4)=.02755,...
       DAI(1)=.038462,DAI(2)=.038462,DAI(3)=.038462,DAI(4)=.000385,...
       TBI(1)=.06,TBI(2)=.05127,TBI(3)=.05127,TBI(4)=.0023076
       PARAMETER ICOUNT=0,ICOMP=0,SSAVG=0.0,DBAVG=0.0,DBBAVG=0.0
PARAMETER RBI=0.0018,HDB=0.001347,SHATR=0.02,...
       LEACHI=0.00136,HMLI=0.02429,HA1=0.036432,HA2=0.025642,...
       HA3=0.025642,HS=0.00804,B=0.0
INCON  IC1=.001,IC2=0.0,IC3=.000716,IC4=0.0,IC5=0.0,VA10=0.0,VA20=0.0,...
       VA30=0.0,VA40=25.0,VB0=560.3,VS0=65.0,VL0=72.0,Q9=8.0,...
       VS=65.0,VA1=0.0,VA2=0.0,VA3=0.0,...
       IQ1=1.0,IQ2=0.48,IQ3=1.0,IQ4=.16,IQ5=0.15,IQ6=0.4,IQ7=0.01,...
       IQ8=0.312,IQ10=3.0,IQ11=0.00153,IQ12=0.005,IQ13=0.2,...
       IQ14=0.2,IQ15=0.00824,IQ16=0.02,IQ17=0.14367,IQ18=0.04859,...
       IQ19=0.31573,IQ20=0.011342,IQ21=1.8221,IQ22=2.59,IQ23=0.23416,...
       IQ24=0.21525,IQ25=0.1,IQ26=0.00319,IVB=560,IVL=72,ISH=5.0,...
       IAC=0.15,VBIN=0.874,VLIN=0.9653
       CONSTANT SSAVG = 0.0,DBAVG = 0.0,DBBAVG = 0.0
CONSTANT HC11=0.00000339,HCI13=0.0697,HC15=0.0115,HCI43=0.0075,...
       HC21=0.000088167,HC61I=0.000004862,HC31=0.0005085,HC24=0.00024,...
       HC34=0.00024,RESP1=0.30398,RESP3=0.2394,RESP4=2,107,P3=0.00586,...
       P4=0.0019,A1=0.5,A2=0.5,A3=0.83,A4=0.92,A5=0.37,D1=0.002198,...
       D3=0.025,FN=0.1,VBQ1=0.00075,...
       VBQ2=0.0001923,VBQ3=0.00040384,VBQ4=0.0000962,VBQ5=0.00003846,...
VBQ6=0.00003846,VBQ7=0.00003846,VLQ8=0.002673,VLQ9=0.0004,...
       SHQ21=0.0207,SHQ22=0.01962,SHQ23=0.002192,SHQ24=0.002192,...
       ADQ17=0.026512,ADQ18=0.00467,ADQ19=0.0467,Q1Q2=0.000962,...
       Q1Q3=0.00384,Q1Q4=0.02308,Q1Q5=0.001922,Q1Q6=0.02308,Q1Q9=.009,...
       Q2Q9=0.00702,Q2Q20=0.0382,Q3SH=0.10192,Q4SH=0.2019,Q5SH=0.0705,...
       Q6SH=0.0529,Q3AD=0.0384,Q3Q9=0.002308,Q3Q15=.01924,...
       Q3Q16=0.01924,Q17Q9=0.0057,Q24Q9=0.04231,Q9Q26=0.00154,...
       Q4AD=0.0962,Q4Q9=0.00481,Q4Q15=0.0673,Q5AD=0.0346,...
       Q5Q7=0.000654,Q17Q20=0.019,Q18SH=0.0641,Q18Q7=0.00519,...
       Q5Q9=0.000654,Q5Q15=0.011538,Q5Q16=0.000654,Q6AD=0.0192,...
       Q7Q9=0.0019,Q8Q9=0.02153,Q8Q20=0.1104,Q10Q3=0.00256,...
       Q10Q8=0.00064,Q18AD=0.02564,Q20AD=0.319,Q10Q9=0.009,...
       Q10Q11=0.00044,Q10Q12=0.00044,Q10Q13=0.00769,Q10Q14=0.01398,...
       Q11SH=0.022,Q11AD=0.0179,Q11Q9=0.03629,Q11Q15=0.038,...
       Q11Q16=0.0135,...
       Q12SH=0.135,Q12AD=0.00462,Q12Q9=0.0019,Q12Q15=0.00231,...
       Q12Q16=0.00077,...
       Q13SH=0.0577,Q13AD=0.0231,Q13Q9=0.00096,Q13Q16=0.000192,...
       Q14SH=0.105,Q14Q7=0.000384,Q14Q9=0.000384,Q14Q16=0.0558,...
       Q15SH=0.346,Q15AD=1.346,Q15Q9=0.0212,Q16SH=0.1934,Q16AD=0.673,...
       Q16Q7=0.192,Q16Q9=0.00718,Q18Q9=0.001346,Q18Q16=0.0064,...
       Q19SH=0.0962,Q19AD=0.0385,Q19Q7=0.00769,Q19Q9=0.00192,...
       Q19Q16=0.0096,Q20SH=0.319,Q20Q9=0.0769,Q21Q22=0.002981,...
