DYNAMICS OF SECONDARY SUCCESSION IN A GRASSLAND ECOSYSTEM

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DYNAMICS OF SECONDARY SUCCESSION IN A

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Dedicated to

Lourdes, Luisito, and Lourdes Maria

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SUMMARY

Ecological succession is the process which dominates the transient behavior of ecosystems as they proceed from their early stage of development to maturity, when the biotic community achieves a condition of equilibrium with its physical environment. When the transients arise in response to a perturbation of the climax ecosystem, the process is referred to as secondary succession. This research has been directed at integrating existing knowledge of ecological succession into a dynamic hypothesis, or theory, in order to account for successional modes of behavior as they arise from the endogenous feedback structure of the ecosystem.

The hypothesis is based on Odum's (1969) tabular model of ecological succession, and traces the mutual causalities between energy flow, abiotic and biotic matter, and species diversity as they interact in time and space to produce secondary succession. Using first and zero-order nonlinear difference equations, a simulation model has been formulated to test the hypothesis, and the results of exercising the model when quantified with grassland data are reported.

The simulations confirm that, within the limitations imposed by the physical environment and other open-loop factors, secondary succession is generated by the closed-loop structure of the ecosystem. They also show that successional modes of behavior are insensitive to parametric and exogenous perturbations as long as they are not exceptionally

large, and that while climatic factors are certainly influential on range productivity in the short run, the endogenous feedback structure which is responsible for succession is also responsible for the performance of the range ecosystem in the long run.

At a time when intensive methods of ecosystem utilization for food production are becoming prohibitive due to short supply and soaring costs of fossil fuels, the research has demonstrated forcefully that synthesis of long term utilization policies can and must be pursued on a successional-dynamic basis, by means of simulated experimentation with computer models such as the one reported here. Abundant opportunities for further research are pointed out, including generalizations of the theory to account for primary succession and the dynamics of senescence, to include other types of ecosystems and to include other types of ecosystem utilization.

CHAPTER I

INTRODUCTION

An understanding of ecological succession provides a basis for resolving man's conflict with nature.

-E. P. Odum, *The Strategy of Ecosystem Development*, 1969.

Statement of the Problem

The research hereby reported addresses the need for a deeper understanding of successional processes in ecological systems (ecosystems) such as lakes, grasslands and forests. In particular, it addresses the need for integrating existing knowledge of ecological succession into a dynamic model, or theory, of how successional transients arise from the endogenous feedback structure of the ecosystem.

Ecological succession is the process which dominates the dynamic behavior of ecosystems as they proceed from their early stage of development to maturity, when the biotic community achieves a condition of equilibrium with its physical environment. It is a universal, exceedingly complex process which involves the ecosystem as a whole and which may be examined from many different points of view (Clements, 1916). Odum (1959) has described the process as follows:

> Ecological succession is the orderly process of community change; it is the sequence of communities which replace one another in a given area. Typically, in an ecosystem, community development begins with pioneer stages which are replaced by a series of more mature communities until a relatively stable community is evolved which is in equilibrium with the local conditions. The whole series of communities which develop in a given situation is called the sere; the relatively transitory

> communities are called seral stages or seral communities, and the final or mature community is called the climax. . . . If succession begins on an area which has not been previously occupied by a community (such as newly exposed rock or sand surface), the process is known as primary succession. If community development is proceeding in an area from which a community was removed (such as a plowed field or cutover forest), the process is called secondary succession. Secondary succession is usually more rapid because some organisms, at least, are present already. Furthermore, previously occupied territory is more receptive to community development than are sterile areas. This is the type which we see all around us. In general, when we speak of ecological succession, we refer to changes which occur in the present geological age, while the pattern of climate remains essentially the same.

This research is concerned with the dynamics of secondary succession. It appears that secondary succession is the critical process to understand and manipulate if we are to manage ecosystems successfully (see, e.g., Ellison, 1960). Furthermore, it is generally acknowledged that energy, biotic and abiotic matter, and community diversity are the fundamental variables which interact in time and space to produce succession (Watt, 1973). The important question is, of course, how do they interact in order to generate ecological succession. Hopefully, answering this question will enable man to better manage his natural resources.

Historical Background

The general pattern of ecological succession is for biomass to accumulate in time and space until a stabilized ecosystem is achieved in which "maximum" biomass and diversity are maintained per unit of energy flow. The energy flow itself increases rapidly during succession in order to satisfy energy requirements for growth, but eventually decreases as the growth rate approaches zero and the total energy flow through the ecosystem becomes allocated to maintenance functions.

Thus, the overall successional mode of behavior can be characterized as growth followed by equilibrium, with possibly biomass and diversity temporarily overshooting their climax values before settling down to their equilibrium levels in the long-run. This overall successional pattern is shared by ecosystems whose variables display quite different numerical values. Figure 1 exhibits similar successional time histories for a forest and a laboratory microcosm.

It is important to explain from the outset the meaning attached here to the phrase "successional modes of behavior." The variables in dynamic systems exhibit modes of behavior such as equilibrium, growth, decline, damped or sustained oscillation, or some combination of these. A certain combination of these modes of behavior is associated with successional dynamics, as illustrated in Figure 1. The point to be stressed immediately is that while these successional modes of behavior are quantitative in the sense that they are generated as time histories of numbers through time, it is not the numbers themselves that matter (from the viewpoint of the present investigation) but the behavioral time patterns. It will be shown that this viewpoint follows naturally from the character of ecological succession and the modelling philosophy of feedback dynamics.

Figure 1 displays the modes of behavior associated with just two successional factors: biomass and bioenergetics. Indeed, many other factors are associated with ecological succession. Odum (1969) has presented a tabular model of ecological succession which summarizes the most important factors, i.e., those ecosystem attributes which are closely

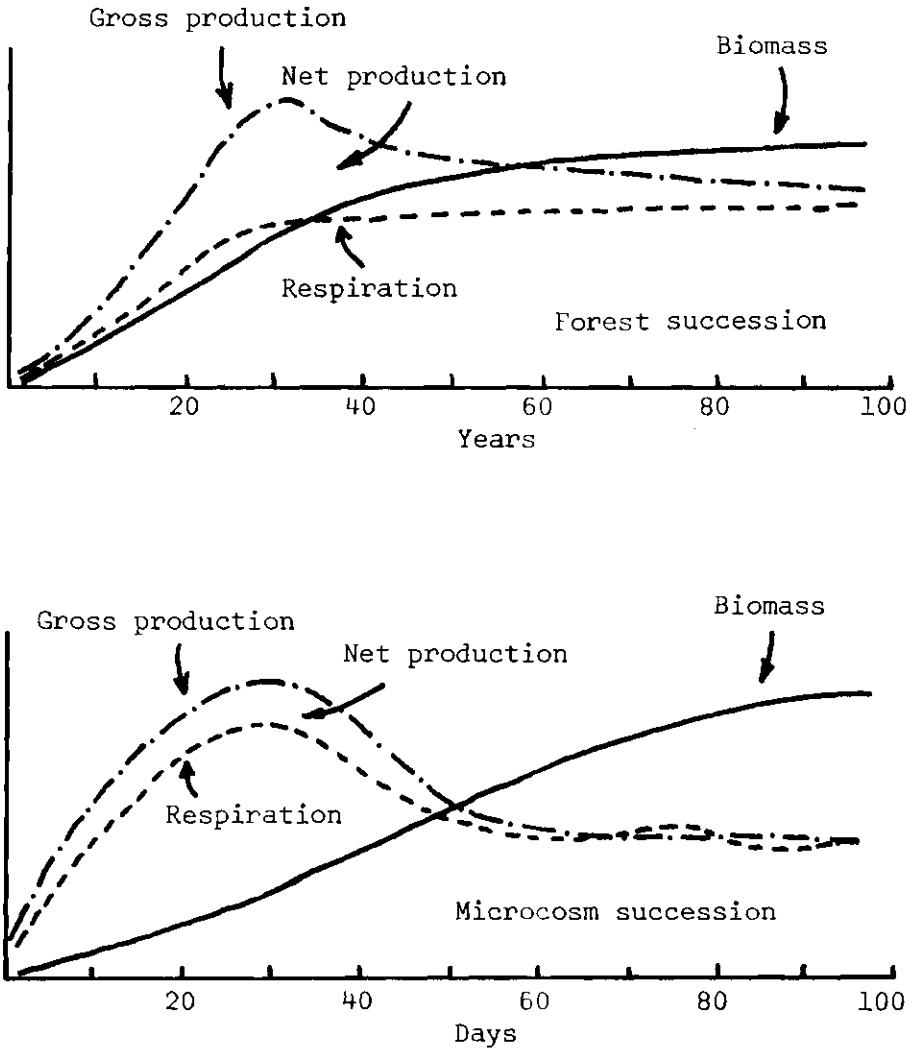

Figure 1. Dynamic Patterns of Ecological Succession in a Forest and a Laboratory Microcosm (Odum, 1969)

related to the successional process. It also indicates the general levels of magnitude characteristic of each factor during the developmental and mature stages of succession. Odum's tabular model is reproduced in Table 1. This table summarizes the available knowledge about ecological succession and therefore sketches the research frontier in the field.

As pointed out in the preceding section, what is needed is a theory, or model, to account for the way in which these factors interact so as to produce secondary succession. While nature's strategy is directed toward achieving a high B/P ratio (see item 2 of Table 1), man's strategy has been precisely the opposite. Only by developing a formal model that relates ecosystem structure to successional behavior will it be possible to attempt a synthesis. In developing this model, the research builds upon three previous lines of development: (1) the methodology of feedback ("industrial") dynamics, developed during the last 15 years, (2) the wealth of descriptive knowledge accumulated during (approximately) the last 100 years about ecological succession under both natural and utilization conditions, and (3) the wealth of structural and functional data on grasslands (and, specifically, on the Pawnee grassland) recently made available through the U.S. IBP Grassland Biome Study. A review of the relevant ecological literature is given below in the present chapter. The technical literature of feedback dynamics will be discussed in the next chapter, together with the presentation of research methodology.

Table 1. Odum's Tabular Model of Ecological Succession (Odum, 1969)

	Ecosystem Attributes	Developmental Stages	Mature Stages
	COMMUNITY ENERGETICS		
1.	Gross production/community respiration (P/R ratio)	Greater or less than 1	Approaches 1
2.	Gross production/standing crop biomass (P/B ratio)	High	Low
3.	Biomass supported/unit energy flow (B/E ratio)	Low	High
4.	Net community production (yield)	High	Low
5.	Food chains	Linear, predominantly grazing	Weblike, predominantly detritus
	COMMUNITY STRUCTURE		
6.	Total organic matter	Small	Large
7.	Inorganic nutrients	Extrabiotic	Intrabiotic
8.	Species diversity--variety component	Low	High
9.	Species diversity-equitability component	Low	High
10.	Biochemical diversity	Low	High
11.	Stratification and spatial heterogeneity (pattern diversity)	Poorly organized	Well-organized
	LIFE HISTORY		
12.	Niche specialization	Broad	Narrow
13.	Size of organism	Small	Large
14.	Life cycles	Short, simple	Long, complex
	NUTRIENT CYCLING		
15.	Mineral cycles	Open	Closed
16.	Nutrient exchange rate, between organisms and environment	Rapid	Slow
17.	Role of detritus in nutrient regeneration	Unimportant	Important
	SELECTION PRESSURE		
18.	Growth form	For rapid growth ("r-selection")	For feedback control ("K-selection")
19.	Production	Quantity	Quality
	OVERALL HOMEOSTASIS		
20.	Internal symbiosis	Undeveloped	Developed
21.	Nutrient conservation	Poor	Good
22.	Stability (resistance to external perturbations)		
23.	Entropy	High	Low
24.	Information	Low	High

Objective of the Research

The ultimate objective of the research started in this dissertation is ecosystem design, i.e., the systematic nondestructive manipulation of ecosystems for human benefit. The immediate objective to be achieved has evolved together with the research as it progressed. The initial objective was to model an ecosystem standing in closed-loop interaction with its users. It was thought at that time that the initial thing to do was to integrate both the successional-dynamic and social-dynamic aspects of ecosystem utilization into the simplest possible model appropriate for policy design, leaving for subsequent research the task of going deeper into each of the sectors in order to address specific problems requiring, for example, explicit consideration of diversity as a successional variable. As the research progressed, however, it became apparent that the most fruitful objective to pursue in the short-run was to develop a more complete ecosystem-specific model of ecological succession than was originally intended. An important consideration for this shift in emphasis was the conclusion, after a considerable amount of research, that for all practical purposes the social dynamics acting upon a *given* ecosystem are determined in open-loop with respect to that *particular* ecosystem. For example, the Taylor Grazing Act was passed by the U. S. Congress (1934) to regulate the utilization of public lands for grazing and therefore was implemented uniformly for all such lands, not only at Pawnee. The dynamics of commodity production cycles are similarly generated at the national level of aggregation (Meadows, 1970), thus transcending the local condition of a given range

ecosystem. At the local level, utilization pressures on the ecosystem appear to be basically dependent on demand from the national commodity market, with regulatory Federal laws, range condition and current climatic conditions acting as constraints. Thus, the coupling between a particular ecosystem and its users appears to be open, at least as long as limiting conditions are not reached. To be meaningful, it therefore seems that the social-dynamic aspect of ecosystem utilization must be studied (for a given class of ecosystems, e.g., rangelands) at the level of the policymaking institutions involved, such as regional rancher's associations, the livestock industry, grazing district administrators, the Bureau of Land Management, the U. S. Forest Service and the U. S. Congress in the case of public grasslands. Conclusions from such a study would provide overall national guidelines for administration of that class of ecosystems, e.g., for all grasslands. Additional concrete guidelines of conservation/utilization practice at the local level (e.g., for a given range ecosystem) are to be formulated on a successional-dynamic basis. Besides, the potential utility of more complete results on the successional-dynamic aspect appears to be tremendous in that they can be subsequently tested at, adapted to, and generalized for other ecosystems throughout the world.

In order to be more specific on the purpose of the research at hand, let us point out that five classes of variables can be abstracted from Table 1 as fundamental to the successional process, on the basis of whether they are related to matter (rows 1, 2, 3, 4, 5, 6, 7, 15, 17, 21, 23, 24), diversity (rows 8, 9, 10, 11, 23, 24), energy (rows 1, 2,

3, 4, 5, 22, 23, 24), space (rows 11, 12, 13, 20) and time (rows 14, 16, 18). Matter and diversity interact with energy flow through the ecosystem in time and space, and succession results. Indeed, it is well known that these are the fundamental variables which determine the behavior of ecosystems whether in succession or steady-state (Watt, 1973). The important question is, of course, how do they interact in order to generate ecological succession. The present dissertation is dedicated to answer this one, deceptively simple question.

The previous discussion implies an important qualification of the research problem, i.e., the research is concerned with explaining successional dynamics as they arise from the internal, closed-loop feedback structure of the ecosystem. Open-loop environmental factors such as temperature and precipitation do have an influence on succession. For example, grasslands are characteristic of regions where precipitation is neither abundant enough to support a forest nor scarce enough to result in a desert. Thus, the average level of precipitation in a given region sets a limit on how far succession can proceed in that particular biome. These open-loop aspects of succession are generally well-known and well-understood. The present contribution focuses on how successional dynamics arise from the internal structure of the ecosystem under a given set of fairly stable environmental conditions. This focus immediately brings to surface another important qualification to the research problem, i.e., to be meaningful, the research must be ecosystem-specific. Once a dynamic hypothesis for ecological succession has been structured and tested for a given ecosystem, its generalization for other ecosystems

can be inductively attempted.

The Pawnee national grassland in northeastern Colorado was chosen as the subject ecosystem for the research. A general description of this ecosystem is given by Jameson and Bement (1969). Pawnee is part of the western grassland biome and, ecologically speaking, is classified as a short-grass prairie. From the viewpoint of land-use management, it is subject to a single use (i.e., grazing) and it is classified as a year-long range, with livestock feeding almost exclusively from native forage plants. It was natural to select this particular grassland as the subject ecosystem for the research. Pawnee is the intensive study site for the U. S. Internal Biological Program (IBP) Grassland Biome Study and, as a result, there exists a wealth of functional and structural information about it which is now available for analysis. At a time when many ecosystems of the world continue to deteriorate under human manipulation, this ecosystem has improved over the last four decades as a result of better ecosystem management (Coleman et al., 1973). Successful utilization of grasslands has come about as a result of practical knowledge gained from earlier (and sometimes disastrous) mistakes in their manipulation. A better understanding of how this pattern of success arises may yield important guidelines for conservation and utilization practice in this and other ecosystems. This consideration further supports grassland succession as the focal point to initiate research on the feedback dynamics of ecological succession.

The preceding discussion leads to a clear focus and a concrete objective to be achieved, i.e., to contribute a simulation-tested

dynamic hypothesis of secondary succession as it is generated by the endogenous feedback structure of a grassland biotic community within the limits imposed by its physical environment.

Review of the Literature

There are two broad categories of scientific literature from which the present research draws: the literature of ecology and the literature of feedback dynamics. It is hoped that this study may prove of use to both ecology-oriented and systems-oriented readers. With this objective in mind, the present section is primarily dedicated to the system-oriented reader unfamiliar with the ecological background underlying the study. It also serves, of course, the purpose of documenting the ecological foundations for the research. Ecology-oriented readers unfamiliar with the technical background of feedback dynamics will find the relevant literature discussed in the next chapter, together with the presentation of research methodology.

Ecology has been defined as the study of the structure and function of nature (Odum, 1963). The spectrum of ecology has traditionally covered natural levels beyond that of the individual organism, i.e., populations, communities, and the biosphere. There appears to be consensus on the fact that term "ecology" was first introduced approximately one century ago (Haeckel, 1866), although it was not recognized as a discipline until the beginning of this century (Odum, 1971). Generally speaking, ecology remained a vaguely-defined science until quite recently, as stated by the British ecologist A. Macfadyen (1957):

> Ecology concerns itself with the interrelationships of living organisms, plant or animal, and their environments; these are studied with a view to discovering the principles which govern the relationships. That such principles exist is a basic assumption--and an act of faith--of the ecologist. His field of inquiry is no less wide than the totality of the living conditions of the plants and animals under observation, their systematic position, their reactions to the environment and to each other, and the physical and chemical nature of their inanimate surroundings. . . . It must be admitted that the ecologist is something of a chartered libertine. He roams at will over the legitimate preserves of the plant and animal biologist, the taxonomist, the physiologist, the behaviourist, the meteorologist, the geologist, the physicist, the chemist, and even the sociologist: he poaches from all these and from other established and respected disciplines. It is indeed a major problem for the ecologist, in his own interest, to set bounds to his divagations.

In 1935, Tansley introduced the concept of ecosystem (ecological system) as a focus for the study of ecological phenomena. Evans (1956) presented the ecosystem as the basic unit of study in ecology. The ecosystem is defined as the biotic community standing in interaction with its physical environment. This important concept provides for the comparative study of similarities and dissimilarities between different kinds of ecosystems, e.g., a lake, a tundra, or a grassland. Thus, it would seem more precise to define ecology as the study of the structure and function of ecosystems.

The ecosystem concept is central to all modern presentations on ecology (see, e.g., Odum, 1959, 1963, 1971; Gates, 1968; Major, 1968; Kormondy, 1969; McNaughton and Wolf, 1973; Watt, 1973). It also appears to be central to applied ecology, i.e., the use of ecological principles for guidance in managing natural environments (Van Dyne, 1968). There are, of course, many different kinds of ecosystems, such as lakes, tundras, deserts, grasslands, and forests. Of primary interest for the

purpose of this research is the literature concerned with grassland ecosystems and their utilization. Grassland ecology has been studied by Hanson (1938, 1950), Carpenter (1940), Barnard (1964), Klapp (1964), Moore (1966), Allen (1967), Daubenmire (1968), Coupland et al. (1969), Costello (1969), and Spedding (1971).

The preceding review, while very abbreviated, is indicative of the enormous reservoir of ecological knowledge available in descriptive form. More recently, increasing recognition of the ecosystem concept and progressive maturity of systems science has led to systems-ecology research, i.e., the application of systems science methodologies to the study of ecosystems (Odum, 1960; Watt, 1966, 1968; Van Dyne, 1968; Dale, 1970; Odum, 1971; Patten, 1971, 1972; Watt, 1973). In the area of grasslands, a significant amount of research has been conducted at Pawnee and other sites by the U. S. IBP Grassland Biome Study. Beyond data collection, systems-ecology research is directed at casting into mathematical models all the knowledge available on the structure and function of grassland ecosystems. This activity has resulted in several large scale state space models (Bledsoe et al., 1971; Innis, 1972a; Patten, 1972) to account for the steady-state dynamics of the Pawnee grassland ecosystem.

While the inclusion of fuzzy biological law coupled with their largeness severely limits the utility of these models (Innis, 1972b), they are contributing significant new insights into the steady-state dynamics of ecosystems. Comprehensive models to account for the transient (i.e., successional) dynamics, on the other hand, are thus far

wanting, although some theoretical models have been presented to account for selected aspects. For example, Monsi and Oshima (1955) contributed a theoretical analysis of production during plant succession. Bledsoe and Van Dyne (1971) have presented a model to account for species substitution during secondary succession in old fields. Williams (1971) developed a computer simulation to quantify Lindeman's classical studies of energy flow and trophic equilibrium in a lake (Lindeman, 1942) but did not account for trophic dynamics during succession. Indeed, a comprehensive model to account for the dynamics summarized in Figure 1 and Table 1 of this chapter is not available. On the other hand, an abundance of descriptive information on successional dynamics has been accumulating for many years in the ecological literature, starting with early studies such as those by Shelford (1911a, 1911b), Clements (1916), Chantz (1917), Cooper (1926), and Tansley (1929, 1935). In his classical paper, Lindeman (1942) was the first one to couple the open-loop flow of energy with the closed-loop cycling of matter as an important aspect (i.e., the "trophic-dynamic" aspect) contributing to the dynamics of ecological succession. More recently, several authors have elaborated on the dynamics of community diversity as another crucial aspect of successional processes leading to climax ecosystems (Margalet, 1963; Gilyarov, 1969; Margalef, 1969; Preston, 1969; Whittaker, 1969). Cooke's experiments with laboratory microcosms (Cooke, 1967) provided empirical evidence on the fact that succession arises from the internal structure and function of the ecosystem even when it is completely closed to all external inputs except light. As previously indicated, Odum's tabular

model (Odum, 1969) has provided a synthesis of the ecological variables which appear to be involved.

The importance of gaining a better understanding of successional dynamics arises from the fact that ecosystems succeed under the pressure of human utilization. In the case of grassland ecosystems used for grazing, it has long been recognized that plant succession results from sustained grazing (Sampson, 1919). Extensive field research has been conducted on the effects of grazing and different grazing systems on range conditions (Pickford, 1932; Albertson et al., 1957; Klipple and Costello, 1960; Ellison, 1960; Reed and Peterson, 1961; Paulsen and Ares, 1962; Jameson, 1963; Smith, 1967; Frischknecht and Harris, 1968; Steger, 1970). The ecological basis for range management is also well developed (Dyksterhius, 1949; Parker, 1954; Osborn, 1956; Costello, 1957; Dyksterhius, 1958; Goekel and Cook, 1960; Humphrey, 1962; DeVos, 1969; Lewis, 1969; Jameson, 1970; Fridrikson, 1972), resulting in enlightened practices of range management whereby many grasslands appear to improve rather than deteriorate under grazing (Williams, 1966; Semple, 1970; Steger, 1970; Vallentine, 1971; Coleman et al., 1973).

Therefore, the long-range effects of secondary succession triggered by grazing may be beneficial or detrimental to the grassland. In his comprehensive survey on the influence of grazing on range succession, Ellison (1960) refers to unregulated livestock overgrazing as the principal cause for deterioration of portions of the western range, and then he states:

> Much of this area is too difficult of access or too low in productivity to warrant intensive pastoral practices, so that

> improvement of its protective plant cover and forage value must be achieved extensively--that is, by natural successional processes. Ecological understanding of these processes, which must form the basis for effective management, is therefore imperative. The achievement of such understanding is a scientific challenge of the first order.

Furthermore, Ellison points out that such understanding cannot be restricted to the destructive effects of overgrazing. In fact, to dwell on this would be an exercise on the obvious. What is most needed from the viewpoint of range ecosystem management is an analysis of secondary succession as provoked by light or moderate grazing (as opposed to heavy grazing) in order to learn to what extent grazing can be manipulated as a constructive ecological force. Unfortunately, the successional response to moderate as opposed to heavy grazing is difficult to observe under actual operating conditions, and field data with regard to small differences (i.e., differences between moderate grazing and no grazing) are both scant and ambiguous. In that it would be practically unfeasible to arrange for controlled (i.e., constant environment) experimental conditions in the field over enough space and time for secondary succession to be observed after an exogenous perturbation, one concludes that such experimentation must be carried out in the model world. It will be shown in the following chapters that feedback dynamics provides an appropriate modeling philosophy for such an investigation. At the Grassland Research Institute in England, feedback dynamics has been applied to investigate the problem of pasture contamination by the excreta of grazing cattle (Spedding, 1971). Otherwise, literature concerned with the application of feedback dynamics to problems of grassland and, for that matter, ecosystem utilization appears to be nonexistent.

CHAPTER II

MODEL STRUCTURE

Our discussion will be adequate if it has as much clearness as the subject-matter admits of, for precision is not to be sought for alike in all discussions. . . . It is the mark of an educated man to look for precision in each class of things just so far as the nature of the subject admits.

-Aristotle, *Nicomachean Ethics*, 384-322 BC

Method of Procedure

The method of procedure to conduct the research has followed the methodology generally known as "industrial dynamics" (Forrester, 1961). Industrial dynamics is a philosophy about systems in general which is essentially qualitative in character, takes the notion of accumulation as the basic building block in the universe, and recognizes that the dynamic behavior of systems is dominated by their feedback loop structure which, in turn, is influenced by the system's performance patterns through time. It is also gradually becoming a body of theory that relates system structure to dynamic behavior (Forrester, 1968b). Due to the vast generality of the subject, the term "industrial dynamics" has become a misnomer. The term "system dynamics" appears frequently in the current literature (Forrester, 1971). In that it is more descriptive of the fundamental assumption guiding the whole approach, "feedback dynamics" appears to be a better term, and it will be used consistently in this presentation.

There is a research methodology associated with the systems philosophy of feedback dynamics. Forrester (1961) originally stated this methodology as follows:

1. Identify a problem.
2. Isolate the factors that appear to interact to create the observed symptoms.
3. Trace the cause-and-effect information feedback loops that link decisions to action to resulting information changes and to new decisions.
4. Formulate acceptable formal decision policies that describe how decisions result from the available information streams.
5. Construct a mathematical model of the decision policies, information sources, and interactions of the system components.
6. Generate the behavior through time of the system as described by the model (usually with a digital computer to execute the lengthy calculations).
7. Compare results against all pertinent available knowledge about the actual system.
8. Revise the model until it is acceptable as a representation of the actual system.
9. Redesign, within the model, the organizational relationships and policies which can be altered in the actual system to find the changes which improve system behavior.
10. Alter the real system in the directions that model experimentation has shown will lead to improved performance.

This methodology covers the identification (items 1, 2, 3, 4), analysis (items 5, 6), validation (items 7, 8) and design (items 9, 10) stages to be covered in addressing problems associated with complex systems in general. A step-by-step elaboration of this methodology with respect to the specific research at hand is in order.

The problem at hand is one of explaining successional modes of behavior as they arise from ecosystem structure under normal environmental conditions. More specifically, it is desired to achieve an ecological understanding of secondary succession processes in a grassland ecosystem, inasmuch as proper manipulation of these processes is required for their preservation and improvement under utilization

conditions.

Odum's tabular model was introduced in the previous chapter as a summary of the factors which appear to interact in generating the ecological symptoms of interest. The "symptoms" in this case are the dynamic time patterns generally associated with ecological succession, as shown in Figure 1 and Table 1. In addition to these overall time patterns, the symptoms of interest include the fact that grasslands usually increase their forage yield and otherwise generally improve under a moderate grazing pressure, the fact that grass composition usually changes for the worst under sustained overgrazing, and so forth. Presumably, the factors listed in Odum's tabular model interact in some complex fashion to generate these desirable or undesirable symptoms.

Structuring these interactions as closed-loop influence diagrams is the most crucial aspect of feedback dynamics as a research methodology. It involves the tracing of feedback influence loops among the identified system variables, the coupling of these loops within a closed system boundary, and the identification of the mechanisms governing the gains and delays within each loop, as well as their polarity. In the context of the investigation at hand, it involves tracing the feedback loops coupling organic matter, inorganic nutrients, species diversity and other internal variables of a grassland ecosystem, as well as identifying the mechanisms to account for both the positive feedbacks dominant during successional development and the negative feedbacks which become dominant as the climax ecosystem is reached. A verbal and/or diagrammatic statement describing the feedback relationships which are believed

to cause the system behavior of interest constitutes a dynamic hypothesis, i.e., a theory of how system behavior results from its internal feedback structure. A dynamic hypothesis for secondary succession in a grassland ecosystem is developed in the next section of this chapter.

Putting forth a hypothesis to explain dynamic phenomena such as ecological succession immediately creates the need for testing it. In feedback dynamics research, model building is undertaken in order to permit simulated experimentation leading to either outright rejection or tentative acceptance of the dynamic hypothesis. The mechanics involved in constructing a detailed mathematical model to quantify the feedback relationships outlined in the dynamic hypothesis are well-developed (Forrester, 1961). According to Forrester (1968b), the feedback structure of a system possesses four significant hierarchies:

THE CLOSED BOUNDARY

THE FEEDBACK LOOPS

LEVELS AND RATES

GOAL STATE
OBSERVED STATE
DISCREPANCY BETWEEN GOAL AND OBSERVED CONDITIONS
CORRECTIVE ACTION

The system boundary is chosen so as to entertain a closed system, i.e., one whose behavior is dominated by internal structure rather than external events, with perhaps one or more exogenous inputs influencing particular modes of behavior. In the context at hand, the closed boundary is of course the natural boundaries of the subject grassland ecosystem. Examples of exogenous inputs to a grassland ecosystem are solar light, precipitation, introduction of domestic animals, etc.

The feedback loop is the basic system component and the identification of the loop or set of interconnected loops which is believed to structure the system constitutes the dynamic hypothesis to be tested. The dynamic hypothesis to be introduced below will include those feedback loops from grassland ecosystem structure which are thought to generate the successional process.

In order to formulate the substructure within each loop, ecosystem variables are to be classified as either levels or rates. Mathematically speaking, levels and rates are formulated as first and zero order difference equations, respectively. Whether a given ecological variable should be formulated as a level or a rate can be ascertained by conceptually bringing the ecosystem to rest. Variables which remain measurable in an ecosystem at rest are properly classified as levels, e.g., weight of plant biomass per unit area. Formulating the substructure of rate variables (e.g., the growth rate of plant biomass) may consist of simple algebraic expressions or involve complex nonlinearities (i.e., table functions) to express flow processes as a function of the current values of the levels. A mathematical model thus constructed will be indicative of the specific data and parameter values needed to quantity the various model relationships; in this research, data required to quantify the model and permit testing of the dynamic hypothesis was abstracted from the ecological literature to the extent of their availability, reasonable numerical values being assumed otherwise. In closing the discussion on the model building aspect of the methodology, it is interesting to note that structuring an ecosystem model in the manner outlined above is in

complete consonance with the best knowledge available on ecological modeling. H. T. Odum (1971), for example, classifies ecosystem components as:

(i) energy storage compartments,

(ii) energy flow pathways,

(iii) energy sources and sinks, and

(iv) complex work functions, to couple the various energy storages and flows throughout the ecosystem.

Compartments (i), (ii) and (iv) of Odum's classification clearly correspond to the levels, rates and table functions, respectively, of the previous discussion. Sources and sinks are also used in feedback dynamics model building, and for the same basic purpose, i.e., to explicity delineate the boundaries of the system being modelled. As indicated by the sixth step of the methodology, the model thus constructed is to be exercised through time in a digital computer. Following generally accepted practice in feedback dynamics research, the model for grassland succession has been developed in DYNAMO (DYNAmic MOdels) language (Pugh, 1963). The detailed formulation of model equations is fully documented in the appendix.

Modeling work as anticipated above eventually leads to a need for model validation. It is important to discuss the validation philosophy to be adopted and the validation methodology to be followed in the research. The validation concept for a given model must be justified in terms of the nature of the model or, equivalently, in terms of the nature of the modeling objectives; validation methodology follows naturally from a well-founded validation philosophy. The validation philosophy of

feedback dynamics has been stated by Forrester (1961) as follows:

> The significance of a model depends on how well it serves its purpose. The purpose of industrial dynamics models is to aid in designing better management systems. The final test is satisfying this purpose must await the evaluation of the better management. In the meantime the significance of models should be judged by the importance of the objectives to which they are addressed and their ability to predict the results of system design changes. The effectiveness of a model will depend first on the system boundaries it encompasses, second on the pertinence of selected variables, and last on the numerical values of parameters. The defense of a model rests primarily on the individual defense of each detail of structure and policy, all confirmed when the total behavior of the model system shows the performance characteristics associated with the real system. The ability of a model to predict the state of the real system at some specific future time is not a sound test of model usefulness.

Feedback dynamics modeling of ecological succession is directed at the qualitative study of dynamic modes of behavior such as the growth-followed-by-equilibrium behavior exhibited by ecosystems during their successional transient. This is in contrast to modeling for the quantitative purpose of computing numbers in a predictive fashion. Modeling dynamic modes of behavior calls for a validation concept which is itself qualitative and dynamic. A dynamic validation concept appropriate for this research is presented in Figure 2.

Modeling was undertaken in response to the successional problematic as it is presently understood and, specifically, as stated in the statement of the research problem above. In addition, modeling has drawn from the currently available reservoir of ecological knowledge and general dynamic system principles, itself the result of previous experimentation with (real-world) systems (denoted by the dotted-line block to the right). The dotted-line block to the left of Figure 2 denotes

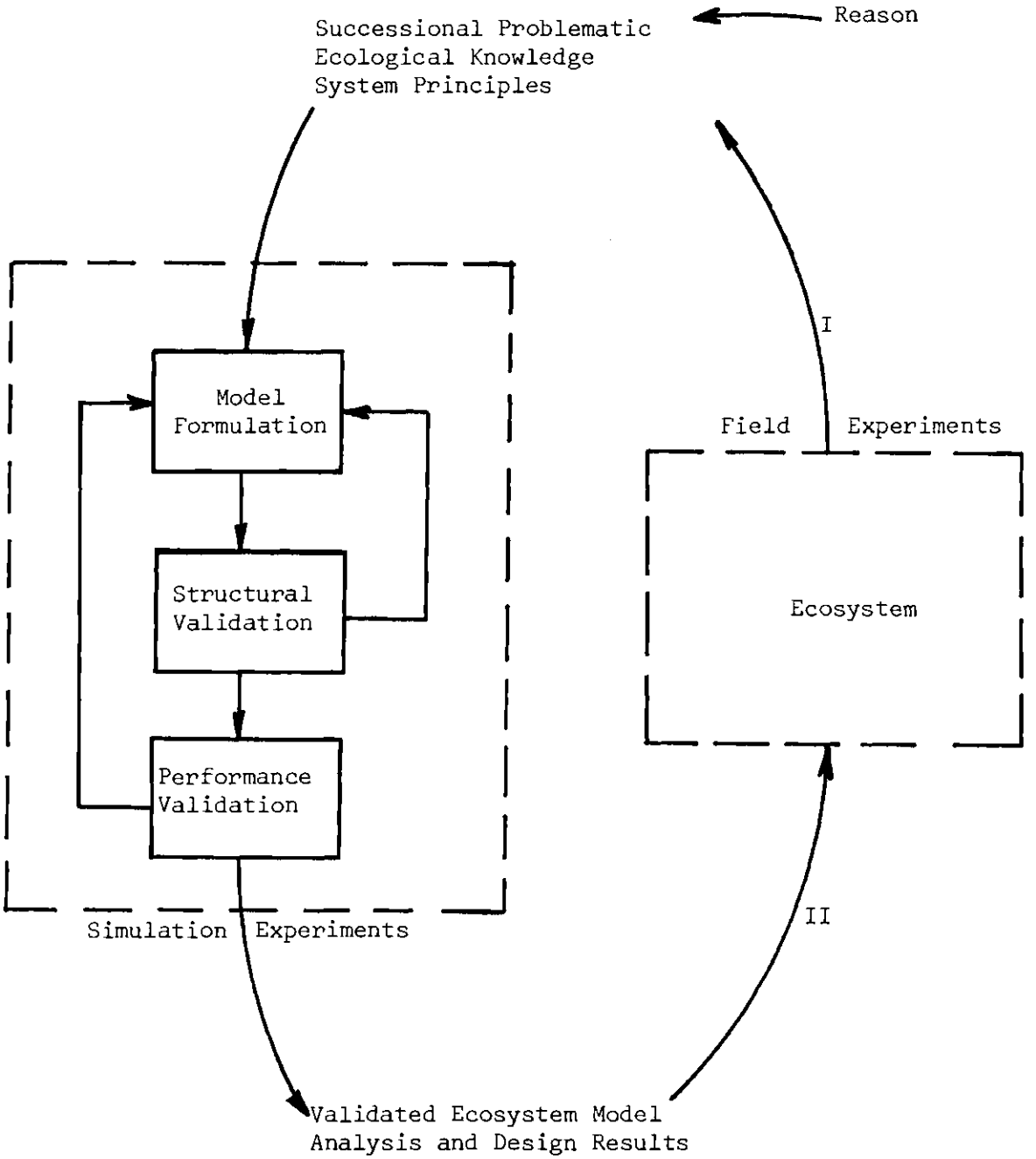

Figure 2. Dynamic Validation Concept

simulation, i.e., experimentation in the model world. The resulting simulation model must be validated with respect to the currently available knowledge from which it was developed.

From the viewpoint of methodology, it is convenient to distinguish between structural validation and performance validation. Both are mutually complementary. Both are highly qualitative in character, but each one merits separate attention. Structural validation verifies that the structure is meaningful and realistic in terms of, and consistent with, all relevant information available on the structure of the subject system. Performance validation verifies that the hypothesized feedback structure generates the same modes of behavior as the system under study, and that the quantification of the model has been accomplished properly. Properly does not necessarily mean accurately. When a structurally validated model reveals insensitivity to the value of a given parameter within its general order of magnitude, "properly" relates to the proper level of magnitude. Needless to say, "properly" means "accurate" in the opposite case; if model behavior is sensitive to a given parameter it becomes desirable to estimate its numerical value as accurately as possible. In feedback dynamics, validation of both model structure and model data should be accomplished in the context of a specific system, a specific system model, and specific objectives. In this investigation, a validated ecosystem model will be one that displays no significant inconsistency with the full range of knowledge available on the subject ecosystem and which proves itself adequate for the study of its successional dynamics.

A point is reached, however, when the ecosystem model is exercised under conditions for which comparable ecosystem-generated behavioral data are not available. This stage will be reached in the process of using the validated ecosystem model for ecological policy design (or redesign). The subject ecosystem can then be altered according to policies that model experimentation has yielded as beneficial to successional performance for a given set of design criteria. The resulting response will contribute to expand the reservoir of available ecological knowledge, and it may or may not motivate a model revision to account for the new knowledge gained. The validation process for dynamic closed-loop models is thus seen as being itself dynamic and closed-loop. It is also highly qualitative, because as feedback systems increase in complexity (high order, inclusion of both negative and positive feedback, nonlinearities, multiple-loops) their dynamic behavior changes in major qualitative ways (Forrester, 1968a); this is indeed the class of systems to which ecosystems belong, and the research objective is precisely the study of how successional dynamics arise from the complex feedback structure of ecosystems. This research traverses the dynamic validation loop from point I to point II of Figure 2, so as to produce an ecosystem model which is validated with respect to the available knowledge and which itself suggests further field experimentation to close the loop and start anew.

Dynamic Hypothesis

The fundamental proposition of this thesis is that, given an exogenous energy source, the successional dynamics of ecosystems arise from their internal feedback structure. In other words, the availability

of physical resources such as space, water and nutrients establishes limits on how far ecosystem development can proceed, but these availabilities by themselves do not generate succession. Given a light input source, a climax autotrophic community succeeds when inoculated into fresh media under laboratory conditions where the microecosystem remains completely closed to other external influences (Cooke, 1967). Given the presence of solar energy input and the presence of levels of precipitation, temperature, etc., which remain approximately constant in the long-run, terrestrial ecosystems succeed to become deserts, tundras, grasslands, forests, etc., as the case may be (Odum, 1969). In both cases, the successional process is internally generated and controlled by the biotic community, not by external factors, although an exogenous perturbation may trigger a climax ecosystem into secondary succession toward either the same climax as before or a permanent disclimax. This viewpoint has important repercussions as to methodology, as discussed in the previous section. The present section abstracts from the ecological literature a dynamic hypothesis for secondary succession in a grassland ecosystem.

