

Technical Report No. 32
SOME CONCEPTS OF MODELLING*

Coordinated by Gordon Swartzman

Faculty and Research Associates:

L. J. Beldsoe
R. C. Francis
N. R. French
D. A. Jameson
F. M. Smith
G. L. Swartzman
G. M. Van Dyne

Graduate Research Assistants:

C. V. Baker
D. L. Bartos
A. F. Galbraith
J. E. Mitchell
D. G. Peden
K. A. Redetzke
D. M. Swift

Major Faculty Consultants:

K. G. Doxtader
J. W. Mayeux
W. D. Striffler

GRASSLAND BIOME

U. S. International Biological Program

February 1971**

* A report of this type represents the amalgamation of ideas and knowledge of many individuals. In effect, it has arisen through reciprocal presentation and open, constructive criticism (sometimes highly spirited) of ideas among most of the Grassland Biome participants. The above-mentioned participants had the responsibility for maintaining continuity and for setting these concepts on paper.

** (This report was originally distributed in April 1970. Because of demand, a reprint has been made including minor editorial changes.)

TABLE OF CONTENTS

	Page
Title Page	i
Table of Contents	ii
Abstract	iv
1. DEVELOPMENTAL HISTORY	1
1.0 Introduction	1
1.1 Magnitude of Effort	4
1.2 State of the Art in the Grassland Biome	5
2. BRIEF CONSIDERATION OF KINDS OF MODELS	5
2.0 Introduction	5
2.1 Compartment Models	6
2.1.1 Forms of compartmental models	7
2.1.2 Some problems in solution of compartmental model equations	9
2.2 Transfer Function Approach	10
2.3 Population Dynamics	18
2.3.1 Population dynamics approaches	18
2.3.2 Population dynamics modelling	18
2.3.3 Life table and Markov models	21
2.4 Electrical Analog Energetics Approaches	24
2.5 Structural and Statistical Models	26
2.5.1 Pattern	28
2.5.2 Classification, ordination, and related multivariate methods	30
2.5.3 Diversity	32
2.5.4 Dispersion and dispersal	33
2.5.5 Migration models	38
2.5.6 Successional, time lag, and autocorrelation models	39
3. GENERALIZED HIERARCHICAL REPRESENTATION OF ECOSYSTEM RELATIONSHIPS	41
3.1 The Hierarchical Concept	41
3.2 Model Formulation from Hierarchical Diagrams	44
3.3 Producers	46
3.3.1 Producer biomass and distribution	46
3.3.2 Internal and external environment	47
3.3.3 Physiological functions	49
3.3.4 Spatial relations	49
3.3.5 Envisioned or possible producer level models	50
3.3.6 Operating producer level models	54

3.4	Consumers	58
3.4.1	Consumer population	58
3.4.2	Consumer weight change of an individual	61
3.4.3	Net energy and those factors which affect it	62
3.4.4	Clarification of consumer hierarchical diagram ambiguities	65
3.5	Detritus Chain	74
3.5.1	Microbial hierarchical diagram structure	74
3.5.2	Detritus chain models	76
3.6	Abiotic: Climatic	76
3.6.1	Net shortwave radiation hierarchical diagram	81
3.6.2	The climatic subsystem	81
3.7	Abiotic: Edaphic	84
3.7.1	Soil water hierarchical diagram	84
3.7.2	Soil water models	88
4.	INTERRELATIONSHIPS BETWEEN MODELS	92
5.	CONCEPTUAL INTERRELATIONSHIPS OF MODELS	100
5.0	Introduction	100
5.1	Whole System Models Built from the Ground Up (Type 1)	100
5.2	Whole System Models Constructed by Interfacing of Submodels (Type 2)	101
5.3	Increasing the Realism and Precision of the Model	103
5.4	Notational Conventions for Model Development	106
6.	MODELS AND EXPERIMENTS	110
6.1	Design and Redesign	110
6.2	A Simplified Example	113
6.3	Evaluation of Experimental Projects and Models	124
6.3.1	An example	126
6.3.2	Deficiencies of the method	129
6.4	Some Possible Extensions and Generalizations	129
6.4.1	Regional grassland models	130
6.4.2	Comparative plant-climate relations	131
6.4.3	World-wide grassland models	131
6.4.4	Interbiome models	132
	REFERENCES	133

ABSTRACT

This technical report, developed through a team approach, gives a summary of the modelling concepts used in the U.S. IBP Grassland Biome. After a brief introduction to the history of the project, the kinds of modelling techniques or approaches are presented including compartment models, transfer functions, population dynamics, electrical analog energetics, structural models, and statistical models. Following this is an introduction to the hierarchical concept and formulation of hierarchical diagrams to represent causal relationships of processes for producers, consumers, detritus chain, climatic, and edaphic variables. The discussion also involves the development of models from these diagrams and the categorization of existing models within the hierarchical framework. After a section on the interrelationships between models and generalized notation conventions for our modelling, a theoretical framework is introduced for the evaluation of experiments in view of their inputs into a model and vice versa. A simplified example of this approach is presented. Finally, our ideas about a series of models applied to areas of varying dimension (e.g., one grassland experiment station, all temperate grasslands, all grasslands, etc.) are given.

1. DEVELOPMENTAL HISTORY

1.0 Introduction

In any consideration of strategy of how to move ahead, it is useful to review how we got where we are. This section, essentially, is an attempt to *"tell it like it is"* with respect to the history and development of modelling and analysis in the Grassland Biome program.

Modelling and analysis has been a central theme in the total planning of the Grassland Biome project. So says the proposal developed in December 1967, and it is reflected in a list of some 10 external scientists who gave advice on modelling and analysis, consideration of modelling problems, and experimental design problems, including a discussion of the role of modelling in synthesis, sensitivity analysis, model validation, and discussion of mathematical models for ecosystem phenomena. A 22-page appendix enumerated examples of mathematical models and evaluated them in the context of the proposed Grassland program. This proposal requested \$1,898,360 for the 12-month period of April 1968 through March 1969, and included support for a mathematical biologist, a biometrician, and a systems analyst in addition to senior scientists to coordinate the data processing and analysis and the several processing laboratories. History shows these funds *did not become available*, nor did the people, but the idea of modelling carried on.

Perhaps the first model developed specifically in and for the Grassland Biome program was a "picture model" developed in March 1968 and used to show the allocation of research projects and research dollars in a proposed revised budget of \$750,000 for a 15-month period beginning in June 1968. This model recognized the following components of the grassland system in a compartmental framework: atmospheric-climatological, live plants, standing dead, plant litter, microflora, soil-hydrological, herbivores, omnivores, carnivores, soil fauna, and animal litter.

Perhaps the next specific attention to modelling occurred in the first information synthesis workshop when a paper was presented which reviewed some of the concepts and examples of mathematical modelling in grasslands. This review leaned heavily on picture models, but also provided examples of numerical implementation of compartmental models solved by either digital or analog computer methods (Van Dyne 1969b).

A large step forward in the history of modelling in the Grassland Biome program was the formulation in December 1968, of a "*can of worms*" model which was included in our progress report and continuation proposal submitted to NSF in January 1969. Also included in that report was a conceptual formulation, later reproduced in another report (Van Dyne 1969a), which recognized the following model segments: system components, driving forces, system parameters, ecological and physiological processes, and human and behavioral controls. The components, driving forces, and parameters were visualized as sets. The emphasis in this conceptualization was on function rather than on structure, although spatial patterns were shown to have effect through the set of control functions and temporal patterns to have effect through lag responses to the past driving forces and system components.

During winter quarter 1969, two of the Grassland Biome program participants involved in teaching an Ecological Simulation course utilized the skills and energies of a group of graduate students (forced labor!) to develop as their final exam problem a large computer program which simulated the nine-compartment (or possibly 10-compartment) total-ecosystem model. This model was based in part on real data, but primarily on extraction of values from the literature. The model had both deterministic and probabilistic components. Essentially, the model worked with major driving forces of

solar energy input, temperature, and precipitation. Temperature and precipitation records were taken directly from Pawnee Site locality and solar energy input was generated for that longitude and latitude. The basic compartments of the system included live plants, standing dead, plant litter, herbivores (antelope), carnivores (coyotes), dead animals, feces, decomposers, and detritus. (An implicit tenth compartment was respiration *in toto*). This computer program was carried only to student-exam level of precision, but reasonable output was obtained and is present elsewhere along with a listing of the program (Van Dyne 1969b).

Problems of modelling and analysis were discussed in all of the information synthesis workshops and many of these concepts and ideas were included in a paper presented in the last workshop in May 1969 (Bledsoe and Jameson 1969). Many of these concepts are referred to herein.

With new money infused into the program for at least a 16-month duration (note: the first 15 months were funded in four segments), effort was made in Autumn 1969, to add to the modelling and analysis capabilities of the staff. Through joint arrangements with three departments on campus, we were able to secure a new systems engineer and biostatistician. During fall quarter these two individuals, along with an existing computer-analytical specialist, interacted strongly with various project scientists, primarily from the Colorado-Wyoming area.

Separate discussion groups were held to evaluate problems of modelling and analysis with specialty area interests in mind. These discussions served to orient both the new analysts in the problems of biology and ecosystems and to orient the physical and biological scientists to the analysts. During the fall and winter weekly discussions were held on problems of modelling

and analysis. This discussion group included the three analysts mentioned above and, usually, three biologists involved in program management and administration, a mathematician with specialization in differential equations, and a few graduate students with special interests and projects in modelling and analysis.

1.1 Magnitude of Effort

It is difficult to estimate the amount of time and funds that have been spent on mathematical modelling per se, because no one individual or group is working solely on this effort. Individuals working in this area split their time among various experimental, data-processing, and modelling efforts. Secondly, it is difficult to indicate when modelling starts, because it requires much discussion and analysis to develop even tentative graphic models before they are eventually implemented into analytical models. However, for purposes of comparison the following estimates are made.

Estimates of manpower input in modelling in
the Grassland Biome program, September 1969
through February 1970.

Individual	Type of Effort:		
	Modelling Planning	Conceptual Development and Reviewing	Analytical Implementation
	Man Days*		
Swartzman	6	30	25
Francis	3	16	15
Bledsoe	8	24	23
Jameson	4	4	1
French	3	2	1
Van Dyne	5	6	1
Project scientists**	5	22	5
Programmers	7	25	100
TOTAL	41	129	171 (Σ 341)

* Estimates are probably $\pm 33\%$

** Based on inputs from about 15 scientists

Nearly 16 man months have been expended in the modelling effort to date. Perhaps 50% of this time has been in the category of analytical implementation, about 33% of the time in conceptual development and reviewing of methods and techniques, and about 10% of the time in planning of the program related to modelling. Categorized in another manner, somewhat over 40% of the time is spent each by analysts per se and by programmers, and somewhat less than 10% of the time by each project scientists and project management personnel. Understandably, these figures are imprecise but provide an "order of magnitude" estimate of the input.

1.2 State of the Art in the Grassland Biome

The following sections of this report have as their major role simply to take stock of what we have done and where we stand. In keeping with the disclaimer notice for the technical report series, this is a preliminary review of concepts and ideas examined within the framework of our modelling efforts in the Grassland Biome. It is through such analysis of efforts we hope to determine where we are going and examine the direction, magnitude, and distribution of our activities. There is no finalty about most of the conclusions in this paper. In addition to this report serving us in our own self-examination, we hope the reader will also offer us constructive criticisms.