```

```
          Q22Q9=0.00248,Q22Q20=0.00248,Q23SH=0.0423,Q23AD=0.063,...
          Q23Q9=0.0211,Q24SH=0.0423,Q24AD=0.063423,Q25Q9=0.02,TAU=0.014,...
          Q3Q0=0.06114,Q4Q0=0.1009,Q5Q0=0.03524,Q6Q0=0.0264,Q7Q0=1.923,...
          Q8Q0=0.8912,Q10Q0=0.333,Q11Q0=0.112,Q12Q0=0.00673,Q13Q0=.04807,...
          Q14Q0=0.0448,Q15Q0=1.73,Q16Q0=0.865,Q17Q0=0.266,Q18Q0=0.0538,...
          Q19Q0=0.0807,Q20Q0=3.84,Q21Q0=0.304,Q22Q0=0.204,Q23Q0=0.128,...
          SHIN=1.2955,ADIN=0.1776,Q26Q0=4.0,Q24Q0=0.128,EFQ25=0.45,...
          Q9F1=0.02,RESP25=0.5
FIXED I
FIXED ITIME
FIXED J
FIXED JJ
FIXED IJ
FIXED JS
FIXED ICOMP
FIXED ICOUNT
DYNAMIC
          SUN=4. + ( 2.*SL )
          TS=SINE(0,.12093,5.904)
          TEMP=(9.+(TS*11.))*.061
          TEMP1=9.0 + (TS*11.0)
          Y=RAMP(B)
          MOIST = MOINT - SLOPE*Y
NOSORT
          IF(Y.GE.51.9) B=B+52.
          IF(Y.GE.50.0) MOIST = MOINT
          IF(MOIST.LT.0.) MOIST=0.
          RB=RBI
          Q25F1=SUN*TEMP*MOIST*EFQ25
          IF(SUN.LT.3.5.OR.SUN.GT.5.0) Q25F1=0.
          IF(SUN.LT.4.0) RB=0.0
          LEACHA=LEACHI
          IF(SUN.LT.4.0) HML=0.0
          IF(SUN.LT.4.0) LEACHA=0.0
          IF(TEMP.LE.0.0) Q25=0.0
          DO 3 I=1,4
          PHOTO(I)=SUN*MOIST*TEMP*EFF(I)
          DA(I)=DAI(I)
          TB(I)=TBI(I)
          IF(SUN.GT.4.5) GO TO 90
          PHOTO(1)=0.0
          DA(1)=DAI(1)*10.0
          TB(1)=0.0
     90   IF(SUN.GT.4.0) GO TO 91
          PHOTO(2)=0.0
          DA(2)=DAI(2)*10.0
          TB(2)=0.0
          PHOTO(3)=0.0
          DA(3)=DAI(3)*10.0
          TB(3)=0.0
     92   IF(SUN.GT.4.0) GO TO 93
          PHOTO(4)=0.0
          DA(4)=DAI(4)*10.0
          TB(4)=0.0
     93   CONTINUE
          FORCE(I)=PHOTO(I)
          ANI(I)=Q9*FNI(I)
          IF(PHOTO(I).GT.ANI(I)) FORCE(I)=ANI(I)
      3   CONTINUE
```

```
      TU=(FORCE(1)+FORCE(2)+FORCE(3)+FORCE(4))/40.0
      TAU=TU/Q9
*
      IF(Y.GE.8.0) SCALE=1.0
      IF(Y.GE.18.) SCALE=0.0
      IF(Y.GE.22.) SCALE=2.5
      IF(Y.GE.26.) SCALE=0.0
      VBV1=SCALE*VBQ1
      VBV2=SCALE*VBQ2
      VLV8=SCALE*VLQ8*0.75
      VLV10=SCALE*VLQ10*0.25
*
      IF(Y.EQ.50.) GO TO 5
      GO TO 60
    5 C1=IC1
      C3=IC3
      C4=IC4
   60 CONTINUE
      P1=0.000121
      HC61=HC61I
      IF(Y.GT.26.0) HC61=HC61I*3.0
    7 CONTINUE
      IF(Y.GE.31.0.AND.Y.LE.47.0) P1=0.0
*     THINGS ABOUT COWS
      IF(Y.LT.4.0) GO TO 8
      IF(Y.GE.26.0) GO TO 8
      P21=0.000208
      P23=0.00208
      HC12=0.00409
      HC22=0.0409
      HC32=0.00448
      HC62=0.00416
      RESP2=0.421505
      IF(Y.GT.5.0) EMC=0.0
      GO TO 9
    8 C2=0.0
      HC12=0.0
      HC22=0.0
      HC32=0.0
      HC62=0.0
      RESP2=0.0
      P21=0.0
      P23=0.0
    9 CONTINUE
*    INSECT PRODUCTION - DEATH - ETC
      IF(Y.LT.9.0) GO TO 20
      IF(Y.GE.24.0) GO TO 20
      P5=0.0166
      RESP5=0.5502
      HCI54=0.004899
      HCI53=0.00011
      HC15=0.0115
      HC25=0.00433
      HC35=0.00733
      HC65=0.00094
      D5=0.0074
      IF(Y.GE.19.0) P5=0.0
      IF(Y.GE.23.9) D5=1.0
      GO TO 21
```

```
   20 CONTINUE
*
      C5=0.0
      SH5=0.0
      Q6Q7=0.0048,Q6Q9=0.00192,Q6Q16=0.0048,Q7SH=0.12,Q7AD=0.115,...
