Introduction

1

Nature abhors a vacuum
—Spinoza (ca. 1677)

1.1 Objectives

When a forest is cut, the land cultivated for a period of time and then abandoned, the resulting "old-field" or bare area is gradually colonized anew by vegetation. After a number of years, the vegetation may come to exhibit the density and composition of the original forest, but not without first passing through a succession of stages with different dominant species. This process whereby nature covers denuded lands with vegetation and, consequently, with animal life as well, is termed ecological succession.

Ecological succession is responsible for 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 the process of ecosystem development. Succession is a universal, exceedingly complex process that involves the ecosystem as a whole and may be examined from many 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.

There appears to be general agreement, however, that secondary succession is a critical process to understand and control if we are to manage ecosystems successfully (see Ellison, 1960; Odum, 1969; Horn, 1975). The basic issues involved are those of productivity and stability. Climax (mature) ecosystems typically exhibit low productivity and high stability, while seral (immature) ecosystems are typically very productive, but also very unstable. Therefore a mature ecosystem such as a climax forest maintains itself and protects itself from environmental perturbations, but does not produce much excess biomass that can be harvested frequently by man. Conversely, if the forest is cut, the land can become very productive if properly cultivated, but then the ecosystem becomes dependent on man's protection and supplementary inputs of energy.

From an ecosystem management perspective, there is a wide spectrum of important cases between conserving an ecosystem in climax condition and sustaining it when the natural vegetation is completely removed and substituted by crops. The importance of gaining a better understanding of successional dynamics arises from the fact that ecosystems succeed in various ways under various modes of human utilization. An excellent case example is provided by the successional response of grasslands when the natural equilibrium between plants and animals is perturbed by the introduction of livestock. It has long been recognized that plant succession results from sustained grazing (Sampson, 1919). 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. What is most needed from the viewpoint of range ecosystem management is an analysis of secondary succession as provoked by light or moderate grazing, so that we can learn to what extent grazing can be manipulated as a constructive ecological force. Unfortunately the successional response to moderate 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 time and space for secondary succession to be observed after an exogenous perturbation, such experimentation must be carried out in the model world.

Some additional considerations that delimit the scope of the present volume are in order. Our 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 mind another important consideration: if a meaningful quantification of the test model is to be achieved, it must be ecosystem-specific. Once a dynamic model 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 test model. A general description of this ecosystem is given by Jameson and Bement (1969). The Pawnee national grassland is under the management of the Forest Service, U.S. Department of Agriculture (USDA). The Central Plains Experimental Range, managed by the Agricultural Research Service, USDA, is located in the southwest corner of the national grassland. As part of the U.S. International

Biological Program (IBP) Grassland Biome Study, the Pawnee site was developed to serve as focus for intensive data collection activity. The Pawnee site consists of portions of the Central Plains Experimental Range and the Pawnee National Grassland. Therefore the Pawnee ecosystem is part of the western grassland biome and, ecologically speaking, is classified as a shortgrass 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. The primary concern of the IBP Grassland Biome study was data collection on intraseasonal as opposed to successional dynamics. Nevertheless, there now exists, as a result, a wealth of functional and structural information about this ecosystem that made it a natural choice as the subject ecosystem for quantification of the test model. Complete long-term successional time histories do not exist for Pawnee or any other large-scale ecosystem. However, fragments exist that permit identification of certain generic time patterns of succession in both aquatic and terrestrial ecosystems. In our work, Pawnee data served to quantify some of the model parameters that determine the physical and biological limits to succession in the shortgrass prairie environment. Descriptive data on succession of grasslands and other ecosystems was used to approximate the model parameters which determine the time constants of succession.

1.2 Ecosystem Analysis Background

There are two reservoirs of knowledge from which the present research draws: the literature of ecological succession and the literature of feedback dynamics. Available accounts of ecological succession are based on numerous field observations, as well as on the general literature of ecology, a venerable body of knowledge under development since ancient times. Feedback dynamics, on the contrary, is a relatively recent development based on cybernetics and computer simulation methods. 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 to document 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 section, together with a discussion 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 a consensus that the term "ecology" was the first introduced in the nineteenth century (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. The British ecologist Macfadyen (1957) has stated:

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, for example, 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 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, the use of ecological principles for managing natural environments (Van Dyne, 1968). Of primary interest for the purpose of the test model to be developed 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 (1968a), Coupland et al.

(1969), Costello (1969), Spedding (1971), and Duffey et al. (1974). 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).