2. BRIEF CONSIDERATION OF KINDS OF MODELS

2.0 Introduction

This section addresses itself to a brief review of the general kinds of models available to and used by ecologists in considering either segments of or entire ecosystems. In many instances the models have been applied in management of renewable resources and some examples come from that area. It does not include a thorough review of all the analytical procedures available.

If a model is an abstraction of a real system then that abstraction must have some real medium of expression. The classical symbology of mathematics is a precise medium for expression of a model; however, it is sometimes desirable to sacrifice precision for ease of communication. Pictorial and diagrammatic models are easier to use for communication of the main ideas of a mathematical model and to summarize the equations. We have found a number of categories of mathematical models and their diagrammatic counterparts useful for various applications. The five categories discussed here are compartment models, transfer functions, population dynamic, electrical analog, and structural models.

The first four categories are analogous in the sense that they are all dynamic (time is the principal independent variable) and that their mathematical analysis may be broken down to or abstracted from differential equations (DE). Each of the first four frameworks is general--they do not necessarily relate to a particular phenomenon--but they do suggest particular methodologies. The population dynamics category, which would seem to be phenomenologically oriented, is used as a generic term for a set of methodologies designed to deal with systems having two-time related variables--time in the usual sense and age. The last category, models for structural properties, is admittedly a "catch-all", but is included primarily to encompass the many kinds of structural, static models in contrast to the dynamic models mentioned above. Even here, the structural models may include dynamic aspects. In these systems the principal independent variable is frequently other than time.

2.1 Compartment Models

Intuitively, a compartment model is an abstraction of a system whose dependent variables can be thought of as describing the contents of various "boxes" or compartments, between which a flow of material or energy, represented

by interconnecting arrows, takes place. This concept is generalized to the point that we might consider using the box and arrow diagram to describe for example, what happens when, in succession, the biomass of species A declines as that of species B increases (Fig. 2.1.1). We are aware that no flow of organic material actually is taking place here, however the analogy is still useful in an abstract sense. The same mathematical form can be employed whether the flow is real or abstract.

2.1.1 Forms of Compartmental Models

Mathematically, a compartment model is, in its most general form, any system of first order differential equations. The system might be a closed, conservative one in which the sum of all the variables is a constant corresponding to some constant amount of material in the system. Or it might be an open, conservative system in which a change in one system variable results in either a change of opposite sign in another variable or in a loss from or gain to the system. Any model in which the principal dependent variables are energy densities is an open, conservative system. Or the abstracted system might have little or no conservative properties, as the successional system mentioned above.

Since the compartment model is so often represented by a box and arrow diagram, many people think it is of limited utility. When one realizes that its most general definition is as a system of first order differential equations the extreme generality of the concept becomes apparent. Under this definition the following categories are subtypes of compartment models in their mathematical form. The *transfer function model* is, in the form most frequently used in biology, a set of first order DE's (higher order forms can be reduced to first order by a transformation of variables). The integral equations of *population dynamics models* are merely nonlinear forms of first

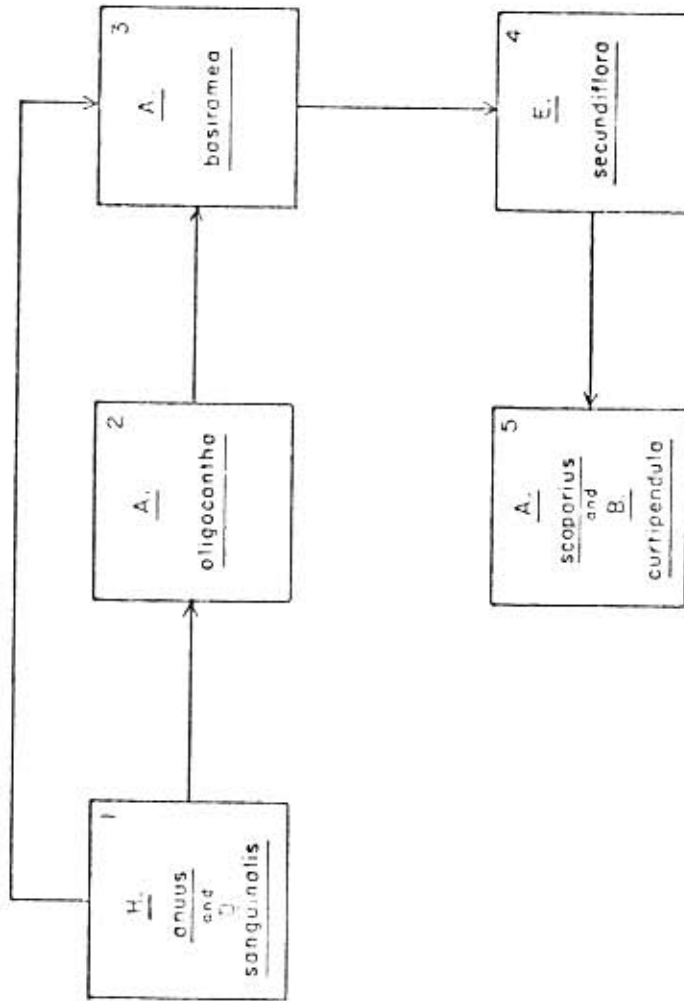


Fig. 2.1.1 Form of initial five compartment model for succession of dominant species on abandoned cropland in central Oklahoma. (From Bledsoe and Van Dyne, 1970)

order DE's. The basic method for analysis of electrical networks is first order, ordinary, linear, constant-coefficient DE's. Thus the *electrical analog model* of an ecosystem can be expected to be no more complex in its abstraction than such a set of equations.

The important facet of these other forms of models is not their mathematical aspect, which, as shown above, is not significantly different from the compartment model, but their diagrammatic counterparts. The box and arrow type diagram is cumbersome and inadequate for representation, for example, of the population dynamics of animals. Any examination of these parts of the grassland ecosystem diagram in Bledsoe and Jameson (1969) should make this apparent. Alternately, the box and arrow diagram is admirably suited to representation of other aspects of the ecosystem (nutrient and energy flow). The diagrammatic representation for a model should be chosen according to the subject matter of the model and the purposes to which the diagram will be put.

2.1.2 Some Problems in Solution of Compartmental Model Equations

The frequent occurrence of nonlinear terms renders an analytical approach to DE solution impractical in ecological simulation.

With the exception of analysis after model construction, a numerical solution via digital computer is preferable to the classical techniques of mathematical analysis. The availability of rapid digital integration techniques coupled with the convenience of computer graphical output display allows the modeller to focus his attention on the ecological rather than mathematical or computational aspects of his problem.

We generally regard integration problems as minor due to numerical approximation techniques. The wide envelope of stability, accuracy, and speed of

Runge-Kutta techniques makes them superior to other multi-step methods which usually involve more complex programming and must be started with the Runge-Kutta procedure in any event. A recent summary of techniques for digital simulation by Benyon (1968) discusses various differential equation solution techniques. Tech. Rep. No. 33 contains a description of ODE, a general purpose routine for numerical integration. ODE allows the user to choose between the speed of the Euler technique for debugging purposes (where accuracy considerations are of low priority) and the high stability and accuracy available from a fifth order Runge-Kutta procedure. The particular implementation of the Runge-Kutta technique automatically varies the integration step size so as to allow a uniform solution accuracy over the entire range of time values. This procedure has proved extremely fast, for a given accuracy, compared to several multi-step methods.

A variety of other techniques for solution and analysis of sets of DE's are available. Some very powerful and general matrix decomposition (eigenvalue-eigenvector) routines have been used on sets of linear equations (Bledsoe 1969). The matrix exponential method (Bellman 1960) of linear constant-coefficient equation solution is programmed and available. The matrizant technique (Amundson 1966) is under investigation for linear DE's with coefficients which are functions of the independent variable. Harmonic analysis procedures including autocorrelation, cross correlation and fast Fourier analysis are in use, both for DE steady-state analysis and investigations of properties of field measurements.

2.2 Transfer Function Approach

The transfer function approach for representation of energy flow through an ecosystem has been offered as an alternative to the conventional compartment representation. In the transfer function approach the lines

(arrows) represent the energy (biomass) compartments and the boxes (transfer functions) represent the processes that transfer energy or biomass between its various forms. In the compartment model, on the other hand, each compartment's biomass is represented by a box, while the processes resulting in biomass interchange are represented by arrows between the boxes. It is apparent that each of these representatives could be looked at as the *dual* of the other.

Figure 2.2.1. shows the compartmental representation of a model for energy flow through an ecosystem. The model is termed a "nine compartment" model in that the energy at any time is distributed between nine "compartments". The triangles (arrows) represent the processes acting to exchange biomass between the compartments. The model was described by Van Dyne (1969b) and a crude, but running form was programmed.

Figure 2.2.2 shows the transfer function diagram for the same nine compartment model shown in Fig. 2.2.1. The energy-converting processes are listed at the top of the page, while the various compartments are identified on the left hand side of the page. Each compartment is identified by a different kind of line, e.g., the dead animal compartment is denoted by a wavy line. A box denotes transfer of energy between compartments and is identified with the process listed directly above it, e.g., photosynthesis is seen as a "box" converting solar energy to live plants. When the energy (biomass) in a compartment comes from more than one source, the energy sources are combined using a circular "summing junction". Initial conditions of the energy in a compartment are denoted by a triangle and feed into a summing junction along with the energy coming from other compartments. Thus, the initial amount of fecal energy (biomass) in the system is fed into a summing junction along with fecal material produced by herbivores and carnivores through defecation (denoted by x's in Fig. 2.2.2)