      VLQ10=0.107,Q1Q0=0.3684,Q2Q0=0.17925,Q25AD=0.634,...
      SL=SINE(0,.12093,0)
      HML=HMLI
   91 IF(SUN.GT.3.7) GO TO 92
      IF(Y.GE.0.0) SCALE=4.0
*     PRODUCTION - RABBITS
      IF(Y.GT.4.0) EMC=0.58135
*     ADDING .00016 AT WEEK 22
      RESP5=0.0
      HCI54=0.0
      HCI53=0.0
*     ALL INPUTS AND OUTPUTS (INSECTS) GO TO 0
      HC15=0.0
      HC25=0.0
      HC35=0.0
      HC65=0.0
   21 CONTINUE
*     COYOTES
      IF(Y.LT.4.0) GO TO 30
*     BIRDS
      IF(Y.GT.20.0) XIM=0.0
      IF(Y.GE.20.0) GO TO 30
      IF(Y.GT.4.0) EM=0.0036
      IF(Y.GT.5.0) EM=0.0
      IF(Y.GE.5.0) D4=0.0000076
      IF(Y.GE.9.0) D4=0.0000126
      IF(Y.GE.19.0) XIM=0.693*C4
      P4=0.0019
      HC24=0.000662
      HC34=0.000662
      HCI54=0.02948
      GO TO 40
   30 CONTINUE
      C4=0.0
      P4=0.0
      HC24=0.0
      HC34=0.0
      HCI54=0.0
   40 CONTINUE
      PP1=P1*VA3
      PP2=P21*VA1 + P23*VA3
      PP3=P3*C1
      PP4=P4*C5
      PP5=P5*VA3
      PI1=PP1/A1
      PI2=PP2/A2
      PI3=PP3/A3
      PI4=PP4/A4
      PI5=PP5/A5
      I1=HC11*VA1+HC21*VA2+HC31*VA3+HC61*VS+PI1
      I2=HC12*VA1+HC22*VA2+HC32*VA3+HC62*VS+PI2
      I3=HCI13*C1+HCI53*C5+HCI43*C4+PI3
      I4=HC24*VA2+HC34*VA3+HCI54*C5+PI4
      I5=HC15*VA1+HC25*VA2+HC35*VA3+HC65*VS+PI5
```

```
        R1=RESP1*C1
        R2=RESP2*C2
        R3=RESP3*C3
        R4=RESP4*C4
        R5=RESP5*C5
        SH1=I1*(1.0-A1)
        SH2=I2*(1.0-A2)
        SH3=I3*(1.0-A3)
        SH4=I4*(1.0-A4)
        SH5=I5*(1.0-A5)
        Q1Q0=SCALE*0.3684*0.5
        Q1Q9=SCALE*0.009*0.5
        Q2Q0=SCALE*0.17925*0.5
        Q2Q9=SCALE*0.00702*0.5
        Q8Q0=SCALE*0.8912*0.375
        Q8Q9=SCALE*0.02153*0.375
        Q10Q0=SCALE*0.333*0.3
        Q10Q9=SCALE*0.009*0.3
SORT
        HA1=HC11+HC12+HC15+P21*2.0
        HA2=HC21+HC22+HC25+HC24
        HA3=HC31+HC34+HC35+HC32+P23*2.0+P5*2.73+P1*2.0
        HS=HC61+HC65+HC62
        HDB=VBV1+VBV2+VBQ3+VBQ4+VBQ5+VBQ6+VBQ7
        HML=VLQ9+VLV10
        LEACH=VLQ9+LEACHA
*
*
        SHIN=0.1*(SH1+SH2+SH3+SH4+SH5)
        GRA=HA1*VA1+HA2*VA2+HA3*VA3+VS*HS
        CUMBIC=VA1+VA2+VA3+VS
*
        ADIN=0.2*(D1*C1+D3*C3+D4*C4+D5*C5)
*
        VA1DOT=FORCE(1)-HA1*VA1-TB(1)*VA1-DA(1)*VA1
        VA1=INTGRL(VA10,VA1DOT)
        VA2DOT=FORCE(2)-HA2*VA2-TB(2)*VA2-DA(2)*VA2
        VA2=INTGRL(VA20,VA2DOT)
        VA3DOT=FORCE(3)-HA3*VA3-TB(3)*VA3-DA(3)*VA3
        VA3=INTGRL(VA30,VA3DOT)
        VA4DOT=FORCE(4)-TB(4)*VA4-DA(4)*VA4
        VA4=INTGRL(VA40,VA4DOT)
        VBDOT=TB(1)*VA1+TB(2)*VA2+TB(3)*VA3+TB(4)*VA4-RB*VB-HDB*VB
        VB=INTGRL(VB0,VBDOT)
        VSDOT=DA(1)*VA1+DA(2)*VA2+DA(3)*VA3+DA(4)*VA4-HS*VS-SHATR*VS
        VS=INTGRL(VS0,VSDOT)
        VLDOT=SHATR*VS-LEACH*VL-HML*VL
        VL=INTGRL(VL0,VLDOT)
*
        C1DOT=I1-R1-SH1-D1*C1-HCI13*C1
        C1=INTGRL(IC1,C1DOT)
        C2DOT=I2-R2-SH2+EMC
        C2=INTGRL(IC2,C2DOT)
        C3DOT=I3-R3-SH3-D3*C3
        C3=INTGRL(IC3,C3DOT)
        C4DOT=I4-R4-SH4-D4*C4-HCI43*C4-XIM+EM
        C4=INTGRL(IC4,C4DOT)
        C5DOT=I5-R5-SH5-D5*C5-HCI54*C5
        C5=INTGRL(IC5,C5DOT)
```

```
*
*
        Q1DOT=VBV1*VB-Q1*(Q1Q2+Q1Q4+Q1Q5+Q1Q6+Q1Q9+Q1Q3+Q1Q0)
        Q2DOT=VBV2*VB+Q1Q2*Q1-Q2*(Q2Q9+Q2Q20+Q2Q0)
        Q3DOT=VBQ3*VB+Q1Q3*Q1+Q10Q3*Q10-Q3*(Q3SH+Q3AD+Q3Q9+Q3Q15+Q3Q16+...