An abundance of descriptive information on successional dynamics in grasslands and other ecosystems has been accumulating for many years in the ecological literature, starting with early studies such as those by Cowles (1899, 1901, 1911), Shelford (1911a, 1911b), Clements (1916), Shantz (1917), Cooper (1926), and Tansley (1929, 1935). In his classical paper, Lindeman (1942) was the first ecologist 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 (Margalef, 1963, 1969; Odum, 1969; Preston, 1969; Whittaker, 1970). Drury and Nisbet (1973) have attempted to explain succession as the outcome of competitive interactions at the organism level. The most comprehensive of recent accounts on succession is possibly that provided by Daubenmire (1968b). He points out that what is known about successional processes has been found by one or more of the following methods of study: repeated observation of permanent plots over a period of time, comparisons of existing vegetation with old records, analysis of age-class distribution in a stand, analysis of the nature and occurence of relics, studies of bare areas of different ages, and analysis of fossil sequences. Another method, involving experiments with laboratory microcosms (Cooke, 1967) has provided empirical evidence that succession arises from the internal structure and function of the ecosystem even when it is completely closed to all external inputs except light.

In recent years, increasing recognition of the ecosystem concept and progressive maturity of systems science has led to systems-ecology research, 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; de Wit and Goudriaan, 1974). In the area of grasslands, a significant amount of research has been conducted at Pawnee and other sites by the 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 laws coupled with their largeness severely limits the utility of these models (Innis, 1972b), they are contributing significant new insights about 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. Leak (1970, 1971), Bledsoe and Van Dyne (1971), and Bartos (1973) have presented dynamic models of species substitution during succession. These models, however, are formulated in open-loop form with respect to nutrient cycling and other ecosystem processes. 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 of ecosystem succession has been reported only recently by the authors (Gutierrez and Fey, 1975a, b, c) and is presently reported in full detail for the first time. We believe that simulation experiments with computer models, if properly used in conjunction with field and laboratory experiments, offer a tremendous potential to advance the study of succession.

1.3 Research Methodology

It must be recognized that simulation experiments cannot possibly provide positive proof of the validity of a given hypothesis. There is always the danger of circular inferences or deductions. However, this danger is also present in other succession analysis methods (Horn, 1975), and computer simulation offers a potential vehicle for hypothesis generating and testing when the size of the system or the duration of the process under study (or both, as in the case of ecosystem succession) make controlled field experimentation difficult. Simulation is rapidly coming of age as a research method in ecology. Watt (1973) already discusses computer simulation, together with the classical inductive and deductive methods and the comparative method of Darwin, as a method of ecological research. He states:

> In the last few years, another method of testing hypotheses has become available: computer simulation. For example, we could program a computer with a mathematical model which mimics the behavior of a forest. Then we could test the hypothesis that of five alternative strategies for managing a forest, over a 100-year period, strategy 5 maximized the long-term productivity of pulpwood from the forest. The hypothesis would be tested by using the computer to simulate, or mimic, the behavior of the forest over the 100-year period, using each of the five alternate strategies. Clearly, this is a type of test that would not be feasible in nature because it would take too long and be too expensive, but using traditional mathematical deduction would not be possible either, because of the great complexity of the system of equations required to describe the behavior of the forest.

The essence and utility of dynamic simulation models have been summarized by ecologists de Wit and Goudriaan (1974) as follows:

> A system has a pattern of behavior which implies that the system changes with time, that it is dynamic. A simplified representation of a dynamic system is a dynamic model. An operational definition of simulation is the building of a dynamic model and the study of its behavior. Simulation is useful if it increases one's insight of reality by extrapolation and analogy, if it leads to the design of new experiments and if the model accounts for most relevant phenomena and contains no assumptions that are proven to be false. The latter requirement seems obvious, but is nevertheless formulated because such assumptions are often made to enable analytical solutions of mathematical models. With more recent simulation techniques this limitation can often be overcome, so that attention may be shifted from solution techniques to the study of behaviour of model and system.

There are, of course, many different types of simulation techniques available to the investigator. The method we have chosen is that originally 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'' has been adopted more recently (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 book.

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 ecosystems, since proper manipulation of these processes is required for their preservation and improvement under utilization conditions. We shall review in the next chapter the various patterns of dynamic behavior that ecosystems exhibit during succession as well as the ecosystem factors or variables that appear to interact to generate succession. 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 involved tracing the feedback loops coupling organic matter, inorganic nutrients, species diversity, and other internal variables of grassland ecosystems, 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 that are believed to cause the system behavior of interest constitutes a dynamic hypothesis, a theory of how system behavior results from its internal feedback structure. We shall be concerned with developing a dynamic hypothesis to integrate ecosystem structure and successional dynamics.