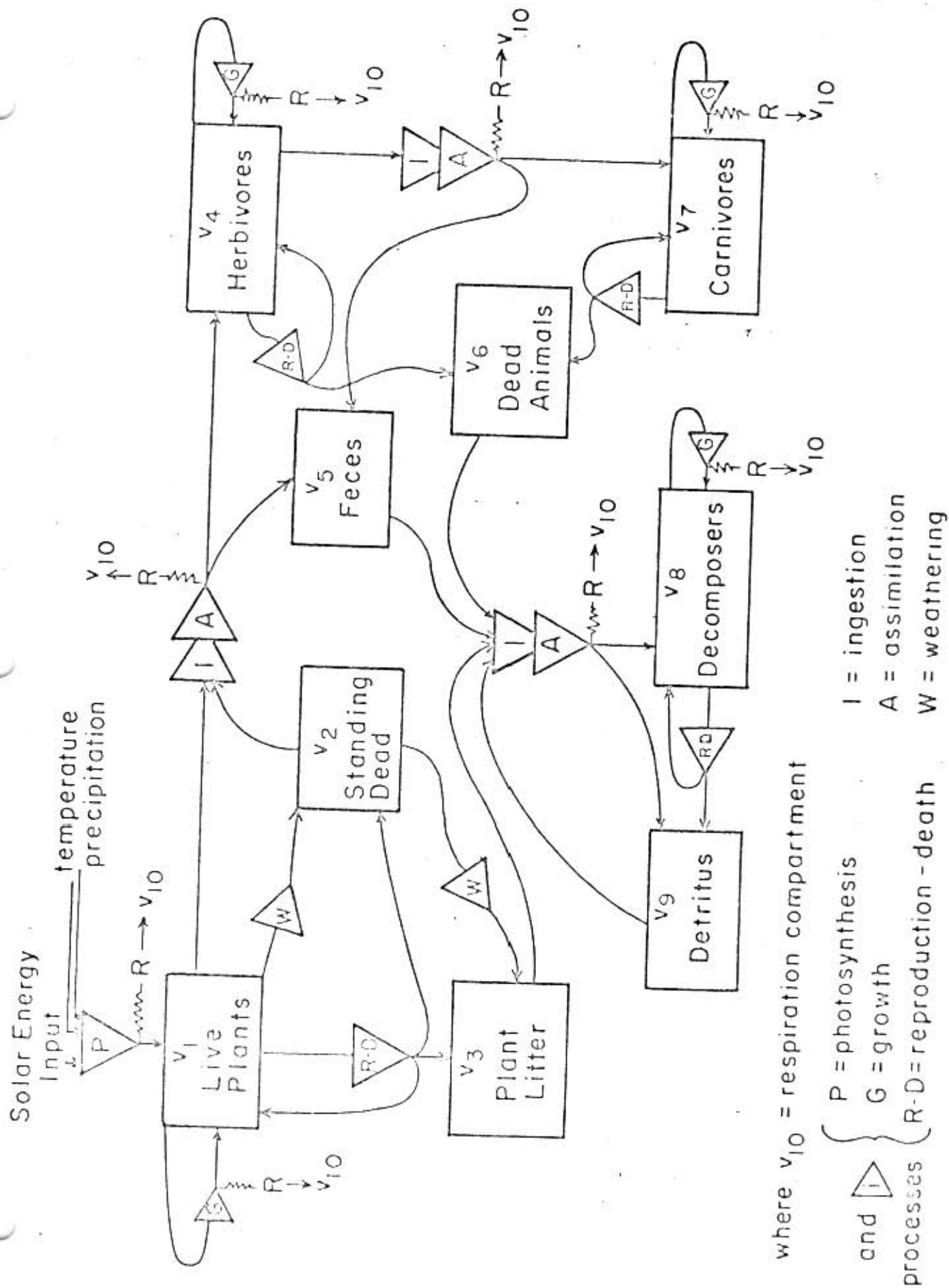


Fig. 2.2.1 A diagram for a 9-compartment multi-trophic level grassland ecosystem. Energy flow is shown by arrows and compartments, in squares, are connected through processes, triangles. At many steps there is a respiratory energy loss, R , to the environment, v_{10} (Van Dyne, 1969)

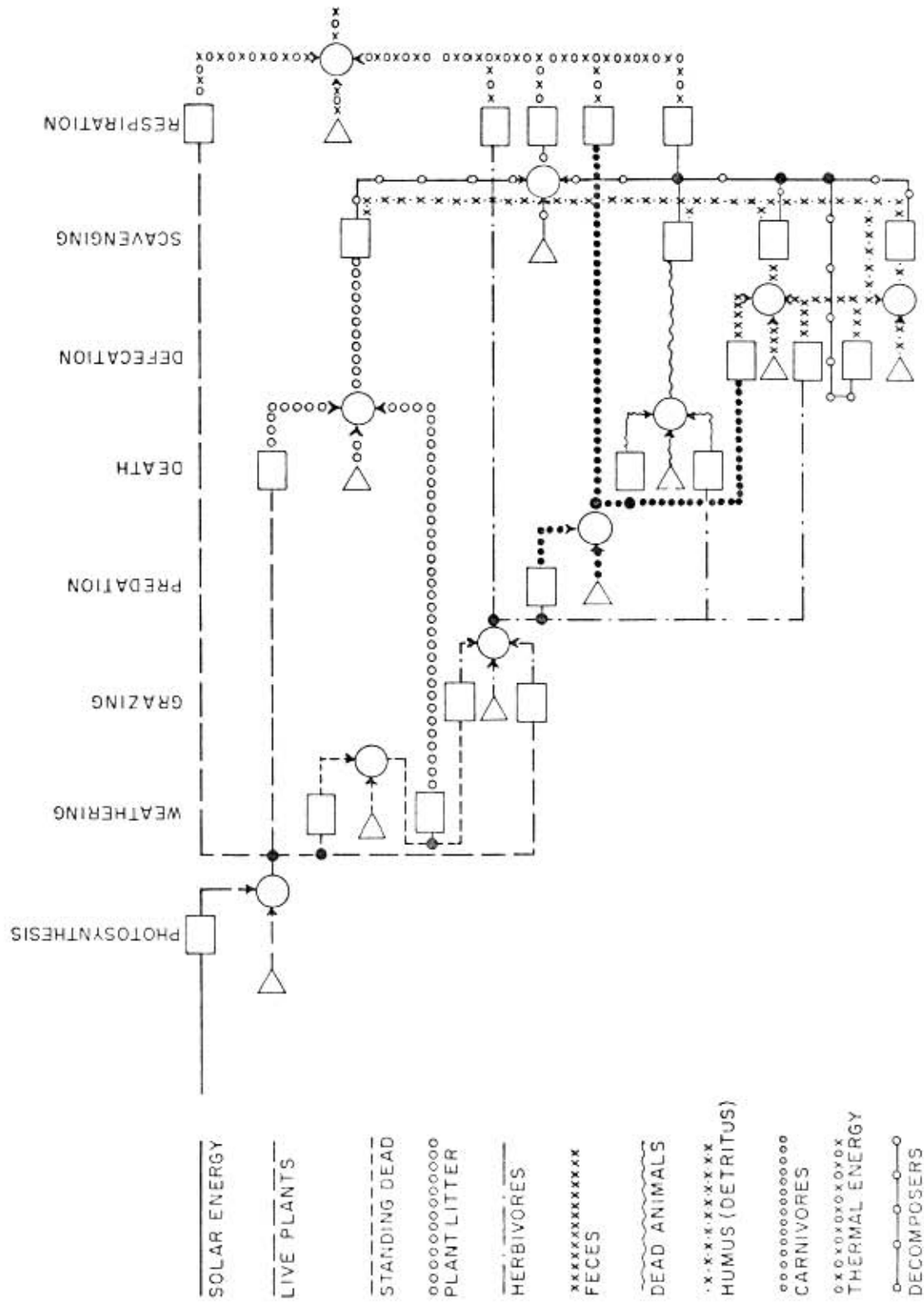


Fig. 2.2.2. A transfer function representation of the model given in Fig. 2.2.1 showing energy transfer through the ecosystem.

to produce the total fecal energy as output from the summing junction. An arrow pointing into the summing junction denotes an input to it.

In comparing Fig. 2.2.1 and 2.2.2, it may be noticed that there are several discrepancies between them. First, it is noticed that although Fig. 2.2.1 is called a nine compartment model (and has nine boxes), there are 11 distinguishable energy forms in Fig. 2.2.2. The two forms missing in Fig. 2.2.1 are solar energy, which is treated as a forcing function input to the diagram, and thermal energy, which is not represented as a box in Fig. 2.2.1, and whose input is derived from respiration.

The processes reproduction and growth, represented in the compartmental approach by feedback relationships from compartments back into themselves, have been omitted in the transfer function approach. This is because these processes do not represent absolute energy transfer between the compartments. Reproduction would result in energy transfer from adults to their young, but to represent this would require a subcompartmentalization for those compartments in Fig. 2.2.1 representing live plants and animals. For a strict nine compartment model these processes should be omitted.

Each respiration transfer box represented in Fig. 2.2.2 corresponds to two respiration processes in Fig. 2.2.1. These are the respiration connected with the growth process and that resulting from activity connected with eating and assimilation. Another discrepancy has to do with the processes of ingestion and assimilation in Fig. 2.2.1 compared with the processes of grazing and predation in Fig. 2.2.2. The grazing and predation processes correspond to ingestion, however, assimilation is omitted since the food in the animal's gut is considered part of the animal's biomass. Thus, in Fig. 2.2.1 the animal components include biomass without uningested food, while in Fig. 2.2.2 the

biomass includes ingested but unassimilated material. Separation of ingestion and assimilation, however, technically requires separate compartments for ingested but undigested plant and animal material.

In the compartment model both temperature and precipitation are drawn as inputs to the diagram. These are not shown in the transfer function diagram because they do not represent energy inputs to the system. The effects of these inputs is, however, certainly important to photosynthesis and would be included as elements in the transfer function for photosynthesis in Fig. 2.2.2 when the diagram is mathematized.

As a display tool, the transfer function approach represents a coherent and instructive method for diagramming energy flow through a system. It may be asked, however, what mathematical applicability this transfer function approach has--that is, when numbers are put into the process boxes representing energy transfers between compartments, what kind of analysis does it suggest?

Each energy transfer function box may be looked at as a mathematical function of time describing the mechanism of the process of energy transfer between two compartments. In systems engineering this time function is often transformed using a Laplace transform (Widder 1947). This transformation, which changes a time function into a function in the complex frequency domain, is generally used for purposes of mathematical simplicity. This is especially true if the transfer process is not represented as a time function per se, but as a differential or integro-differential equation.

Take for example the transfer process photosynthesis, which transfers solar energy into plant biomass. The rate of increase of plant biomass due to photosynthesis is dependent upon solar energy, temperature, soil moisture, soil nutrient status and amount of plant biomass. For simplicity, let us suppose this rate to be dependent upon these factors combined in a linear

fashion. That is it may be represented by the differential equation below.

$$\frac{dx}{dt} = \dot{x}(t) = ax(t) + bT(t) + cS(t) + dN(t) + eE(t)$$

where $x(t)$ = amount of photosynthate at time t

$T(t)$ = temperature at time t

$S(t)$ = soil moisture status at time t

$N(t)$ = nutrient status at time t

$E(t)$ = photosynthetically active solar radiation at t (PHAR)

and $a, b, c, d,$ and e are coefficients.

The Laplace transform of any function $x(t)$ is given by $x(s)$ where s is the frequency. The Laplace transform of the above differential equation is given by

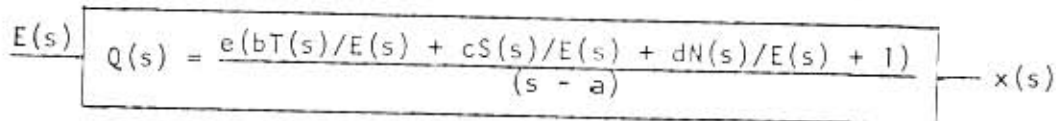
$$sx(s) = ax(s) + bT(s) + cS(s) + dN(s) + eE(s)$$

The transfer function between plant biomass and solar energy is $\frac{x(s)}{E(s)}$ and is given by $Q(s)$:

$$Q(s) = \frac{x(s)}{E(s)} = \frac{e(bT(s)/E(s) + cS(s)/E(s) + dN(s)/E(s) + 1)}{(s - a)}$$

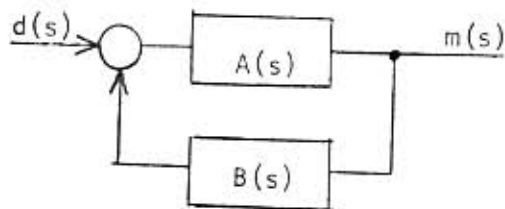
This represents the Laplace transform of the ratio of output (photosynthate) to input (photosynthetically active radiation).

The transfer function representation of the photosynthesis process would then be diagrammed as below



The problem then becomes one of finding the inverse Laplace transform for $Q(s)$ which is, in effect, the solution to the above differential equation.