        Q3Q0)
        Q4DOT=VBQ4*VB+Q1Q4*Q1-Q4*(Q4SH+Q4AD+Q4Q9+Q4Q15+Q4Q0)
        Q5DOT=VBQ5*VB+Q1Q5*Q1-Q5*(Q5SH+Q5AD+Q5Q7+Q5Q9+Q5Q15+Q5Q16+Q5Q0)
        Q6DOT=VBQ6*VB+Q1Q6*Q1-Q6*(Q6SH+Q6AD+Q6Q7+Q6Q9+Q6Q16+Q6Q0)
        Q7DOT=VBQ7*VB+Q5Q7*Q5+Q6Q7*Q6+Q14Q7*Q14+Q16Q7*Q16+Q18Q7*Q18+...
        Q19Q7*Q19-Q7*(Q7SH+Q7AD+Q7Q9+Q7Q0)
        Q8DOT=VLV8*VL+Q10Q8*Q10-Q8*(Q8Q9+Q8Q20+Q8Q0)
        Q9DOT=VLQ9*VL+Q1Q9*Q1+Q2Q9*Q2+Q3Q9*Q3+Q4Q9*Q4+Q5Q9*Q5+Q6Q9*Q6+...
        Q7Q9*Q7+Q8Q9*Q8+Q11Q9*Q11+Q12Q9*Q12+Q13Q9*Q13+Q14Q9*Q14+Q15Q9*...
        Q15+Q16Q9*Q16+Q17Q9*Q17+Q18Q9*Q18+Q19Q9*Q19+Q20Q9*Q20+Q22Q9*...
        Q22+Q23Q9*Q23+Q24Q9*Q24+Q10Q9*Q10+Q9F1+Q25Q9*Q25-Q9*(Q9Q26+TAU)
        Q10DOT=VLV10*VL-Q10*(Q10Q3+Q10Q8+Q10Q11+Q10Q12+Q10Q13+Q10Q14+...
        Q10Q0+Q10Q9)
        Q11DOT=Q10Q11*Q10-Q11*(Q11SH+Q11AD+Q11Q9+Q11Q15+Q11Q16+Q11Q0)
        Q12DOT=Q10Q12*Q10-Q12*(Q12SH+Q12AD+Q12Q9+Q12Q15+Q12Q16+Q12Q0)
        Q13DOT=Q10Q13*Q10-Q13*(Q13SH+Q13AD+Q13Q9+Q13Q16+Q13Q0)
        Q14DOT=Q10Q14*Q10-Q14*(Q14SH+Q14Q7+Q14Q9+Q14Q16+Q14Q0)
        Q15DOT=Q11Q15*Q11+Q12Q15*Q12+Q3Q15*Q3+Q4Q15*Q4+Q5Q15*Q5-Q15*(...
        Q15SH+Q15AD+Q15Q9+Q15Q0)
        Q16DOT=Q3Q16*Q3+Q5Q16*Q5+Q6Q16*Q6+Q11Q16*Q11+Q12Q16*Q12+Q13Q16*...
        Q13+Q14Q16*Q14+Q18Q16*Q18+Q19Q16*Q19-Q16*(Q16SH+Q16AD+Q16Q7+...
        Q16Q9+Q16Q0)
        Q17DOT=ADQ17*AD-Q17*(Q17Q9+Q17Q20+Q17Q0)
         Q18DOT=ADQ18*AD-Q18*(Q18SH+Q18AD+Q18Q7+Q18Q9+Q18Q16+Q18Q0)
        Q19DOT=ADQ19*AD-Q19*(Q19SH+Q19AD+Q19Q7+Q19Q9+Q19Q16+Q19Q0)
        Q20DOT=Q2Q20*Q2+Q8Q20*Q8+Q17Q20*Q17-Q20*(Q20SH+Q20AD+Q20Q9+Q20Q0)
        Q21DOT=SHQ21*SH-Q21*(Q21Q22+Q21Q0)
        Q22DOT=SHQ22*SH+Q21Q22*Q21-Q22*(Q22Q9+Q22Q20+Q22Q0)
        Q23DOT=SHQ23*SH-Q23*(Q23SH+Q23AD+Q23Q9+Q23Q0)
        Q24DOT=SHQ24*SH-Q24*(Q24SH+Q24AD+Q24Q9+Q24Q0)
        Q25DOT=Q25F1-Q25Q9*Q25-RESP25*TEMP1*Q25
        Q26DOT=Q9Q26*Q9-Q26*Q26Q0
        SHDOT=SHIN+Q3SH*Q3+Q4SH*Q4+Q5SH*Q5+Q6SH*Q6+Q7SH*Q7+Q11SH*Q11+...