It has been pointed out (Watt, 1973) that energy, matter, diversity, space and time are the fundamental ecological variables. Figure 3 exhibits a hypothesis on the feedback structuring of these fundamental variables. In order to be specific, the discussion will be focused on the case of a grassland ecosystem which has been perturbed so as to trigger secondary succession. Solar energy is absorbed by the green plants and converted to fixed energy by the biochemical process of

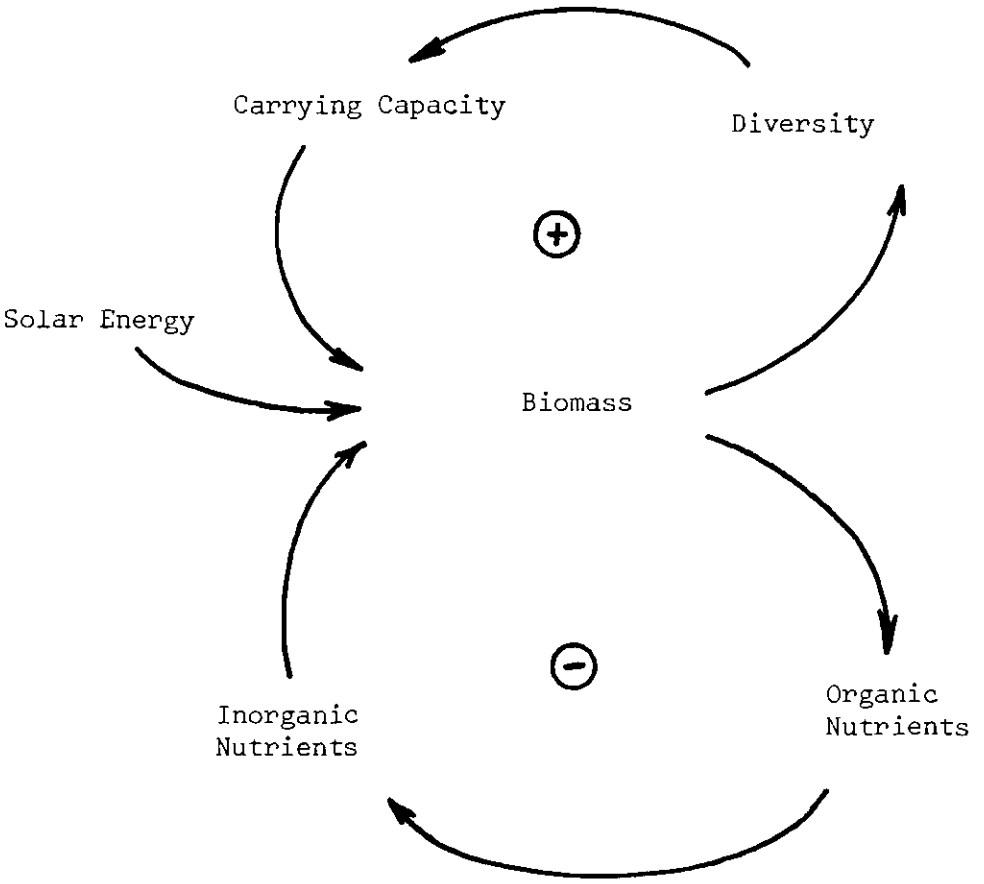

Figure 3. Fundamental Feedback Structure of an Ecosystem

photosynthesis. The energy becoming available (i.e., being fixed) can be allocated to either growth or maintenance functions. By growth is meant the quantitative accumulation of living matter which results when energy is spent in fixing nutritive abiotic matter into biotic matter, or biomass. The energy expenditure necessary to accomplish this transition must come either from an internal source of stored energy or from the sun. In the early stages of development, the internal reservoir of stored energy is insignificant, and therefore the ecosystem is highly dependent on solar energy for its survival and development. Given a constant environment that includes the availability of incoming solar energy, vegetation builds up as long as soluble inorganic nutrients are available and the carrying capacity of the soil remains unsaturated. The lower loop in Figure 3 accounts for the closed-loop cycling of nutrients throughout the ecosystem; it is well known (Lindeman, 1942; Borman and Likens, 1967, 1970) that it possesses negative polarity, returning the ecosystem to a state of trophic equilibrium after an exogenous perturbation. The upper loop, on the contrary, exhibits positive polarity, and is postulated as the dominant force behind the community-controlled growth dynamics associated with ecological succession. When the carring capacity of the soil becomes saturated, energy becoming available which can no longer be used for further quantitative growth is allocated to quality functions, such as building up community diversity. Exploitation of specialized inches by emerging species effectively results in increased carrying capacity, which in turn allows for further build up of plant biomoss, thus setting the stage for still further

diversification, and so forth. This hypothesis is in consonance with Margalef's theory that "succession is simply the exchange of an excess available energy in the present, for a future increase in biomass" (Margalef, 1963). Eventually, however, a point is reached in which further diversification does not result in increased carrying capacity either because (i) niche specialization cannot proceed any further or (ii) because trophic equilibrium becomes limiting, or (iii) because some environmental factor such as temperature or precipitation becomes limiting. As this point is approached, the gain of the positive feedback gradually vanishes, and succession proceeds no further.

The coupled feedback loops of Figure 3 provide a dynamic hypothesis of ecological succession which is highly parsimonious, i.e., it accounts for only the five fundamental ecological variables (energy, matter, diversity, time and space) and the way they are postulated to interact in producing succession. The lower loop accounts for the circulation of matter. The upper loop accounts for diversity and space, the latter expressed functionally in terms of carrying capacity. Energy flows into the ecosystem and is either stored or gradually dissipated in the performance of work around the loops. Finally, this structure generates successional behavior as a function of time, i.e., each arrow in the diagram of Figure 3 denotes a time delay.

It is illuminating to consider how all the factors listed by Odum in his tabular model (Table 1) relate to this hypothesis and, at the same time, are indicative of how it should be further structured in developing a testable model. Gross production/community respiration,

gross production/standing crop biomass, and biomass supported/unit energy flow (attributes 1, 2 and 3 of Table 1) are quantitative indices of how the positive and negative feedbacks interact in allocating incoming energy for biomass production and other functions. Figure 3 explicitly recognizes that, given availability of nutrients and an unsaturated carrying capacity, incoming energy is to be primarily allocated to production of biomass. This is in consonance with the trends listed for these ratios in the tabular model, as well as with the trend listed for net community production, or yield (attribute 4). Figure 3 also indicates that a build-up of biomass gradually has a positive influence on diversity, but lacks content on the feedback structure which increasingly allocates energy to diversification and other quality functions as maturity is approached; this is, of course, a clear indication that further structuring of this aspect of the hypothesis is in order.

In the lower loop of Figure 3, the values of the delays around the loop are not limiting during the early unfolding of the successional process, and they do not become limiting as long as the reservoir of soluble nutrients remains high in relation to the standing crop. Therefore, functioning of the food chains (attribute 5) is effectively open and determined by grazing activity in the developmental stages; on the contrary, as trophic equilibrium is approached in the mature stages, the functioning of the food chain increasingly depends on the capacity for recycling of nutrients. A detritus food chain, however, is not explicitly incorporated. The lower loop of Figure 3 also accounts for total organic matter (attribute 6) and inorganic nutrients (attribute 7), with

the trends listed for these attributes being the consequence of this loop reaching traffic equilibrium. The dynamics of nutrient cycling as listed further down in the tabular model also arise from this loop. Thus, mineral cycles (attribute 15) become effectively closed, nutrient exchange rate (attribute 16) slows down, and the rate of detritus in nutrient regeneration (attribute 17) becomes increasingly important to keep the whole ecosystem alive as the regulatory action of this loop becomes dominant at the climax.

Attributes 8 through 14 are certainly associated with the positive feedback mechanism behind succession, but the mutual causalities among these and other successional factors are for the most part unknown. For example, "the question of whether the seemingly direct relationship between organism size and stability is the result of positive feedback or is merely fortuitous remains unanswered" (Odum, 1969). Odum concludes that "whether or not species diversity continues to increase during succession will depend on whether the increase in potential niches resulting from increased biomass, stratification and other consequences of biological organization exceeds the countereffects of increasing size and competition" (Odum, 1969). Therefore, it appears reasonable to assume that different processes of diversification (attributes 8 through 11) proceed in parallel and reinforce each other, that the resulting niche specialization (attribute 12) has the net effect of increasing carrying capacity up to certain limits, and that these developments reinforce, and are reinforced by, the ongoing build-up of biomass during succession; thus the upper loop of Figure 3. With respect to

size of organism and life cycles (attributes 13 and 14), Odum (1969) states:

> In a mineral nutrient-rich environment, small size is of selective advantage, especially to autotrophs, because of the greater surface-to-volume ratio. As the ecosystem develops, however, inorganic nutrients tend to become more and more tied up in the biomass (that is, to become intrabiotic), so that the selective advantage shifts to larger organisms (either larger individuals of the same species or larger species, or both) which have greater storage capacities and more complex life histories, thus are adapted to exploiting seasonal or periodic releases of nutrients or other resources.

In that no mutual causalities appear to be discernible between these and other successional trends, they are not explicitly included in the tentative hypothesis of Figure 3. Finally, attributes 18 through 24 are not themselves variables, but rather consequences of the dynamic interaction between the positive and negative feedbacks hypothesized in Figure 3 which become observable as succession unfolds. These positive and negative feedbacks are the force behind all these observables.

Thus, the "simple" hypothesis of Figure 3 establishes a framework which encompasses (either explicitly or implicitly) all attributes of Odum's tabular model. In order to construct a testable model, however, this hypothesis must be articulated in terms of quantifiable interloop and intraloop relationships. Taking the feedback structure of Figure 3 as point of departure, further articulation of the hypothesis will consist of (i) structuring the intra-loop relationships of the negative feedback, i.e., the nutrient cycling process, (ii) structuring the intra-loop relationships of the positive feedback, i.e., the diversification process, and (iii) structuring the energy flow relationships through which the positive and negative feedbacks stand in interaction.

Nutrient Cycling Dynamics

The dynamics of ecosystem nutrient cycles have been extensively studied in ecology, although some of the specific processes involved are extremely complex and still poorly understood. The cycling of nutrients and the flow of energy are closely interconnected, and constitute the trophic-dynamic aspect of ecosystems (Lindeman, 1942). According to Lindeman's description, the inner structure of the lower loop in Figure 3 is composed of four major sectors: abiota, producers, consumers and decomposers. The feedback structuring of these sectors is traced in Figure 4. This influence diagram accounts for the traffic dynamics of the ecosystem under the influx of solar energy and otherwise constant environmental conditions. It is composed of five levels: inorganic nutrients, producers biomass, consumers biomass and organic nutrients. The inorganic nutrients level stands for the lumped sum of nutritive minerals available in soluble (i.e., absorbable) form in the soil of the grassland. The producer and consumer levels account for the sum total of grass and animal biomass, respectively. Similarly, the level of decomposers refer to the total amount of soil micro-organism biomass available to decompose dead biomass, plant and animal litter and other soil organic matter back into soluble inorganic form. The organic nutrients level lumps together all nutrients in organic form (i.e., organic debris) undergoing the process of decomposition.

The basic building block in the influence diagram of Figure 4 is the (biotic or abiotic) level, together with its "inner" feedback loop structure. To illustrate, Figure 5 isolates the basic building block

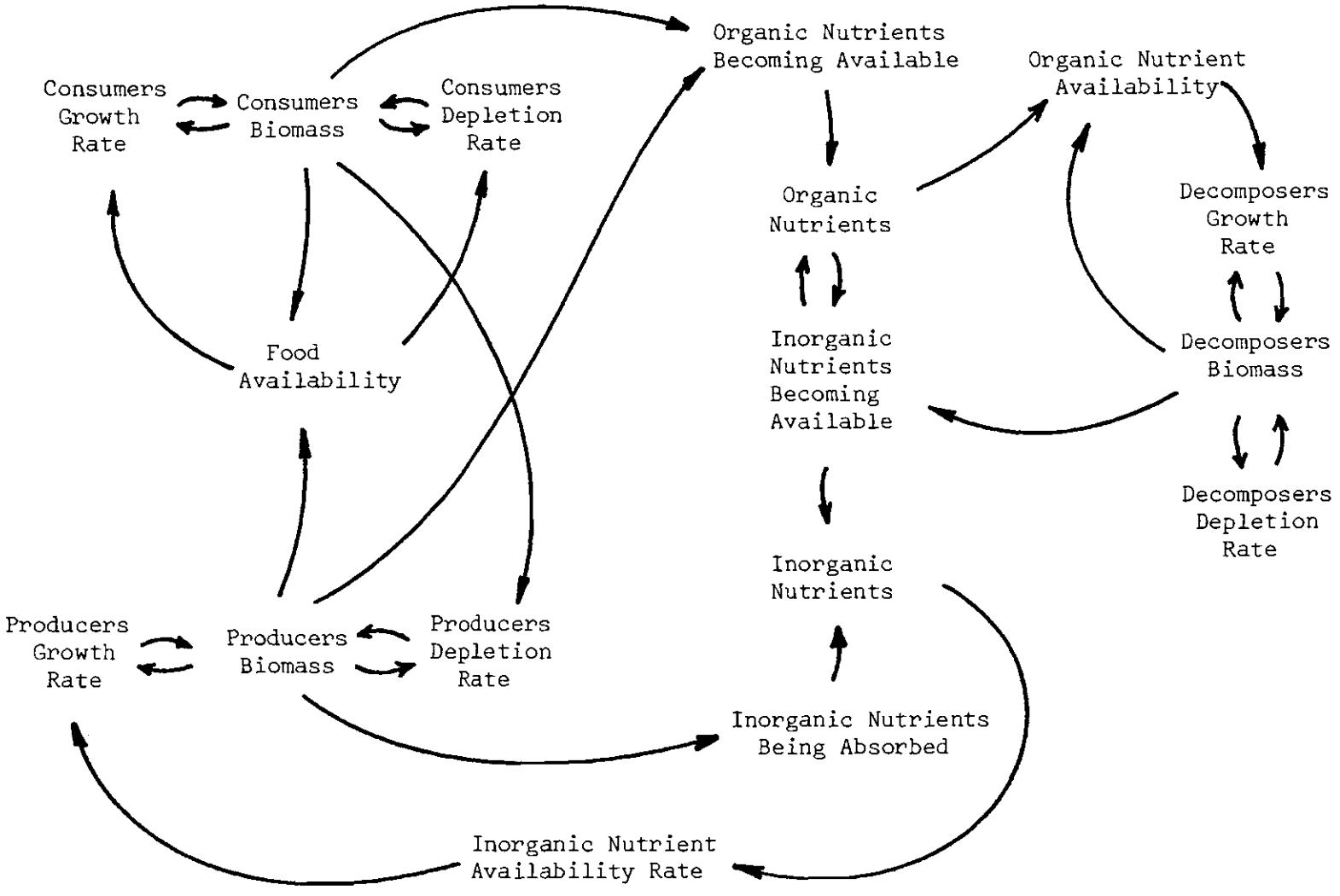

Figure 4. Nutrient Cycling

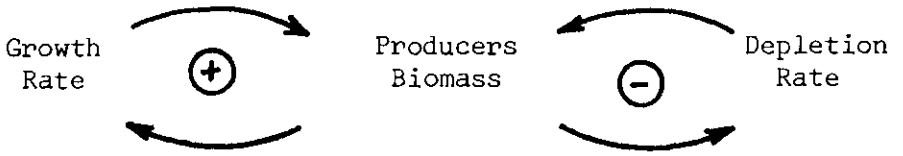

Figure 5. Basic Trophic Structure

for the producers: a biomass accumulation and the positive and negative feedback loops associated with biomass growth and regulation. The level of producers biomass increases or decreases dynamically depending on whether the gain of the positive growth loop is greater than the gain of the negative decay loop, or vice versa.

In the present discussion on the structure of Figure 4, energy flow will be taken for granted; it will be formally accounted for later in this chapter. In Figure 4, producers biomass is shown as growing under the influence of its own machinery and the availability of soluble inorganic nutrients in the soil. On the other hand, the standing crop of grasses is regulated by its own rate of decay and by consumption, i.e., grazing by the primary consumers. Clearly, there must be other constraints on the growth of plant biomass besides nutrients availability. Even if nutrient resources do not become limiting, grasses will grow in a given grassland only to a certain saturation density which is a function of the local environment as reflected on soil carrying capacity. Accordingly, the feedback structure of the producers sector is further detailed in Figure 6. It shows producers growth rate as being the result of both replacement growth and new growth. This recognizes that grasses replace themselves from year to year and, in addition,

generate new growth each year as succession unfolds. New growth rate vanishes when either the nutrients become limiting or the soil becomes saturated; replacement growth rate, on the other hand, perpetuates biomass production year after year, so as to approximate each year the standing crop level of the previous year, as long as nutrients continue to be available. In the diagram of Figure 6, inorganic nutrients, soil carrying capacity, grazing pressure and production efficiency appear as constants, where in fact they are not. Assuming for the moment a fixed, finite soil carrying capacity, a continuous nonlimiting supply of nutrients, a constant production efficiency and no grazing, let us consider the closed-loop dynamics of this feedback structure. This is best accomplished by first breaking it down into its component loops. The positive feedback loop which is hypothesized as generating new growth of plant biomass is isolated in Figure 7. When the standing crop is below the level which can be carried by the soil of the grassland, gross new growth results as the plant machinery acts to take advantage of soil availability. Part of this new growth results in net new growth, the respiration loss depending on the production efficiency of the plants. There is, of course, a time delay elapsing before the new growth indicated by this production process actually impacts new growth rate, assuming (see Figure 6) that there exists a nutrient availability rate remaining for new growth after the nutrient absorption requirements for replacement growth have been satisfied. Thus, in the new growth loop of Figure 7, growth of plant biomass results in still further growth of plant biomass as long as soil carrying capacity remains unsaturated.

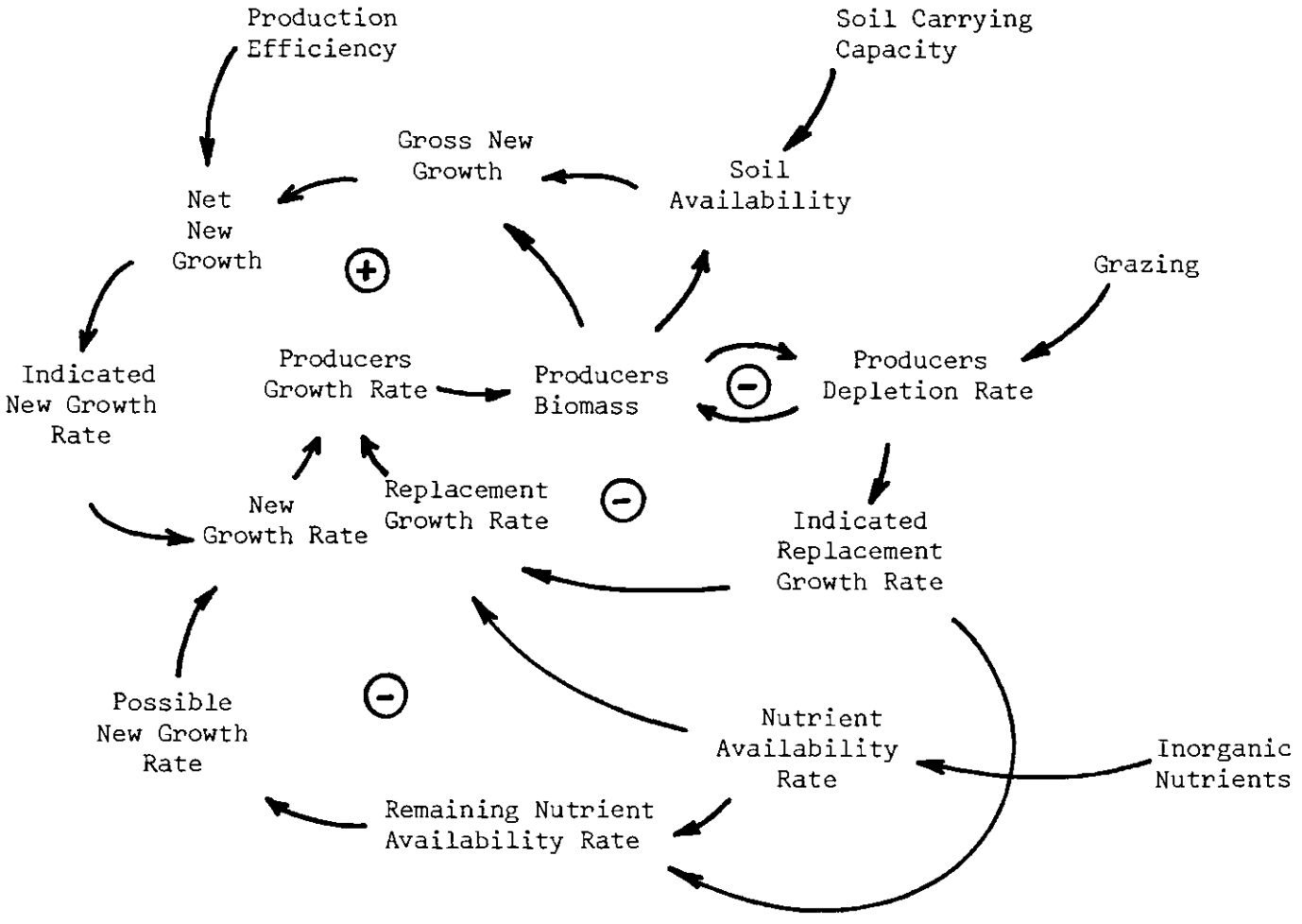

Figure 6. Producers Sector

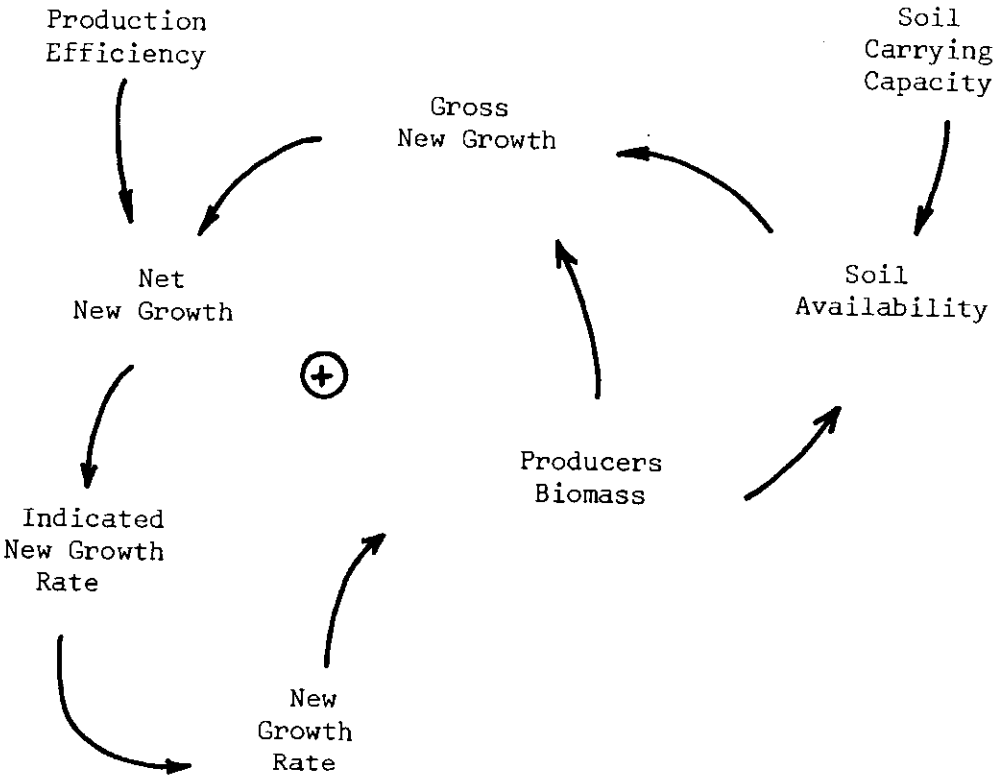

Figure 7. New Growth Loop

As the standing crop approaches the level of soil saturation, the gain around this loop should vanish. In Figure 8, an assumption is presented on how new plant biomass production becomes limited by soil saturation.

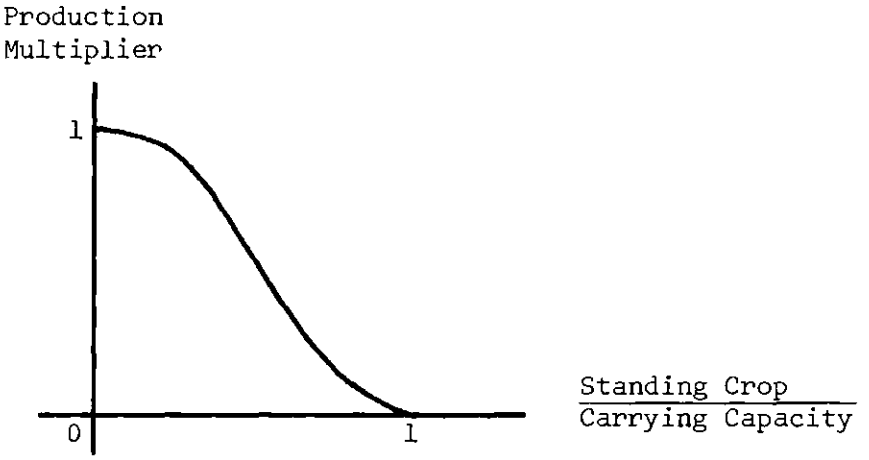

Figure 8. New Production Multiplier as a Function of Soil Availability

When the ratio of standing crop over soil carrying capacity is close to zero, the production of new plant biomass is limited only by the capacity of the plant machinery to do the work. As this soil availability ratio approaches one, however, production for new growth will gradually vanish under the pressures of a saturated environment, gross new production in Figure 7 becomes inactive, and the gain around the loop vanishes.

The positive new growth loop of Figure 7 stands in interaction with the replacement growth loop, isolated in Figure 9. While the new growth loop is active only during succession, the replacement loop continues to work after the standing crop has reached its climax level, to keep it there year after year.

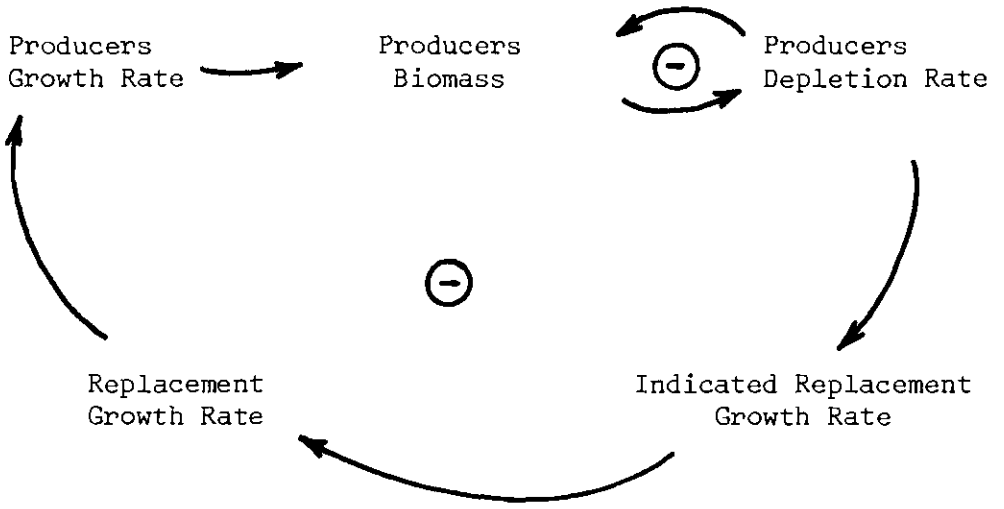

Figure 9. Replacement Growth Loop

It possesses negative polarity, i.e., the decay rate currently depleting plant biomass becomes the replacement growth rate indicated for the following year, bringing plant biomass back to its steady state climax value. As indicated in Figure 6, the ability of this replacement process to perform its function is constrained by the availability rate of nutrients. Plants can continue to replace themselves only as long as inorganic nutrients continue to become available for absorption. Destroying the negative feedback gain of this loop results in a gradual decay of standing crop. Indeed, other factors besides limiting nutrients may constrain the continued performance of this replacement process. It is interesting to note that factors affecting the gain of the replacement growth loop in a detrimental fashion may be the dominant force behind senescence, i.e., the process whereby mature ecosystems sometimes age and decay after a (possibly very long) climax period. These

considerations go, however, clearly beyond the scope of the present hypothesis.

At this point, the question arises as to whether development of the plant community is also influenced directly by natural consumers. Ellison (1960) conducted an extensive investigation on this matter. After reviewing all the available evidence, he concludes ". . . that the evidence of grazed plants' dependence on grazing animals is rather negative: the relation appears to be essentially one of parasitism by the animals." This conclusion implies that the growth of consumers lags behind the growth of producers during succession, and is, therefore, in consonance with the influence diagram of Figure 4, which shows consumers influencing the depletion rate of producers, but not their growth rate. The growth of consumers, on the other hand, is highly dependent on food availability, i.e., the availability of abundant grass cover in the case of a grassland ecosystem.

The consumers biomass level in the diagram of Figure 4 is also aggregated to include all kinds of consumers, both primary and secondary. The feedback structure of this sector is somewhat further detailed in Figure 10. Under the benefit of a constant, presumably healthy environment, consumers biomass grows and decays in response to the relative availability of food, i.e., the ratio of food available over food required. When the grassland is in good condition and food is plentiful, consumers grow as a result of their ability to reproduce and multiply, and the abundant food supply. Eventually, however, growth ceases either because the food supply becomes depleted due to the increase in

consumption resulting from previous growth, or as a consequence of inter-specific competition, or both. These dynamics are accounted for by the positive and negative feedback loops to the left of Figure 10.

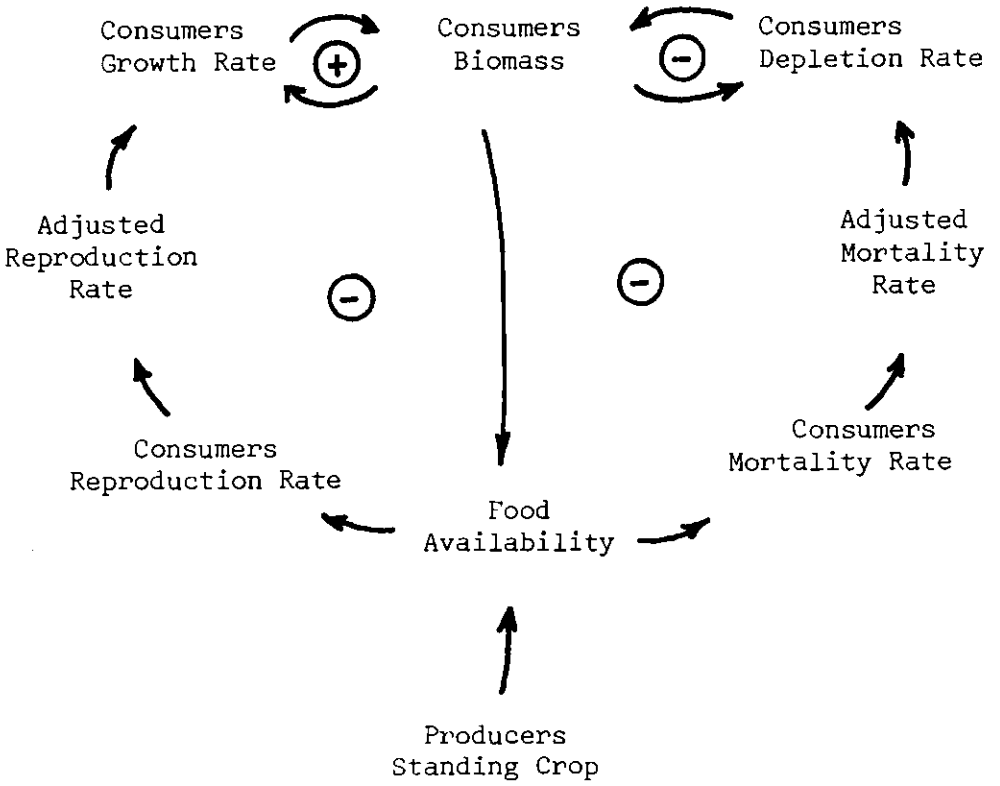

Figure 10. Consumers Sector

The negative feedback loops to the right-hand side of the diagram are indicative of the fact that the total amount of living biomass in the consumers sector is regulated by both aging and food availability. There will be a time delay involved in adjusting either the reproduction rate or the mortality rate in response to changes in food availability. For a given level of food supply, an equilibrium level for consumers biomass

will be approached in the long-run, as graphically stated in Figure 11. According to the functions hypothesized in Figure 11, mortality rate has a "normal," constant value when food is plentiful, i.e., animals die of causes other than food scarcity. On the other hand, it rises sharply as food scarcity becomes acute. The reproduction rate, on the other hand, rises in response to food availability, but only to a certain extent. If the standing crop of grass goes beyond (say) twice what is required to sustain the consumers, other factors such as space are assumed to become limiting on their further growth.

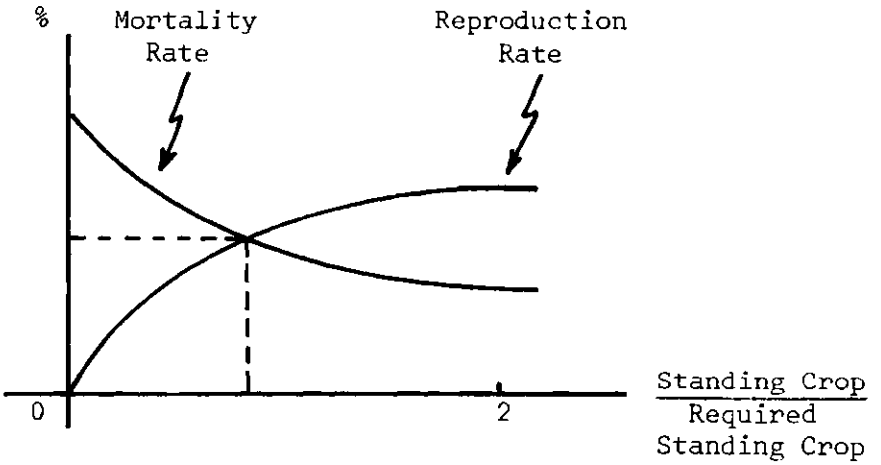

Figure 11. Consumers' Reproduction and Mortality Rates as a Function of Food Availability

As indicated in Figure 4, dead plants and animals, as well as their litter, accumulate as organic matter available for decomposition. As this accumulation of organic matter to be decomposed builds up during succession, a corresponding increase in decomposers is indicated in order to break down the nutrients trapped in organic form back into soluble inorganic form. In the decomposers sector, the availability of

decomposable biomass can play a role similar to the availability of plant biomass in the consumers sector. For the purposes at hand, an even more simplified hypothesis is suggested in Figure 12.

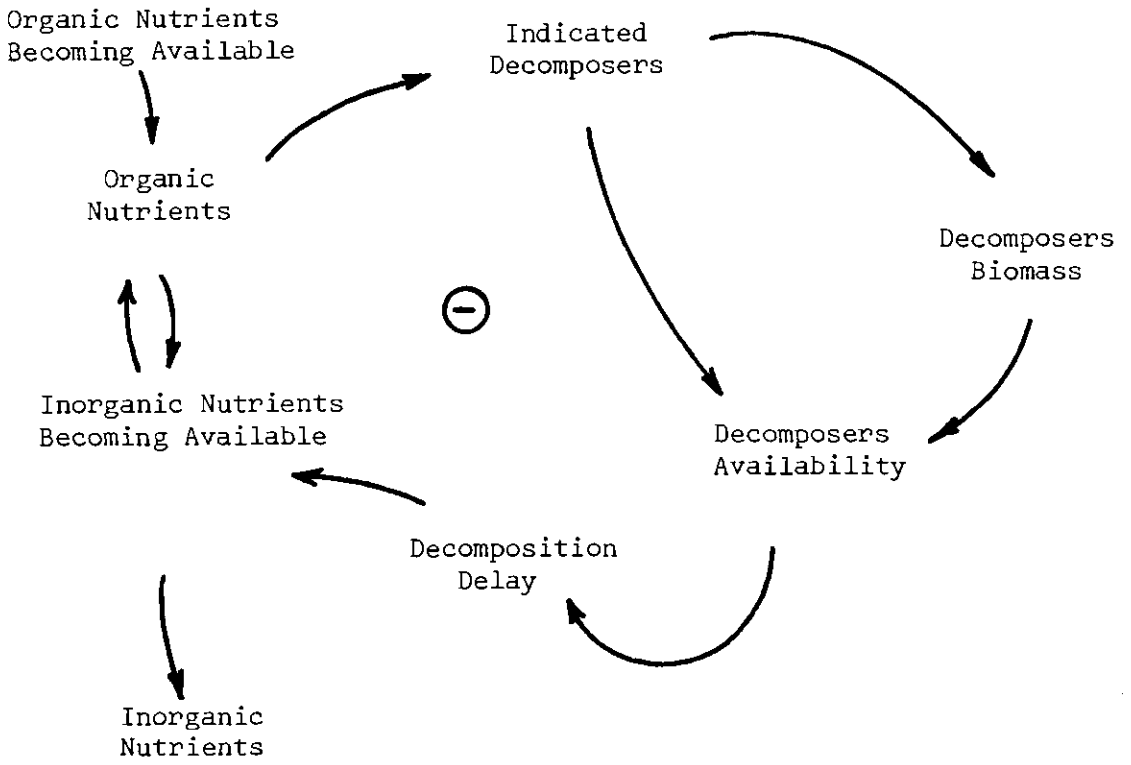

Figure 12. Decomposers' Sector

According to this influence diagram, a buildup in organic nutrients is indicative of the need for a proportional buildup in decomposers biomass; the latter reacts by gradually growing to the new required level. Naturally, a reduction in the level of organic nutrients would reverse the trend of the response. If decomposers availability is taken as the

ratio of decomposers indicated (i.e., needed to accomplish decomposition) over decomposers available to do the work, then it seems reasonable to assume that the decomposition delay will be some monotonically increasing function of decomposers availability. Figure 13 displays a linear approximation for this relationship.

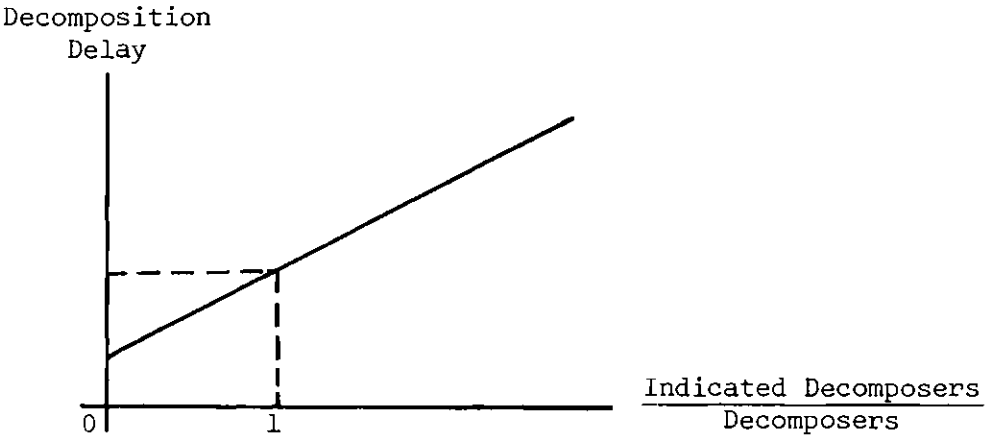

Figure 13. Decomposition of Delay as a Function of Decomposers Availability

Clearly, the decomposition delay will be longer the greater the value of the decomposers availability ratio, and will shorten to some minimum time as the value of the ratio approaches zero. During the successional transient, the negative feedback loop of Figure 12 will stimulate the growth of decomposers biomass so as to keep the recycling of nutrients going; as the ecosystem approaches maturity, it will regulate decomposers biomass about an equilibrium level such that the value of this ratio remains close to unity, thus yielding some "normal" decomposition delay when the ecosystem is in steady-state.

Diversification Dynamics

A biotic community develops both by quantitative growth and by qualitative diversification. It modifies its physical environment so as to enhance its carrying capacity and pave the way for further community development, and it continues to do so until constrained by physical and biological limits such as unavailability of space, niches, nutrients, etc. This process is community-controlled (Odum, 1969). As the limits of the environment are approached, a transition from growth to equilibrium is observed, eventually resulting in a stabilized climax community. These well-known observations constitute the basis for the upper loop of the dynamic hypothesis in Figure 3, which shows the closed-loop interaction between species diversity, soil-carrying capacity and biomass production. A more explicit influence diagram for this aspect of the hypothesis is articulated in Figure 14.

In discussing this feedback structure as an explanatory hypothesis for successional modes of behavior as displayed in Figure 1, it is first necessary to point out that successional patterns are not necessarily smooth. In fact, according to Lindeman (1942), smooth growth patterns are

> seldom found in natural succession, except possibly in such cases as bare areas developing directly to the climax vegetation type in the wake of a retreating glacier. Most successional seres consist of a number of stages. . . . so that their productivity-growth curves will contain undulations corresponding in distinctness to the distinctness of the stages. The presence of stages in a successional sere apparently represents the persistent influence of some combination of limiting factors, which, until they are overcome by species-substitution, etc., tend to decrease the acceleration of productivity and maintain it at a more constant rate.

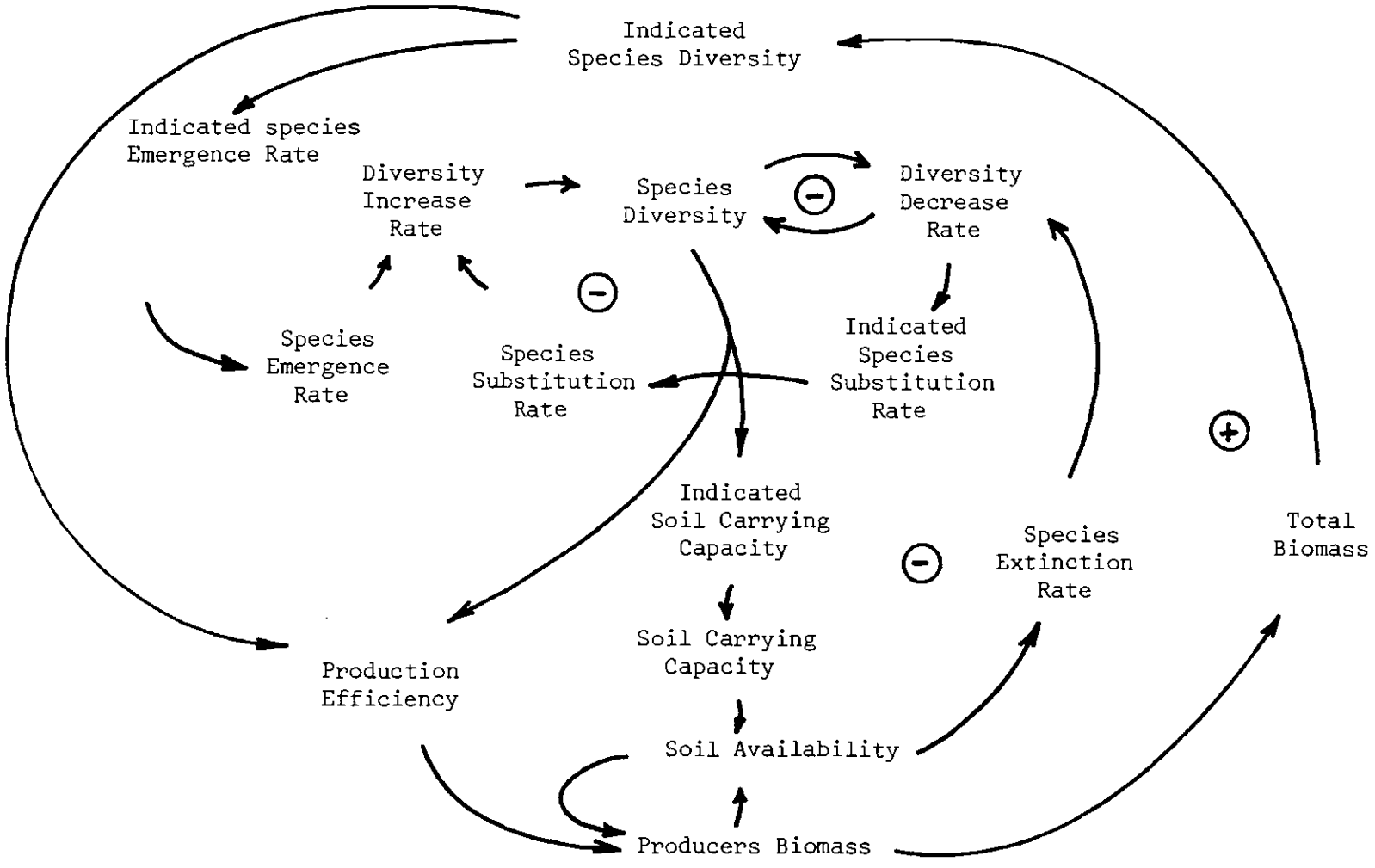

Figure 14. Diversification

Thus, it seems that at the beginning of succession, soil carrying capacity (refer to Figure 14) would be typically modest, permitting only a correspondingly modest amount of further growth in biomass. As the current carrying capacity of the soil becomes saturated, two things happen: on the one hand, some species currently on the grassland may disappear under the pressures of competition and other factors arising from the current saturation of the physical environment; on the other hand, available energy which cannot be allocated any more to growth of more biomass will be allocated for diversification. While energy flow will not be formally accounted for until the next section, its presence is again assumed for the present discussion.