Each of the processes in Fig. 2.2.2 may be represented by transfer functions if the time relationships between input and output are known in equation form and are linear. The major strength in the transfer function as a mathematical tool is the convenient set of rules for combination of transfer function boxes. Two boxes in series may be combined into a single box by taking the product of the two transfer functions. Feedback loops may be eliminated and a single transfer function box produced. As an example of feedback consider microbial scavenging. The scavenging of detritus produces biomass of microbiota but also feeds back into more detritus biomass. This set of transfer processes could be represented through Laplace transforms by



Where $A(s)$ represents the transfer function for detritus into microbial biomass through scavenging and $B(s)$ represents the portion fed back as detritus biomass. This whole feedback loop may be simplified, using Laplace transform theory, into a single equivalent transfer function $C(s) = \frac{m(s)}{d(s)}$ representing the actual scavenging detritus into microbial biomass. Here

$$C(s) = \frac{A(s)}{1 - A(s)B(s)}$$

Several sections of Fig. 2.2.2 may be combined to investigate the effects of say live plants upon detritus biomass--the total transfer function between these two elements being a combination of transfer functions due to weathering, grazing, predation, death, defecation, and scavenging. This would indeed be a

complicated transfer function. Techniques developed from Laplace transform theory (e.g., Bode and Nyquist diagrams) allow for investigation of system stability without actual inversion of the Laplace transform to get a time-varying transfer function.

Thus, the transfer function approach lends itself to a system engineering analysis of the ecosystem with its allied concepts of feedback and systems stability. Such analysis, however, may well be impractical given the present state of knowledge and data collection ability in ecological systems. This procedure has not been used widely in ecology, although Watts and Loucks (1969) have provided such diagrams for aquatic systems.

The apparent neatness of the diagram of Fig. 2.2.2 might well dissolve if too many compartments or energy states are represented. Also, the apparent neatness of the Laplace representation dissolves if the relationships are nonlinear where often a transform does not exist.

2.3 Population Dynamics

2.3.1 Population Dynamics Approaches

Four general kinds of population dynamics models are considered: (i) differential equation models, (ii) integro-differential equation models, (iii) life table and Markov models. General references for these models include Watt (1968), Trucco (1965), and, especially from the demographic side, Keyfitz (1968) and Barclay (1958).

2.3.2 Population Dynamics Modelling

The primary objectives of population dynamics modelling are twofold: to give insight into the biological mechanisms operating in the system being modelled, and, to produce a model of community interactions which predicts changes in abundances (numbers) of community species. A model must be flexible enough so that it can reliably be applied, with changes in parameter values, to populations in geographical locations other than the one from which it was derived.

Up until recently in the IBP Grasslands Biome, population dynamics models have been solely time-oriented. In other words, a uniform spatial and age distribution of the population being modelled is assumed. The models have taken the following general format:

$$\dot{N}(t) = I(t) - E(t) + B(t) - M(t)$$

$$\dot{w}(t) = A(t) - RE(t)$$

$$W(t) = N(t) w(t)$$

where

$\dot{N}(t)$ = rate of change of the population density at time t ($\frac{dN}{dt}$)	}	(1/cm ² - sec)
$I(t)$ = immigration rate at time t		
$E(t)$ = emigration rate at time t		
$B(t)$ = birth rate at time t		
$M(t)$ = mortality rate at time t		
$\dot{w}(t)$ = rate of change of an average individual's weight at time t		(g/sec)
$A(t)$ = assimilation rate at time t		
$RE(t)$ = respiration rate at time t		
$W(t)$ = population biomass density at time t		(g/cm ²)

An example of this type of model is given in the IBP Grassland Biome Tech. Rep. 3.

Integro-differential equations (IDE) for population dynamics phenomena. A somewhat more sophisticated approach to animal population dynamics, still using continuous variable mathematics, takes into account the age structure of a population by using a generalized lag term for the probabilities of births and deaths. This lag term takes the form of a weighted integral over the past history of the population. One form of this equation has been presented in the paper by Bledsoe and Jameson (1969). Their formulation lacks complete generality but the resulting differential equation is easy to integrate numerically. A more

general formulation has been given by Bartlett (1960) who derives some numerical population parameters and quotes an example from studies on *Tribolium* (flour beetle).

A more extensive discussion of the IDE approach can be found in Trucco (1965). This paper refers to early work by Von Foerster (1959, 1961), who was interested in distribution functions for mitotic and generation times. Trucco's equation defines the age density function which is the basis for this approach to population dynamics. It is given below

$$N(t) = \int_0^{\infty} n(t,a) da$$

where

a = age

t = time

n(t,a) = age and time specific population density function.

N(t) = time specific population density function.

Trucco derives the partial differential equation formulation known as Von Foerster's equation from the fundamental age density function. Von Foerster's equation follows

$$\frac{\partial n(t,a)}{\partial t} + \frac{\partial n(t,a)}{\partial a} = - \lambda(t,a,\dots) n(t,a)$$

where

$\lambda(t,a,\dots)$ = instantaneous population loss as a function of time,
age, and environmental variables.

In view of the generally accepted importance of lag functions in population dynamics work it would seem that this formulation, involving a very generalized form of lag (an integral over the past population history), could be very useful in the modelling of animal populations. In particular in the Grassland

Biome it is planned to use a formulation of this sort for insect population dynamics in which a separate variable will refer to the different insect life forms or instars. A similar approach is planned for modelling of small mammal populations.

2.3.3 Life Table and Markov Models

In some areas of resource biology, large sampling programs have been mobilized to obtain data to build life tables from which population dynamics models may be developed. In such studies, an account is made of the numbers of individuals of different age, sex, and generation groups and how they vary through time in association with such independent variables as meteorological events, food supply, etc. A similar approach is that of the "key factor" method where only one population fix per generation is examined. A third population dynamics approach of this type is the "process" approach where perhaps only one part of the system is examined at a time. Sampling error is generally not the main reason for the lack of success of these models as predictors, but lack of success probably is because there are not enough variables considered therein. Interactions of environmental variables generally are ignored in many of the models derived from life tables, perhaps a characteristic of poor model building rather than the approach itself. Results from these models usually show that one or two age intervals in the population are most important. Example applications of this type of modelling for forest insect populations are given by the Forest Service (1969). Most life table approaches have the following general form:

Let $n_i(t)$ = number of individuals of age i alive at time t .

f_i = unit time interval fecundity rate of age class i .

p_i = probability that an individual of age i survives a unit time interval $(t, t+1)$.

k = number of age classes in the population.

$$\text{Then } n_0(t+1) = f_0 n_0(t) + f_1 n_1(t) + \dots + f_k n_k(t)$$

$$n_i(t+1) = p_{i-1} n_{i-1}(t) ; i=1, \dots, k$$

This model can be put into the following matrix form:

$$n_{t+1} = \begin{bmatrix} n_0(t+1) \\ n_1(t+1) \\ \vdots \\ n_k(t+1) \end{bmatrix} = \begin{bmatrix} f_0 & f_1 & \dots & f_k \\ p_0 & 0 & \dots & 0 \\ 0 & p_1 & \dots & 0 \\ & \ddots & & \vdots \\ & & p_{k-1} & 0 \end{bmatrix} \begin{bmatrix} n_0(t) \\ n_1(t) \\ \vdots \\ n_k(t) \end{bmatrix}$$

$$= M n_t$$

The matrix M is called the survival-fecundity (Leslie) matrix for the population under consideration. It was originally introduced some time ago by Leslie (1945, 1948). In addition, the natural logarithm of the dominant latent root (λ), or eigenvalue, of the survival-fecundity matrix is called the intrinsic rate of increase for the population (i.e., there exists a constant λ such that $n_{t+1} = \lambda n_t$ for t sufficiently large).

From studies of the above types of matrices, a steady state or stable age distribution vector can be estimated. It can thus be determined how close a population is to an equilibrium state as far as the relative numbers of individuals in each age class are concerned.

A related group of procedures utilize Markov chains to predict dynamics of population or even of communities. Thus, for example, Leak (1968) has illustrated, but not implemented, a scheme using a computational procedure similar to an absorbing Markov chain to predict regeneration of cut-over birch forests. Olson and Uppuluri (1966) show how a similar procedure can be used for predicting ecosystem maintenance and transformations. Olson et al.

(1965) and Waggoner (1969a) both have used examination of aerial photographs or plot records of forested areas to develop transition probability matrices which were used in first-order Markov chains to predict the population dynamics of communities, i.e., specifically secondary succession.

Generally, these techniques do not offer much to the modelling of complex ecosystem relationships. One reason is because of the difficulty of including mechanistic events, forcing functions, and the full complexity of the system. However, the procedures may be very useful for empirical models of change within the system. It may be possible to utilize the calculation techniques but to alter some of the coefficients in the transformation matrices to be functional elements dependent upon the state of the system.

A closely related type of conceptual operation with application to ecosystem studies is the Ashby (1963) type transformations for state and change of state of systems. These transformations could be utilized on a computer containing software in which logical variables are available. The concepts are most useful, however, in formulating possible mechanisms and reasoning for change of state of systems, rather than for actual implementation and calculations.

The population dynamics models thus far developed have been species or functional group models. The format used necessitates the assumption of uniform population density over the area being modelled. Unfortunately most populations do not behave in this way. Thus we are looking for a change in the general mathematical formulation of the population dynamics model. This change will include a way to superimpose the spatial distribution on a time-specific model. Two possible approaches come to mind: using partial

differential equations as opposed to ordinary differential equations, and dividing the total area of concern up into grids, within which the spatial distribution is assumed to be constant. A system of differential equations, such as the ones presented above, would represent the change in the population within each grid at any time. Movement between bordering grids would be reflected in the immigration and emigration terms $[I(t), E(t)]$.

In order to model spatial distributions of populations over time, one must be able to observe and record these phenomena in the field. This will involve simultaneous measurements of species abundances and movements over time. Field tagging of individual population elements seems to be the logical starting point for an attack on this problem.

Once the field measurements are analyzed and understood, the revealed patterns must be translated into mathematic format amenable to mathematical modelling. Obviously this is an easy task. After individual species or functional group models are developed, they must be interfaced in order to form community models. One possible approach to this problem is to have a separate coordinating model which links together several species or functional group models. Such a model would take into account pressures generated by a lack of food supply and high population densities (i.e., competition between various species). It would also incorporate the re-orientation of a species or functional group when it is forced out of its particular location in space by competitive pressures.

2.4 Electrical Analog Energetics Approaches

An area of modelling of ecosystems, closely related to standard analog

computer techniques, is that originated by H. T. Odum and is concerned with representing biological energy circuits with electrical analogs. Examples of this work originate in Odum's early paper on the subject (Odum and Pinkerton 1955), followed by extensions for ecological potential and analog circuits (Odum 1960), and applications to teaching ecological theory (Odum 1962) as well as specific analysis of marine examples (Odum 1966), and application to energetics of world food production (Odum 1967). Recently a complete manual and explanation of this approach has become available (Odum 1969) as well as a book (Odum 1971).

Essentially, this is simply a type of ecological flow chart using certain standardized symbols. Odum uses a compartmental system for energetic flows but with specialized energy network symbols for such items as energy source, passive energy storage, heat sink, potential generating work, pure energy receptor, work gate, self-maintaining consumer population, plant populations, and economic transactor. Each of these network symbols implies mathematical conventions. In effect, he is describing a unidirectional flow of energy in accordance with the second principle of thermodynamics. He draws heavily from the conventions used in the designing of electronic gear. The circuit lines in these symbols represent pathways of energy flow, and there is an entropy increase with each process. The technique can be generalized for circuits of matter, but this has not been done.

The major difference from conventional analog techniques is that Odum's scheme uses passive electrical analog principles rather than the standard voltage analog method. He considers Ohm's Law in the passive system as analogous to the biological system for flow of organic matter. Organic

matter, containing proportional energy, flows in proportion to the "thrust" exerted by concentrations of organic matter "upstream." The energy may be obtained from the electrical flows but not by computing the electrical energy of the analog. Odum suggests that potential energies for driving concentrations in many ecological instances are within about 15% of being constant per unit of weight. Furthermore, the potential function of storage is proportional to concentration of organic material rather than its logarithm. Thus, the pounds of organic matter in a consumer drives the consumption of elements by that consumer, but in a different manner for each consumer.