        Q12SH*Q12+Q13SH*Q13+Q14SH*Q14+Q15SH*Q15+Q16SH*Q16+Q18SH*Q18+...
        Q19SH*Q19+Q20SH*Q20+Q23SH*Q23+Q24SH*Q24-SH*(SHQ22+SHQ23+SHQ21)
        ADDOT=ADIN+Q3AD*Q3+Q4AD*Q4+Q5AD*Q5+Q6AD*Q6+Q7AD*Q7+Q11AD*Q11+...
        Q12AD*Q12+Q13AD*Q13+Q15AD*Q15+Q16AD*Q16+Q18AD*Q18+Q19AD*Q19+...
        Q20AD*Q20+Q23AD*Q23+Q24AD*Q24-AD*(ADQ17+ADQ18+ADQ19)
*
*
        Q1=INTGRL(IQ1,Q1DOT)
        Q2=INTGRL(IQ2,Q2DOT)
        Q3=INTGRL(IQ3,Q3DOT)
        Q4=INTGRL(IQ4,Q4DOT)
        Q5=INTGRL(IQ5,Q5DOT)
        Q6=INTGRL(IQ6,Q6DOT)
        Q7=INTGRL(IQ7,Q7DOT)
        Q8=INTGRL(IQ8,Q8DOT)
        Q9=INTGRL(IQ9,Q9DOT)
        Q10=INTGRL(IQ10,Q10DOT)
        Q11=INTGRL(IQ11,Q11DOT)
        Q12=INTGRL(IQ12,Q12DOT)
        Q13=INTGRL(IQ13,Q13DOT)
        Q14=INTGRL(IQ14,Q14DOT)
```

```
      Q15=INTGRL(IQ15,Q15DOT)
      Q16=INTGRL(IQ16,Q16DOT)
      Q17=INTGRL(IQ17,Q17DOT)
      Q18=INTGRL(IQ18,Q18DOT)
      Q19=INTGRL(IQ19,Q19DOT)
      Q20=INTGRL(IQ20,Q20DOT)
      Q21=INTGRL(IQ21,Q21DOT)
      Q22=INTGRL(IQ22,Q22DOT)
      Q23=INTGRL(IQ23,Q23DOT)
      Q24=INTGRL(IQ24,Q24DOT)
      Q25=INTGRL(IQ25,Q25DOT)
      Q26=INTGRL(IQ26,Q26DOT)
      SH=INTGRL(ISH,SHDOT)
      AD=INTGRL(IAD,ADDOT)
      GRAZ=HA1*VA1+HA2*VA2+HA3*VA3
      BUGS=C5+Q16+Q18+Q23+Q24+Q19+Q5+Q6
*
*
      PHOTO1=PHOTO(1)
      FORCE1=FORCE(1)
NOSORT
   84 ICOMP = ICOMP + 1
      X(1)=VA1
      X(2)=VA2
      X(3)=VA3
      X(4)=VA4
      X(5)=VB
      X(6)=VS
      X(7)=VL
      X(8)=C1
      X(9)=C2
      X(10)=C3
      X(11)=C4
      X(12)=C5
      X(13)=Q1
      X(14)=Q2
      X(15)=Q3
      X(16)=Q4
      X(17)=Q5
      X(18)=Q6
      X(19)=Q7
      X(20)=Q8
      X(21)=Q9
      X(22)=Q10
      X(23)=Q11
      X(24)=Q12
      X(25)=Q13
      X(26)=Q14
      X(27)=Q15
      X(28)=Q16
      X(29)=Q17
      X(30)=Q18
      X(31)=Q19
      X(32)=Q20
      X(33)=Q21
      X(34)=Q22
      X(35)=Q23
      X(36)=Q24
      X(37)=Q25
```

```
      X(38)=Q26
      X(39)=SH
      X(40)=AD
      DO 24 I = 1 , 1681
      F(I)=0.0
   24 A(I) = 0.0
      A(5)   =TB(1)
      A(6)   =DA(1)
      A(8) = HC11*A1
      A(9) = HC12*A2 + P21
      A(12) = HC15*A5
      A(46) =TB(2)
      A(47) =DA(2)
      A(49) = HC21*A1
      A(50) = HC22 * A2
      A(52) = HC24*A4
      A(53) = HC25*A5
      A(87) =TB(3)
      A(88) =DA(3)
      A(90) = HC31*A1 + P1
      A(91) = HC32*A2 + P23
      A(93) = HC34*A4
      A(94) = HC35*A5 + P5
      A(128)=TB(4)
      A(129)=DA(4)
      A(177) =VBV1
      A(178) =VBV2
      A(179) =VBQ3
      A(180) =VBQ4
      A(181) =VBQ5
      A(182) =VBQ6
      A(183) =VBQ7
      A(205) =RB
      A(212)=SHATR
      A(213)=HC61
      A(214)=HC62
      A(217) =HC65
      A(266) =VLV8
      A(267) =VLQ9
      A(268) =VLV10
      A(287) =LEACH
      X1TOT=X(33)+X(34)+X(35)+X(36)
      X2TOT=X(17)+X(18)+X(19)
      SH11=0.9*SH1
      SH22=0.9*SH2
      SH33=0.9*SH3
      SH44=0.9*SH4
      SH55=0.9*SH5
      D11=0.8*D1
      D33=0.8*D3
      D44=0.8*D4
      D55=0.8*D5
      IF(X2TOT.EQ.0.0) GO TO 32
      A(304) =D11*X(17)/X2TOT