After a certain time delay, the allocation of energy to diversification gradually gives rise to a bloom in species diversity. This bloom is brought about both by recolonization of previously occupied niches and by colonization of new niches. These diversification activities are denoted in Figure 14 as species substitution rate and species emergence rate, respectively. Now, a more diversified community is not only bound to exploit a greater number of available specialized niches, but also to act on the soil so as to, effectively speaking, increase its carrying capacity after some time has elapsed. Increased carrying capacity means, in turn, the ability of the soil to sustain a greater standing crop of the now more diversified community; after another period of time, the new growth in standing crop saturates once more the new carrying capacity of the soil, thus paving the way for still further diversification and the next successional stage. This stage-by-stage

process eventually must come to an end, however, and the transition from growth to equilibrium arises from the intraloop relationships which govern the gain of the positive feedback.

There are four complex relationships in the structure of Figure 14: indicated diversity as a function of total biomass, indicated soil carrying capacity as a function of diversity, species extinction rate as a function of soil saturation, and production efficiency as a function of relative diversity, the ratio of species diversity to indicated species diversity. A fifth relationship, indicated species substitution rate as a function of diversity decrease rate, is clearly analogous to indicated replacement growth rate as a function of producers decay rate (see Figures 6 and 9). Among these relationships, the most crucial are the first two, because they provide the basic positive feedback mechanism (see Figure 18). With regard to indicated diversity as a function of total biomass, Odum (1969) points out that

> whether or not species diversity continues to increase during succession will depend on whether the increase in potential niches resulting from increased biomass, stratification (Table 1, item 9) and other consequences of biological organization exceeds the countereffects of increasing size and competition.

A functional relationship which may be assumed between total biomass and indicated diversity is shown in Figure 15. Obviously, indicated diversity is zero if total biomass is zero. Indicated diversity is assumed to be a monotonically nondecreasing function of biomass accumulation; gradually, a stage of development is reached in which (due to any one of many possible limiting factors; e.g., competition) further accumulation of biomass does not result in further diversification.

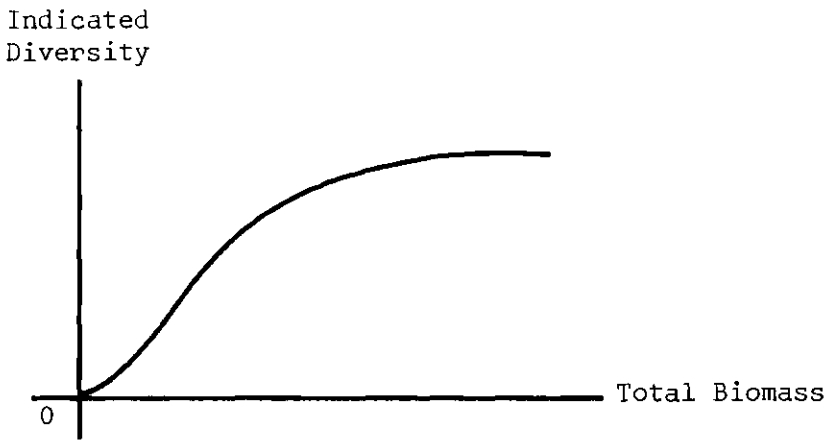

Figure 15. Indicated Species Diversity as a Function of Total Biomass

Incorporation of this relationship immediately provides a mechanism for the transition from growth to equilibrium, i.e., the gain of the positive feedback would gradually vanish as the horizontal asymptote of the nonlinearity in Figure 15 is approached.

The causal relationship between total biomass and species diversity is not unidirectional, however. The mutual causality which exists is evident from Odum's statement. Elsewhere, DeVos (1969) also observes that ". . . production, both primary (by green plants) and secondary (by consumers) in an ecosystem is apparently increased by species variety because this permits the occupancy of more niches in the habitat." Consequently, it appears reasonable to assume that the effective carrying capacity per unit area of the soil increases as diversity increases, and that succession ends when further diversification does not result in increased soil carrying capacity due to an exhaustion of specialized niches in which to pursue further growth. This assumption is expressed

graphically in Figure 16, which postulates that the actual carrying capacity of the soil ranges from a modest value when diversity is low to some upper bound for a highly diversified community. It follows, then, that the gain of the positive feedback loop of Figure 18 will vanish as either the upper bound of Figure 15, or the upper bound of Figure 16, or both, are approached.

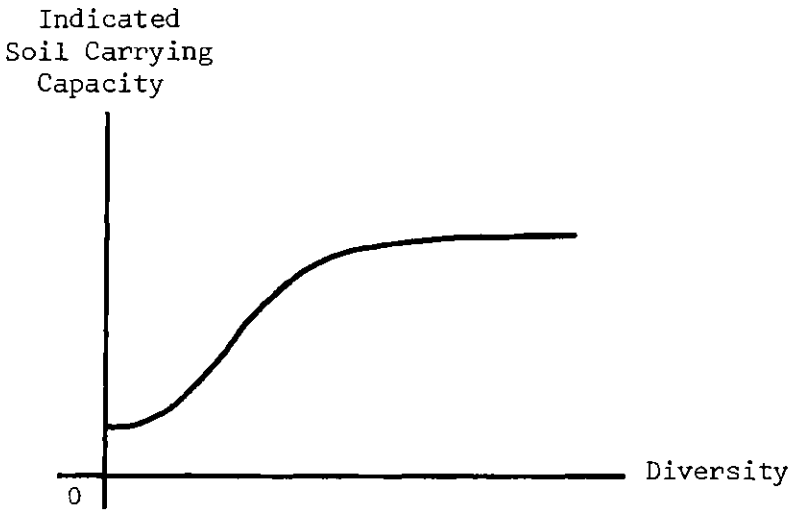

Figure 16. Indicated Soil Carrying Capacity as a Function of Diversity

Figure 17 displays the assumed nonlinear influence of soil saturation on species mortality rate. As standing crop approaches its equilibrium value with soil carrying capacity in the mature stages of succession, extinction and substitution of species either continues at a very low rate or ceases altogether (i.e., a zero species mortality rate). On the other end, the relationship simply recognizes the obvious fact

that all species would become extinct if the whole standing crop is destroyed. Note that according to the nonlinearity of Figure 17, the species extinction rate is activated only when the standing crop is less than the carrying capacity. Even if the standing crop is only partially destroyed, some of the species on the range are bound to be driven away (at least temporarily) by the resulting scarcity of food, competition pressure, selective grazing, etc.; thus the gradually decreasing shape of the postulated curve.

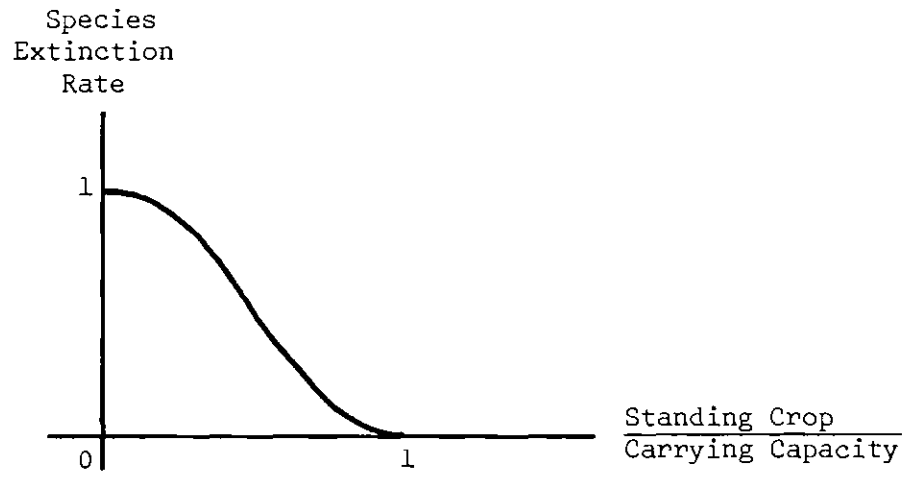

Figure 17. Species Extinction Rate as a Function of Soil Availability

In the hypothesis structured in Figure 14, the positive feedback isolated in Figure 18 would be activated by the closed-loop interaction of the relationships previously discussed, even if production efficiency were to remain constant throughout the successional process. Production efficiency does change during succession, however, under the influence of a multitude of factors. Productivity will increase if diversity is

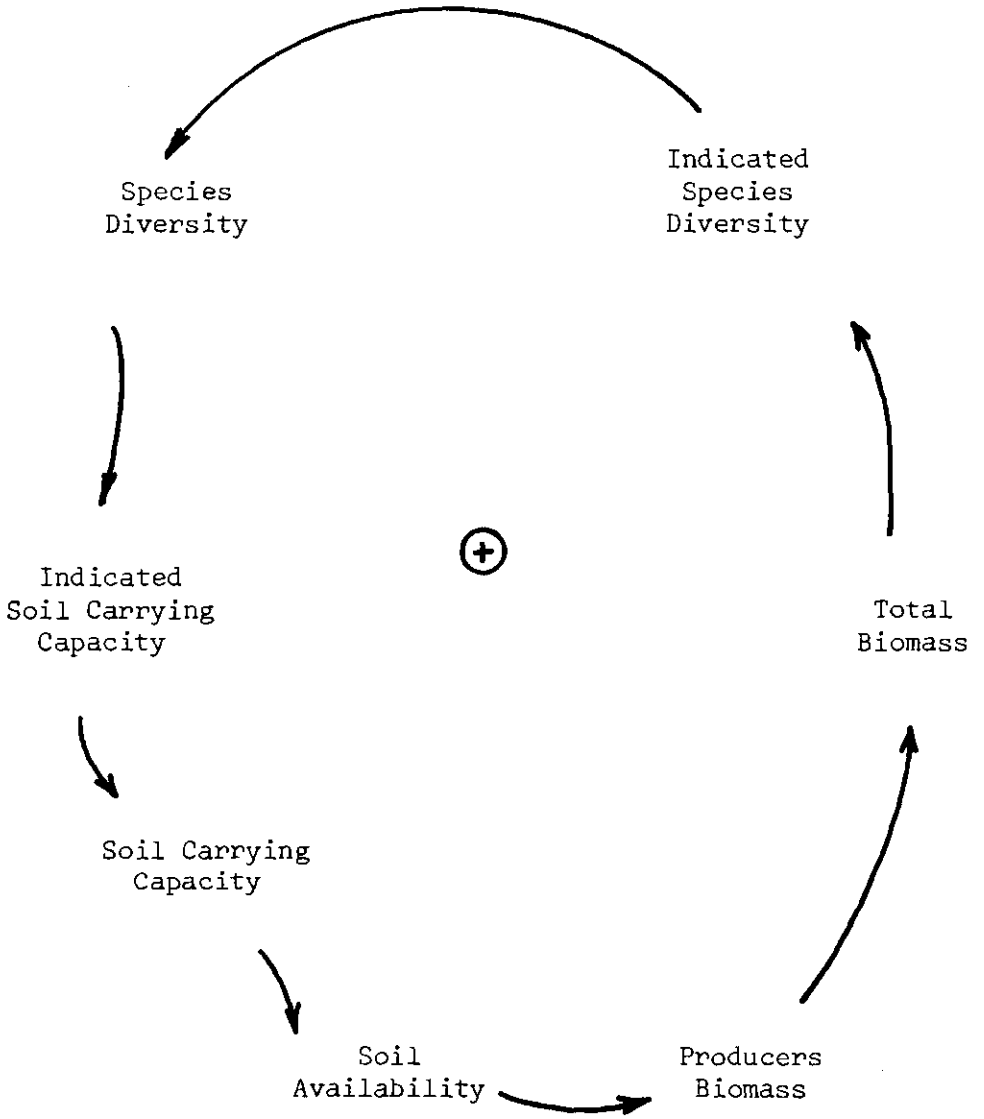

Figure 18. Positive Feedback Between Biomass and Diversity

suddenly destroyed in a mature ecosystem. This influence can be explicitly incorporated into the hypothesis by making production efficiency a function of relative diversity, i.e., actual diversity over indicated diversity, as stated graphically in Figure 19. Following the same reasoning as before, the assumption implicit in Figure 19 is that production efficiency would stabilize at some low value under undisturbed climax conditions, but would rise to a much higher value were diversity to be destroyed completely (as in monocultures), with some intermediate values in between. These and other refinements can be incorporated to test the sensitivity of the hypothesis to various factors. It is emphasized, however, that the upper loop of Figure 3 stands as the fundamental internal driving force behind the successional response of ecosystems to perturbation of their climax.

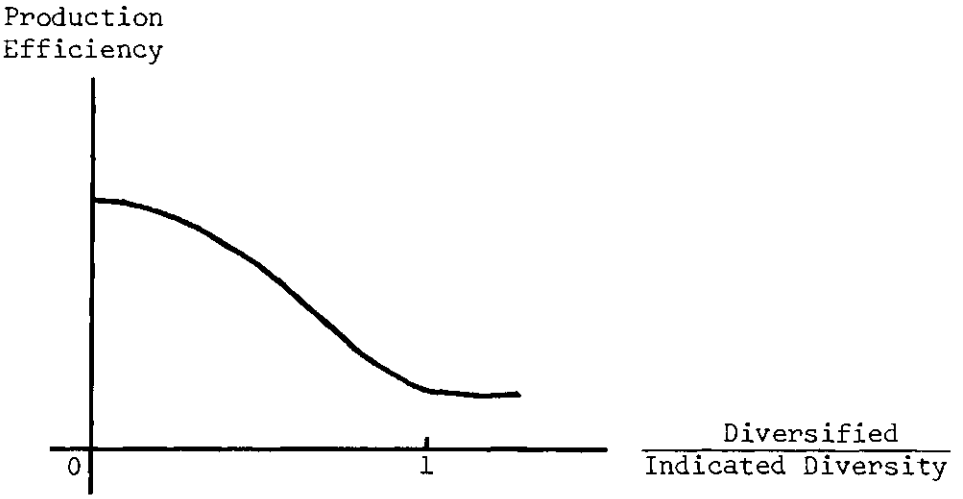

Figure 19. Production Efficiency as a Function of Relative Diversity

Energy Flow Dynamics

In the preceding section, it was assumed that energy was available to flow through the ecosystem as necessary for growth and maintenance of both biomass and diversity. While upholding the necessary assumption that solar energy is available to the grassland, the present section attempts to account for the energy flow underlying the dynamics of succession.

In contrast with the closed-loop flow of nutrients, the flow of energy through an ecosystem is unidirectional (see, e.g., Lindeman, 1942; Phillipson, 1966; Kormondy, 1969; Odum, 1971); thus the need for the sun as a continuous source of primary energy. In the context of the structure presented in Figure 3, solar energy is fixed by the green plants of the grassland and then it is either used (i.e., dissipated) for various purposes or stored in various forms as it flows through both feedback loops, providing the ability for the biotic community to do work. As it flows through either loop, energy is conserved as it is successively transformed from one form into another, and at the same time it becomes successively degraded into increasingly dispersed forms which sooner or later become useless to the community. These facts follow from the first and second laws of thermodynamics. More specifically, energy flows through the lower feedback loop of Figure 3 and is either temporarily stored as biomass, or dissipated as heat; it also flows through the upper loop, and is dissipated in the performance of quality functions (e.g., diversification) and in the performance of work on the physical environment. Let us consider the flow of energy through each

one of these loops as it relates to successional dynamics.

The successive transformation and degradation of energy around the negative feedback of Figure 3 proceed concurrently with the dynamics of nutrients cycling, as diagrammed in Figure 4. Food energy is successively fixed and transferred around the loop, with respiratory losses taking place at each trophic level. In other words, production of biomass plus respiration equals energy flow through each trophic level. The energy allocated for production is thus gradually dissipated as it goes from trophic level to trophic level around the loop. These are, of course, the energetics associated with the trophic-dynamic aspect of ecosystems. as previously cited from the work of Linderman (1942). In brief, it means that an open-loop flow of energy underlies the closed-loop flow of nutrients as traced in Figure 4 and that, under any circumstances, activation of the latter would be impossible in the absence of the former. However, this accounts only partially for successional behavior, since trophic-dynamic interactions and the resulting growth in living matter would permit successional development to proceed only to a limited extent in the absence of diversification.

It seems clear that the qualitative work associated with diversification and other quality functions requires energy, just as the work associated with biomass production and maintenance requires energy. As succession unfolds, energy becoming available through photosynthesis must be allocated either for biomass production and maintenance, or for qualitative functions such as diversification. In other words, it must be allocated for the performance of work around either the lower loop or

the upper loop of Figure 3. Work performed around the upper loop includes that required for maintaining the interactions among the species. For example, it is clear that energy is dissipated by both the predator and the prey as predator-prey interactions take place through time. In discussing the relationship between quantitative growth, qualitative change, and the energetics of succession, Margalef (1963) points out that it is necessary to distinguish between the energetics associated with biomass production and maintenance and those associated with the generation and maintenance of diversity and other aspects of structural complexity, and he concludes:

> It seems safe to assume that maturity has a double measure: In its structural aspect, it can be measured in terms of diversity or of complexity over a certain number of levels. In the aspects relating to matter and energy, it can be measured as primary production per unit of total biomass. The connections between complementary aspects and measures require theoretical consideration.

What is needed is a tentative theoretical model, or hypothesis, to account for the structuring of these connections or, in other words, to account for the dynamic allocation of excess available energy to either further growth or further diversification so as to bring about successive stages of development. The influence diagram of Figure 20 displays a dynamic hypothesis for successional energetics. This hypothesis is based on admittedly sketchy descriptive information, such as Margalef's observations as quoted above. It exhibits the feedback structure which is assumed to determine the dynamic allocation of energy for storage and/or dissipation in the performance of work around the positive and negative feedback loops of Figure 3.

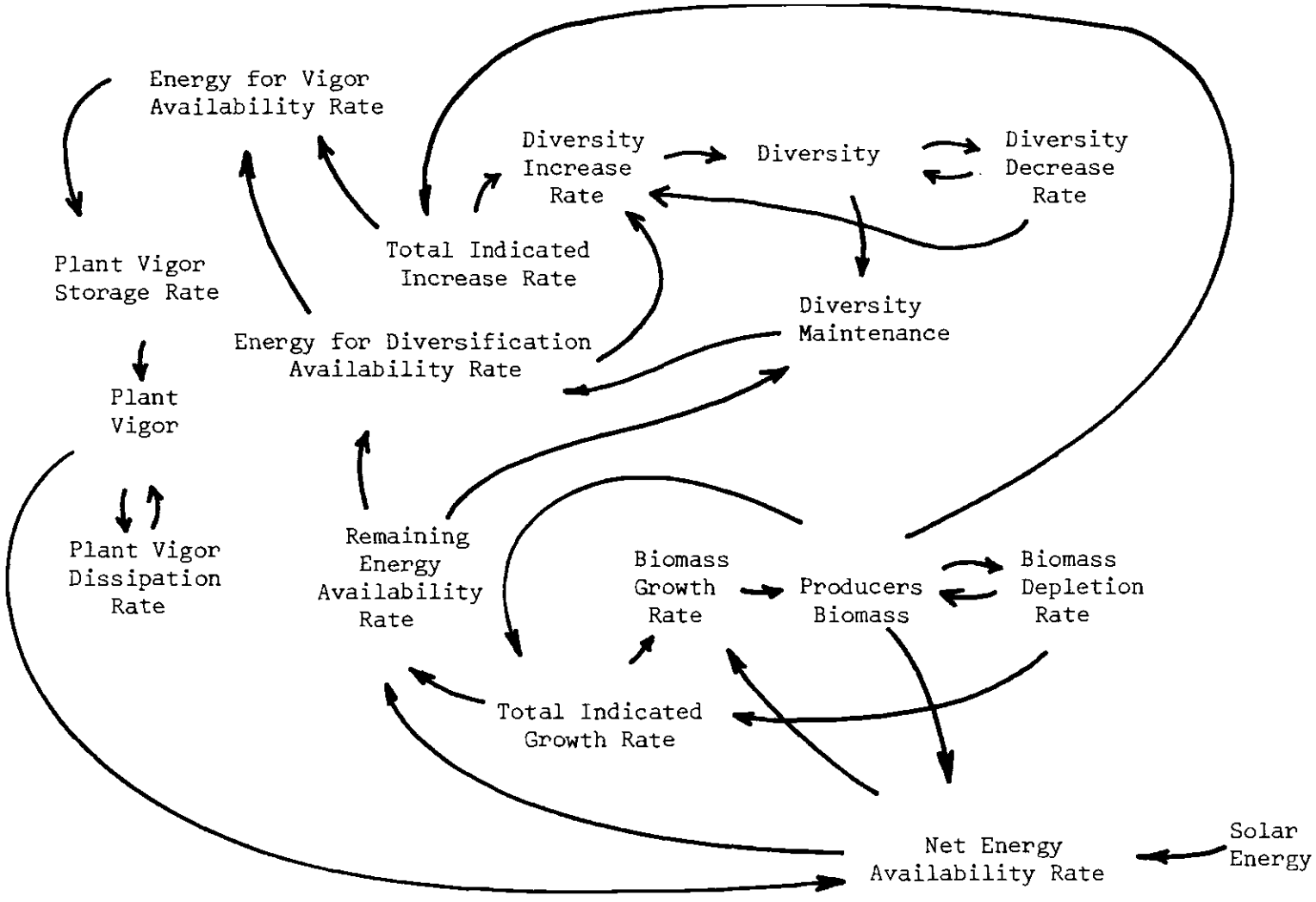

Figure 20. Energetics

The net availability of energy to be allocated (i.e., the energy availability rate in excess of that required for biomass production and maintenance) depends on both the rate of solar energy fixation and the reservoir of internally stored energy, denoted in the diagram as "plant vigor." The rate of solar energy fixation depends, of course, on the availability of green plants machinery coupled with incoming solar radiation. It is assumed that this net energy availability rate will be allocated to further growth of biomass as long as such growth can continue without saturating the carrying capacity of the soil, i.e., as long as the new growth loop of Figure 7 remains active for a given stage of successional development. Presumably, generation of new growth requires a consumption of energy in proportion to the amount of new biomass to be produced. The energy availability rate remaining after both replacement growth and new growth requirements have been satisfied is allocated to the performance of quality functions, primarily diversification. Some energy expenditure is required to maintain diversity at a given level, the level of necessary expenditure being proportional (as a first approximation) to the level of diversity. If the energy availability rate remaining from growth is inadequate for this maintenance function, diversity is bound to decrease. On the other hand, if energy is becoming available at a rate in excess of that required to sustain the present levels of both biomass and diversity (possibly as a result of no further growth currently being possible), such excess energy availability rate becomes available for further diversification. This energy provides the ability to perform all kinds of work associated with

increasing the carrying capacity of the soil to a new level, so as to bring about the next stage of successional development; again as a first approximation, it may also be assumed that the energy thus dissipated will be in proportion to the intensity of diversification activity, as measured by the rate of increase in species diversity. As the climax is approached, however, both total biomass and species diversity gradually approach steady-state levels, and the question arises as to the destination of energy availability rate in excess of that required for continued maintenance of biomass and diversity at their steady-state levels. Presumably, as the ecosystem continues to mature such excess energy can be allocated to do further work on other quality functions such as biochemical and genetic diversification, which provide for higher resistance to disease and other external perturbations. Therefore, this excess energy is assumed to be stored as potential energy in various forms which in the diagram of Figure 20 are lumped together under a level of stored energy, or vigor. This hypothesis provides a rationale to explain the ability of grasslands, for example, to "bounce back" under grazing stress, at least to a certain extent. For, energy stored under various forms of plant vigor is potentially available for biomass production work, as pointed out before. As indicated by the influence diagram, however, energy can be stored for a limited period of time; due to leaching, fossilization and other internal factors, plant vigor dissipates if it goes unused for too long. Thus, the hypothesis accounts for the eventual disposition of all energy allocated for diversification and other quality work; although not explicitly shown in the diagram of

Figure 20, it is of course understood that energy allocated for growth is gradually dissipated as it is successively transferred from one trophic level to another throughout the food chain.

In consonance with the research methodology outlined at the beginning of this chapter, the basic dynamic hypothesis of Figure 3 has been structured into a number of interconnected feedback loops, with each loop further structured in terms of levels and rates. The next step is the detailed analytical formulation of the hypothesis to permit its testing. Levels are to be formulated as first-order difference equations. The rates will be formulated as zero order (i.e., algebraic) equations, with nonlinearities possibly involved in coupling rates of flow to the current values of the levels, as indicated in the preceding sections. The analytical formulation of the simulation model constructed to test the hypothesis is fully documented in the appendix.

Structural Validation of the Dynamic Hypothesis

It was pointed out in the first section of this chapter that (short of empirical verification) the dynamic hypothesis under consideration can be validated on the grounds that (i) its structure is consistent with available knowledge on the structure and function of grassland ecosystems, and (ii) it generates the same successional modes of behavior it is intended to account for when exercised as a simulation model. The results obtained in pursuing the latter form of hypothesis testing (i.e., performance validation) are reported at length in the following chapters; the former aspect, structural validation, is presently addressed.

The consistency (or, at the very least, lack of inconsistency)

between each structural element of the proposed dynamic hypothesis and the full range of knowledge available on ecological succession has been carefully documented in the preceding sections. To a significant extent, the hypothesis developed in this chapter is simply a formalization of existing empirical and conceptual information on ecological succession--thus far available in descriptive form only--into a closed feedback system which is mathematically realizable and therefore testable by means of simulation experiments. Where a search of the relevant literature proved unfruitful in yielding the desired information, plausible provisional assumptions necessary for the hypothesis to be self-contained were introduced, concurrently with consultations with professional ecologists. Let us briefly summarize the grounds on which each hierarchy of the hypothesis rests.

First, the closed boundary. The system boundary assumed by the hypothesis--the natural boundary of a grassland ecosystem--is consistent with the well-established concept that ecosystems are the basic units of study in ecology. Indeed, successional phenomena is but one class of ecosystem phenomena. By the assumed closeness of the boundary, the hypothesis qualifies itself as attempting to explain succession inasmuch as it is generated and controlled internally by the biotic community.

Second, the feedback structure. In the preceding sections, the structuring of each loop or subloop of the hypothesis, as well as the interconnections among the loops, was paralleled by reference to and quotations from the information sources prompting its incorporation to the hypothesis. It does not seem necessary to refer back in detail to

the evidence presented in support of each loop. In each case, it was pointed out whether the descriptive information available was sufficient to structure the entire loop, whether gaps had to be filled with plausible assumptions, and whether its relationship with the basic hypothesis of Figure 3 is or is not widely recognized in modern ecological research. On balance, the feedback structures of Figures 3, 4, 5, 6, 7, 9, 10, 12, 14 and 20 appear to be in agreement with the best information available in terrestrial ecology and, in particular, grassland ecology.

Third, the relationships between levels and rates within each loop. Of special interest are, of course, the functional relationships assumed in Figures 8, 11, 13, 15, 16, 17, and 19. When looking at a grassland ecosystem through the "macroscope," as in this research, these relationships subsume complex webs of factors and interactions about which it is not useful to think in detail--even if this were possible. While each one of them seems consistent with either intuition, or empirical evidence, or both, it is admitted that they may be simplistic and, perhaps, even naive. Still, they provide a rationale to develop a testable model, as mathematically formulated in the appendix. The simulation results reported in the next chapter will be indicative of whether these relationships are realistic, whether successional behavior is sensitive to them, and whether they must be understood in greater detail before a better understanding of ecological succession can be sought.

In brief, it is believed that the structure of the dynamic hypothesis does not exhibit any significant inconsistency with Odum's tabular model (Odum, 1969) or any other relevant information. It is

also believed that it will contribute insights into successional dynamics which deepen those yielded by the tabular listing of variables which are known to be successionally significant. At this point, the reader interested in the analytical formulation of the model may wish to turn to the appendix. Otherwise, he may proceed to the next chapter without loss of continuity.

CHAPTER III

MODEL TESTING UNDER NATURAL CONDITIONS

In the great chain of causes and effects no thing and no activity should be regarded in isolation.

-Alexander von Humboldt, 1807

Successional Dynamics of the Grassland Ecosystem

It was pointed out in Chapter I that the overall successional mode of behavior can be characterized as growth (possibly with a varying rate, as from stage to stage) followed by equilibrium, with possibly biomass and diversity temporarily overshooting their long-run climax levels. Graphical and tabular summaries of the significant trends involved were given in Figure 1 and Table 1, respectively. These trends apply to ecosystems in general, including grasslands. With regard to grassland succession in particular, Odum (1959) states:

> Secondary plant succession is equally striking in grassland regions as in the forest even though only herbaceous plants are involved. . . . While the species vary geographically the same pattern everywhere holds. This pattern involves four successive stages: (1) annual weed stage (2 to 5 years), (2) short-lived grass stage (3 to 10 years), (3) early perennial grass stage (10 to 20 years) and (4) climax grass stage (reached in 20 to 40 years). Thus, starting from bare or plowed ground, 20 to 40 years are required for nature to "build" a climax grassland, the time depending on the limiting effect of moisture, grazing, etc. A series of dry years or overgrazing causes the succession to go backwards towards the annual weed stage; how far back depends on the severity of the effect.

The present chapter is devoted to present the simulation results obtained by testing the dynamic hypothesis of the previous chapter (using

the model formulated in the appendix) and to discuss these results vis-a-vis those which are known to be associated with secondary succession in grasslands under natural conditions. Let us consider first the behavior associated with the nutrients cycling loop (i.e., the lower loop of Figure 3) alone. Figure 21 exhibits a 60-year (720 months) simulation of this loop, structured in accordance with the hypothesis elaborated in Figures 4, 6, 7, 9, 10 and 12. Thus, in conducting the simulation run of Figure 21, diversity was ignored, energy flow was taken for granted, and both production efficiency and soil carrying capacity were assumed to possess constant values. For this particular run, the value of production efficiency was set at 10 per cent, and the value of soil carrying capacity at its climax value of 103.3 grams per square meter of plant biomass. The initial conditions were set so as to represent severe trophic disequilibrium, i.e., a very small standing crop and a very large reservoir of nutrients available for absorption. Figure 21 displays the transients which arise in the process of approaching trophic equilibrium. The variables plotted are N = nutrients, O = organic nutrients (i.e., nutrients in organic matter undergoing decomposition), G = gross production, R = respiration, P = producers biomass, C = consumers biomass, and D = decomposers biomass. These correspond to N, ON, GPGR, RESP, P, NC and D, respectively, in terms of the notation used for the formulation of the model in the appendix. Note that G and R, N and O, P, C, and D are plotted in their own scales. Gross production and respiration increase rapidly in response to the abundant supply of nutrients and uncolonized soil. A build-up of the standing crop

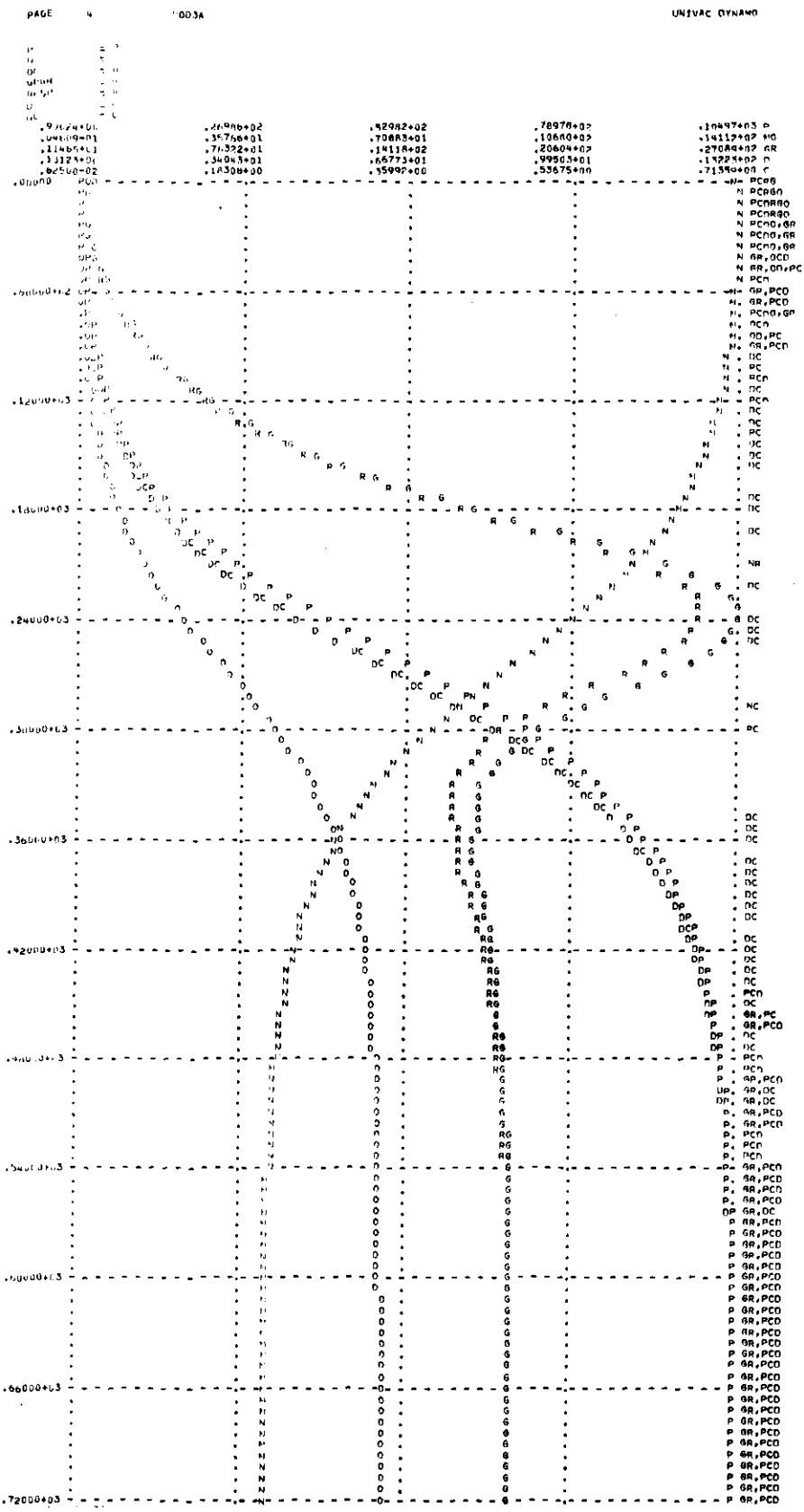

Figure 21. Dynamics of the Nutrient Cycling Loop

gradually follows, and continues until the saturation value assumed for soil carrying capacity is approached. Consumers and decomposers lag behind plants in the growth process. After reaching a peak during the most active years of production, both gross production and respiration decline and level off at the maintenance level. Toward the end of the simulation, the ecosystem is clearly approaching steady-state, with most of the nutrients now forming part of either living biomass (plants and animals) or organic matter in the process of decomposition. The biomass levels of producers, consumers and decomposers approach maximum values of 104.97, 0.71 and 13.22 grams per square meter, respectively, which correspond approximately to the actual values at Pawnee, which are 103.3, 0.70 and 12.4 (Patten, in preparation). Most of the growth has been accomplished after 30 to 40 years, with production activity peaking at about 20 years.

These results compare with the successional patterns of Figure 1 and are consistent with items 1, 2, 4, 6, 7, 16 and 17 of Table 1. The ratio of gross production over community respiration is greater than one during the first 30 to 40 years, but gradually approaches one in later years as production and respiration become equal. The ratio of gross production over standing crop biomass goes from a value greater than one at the beginning of the simulation to a value smaller than one as equilibrium is approached. Presumably, energy flow would be proportional to the level of production and respiration, so there is also implicit consistency with item 3 of Table 1, i.e., the ratio of biomass supported per unit energy flow goes from a low to a high value as the transients

unfold through time. Net production (item 4 in Table 1) is, of course, the difference between gross production and respiration losses; it gradually vanishes toward the end of the simulation. The food chain is grazing-oriented, with plants drawing from abundant nutrients and consumers drawing from abundant plants as rapidly as their own growth machinery allows. Total organic matter (item 6) accumulates to its maximum feasible value and therefore most of the inorganic nutrients become intrabiotic (item 7). As the amount of dead organic matter accumulates, the nutrients recycling role of decomposers becomes critical for continued survival of the biotic community (item 17), although nutrient exchange rate (item 16) slows down and nutrients recycling never becomes limiting in this case. Growth proceeds until limited by the saturation of soil carrying capacity.

The dominant force behind the growth process shown in Figure 21 is, of course, the new growth loop of Figure 7. When the (constant) soil carrying capacity level is approached, the gain of the positive feedback gradually vanishes (as a result of the nonlinearity of Figure 8), and production activity becomes regulated solely by the replacement growth loop of Figure 9. In brief, the standing crop builds up to the limit imposed by soil carrying capacity, or to the limit imposed by the nutrients availability rate resulting from nutrient recycling, whichever is reached first. Changing the values of soil carrying capacity and/or the delays involved in nutrient cycling will affect the limits of growth, but the modes of behavior shown in Figure 21 would remain the same. Similarly, changing the value of production efficiency and/or the

valuation of the nonlinearity of Figure 8 (without changing the shape of the curve) would affect the gain of the loop, and therefore would result in slower or faster growth, as the case may be, but the overall dynamic patterns would still be the same.

Parametric sensitivities of the model will be explored in the next section. At this point, it is interesting to observe that the growth pattern for biomass in Figure 21 approaches the limit asymptotically, i.e., there is no overshoot by the community before settling down to steady-state. In the model used for this run, the indicated replacement growth rate (refer to Figure 6) was formulated as a delay of the total plant depletion rate, including both depletion due to natural decay and depletion due to grazing by the consumers. It was found that overshooting occurs when the indicated replacement growth rate is reformulated as a delay of plant depletion due to natural decay only. The results are shown in Figure 22. When the indicated replacement growth rate is reformulated in this manner, grasses eaten away by the consumers must be restored by new growth rather than replacement growth, a longer adjustment delay is involved, and overshooting results. The difference between gross production and community respiration for the producers no longer tends to zero, but rather to a positive steady-state value corresponding to the net yield required year after year by the consumers. The reformulation also results in a weakening of the new growth loop, due to the reduced rate of accumulation of standing crop which in turn results from the weakened replacement growth loop; as a result, the steady-state is approached at a level which is below either the limit

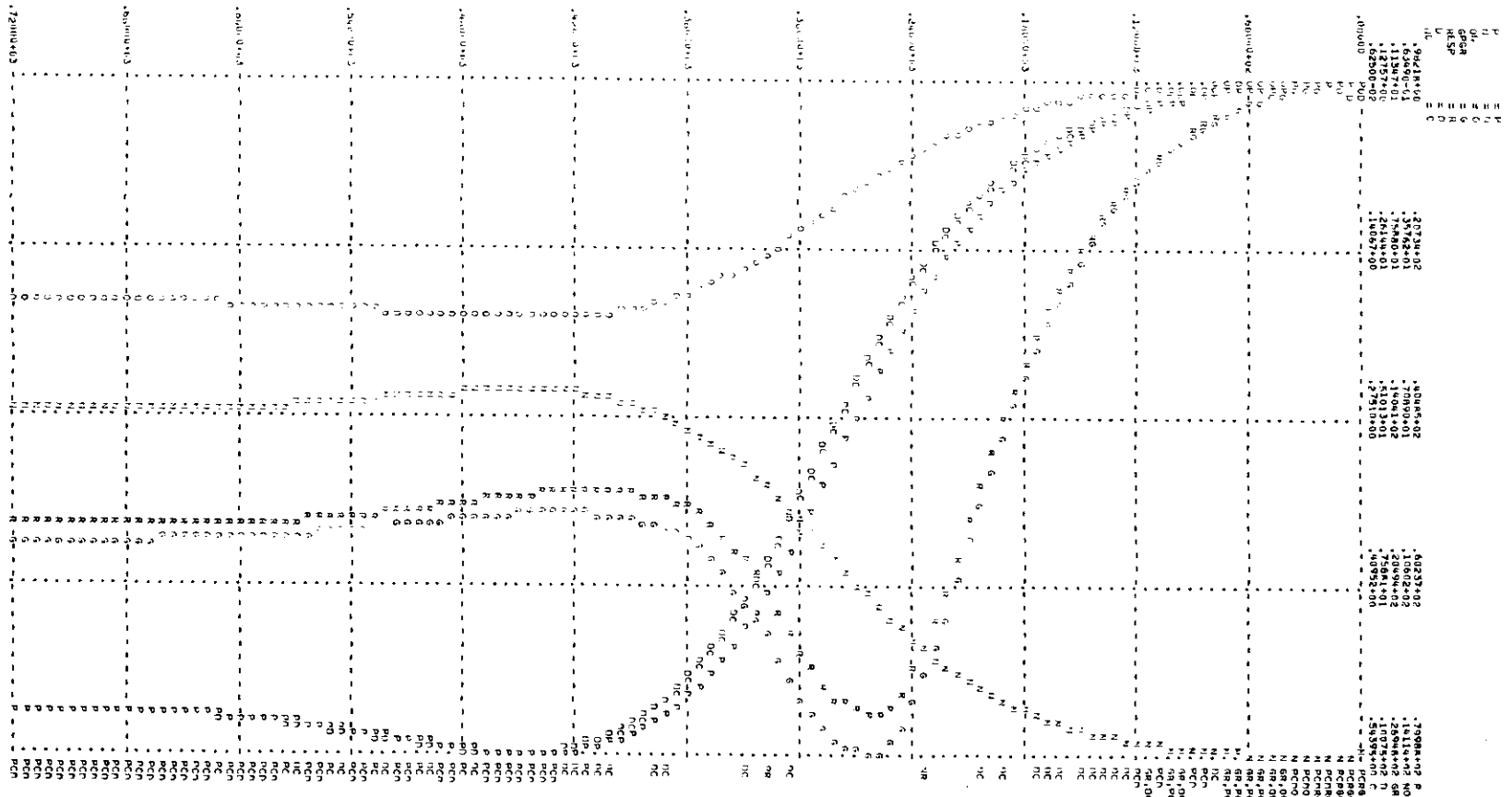

Figure 22. Dynamics of the Nutrient Cycling Loop
with Revised Replacement Subloop

imposed by soil carrying capacity or the limit imposed by the rate of recycling of nutrients. The revised formulation of indicated replacement growth rate may be realistic in that it introduces the tendency of the growth process to overshoot before approaching steady-state, and this is the formulation used in the balance of the simulations. Whether one formulation or the other is used, however, the nutrient cycling loop alone does not explain how successional dynamics arise. The actual carrying capacity of the soil is usually very modest at the beginning of succession, and will not increase unless acted upon by the community. In order to account for ecological succession as a community-controlled process, the upper and lower loops of Figure 3 must stand in interaction.