Although extremely interesting and thought provoking, this approach has not been widely adapted to modelling ecological systems. Perhaps one concern is that of the general limitation of most analog computer systems for processing and analyzing large blocks of real-life data from ecological studies. However, extremely interesting comparisons are made of different types of systems using this network notation (Odum 1967).

2.5 Structural and Statistical Models

This section is the most difficult to write as it contains the greatest diversity of models, including those concerned with the numerical quantification of groups of plants and animals. The ideas discussed can be incorporated at least in a qualitative manner into models of ecological systems. An example, arbitrary grouping of these models is given in Table 2.5.1 Only a few of these will be discussed here.

When ecological sampling is performed, several variables (not necessarily independent) generally are measured. Thus the mathematical and statistical models employed must be multivariate in nature.

In what follows three ecological concepts are considered: pattern, classification and ordination, and diversity.

Table 2.5.1. An example, initial approach to grouping
spatial, statistical and structural models

- .1 Concepts and Models involving only biota
 - .1.1 Euclidean Space specific
 - a) Pattern,
distribution indices
mean squares statistical distribution (Pielon) space
 - b) Dispersal
density probability
random walk
 - .2.2 Hyperspace organization (non-metric)
 - a) Diversity
entropy of foodwebs
information statistics
 - b) Classification
discriminant and cluster analysis
canonical analysis
 - c) Ordination
principal component analysis
factor analysis
- .2 Concepts and models involving biota and phsycal environment
 - .2.1 Euclidean space specific
 - a) Pattern (see 2.5.1.1.a)
 - b) Dispersal (see 2.5.1.1.b)
 - .2.2 Hyperspace organization (non-metric)
 - a) Ordination
multivariate analysis
multiple regression, canonical correlation (see 2.5.1.2.b)
 - b) Discretized processes
diet analysis lag model
autoregression
autocorrelation
cross correlation
 - c) Niche analysis
concepts of Hutchinson and MacArthur
discriminant analysis
principal component analysis
factor analysis (see 2.5.1.2.c)

2.5.1 Pattern

Pattern analysis concerns itself with how organisms distribute themselves in space (Pielou 1969). Since little has been done to link distributions over space with distributions over time, sessile or sedentary organisms (mainly plants) have been studied in this respect. In general organisms can be put into three groups to which pattern analysis can be applied:

- (i) organisms confined to discrete habitable sites (pest species that attack shoots of a tree);
- (ii) organisms that can occupy a continuum of space and occur themselves in discrete units (trees in a forest);
- (iii) organisms which do not occur as distinct individuals amenable to counting (sod forming grasses).

Most tests of pattern are tests for random (or non-random) distributions, either of individuals or clusters of individuals, and are based on the Binomial and Poisson probability distributions. More complex tests can be developed on the basis of the many "contagious" discrete distributions, generally compounded from the Poisson, Binomial or Hypergeometric (Patil 1968). Once the theoretical distribution of the variable being measured is determined, the observed distribution is tested against it by means of a χ^2 test.

In case (i) all that is usually determined is whether individuals within each discrete site are distributed in a random fashion. Distribution over any larger space is also a function of the distribution of the habitable sites.

In case (ii) the methods of sampling for pattern analysis can be divided into two groups:

- (a) The commonest method is to sample within randomly placed quadrats. One counts the number of individuals in each quadrat. The major drawback to this type of sampling is that a measurement of aggregation (clumping, clustering,

or contagion) is affected by the size and location of the quadrats. In many cases the relative size of clumps to quadrats is extremely important to the analysis. To remedy this situation a sampling scheme is often employed in which quadrats are systematically changing in size.

(b) The second method of sampling for case (ii) is called "plotless" or distance sampling. Two techniques are employed here: (1) the sampling points are located at random throughout the area and the distance from each point to the nearest neighbor is measured, and (2) individuals are selected at random and the distance from each of these individuals to the nearest neighbor is measured.

The theoretical distribution, in randomly dispersed populations, of the measure employed is then determined and compared to the observed measures.

In case (iii) patterns exhibited by vegetatively reproducing plants occur as extensive clumps or shoots, within which individual elements cannot be distinguished. In this case the clumps are treated as the entities to be studied. In its simplest manifestation, studying a single plant species, the mapped pattern of the clumped individuals results in a two-phase mosaic. A patch (phase) is a clump where the plant occurs and a gap (phase) is a clump where the plant is absent. Tests of randomness can be derived from the study of the mathematical properties of "random mosaics".

Spatial relationships of two or more species can be studied simultaneously. Determination of whether or not species occur independently over space is usually made. A measure of the strength of association between species, coefficient of association, is employed. A coefficient of association between two species close to +1 implies that both species tend to occur together in space, and a coefficient of association which is close to -1 implies that when one species is present the other species is most likely absent.

2.5.2 Classification, Ordination, and Related Multivariate Methods

Ecological samples usually involve lists (qualitative) or amounts (quantitative) of species in each sampling unit (quadrat). It is often of interest to know if these sampling units, or quadrats, are systematically classifiable into distinct groups. This question is generally posed with reference to vegetation groups. If classification is inappropriate one may still wish to condense (and hopefully clarify) a mass of field observations by arranging the multivariate data from the quadrats in some coordinate frame to display their interrelationships using as few dimensions as will suffice. This is called *ordination*.

Classification can be approached from two directions: (i) Agglomerative--start with individual quadrats and progressively classify them into larger groups of "similar" quadrats, and (ii) Divisive--start with one large group of quadrats and divide and redive it into smaller groups of "similar" quadrats.

In most classifying procedures one looks at measures of association or "similarity" between quadrats and classifies them into groups based upon these measures.

Another approach to classification occurs when individual measurements (multivariate) are assigned to pre-determined classes or groups based upon similar assignments of individuals whose class was already known. Of course, before observations can be assigned to groups, it must be determined if these groups can be distinguished upon the basis of multivariate measurements taken. This whole topic falls under the heading of *discriminant analysis* as described in texts on multivariate statistical methods.

When classification seems extremely arbitrary, i.e., distinguishable groups do not manifest themselves under existing techniques, ordination becomes a useful tool in simplifying ecological data. Ordination involves plotting n

sample points of s variates in a space of less than or equal to s dimensions in such a way that none of the important features of the original s -dimensional pattern is lost. Two ordination techniques are briefly discussed below.

In *principal component analysis* the original s -dimensional space is projected into a space of dimension less than or equal to s , with all components of the new space being independent linear combinations of the elements of the old space. In many cases the behavior of the s -variate system can be readily understood when that system is transformed into its principal components. In addition much statistical theory based upon independent variates can be applied to ecological data once it has been transformed into an independent format such as its principal components.

Principal component analysis involves two steps: first, determination of measure of "difference" between individual quadrats, and second, construction of a plot of the data points in a new coordinate system such that (i) each point represents a quadrat, and (ii) the distance between any two points is equal to the "difference" between the quadrats represented by those points. Thus if the number of principal coordinates can be reduced to two, the "differences" between individual quadrats can be represented graphically, and it is possible that some natural groupings might manifest themselves.

Principal component and factor analyses methods are useful as a preliminary step in multiple regression problems. That is, if we have a large set of inter-related variables, principal components or factor analysis can reduce this large set to a smaller set of unrelated variables. Often such problems are complex and may require considerable insight; techniques such as both non-rotated and rotated factor analysis may be helpful in determining the minimal set of variables which could be retained. Supplemental interpretative aids can be provided by matrices of partial and simple correlation coefficients.

Factor analysis can also be used directly to examine a data set to determine the number of functions expressed in the data. For example, analysis of say 1000 bacterial samples may reveal some 50 major bacteria taxa. Examination of such a data set by principal components or factor analysis will suggest how many different subsets are in fact in the data, and may, by including knowledge of certain taxa in the group, suggest which processes are dominant in the microbial milieu.

In our research program we have been conducting in-depth research on nitrogen, and are considering similar research on phosphorus. Among the nutrient elements, these have been selected as priority items because of their probable critical role in the ecosystem, and the flow of these nutrients in the plants and soil is being modelled in a mechanistic sense. Other nutrient elements, however, are being approached as a group in a non-mechanistic fashion. A series of soil and aboveground plant tissue samples are taken from a variety of sites and analyzed for such elements as N, P, K, Fe, Ca, Mg, S, and Mn. The levels of these nutrient elements in the plant tissue may be related to the amounts in the soil and may also be interrelated to each other. For example, a high Ca:P ratio in the soil may result in a low P content in the plant tissue. For such purposes we use a canonical correlation to express the overall relationship between independent (soil) and dependent (vegetation) factors.

2.5.3 Diversity

An index of diversity is a single statistic in which the following two independent properties of a population or community are confounded: (i) the number of species it contains; and (ii) the evenness of the abundance of those species.

Let N_1, N_2, \dots, N_s refer to the numbers of each of s species in a population. Then the population is said to have maximum evenness if all species abundances

(N_j) are equal. The greater the disparities among the N_j the more uneven the population is said to be.

A collection is said to have high diversity if it has many species and their abundancies are fairly even. Conversely, the diversity is said to be low when the species are few and their abundancies are uneven. Due to the fact that diversity is a measure of two independent properties of a population or community it has possible ambiguities built into it. A collection with few species and high evenness could have the same diversity as another collection with many species and low evenness. Pielou (1969) gives several measures of diversity for infinite and finite collections, as well as a measure of evenness.

2.5.4 Dispersion and Dispersal

If we look at the spatial display of an ecosystem in appropriate time spans, such as one day, we see an essentially static array of plants. Through this static network we see the dynamic movement of other components of the system such as air, water, and animals.

Such conceptualizations come immediately to a problem of scale. It would be inappropriate for example to consider the movement of a tenebriad beetle from one grazed pasture to another, and it would be equally inappropriate to consider the movement of an antelope from one grass blade to another. It would be most appropriate, however, to consider things like:

Biome and sub-biome distribution-air mass movements

Topographic relief or vegetation type-rabbit movements

Grazed pasture-bird movement

Soil series and type-mammals burrow location

Prickly pear pattern-grasshopper distribution

Grass culm location-beetle movements

Soil particle distribution-soil water movement.

Thus a structural study should consider a series of large to small study areas, each with an appropriate scale. Various ecological distributions and their meanings have been discussed and argued by ecologists for some time.

Animal dispersion has been investigated by studying the distribution of centers of activity. The center of activity of an animal is the average location of all the points at which the individual has been detected by trapping or other means. Several tests can be used for examination of randomness of distribution of the centers of activity. In fact, several must be used because each test determines whether or not dispersion is non-random, but does not tell if the dispersion is, in fact, random. Therefore, the concurrence of several tests is required to indicate whether a truly random distribution of organisms exists within an area at a given time. There are several test of non-randomness that can be applied in this fashion. They are similar to the tests for patterns discussed in 2.5.1. Some examples follow:

(i) A test of geographical homogeneity may be performed on several subsections of the area when the area is equally divided. Essentially this method compares the numbers of individuals in each subsection with the numbers expected on the basis of a random distribution, but utilizing a Chi-square test. By dividing the area in different ways, that is, equal rectangles, or equal squares, some indication of gradients in the dispersion pattern can result.