      A(305) =D11*X(18)/X2TOT
      A(306) =D11*X(19)/X2TOT
      A(386)  =D33*X(17)/X2TOT
      A(387)  =D33*X(18)/X2TOT
      A(388)  =D33*X(19)/X2TOT
```

```
      A(427)  =D44*X(17)/X2TOT
      A(428)  =D44*X(18)/X2TOT
      A(429)  =D44*X(19)/X2TOT
      A(468)  =D55*X(17)/X2TOT
      A(469)  =D55*X(18)/X2TOT
      A(470)  =D55*X(19)/X2TOT
   43 IF(X(8).EQ.0.0) GO TO 34
      IF(X1TOT.EQ.0.0) GO TO 51
      A(297) =HCI13
      A(320) =SH11*X(33)/(X1TOT*X(8))
      A(321) =SH11*X(34)/(X1TOT*X(8))
      A(322) =SH11*X(35)/(X1TOT*X(8))
      A(323) =SH11*X(36)/(X1TOT*X(8))
      A(326) =0.1*SH1/X(8)
      A(327) =0.2*D1/X(8)
      A(328) =RESP1
      GO TO 41
   51 A(320) =0.0
      A(321) =0.0
      A(322) =0.0
      A(323) =0.0
      A(326) =0.1*SH1/X(8)
      A(327) =0.2*D1/X(8)
      A(328) =RESP1
   41 IF(X(9).EQ.0.0) GO TO 35
      IF(X1TOT.EQ.0.0) GO TO 52
      A(361) =SH22*X(33)/(X1TOT*X(9))
      A(362) =SH22*X(34)/(X1TOT*X(9))
      A(363) =SH22*X(35)/(X1TOT*X(9))
      A(364) =SH22*X(36)/(X1TOT*X(9))
      A(367) =0.1*SH2/X(9)
      A(369) =RESP2
      GO TO 42
   52 A(361) =0.0
      A(362) =0.0
      A(363) =0.0
      A(364) =0.0
      A(367) =0.1*SH2/X(9)
      A(369) =RESP2
   42 IF(X(10).EQ.0.0) GO TO 36
      IF(X1TOT.EQ.0.0) GO TO 53
      A(402)  =SH33*X(33)/(X1TOT*X(10))
      A(403)  =SH33*X(34)/(X1TOT*X(10))
      A(404)  =SH33*X(35)/(X1TOT*X(10))
      A(405)  =SH33*X(36)/(X1TOT*X(10))
      A(408)  =0.1*SH3/X(10)
      A(409)  =0.2*D3/X(10)
      A(410)  =RESP3
      GO TO 44
   53 A(402)  =0.0
      A(403)  =0.0
      A(404)  =0.0
      A(405)  =0.0
      A(408)  =0.1*SH3/X(10)
      A(409)  =0.2*D3/X(10)
      A(410)  =RESP3
   44 IF(X(11).EQ.0.0) GO TO 37
      IF(X1TOT.EQ.0.0) GO TO 54
      A(420) = HCI43
```

```
      A(443)  =SH44*X(33)/(X1TOT*X(11))
      A(444)  =SH44*X(34)/(X1TOT*X(11))
      A(445)  =SH44*X(35)/(X1TOT*X(11))
      A(446)  =SH44*X(36)/(X1TOT*X(11))
      A(449)  =0.1*SH4/X(11)
      A(450)  =0.2*D4/X(11)
      A(451)  =RESP4+XIM/X(11)
      GO TO 45
   54 A(443)  =0.0
      A(444)  =0.0
      A(445)  =0.0
      A(446)  =0.0
      A(449)  =0.1*SH4/X(11)
      A(450)  =0.2*D4/X(11)
      A(451)  =RESP4+XIM/X(11)
   45 IF(X(12).EQ.0.0) GO TO 38
      IF(X1TOT.EQ.0.0) GO TO 55
      A(461) = HCI54
      A(484)  =SH55*X(33)/(X1TOT*X(12))
      A(485)  =SH55*X(34)/(X1TOT*X(12))
      A(486)  =SH55*X(35)/(X1TOT*X(12))
      A(487)  =SH55*X(36)/(X1TOT*X(12))
      A(490)  =0.1*SH5/X(12)
      A(491)  =0.2*D5/X(12)
      A(492)  =RESP5
   55 A(484)  =0.0
      A(485)  =0.0
      A(486)  =0.0
      A(487)  =0.0
      A(490)  =0.1*SH5/X(12)
      A(491)  =0.2*D5/X(12)
      A(492)  =RESP5
      GO TO 46
   34 A(320) =0.0
      A(297) = 0.0
      A(321) =0.0
      A(322) =0.0
      A(323) =0.0
      A(326) =0.0
      A(327) =0.0
      A(328) =0.0
      GO TO 41
   35 A(361)=0.0
      A(362)=0.0
      A(363)=0.0
      A(364)=0.0
      A(367)=0.0
      A(368)=0.0
      A(369)=0.0
      GO TO 42
   36 A(402)=0.0
      A(403)=0.0