Figure 23 displays the result of testing the model for the full dynamic hypothesis, which integrates the dynamics of nutrient cycling, diversification and energy flow. Soil carrying capacity and production efficiency are now functions of diversity and relative diversity, respectively, as defined in the preceding chapter. Starting with a modest value of approximately 20 grams per square meter, soil carrying capacity built up during the simulation to 120 grams per square meter in response to community development and diversification. Production efficiency assumed values ranging from 10 to 40 per cent, depending on the stage of successional development. Starting with Figures 23, two additional variables are plotted: Y = diversity and V = vigor, corresponding to the levels denoted as DIV and PV, respectively, in the appendix. The other plotted variables continue to have the same interpretation as

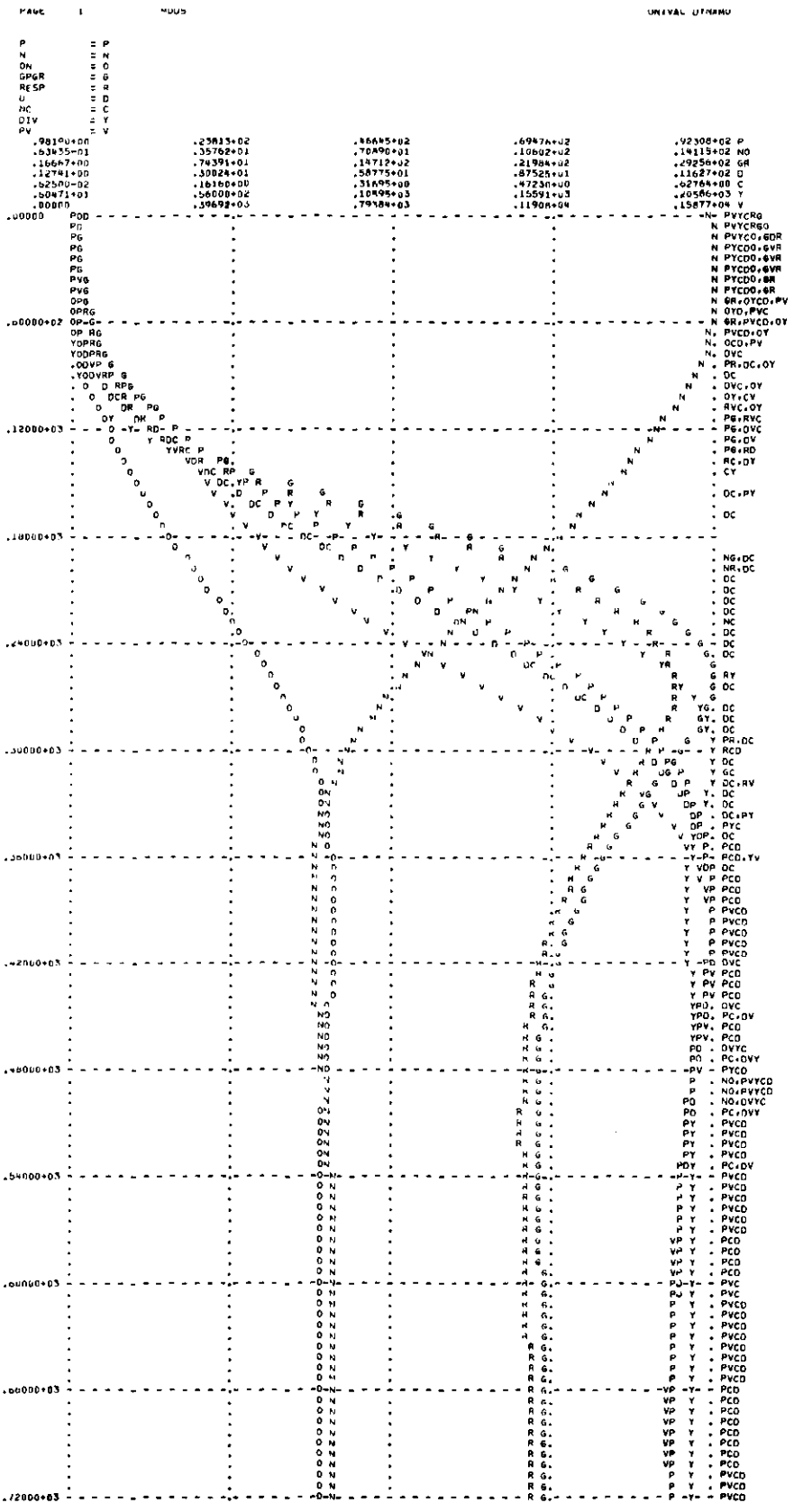

Figure 23. Dynamics of Secondary Succession

before. It must be pointed out that, while the appearance of the P, C, D, G, R, N and O curves resembles that of the previous runs, the controlling force now is the community (i.e., the upper loop of Figure 3), whereas before it was simply the combined effect of assuming a high fixed value for soil carrying capacity and setting the initial conditions at non-steady-state levels, together with the growth machinery of plants and the physical tendency toward equilibrium in the distribution of matter around the nutrient cycling loop.

According to the results in Figure 23, diversity increases and peaks first, then comes the peak in biomass, and lastly the buildup in energy stored, or vigor. The process of species diversification (item 8 of Table 1) presumably results in increased niche specialization (item 12 of Table 1) which in turn has a positive influence on soil carrying capacity (Figure 16), which in turn allows for further growth of biomass (item 6 of Table 1), which of course results in still further diversification (Figure 15). As growth and diversification eventually become limited by space saturation, inter-specific competition, etc., energy flow increasingly becomes allocated to storate as vigor and, eventually, to dissipation in the performance of other quality functions. As the potential for both quantitative and qualitative growth becomes exhausted, the steady-state or climax condition is approached. The time histories of Figure 23 constitute the basic simulation result of the research. They display the energetically-based dynamic behavior which arises in time and space from the feedback coupling of abiotic and biotic matter, species differentiation and energy flow. In brief,

Figure 23 exhibits the dynamic patterns of secondary succession in a grassland ecosystem.

Sensitivity to Parametric Perturbations

The dynamic behavior discussed in the previous section arises from the feedback structure of the ecosystem. More specifically, the modes of behavior which appear in Figure 23 arise from the feedback structure of the dynamic hypothesis in Chapter II. Parameter values determine, of course, the levels of magnitude associated with the various successional variables, the period and limits of succession, the amplitude of oscillations, etc. However, they determined neither the occurrence of succession nor the dynamic patterns associated with its unfolding. In order to verify that this is indeed the case, the simulation model was exercised repeatedly to test the sensitivity of successional behavior to changes in each one of the model parameters. Sensitivity analyses for each parameter were conducted on a one-at-a-time basis by perturbing its numerical value over a wide range and rerunning the model while keeping everything else constant. Additional simulations to test the effect of parameter variations on a several-at-a-time basis were conducted in a selective manner, with emphasis on those parameters which appear to have special relevance to ecological succession.

The parameters required to quantify the dynamic hypothesis under consideration are basically of three kinds, i.e.: conversion coefficients, time delays and table functions. Conversion coefficients include the amount of nutrients required to produce one unit of plant biomass, the amount of energy per unit time required to maintain one unit of

plant biomass, the amount of plant biomass required to sustain one unit of consumers biomass, the amount of energy per unit time required to maintain each one of the species in the community, and so forth. Time delays include the average lifetimes of plants and animals, the time required for the production machinery of plants to respond to favorable growth conditions, the delay involved in the substitution of species, the average amount of time that energy can be stored before it becomes fossilized, etc. Table functions refer to the valuation of the complex ecological functions hypothesized in Figures 8, 11, 13, 15, 16, 17 and 19. It would not seem necessary to display and discuss all the simulations conducted for sensitivity analysis purposes. However, a discussion of some selected cases is appropriate. In order to follow the discussion, it will not be necessary for the reader to study in detail the analytical formulation of the simulation model, as presented in the appendix. However, the discussion will include parenthetical references to the formal notation used in the appendix, for the benefit of the reader who wishes to do so.

Let us consider first the effect of delays on successional dynamics. In the simulation of Figure 23 (hereafter taken as the "standard run" for comparative discussion purposes), the average lifetime for the standing crop of grasses (denoted as PDD in the appendix) was assumed to be six months. The results of assuming a lifetime of only three months for grasses are shown in Figure 24. The effect of shortening the lifetime of grasses by one half is shown to be basically twofold: production activity peaks approximately ten years *later*, and the standing

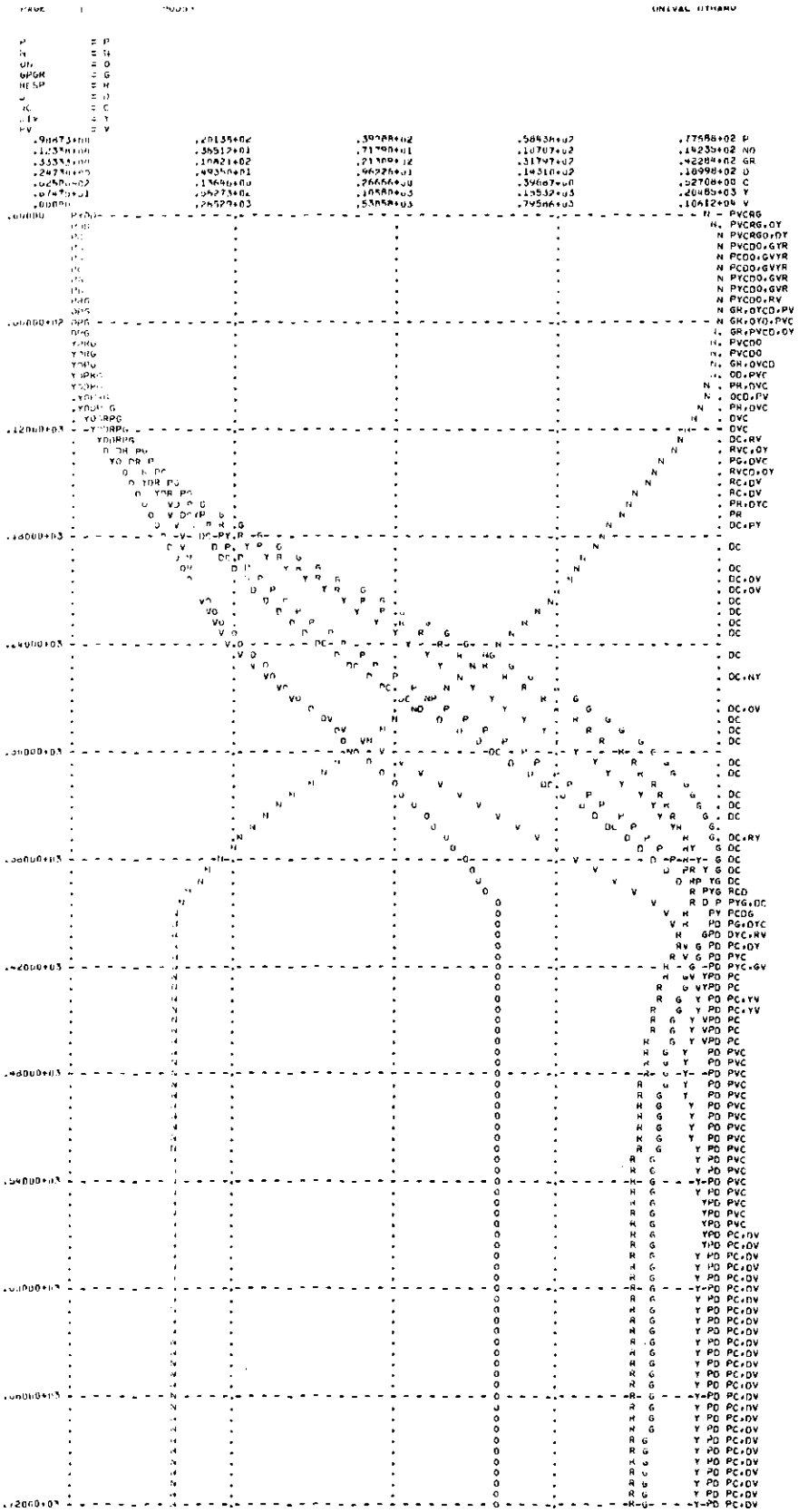

Figure 24. Effect of Reducing the Lifetime of Grasses by One Half

crop of grasses levels off after succession at a *lower* steady-state level. Succession takes longer because shortening the life span of grasses reduces the accumulation of standing crop, which in turn reduces the production capacity of the plant community and results in a weakening of the new growth loop gain. It results in a lower climax level for plant biomass because the rate of availability of soluble inorganic nutrients becomes limiting as a result of the great quantity of nutrients which accumulate in organic form (i.e., trapped in organic matter in process of being decomposed). The effect of assuming that the average lifetime of grasses is longer than six months would be exactly the opposite: production activity would peak sooner, and the climax standing crop would be greater than in Figure 23. In either case, however, the same modes of successional behavior occur; changing the numerical value of this delay changes the period of the successional patterns and their limits, but the patterns themselves do not change. With regard to Figure 24, it is interesting to observe that while the climax accumulation of biomass is smaller than before, gross production peaks and then approaches steady-state at levels higher than before. This means that a greater amount of the energy flow is consumed in the long run for production purposes (as evidenced also by the reduced climax level of energy stored as vigor) and reveals that a plant community characterized by short-lived plants will tend toward a higher gross production over standing crop biomass ratio and a lower amount of biomass supported per unit energy flow than a community where long-lived plants predominate. Conversely, the longer the average life span of plants is, the lower the

gross production over standing crop biomass ratio and the higher the biomass supported over unit energy flow ratio to be approached in the mature stages. The smaller climax accumulation of plant biomass and the greater accumulation of organic debris which result when plants are short-lived also result in smaller and greater climax levels of consumers and decomposers biomass, respectively. Species diversity, on the other hand, does not seem to be affected in any significant way by the average lifetime of plants.

Delays also can affect successional transients by introducing oscillations. For example, Figure 25 shows the effect of increasing the species colonization delay (ISEAD in the appendix) by a factor of two, from five to ten years. Increasing the value of this delay means that it will take longer for new species to appear on the grassland in response to the ongoing build-up of biomass. The result is a slower takeoff of species diversity, followed by a diversification pattern which overshoots and then exhibits damped oscillations as it approaches its climax level. This behavior is intuitively appealing from the ecological viewpoint. The potential of the ecosystem as a site for colonization by new species accumulates as a result of the slow response to biomass accumulation. This potential eventually results in a diversification boom which brings to the grassland new species in numbers exceeding the natural niches available. Fierce inter-specific competition results, and diversity declines. It declines too much, however, due to the severity of competition and/or the unsuitability of some of these species for the local niches. As a result, some niches are left

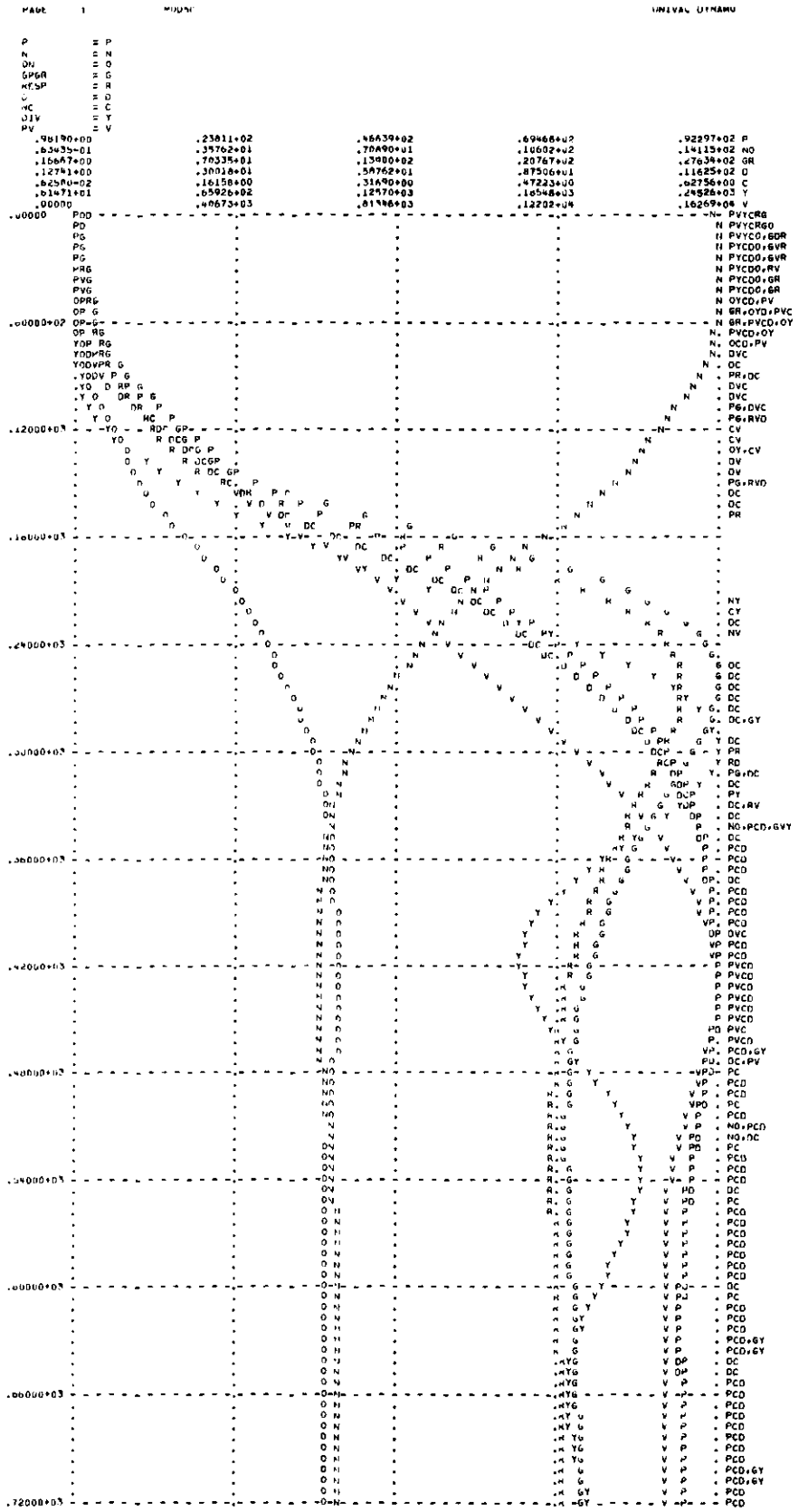

Figure 25. Effect of Increasing the Species Emergence Delay by a Factor of Two

uncolonized, creating again the potential for the arrival of new species, which again compete for the remaining niches, and a new diversification cycle takes place. The gradual exhaustion of niches remaining after each cycle brings about a gradual vanishing of the potential for further diversification and eventually leads to steady-state after several cycles of decreasing amplitude. In Figure 25, successional development otherwise unfolds as before, but it would be affected eventually if the delay under consideration continues to increase. If the length of the delay were to become infinite (meaning that diversification response to biomass growth never materialized) the carrying capacity of the soil would remain stagnant and successional development would abort.

There are three important delays in the positive feedback loop of Figure 18. One is of course the delay associated with the production of plant biomass. Another is the delay involved in the appearance of new species in response to biomass accumulation, as discussed in the previous paragraph. The third one is the delay involved in the complex array of community activities which eventually results in increased soil carrying capacity. In the simulation of Figure 23, this delay (which is denoted as SCCAD in the appendix) was assumed to have a value of 12 months. In other words, it was assumed that the impact of new species on soil carrying capacity becomes operative one year after the arrival of the new species. The effect of a tenfold increase in the value of this delay is shown by the simulation of Figure 26. Successional modes of behavior remain invariant, as well as the climax levels eventually reached by the various variables, but the smoothness of the process is broken into

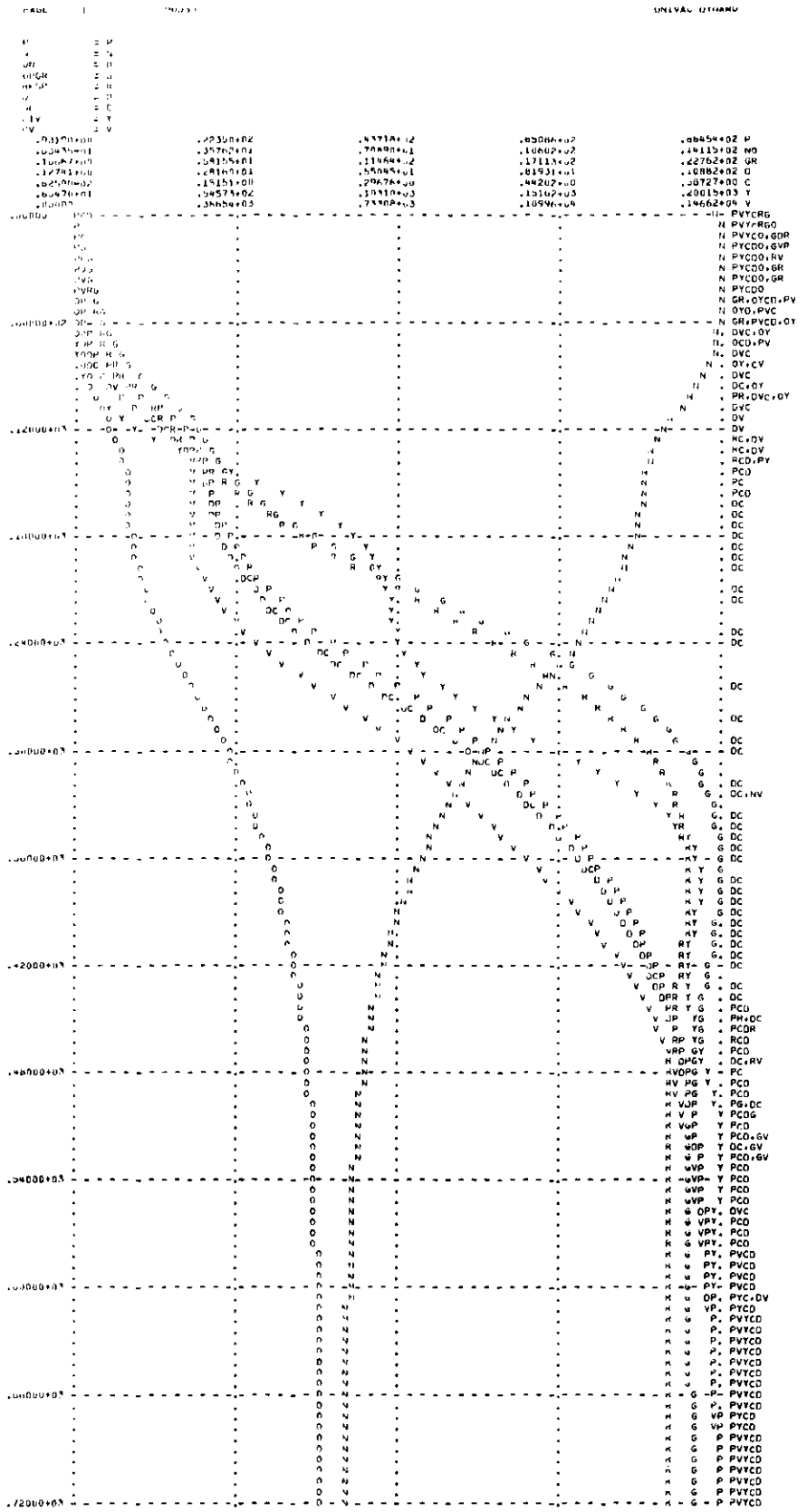

Figure 26. Effect of Increasing the Soil Carrying Capacity Adjustment Delay by a Factor of Two

distinct stages of development. Thus, production activity and therefore plant biomass grow rapidly at the beginning, as before. After ten years or so, however, biomass production and the accumulation of standing crop slow down due to the limiting effect of soil carrying capacity, until this limit is relaxed by species substitution and the (now slower) activity of the increasingly diversified community.

Simulation runs conducted to test the effect of perturbing the value of other delays revealed a high degree of model insensitivity to wide variations in these parameter values. As expected, successional transients retained the same behavioral patterns in all cases. Sufficiently large values for some of the delays, however, have a limiting effect on succession. For example, the nutrient availability rate of Figure 6 is directly proportional to the reservoir of soluble inorganic nutrients available in the soil and inversely proportional to the nutrient absorption delay (NAD in the appendix), which in turn depends on the availability of water and other factors. Thus, for a given reservoir of nutrients, increasing the nutrients absorption delay decreases the nutrient availability rate; the longer this delay is, the sooner nutrient availability becomes a limiting factor of succession. Similar remarks apply with regard to the delay involved in the decomposition of organic matter. This delay depends on the availability of decomposers to do the job (see Figures 12 and 13), and decomposers grow in response to the accumulation of organic debris. If their response delay (DRD in the appendix) is very large, decomposers will grow slowly, organic debris will accumulate at a rate faster than the decomposition rate in the

meantime, the decomposition delay will increase, the rate of inorganic nutrients becoming available will decrease, the reservoir of soluble inorganic nutrients in the soil will also decrease, and again the nutrient availability rate will become limiting sooner than if the decomposers grow quickly in response to the buildup in organic matter, with the limiting effect persisting at least until the actual level of decomposers catches up with the required level. Needless to say, if the length of the decomposers response delay were to become infinite, organic matter would accumulate without being decomposed, the recycling of nutrients would stagnate, and the growing standing crop would first level off and then eventually decline as nutrients continue to become available neither for new growth nor for replacement growth. In any of these cases, successional transients unfold as usual until suppressed by the limiting effect of the delay.

Let us consider next the sensitivity of successional behavior to the values of conversion coefficients. The gain of each feedback loop in the structure of the ecosystem depends on the numerical values of the parameters in that loop, whether they are time delays or conversion coefficients. When the gain in any one of the loops of the multi-loop structure becomes limiting, succession is suppressed. This is the case whether a loop gain becomes limiting as a consequence of a coefficient or as a consequence of a delay. For example, consider again the possibility that the availability rate of nutrients (see Figure 6) becomes limiting. It was pointed out above that the nutrient availability rate is proportional to the amount of inorganic nutrients available in the

soil and inversely proportional to the nutrient absorption delay. Therefore, the maximum production rate of plant biomass which is feasible as far as nutrient availability is concerned (denoted as NRPGR in the appendix) is equal to the nutrient availability rate divided by the quantity of nutrients which are necessary to produce one unit of plant biomass (i.e., the coefficient NPRC in the appendix). Evidently, the greater the value of this coefficient, the sooner nutrient availability effectively becomes a limiting factor of succession. It follows then that for a given inventory of nutrients, actual nutrient availability becomes limiting sooner if either the nutrient absorption delay, or the nutrient conversion coefficient, or both, are increased. Whether it is the time delay or the conversion coefficient that causes nutrient availability to become limiting, successional transients continue their course until constrained by the limiting factor.

Similar remarks apply to other conversion coefficients in the various loops. Energy flow, of course, also can be made limiting by increasing one or more of the conversion coefficients involved. For example, the maximum production rate of plant biomass which is energetically feasible (EPPGR in the appendix) is equal to the rate of energy becoming available from photosynthesis plus the rate of energy becoming available from storage, all divided by the quantity of energy which is required to produce one unit of plant biomass (EPRC in the appendix). Again, the greater the value of this coefficient, the sooner energy availability becomes limiting on succession. Short of becoming a limiting factor on growth and diversification, either decreasing energy flow

or assuming that more of it must be used for production and/or diversification work results in weakened plant vigor during succession. An illustrative example is given by the simulation run of Figure 27, which exhibits the effect of increasing the energy requirement coefficient for diversity maintenance (DIVMC in the appendix) by a factor of five. According to the influence diagram of Figure 20, this would affect the rate of energy remaining for storage, or vigor. The simulation shows that plant vigor, and therefore the ability of the plant community to draw from stored energy in order to sustain external perturbations (see item 22 of Table 1) is detrimentally affected during succession, and also approaches a lower climax level. The same effect results from reducing, for example, the assumed energy fixation rate per unit of standing crop (EFR in the appendix). This is of course due to the higher priorities enjoyed in the hypothesis by production and diversification work, and the open-loop character of energy flow.

Finally, let us discuss the sensitivities associated with the non-linearities of Figures 8, 11, 13, 15, 16, 17 and 19. Structurally speaking, these functions are actually variable coefficients. They influence system behavior in ways similar to time delays and conversion coefficients, but in varying degrees depending on the value of the independent variable, which in each case is both an integral element of the feedback structure and an indicator of the stage of successional development. Thus, the changes in the values of these variable coefficients are internally generated over time by the feedback structure of the ecosystem, and they both influence and are influenced by the unfolding of

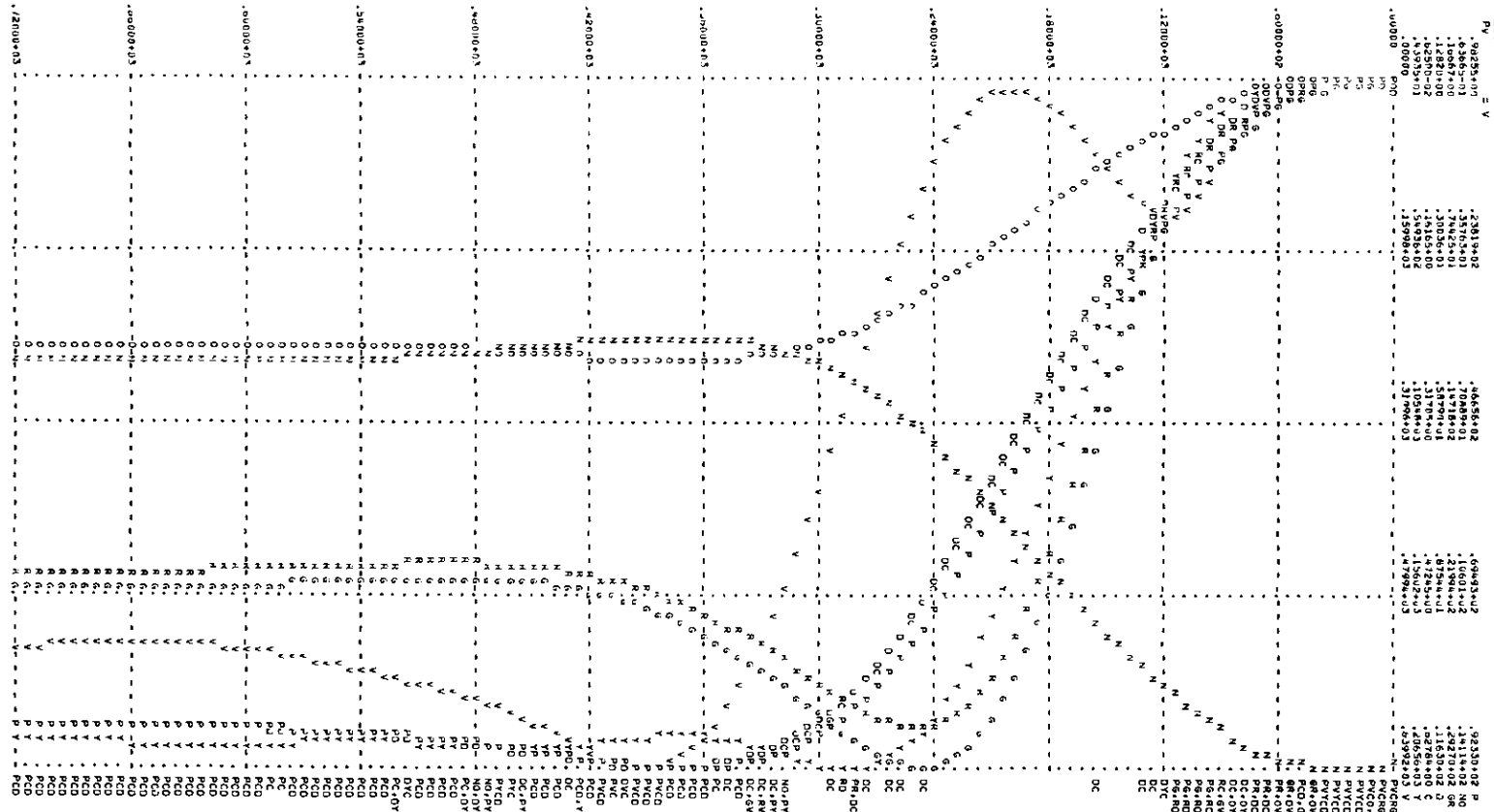

Figure 27. Effect of Increasing Energy Requirement for Diversity Maintenance by a Factor of Five

successional transients. In each case, sensitivities will depend on both the shape and the numerical valuation of the curve. The shape of each curve is as assumed in the dynamic hypotheses of the previous chapter, and remain invariant (except for some linearization trials) for all simulations conducted during the research. The upper and lower limits of each function also remained constant for all simulations; in each case, the perturbation made for the sensitivity analysis runs consists of either inflating or deflating the numerical values of the curve within the hypothesized range. The interested reader may refer to Figures 42 and 46 in the appendix for the numerical values used.

As it was with regard to time delays and conversion coefficients, the most interesting sensitivities related to nonlinearities (table functions) were found to be associated with those belonging to the positive loop of Figure 18. For example, the effect of inflating the values of the production efficiency curve (refer to Figures 19 and 46) is shown in the simulation run of Figure 28. The consequence of a higher-valued production efficiency curve is of course to increase the gain of the new growth loop of Figure 7. As a result, the rate of production of plant biomass accelerates much faster and overshoots, generating oscillations of standing crop and species diversity before the ultimate climax is approached. A comparison with the time patterns of Figure 1 suggests that the production efficiency curve used for this simulation probably was too inflated.

Interesting results were also obtained by perturbing the indicated-diversity-as-a-function-of-total-biomass and the indicated-

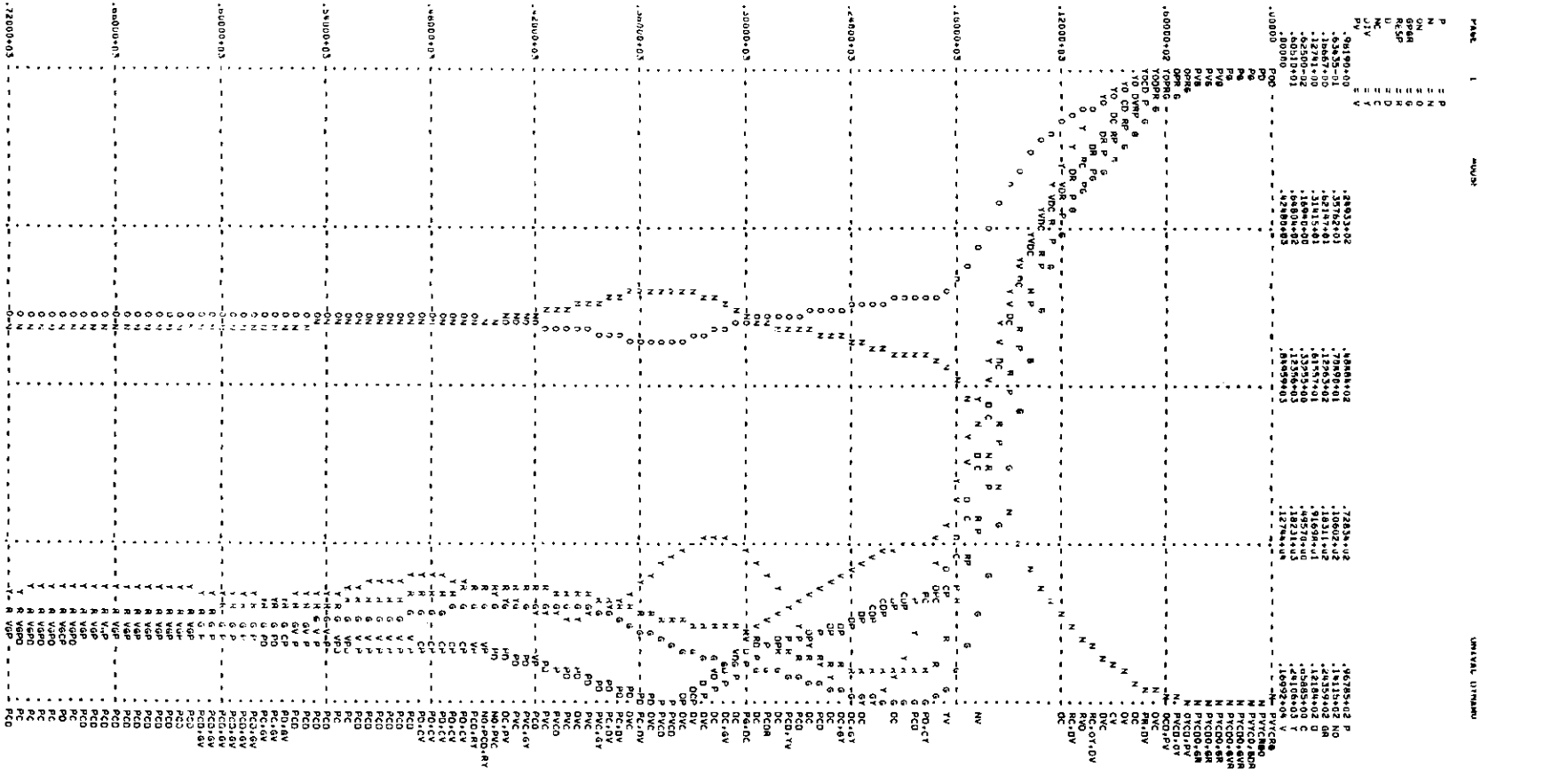

Figure 28. Effect of Higher-Valued Production Efficiency Curve

soil-carrying-capacity-as-a-function-of-diversity curves of Figures 15 and 16, either one at a time or jointly. It was found that the distinctness between successive stages of ecosystem development becomes more apparent as a result of either increasing the delays around the loop (as in the simulation of Figure 26), or perturbing the nonlinearities involved, or both. Figure 29 displays the effect of jointly deflating the diversity curve and linearizing the soil carrying capacity curve (see Figures 44 and 45 for the actual values used). It is illuminating to examine the results of Figure 29 vis-a-vis the results presented before in Figure 26. While diversity leads biomass during most of the transient period in Figure 26, the reverse is the case in Figure 29. This is because the joint perturbation introduced in the latter case effectively shifts dominance during the early stages of succession to the gain associated with the soil carrying capacity curve. In Figure 26, successive stages become distinct simply because of the delay involved in going from one to another; in Figure 29, on the contrary, they become distinct because the more-growth versus more-diversity strategy of the early grassland community is assumed to shift in favor of increasing the carrying capacity of the soil presumably to allow for faster growth. Nevertheless, the net result of assuming this change in community strategy is to reach the climax more or less at the same time as in Figure 26 and approximately 10 to 15 years later than in the simulation of the standard run. Attempting to expand the carrying capacity of the ecosystem without (of even with less) species diversification results in oversaturation of the colonized niches, while leaving other niches unexploited. After a

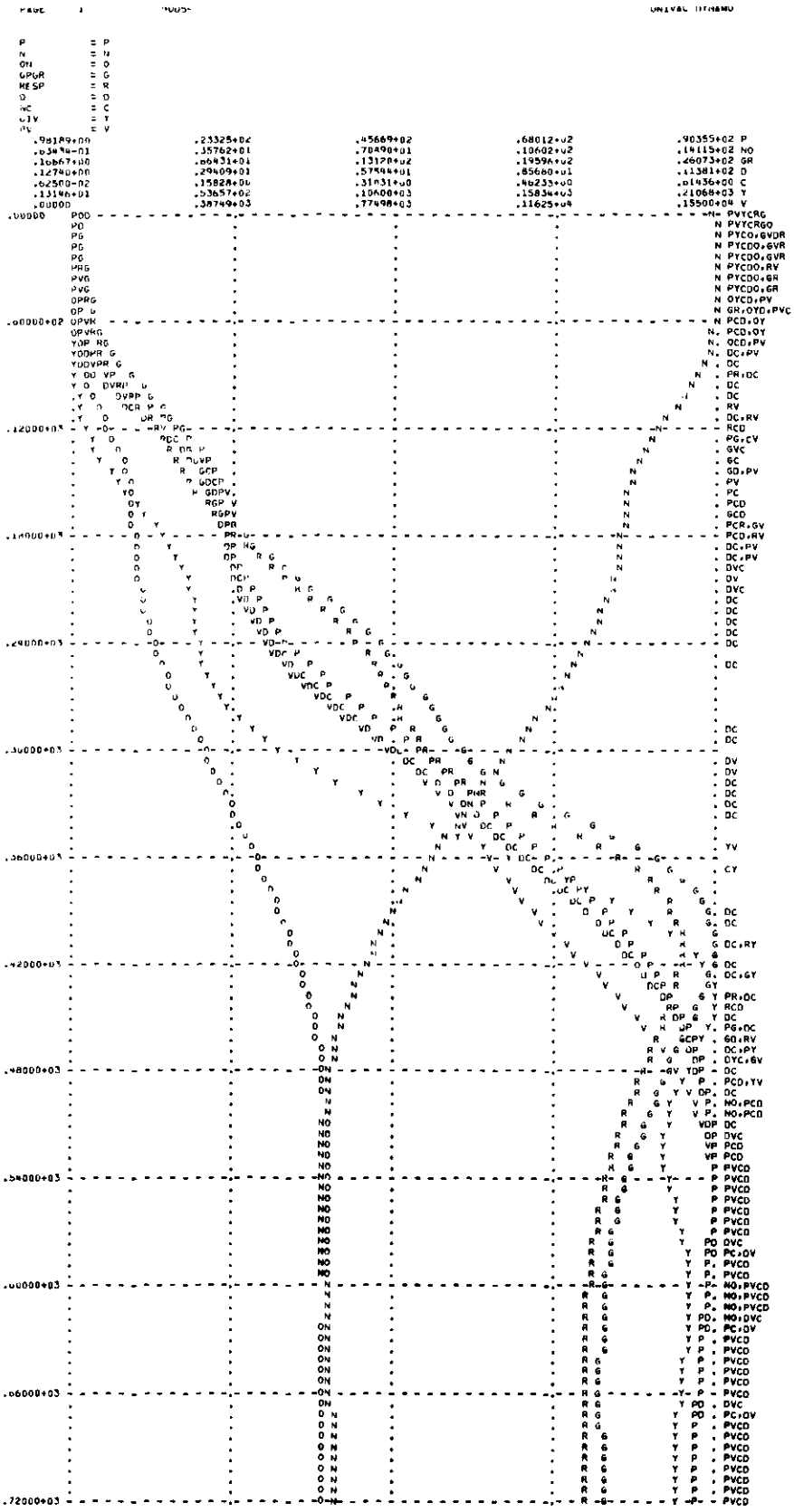

Figure 29. Joint Effect of a Lower-Valued Diversity Curve and a Linearized Soil Carrying Capacity Curve

few years, growth must slow down to give time for a more diversified community to pursue a more comprehensive colonization of the grassland; then, succession proceeds. With regard to the simulation of Figure 29, it is also interesting to observe that it displays stages of grassland development which closely resemble (time wise) those described in Odum's quotation at the beginning of this chapter.