(ii) The observed distribution may be compared to a calculated Poisson distribution having a mean equal to the mean density of individuals in the study area. The area is divided into small subsections because in a Poisson distribution the probability of any single point falling into any single subsection must be small. Comparison of expected numbers with observed numbers in the subsections is again based on the Chi-square test.

(iii) The proportion of individuals that form reflexive pairs is characteristic of a random distribution. Two points that are closer to each other than either is to any other point form a reflexive pair. In a random distribution the proportion of individuals involved in reflexive pairs is 0.6215. This provides an expected value to which the actual values may be compared by means of a Chi-square test.

(iv) In a randomly distributed population a definite proportion of individuals is known to be nearest neighbors to 1, to 2, or to 3 or more other individuals. The proportion expected to be nearest neighbor to 0, is 0.297, nearest neighbor to 1 is 0.453, to 2, 0.225, and to 3 or more others is .025. Again the observed proportions are compared to the theoretical distribution by means of a Chi-square test. M. S. Bartlett (in press) has expanded on the ecological applications of two-dimensional nearest neighbor systems.

(v) The mean distance between neighbors can be compared to the mean nearest neighbor distance of a random population having the same density as the sample population. The ratio of the observed value to the expected value is the measure of departure of the sample population from a random distribution. If the sample population presents random distribution, the ratio is equal to one. With maximum clumping of individuals the ratio is 0, and with maximum spacing of individuals the ratio is 2.1491. A test of significance has been developed by Clark and Evans (1954) for testing departure of the ratio from a value of 1. The test is to calculate the normal variate or the standard variate of the normal curve. The normal variate values of 1.96 and 2.58 represent respectively the 5% and 1% levels of significance. Munroe (1963) attempts to provide a conceptual link between population ecology and zoogeography by showing that transition matrices of Markov chains provide a succinct means of expressing the temporal change in numbers at a point and also the temporal change in numbers at a set of points.

Movement models are best developed at the two extremes. Air mass movement has long been worked on by climatologists, and the work of Bryson (1957, and Sabbagh and Bryson 1962) has handled annual distribution of precipitation in an excellent fashion by maps or parameters developed by Fourier analysis. At the other extreme, there are studies of unsaturated flow through porous media which apply to the water movement problem.

Between these extremes, however, the modelling of movements is very sketchy and poorly developed. Some examples from the literature are Francis (1970), who worked on salmon movements in relation to offshore islands near British Columbia, and arrived at solutions based on long run computer simulations rather than sophisticated mathematical formulations.

It appears that new concepts are needed for the pattern movement studies. A partial differential equation approach would be extremely difficult because of the solution problems involved with irregularly distributed systems. On the other hand, discretizing space soon leads to dimensionality and computer storage problems. Application of random walk to animal movements has been attempted (Holgate, in press) but results do not as yet approach reality. Siniff and Jessen (1969) have evaluated an immense amount of information on animal behavior utilizing a simulation model of animal movements, and have gained insight into the manner in which certain species utilize their home ranges.

Some attempts have been made to modify the old concept that an animal's home range is represented by a fixed area circumscribed by a fixed boundary. The modifications involve attempts at expressing an animal's movements around the center of activity on the basis of a series of concentric circles, each

representing some decreasing probability of the animal's occurrence. This concept was initially presented by Dice and Clark (1953). They replace the concept of home range with a statistical concept and expressed the home range in terms of the "recapture radius". The method was elaborated by Calhoun and Casby (1958) who derived an elaborate probability-density function for the expression of activity range derived from a series of recapture data. The main objection that has been raised to this approach is that it of necessity considers the activity range of an animal to be circular. An alternative that does not require the circularity consideration has been presented by Jenrich and Turner (1968).

In the evaluation of distances of movement recorded for animals, efforts have been primarily to determine if the data indicate that movements are random as opposed to purposeful and directed movements. Two approaches used are examination of the distances moved and examination of the directions of movement. There are no cases where both have been combined in the same analysis. To evaluate distances of movement, comparisons to a theoretical Poisson distribution have been made. The Poisson distribution describes the occurrence of isolated events in a continuum and can be applied to a set of data if the quantity z is derived from the data, z being the average number of occurrences of the event. A Poisson distribution is computed on the basis of the data and the results are compared to the observed data by means of a Chi-square test. A simpler test of the Poisson distribution is to examine the mean and variance computed from the records of distances. In a Poisson distribution the variance is equal to the mean.

Dobzhansky and Wright (1943, 1947) investigated the movements of *Drosophila* by comparison with the frequency distribution of individual movements with a

normal curve. They reasoned that movements out from a central point, where they released a large number of flies, would represent a radially symmetrical bivariate normal distribution so that the results from each sector of the circle may be combined and treated as though all were taken along a straight line through the center. The value then represents a frequency distribution which may be compared with a normal curve. If dispersal is not random but is characterized by excessive frequencies at greater distances and low frequencies near the center the distribution is platykurtic instead of normal, in a normal frequency distribution the fourth moment about the mean is $3\sigma^4$ where σ is the standard deviation about the mean. Computation of these values and comparison with the appropriate tables will indicate whether or not the data significantly differ from a distribution represented by a normal curve.

Another way of analyzing animal movement is by treating them as circular distributions. This utilizes the angle of the direction of movements with reference to a particular axis and disregards the distance. The statistics of circular distributions has been worked out in an elaborate monograph by Batschelet (1965). He provides methods for evaluating the mean, the dispersion and the skewness of circular distribution. This is useful in the analysis of data such as migratory movements or homing movements of birds and in certain biological rhythms. There are also tests given for comparison of observed distributions with a circular normal distribution.

2.5.5 Migration Models

In the grassland ecosystem many major organisms (and perhaps many minor organism as well) are not resident, but migratory. Studies at any one location, therefore, are not directly concerned with the total picture of these taxa, such as population dynamics and demographic models, but rather are only concerned with

the dynamics of arrival and departure. Preston (1966) has presented a mathematical formulation for migration as viewed from a single location. He found that migration can be expressed by

$$\frac{y}{y_0} = (\sin x + b \sin 2x)^{n_1} (1 + k \sin x)$$

y = level of migration

y_0 = y at peak of migration

x = time in radians

In this equation b decides the interval between migration peaks, n_1 decides the average tightness or average deviation in the spring and fall migrations, and k decides the difference between the standard deviation of the spring and fall migrations. Preston concludes that, from a practical point of view, it is usually better to take spring and fall migrations as separate events and use a simpler formulation than that shown above. This approach should be very useful for grassland species, such as the lark bunting, which are marked primarily by their migration habits.

2.5.6 Successional, Time Lag, and Autocorrelation Models

Grassland ecology has long been concerned with succession, and a vast literature is available on this subject. This is, therefore, a fruitful area for modelling. A deterministic model of plant succession from a compartment analysis point of view has been presented by Bledsoe (1969) and a stochastic succession model based on probability of plant establishment and survivorship tables of grazing species has been developed by Jameson (1969). Margalef (1968) suggested that succession can be thought of as a self-organizing adaptive system. None of these concepts are at all contradictory to one another, and all are mathematically tractable. Haug (1970) has thoroughly reviewed the literature on grassland succession but has not developed a model from his work.

At the outset of the Grassland Biome program it was determined, however, that the life expectancy of the program was short in comparison to the time required for grassland succession, and that direct experimentation on the succession would not be feasible. If we restrict our thinking to higher plant succession, and disregard or filter out annual noise, this is certainly true. If, however, we consider successional patterns in organisms such as bacteria, protozoa, fungi, and certain insect taxa, we are able to collect sample data for successional models within a short time.

Consider, for example, a year on the grasslands with a dry, early summer. Temperatures would be adequate for biological response, but moisture would be severely limiting. With a single rain the grasslands is transformed; if the rain is adequate to change soil moisture from wilting point to field capacity a unit impulse can be assumed to represent the rain (it may be, on the other hand, better to consider a unit step function). The response of various short generation time taxa to this impulse would be an appropriate study from a classical control theory point of view. From the ecological viewpoint, it can be considered as a successional model. Relationships between taxa can be investigated by autocorrelation techniques. If the responses are monotonic rather than cyclic, a curve fitting technique such as used by Martel and Bledsoe (1970) for functional groups of micro-organisms is appropriate.

We have not yet fully developed concepts of successional modelling for our purposes but recognize the potential and importance of so doing.

3. GENERALIZED HIERARCHICAL REPRESENTATION OF ECOSYSTEM RELATIONSHIPS

3.1 The Hierarchical Concept

The hierarchical representation for energy flow within a particular ecological community is used as a *method of developing the models* to represent a particular system. The hierarchical diagram shows the breakdown of the various general or specific processes influencing change on a particular variable of interest in a branching hierarchical fashion (e.g., producer biomass, animal numbers, etc.). The hierarchy of causality is outlined until all processes are related back to driving forces or static conditions.

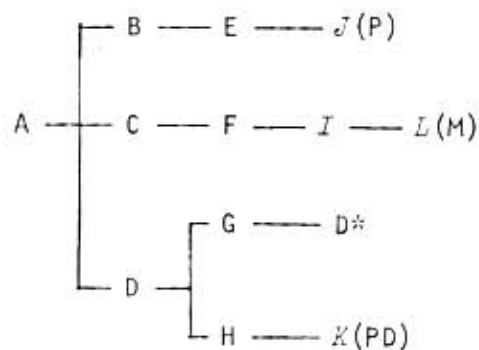
Hierarchical diagrams are presented for consumers, producers, decomposers, and abiotic groupings. Further subdivision is then made according to various separable compartments within these groupings. Each diagram attempts to show the causal relationships that affect energy/matter flow within that compartment, as well as the influence of elements in other compartments upon these flows.

For the producers, a single diagram for producer biomass density and distribution is used. Within the consumer grouping, diagrams are drawn for population size and individual weight change. For the decomposers, the diagrams are for biotic nutrient cycling as a function of decomposer activity. The abiotic grouping includes diagrams for water cycling and net radiation.

Causality in each diagram is shown by having the dependent elements to the left of the causal elements and hierarchically connected to them. That is, if

A depends upon B, C, and D, then A would appear to the left of B, C, and D in the hierarchical diagram and would be connected to them by hierarchical brackets. This relationship is shown in Fig. 3.1.1.

Fig. 3.1.1. Generalized example of a hierarchical diagram.



The elements B, C, and D may then be further dependent upon other elements and would then "bracket" these elements. Thus a complete diagram can be generated and would show *second* (e.g., effect of G on A), *third* (effect of K on A), and *higher order* (the effect of L on A - a fourth order effect) causal effects on various elements in the diagram. Independent forcing functions or inputs from other diagrams are shown with a parenthesis after them, with the parenthesis referring to the particular diagram the input comes from. In this way interactions between the various trophic levels are shown. The elements in parentheses in the specific diagrams presented below are abiotic (A), producer (P), consumer population (PD), microbial (M), general consumer (C), and human intervention (HI).

The elements at the lowest levels (to the right) of the diagram may be generated in several ways, as follows:

- (i) *External control*: a factor which is under human control and represents a method of manipulating the environment, e.g., fertilizer treatments.
- (ii) *Other subgroups*: a factor generated by a subgroup external to the diagram under consideration. This is followed by a parenthesis indicating which other subgroup is being referred to.
- (iii) *Feedback relation*: one or more of the factors of a diagram providing input at another level in the diagram in a feedback relation. These are followed by an asterisk.
- (iv) *Other*: Generally parameters or phenological characteristics such as animal breeding times, constant soil characteristics, field measurements, simple statistical mechanisms.