      A(404)=0.0
      A(405)=0.0
      A(408)=0.0
      A(409)=0.0
      A(410)=0.0
      GO TO 44
   37 A(443)=0.0
```

```
      A(420) = 0.0
      A(444)=0.0
      A(445)=0.0
      A(446)=0.0
      A(449)=0.0
      A(450)=0.0
      A(451)=0.0
      GO TO 45
   38 A(484)=0.0
      A(461) = 0.0
      A(485)=0.0
      A(486)=0.0
      A(487)=0.0
      A(490)=0.0
      A(491)=0.0
      A(492)=0.0
      GO TO 46
   32 A(304)=0.0
      A(305)=0.0
      A(306)=0.0
      A(297)=0.0
      A(386)=0.0
      A(387)=0.0
      A(388)=0.0
      A(420)=0.0
      A(427)=0.0
      A(428)=0.0
      A(429)=0.0
      A(468)=0.0
      A(469)=0.0
      A(470)=0.0
      A(461)=0.0
      GO TO 43
   33 A(320)=0.0
      A(321)=0.0
      A(322)=0.0
      A(323)=0.0
      A(326)=0.0
      A(327)=0.0
      A(361)=0.0
      A(362)=0.0
      A(363)=0.0
      A(364)=0.0
      A(367)=0.0
      A(368)=0.0
      A(402)=0.0
      A(403)=0.0
      A(404)=0.0
      A(405)=0.0
      A(408)=0.0
      A(409)=0.0
      A(443)=0.0
      A(444)=0.0
      A(445)=0.0
      A(446)=0.0
      A(449)=0.0
      A(450)=0.0
      A(484)=0.0
      A(485)=0.0
```

```
      A(486)=0.0
      A(487)=0.0
      A(490)=0.0
      A(491)=0.0
   46 A(505)   =Q1Q2
      A(506)   =Q1Q3
      A(507)   =Q1Q4
      A(509)   =Q1Q6
      A(512)   =Q1Q9
      A(533)   =Q1Q0
      A(554)   =Q2Q9
      A(565)   =Q2Q20
      A(574)   =Q2Q0
      A(595)   =Q3Q9
      A(601)   =Q3Q15
      A(602)   =Q3Q16
      A(613)   =Q3SH
      A(614)   =Q3AD
      A(615)   =Q3Q0
      A(636)   =Q4Q9
      A(642)   =Q4Q15
      A(654)   =Q4SH
      A(655)   =Q4AD
      A(656)   =Q4Q0
      A(675)   =Q5Q7
      A(677)   =Q5Q9
      A(683)   =Q5Q15
      A(684)   =Q5Q16
      A(695)   =Q5SH
      A(696)   =Q5AD
      A(697)   =Q5Q0
      A(716)   =Q6Q7
      A(718)   =Q6Q9
      A(725)   =Q6Q16
      A(736)   =Q6SH
      A(737)   =Q6AD
      A(738)   =Q6Q0
      A(759)   =Q7Q9
      A(777)   =Q7SH
      A(778)   =Q7AD
      A(779)   =Q7Q0
      A(800)   =Q8Q9
      A(811)   =Q8Q20
      A(820)   =Q8Q0
      A(858)   =Q9Q26
      A(861)   =TAU
      A(876)   =Q10Q3
      A(881)   =Q10Q8
      A(882)   =Q10Q9
      A(884)   =Q10Q11
      A(885)   =Q10Q12
      A(886)   =Q10Q13
      A(887)   =Q10Q14
      A(902)   =Q10Q0
      A(923)   =Q11Q9
      A(929)   =Q11Q15
      A(930)   =Q11Q16
      A(941)   =Q11SH
      A(942)   =Q11AD
```

```
A(943)  =Q11Q0
A(964)  =Q12Q9
A(970)  =Q12Q15
A(971)  =Q12Q16
A(982)  =Q12SH
A(983)  =Q12AD
A(984)  =Q12Q0
A(1005) =Q13Q9
A(1012) =Q13Q16
A(1023) =Q13SH
A(1024) =Q13AD
A(1025) =Q13Q0
A(1044) =Q14Q7
A(1046) =Q14Q9
A(1053) =Q14Q16
A(1064) =Q14SH
A(1065) =Q14AD
A(1066) =Q14Q0
A(1087) =Q15Q9
A(1105) =Q15SH
A(1106) =Q15AD
A(1107) =Q15Q0
A(1126) =Q16Q7
A(1128) =Q16Q9
A(1146) =Q16SH
A(1147) =Q16AD
A(1148) =Q16Q0
A(1169) =Q17Q9
A(1180) =Q17Q20
A(1189) =Q17Q0
A(1208) =Q18Q7
A(1210) =Q18Q9
A(1217) =Q18Q16
A(1228) =Q18SH
A(1229) =Q18AD
A(1230) =Q18Q0
A(1249) =Q19Q7
A(1251) =Q19Q9
A(1259) =Q19Q16
A(1269) =Q19SH
A(1270) =Q19AD