The simulations reported in this section have shown that perturbing ecosystem parameters affect the limits of succession, the period of transient successional response, the period and amplitude of oscillations, and so forth. However, the dominant dynamic modes of successional behavior (as in Figure 1 and Table 1) arise from the feedback structure of the ecosystem and are insensitive to parametric variations. In generating succession, all elements of the ecosystem interact according to the mutual causalities involved, with no one standing in isolation from the others. Precisely because of this, any factor which becomes limiting for the successional development of one element of the ecosystem structure becomes limiting for the whole ecosystem.

Response to Exogenous Perturbations

While the previous section explored sensitivities to ecological parameters as the ecosystem succeeds from youth to maturity, the present one describes the transient successional response of the climax grassland ecosystem to natural exogenous perturbations such as fire, drought, etc. It has been shown how the positive feedback loop of Figure 18 has a controlling influence on successional transients. Therefore, it appears appropriate to test model performance under natural exogenous

perturbations which periodically result in destruction of standing crop and/or species diversity. A set of simulation runs was conducted for this purpose, and the results are illustrated by Figures 30 and 31. These simulations were accomplished by letting the model run during 60 years and then, with the ecosystem in steady-state (climax) condition, applying a severe pulse increment to the rates of depletion of plant biomass and species diversity (PDR and DDR in the appendix, respectively).

Figure 30 displays the successional response to a sudden destruction of approximately 50 per cent of the standing crop of grasses. The net effect of the disturbance is to push the grassland back to a younger stage of successional development. Grass production (and therefore plant respiration also) declines during the year following the disturbance, due to the reduction in production machinery associated with the destruction of plant biomass. As a result, the standing crop for the year immediately following the perturbation is greatly reduced. The number of species in the community declines slightly, presumably the result of the weakest species abandoning the range under the pressure of increased competition brought about by the scarcity of food. Finally, plant vigor also declines in the aftermath, because the reduction in photosynthetic activity reduces energy flow below the level necessary for immediate replacement of energy being dissipated from storage. Beginning with the second year after the destruction, however, the grassland bounces back. Both gross and net production increase, plant biomass builds up, some of the abandoned riches are colonized anew, and the interplay between plant production and the still highly diversified community gradually drives

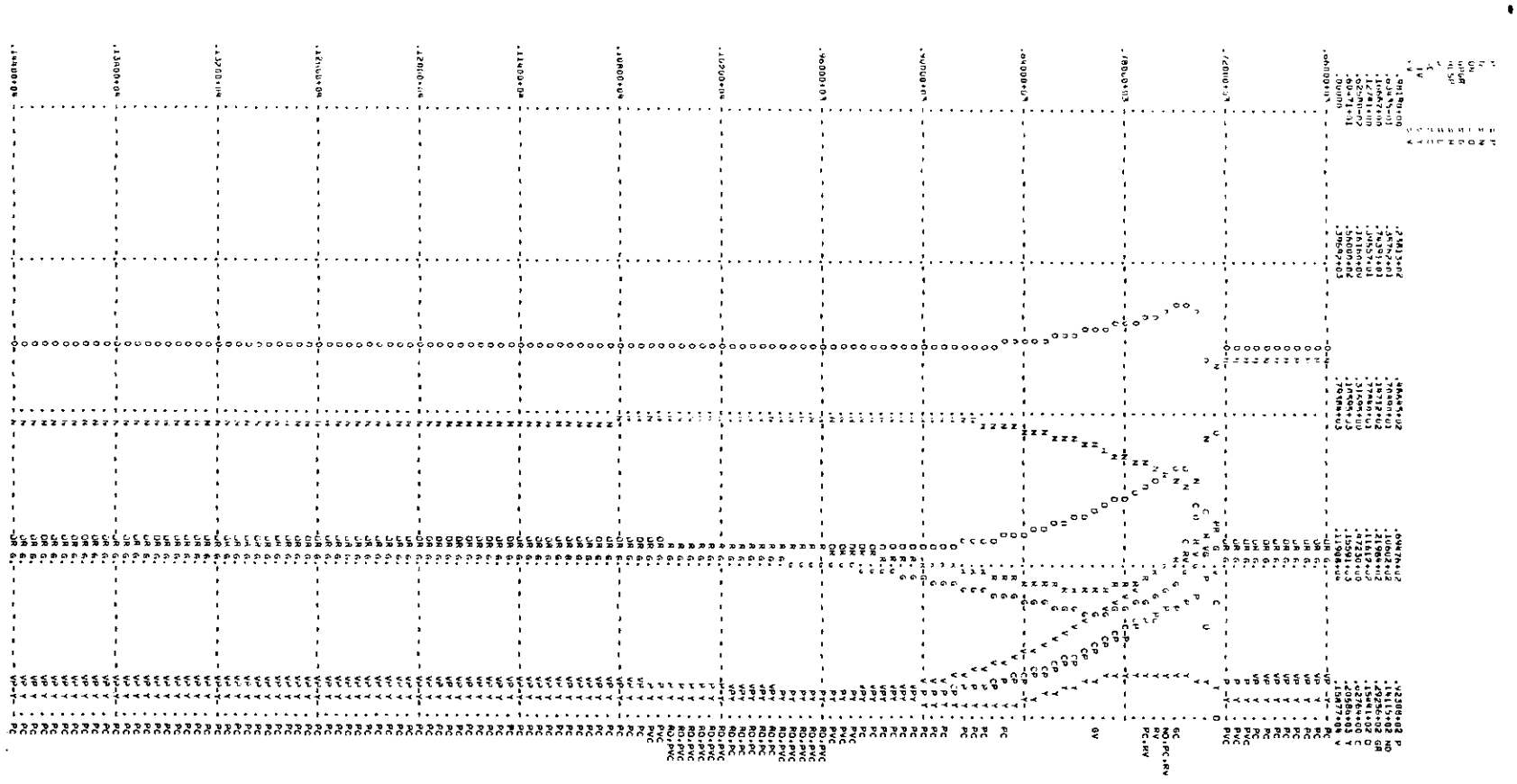

Figure 30. Response to Sudden Partial Destruction of Standing Crop

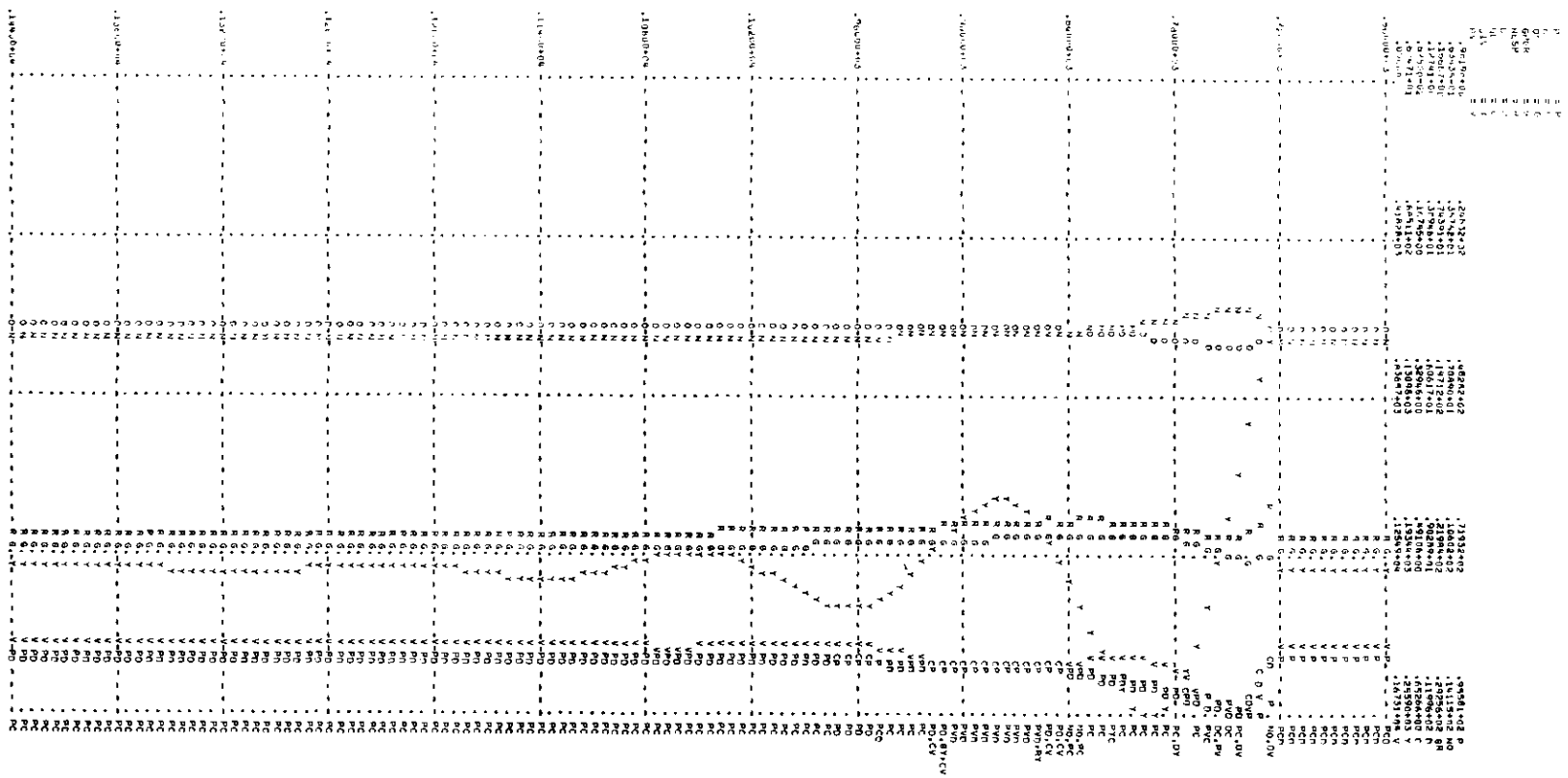

Figure 31. Response to Sudden Partial Destruction of Species Diversity

the grassland back to its climax in approximately 10 to 15 years.

Figure 31, on the other hand, exhibits the successional transient which arises from suddenly forcing about 50 per cent of the species in the biotic community out of the grassland. The initial reaction to the sudden decrease in diversity is an increase in gross production, and even greater increase in net production, and therefore a boom in the level of standing crop. Both the standing crop and its vigor flourish in the years immediately following the disturbance. This is made possible by the reduced demand of energy for diversity maintenance work, which results in increased amounts of energy flow being allocated to production of biomass and the performance of quality functions other than diversification, with increased plant vigor as the net effect. Naturally, the bloom in productivity and the abundance of food which the accumulation of standing crop brings about immediately creates a high potential for community diversification. Too many species respond to the favorable conditions for colonization and overshooting results, followed by damped oscillations as again the grassland is internally driven back to its climax by its own feedback mechanisms.

Other exogenous perturbations may be of some consequence in generating successional transients. For example, a disturbance causing a temporary destruction of decomposers would result in a slowdown of decomposition processes and, as a result, nutrient availability may become limiting and the standing crop (and even species diversity) may suffer a temporary decline until decomposers regenerate and an adequate rate of nutrients recycling is restored. On the other hand, a disturbance

leading to a temporary extermination of consumers would relax the grazing pressure on grasses and they would tend toward a new steady-state level involving no net new production until the animals come back. As discussed in the preceding section (in connection with sensitivity to nutrient availability delay, NAD) a disturbance causing water shortage may have the same limiting effect as destroying the decomposers. The concentration of soluble inorganic nutrients in the soil may be adequate, but nutrient availability still becomes limiting if they cannot be absorbed at the required rate. As was the case with parametric variations external disturbances such as these may have an indirect (e.g., limiting) effect on successional transients, but the most interesting responses arise when perturbations are applied to the loop coupling standing crop and species diversity.

With regard to the results of both Figure 30 and Figure 31, it is also interesting to note that the same feedback structure which generates and controls ecosystem succession is also responsible for its ability to bounce back from the destructive effect of external disturbances. In the next chapter, it will become apparent how the very same feedback structure of the ecosystem is again responsible for its ability to endure sustained utilization stress, at least to a certain extent.

Performance Validation of the Dynamic Hypothesis Under Natural Conditions

The last section of Chapter II provided evidence on the structural validity of the dynamic hypothesis under consideration. The hypothesis (and therefore the model of the appendix, which is based on the

hypothesis) was defended on the basis of the system boundaries chosen, the pertinence of the variables included, and the consistency between the feedback couplings assumed by the hypothesis and those which are known to exist in grassland ecosystems. According to Forrester (1961) ". . . the defense of a model rests primarily on the individual defense of each detail of structure and policy, all confirmed when the total behavior of the model system shows the performance characteristics associated with the real system." Having discussed the structural validation aspect before, let us summarize the simulation results of the present chapter insofar as they confirm the validity of the hypothesis.

The performance characteristics associated with ecological succession in real ecosystems are as shown in Figure 1 and tabulated in Table 1. Therefore, for purposes of performance validation, the basic comparison to be made is between these performance patterns and the performance patterns of the model, as shown in Figure 23. It might seem at first glance that Figure 1 is best resembled by the simulation of Figure 21. However, in comparing Figures 1 and 23, it is important to recall that while R stands for total community respiration in Figure 1, it accounts for producers respiration only in the case of Figure 23; since a net yield is required year after year by the consumers, the difference between gross production and respiration does not tend to zero in the simulations. Since the energetics of consumers and decomposers are not explicitly taken into account by the model, it is not possible to compute total community respiration, but this in no way affects the overall successional behavior of the model. It is also important to recall that

while total biomass approaches its climax level asymptotically in Figure 1, it was considered more realistic to incorporate into the model the tendency of the biotic community to overshoot before settling down to its post-successional steady state. Otherwise, the modes of behavior which Figures 1 and 23 exhibit are the same.

With regard to Figure 1, it would seem that the actual pattern of grassland succession should fall somewhere in between those of microcosm succession and forest succession, probably closer to the latter. While the simulated patterns, especially those of gross production and respiration, appear to be more in consonance with those of the forest ecosystem, the relative magnitude of net production in the simulations is reminiscent of the small laboratory ecosystem. It must be pointed out that while the microcosm succession patterns of Figure 1 are based on empirical data (Cooke, 1967), those for forest succession are hypothetical (Kira and Shedei, 1967). Under closer scrutiny, it becomes apparent that the growth patterns hypothesized by Kira and Shedei during the first 30 years of forest succession are, at best, debatable. They seem to imply that during this period total biomass increases only linearly as a function of time, while net production (i.e., the difference between gross production and respiration) increases at an accelerated rate. In this respect, the simulated patterns appear to be more realistic.

The simulated time patterns of Figure 23 are also consistent with other trends to be expected in ecological succession, as listed in Odum's tabular model (Table 1). Comparative discussions of trends in Table 1 vis-a-vis simulated trends were provided in previous sections of this

chapter, and will not be repeated here. These discussions showed that trend items 1, 2, 3, 4, 6, 7 and 8 of Table 1, and therefore items 23 and 24 also, are reproduced by the simulations with a high degree of fidelity. While not directly measurable in terms of model variables, trend items 5, 15, 16, 17, 20 and 22 are descriptive of the way the model actually works. Item 21 is automatically implied by the choice of a closed boundary. Finally, it appears very reasonable to suppose that in real ecosystems the trends numbered 9 to 14, 18 and 19 unfold in parallel with those generated in the simulations. Although these factors were not explicitly included as separate variables in the hypothesis or the simulation model, their importance is recognized in some of the complex functions relating the other variables. For example, trend item 12, niche specialization, is an important element in the rationale underlying the relationship between diversity and carrying capacity. In brief, then, the simulated patterns of Figure 23 are consistent (or, at least, not inconsistent) with each one of the trends which is known to be associated with ecological succession. In addition, the simulations of Figures 24 to 31 verify that the successional dynamics generated by the model remain well behaved under both parametric and exogenous perturbations, and further confirm the adequacy of the dynamic hypothesis.

CHAPTER IV

MODEL TESTING UNDER UTILIZATION CONDITIONS

All flesh is grass.

-Isaiah 40:6

Influence of Grazing on Grassland Succession

Animal life, human life, and indeed all economic activity are ultimately based on the fact that grasses and other plants capture solar energy at a rate greater than that necessary for their own maintenance. The objective of the present chapter is to report the extent to which successional responses to a systematic exploitation of this surplus can be explained by the dynamic hypothesis of Chapter II.

Land may be used for urban development, for recreation, agriculture, forestry, grazing, etc. Only the last mode of utilization will be considered here, as it is the typical mode of utilization for natural grasslands such as Pawnee. When a grassland is used as a range for livestock, the long-run consequences of the grazing stress may be either beneficial or detrimental to the range resource. It is well known that overgrazing sooner or later induces a depletion of palatable grasses and their substitution by undesirable species, as well as soil erosion and other harmful effects. On the other hand, it is also well known that field research conducted during the last few decades has resulted in grazing systems under which grasslands can endure sustained grazing pressure and even improve while being grazed. What is the basis for the (at

least potentially) beneficial influence of grazing on grassland succession? The simulations reported in this chapter were directed at secondary succession as provoked by light or moderate grazing (as opposed to heavy grazing) in an attempt to establish to what extent grazing can be manipulated as a constructive ecological force. In so doing, we shall be testing the adequacy of the dynamic hypothesis to explain successional behavior under utilization conditions.

Needless to say, the crucial difference between natural exogenous disturbances such as fire, drought, etc., and man-made or utilization perturbations is that while the former are momentary, the latter are usually sustained over long periods of time. When a severe conflagration takes place, the heat results in a sudden destruction of biomass and/or diversity, but then the community is left alone to reconstruct itself back to the climax. Let us examine now the effect of sustained stress on plant biomass and/or species diversity. The end result of an exogenous sustained grazing pressure is to push the ecosystem back to a younger successional stage and keep it there. Figure 32 shows this effect, as it would arise by introducing domestic consumers to harvest the standing crop of grasses on a continuous basis. The variables plotted in the simulations of this chapter are the same as in the previous chapter. In Figure 32, the induced depletion of plant biomass brings about an increase in both gross and net production, which is sustained because of the sustained grazing pressure. The grazing activity of the domestic consumers also has a negative influence on the availability of food for natural consumers, which decline in proportion to the decline of plant

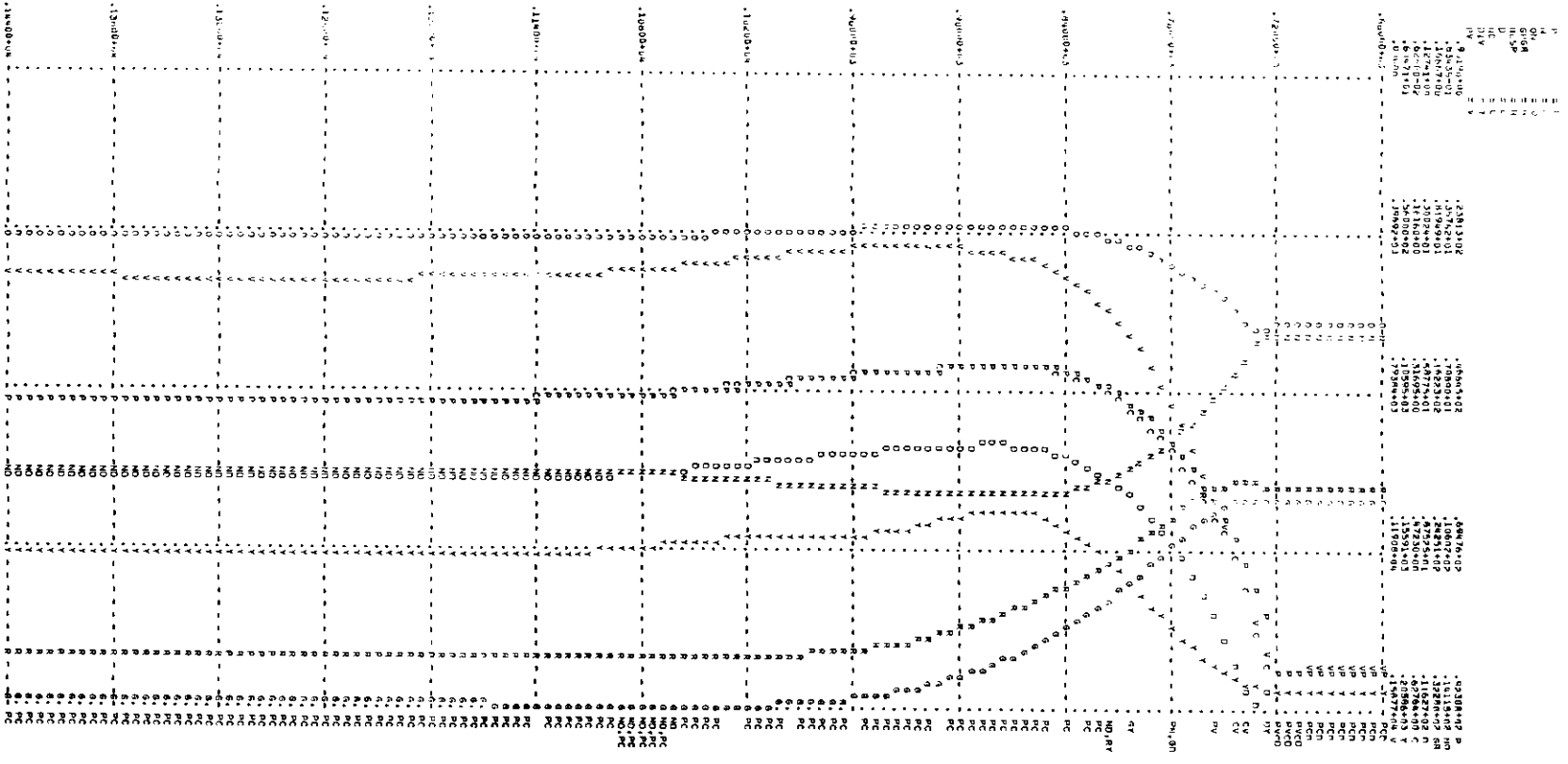

Figure 32. Response to Sustained Partial Destruction of Standing Crop

biomass. The reduction of standing crop under grazing is then followed by declines in vigor and diversity. The vigor of plants decreases because now they must spend a greater proportion of energy flow on production work. Diversity also suffers after a few years of continuous grazing because some of the species on the range are driven away (as postulated in Figure 17) by the reduced supply of food, increased competition pressures, the cattle's preference for palatable grasses, etc., and also because the various activities of the domestic animals may force vacancy of some of the niches in the grassland (refer to Figures 15 and 16).

It is also interesting to observe the patterns of organic and inorganic nutrients which arise in the simulation run of Figure 32. In parallel with the pattern of standing crop, the accumulation of organic debris first increases a bit, then decreases toward a new equilibrium level. The pattern of decomposers reflects of course the pattern of organic matter available for decomposition; they increase when it increases, decrease when it decreases. The quantity of inorganic nutrients in the soil, on the other hand, increases to a new level which is higher than the climax level previously attained in the absence of the exogenous grazing stress. This is a consequence of the closed nature of the model and the law of conservation of matter, i.e., since the system is closed, all nutrients in plant matter eaten away by either wild or domestic consumers are recycled. As the size of the standing crop declines, more inorganic nutrients are left unused in the soil, and thus the reservoir of nutrients accumulates to a higher level, as shown in

Figure 32. The implications of this assumption, as well as the result of an alternative assumption on the dispostion of nutrients contained in harvested grasses, are discussed later in this section.

Let us consider now the simulation of Figure 33, which shows the outcome of simultaneously applying a sustained stress on standing crop and community diversity. More specifically, exogenous step perturbations were applied to both plant depletion rate and diversity decrease rate (PDR and DDR in the appendix, respectively). This joint perturbation amounts to both introducing the cows and shooting the wolves, so to speak, and to keep doing so on a continuous basis, presumably in an attempt to keep undesirable species out of the range. As soon as the joint perturbation is applied, biomass and diversity start declining. However, as diversity continues to be destroyed, the resulting surplus of energy flow generates a dramatic increase in net production, and after two or three years the standing crop "bounces back" toward its climax level. The levels of wild consumers and decomposers, as well as the levels of organic and inorganic nutrients, follow the oscillations of standing crop. Artificial elimination of some species, however, has consequences which go beyond those species simply vanishing from the range. It also results in the species substitution mechanism (see Figure 14) of the ecosystem being activated, and after a few years other species (presumably resistant to the perturbation technology being used) gradually start arriving to take their place. After about five years the new upsurge of diversification forces a decline in productivity, and both plant biomass and plant vigor start again on a downward pattern.

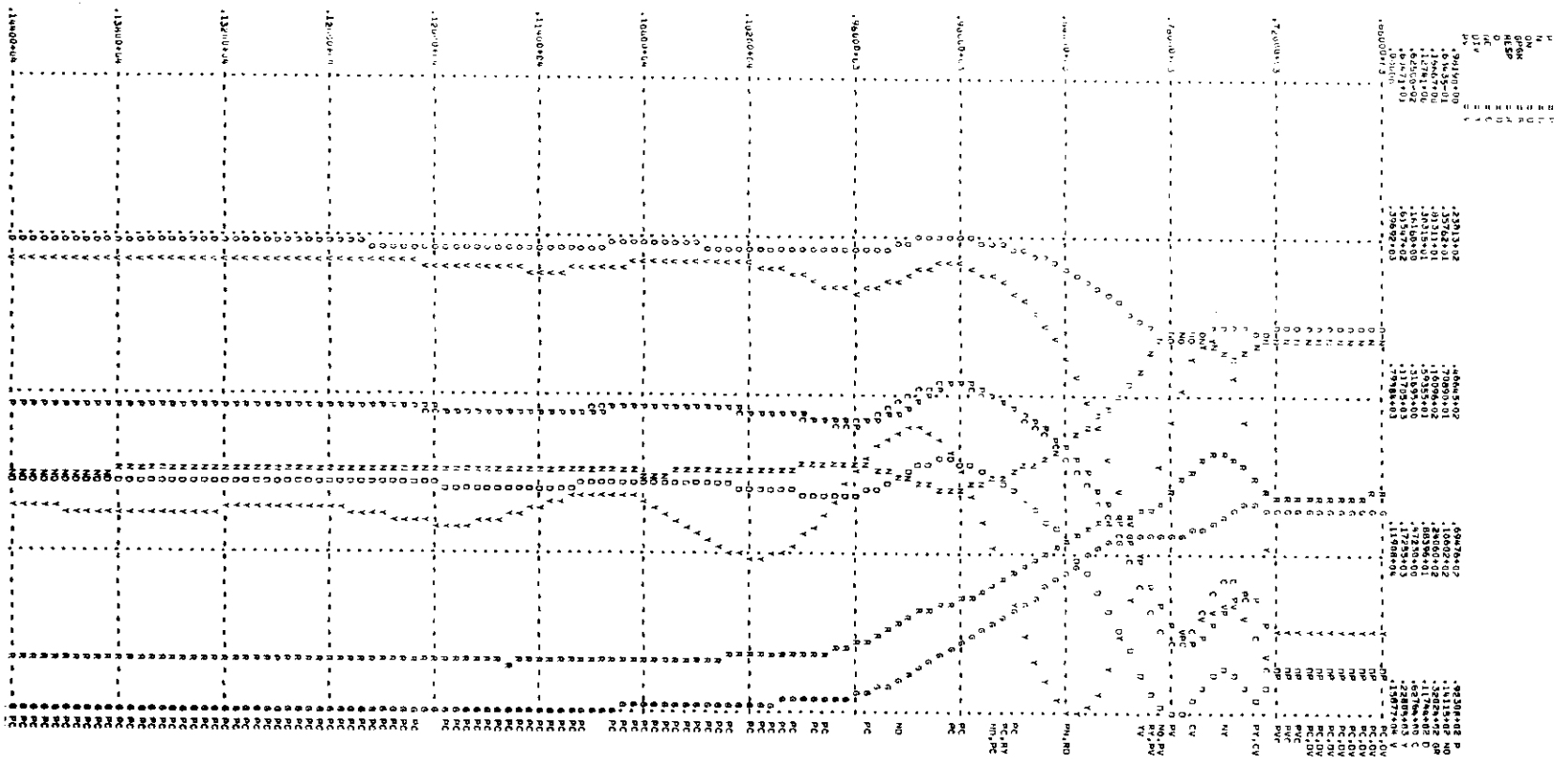

Figure 33. Response to Sustained Partial Destruction of Standing Crop and Species Diversity

From that point on, they both decrease with damped oscillations toward lower steady state levels while interacting with oscillations in species diversity. The latter arise here for the same reasons as in the simulation of Figure 31. After several decades of continuous stress, standing crop approaches the same lower level in Figure 33 as it did in Figure 32, while diversity and vigor approach even lower levels of equilibrium. Thus, it is evident that destroying diversity in order to enhance the ability of the plant community to bounce back (production wise) in the short-run is, at best, ineffective in the long-run, and it may be that it actually causes more harm than good to the ecosystem. The more resistant species which replace the original ones may or may not be as desirable, but such a consideration is clearly beyond the scope of the model.

As pointed out before, another aspect of the model which is clearly oversimplified is the supply of nutrients. In the simulations of Figures 32 and 33, as in those of the previous chapter, it is assumed that all nutrients contained in grasses eaten by either natural or domestic consumers are conserved. As long as nutrients are conserved while they flow around the nutrient cycling loop (recall the lower loop of Figure 3) the accumulation of nutrients in the soil depends on the level of the standing crop. The higher the proportion of nutrients in biotic form, the lower the proportion of nutrients remaining in abiotic form in the soil, and vice versa; thus the trends of O and N observed in the simulations. Actually, nutrients contained in plant biomass consumed by domestic animals may or may not be returned to the soil of the range.

Figure 34 displays the effect of assuming that they are not returned. It shows the response to a sustained grazing pressure of light intensity, but assuming that all plant material which is eaten by the livestock, and therefore the nutrients contained therein, exit the system. The effect of assuming this net loss of nutrients is reflected in the trend of N, the concentration of inorganic nutrients in the soil. In less than 40 years, nutrients become limiting and the standing crop begins to decline from the level otherwise sustainable under this intensity of continuous grazing. After 60 years, the grazing stress is removed. However, since the reserve of nutrients in the ecosystem has been exhausted without replenishment, new growth is suppressed and the standing crop never recuperates. What actually happens is of course somewhere in between the two extreme assumptions of either total conservation or total loss of nutrients under utilization conditions. There may also be net gains of nutrients coming into the ecosystem in diverse forms from external sources. This bring the discussion, however, to open-loop considerations which are outside the scope of the present research. Therefore, while bearing in mind the limitations involved, the rest of the simulations reported in this chapter were again conducted assuming the grassland ecosystem to be completely closed or, equivalently, that it receives from external sources as much nutrients as are extracted from it through grazing.

The simulation results under consideration reflect the influence of grazing on grassland succession inasmuch as grazing activates some of the feedback mechanisms coupling the variables included in the dynamic

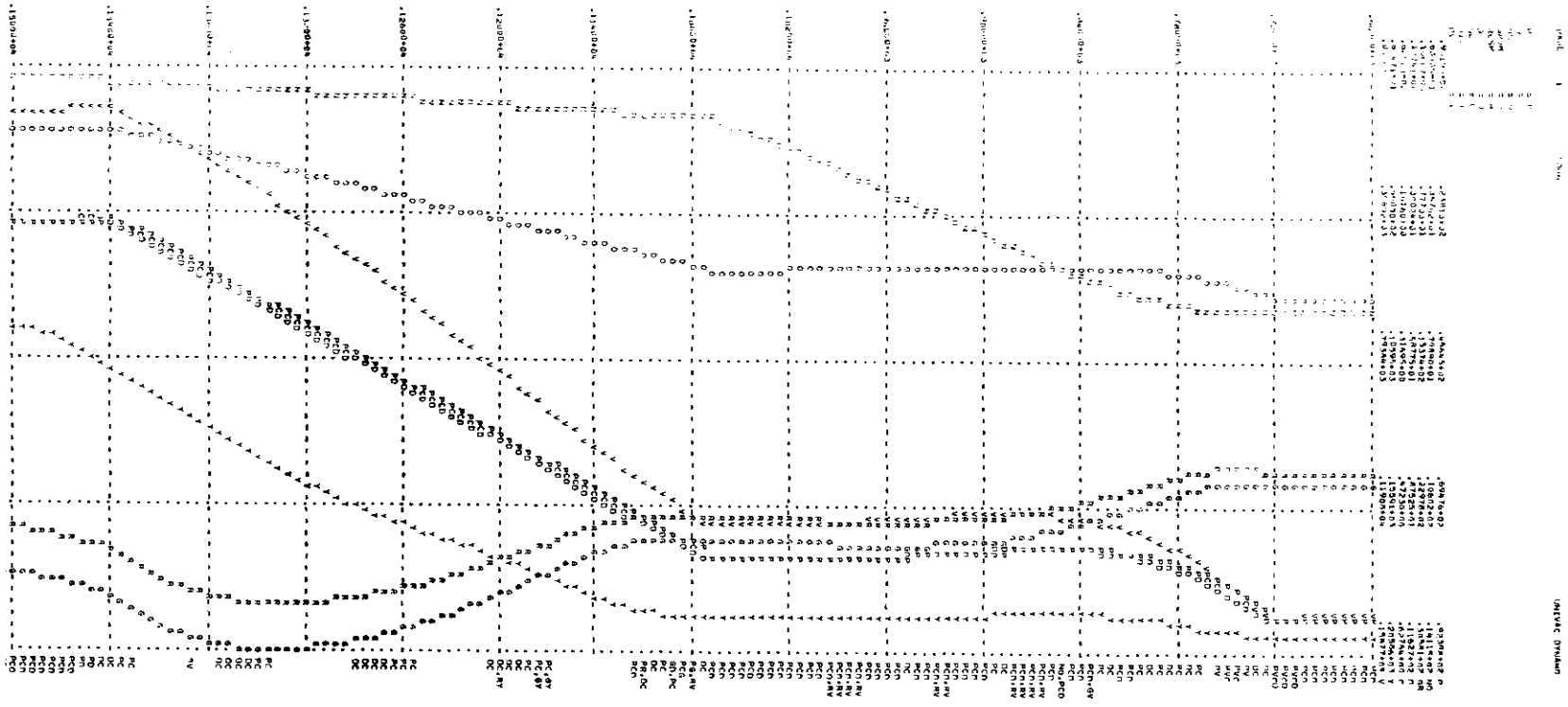

Figure 34. Response to Sustained Harvesting of the Standing Crop with Net Loss of Nutrients

hypothesis. It is by no means claimed that the present model accounts for the full spectrum of effects which grazing brings about. In addition to reducing the volume of herbage and therefore the area of photosynthetic surface, grazing animals may exert influence on the range by trampling, fertilizing the soil, disseminating plant seeds, shifting the species composition of plants, etc. According to Ellison (1960) whether these effects are actually beneficial or detrimental for the grassland is a matter for which conclusive experimental evidence is lacking. Thus, it appears that as long as denudation does not result in soil erosion, which is irreversible and clearly not a successional phenomenon, the overall response to grazing is toward less vegetation with less diversity and vigor, and with the intensity of the successional transient being roughly proportional to grazing intensity. Ellison (1960) also points out, however, that "unless soil erosion is very active, denudation of vegetation is followed by an orderly succession," and Dyksterhius (1958) reports that secondary succession is the dominant force underlying range dynamics, although successional patterns in the field may be obscured in time and space by climatic and edaphic factors of the physical environment, and their complex interactions and gradients. On this basis, it appears reasonable to conclude then that the successional patterns of Figure 32 are the dominant response to sustained grazing, other effects being "lost in the blur" so to speak. In Figure 35, a constant grazing pressure was exogenously applied as before, and the simulation was extended to include the successional recovery of the range when the continuous grazing stress is removed after 60 years; indeed (since any

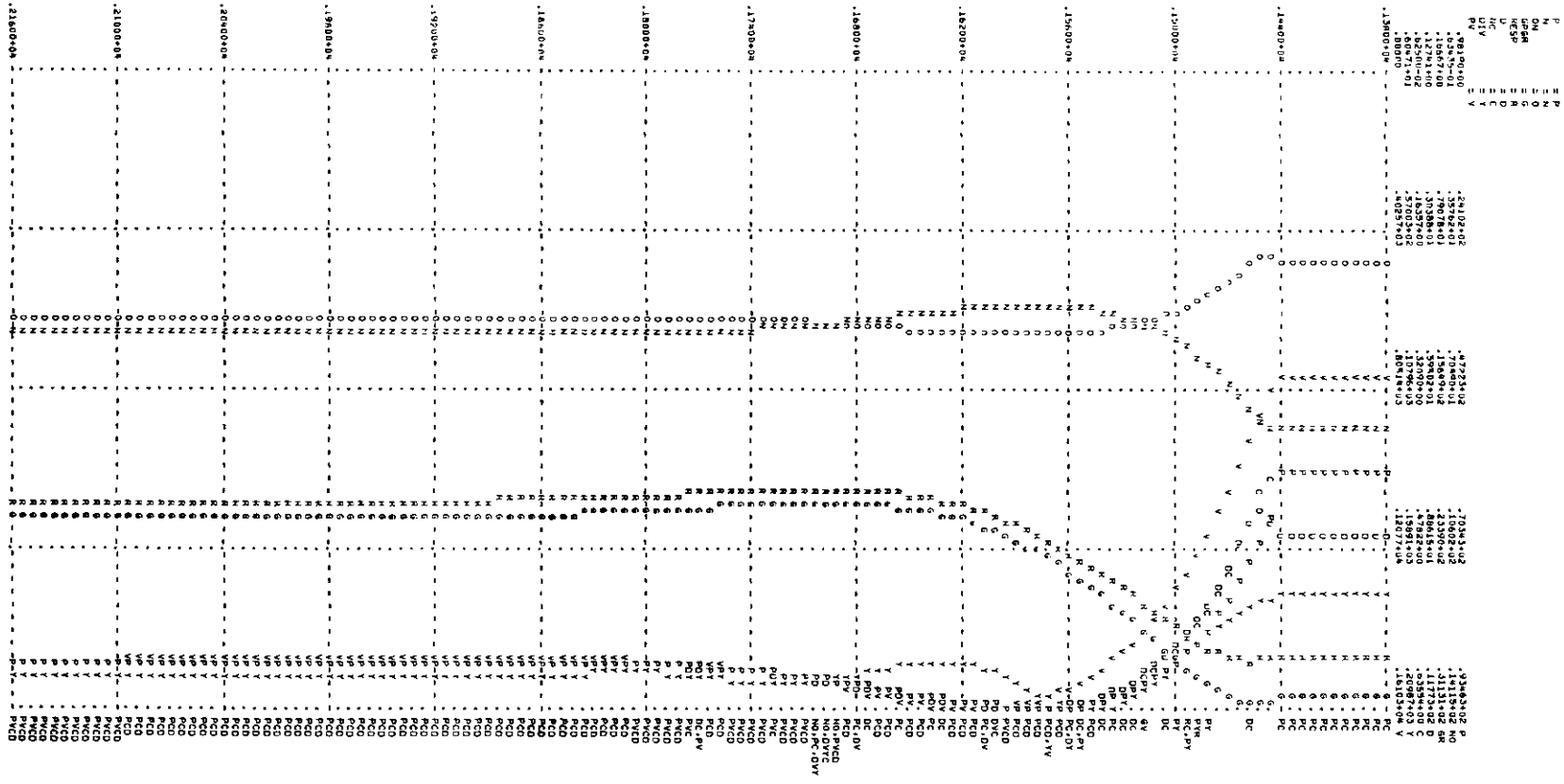

Figure 35. Successional Dynamics After an Extended Period of Grazing Pressure

consideration of soil erosion is absent from the model) orderly succession gradually brings the ecosystem back to climax condition.

Response to Alternative Stocking Policies

What are the implications of successional dynamics for range management? Needless to say, range preservation is an important consideration in the design of grazing policies, but not the only one. Grasses are the crop of the grassland, but they go to the market in the form of meat and other dairy products. As pointed out in the first chapter, grazing policy design must taken into account both the successional dynamics of the grassland and the market dynamics associated with the commodity being produced. Let us restrict our attention here to grazing for meat production. The stockman has to be concerned with grass production inasmuch as it influences livestock gain, with preservation of the range resource, and with the dynamics of the economic system in which he operates. His objective is presumably to maximize profits. As he pursues this basic objective and adapts to pressures from the marketplace, he may or may not be looking for maximum grass and/or meat production. Economic considerations are outside the scope of the present work, however, and the following discussion will elaborate on the successional-dynamic aspect only, assuming the more simplistic objective of obtaining maximum yield consistent with range preservation.

Assuming that what really matters to the stockman is yield in the form of livestock gain, the problem is to determine what grazing system will extract the maximum of such gain from a particular pasture while preserving (or even improving) range condition. The key words here are

"livestock gain," "range condition" and "grazing system." It is desirable to delve a bit on the meaning of these terms; then we shall be able to discern to what extent the model accounts for the factors involved and therefore to what extent it is relevant not only to range ecology, but also to range management.

All other things (e.g., grass palatability, nutritive value, etc.) being equal, it is evident that "livestock gain" depends on the abundance of herbage available for consumption, and it would seem that maximum yield should follow from maximum grass production. Actually, yield will depend on both the total amount of grass production and the efficiency of its utilization, the latter being defined as the proportion of herbage that is actually harvested by the animals. The matter of assessing utilization efficiency is by no means straightforward. Spedding (1971) points out that the amount of grass production which is harvested is a quantity which can be measured directly and otherwise presents no problems. Grass production, however, gives only the absolute level of utilization and must be supplemented by some indicator of utilization efficiency. He proposes the following ratios as indicators of utilization efficiency:

$$\frac{\text{amount harvested}}{\text{amount present at the beginning of the harvesting period}} \qquad \text{(A)}$$

$$\frac{\text{total amount harvested}}{\text{total actually grown over a period of time}} \qquad \text{(B)}$$

$$\frac{\text{total amount harvested}}{\text{potential growth}} \qquad \text{(C)}$$

Spedding's point is that both the level and the efficiency of utilization must be evaluated over time. Ratio (A) assesses utilization by a harvesting method (i.e., grazing by a given mix of animals at a given stocking density) on one harvesting period. It is simply the proportion of grass commodity present at one point in time which is actually harvested by the animals. Ratios (B) and (C), on the other hand, assess utilization by a harvesting pattern (i.e., a given sequence of frequency and severity in the application of a given harvesting method) over time in terms of actual and potential grass production, respectively. After discussing the relative merits and demerits of (A), (B), and (C) as indicators of utilization efficiency, Spedding concludes:

> It seems obvious that what is required for agricultural purposes is both efficient utilization in sense (A), and very high crop production. Thus (C) would appear to be the most useful expression. To some extent this is so, and it is legitimate to ask at what percentage values for (A) and (B) is (C) maximized for different animals, pastures, and harvesting patterns.

It is clear then, that in order to be of value for range management, a dynamic model should account for the behavior that the ratios (A), (B) and (C) exhibit in response to alternative stocking policies. In particular, it should account for range condition, as implied by the denominator of (C), the utilization efficiency in terms of growth potential. While livestock gain may be the primary short-term consideration, in the long-run it is also necessary to pay attention to the condition of the range.