Each of the diagrams presented in the following sections is general and does not refer to a particular species, community, etc. However, the diagram may be *applied* to a specific population or community, in which case the nature of the causal effects may be made more specific. Thus, for example, the consumer population diagram applied to a given species would be no different from the diagram applied to the entire consumer trophic level except that when models are developed from these diagrams, the parameters, and frequently the form of the models displaying the causal relationships, would be different.

One quality of a model, known as its resolution (Bledsoe and Jameson 1969), relates to the relative number of causal connections in the structural diagram encompassed by the model. A model of very high resolution takes into account the full range of causal phenomena. A model of low resolution "finesses" the causal relationships below a certain point by ignoring them entirely or by using an empirical or curve fitting model for their representation.

3.2 Model Formulation from Hierarchical Diagrams

The diagrams mentioned above would be used as a framework, within which to develop models which can be used to represent a particular ecosystem. These models can be of varying degrees of complexity, generality, and resolution. A model could be constructed from the diagram by drawing an enclosure (imaginary) around a number of related elements in the diagram. The model then describes the mechanistic relationship between these elements. Any one of these enclosures, however, may have only one element from the left-most hierarchical level within it. For example, in the consumer population diagram (Fig. 3.2.1), the consumer population size is directly linked to immigration, emigration, mortality, and natality. Several models may be developed from this segment of the population diagram. An enclosure around only the "animal numbers" element would denote a model unconnected to any other element. An enclosure around all five of these elements would be a model involving all the causal connections in the hierarchical diagram. Similarly, other models could be denoted by enclosing between two and four elements of the system although all of these must include the first element--the population size.

The model developed solely from the animal numbers element in the consumer population diagram (Fig. 3.2.1) may be seen as an empirical curve fitting population model. This is a simple empirical model, i.e., does not depend upon the elements directly to the right of it in the hierarchy for its inputs. An example of such a model would be an equation for the

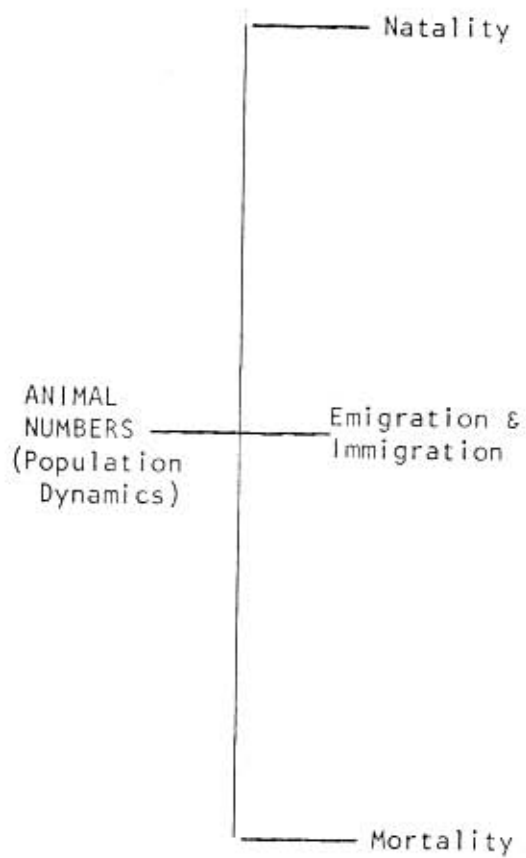


Fig. 3.2.1. A simplified structure for a hierarchical model (from Fig. 3.4.1.1).

seasonal variation in bird population based solely on bird count data and fitting the data as closely as possible. The model developed from the enclosing of all five of these elements (Fig. 3.2.1) is a mechanistic model, since it includes the causal relationships connecting the animal numbers element with those elements directly to the right of it in the hierarchy and must describe in some fashion the mechanism of this causality. The four elements to the right of the animal numbers element in the hierarchical diagram may either be determined empirically, be developed from the lower levels in the hierarchical diagram, or be deduced using other means (e.g., literature). This model then would give the functional effect of emigration, immigration, mortality, and natality, upon the consumer population. Such a model would be either empirical (inductive) or deductive, but would definitely contain some mechanistic elements. An example of this type of model is the lark bunting population dynamics model given in Tech. Rep. 3.

The development of individual models from each of the hierarchical diagrams is further described below. The hierarchical diagrams presented below are not unique. They are drawn by individual groups of scientists and contain their prejudices and preferences. However, an effort toward completeness and generality has been made. The diagrams may be used to develop an array of submodels to cover the whole ecosystem. As the project progresses, it may be necessary to develop parallel structure for parts of the ecosystem in order to get different viewpoints of grassland function and structure.

3.3. Producers

3.3.1 Producer Biomass and Distribution

In most grasslands the greatest part of aboveground plant biomass is produced during brief periods when soil moisture and temperature are adequate.

Internal plant processes in this situation are subject to wide day-to-day fluctuations depending on the immediate environmental conditions.

Particular attention needs to be paid to the influences of the environment on processes within the plant. The concept of external and internal environments was used in developing the producer hierarchical diagram in Fig. 3.3.1.

3.3.2 Internal and External Environment

Input functions such as the consumer element, microbial activity, soil, and climate compose the *external environment* for the producers. The external environment influences the *internal conditions* of the plant, such as the photo-thermal status and water status, which combine to form the internal environment for producers. Any of the internal conditions can be influenced to varying degrees by any of the factors of the external environment. The internal nutrient status of a plant at any given time, for example, is a function of soil characteristics, climate, microbial activity and its previous status, i.e., internal feedback. Feedback is included by having "producer" appear at the right in the hierarchy as well as at the extreme left with an asterisk after it (see Fig. 3.3.1). The presence or absence of given nutrients in the plant's environment will depend on the fertility of the soil, while the availability of these nutrients depends upon climate conditions and nutrient cycling by microbial activity. Here all of the external conditions are of major importance. The plant's water status, however, is mainly influenced by the climate through precipitation, and by the soil through its water-holding capacity, with a less direct effect from microbial activity through competition for moisture. The effect of consumers on water status would primarily be through the influence of physical disturbances of the soil such as compaction and burrowing and through man's impact via herbicides and selective cultivation.

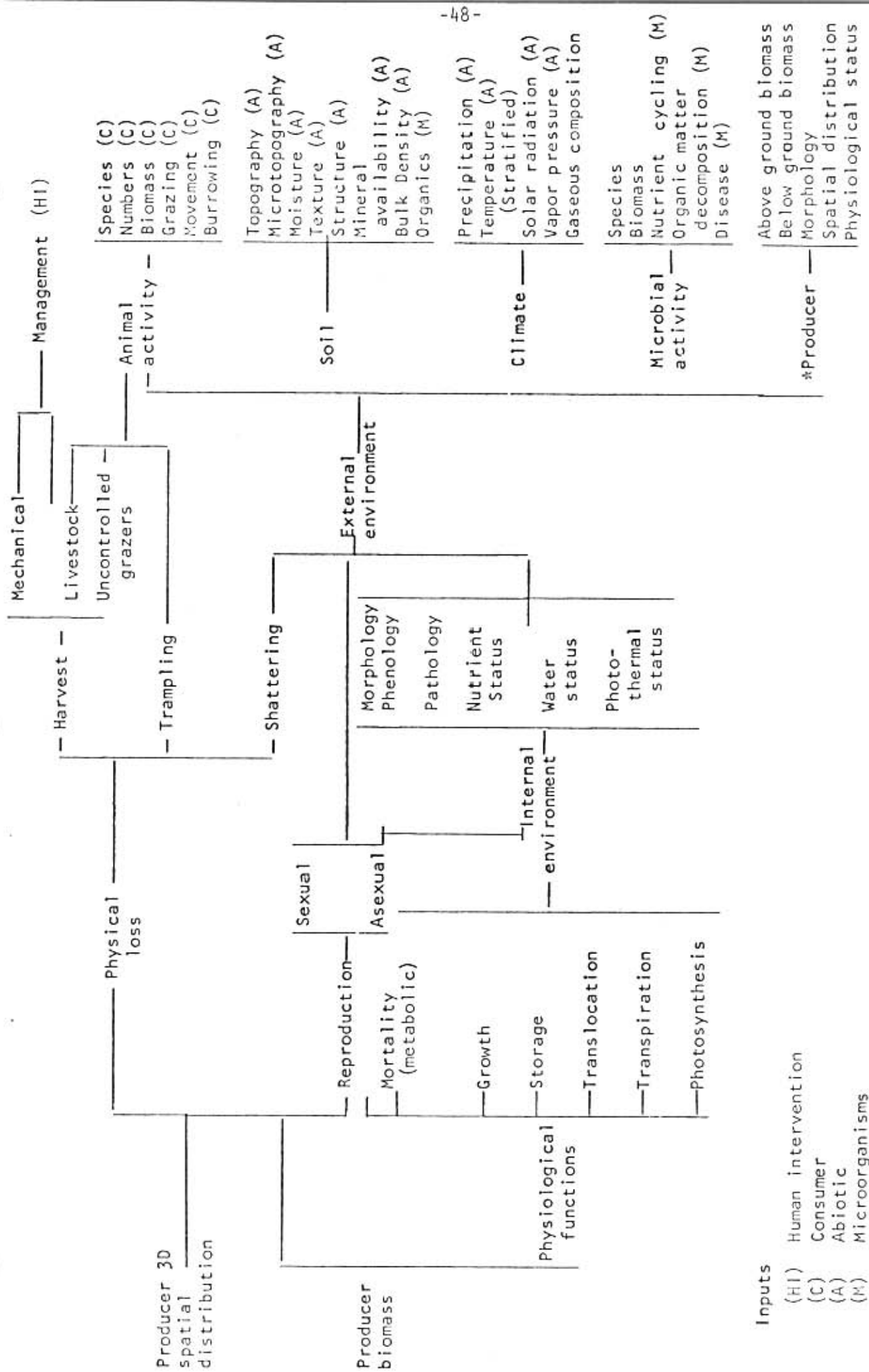


Fig. 3.3.1. Hierarchical diagram of producer compartment (tentative).

3.3.3 Physiological Functions

The balance of the internal conditions composing the internal environment affects specific physiological functions in plants. The current conditions will determine the rate of reaction for any given physiological function. For example, in photosynthesis the rate of reaction is dependent on temperature and the availability of light, water and nutrients (such as CO_2), and enzyme-activating minerals. The plants phenological development (growth stage) determines its morphology (structure) and the amount of actively photosynthesizing tissue. Pathology influences photosynthesis by disrupting the balance of internal conditions. Respiration and translocation influence photosynthesis by removing the carbohydrate produced from the reaction site, thereby perpetuating the reaction.

3.3.4 Spatial Relations

The spatial relations of the producer trophic level are a function of the external environment variables described above, of an input from the consumer hierarchy through physical losses, and of reproduction. The external environment affects plant reproduction directly through pollen dissemination, seed dispersal, seed implantment, and stolon fragmentation. Local soil conditions are particularly influential in determining species distribution and composition, as are consumers through selective grazing patterns. Climate is influential in direct physical loss of plant material through wind, hail, and other catastrophic events. Consumers cause physical loss other than by trampling and harvesting activities, such as by burrowing. In addition, the consumers affect physical losses through mechanical harvesting devices, grazing, and associated trampling by domestic and uncontrolled herbivores. The producer biomass and distribution at any

given time is effected by changes in the physiological functions and spatial relations in the fashion outlined in Fig. 3.3.1. Example models developed from this diagram, along with explanations follow. One thing to realize is that in developing models from the diagram not all the causal links from one level to the next need to be considered since some elements have a greater effect than others.