A(1271) =Q19Q0
A(1292) =Q20Q9
A(1310) =Q20SH
A(1311) =Q20AD
A(1312) =Q20Q0
A(1346) =Q21Q22
A(1353) =Q21Q0
A(1374) =Q22Q9
A(1385) =Q22Q20
A(1394) =Q22Q0
A(1415) =Q23Q9
A(1433) =Q23SH
A(1434) =Q23AD
A(1435) =Q23Q0
A(1456) =Q24Q9
A(1474) =Q24SH
A(1475) =Q24AD
A(1476) =Q24Q0
```

```
      A(1497) =Q25Q9
      A(1517) =RESP25*TEMP1
      A(1558) =Q26Q0
      A(1591) =SHQ21
      A(1592) =SHQ22
      A(1593) =SHQ23
      A(1628) =ADQ17
      A(1629) =ADQ18
      A(1630) =ADQ19
      A(1641)=FORCE(1)
      A(1642)=FORCE(2)
      A(1643)=FORCE(3)
      A(1644)=FORCE(4)
      A(1649)=EMC
      A(1651) =EM
      A(1677) =Q25F1
      X(41)=1.0
      DBBAR=0.0
      XBTOT=0.0
      DO 64 J = 1 , 40
   64 XBTOT = XBTOT + X(J)
      DO 65 J = 1 , 40
      QB(J) = X(J)/XBTOT
      IF(QB(J).LE.0.0000001) GO TO 65
      DBBAR = DBBAR - 1.442695 * QB(J) * ALOG(QB(J))
   65 CONTINUE
      IJ = 0.0
      DO 11 I = 1 , 40
      SUM(I) = 0.0
      DO 10 J = 1 , 41
      JJ = J + IJ
   10 SUM(I) = SUM(I) + A(JJ)
   63 IJ = 41 * I
   11 SUM(I) = SUM(I) * X(I)
      SUMTOT = 0.0
      DO 12 J = 1 , 40
   12 SUMTOT = SUMTOT + SUM(J)
      DO 13 J = 1 , 40
   13 Q(J) = SUM(J)/SUMTOT
      IJ = 0
      DO 19 I = 1 , 40
      DO 14 J = 1 , 41
      P(J) = 0.0
      JJ = J + IJ
      IF(SUM(I).EQ.0.0) GO TO 71
   14 F(JJ) = A(JJ) * X(I) / SUM(I)
   71 IJ = 41 * I
   19 CONTINUE
      IJ = 0
      DO 22 I = 1 , 40
      DO 15 J = 1 , 41
      JJ = J + IJ
   15 P(J) = P(J) + Q(I)*F(JJ)
      IJ = 41 * I
   22 CONTINUE
      DBAR = 0.0
      DO 16 I = 1 , 40
      IF(Q(I).LE.0.0000001) GO TO 16
      DBAR = DBAR - 1.442695 * Q(I) * ALOG(Q(I))
```

```
   16 CONTINUE
      AMI = 0.0
      IJ = 0
      DO 23 I = 1 , 40
      DO 17 J = 1 , 41
      JJ = J + IJ
      IF(F(JJ).EQ.0.0.OR.P(J).EQ.0.0) GO TO 17
      DIV1 = F(JJ)/P(J)
      IF(DIV1.LE.0.0000001) GO TO 17
      AMI = AMI + 1.442695*Q(I)*F(JJ)*ALOG(F(JJ)/P(J))
   17 CONTINUE
      IJ = 41 * I
   23 CONTINUE
      S = DBAR - AMI
      IF(ICOMP.LE.5) GO TO 96
      GO TO 97
   96 SSAVG = SSAVG + S
      DBAVG = DBAVG + DBAR
      DBBAVG = DBBAVG + DBBAR
      SS(ICOMP) = S
      ST(ICOMP) = DBAR
      SB(ICOMP) = DBBAR
      GO TO 98
   97 DIFF1 = S - SS(1)
      DIFF2 = DBAR - ST(1)
      DIFF3 = DBBAR - SB(1)
      DO 99 J = 1 , 4
      JS = J + 1
      SS(J) = SS(JS)
      ST(J) = ST(JS)
   99 SB(J) = SB(JS)
      SS(5) = S
      ST(5) = DBAR
      SB(5) = DBBAR
      SSAVG = SSAVG + DIFF1
      DBAVG = DBAVG + DIFF2
      DBBAVG = DBBAVG + DIFF3
      ICOMP = 5
   98 SAVG = SSAVG/ICOMP
      DAVG = DBAVG/ICOMP
      DDAVG = DBBAVG/ICOMP
      WRITE(6,95)ICOMP,TIME,S,SAVG,DBAR,DAVG,DBBAR,DDAVG,AMI
   95 FORMAT(5X,I5,2X,F10.2,7(2X,F10.5))
       METHOD RKSFX
      TIMER DELT=.1,FINTIM=1063.0,OUTDEL=10.0
END
STOP
ENDJOB
//
```

VITA

Robert Wayne Rutledge

Candidate for the Degree of

Doctor of Philosophy

Thesis: ECOLOGICAL STABILITY: A SYSTEMS THEORY VIEWPOINT

Major Field: Electrical Engineering

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