Clawson et al. (1960) review the concept of "range condition" as ". . . an attempt to estimate the productive potential of each range site, and then to rate the present condition of the range in relation to that potential." While it is true that the productive potential of a range depends to a certain extent upon external factors such as precipitation and temperature, it will be shown that its stage of successional development is the principal determinant. Indeed, range condition is a dynamic concept. A given range is generally improving or deteriorating in response to the grazing policies being applied. Thus, it becomes necessary to measure range condition in a reliable manner. As pointed out by Clawson et al., there are many factors to be taken into account when assessing range condition, but the following are particularly significant: density of plant cover, its species composition, the vigor of individual plants, accumulations of plant litter, and soil stability. According to Dyksterhuis (1949) species composition provides the most reliable indicator of range condition. Our model is not of much help here, however, because although it takes diversity into account, it does not take explicitly into account the relative proportion of decreasers, increasers and invaders in the plant community. The matter of soil stability (or soil erosion) is also outside the scope of the model. On the other hand, the model does account (albeit in a very aggregated manner) for the other three indicators: density of plant cover, plant vigor, and the accumulation of organic debris. While species composition may in fact be an excellent measure, it is also true that the other indicators contain valuable information on range condition (Dyksterhuis,

1958). Therefore, the model accounts for the dynamics of range conditions inasmuch as it is reflected by the levels of standing crop, plant vigor and organic matter. More importantly, it accounts for the productive potential of the range inasmuch as it is determined by successional processes.

With regard to policy, there are three variables which are essential in the formulation of a "grazing system:" stocking rate, livestock class, and grazing periodicity. According to Steger (1970) range managers attempt to use a stocking rate which fits the range, animals which are right for the forage, and grazing periods keyed to the major plant species. A given stocking rate, or stocking density per unit time, results in a given quantity of forage being harvested per unit time by the livestock. The model is of course testable in this sense, as illustrated in Figures 32 to 35. As shown in these simulations, successional trends of the vegetation are roughly proportional to grazing intensity or, in other words, to stocking rate. What mix of animals is right for a given site is, however, a consideration which is clearly beyond the scope of this model, since standing crop is aggregated as a single accumulation of plant biomass, and it is therefore taken for granted that all forage is grazed uniformly. Whether the model is relevant for consideration of grazing periodicity depends on whether it is intra-year or inter-year grazing periods that matter. The model developed in this research explains the successional dynamics of the range as they unfold from year to year, but without taking into account differences between the seasons of each year. The model would be inadequate, for example, to examine

whether it is better to graze the range before or after seed maturity each year; continuous yearlong grazing is assumed. On the other hand, the model provides insight on the interplay between stocking cycles and secondary succession. The effect of grazing intensities associated with alternative stocking rates was discussed in the previous section. Assuming a fixed stocking rate and the right kind of livestock, let us consider now the interplay between stocking cycles and secondary succession, and how secondary succession can be manipulated to maximize grassland yield in the long run.

What is the best successional stage for grazing? Figures 36, 37 and 38 exhibit the successional trends associated with 10-, 20- and 30-year stocking cycles, respectively. This means that the range was assumed to be continuously grazed, then continuously rested in successive periods of 5, 10, and 15 years, respectively, each cycle being composed of a period of uninterrupted grazing followed by a period of uninterrupted recovery. The simulations were accomplished by turning on and off the exogenous step perturbations on plant depletion rate of the indicated intervals. Let us consider the effect of these harvesting patterns from the viewpoint of grass production and utilization efficiency.

Under the 10-year stocking cycle policy, livestock is introduced to the range at a time of great net production. On the other hand, when the 20-year grazing cycle is used, livestock is brought in for grazing at the time when the standing crop of grasses is peaking. Deferring grazing over cycles longer than 30 years clearly results in the animals grazing at a time when the grasses are neither generating the highest

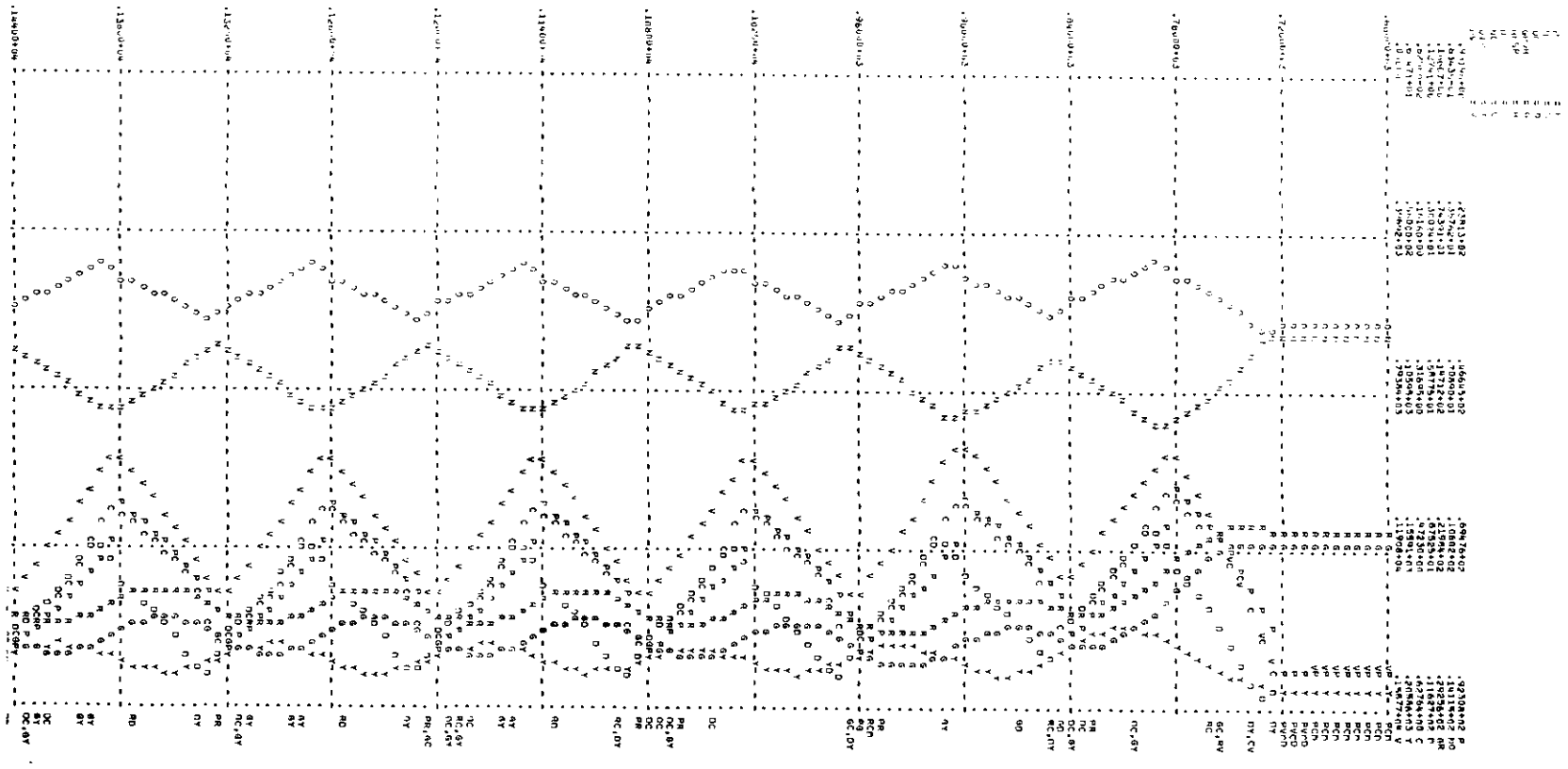

Figure 36. Successional Dynamics Under a 10-Year Stocking Cycle

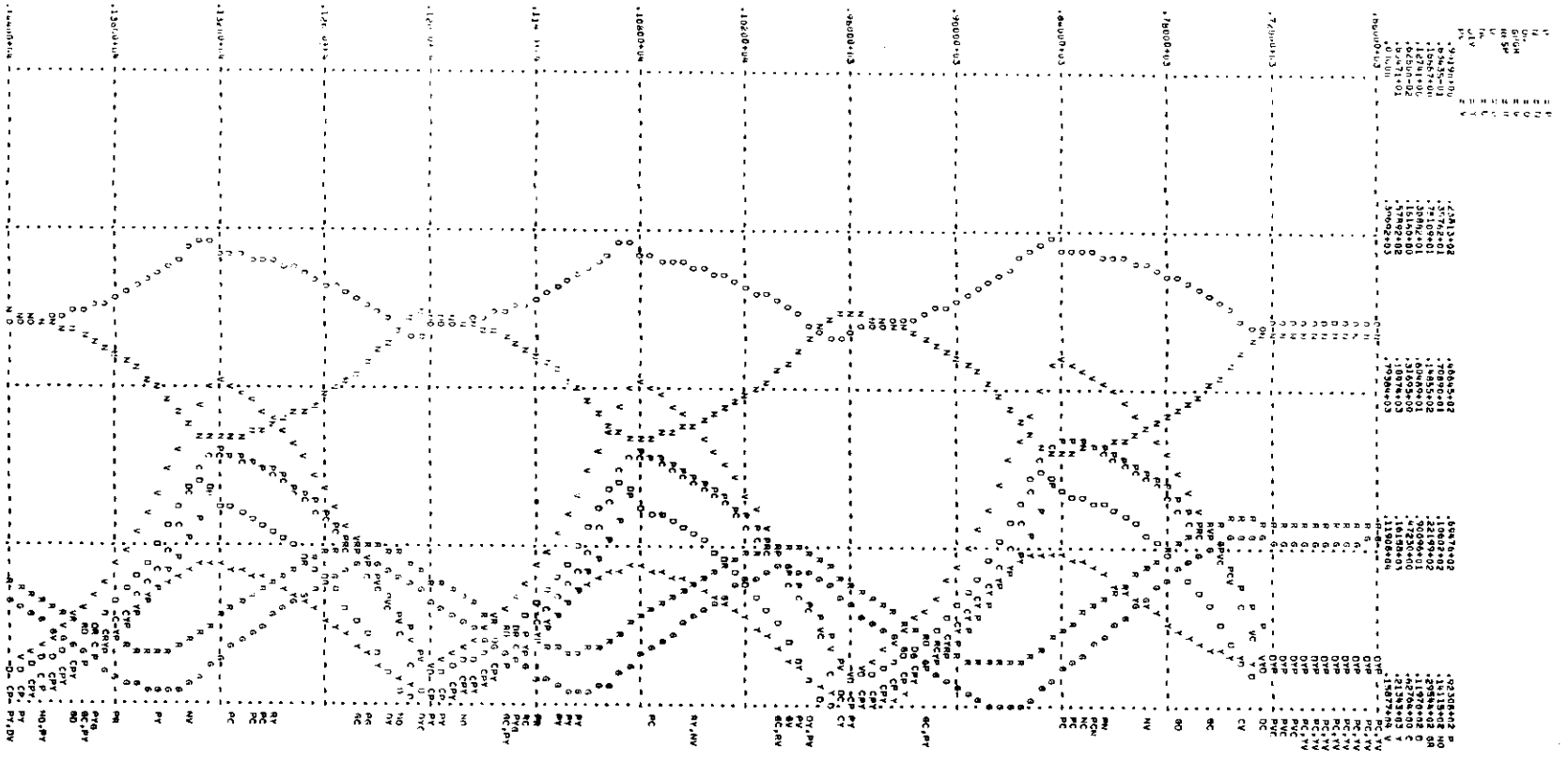

Figure 37. Successional Dynamics Under a 20-Year Stocking Cycle

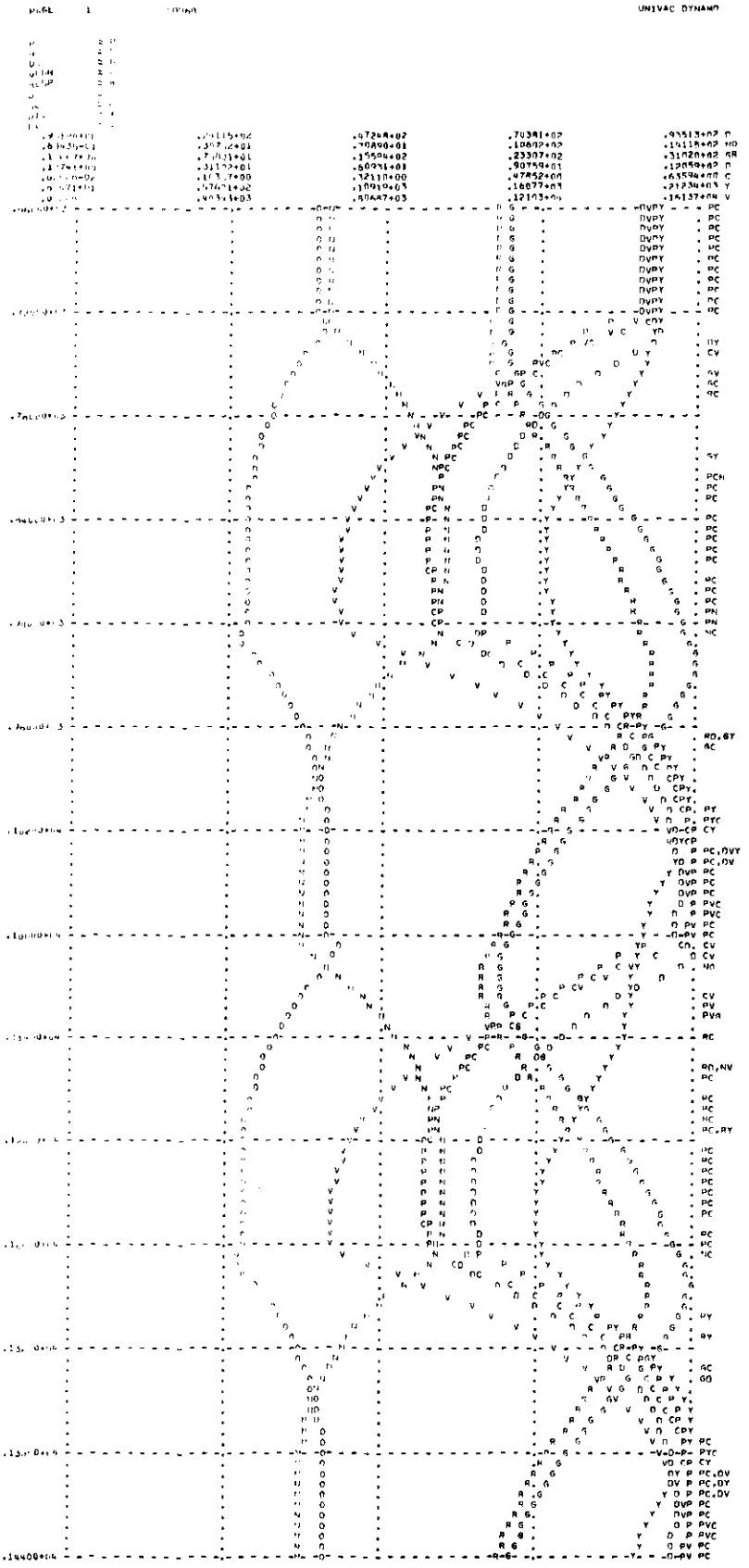

Figure 38. Successional Dynamics Under a 30-Year Stocking Cycle

possible yield nor covering the range in maximum quantity (recall that, after peaking, the standing crop will settle down to a lower climax level); conversely, succession-generated increases in either net production or standing crop would be negligible under grazing cycles shorter than ten years. Thus, on the basis of grass abundance alone, the simulations suggest that a stocking cycle of approximately 20 years is optimal in the sense that, for this stocking density, it sets in motion successional processes which bring the standing crop to the highest possible level at the start of each grazing cycle. Other things being equal, this would be the stocking cycle to use if grass abundance makes grazing easier and results in maximum livestock gain. On the other hand, if maximization of net plant production were to be taken as the decision criterion, the 10-year cycle would seem better. This suggests that analysis and synthesis of grazing patterns in the successional time scale may be a valuable complement to policies formulated under a shorter time resolution. Grazing systems such as seasonal, deferred, rotation, rest rotation, deferred rotation, etc., manipulate the livestock from range to range on the basis of intra-year or, at the most, year to year considerations; thus, rotation grazing dictates that a given range should not be used at the same season every year, rest rotation implies that each range is periodically rested for one full year, etc. Assuming year-long grazing, the simulations suggest that if secondary succession is to be manipulated for increased grass production (and, presumably, increased livestock gain) some sort of multi-year rotation may be desirable whereby a range is continuously grazed during several years, then rested for

several years in order to allow secondary succession to either expand net production or generate a peak standing crop before using it again, depending on what criterion is relevant from the viewpoint of net production. It may be possible to integrate intra-year and inter-year considerations into grazing systems which take both into account.

Let us reexamine the performance patterns of Figures 36 to 38 in the light of the efficiencies (A), (B) and (C). Recall that the numerator of each ratio remains constant throughout each grazing period in the simulations. If this grazing pressure were to be sustained indefinitely, the reader will recall (refer back to Figure 32) that the standing crop would decline gradually, then approach a lower steady-state level. Efficiency (A) is defined as the ratio of the amount harvested over the standing crop of each year, taking one year as the harvesting period. Since the amount harvested remains constant year after year while the standing crop declines, the ratio (A) would indicate that the efficiency of utilization is increasing from year to year as long as the standing crop continues to decline. In Figures 36 and 37, it would continue to increase from year to year during the grazing period of each cycle, implying maximum efficiency in the last year of each period, when the standing crop is lowest. Thus, while the ratio (A) is a relevant measure of efficiency for a given year, it is meaningless for a multi-year planning horizon; a very high level of type (A) efficiency in a given year may render the range useless on the following year and, in cases of extreme defoliation, may induce detrimental effects such as soil erosion. It seems reasonable to assume that on the basis of empirical

considerations, an experienced stockman knows the maximum efficiency of type (A) that he can obtain in a given year without harming the range in any significant way. Accordingly, let us assume that the amount of grass being harvested each year under the stocking rates of Figures 36 to 38 maximizes efficiency in this sense. What about the efficiencies (B) and (C)?

As long as the grazing efficiency of the animals remains invariant, efficiency type (B) provides the same information as efficiency type (A) when computed on a yearly basis. The grazing efficiency of the animals may be affected by changes in crop growth rate and/or changes in species composition and sward structure, but such considerations would fall outside the scope of the present model. Thus, in the present context, (B) becomes meaningful when applied on a multi-year basis. A consideration of (B) and the simulated patterns on a multi-year basis does indicate, for example, that the 30-year grazing cycle is indeed too long. Clearly, the average value of (B) over the grazing cycle decreases due to several peak crops going ungrazed before cattle is brought back into the range. On the other hand, efficiency type (C) once again hints that stocking cycles shorter than 10 years, while increasing utilization efficiency in the sense of (B) may decrease the utilization of crop potential (C) by inhibiting the unfolding of secondary succession. If the total amount of herbage actually grown is less than the total amount that could have been grown, we would suspect that actual livestock gain is also less than could have been obtained. However, since the total amount harvested per year is always the same in the simulations

regardless of the amount grown, it is not possible to arrive at more definitive conclusions. While the simulations indicate a range of stocking cycles (between 10 and 20 years) that should be approximately optimal with respect to both level and efficiency of utilization, more definitive and meaningful conclusions on efficiency will require a closed-loop coupling between standing crop and livestock gain.

Although detailed grazing policy design as such is beyond the scope of the present research, the preceding discussion is indicative of the relevance of successional dynamics to range management. The simulations confirm that secondary succession is the principal process to be taken into account in long-range planning of grazing patterns. While range productivity may be considerably influenced in the short run by variable climatic factors, successional processes are the dominant influence in the long run; thus the potential utility of a model which allows simulated experimentation in the successional time scale and under ideal management conditions. Simplicity and insensitivity are seen as the most attractive attributes of grazing patterns designed on a successional-dynamic basis, the assurance of success in the long-run resting on the fact that, when following a grazing pattern so planned, the stockman would be working with nature, rather than against it. Successional-dynamic design of grazing patterns should result in yield performance insensitive to external disturbances and, at the same time, should provide simple schemes of operation which take into account the dominant factors in the situation so exceedingly complex that trying to take all factors into account would result (if it results in anything) in

recommendations which are difficult or even impossible to apply in practice. On the other hand, long-term grazing guidelines based on successional criteria--basically, that combination of stocking rate and stocking cycle which appears to give the best tradeoff between range yield and range condition--would be simple to follow, leaving short-term considerations to be worked out on an empirical basis. Due to the insensitivity of the design, the actual harvesting patterns which result from short-term adjustments should not differ significantly from the ideal one as far as yield and utilization efficiency are concerned.

These considerations are not to be regarded as a claim that anything but very tentative conclusions can be drawn from simulations of the present model. They merely illustrate the feasibility of designing ecosystem utilization policies on a successional-dynamic basis. Even under the simplistic assumption that maximum sustained yield is desirable, further elaboration of the ecosystem model itself may be necessary to account for the possibility of irreversible deterioration due to soil erosion, changes in the species composition of grasses, and hysteresis effects in the production efficiency curves, among other factors. As pointed out from the outset, mutual causalities between livestock gain and standing crop, and between livestock gain and the economic system into which the cattle are fed, should be taken into account in a realistic design model. Then it will be possible to address the complex issue of designing grazing policies which are both economically and ecologically sound.

Performance Validation of the Dynamic Hypothesis Under Utilization Conditions

The simulation experiments reported in this chapter display range succession dynamics as they arise under the influence of sustained grazing pressure. The model appears to be well behaved under sustained stress. These results, together with the simulations of the previous chapter, provide strong evidence that the dynamic hypothesis of Chapter II does generate the performance patterns associated with secondary succession, be it the result of either transitory or sustained perturbations to the climax grassland.

It must be pointed out that the basis for comparison here is non-quantitative and, for the most part, nonexperimental. Indeed, it would be very difficult to conduct field experiments to study successional trends under ideal management conditions and, in particular, under moderate grazing pressure; most grazing experiments documented in the literature refer to extreme cases of overgrazing and therefore do not constitute a good basis for comparison (Ellison, 1960). Documented descriptions of the effects of grazing as observed in the field (see, e.g., Klipple and Costello, 1960) are very confusing due to the multitude of external factors (climatic and otherwise) which obscure the successional patterns of the range under uncontrolled conditions. Nevertheless, the simulations demonstrate that the dynamic hypothesis is valid in the sense that it provides the feedback structure which generates secondary succession and which, therefore, generates the dominant modes of behavior which in the long run determine the condition of the range and its productive potential. It cannot be overemphasized that this

appears to be the case under any set of circumstances short of irreversible site destruction by overgrazing. To illustrate the point one bit further, consider the simulation of Figure 39, which shows the successional transients which arise under joint natural and man-made perturbations. The simulation was conducted using a 20-year stocking cycle, with stocking density at the same level as in Figure 37. Superimposed to this sustained perturbation, momentary natural perturbations further depleted plant biomass at 15-year intervals. As a result, the neat successional patterns of Figure 37 become somewhat obscured in Figure 39, but they are not destroyed, and they continue to emerge in the long run because they are not produced by the exogenous inputs but by the internal feedback mechanisms of the ecosystem. Superimposing other external sources of variability (e.g., the effect of changes in climatic factors such as temperature, precipitation, etc.) would have the same effect as introducing noise; the dynamic trends of Figure 27 would be further obscured, but the underlying trends would remain invariant as long as the feedback structure of the ecosystem is not altered. Therefore, the dynamic hypothesis appears to be valid on the basis of the performance patterns which it generates endogenously, either in the presence of any set of reasonable exogenous perturbations, or in their absence.

Needless to say, the model does not account for successional effects of grazing (or any other disturbance) whose analysis would require a different level of model aggregation. A good example is the trends which are known to arise in the species composition of grasses when they are grazed; generating these trends would require modeling the plant

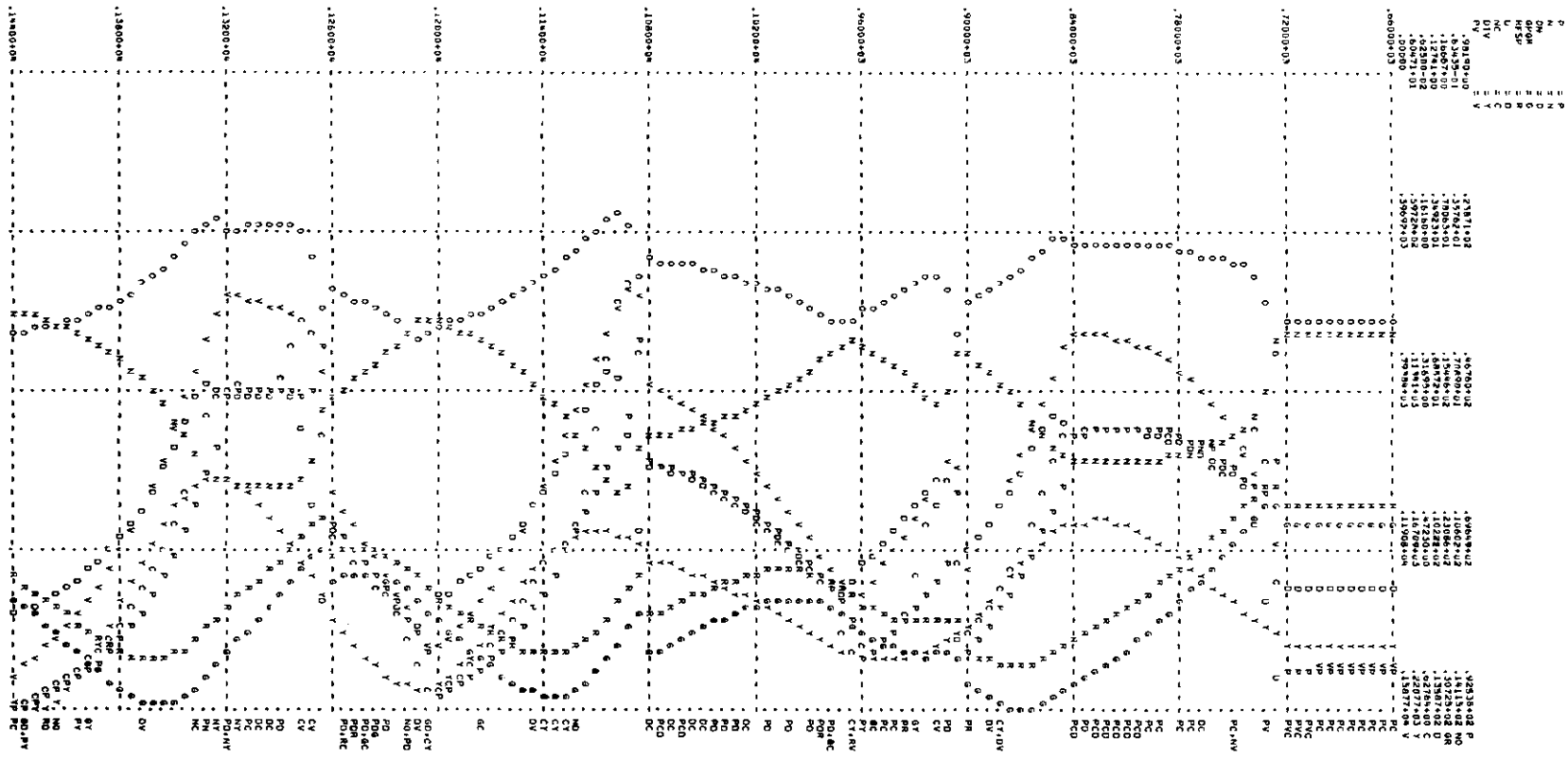

Figure 39. Successional Dynamics Under Both Transitory and Sustained Perturbations

community at a lower level of aggregation, one which decomposes total plant biomass into palatable and unpalatable grasses, for example, and modeling the feedback interaction of these plant compartments with each other and with other sectors of the ecosystem. Therefore, the simulations of this chapter simultaneously confirm the validity of the dynamic hypothesis and point out its limitations. While these limitations are suggestive of further modeling work needed in pursuing better ecosystem design, they in no way invalidate model performance with regard to the immediate research objective as set forth in the first chapter.

CHAPTER V

CONCLUSIONS AND RECOMMENDATIONS

In its early, naive stage, science . . . imagined that we could observe things in themselves, as they would behave in our absence. Naturalists . . . are now beginning to realize that even the most objective of their observations are steeped in the conventions they adopted at the outset . . . so that, when they reach the end of their analyses they cannot tell with any certainty whether the structure they have made is the essence of the matter they are studying or the reflection of their own thought.

-Pierre Teilhard de Chardin
The Phenomenon of Man, 1955

Significance of the Research

It is appropriate to conclude with an assessment of what has been accomplished in this project. In so doing we shall be setting the stage for discussing what is yet to come, for it is hoped that this research does not lead to a dead end but, on the contrary, opens up an important area of research of the application of feedback dynamics to systems ecology.

This research has been concerned with successional dynamics as they arise from the endogenous feedback structure of ecosystems. More specifically, a feedback dynamics model of secondary succession in a grassland ecosystem has been structured, formulated in terms of first- and zero-order difference equations, and tested by means of simulation experiments. The research was motivated by strong evidence that ecological succession must be better understood if harmony between man and

nature is to be established (Odum, 1969). At a time when intensive methods of ecosystem utilization for food production are becoming prohibitive due to short supply and soaring costs of fossil fuels (Pimentel et al., 1973), it is imperative to learn how to make efficient use of ecosystems by extensive methods, i.e., by manipulation of secondary succession processes. The case of a grassland ecosystem used for grazing seemed an excellent place to start due to the availability of some structural and functional data, the fact that grasslands constitute a major source of meat production all over the world, and the fact that they are known to endure and even improve under grazing when the stockman works with the grassland rather than against it. Understanding why and how these desirable behavior patterns arise may lead to better utilization policies for grasslands and, by analogy, for other ecosystems as well.

The basic significance of the research is that it contributes (for the first time) an endogenic theory of secondary succession, i.e., a theory which accounts for secondary succession as generated by the endogenous structure of the ecosystem. It also provides a simulation model to test the theory, and the results of testing the model when quantified with grassland data. The simulations confirm that, within the limitations imposed by the physical environment and other open-loop factors, secondary succession is generated by the closed-loop structure of the ecosystem. They also show that successional *modes* of behavior are insensitive to parametric and exogenous perturbations as long as they are not unrealistically large, and that while climatic factors are

certainly influential on range productivity in the short run, the endogenous feedback structure which is responsible for succession is also responsible for the performance of the range ecosystem in the long run. Indeed, these facts have been observed for a long time, and the resulting conclusions are not new; what is new is the knowledge gained as to what is the structure of the ecological mechanism which generates the observed dynamic patterns and the insights gained about secondary succession as the process to be manipulated in using ecosystems for productive purposes. Needless to say, the model produced by the research is by no means definitive. Let us attempt to qualify the model and the simulations with regard to their validity, generality and utility.

It is felt that strong evidence has been provided on the validity of the dynamic hypothesis. It appears to be valid on the grounds that its structure is consistent with the full range of pertinent ecological knowledge and, furthermore, generates the successional modes of dynamic behavior it is intended to account for. By assuming a closed ecosystem boundary, the hypothesis restricts itself to explain secondary succession inasmuch as it is generated and controlled endogenously by the biotic community. Within this context, however, abundant documentary evidence is given on the adequacy of the feedback loop structure and the relationships coupling levels and rates within each loop. The actual quantification of the simulation model was arbitrary to the extent dictated by availability of data, but this is not a major source of concern in view of the model's insensitivity to parametric variations, at least as far as overall behavior patterns are concerned. The fact that the model is

well behaved under both transitory and sustained exogenous disturbances further confirms the adequacy of the theoretical model. While these considerations increase our confidence in the soundness of the model, they do not, of course, constitute positive proof of its absolute validity. As Box and Jenkins (1970) have stated so well:

> A model is only capable of being "proved" in the biblical sense of being put to the test. As was recommended by Saint Paul in his first epistle to the Thessalonians, what we can do is to "Prove all things: hold fast to that which is good."

Putting the model to the test beyond simulated experimentation is a matter of field research which is clearly beyond the scope of the present work. As it stands, however, the dynamic hypothesis holds fast to well-established ecological knowledge and principles. It results in a parsimonious yet comprehensive model, one which explains successional dynamics in terms of the fundamental ecological variables, i.e., energy, matter, diversity, space and time, albeit that in a restricted sense for each. In other words, the model does not account for all possible implications of each one of these variables, but only those which were found to be indispensable to account for secondary succession. Thus the closed-loop recycling of matter between biotic and abiotic states was accounted for, but without differentiating between different kinds of minerals and assuming the existence of water, soil and air. The open-loop flow of energy was accounted for inasmuch as its allocation to either plant production or other functions influences the unfolding of successional development. Only the variety component of species diversity was considered; while other aspects of diversity are also important,

this component appears to be most directly associated with succession due to its influence on niche specialization. Space is considered in the functional sense only, i.e., in the sense of carrying capacity per unit area of soil surface. This simplification appears to be justified on the basis that while succession takes place in time and space, it is a predominantly time-oriented process. Time is, of course, the independent variable of the model, and the simulations display performance patterns through time which are in complete consonance with actual successional dynamics. In brief, as far as can be ascertained both structural and performancewise, the theory is valid, the model adequate. Model inadequacies will have to be discovered in the context of specific applications suggestive of appropriate modifications, as discussed below under recommendations for systems research.

With regard to generality, the dynamic hypothesis accounts only for secondary succession; primary succession, involving much longer time constants and the formation of soil out of bare rock, is clearly not covered since the existence of soil is taken for granted. In the context of secondary succession, the basic dynamic hypothesis of Figure 3 possesses a high degree of generality, but at the expense of content. In other words, Figure 3 provides a feedback-dynamic theory of secondary succession for ecosystems in general, but none in particular. As more content was added to it, the degree of generality was bound to decline and we ended up with a simulation model of secondary succession in a short-grass prairie ecosystem, one that can be exercised assuming either natural conditions or a single mode of utilization, i.e., grazing.

Subsequent research will have to proceed inductively in order to generalize the model with respect to successional time frame, class of ecosystems, and type of utilization. The theory needs to be extended to account for both primary and secondary succession, and to account for the longer term dynamics that sometimes would make the prairie develop eventually into a forest were it not for grazing and the periodic occurrence of fires. More generally, it needs to be extended to account for the dynamics of senescence, i.e., the dynamics whereby ecosystems sometimes grow, mature, age, and eventually decay, perhaps to start all over again (resulting in a cyclic climax) or to permit the energency of a new ecosystem. The model needs to be extended and/or modified to account for successional dynamics in other grasslands (e.g., tall-grass and mixed prairies), in other terrestrial ecosystems and eventually in aquatic ecosystems, by taking into account the similarities and dissimilarities which exist among them. Finally, the successional response of ecosystems to types of utilization other than grazing must be investigated, as well as the successional response in the most complex situation, that where the ecosystem is subject to multiple modes of utilization. These considerations point out both the limitations of the present model with regard to generality and the long road ahead, but they also stress the significance of this research in that it opens the way toward developing a more general feedback dynamic theory of ecological succession.

To conclude, let us discuss the matter of utility. Innis (1972b) has pointed out that modeling complex biological systems may yield conceptual, developmental and output utilities. Conceptual utility results

from looking at the ecosystem through the framework provided by a given modeling philosophy. Developmental utilities arise during the learning process involved in accomplishing a precisely (if not accurately) formulated model. Finally, output utility is the useful information that exercising the model may produce for persons other than the modeler.

At this time, the only claim we can make with certainty is that both the dynamic hypothesis and the simulation model reported above possess conceptual and developmental utility in a significant degree; whether they really possess output utility or not is something that must wait the test of time. Conceptually, this research has integrated a vast amount of dispersed (and sometimes quite old) descriptive knowledge into a formal feedback structure which shows how all the pieces in the puzzle of Table 1 fit together and mutually interact to generate secondary succession. This conceptual utility is enhanced by the research emphasis on interpreting all these pieces in terms of energy, matter, diversity, space and time as the fundamental ecological variables, which results in a highly parsimonious frame of reference. It goes without saying that the structuring of Figure 3 into a dynamic hypothesis for secondary succession (as in Chapter II) and its subsequent formulation as a precise simulation model (as in the Appendix) was not a straightforward modeling process. A considerable amount of iteration was necessary between hypothesis and model formulation, structural validation and performance validation (refer to Figure 2) before the hypothesis was cast into a model which generates the desired patterns. However, it is

felt that the greatest developmental utility of the model is still to come, and will materialize as seasoned ecologists study the model, find faults with it and, hopefully, improve upon it. Certainly, the model is not ready for use as a self-sufficient planning tool by the range manager. It accounts for closed-loop dynamics only, and this at a very high level of aggregation. It ignores open-loop, short-term considerations which constitute the day-to-day, year-to-year concern of the stockman. Its numerical quantification would have to be empirically worked out in the context of ecosystem-specific applications. Still, it is felt that the output utility of the model is significant in that it forcefully demonstrates that synthesis of long-term grazing policies can and must be pursued on a successional-dynamic basis; this is the way to go if extensive methods of land use are to be developed whereby ecosystems can be productively used without prohibitive expenditures of scarce fossil fuel energy.

Recommendations for Further Research

From the discussion of the previous section, it is not difficult to discover implications for both field and systems research. As anticipated in Figure 2, the results reported herein are based on experimentation in the model world and should be followed up by testing on the field. In turn, such field experimentation may yield new insights indicative of revisions necessary to improve our model of successional dynamics.

The main problem here will be the practical difficulty of conducting field experiments under controlled conditions when the unit of

study is the total ecosystem. It is not feasible to replicate Cooke's laboratory experiments of autotrophic succession (Cooke, 1967) with large-scale heterotrophic ecosystems such as grasslands. If anything, this stresses the necessity for building simulation models as tools for experimentation in this area. The implications for field research here may not lie so much in attempting to conduct the same simulation experiments with an actual grassland, but rather in taking the model as a guide for data requirements. For a given grassland ecosystem, the model indicates the delays, coefficients and complex functional relationships that must be measured (at least to a level of magnitude approximation) for simulation studies of its successional dynamics. Data which are necessary but not available can be collected, but exhaustive collection of floristic data and other data of little relevance to successional dynamics can be avoided by letting the model be the guide in data collection activity. Some of the parameters in the present theory may prove difficult to measure in practice. For example, it may be more convenient to express plant vigor in units other than stored energy per unit area, it may be unfeasible to measure how much energy flow must be allocated to maintain one unit of species diversity in a community, and so forth. Such difficulties lead back to systems research because they would imply the need for revising the model so as to obtain a formulation which is functionally equivalent but expressed in terms of conveniently measurable relationships. The present model stands for examination by grassland ecologists who will determine the data which are already available, those which are not but can be collected, and those which are

impractical to collect and therefore require a reformulation of the theory which avoids the difficulty. In the context of a particular ecosystem, it may be of interest to quantify both the closed-loop model and the open-loop time series of climatic and other exogenous factors which set limits to the successional process; if the latter are then related to the model as exogenous inputs to the appropriate parameters, a very realistic simulation tool may be obtained, one that may serve for both short- and long-term planning.

It is anticipated that, in parallel with field research, the model presented herein will bring about abundant opportunities for systems research. The model itself is suggestive of the possibilities. For example, although the average lifetime of grasses tends to increase in successive stages of secondary succession (Odum, 1959) the present model assumes it to be a constant. What is the lifetime of grasses a function of? Is it a function of factors already included in our closed-loop theory? Is there a mutual causality between successional dynamics and the value of this delay, or is the latter simply the result of the former? Almost any other detail of model structure is subject to further investigation. The nonlinearities of Figures 8, 11, 13, 15, 16, 17 and 19 are a case in point. In particular, the lower ends of the curves in Figures 8 and 19 need verification. If these curves were to rise, peak and then decline within the range of the independent variable, or if hysteresis effects were to be present, these curves could be critical for utilization studies. It also seems desirable to investigate alternative formulations of production efficiency, for instance, by making it

a function of grazing pressure, a function of diversity alone, or a function of other variables which are known to influence plant growth rate. Finally, it seems desirable to investigate alternative ways to incorporate diversity into the feedback loop structure. Is diversity the result of a build-up in vegetation, or rather the result of the accumulation of humus which in turn results from a buildup of vegetation? What about biochemical diversity? Biochemical diversity is very important and may be critical for utilization studies, and there must be a good way of incorporating it as an explicit sector of the diversification loop. As a tool for exploring questions such as these, there is a lot of research mileage left in the present model.

From the viewpoint of applications, it might seem that the main limitation of the present model is that it always will "bounce back" to the original climax after the stress is removed; some ingredient is missing to account for the case where a severe stress eventually results in a permanent disclimax. In a closed-loop context, irreversible deterioration occurs when the gain of one or more of the growth loops are destroyed. This may be the case when resources become limiting; net loss of nutrients without replacement and soil depletion due to erosion are typical examples. Percentage area destroyed may be another variable to include, for the ability of the ecosystem to recover is clearly dependent on the spread of the damage. For certain applications, it may be of interest to explore how much pressure (e.g., how much overgrazing) can be sustained by the grassland without suffering irreversible deterioration. Irreversibility is, of course, a relative matter, depending on

the time horizon under consideration; what appears to be an irreversible situation in the time span of secondary succession may nonetheless be reversible in the context of longer term dynamics. Therein lies perhaps the greatest potential of the model. It is evident that the model can be extended to account for primary succession by introducing a soil formation delay and otherwise adjusting the time constants appropriately. It should be possible also to extend the model as necessary to account for the dynamics of senescence and explain how and why "development at the ecosystem level differs from development at the individual level in that aging and death do not inevitably follow achievement of maturity, as is the case in the individual organism" (Odum, 1972). It may be possible to accomplish this at least in part by developing the ecosystem-level analogue of a recently proposed theory which suggests that "cell and tissue aging is the result of transitions from cycling to noncycling cells" (Gelfant & Smith, 1972). Fossilization, for example, may result in gradually inhibiting the cycling of nutrients to a point where they become limiting and suppress not only new growth, but also replacement growth. Other complex factors may be involved, so this is an area where much remains to be done modeling wise.

As implied at the end of the previous section, another important area of followup research will consist of developing the many possible generalizations with respect to type of ecosystem, type of utilization, or both. Similarities and dissimilarities among them will have to be sorted out in examining specific ecosystems subject to specific modes of exploitation. For example, it is known that grasslands differ in their

response to heavy grazing depending on whether it is a short-grass, tall-grass, or mixed prairie which is being grazed. While the response of the short-grass prairie is a shift in the proportion of above and below ground plant biomass toward more of the latter, the response of the tall-grass and mixed prairies is reflected on the species composition of grasses (Coleman et al., 1973). Thus, accounting for these grazing effects in the model would dictate breaking down the level of plant biomass into (say) above ground/below ground biomass or palatable/unpalatable grasses, respectively. Extensions to other terrestrial ecosystems, and eventually to aquatic ecosystems, will be a greater challenge which may require more fundamental generalizations of the feedback structure. In the tropical rain forest, for instance, the vegetation is dense enough to become a significant factor in determining its own microclimate, which in turn affects its growth machinery (Watt, 1973); thus while climate may still interact in open-loop fashion with a forest ecosystem, it may be necessary to include microclimate as an integral element of its closed-loop structure. Generalizations to account for successional response to different modes of utilization are even more important, for they bear directly on the issue of human development. A lot remains to be done and the complexity involved appears overwhelming, but this research has made visible a way of dealing with it and achieving a better understanding of the ecosystems we are seeking to save, and effectively utilize.