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, 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 ecosystem. Exogenous inputs to a grassland ecosystem, for example, are solar light, precipitation, and introduction of domestic animals.

The feedback loop is the basic system component, and the identification of the loop or set of interconnected loops believed to structure the system constitutes the dynamic hypothesis to be tested.

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 that remain measurable in an ecosystem at rest are properly classified as levels, such as 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 quantify the various model relationships; in this research, data required to quantify the model and permit testing of the dynamic hypothesis were abstracted from the literature on grassland ecosystems to the extent of their availability, but otherwise reasonable numerical values were assumed. In closing the discussion on the model-building aspect of the methodology, it is interesting to note that structuring an ecosystem model in this manner is in complete consonance with the best knowledge available on ecological modeling. H. T. Odum (1971), for example, classifies ecosystem components as (1) energy storage compartments, (2) energy flow pathways, (3) energy sources and sinks, and (4) complex work functions, to couple the various energy storages and flows throughout the ecosystem.

Subdivisions (1), (2), and (4) 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, to explicitly delineate the boundaries of the system being modeled. 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 test model for grassland succession has been developed in the DYNAMO (DYNAmic MOdels) language (Pugh, 1963).

Modeling work 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 in 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 that is itself qualitative and dynamic. A dynamic validation concept appropriate for this research is presented in figure 1.1.

Development of simulation models of ecosystem succession will draw from the currently available reservoir of ecological knowledge and general dynamic system principles, themselves the result of previous experimentation with (real-world) systems (denoted by the dashed-line block at the right in figure 1.1.) The block of dashed lines at the left of the figure denotes simulation, that is, 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 causal relationships between the variables are meaningful and realistic in terms of, and consistent with, all relevant information available on the structure of

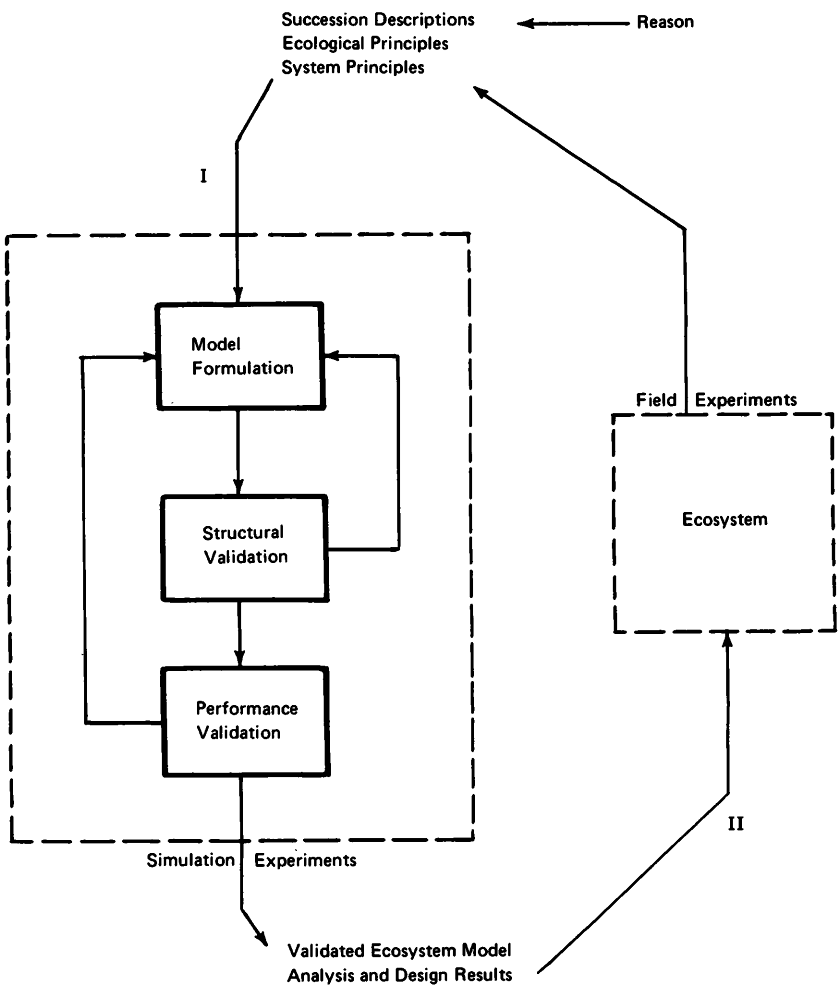

Figure 1.1
Dynamic validation concept.

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, involving 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 II of figure 1.1, 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.