APPENDIX

MODEL FORMULATION

Preliminaries

The model on ecological succession hypothesized in the second chapter of this thesis is, indeed, a provisional one. In this appendix, the dynamic hypothesis of Chapter II is cast into concise mathematical formal and numerically quantified in order to (i) permit its testing by means of simulation experiments, and (ii) provide the means for it to be fully exploited and/or easily revised as time or fuller knowledge allows.

The simulation model was formulated in consonance with the notation and conventions of the DYNAMO (DYNAmic MOdels) language (Pugh, 1963). DYNAMO is a special purpose compiler that was developed for the digital simulation of industrial dynamics models, and is well established as the standard simulation technique in the field (Forrester, 1968).

According to the methodology outlined in Chapter II, dynamic models are formulated in terms of algebraic and first-order difference equations. Corresponding to these, DYNAMO programs are written in terms of rate and level equations. Rate equations can have any appropriate algebraic form. In the present context, they quantify the flow processes in the ecosystem. Level equations, on the other hand, account for accumulations (of information, biomass, nutrients, etc.) within the ecosystem, and they have the form

$$LEVEL.K = LEVEL.J+(DT)(INR.JK-OUTR.JK) \quad (1)$$

where LEVEL.K = Value of LEVEL at time K.

LEVEL.J = Value of LEVEL at time J.

DT = Delta time (solution interval).

INR.JK = Input rate during time interval JK.

OUTR.JK = Output rate during time interval JK.

A graphical explanation of the time notation used in DYNAMO is given in Figure 40.

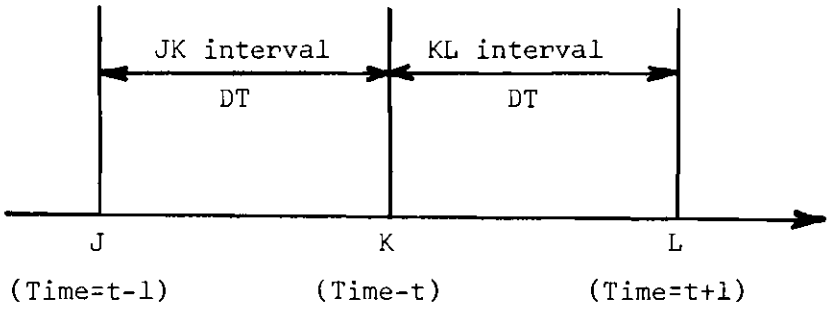

Figure 40. Time Notation Used in DYNAMO

The main purpose of the time notation is to guide the formulation of equations in such a way that they are compatible with the procedure followed by the computer in calculating all equations at each iteration. Thus, during the simulation runs, levels will be computed at each point in time, say for example time t = K, based on the previous values of the levels at time t = J and the values of the rates during the interval JK. This is, of course, a discrete-time approximation of

$$\text{LEVEL} = \text{LEVEL}_{t=o} + \int_{o}^{t} \{\text{INR}(t)-\text{OUTR}(t)\}dt \qquad (2)$$

i.e., the theoretical formulation of levels in dynamic models when using an integral equation formulation. In that the formulation of the rates may involve complex interactions between two or more levels, auxiliary equations are sometimes used as intermediate analytical steps in computing levels and rates. At each iteration, then, the order of computation is first levels, then auxiliaries, and finally rates. In addition to levels and rates, DYNAMO programs include supplementary, constant and initial-value equations. Supplementary equations are used for ancillary computations related to printing and plotting of the results, but otherwise have no impact on the logic of the model. Constant and initial-value equations are convenient means for the numerical quantification of the model. DYNAMO also offers a number of special functions which are convenient for model building and/or simulated experimentation, such as step and ramp functions; maximum, minimum and switching functions; table functions, etc. For further details on these and other features of the DYNAMO package, the reader is referred to the DYNAMO Users Manual (Pugh, 1963).

The following section documents the DYNAMO model that was employed to test the dynamic hypothesis of Chapter II, equation by equation. Standard DYNAMO notation and flow diagramming conventions (as in Forrester, 1961) will be adhered to. Justification for the closed ecosystem boundary, the feedback loops included, the levels and rates included in each loop, and the main nonlinearities involved, follows from the dynamic

hypothesis. Two tasks remain for the hypothesis to become testable by simulated experimentation: casting each relationship into precise mathematical format, and quantifying each relationship by means of appropriate numerical values. With regard to the former, the approach will be to use the simplest plausible mathematical formalization for each relationship, e.g., as a linear function unless ecological considerations clearly dictate a nonlinear one. With regard to numerical valuation of model parameters, data from the Pawnee grassland ecosystem in northeastern Colorado were used. The major data sources used were Bledsoe et al. (1971) and Patten (in preparation). Other sources of representative data and (as a last resort) tentative guesses were used to valuable parameters not covered in these major sources. The basis for each analytical and numerical assumption is given in this appendix; implications on model performance are discussed in Chapters III and IV.

The Simulation Model

Figure 41 exhibits a flow diagram of the DYNAMO simulation model constructed for the research. As customary in DYNAMO flow diagrams, rectangles, valves, and circles represent levels, rates and auxiliary functions, respectively; solid lines represent physical flows (of biomass, nutrients, etc.) and dashed lines represent flows of information. The equations for each element of the diagram, as well as the nominal numerical values for initial conditions and model parameters, are listed in Table 2. The discussion that follows attempts to establish the ecological basis for each detail of the model. As the discussion unfolds, the reader may wish to refer back concurrently to the influence diagrams

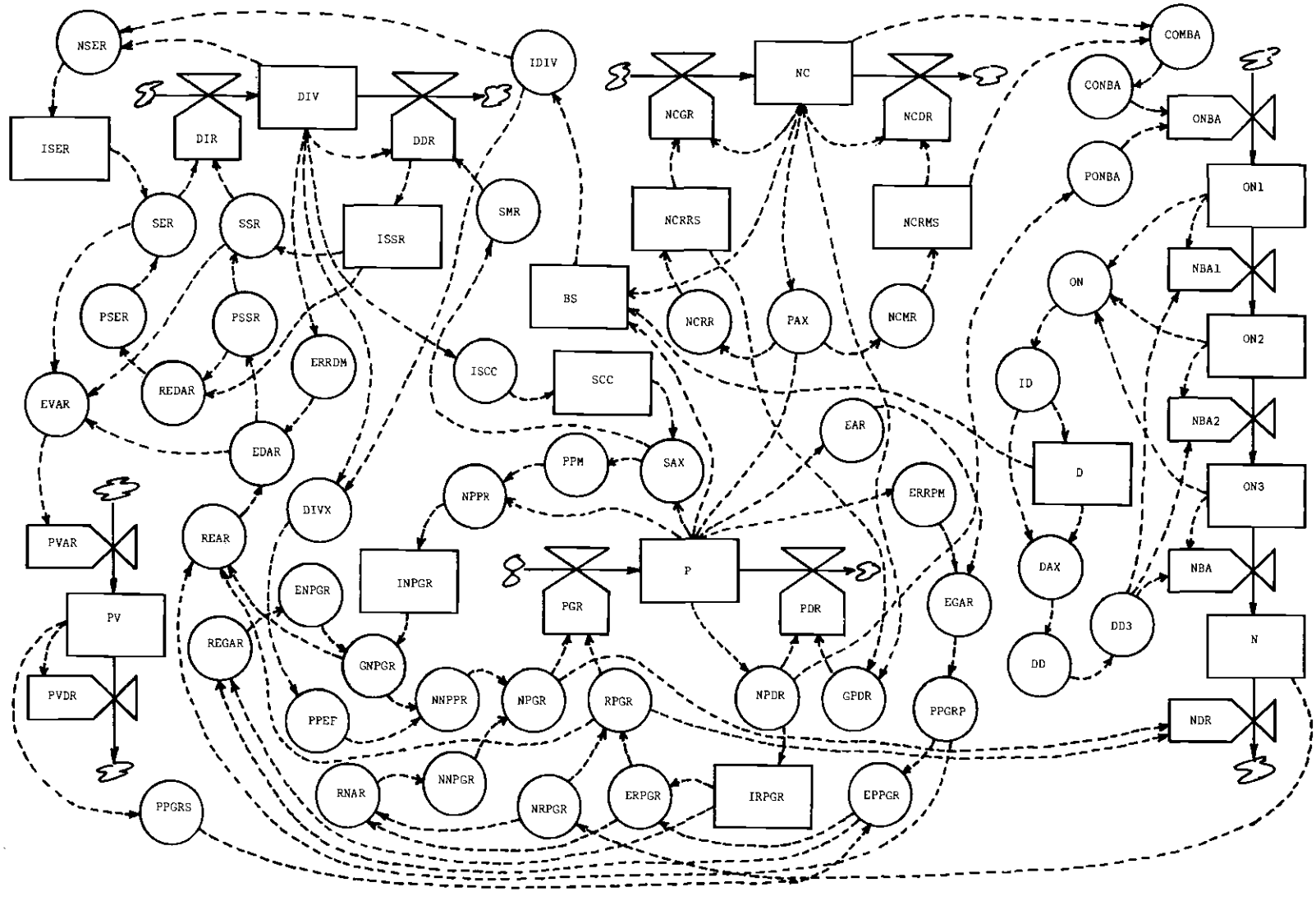

Figure 41. Flow Diagram of DYNAMO Simulation Model.

Table 2. Program Listing of DYNAMO Simulation Model

```
NOTE  SUCCESSIONAL DYNAMICS (TROPHIC LEVELS,DIVERSITY,ENERGETICS)
NOTE
1L    P.K=P.J+(DT)(PGR.JK-PDR.JK)
1L    ON1.K=ON1.J+(DT)(ONBA.JK-NBA1.JK)
1L    ON2.K=ON2.J+(DT)(NBA1.JK-NBA2.JK)
1L    ON3.K=ON3.J+(DT)(NBA2.JK-NBA.JK)
1L    N.K=N.J+(DT)(NBA.JK-NDR.JK)
3L    IRPGR.K=IRPGR.J+(DT)(1/PDRSD)(NPDR.J-IRPGR.J)
3L    INPGR.K=INPGR.J+(DT)(1/INGAD)(NPPR.J-INPGR.J)
3L    D.K=D.J+(DT)(1/DRD)(ID.J-D.J)
1L    NC.K=NC.J+(DT)(NCGR.JK-NCDR.JK)
3L    NCRRS.K=NCRRS.J+(DT)(1/NCRD)(NCRR.J-NCRRS.J)
3L    NCMRS.K=NCMRS.J+(DT)(1/NCRD)(NCMR.J-NCMRS.J)
3L    ISSR.K=ISSR.J+(DT)(1/SSD)(DDR.JK-ISSR.J)
3L    ISER.K=ISER.J+(DT)(1/ISEAD)(NSER.J-ISER.J)
1L    DIV.K=DIV.J+(DT)(DIR.JK-DDR.JK)
3L    SCC.K=SCC.J+(DT)(1/SCCAD)(ISCC.J-SCC.J)
4L    BS.K=BS.J+(DT)(1/BSD)(P.J+NC.J+D.J-BS.J+0+0)
1L    PV.K=PV.J+(DT)(PVAR.JK-PVDR.JK)
NOTE
58A   PPEF.K=TABHL(PPET,DIVX.K,0,1,0.1)
20A   DIVX.K=DIV.K/IDIV.K
20A   SAX.K=P.K/SCC.K
58A   PPM.K=TABHL(PPMT,SAX.K,0,1,0.1)
20A   DD3.K=DD.K/3
14A   DD.K=DDMIN+(DDS)(DAX.K)
20A   DAX.K=ID.K/D.K
20A   ID.K=ON.K/ONDRC
58A   NCRR.K=TABHL(NCRT,PAX.K,0,2,0.2)
58A   NCMR.K=TABHL(NCMT,PAX.K,0,2,0.2)
42A   PAX.K=P.K/((PNCRC)(NC.K))
20A   NPDR.K=P.K/PDD
13A   GPDR.K=(NC.K)(NCRRS.K)(NCPRC)
44A   PONBA.K=(P.K)(NPRC)/PDD
13A   CONBA.K=(COMBA.K)(NCPRC)(NPRC)
12A   COMBA.K=(NC.K)(NCMRS.K)
8A    ON.K=ON1.K+ON2.K+ON3.K
58A   IDIV.K=TABHL(DIVT,BS.K,0,100,10)
12A   SMR.K=(SMRN)(PPM.K)
58A   ISCC.K=TABHL(SCCT,DIV.K,0,100,10)
```

```
54A     SSR.K=MIN(PSSR.K,ISSR.K)
7A      REDAR.K=PSSR.K-ISSR.K
56A     PSER.K=MAX(0,REDAR.K)
54A     SER.K=MIN(ISER.K,PSER.K)
7A      APGR.K=NPGR.K+RPGR.K
54A     RPGR.K=MIN(NRPGR.K,ERPGR.K)
42A     NRPGR.K=N.K/((NPRC)(NAD))
54A     ERPGR.K=MIN(IRPGR.K,EPPGR.K)
7A      EPPGR.K=PPGRP.K+PPGRS.K
7A      RNAR.K=NRPGR.K-ERPGR.K
7A      REGAR.K=EPPGR.K-IRPGR.K
54A     NPGR.K=MIN(NNPGR.K,NNPPR.K)
56A     NNPGR.K=MAX(0,RNAR.K)
12A     NNPPR.K=(PPEF.K)(GNPGR.K)
54A     GNPGR.K=MIN(INPGR.K,ENPGR.K)
56A     ENPGR.K=MAX(0,REGAR.K)
12A     NPPR.K=(P.K)(PPM.K)
19A     REAR.K=(EPRC)(PPGRP.K-GNPGR.K-RPGR.K+0)
42A     PPGRS.K=PV.K/((EPRC)(PVDD))
19A     EVAR.K=(ESRC)(EDAR.K-SSR.K-SER.K+0)
21A     NSER.K=(1/SED)(IDIV.K-DIV.K)
21A     EDAR.K=(1/ESRC)(REAR.K-ERRDM.K)
56A     PSSR.K=MAX(0,EDAR.K)
12A     ERRDM.K=(DIV.K)(DIVMC)
12A     EAR.K=(P.K)(EFR)
12A     ERRPM.K=(P.K)(PMC)
7A      EGAR.K=EAR.K-ERRPM.K
20A     PPGRP.K=EGAR.K/EPRC
NOTE
7R      PDR.KL=NPDR.K+GPDR.K
7R      ONBA.KL=PONBA.K+CONBA.K
20R     NBA1.KL=ON1.K/DD3.K
20R     NBA2.KL=ON2.K/DD3.K
20R     NBA.KL=ON3.K/DD3.K
18R     NDR.KL=(NPRC)(RPGR.K+NPGR.K)
12R     NCGR.KL=(NC.K)(NCRRS.K)
12R     NCDR.KL=(NC.K)(NCMRS.K)
12R     DDR.KL=(DIV.K)(SMR.K)
7R      DIR.KL=SER.K+SSR.K
6R      PGR.KL=APGR.K
56R     PVAR.KL=MAX(0,EVAR.K)
20R     PVDR.KL=PV.K/PVDD
NOTE
7S      GPGR.K=GNPGR.K+RPGR.K
7S      RESP.K=GPGR.K-NNPPR.K
NOTE
6N      N=14
6N      P=1
20N     IRPGR=P/PDD
6N      INPGR=0
46N     ON1=(P)(DD3N)(NPRC)/((PDD)(1)(1))
6N      ON2=ON1
6N      ON3=ON2
26N     D=(ON1+ON2+ON3)/(ONDRC+0+0)
6N      NC=0.00625
6N      NCRRS=0.096
6N      NCMRS=0.074
```

```
6N      ISER=0
12N     ISSR=(0IV)(SMRN)
6N      PV=0
8N      BS=P+NC+D
58N     DIV=TABHL(DIVT,BS,0,120,10)
58N     SCC=TABHL(SCCT,DIV,0,100,10)
NOTE
C       PDD=6
C       NAD=3
C       PDRSD=12
C       INGAD=60
C       DDMIN=6
C       DDS=6
C       DD3N=12
C       DRD=3
C       NCRD=6
C       NPRC=0.03
C       ONDRC=0.5
C       PNCRC=147.1
C       NCPRC=14.71
C       PPMT*=1/0.96/0.88/0.70/0.50/0.34/0.20/0.10/0.04/0.01/0
C       NCRT*=0/0.01/0.02/0.04/0.06/0.083/0.096/0.106/0.114/0.118/0.12
C       NCMT*=1/0.21/0.16/0.12/0.098/0.083/0.074/0.068/0.064/0.062/0.06
C       SED=12
C       SMRN=0.01
C       SSD=60
C       ISEAD=60
C       SCCAD=12
C       ESRC=1
C       EFR=2
C       EPRC=1
C       BSD=12
C       PVDD=12
C       DIVMC=0.1
C       PMC=0.1
C       SCCT*=20/23/32/57/84/102/112/116/118/119/120
C       DIVT*=0/46/76/104/128/148/164/176/188/196/200
C       PPET*=0.5/0.49/0.46/0.43/0.39/0.35/0.25/0.18/0.13/0.11/0.10
NOTE
PLOT    P=P/N=N,ON=0/GPGR=6,RESP=R/D=D/NC=C/DIV=Y/PV=V
SPEC    DT=1.0/LENGTH=720/PRTPER=6/PLTPER=6
RUN     MOD5A
C       DIVMC=0.5
RUN     MOD5B
C       PDD=3
RUN     MOD5C
C       ISEAD=120
RUN     MOD5D
C       SCCAD=120
RUN     MOD5E
C       PPET*=0.5/0.5/0.49/0.48/0.47/0.46/0.43/0.37/0.30/0.18/0.10
RUN     MOD5F
C       SCCT*=20/30/40/50/60/70/80/90/100/110/120
C       DIVT*=0/10/24/41/64/91/125/156/180/195/200
END
```

of Chapter II and to the simulation results of Chapters III and IV.

In the presence of a constant physical environment (i.e., constant temperature, water supply, light intensity, etc.) grassland plants make themselves out of soluble inorganic nutrients by the process of photosynthesis. Thus, plant biomass grows at a certain rate. It also declines at a certain rate, due to either natural decay or grazing by the consumers. Until such time as grasses die or are grazed away, plant biomass accumulates on the soil as standing crop. The stock of grasses standing at any given time is given by the level equation

$$P.K = P.J+(DT)(PGR.JK-PDR.JK) \qquad (3)$$

$$P = 1$$

where P = plant biomass ($g_p m^{-2}$)

PGR = plant growth rate ($g_p m^{-2}$/month)

PDR = plant depletion rate ($g_p m^{-2}$/month)

and the initial value reflects what is presumably a modest standing crop at the beginning of secondary succession. Alternatively, the initial value could be set so as to assume the grassland is initially at its climax--approximately 100 gm^{-2} in the case of the Pawnee grassland (Patten, in preparation). Initialization of the model for a particular simulation run depends, of course, on the purpose of the experiment: it may be to study the full successional process from youth to maturity, or it may be to study the successional response of the mature grassland to a moderate (either natural or man-made) perturbation. Both cases are

discussed in Chapter III and IV. In this appendix, initial values will be indicative of a grassland that has been pushed back to the early stage of its successional development.

When the grassland ecosystem is in steady-state, or climax condition, grasses grow, mature and either are eaten away or decay in (say) yearly cycles. They replace themselves from year to year, the standing crop for each year being the same as the standing crop for the previous year. During succession, however, they not only replace themselves from year to year but, in addition, generate new growth each year as succession unfolds. Therefore,

$$PGR.KL = NPGR.K+RPGR.K \tag{5}$$

where PGR = plant growth rate ($g_p m^{-2}$/month).

NPGR = new plant growth rate ($g_p m^{-2}$/month).

RPGR = replacement plant growth rate ($g_p m^{-2}$/month).

Plant depletion rate, on the other hand, depends not only on the natural decay rate of plant biomass, but also on consumption rate by the consumers; thus,

$$PDR.KL = NPDR.K+GPDR.K \tag{6}$$

where PDR = plant depletion rate ($g_p m^{-2}$/month).

NPDR = natural plant decay rate ($g_p m^{-2}$/month).

GPDR = grazing plant depletion rate ($g_p m^{-2}$/month).

It will be assumed that the natural plant decay rate NPDR is inversely proportional to the average half-life of the grasses, i.e.,

$$NPDR.K = P.K/PDD \tag{7}$$

$$PDD = 6$$

where NPDR = natural plant decay rate ($g_p m^{-2}$/month).

P = plant biomass ($g_p m^{-2}$).

PDD = plant decay delay (months).

The component of plant depletion rate which is due to grazing, GPDR, depends on the food requirements of the consumers and will be formulated later. At this time, let us consider the formulation of the "new growth" and "replacement growth" components of Equation (5). Adequate availability rates of energy and absorbable nutrients are required (in addition, of course, to plant machinery) for replacement growth to continue; new growth requires, in addition, the availability of unsaturated soil carrying capacity. Let us consider first the replacement growth rate, RPGR. Since either nutrient availability rate or energy availability rate is limiting,

$$RPGR.K = MIN(NRPGR.K,ERPGR.K) \tag{9}$$

where RPGR = replacement plant growth rate ($g_p m^{-2}$/month).

NRPGR = nutrient-limiting replacement plant growth rate ($g_p m^{-2}$/month).

ERPGR = energy-limiting replacement plant growth rate ($g_p m^{-2}$/month),

and, under the assumption of a constant water supply, it appears reasonable to assume that (as far as nutrients are concerned) the feasible limit to production of plant biomass is proportional to the reservoir of soluble inorganic nutrients in the soil, i.e.,

$$NRPGR.K = N.K/(NPRC)(NAD) \quad (10)$$

$$NPRC = 0.03 \quad (11)$$

$$NAD = 3 \quad (12)$$

where NRPGR = nutrient-limiting replacement growth rate ($g_p m^{-2}$/month).

N = nutrients available ($g_n m^{-2}$).

NPRC = nutrient-to-plant requirement coefficient (g_n/g_p).

NAD = nutrient absorption delay (months).

The quotient N.K/NAD gives the nutrient availability rate, with NPRC providing the conversion from grams of abiotic matter, or nutrients (g_n) to grams of plant biomass (g_p). Thus, in words, Equation (10) simply means that the production rate of plant biomass is limited in proportion to the availability rate of nutrients. As a first approximation the value of NPRC was abstracted from Pawnee data (Patten, in preparation) by simply taking the quotient of the aggregate steady-state value of nitrogen compartments (3.51 $g_n m^{-2}$) over the aggregate

steady-state value of plant biomass compartments (103.3 $g_p m^{-2}$) and taking the result (approximately 0.03) as indicative of mineral fixation requirement per unit of biomass production. A nominal value of three months was arbitrarily attached to NAD in the absence of specific data for this parameter. The (admittedly naive) numerical valuation of NPRC and NAD is illustrative of the approach consistently followed in the research: to construct a model which is theoretically (i.e., structurally) sound, to quantify the model relationships with reasonable numerical values and to exercise the model in order to detect sensitive parameters which merit more accurate field estimation, as discussed in Chapter III and IV of this dissertation.

The energy-limiting replacement growth rate, ERPGR, is formulated as follows:

$$ERPGR.K = MIN(IRPGR.K,EPPGR.K) \tag{13}$$

where ERPGR = energy-limiting replacement plant growth rate ($g_p m^{-2}$/month).

IRPGR = indicated replacement plant growth rate ($g_p m^{-2}$/month).

EPPGR = energetically possible plant growth rate ($g_p m^{-2}$/month).

The indicated replacement plant growth rate, IRPGR, is simply the value of the natural plant decay rate, NPDR, delayed so as to account for the yearly replacement cycle of grasses, i.e.,

$$IRPGR.K = IRPGR.J+(DT)(1/PDRSD)(NPDR.J-IRPGR.J) \tag{14}$$

$$IRPGR = P/PDD \tag{15}$$

$$PDRSD = 12 \tag{16}$$

where IRPGR = indicated replacement plant growth rate ($g_p m^{-2}$/month).

PDRSD = plant decay rate smoothing delay (months).

NPDR = natural plant decay rate ($g_p m^{-2}$/month).

P = plant biomass ($g_p m^{-2}$).

PDD = plant decay delay (months).

Note that according to Equation (14) the replacement function is assumed to take care only of replacing grasses which matured and decayed according to their own life cycle; grasses grazed by consumers are to be replaced by new growth. The replacement loop would take care of both if this equation is reformulated with PDR in place of NPDR. The other limiting factor in Equation (13), EPPGR, is equal to the plant growth rate which is possible using energy becoming available through photosynthesis, plus that which is possible by drawing from stored energy:

$$EPPGR.K = PPGRP.K+PPGRS.K \tag{17}$$

where EPPGR = energetically possible plant growth rate ($g_p m^{-2}$/month).

PPGRP = possible plant growth rate--photosynthesis ($g_p m^{-2}$/month).

PPGRS = possible plant growth rate--storage ($g_p m^{-2}$/month).

PPGRS, the possible plant growth rate using stored energy, is proportional to the rate at which stored potential energy (i.e.,

"vigor") can be made available for production purposes:

$$PPGRS.K = PV.K/(EPRC)(PVDD) \quad (18)$$

$$EPRC = 1 \quad (19)$$

$$PVDD = 12 \quad (20)$$

where PPGRS = possible plant growth rate--storage ($g_p m^{-2}$/month).

PV = plant vigor (cal m^{-2}).

EPRC = energy-to-plant requirement coefficient (cal/g_p).

PVDD = plant vigor dissipation delay (months).

On the other hand, the possible plant growth rate using photosynthetic energy, PPGRP, is to be computed at each point in time from the following set of equations:

$$PPGRP.K = EGAR.K/EPRC \quad (21)$$

$$EGAR.K = EAR.K-ERRPM.K \quad (22)$$

$$EAR.K = (P.K)(EFR) \quad (23)$$

$$ERRPM = (P.K)(PMC) \quad (24)$$

$$EFR = 2 \quad (25)$$

$$PMC = 0.1 \quad (26)$$

where PPGRP = possible plant growth rate--photosynthesis ($g_p m^{-2}$/month).

EGAR = energy for growth availability rate (cal m^{-2}/month).

EPRC = energy-to-plant requirement coefficient (cal/g_p).

EAR = energy availability rate (cal m^{-2}/month).

ERRPM = energy rate required for plant maintenance (cal m^{-2}/month).

EFR = energy fixation rate (cal g_p^{-1}/month).

PMC = plant maintenance coefficient (cal g_p^{-1}/month).

P = plant biomass ($g_p m^{-2}$).

The set of Equations (10) to (26) account in a very simplified fashion for the initial disposition of photosynthetic energy, the maintenance and replacement of plant biomass, and the fixing of mineral nutrients as part of this production process. The photosynthetic machinery of plants fixes solar energy in a rate proportional to the standing crop (Equation (23)). Part of this energy is immediately dissipated in the performance of maintenance functions (Equation (24)), and the remaining energy becomes available for production functions (Equation (22)). Assuming that it takes so many calories to produce a gram of plant biomass, the production rate which is energetically possible (Equation (17)) is proportional to the energy becoming available from photosynthesis (Equation (21)) plus the energy becoming available from storage (Equation (18)). The plant community is assumed to attain either this production rate (Equation (17)) or the production rate indicated for replacement purposes (Equation (14)), whichever is less (Equation (13)). The "attempt" is successful if the nutrient availability rate (Equation (10)) is not limiting; otherwise, the actual

production rate accomplished is as limited by the availability rate of nutrients (Equation (9)). The values for EPRC, EFR and PMC were deliberately chosen so as to ensure a nonlimiting availability of energy; no empirical basis for these numbers is claimed.

Let us consider now the new growth component of plant growth rate, NPGR. New growth, in addition to replacement growth, can be accomplished if there are excess availability rates of energy and nutrients and, in addition, available space or soil in which additional growth can be attempted. If all these resources are available, it is assumed that the plant community will attempt further growth before allocating excess energy to other functions. With these considerations in mind, the component NPGR of Equation (5) can be formulated as

$$NPGR.K = MIN(NNPGR.K,NNPPR.K) \tag{27}$$

where NPGR = new plant growth rate ($g_p m^{-2}$/month).

NNPGR = nutrient-limiting new plant growth rate ($g_p m^{-2}$/month).

NNPPR = not new plant growth rate ($g_p m^{-2}$/month).

The nutrient-limiting new plant growth rate is the nonnegative number

$$NNPGR.K = MAX(0,RNAR.K) \tag{28}$$

where NNPGR = nutrient-limiting new plant growth rate ($g_p m^{-2}$/month).

RNAR = remaining nutrient availability rate ($g_p m^{-2}$/month),

and the remaining nutrient availability rate is of course what is left unused after replacement growth requirements have been satisfied, i.e.,

$$RNAR.K = NRPGR.K - ERPGR.K \tag{29}$$

where RNAR = remaining nutrient availability rate ($g_p m^{-2}$/month).

NRPGR = nutrient-limited replacement plant growth rate ($g_p m^{-2}$/month).

ERPGR = energy-limited replacement plant growth rate ($g_p m^{-2}$/month).

The other limiting factor in Equation (27) is NNPPR, the new net plant production rate: this is, of course, the percentage of the gross new plant rate which is not lost as respiration:

$$NNPPR.K = (PPEF.K)(GNPGR.K) \tag{30}$$

where NNPPR = net new plant growth rate ($g_p m^{-2}$/month).

PPEF = plant production efficiency factor (dimensionless).

GNPGR = gross new plant growth rate ($g_p m^{-2}$/month).

It is possible to assume that the efficiency factor PPEF is either a constant or a variable. A constant value in the range of 10 to 50 per cent would be a reasonable approximation. In consonance with the discussion of Figure 19, Chapter II, it will be formulated later as a function of relative diversity. Gross new plant growth rate, GNPGR, is the minimum of that which is energetically possible and that which is indicated by the availability of physical space in which to grow, thus,

GNPGR.K = MIN(INPGR.K,ENPGR.K) (31)

where GNPGR = gross new plant growth rate ($g_p m^{-2}$/month).

INPGR = indicated new plant growth rate ($g_p m^{-2}$/month).

ENPGR = energetically possible new plant growth rate ($g_p m^{-2}$/month).

Using the same technique employed before to compute the excess availability of nutrients, we can write

ENPGR.K = MAX(0,REGAR.K) (32)

and

REGAR.K = EPPGR.K-IRPGR.K (33)

where ENPGR = energetically possible new plant growth rate ($g_p m^{-2}$/month),

REGAR = remaining-energy-for-growth availability rate ($g_p m^{-2}$/month),

EPPGR = energetically possible plant growth rate ($g_p m^{-2}$/month),

IRPGR = indicated replacement plant growth rate ($g_p m^{-2}$/month),

to compute the excess availability rate of energy for growth. The indicated new plant growth rate, INPGR, is computed as follows:

INPGR.K = INPGR.J+(DT)(1/INGAD)(NPPR.K-INPGR.J) (34)

INPGR = 0 (35)

INGAD = 6 (36)

NPPR.K = (P.K)(PPM.K) (37)

PPM.K = TABHL(PPMT,SAX.K,0,1,0.1) (38)

PPMT* = 1/0.96/0.88/0.70/0.50/0.34/0.20/0.10/0.04/0.01/0 (39)

SAX.K = P.K/SCC.K (40)

where INPGR = indicated new plant growth rate ($g_p m^{-2}$/month).

INGAD = indicated new growth adjustment delay (months).

NPPR = production capacity for new plant growth rate ($g_p m^{-2}$/month).

P = plant biomass ($g_p m^{-2}$).

PPM = plant production multiplier ($month^{-1}$).

SAX = soil availability index (dimensionless).

SCC = soil carrying capacity ($g_p m^{-2}$).

PPMT = plant production multiplier table ($month^{-1}$).

Thus when the ratio P.K/SCC.K is small (i.e., when there is plenty of unutilized soil carrying capacity), plant machinery responds by increasing its production activity beyond that required for replacement purposes; the result is new growth. Equation (38) gives the DYNAMO statement for the nonlinearity involved. It means that PPM.K is a table function of the independent variable SAX.K, that the range of SAX.K is between zero and one, and that the values of PPM.K as a function of SAX.K are stored in table PPMT at 0.1 increments of the independent variable (Equation (39)). At each iteration, PPM.K is computed from the table by linear interpolation. Figure 42 shows alternative numerical valuations of PPMT. The shape of the curve is as hypothesized in Chapter II. The intensity of the new growth response to available space is, of course,

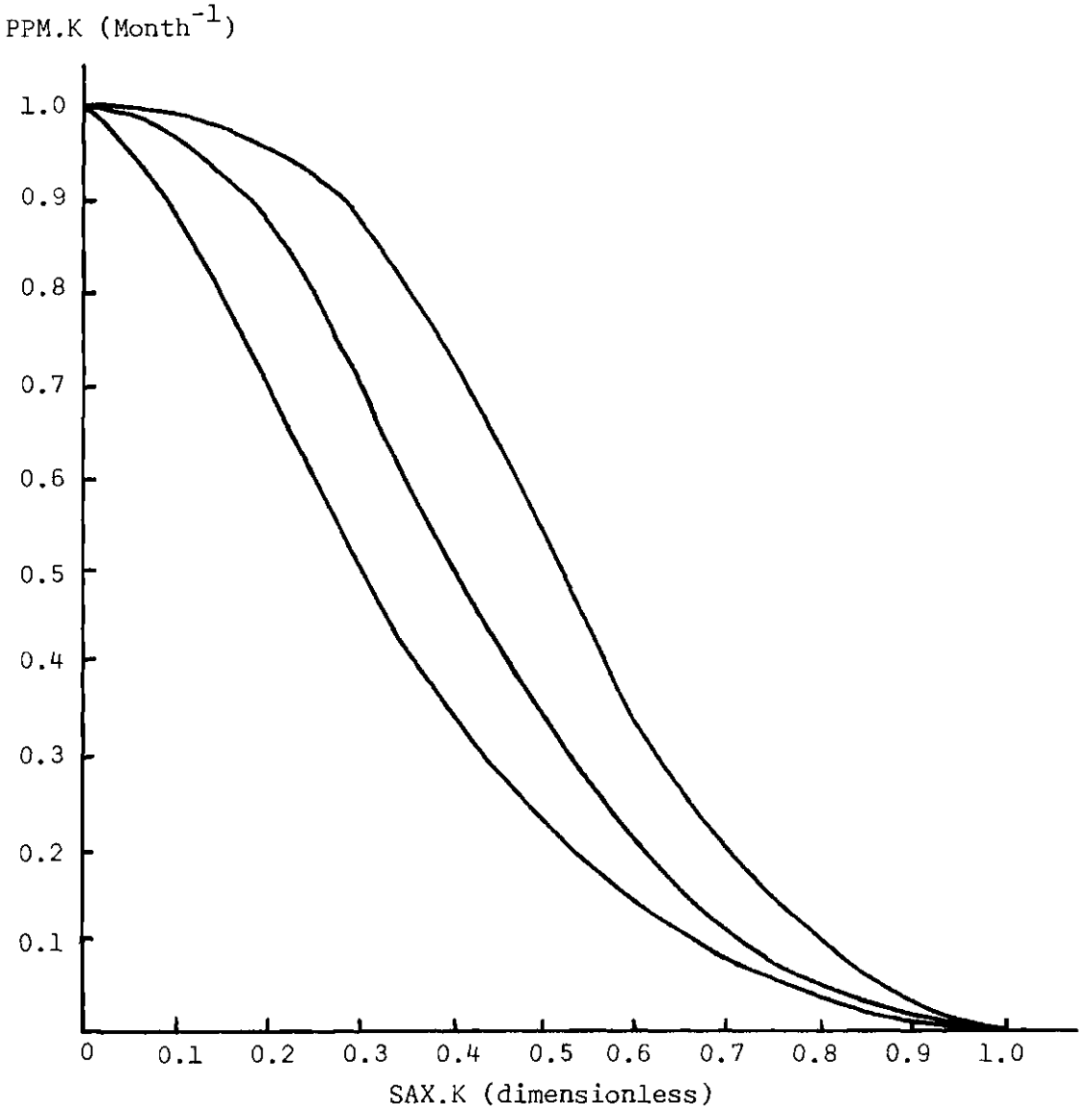

Figure 42. New Production Multiplier (PPM.K) as a Function of Soil Availability (SAX.K)

proportional to the amount of plant machinery available in the grassland (Equation (37)). Furthermore, the new growth response is not instantaneous. In fact, it may take a significant amount of time (say, five years) for the plant community to adjust its production machinery so as to exploit a growth situation; thus the level Equation (34). It delays (i.e., smoothes) the value of new plant production rate, so that the current indicated value of new plant growth rate reflects the time delay involved in the adjustment process. This completes the feedback structure controlling the growth and decay of grasses. Several links with other sectors of the ecosystem, however, remain unformulated: soil carrying capacity (SCC), plant production efficiency factor (PPEF), and the plant depletion rate due to grazing (GPDR). Let us consider the last one first.

The rate at which grasses are eaten away from the soil depends on the density and growth rate of consumers. The biomass density of natural consumers is given by

$$NC.K = NC.J+(DT)(NCGR.JK-NCDR.JK) \tag{41}$$

$$NC = 0.00625 \tag{42}$$

where NC = natural consumers biomass ($g_c m^{-2}$).

NCGR = natural consumers growth rate ($g_c m^{-2}$/month).

NCDR = natural consumers depletion rate ($g_c m^{-2}$/month).

NC is, of course, a highly aggregated level which lumps together all kinds of consumers, both primary and secondary. It might seem that this is an oversimplification in modeling the grassland ecosystem. But

the purpose of the research, and therefore the purpose of the model, is not to account for specific dynamic processes such as, for example, predator-prey interactions; the objective at hand is to account for successional dynamics. From a successional-dynamic viewpoint, what matters is not so much the manyfold pathways followed by nutrients as they are transferred from trophic level to trophic level, as it is the overall time constants of the cycling process. The producers community is really the one that generates succession, and succession will proceed up to the limits imposed by the physical environment as long as the cycling of nutrients does not become limiting. In accounting for nutrients cycling in the sense, it does not seem necessary to decompose trophic levels beyond the basic categories, i.e., producers, consumers and decomposers. In fact, the whole nutrients recycling process could be formulated as a high order delay without significantly affecting the growth dynamics of the model. For subsequent utilization studies, however, it will be desirable to investigate, for example, the effect of augmenting consumers with domestic consumers, the effect of destroying the decomposers, and so forth. With these considerations in mind, it was decided to account for the various trophic levels in an explicit manner, though at the highest possible level of aggregation.

The level of natural consumers biomass, NC, grows and declines in response to the availability of grasses. If we take the ratio

$$PAX.K = P.K/(PNCRC)(NC.K) \tag{43}$$

$$PNCRC = 147.1 \tag{44}$$

where PAX = plant biomass availability index (dimensionless),

P = plant biomass ($g_p m^{-2}$),

NC = natural consumers biomass ($g_c m^{-2}$).

PNCRC = plants-to-natural consumers requirement coefficient (g_p/g_c),

as an index of food availability for the consumers (note that the right-hand side of Equation (43) is simply the ratio of plant biomass available over plant biomass required), then the reproduction and mortality rates of natural consumers would be functions of this index, as postulated in Chapter II, Figure 11. Thus,

NCRR.K = TABHL(NCRT,PAX.K,0,2,0.2) (45)

NCRT* = 0/0.01.0.02,0.04/0.06/0.083/0.096.0.106.0.114.0.118.0.12 (46)

NCMR.K = TABHL(NCMT,PAX.K,0,2,0.2) (47)

NCMT* = 1/0.21/0.16/0.12/0.098/0.083/0.074/0.068/0.064/0.062/0.06 (48)

where NCRR = natural consumers reproduction rate ($month^{-1}$).

NCMR = natural consumers mortality rate ($month^{-1}$).

PAX = plant biomass availability rate (dimensionless).

NCRT = natural consumers reproduction table ($month^{-1}$).

NCMT = natural consumers mortality table ($month^{-1}$).

According to Patten (in preparation), the steady-state values of aggregate consumers biomass and aggregate plant biomass are approximately 0.7 $g_c m^{-2}$ and 103 $g_p m^{-2}$, respectively; thus the value assigned to PNCRC (103 ÷ 0.7 = 147.1). The tables NCRT and NCMT used for the

simulations are shown in Figure 43. The superimposed graphs of NCRT and NCMT show that equilibrium occurs at PAX = 1, i.e., the situation where food available is equal to food required. According to the values assumed in Figure 43, this equilibrium would result in reproduction and mortality rates of 0.083, which implies a yearly turnover of consumers biomass. If plant biomass exceeds the required value (PAX>1) the reproduction rate will be greater than the mortality rate, and the level of natural consumers will increase; on the other hand, when food becomes scarce (PAX<1) the mortality rate will be higher than the reproduction rate, and the level of natural consumers will decline. In the extremes, if the standing crop of plants is completely destroyed (PAX=0), the reproduction rate of consumers will become zero, and mortality rate will increase dramatically. Consequently, the level of natural consumers will gradually vanish. On the other hand, an abundance of plant biomass generates further growth in natural consumers only to a certain extent. If there is an overabundance (e.g., PAX>2) of grasses, other factors will become limiting and both NCRR and NCMR level off at their maximum and minimum levels, respectively. It takes some time, however, for animals to adjust their numbers (either upward or downward) in response to the food supply; therefore, it was chosen to formulate the growth and death rates of natural consumers as follows:

$$NCGR.KL = (NC.K)(NCRRS.K) \tag{49}$$

$$NCRRS.K = NCRRS.J+(DT)(1/NCRD)(NCRR.J-NCRRS.J) \tag{50}$$

$$NCRRS = 0.096 \tag{51}$$

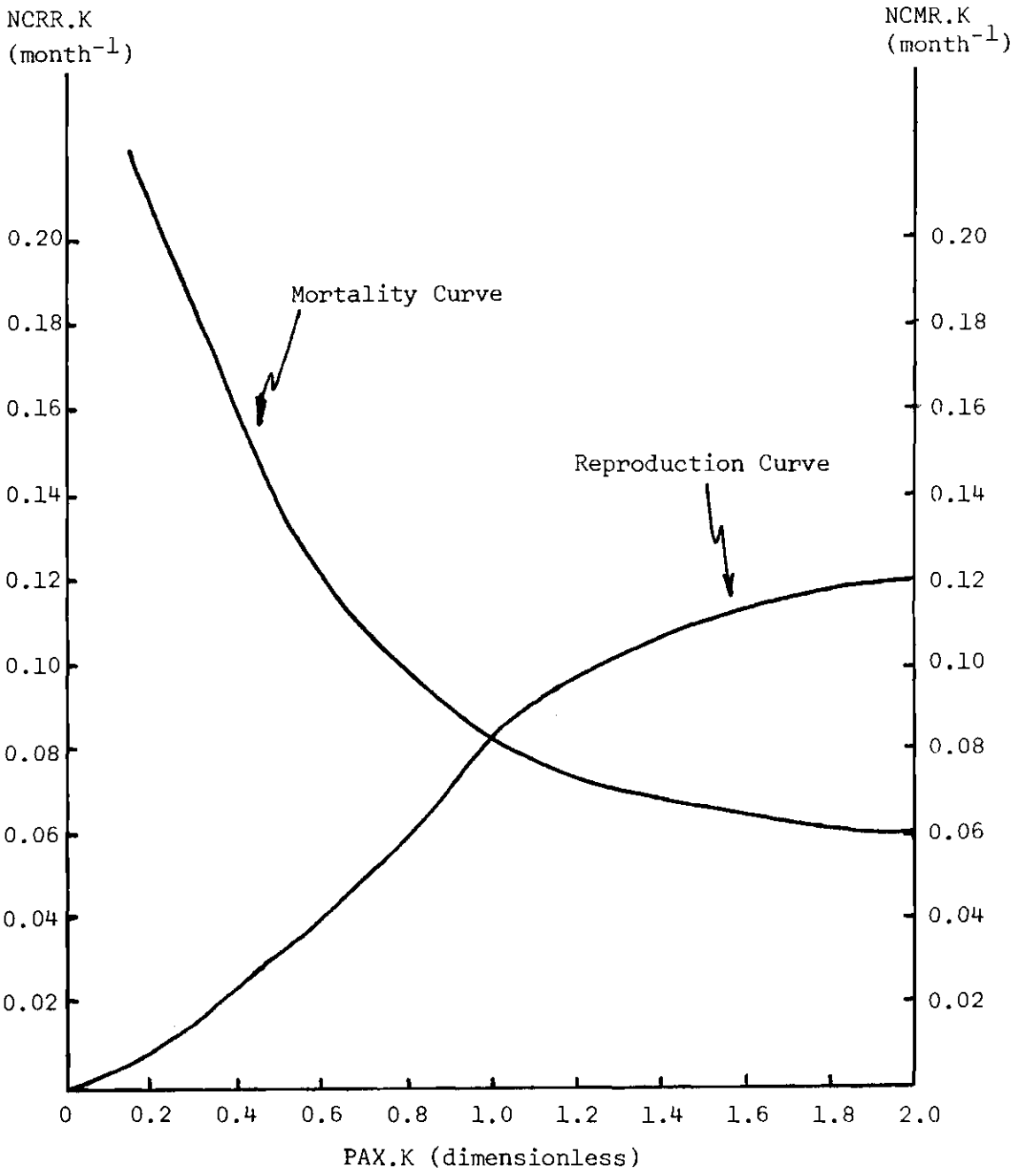

Figure 43. Natural Consumers Reproduction Rate (NCRR.K) and Mortality Rate (NCMR.K) as a Function of Plant Availability Index (PAX.K)

NCDR.KL = (NC.K)(NCMRS.K) (52)

NCMRS.K = NCMRS.J+(DT)(1/NCRD)(NCMR.J-NCMRS.J) (53)

NCMRS = 0.074 (54)

NCRD = 6 (55)

where NCGR = natural consumers growth rate ($g_c m^{-2}$/month).

NC = natural consumers biomass ($g_c m^{-2}$).

NCRRS = natural consumers reproduction rate smoothed ($month^{-1}$).

NCDR = natural consumers depletion rate ($g_c m^{-2}$/month).

NCMRS = natural consumers mortality rate smoothed ($month^{-1}$).

NCRD = natural consumers response delay (months).

NCRR = natural consumers reproduction rate ($month^{-1}$).

NCMR = natural consumers mortality rate ($month^{-1}$).

As stated before, the rate at which grasses are consumed depends on the density and growth rate of animals. The formulation

GPDR.K = (NC.K)(NCRRS.K)(NCPRC) (56)

NCPRC = 14.71 (57)

where GPDR = grazing plant depletion rate ($g_p m^{-2}$/month),

NC = natural consumers biomass ($g_c m^{-2}$),

NCRRS = natural consumers reproduction rate smoothed ($month^{-1}$),

NCPRC = natural consumers--plant requirement coefficient (g_p/g_c),

lumps together food intake rate requirements for both growth and

maintenance, with NCPRC set at 10 per cent of PNCRC. Admittedly, this is simplifying things quite a bit, but let us recall that the objective at hand is to account for the delays involved in the cycling of nutrients, rather than to account for specific processes within each trophic level.

As either plants or animals die, the dead organic matter must be broken down to complete the cycling of the nutrients back to soluble inorganic form. The delays involved in this process were modeled as follows. The rate of nutrients becoming available in organic form is formulated as the nutrient equivalent of decaying biomass:

$$ONBA.KL = PONBA.K+CONBA.K \tag{58}$$

$$PONBA.K = (P.K)(NPRC)/PDD \tag{59}$$

$$CONBA.K = (COMBA.K)(NCPRC)(NPRC) \tag{60}$$

$$COMBA.K = (NC.K)(NCMRS.K) \tag{61}$$

where ONBA = organic nutrients becoming available ($g_n m^{-2}$/month).

PONBA = plant organic nutrients becoming available ($g_n m^{-2}$/month).

CONBA = consumer organic nutrients becoming available ($g_n m^{-2}$/month).

COMBA = consumer organic matter becoming available ($g_c m^{-2}$/month).

P = plant biomass ($g_p m^{-2}$).

NC = natural consumers biomass ($g_c m^{-2}$).

NPRC = nutrients-to-plant requirement coefficient (g_n/g_p).

NCPRC = natural consumers--plant requirement coefficient (g_p/g_c).

PDD = plant decay delay (months).

NCMRS = natural consumers mortality rate smoothed ($g_c m^{-2}$/month).

Decaying biomass accumulates in the soil, and is gradually broken down by the decomposers. The delay incurred in the process depends, of course, on the relative availability of decomposers to accomplish the breakdown. Due to the complex processes involved, the conversion of nutrients from organic to inorganic form is more gradual than would be implied by a first-order delay. In this model, this transition to complete the cycling of nutrients was formulated as a third-order delay, with the overall average delay being a function of the level of decomposers available. The equations

ON1.K = ON1.J+(DT)(ONBA.JK-NBA1.JK) (62)

ON1 = (P)(DD3N)(NPRC)/PDD (63)

DD3N = 12 (64)

NBA1.KL = ON1.K/DD3.k (65)

ON2.K = ON2.J + (DT)(NBA1.JK-NBA2.JK) (66)

ON2 = ON1 (67)

NBA2.KL = ON2.K/DD3.K (68)

ON3.K = ON3.J+(DT)(NBA2.JK-NBA.JK) (69)

ON3 = ON2 (70)

$$NBA.KL = ON3.K/DD3.K \tag{71}$$

where ONBA = organic nutrients becoming available ($g_n m^{-2}$/month),

ON1 = organic nutrients--stage one ($g_n m^{-2}$),

NBA1 = nutrients becoming available--stage one ($g_n m^{-2}$/month),

ON2 = organic nutrients--stage two ($g_n m^{-2}$),

NBA2 = nutrients becoming available--stage two ($g_n m^{-2}$/month),

ON3 = organic nutrients--stage three ($g_n m^{-2}$),

NBA = nutrients becoming available ($g_n m^{-2}$/month),

P = plant biomass ($g_p m^{-2}$),

DD3N = decomposition delay three--normal (months),

NPRC = nutrients-to-plants requirement coefficient ($g_n g_p$),

PDD = plant decay delay (months),

DD3 = decomposition delay three (months),

account for the physical flow of nutrients undergoing the decomposition process. The delays DD3 vary as a function of the relative abundance of decomposers. In time, the level of decomposers depends on the level of organic matter available for decomposition. In order to see how the closed-loop interaction between organic matter and decomposers biomass arises, let's consider the total accumulation of organic nutrients

$$ON.K = ON1.K+ON2.K+ON3.K \tag{72}$$

where ON = organic nutrients ($g_n m^{-2}$).

ON1 = organic nutrients--stage one ($g_n m^{-2}$).

ON2 = organic nutrients--stage two ($g_n m^{-2}$).

ON3 = organic nutrients--stage three ($g_n m^{-2}$).

It was assumed that, for decomposition to be accomplished in a normal amount of time, the indicated level of decomposers is proportional to the total amount of organic nutrients, ON. More specifically,

$$ID.K = ON.K/ONDRC \tag{73}$$

$$ONDRC = 0.5 \tag{74}$$

where ID = indicated decomposer biomass ($g_d m^{-2}$),

ON = organic nutrients ($g_n m^{-2}$),

ONDRC = organic nutrients--decomposers requirement coefficient (g_n/g_d),

and the value of ONDRC was again abstracted from Patten's data (Patten, in preparation) by taking the quotient of steady-state organics (completed to be approximately 6 $g_n m^{-2}$) over steady-state decomposers standing crop (approximately 12.4 $g_d m^{-2}$). Decomposers are simply assumed to react to a buildup in organic matter by growing to the indicated level, i.e.,

$$D.K = D.J+(DT)(1/DRD)(ID.J-D.J) \tag{75}$$

$$D = (ON1+ON2+ON3)/ONDRC \tag{76}$$

$$DRD = 3 \tag{77}$$

where D = decomposers biomass ($g_d m^{-2}$).

ID = indicated decomposers biomass ($g_d m^{-2}$).

DRD = decomposers response delay (months).

ON1 = organic nutrients--stage one ($g_n m^{-2}$).

ON2 = organic nutrients--stage two ($g_n m^{-2}$).

ON3 = organic nutrients--stage three ($g_n m^{-2}$).

ONDRC = organic nutrients--decomposers requirement coefficient (g_n/g_d).

The relative availability of decomposers is then given by the ratio

$$DAX.K = ID.K/D.K \tag{78}$$

where DAX = decomposers availability index (dimensionless),

ID = indicated decomposers biomass ($g_d m^{-2}$),

D = decomposers biomass ($g_d m^{-2}$),

and the decomposition delay which results from a given value of DAX was formulated (following the hypothesis of Figure 13, Chapter II) as follows:

$$DD.K = DDMIN+(DDS)(DAX.K) \tag{79}$$

$$DDMIN = 6$$

$$DDS = 6 \tag{81}$$

$$DD3.K = DD.K/3 \tag{82}$$

where DD = decomposition delay (months).

DDMIN = decomposition delay minimum (months).

DDS = decomposition delay slope (months).

DD3 = decomposition delay three (months).

The auxiliary variable DD3 is simply the prorating of the total decomposition delay DD to each stage in the third-order delay process (see Equations (65), (68), and (71)). Nutrients becoming available as a result of decomposition accumulate in the soil and are ready once more for utilization by the producers. It remains only to formulate this level to close the nutrients cycling loop in the model; thus, we can write

$$N.K = N.J+(DT)(NBA.JK-NDR.JK) \tag{83}$$

$$N = 14 \tag{84}$$

where N = nutrients available ($g_n m^{-2}$).

NBA = nutrients becoming available ($g_n m^{-2}$/month).

NDR = nutrients depletion rate ($g_n m^{-2}$/month).

The rate of nutrients becoming available, NBA, was formulated in Equation (71). As nutrients become available in the soil, however, they are consumed again by the producers at a rate which is proportional to both the replacement and new growth rates, i.e.,

$$NDR.KL = (NPRC)(RPGR.K+NPGR.K) \tag{85}$$

where NDR = nutrients depletion rate ($g_n m^{-2}$/month).

NPRC = nutrients-to-plants requirement coefficient (g_n/g_p).

RPGR = replacement plant growth rate ($g_p m^{-2}$/month).

NPGR = new plant growth rate ($g_p m^{-2}$/month).

In other words, nutrients depletion rate equals the rate at which

they are absorbed by the plants, to start a new cycle. Thus, in this model, the rate of circulation of nutrients may change, as well as the distribution of the total amount of nutrients to the various traffic levels, but the total amount in circulation remains invariant with time; this is, of course, as it would be in a closed ecosystem. The model equations fully account for the closed-loop flow of nutrients. Energy flow, on the other hand, is open. Energy fixed as biomass is gradually dissipated as it is transferred from one trophic level to another, never to become usable again to the grassland community. Bey ond the producers, biomass flow and energy flow are one and the same; only that, while nutrients are conserved, energy is not.

The model as formulated thus far does not account for one critical aspect of succession, namely, the ability of the biotic community to increase the carrying capacity of the physical environment. In the case of a grassland ecosystem, the carrying capacity of the physical environment is basically the carrying capacity of the soil. In consonance with the hypothesis of Chapter II, the model assumes that increments in soil carrying capacity are effectively brought about by the diversification which follows a buildup in biomass and which "permits the occupancy of more niches in the habitat" (DeVos, 1969). The enhanced soil carrying capacity, in turn, propitiates further growth. The analytical formulation of this positive feedback was accomplished as follows:

Species diversity is the total number of species in the community and given by

$$DIV.K = DIV.J+(DT)(DIR.JK-DDR.JK) \qquad (86)$$

$$DIV = 1 \tag{87}$$

where DIV = species diversity (species).

DIR = diversity increase rate (species/month).

DDR = diversity decrease rate (species/month).

Diversity decreases when species disappear. It increases with the emergence of new species and/or substitution of those which have vanished. During succession, species come and go. Those which go after each successional stage must be substituted by others, better adapted to the forthcoming stage; furthermore, completely new species emerge as succession unfolds, resulting in successive net diversity increments. As the climax is approached, however, both DIR and DDR should approach zero. The soil availability index of Equation (40), SAX.K = P.K/SCC.K, provides valuable information on the benevolence of current conditions toward species currently on the grassland. Thus, a value of SAX.K close to zero is indicative of a new successional stage being at hand; conditions are bound to change, competition is bound to increase, and as a result, species will begin to disappear at some nominal rate. On the other hand, a value of SAX.K close to one is indicative of maturity and stability, and therefore indicative of zero species decrease rate. With these considerations in mind, the diversity decrease rate was formulated as

$$DDR.KL = (DIV.K)(SMR.K) \tag{88}$$

$$SMR.K = (SMRN)(SMRM.K) \tag{89}$$

SMRM.K = TABHL(SMRT,SAX.K,0,1,0.1) (90)

SMRT* = 1/0.96/0.88/0.70/0.50/0.34/0.20/0.10/0.04/0.01/0 (91)

SMRN = 0.01 (92)

where DDR = diversity decrease rate (species/month),

DIV = species diversity (species),

SMR = species extinction rate ($month^{-1}$),

SMRN = species extinction rate--normal ($month^{-1}$),

SMRM = species extinction rate multiplier (dimensionless),

SAX = soil availability index (dimensionless),

SMRT = species extinction rate table (dimensionless),

PPMT = plant production multiplier table (dimensionless),

and SMRT is equated with PPMT, since a nonlinearity of the same shape (see Figure 42) would apply. The reader will note that, in the model listing of Table 2, Equation (89) is written as SMR.K = (SMRN)(PPM.K), which eliminates the need for Equation (90) and (91). Both versions are computationally equivalent, but the theoretically correct formulation is as written above.

The diversity increase rate, as stated before, is the result of both species substitution and the emergence of additional new species, i.e.,

DIR.KL = SER.K+SSR.K (93)

where DIR = diversity increase rate (species/month).

SER = species emergence rate (species/month).

SSR = species substitution rate (species/month).

Given the potential for further niche specialization, two resources are required for diversification to take place: biomass and energy. These factors are limiting on the diversification process in a way similar to the limits imposed on the growth process by space, nutrients and energy. Thus, the species substitution rate SSR was formulated as

$$SSR.K = MIN(PSSR.K, ISSR.K) \tag{94}$$

where SSR = species substitution rate (species/month).

PSSR = possible species substitution rate (species/month).

ISSR = indicated species substitution rate (species/month).

The rate of species substitution which is "indicated" is the rate necessary to replace species which have abandoned the ecosystem in the recent past (say, during the last few years) as a result of successional developments. Therefore, the indicated species substitution rate is equal to the value of diversity decrease rate Equation (88) after a substitution delay, i.e.,

$$ISSR.K = ISSR.J+(DT)(1/SSD)(DDR.JK-ISSR.J) \tag{95}$$

$$ISSR = (DIV)(SMRN) \tag{96}$$

$$SSD = 60 \tag{97}$$

where ISSR = indicated species substitution rate (species/month).

SSD = species substitution delay (months).

DDR = diversity decrease rate (species/month).

DIV = species diversity (species).

SMRN = species mortality rate--normal ($month^{-1}$).

The rate of species substitution which is actually possible, however, is a function of the availability of energy for diversification, which in turn depends on energy availability in excess of that required for growth work. In order to account for the limiting effect of energy on diversification, PSSR is computed at each point in time from the following set of equations:

$$PSSR.K = MAX(0,EDAR.K) \quad (98)$$

$$EDAR.K = (1/ESRC)(REAR.K-ERRDM.K) \quad (99)$$

$$ESRC = 1 \quad (100)$$

$$REAR.K = (EPRC)(PPGRP.K-GNPGR.K-RPGR.K) \quad (101)$$

$$ERRDM.K = (DIV.K)(DIVMC) \quad (102)$$

$$DIVMC = 0.1 \quad (103)$$

where PSSR = possible species substitution rate (species/month).

EDAR = energy for diversification availability rate (species/month).

ESRC = energy-to-species requirement coefficient (cal m^{-2}/species).

REAR = remaining energy availability rate (cal m^{-2}/month).

DPRC = energy-to-plants requirement coefficient (cal/g_p).

PPGRP = possible plant growth rate--photosynthesis ($g_p m^{-2}$/month).

GNPGR = gross new plant growth rate ($g_p m^{-2}$/month).

RPGR = replacement plant growth rate ($g_p m^{-2}$/month).

ERRDM = energy rate required for diversity maintenance (cal m^{-2}/month).

DIV = species diversity (species).

DIVMC = diversity maintenance coefficient (cal m^{-2}/month/species).

The set of Equations (98) to (103) simply converts the energy availability rate remaining from growth (RDEAR, Equation (101)) to its equivalent in terms of further diversification potential (Equation (99)), taking into account that some energy is required just to maintain the current level of diversity (Equation (102)). Empirical data on the energetic coefficients associated with diversification work appear to be unavailable in the literature, so the values assumed above (Equation (100) and (103)) are purely hypothetical.

Energetic limits to the emergence of additional new species as succession unfolds follow from the previous accounting of energy availability rate and can be formulated as

SER.K = MIN(ISER.K,PSER.K) (104)

where SER = species emergence rate (species/month),

ISER = indicated species emergence rate (species/month),

PSER = possible species emergence rate (species/month),

and PSER is the species emergence rate which still is energetically possible after energy expenditures for diversity maintenance and species substitution have been accounted for, i.e.,

PSER.K = MAX(0,REDAR.K) (105)

REDAR.K = PSSR.K-ISSR.K (106)

where PSER = possible species emergence rate (species/month).

REDAR = remaining energy-for-diversification availability rate (species/month).

PSSR = possible species substitution rate (species/month).

ISSR = indicated species substitution rate (species/month).

The "indicated" species emergence rate, on the other hand, represents the appearance of additional new species which is brought about by the ongoing buildup of total biomass in the community. Grasses, of course, constitute the major portion of this buildup. However, the total amount of biomass as it accumulates in the ecosystem can be consolidated by means of the level equation

BS.K = BS.K+(DT)(1/BSD)(P.J+NC.J+D.J-BS.J) (107)

BS = P + NC + D (108)

BSD = 12 (109)

where BS = total biomass smoothed ($g\ m^{-2}$).

BSD = total biomass smoothing delay (months).

P = plant biomass ($g_p m^{-2}$).

NC = natural consumers biomass ($g_c m^{-2}$).

D = decomposers biomass ($g_d m^{-2}$).

At any given successional stage, further accumulation of biomass in the ecosystem is indicative of increased species diversity forthcoming in the near future. It is also indicative of previous increases

in diversity which brought about the increased carrying capacity that, in turn, resulted in the present buildup of biomass. Let us consider first the former side of this mutual causality, i.e., the positive influence of community growth on community diversity. Following the hypothesis of Figure 15 in Chapter II, it can be assumed that the level of species diversity which is indicated at any given time is functionally related to current accumulation of total biomass,

$$IDIV.K = TABHL(DIVT,BS.K,0,100,10) \quad (110)$$

$$DIVT* = 0/46/76/104/128/148/164/176/188/196/200 \quad (111)$$

where IDIV = indicated species diversity (species),

DIVT = diversity table (species),

BS = total biomass smoothed (g m^{-2}),

but empirical data on the graphical appearance of DIVT (i.e., the shape of the functional relationship) does not appear to be available. On the basis of descriptive evidence as pointed out in Chapter II, it seems reasonable to assume that increase in species diversity are roughly proportional to increase in total biomass as succession goes on. Alternatively, it may be assumed that the relationship is nonlinear, with biomass accumulation ceasing to generate further diversification after a certain point, possibly due to an increase in the size of organisms, the length and complexity of life histories, and interspecific competition resulting in the elimination of some species. Alternative assumptions for DIVT are shown explicitly in Figure 44. The rationale behind the numerical values attached to the horizontal and vertical axis is simple

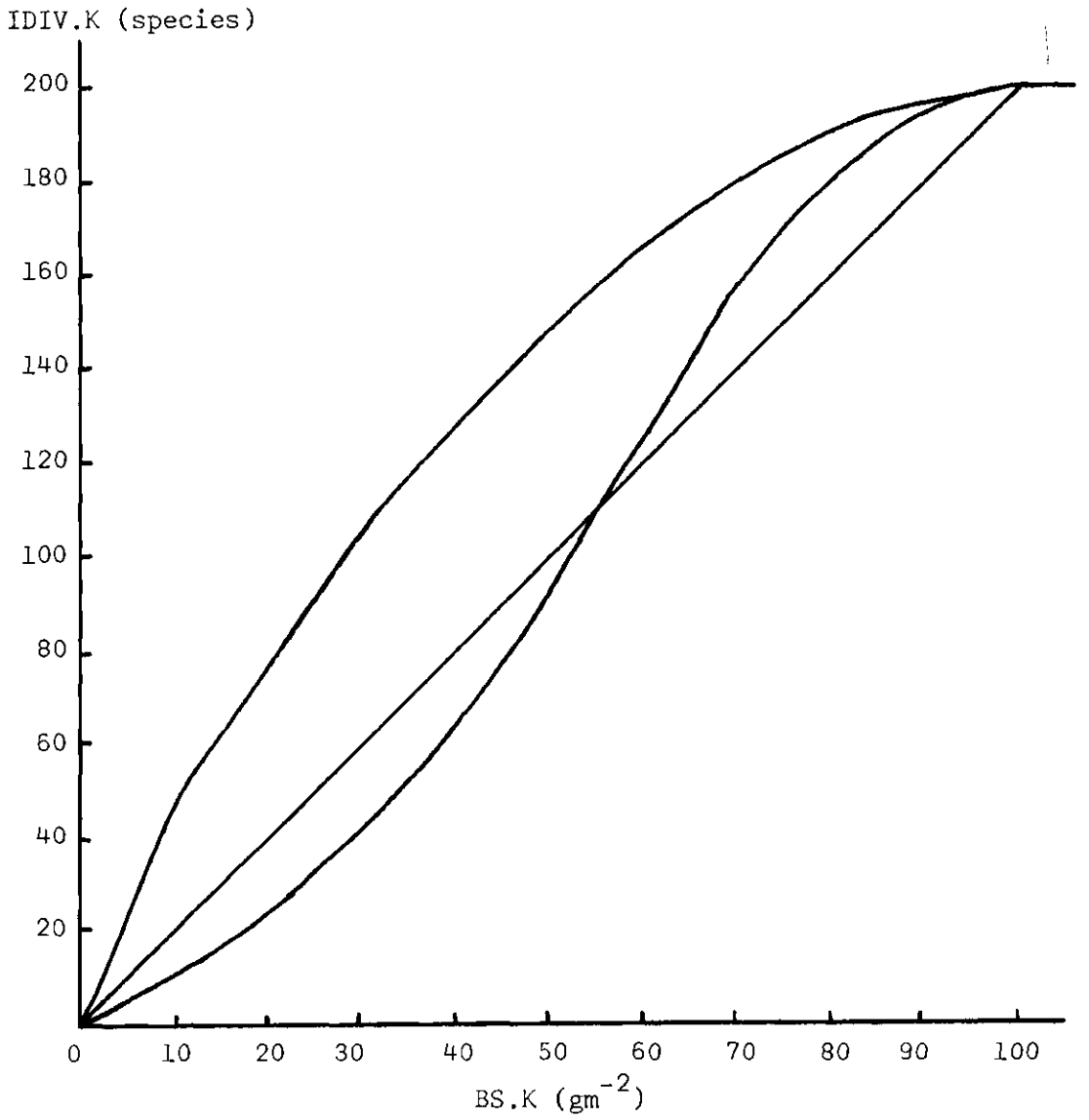

Figure 44. Indicated Diversity (IDIV.K) as a Function of Total Biomass (BS.K)

enough. The maximum accumulation of total biomass at the Pawnee grassland ecosystem appears to be approximately 120 gm^{-2} (Patten, in preparation). The maximum number of species has never been counted for this or, for that matter, for any large ecosystem. The maximum indicated number of species shown in Figure 44 is 200. The actual number may be lower or higher. The important thing is that under natural conditions it has a high value, and the influence of total biomass on community diversity continues to be positive as long as the curve does not level off. Then, the emergence rate of new species which is indicated in order to correct the difference between indicated, or goal diversity and current diversity is

$$NSER.K = (1/SED)(IDIV.K-DIV.K) \quad (112)$$

$$SED = 12$$

where NSER = new indicated species emergence rate (species/month),
SED = species emergence delay (months),
IDIV = indicated species diversity (species),
DIV = species diversity (species),

assuming new species appear for the first time on the year after successional development has reached the stage appropriate for their emergence. It does not seem reasonable, however, to assume that all new species will appear as soon as they potentially can do so. To take into account the gradual character of diversification, the indicated species emergence rate ISER of Equation (104) was formulated as the value of NSER smoothed

over a period of time (a few years, in the case of secondary succession) as follows:

$$ISER.K = ISER.J+(DT)(1/ISEAD)(NSER.J-ISER.J) \quad (113)$$

$$ISER = 0 \quad (114)$$

$$ISEAD = 60 \quad (115)$$

where ISER = indicated species emergence rate (species/month).
ISEAD = indicated species emergence adjustment delay (months).
NSER = new indicated species emergence rate (species/month).

Having accounted for the influence of biomass on diversity, let us account for the influence of diversity on biomass. As pointed out in the statement of the dynamic hypothesis (Chapter II), when the biotic community diversifies it is bound to exploit a greater number of specialized niches in the soil, and it is also bound to modify the soil so as to, effectively speaking, increase its carrying capacity after some time has elapsed. Two notions are subsumed in this statement: the notion that diversification implies further niche specialization and in turn greater soil carrying capacity, and the notion that it takes a certain amount of time (again, a few years in the case of secondary succession) for the newly diversified community to exercise its influence on the soil. These two notions find analytical expression in the following manner:

$$ISCC.K = TABHL(SCCT,DIV.K,0,100,10) \quad (116)$$

SCC.K = SCC.J+(DT)(1/SCCAD)(ISCC.J-SCC.J) (117)

SCC = TABHL(SCCT,DIV,0,100,10) (118)

SCCT* = 20/23/32/57/94/102/112/116/118/119/120 (119)

SCCAD = 60 (120)

where ISCC = indicated soil carrying capacity ($g_p m^{-2}$).

SCCT = soil carrying capacity table ($g_p m^{-2}$).

DIV = species diversity (species).

SCCAD = soil carrying capacity adjustment delay (months).

SCC = soil carrying capacity ($g_p m^{-2}$).

Figure 45 exhibits alternative assumptions about the functional relationship SCCT. In either case, the positive influence of diversity on carrying capacity is assumed to level off as the potential for further niche specialization and further soil improvement is gradually exhausted. Again, the aggregate climax value (approximately 100 $g_p m^{-2}$) of vegetation at Pawnee (Patten, in preparation) is taken as the ultimate limit for the process. As the physical environment becomes fully saturated, the capacity of the soil gradually vanishes. Therefore, the gain of the positive feedback between biomass and diversity gradually vanishes as either the nonlinearity of Figure 44, or the nonlinearity of Figure 45, or both, become limiting.

Needless to say, community diversification impacts many other factors of the ecosystem in addition to soil carrying capacity. One example, pointed out in the dynamic hypothesis of Chapter II, is the

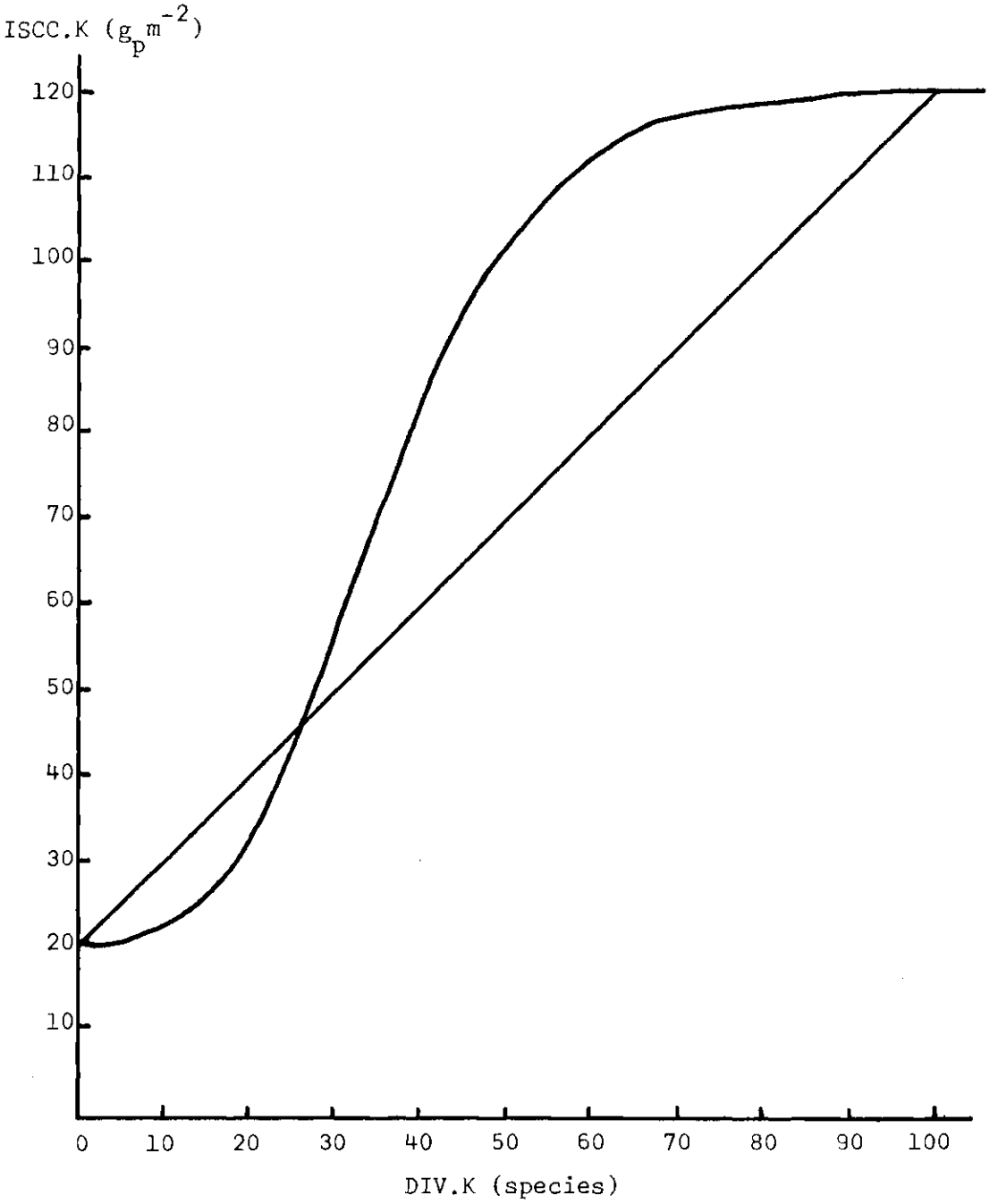

Figure 45. Indicated Soil Carrying Capacity (ISCC.K) as a Function of Species Diversity (DIV.K)

relationship between diversity and productivity. Within certain limits, productivity increases when diversity decreases, and vice versa. This notion can be used to formulate the plant production efficiency factor of Equation (30) as a function of relative diversity, where the latter index is defined as the ratio of diversity over indicated diversity. The equations are

$$PPEF.K = TABHL(PPET,DIVX.K,0,1,0.1) \tag{121}$$

$$PPET^* = 0.5/0.49/0.46/0.43/0.39/0.35/0.25/0.18/0.13/0.11/0.10 \tag{122}$$

$$DIVX.K = DIV.K/IDIV.K \tag{123}$$

where PPEF = plant production efficiency factor (dimensionless).

PPET = plant production efficiency table (dimensionless).

DIVX = diversity index (dimensionless).

DIV = species diversity (species).

IDIV = indicated species diversity (species).

Alternative assumptions can be made with respect to the non-linearity PPET. Some possibilities are graphed in Figure 46. The simplest possible alternative is, of course, to assume that production efficiency is constant. It would seem more realistic to assume, however, that production efficiency stabilizes at some modest value under undisturbed climax conditions, but rises to much higher values when diversity is either partially or completely destroyed. The range of numerical values used to quantify the function are consistent with

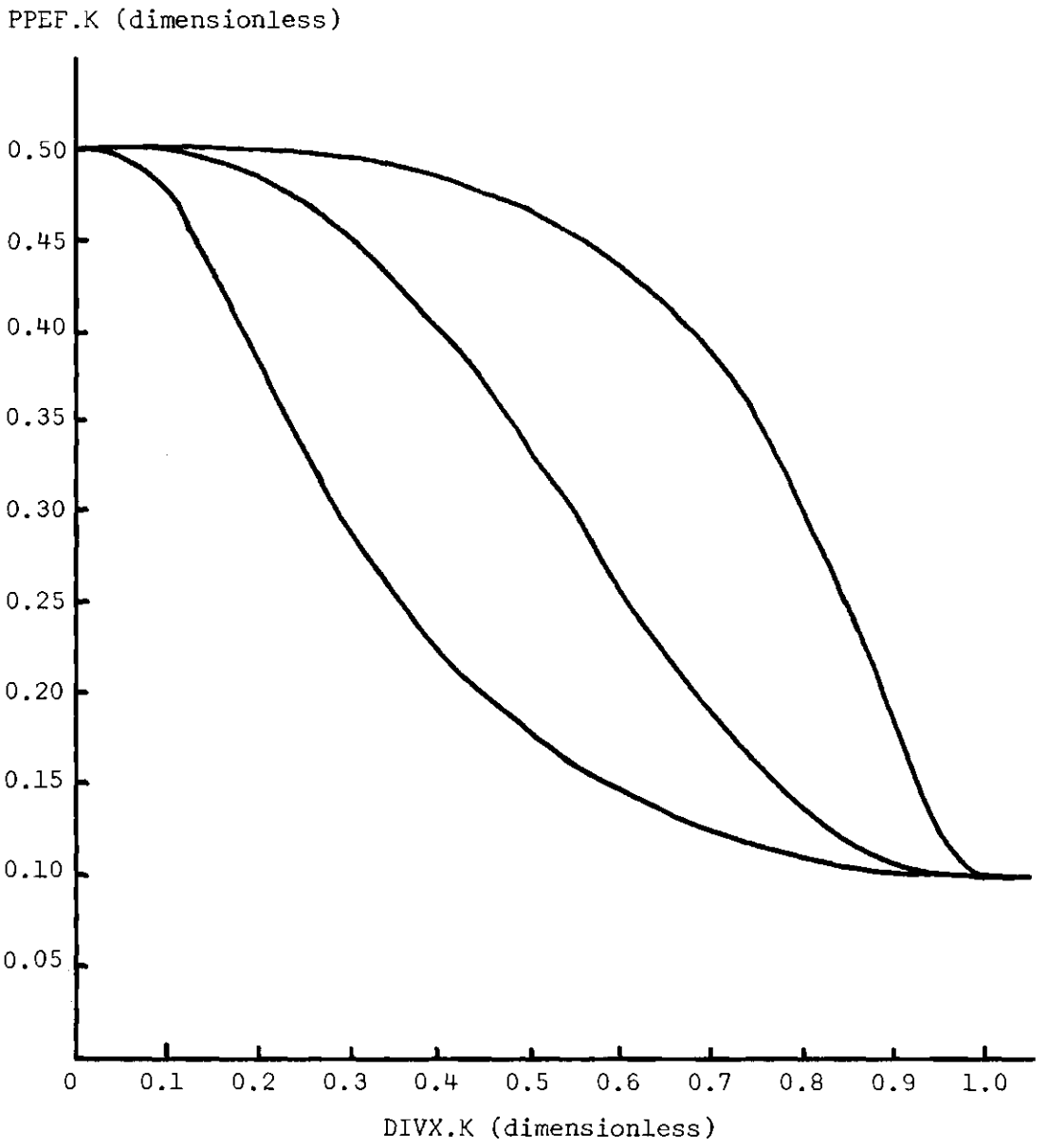

Figure 46. Plant Production Efficiency Factor (PPEF.K) as a Function of Diversity Index (DIVX.K)

empirical evidence (see, for example, Lindeman, 1942) although the numerical values themselves are not the result of field measurement. As stated before, the sensitivity of the model to these and other parameter values is reported in Chapter III.

To complete the formulation of the model, it only remains to account for the disposition of energy flow through the producers which is neither used for growth nor for diversification. For, as pointed out before, the energetics of succession are controlled by the energy strategy of the producers. As energy becomes available to the plant community, it is allocated first for production work, then to diversification work. The basic question is, of course, what happens with any energy availability rate remaining after the current energy consumption rate requirements for production and diversification work have been satiated. The hypothesis suggested in Chaper II is that such excess energy is stored as potential energy in various forms (biochemical diversity, genetic diversity, etc.) which can be lumped together as a level of stored energy or, for lack of a better term, plant vigor. Energy can be stored for a limited period of time, however; eventually, it is either dissipated in the performance of other quality functions, or be comes fossilized. In either case, after a certain amount of time it is no longer available as a supplementary source of energy for production purposes (see Equation (18)). The formulation of this part of the model was accomplished as follows:

$$PV.K = PV.J+(DT)(PVAR.JK-PVDR.JK) \qquad (124)$$

$$PV = 0 \tag{125}$$

$$PVAR.KL = MAX(0,EVAR.K) \tag{126}$$

$$EVAR.K = (ESRC)(EDAR.K-SSR.K-SER.K) \tag{127}$$

$$PVDR.KL = PV.K/PVDD \tag{128}$$

where PV = plant vigor (cal m^{-2}).

PVAR = plant vigor accumulation rate (cal m^{-2}/month).

PVDR = plant vigor dissipation rate (cal m^{-2}/month).

EVAR = energy-for-vigor availability rate (cal m^{-2}/month).

ESRC = energy-to-species requirement coefficient (cal m^{-2}/species).

EDAR = energy-for-diversification availability rate (species/month).

SSR = species substitution rate (species/month).

SER = species emergence rate (species/month).

PVDD = plant vigor dissipation delay (months).

It is important to verify whether the flow of energy through the producers is fully accounted for. When the ecosystem is in steady-state, the difference between the rates of energy flowing in and out of the ecosystem should tend to zero. The energy balance for the model is given by the equation

$$EB.K = EAR.K-EUR.K \tag{129}$$

where EB = energy balance (cal m^{-2}/month).

EAR = energy availability rate (cal m^{-2}/month).

EUR = energy utilization rate (cal m^{-2}/month).

Energy availability rate is the energy influx to the ecosystem, as given by Equation (23). Energy utilization rate, on the other hand, is equal to the summation of energy expenditure rates associated with the various work functions of the community, i.e.,

$$EUR.K = EEP.K+ERRPM.K+EED.K+ERRDM.K+EEV.K \quad (130)$$

$$EEP.K = (EPRC)(GNPGR.K+RPGR.K) \quad (131)$$

$$EED.K = (ESRC)(SER.K+SSR.K) \quad (132)$$

$$EEV.K = PV.K/PVDD \quad (133)$$

where EUR = energy utilization rate (cal m^{-2}/month),

EEP = energy expenditure rate for production (cal m^{-2}/month),

ERRPM = energy rate required for plant maintenance (cal m^{-2}/month),

EED = energy expenditure rate for diversification (cal m^{-2}/month),

ERRDM = energy rate required for diversity maintenance (cal m^{-2}/month),

EEV = energy expenditure rate due to vigor dissipation (cal m^{-2}/month),

EPRC = energy-to-plants requirement coefficient (cal/g_p),

GNPGR = gross new plant growth rate ($g_p m^{-2}$/month),

RPGR = replacement plant growth rate ($g_p m^{-2}$/month),

ESRC = energy-to-species requirement coefficient (cal m^{-2}/species),

SER = species emergence rate (species/month),

SSR = species substitution tare (species/month),

PV = plant vigor (cal m^{-2}),

PVDD = plant vigor dissipation delay (months),

and the terms ERRPM and ERRDM are given by Equations (24) and (102), respectively. Simulation exercises with the model confirmed that, in fact, the difference of Equation (129) vanishes in the steady-state. Another difference that should vanish, and in fact does, is the difference between gross production and community respiration. If respiration is defined as gross production minus net production, gross production and respiration are given by the equations

GPGR.K = GNPGR.K+RPGR.K (134)

and

RESP.K = GPGR.K-NNPPR.K (135)

where GPGR = gross plant growth rate ($g_p m^{-2}$/month).

GNPGR = gross new plant growth rate ($g_p m^{-2}$/month).

RPGR = replacement plant growth rate ($g_p m^{-2}$/month).

NNPPR = net new plant growth rate ($g_p m^{-2}$/month).

The terms RPGR, NNPPR, and GNPGR are given by Equations (9), (30), and (31), respectively. Equations (134) and (135) could be expressed in energetic units (cal m^{-2}/month) just as well by simply introducing the appropriate conversion factor, EPRC (cal/g_p). Equation (135) can be reformulated as community (rather than plant) respiration by adding the

respiration terms for consumers and decomposers. While these supplementary equations (129 to 135) in no way influence the feedback structure of the model, they were useful in printing and plotting variables of interest for model verification, as reported in Chapter III.

For the simulation experiments discussed in Chapters III and IV, it was also necessary to incorporate into the model the ability to introduce exogenous perturbations to test model performance under both natural and utilization conditions. Thus, perturbation terms were added to plant depletion rate (Equation (6)) and diversity decrease rate (Equation (88)) to test model response to destructive natural perturbations such as fire, drought, etc. Terms to account for the introduction of domestic consumers were added to grazing plant depletion rate (Equation (56)) and consumer organic nutrients becoming available (Equation (60)) to test model response to grazing pressure. The analytical formulation of these perturbation terms is straightforward, i.e., simple pulse and step input functions of constant amplitude to simulate the effect of transitory and sustained perturbations, respectively. The simulation runs were performed by exercising the model using a solution interval of one month. Needless to say, the model can be exercised in any digital computer for which the DYNAMO compiler is available.

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