3.3.5 Envisioned or Possible Producer Level Models

(i) External Environment

$$\text{Ext Env} = f(\text{Mic}, \text{Clim}, \text{Soil}, \text{Cons}, \text{An.A})$$

Where Mic = Microbial Activity
 Cons = Consumers
 Clim = Climate
 An.A = Animal Activity

The external environment is the result of varying combinations of the input functions. Microbial activity here includes both decomposer and pathogen activities which effect nutrient cycling, organic matter decomposition, and disease. Climate includes solar radiation, precipitation, temperature at varying levels below and above the ground surface, relative humidity, and gaseous composition of the ambient air. The soil input function includes soil moisture, texture, structure, bulk density, base saturation of the soil solution, and organic content (see Fig. 3.3.1). The animal activity function includes input of the species, numbers, and physical activity of all animals. The producer input represents an *internal feedback* of plant biomass and distribution. Also included is an effect due to the plants previous physiological status.

(ii) Internal Environment

$$\text{Int Env} = f(\text{PT}, \text{WS}, \text{NS}, \text{Path}, \text{Phen}, \text{Morph})$$

Where PT = Photo-Thermal Status
 WS = Water Status
 NS = Nutrient Status
 Path = Pathology
 Phen = Phenology
 Morph = Morphology

The internal environment is the result of varying combinations of the plants internal conditions which are in turn altered by the external environment.

a. Photo-Thermal Status

$$P-T = f(\text{Prod, Clim, Soil})$$

b. Water Status

$$WS = f(\text{Prod, Clim, Soil, Mic})$$

c. Nutrient Status

$$NS = f(\text{Mic, Prod, Clim, Soil, Cons})$$

d. Pathology

$$\text{Path} = f(\text{Mic, Clim, Soil})$$

e. Phenology

$$\text{Phen} = f(\text{Prod, Clim, Soil})$$

f. Morphology

$$\text{Morph} = f(\text{Prod, Clim, Soil, An.Act.})$$

(iii) Photosynthesis

$$\text{Photo} = f(\text{Int Env, Trnsl, Res})$$

Where Trnsl = Translocation
 Res = Respiration

All factors of the internal environment have an effect on photosynthesis. Greatest effects are due to photo-thermal, water, and nutrient status, where nutrient status includes minerals, gases, and required organic materials. Removal of the product of photosynthesis by translocation and respiration also influences the rate of the reaction.

(iv) Respiration

$$\text{Res} = f(\text{Int Env, Photo, Trnsl})$$

The photo-thermal, nutrient, and water statuses are the most influential factors of the internal environment affecting respiration. Respiration rate also will respond directly to an increase in carbohydrate resulting from respiration or translocation.

(v) Translocation

$$\text{Trnsl} = f(\text{Int Env, Photo, Res, Stor, Mort, Growth})$$

Where Mort = Mortality
 Stor = Storage

The primary elements of the internal environment effecting translocation are phenology, nutrient, water, and photo-thermal status. The accumulation of carbohydrate in photosynthesizing tissue cause an increase in translocation. Respiration also necessitates translocation of carbohydrate and removal of waste products. Growth and storage processes accumulate organic materials which must be translocated.

(vi) Transpiration

$$\text{Trnsp} = f(\text{Int Env, Res, Trnsl, Photo})$$

Transpiration is influenced primarily by the plants internal water status. The photo-thermal status, translocation, and photosynthesis influences transpiration through their effects on the stomatal openings.

(vii) Growth

$$\text{Growth} = f(\text{Int Env, Photo, Trnsl, Stor, Res})$$

The internal photo-thermal status and plant phenology provide the necessary conditions for growth. Photosynthesis, translocation, storage, nutritional and water status, and respiration either provide or deplete the materials needed for growth.

(viii) Storage

$$\text{Stor} = f(\text{Int Env, Photo, Trnsl, Growth, Res})$$

Storage is affected by essentially the same factors as growth.

(ix) Mortality

$$\text{Mort} = f(\text{Int Env})$$

Metabolic mortality is influenced by all of the elements of the internal environment in a direct manner. Any serious imbalance in these

factors can result in death of all or part of the plant by metabolic disruption.

(x) Reproduction

$$\text{Rep} = f(\text{Asex}, \text{Sex})$$

Where Asex = Asexual
 Sex = Sexual

a. Asexual

$$\text{Asex} = f(\text{Int Env}, \text{Ex Env}, \text{Photo}, \text{Trns1})$$

b. Sexual

$$\text{Sex} = f(\text{Int Env}, \text{Ex Env}, \text{Photo}, \text{Trns1})$$

Both asexual and sexual reproduction are sensitive to all of the factors of the internal environment. In addition the external environment affects reproduction through transport of pollen and seeds, and implantation of seeds and stolons. Photosynthesis and translocation provide the carbohydrate needed for this process.

(xi) Producer Biomass

$$\text{PB} = f(\text{Phy F}, \text{Phy L})$$

Where Phy F = Physiological Functions
 Phy L = Physical Loss

Physiological functions affect producer biomass by addition of material through processes of photosynthesis and losses of material through respiration and metabolic mortality. Physical loss represents a direct removal.

(xii) Producer Three-Dimensional Spatial Distribution

$$\text{3D} = f(\text{Rep}, \text{Phy L})$$

Where Rep = Reproduction

The three-dimensional distribution describes the horizontal layering of plant parts above and below ground as well as the positioning of plants

with respect to each other on the ground surface. Reproduction and physical loss have an effect through establishment and loss of individuals.

(xiii) Physical Loss

$$\text{Phy L} = f(\text{Ex Env, Harv, Tramp})$$

Where Tramp = Trampling

The external environment affects plant loss directly through destruction of plants by climatic conditions and through the activities of animals, other than by grazing. Trampling is meant to include the destruction of plant material associated with grazing, and harvest represents the removal of material that is cycled through the consumer trophic level.

(xiv) Harvest

$$\text{Harvest} = f(\text{Unc, Livestock, Mechanical})$$

Where Unc = Uncontrolled

The uncontrolled input of the harvest function includes all removal by free-ranging fauna while removal by livestock and mechanical means represent the managed harvest via man's intervention.

3.3.6 Operating Producer Level Models

Several specific models are described below to give the reader some idea of what kinds of models we are working with. Each of the models will then be related to the producer hierarchical diagram of Fig. 3.3.1.

(i) A model for net photosynthesis has been produced and currently is in operating condition. This model is an implementation of Waggoner's (1969b) simulator of net photosynthesis in a single leaf. This model is part of the overall producer biomass model. The dependent variables or outputs are net photosynthesis, dark respiration, and light respiration. It requires as building blocks or inputs, models of photo-thermal status and nutrient status of the plants. The equations used are algebraic.

The primary equation of the model is

$$\text{Net Photosynthesis} = \frac{C - W(R_i + R_c)}{R_a + R_s + R_o + R_i + R_c}$$

where the input data (parameters) are

C = CO_2 in free air

R_i = internal resistance

R_a = air resistance

R_o = physiological resistance

and where the intermediate system variables are

W = respiration

R_c = chemical resistance

R_s = stomatal resistance

The time increment of the model is one second and the unit of space over which it operates is a single plant leaf.

(ii) A further photosynthesis model has been developed by Bledsoe and Jameson (1969) which implements work by Budagovski and Ross (1967), and Gates (1968). The single dependent variable output by this model is P_n , net photosynthesis. It uses a single algebraic equation:

$$P_n = \begin{cases} C[V_1 L]k_1 \left[\frac{s}{1+k_3 s} - \frac{s_c}{1+k_3 s_c} \right] \cdot \\ \quad [(T_{20} - T_2)e^{-k_2(T_{20} - T_2)}] M_n \text{ if } s > s_c \text{ and } T_2 < T_{20} \\ -C V_1 k_4 [(T_2 - T_{20})e^{-k_5(T_2 - T_{20})}] M_n \text{ if } s > s_c \text{ and } T_2 > T_{20} \\ -C V_1 k_6 \left[\frac{s_c - s}{s_c} \right] [T_2^{k_7} e^{k_7/k_8(1 - T_2^{k_8})}] M_n \text{ if } s < s_c \end{cases}$$

where driving functions are

T_2 = air temperature

S = solar radiation

V_1 = above ground biomass

L = leaf area index.

The intermediate system variables are

M = function of soil moisture

N = function of soil nitrogen,

while the constants are

T_{20} = compensation point for net photosynthesis with respect to leaf temperature

S_c = photosynthetic compensation point with respect to sunlight intensity

k_i = empirically determined constants, $i = 1 \dots 8$.

The time increment of this model is one second and the unit area is one square centimeter.

(iii) A herbage dynamics model with vegetative structure detail was also developed by Bledsoe and Jameson (1969). The output of this model includes V_A , aboveground biomass in reproductive structures. It uses a set of three differential equations for each of n species of plants. The set is:

$$\begin{aligned}\dot{V}_A &= P_n - (T_B + T_R + D_A + H_A) \\ \dot{V}_B &= T_B - (D_B + H_B + V_B R_B(T_3)) \\ \dot{V}_R &= T_R - (D_R + H_R + V_R R_R(T_2))\end{aligned}$$

where driving variables are

P_n = net photosynthesis

T_2 = air temperature

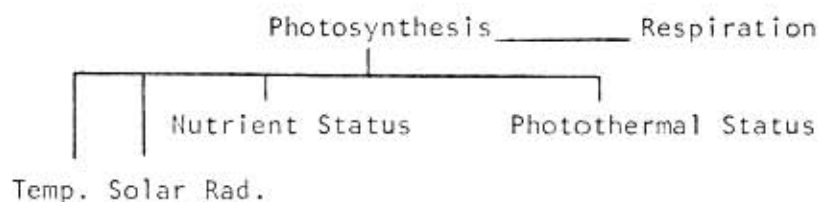
T_3 = soil temperature

and where system variables are

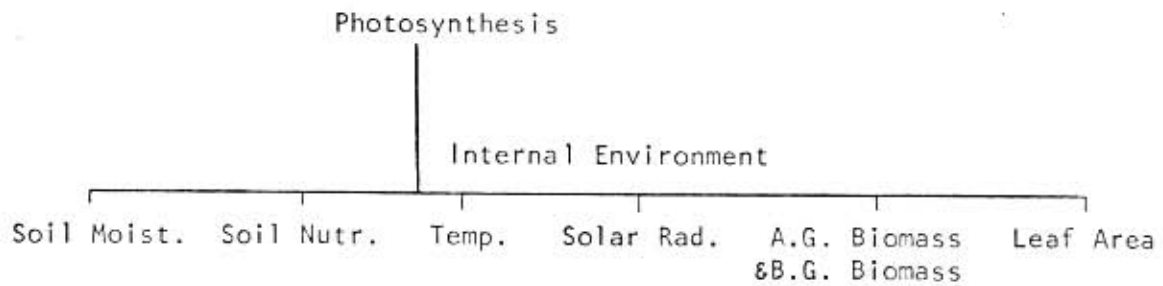
- T_B = translocation to belowground parts
- T_R = translocation to reproductive structures
- D_A = death rate of aboveground parts
- H_A = aboveground harvest rate
- D_B = belowground death rate
- H_B = belowground harvest rate
- V_B = belowground biomass
- R_B = belowground respiration
- D_R = death rate of reproductive parts
- H_R = harvest rate of reproductive parts
- V_R = reproductive structure biomass
- R_R = respiration of reproductive structures

The model operates on a per second time scale and per square centimeter area scale.

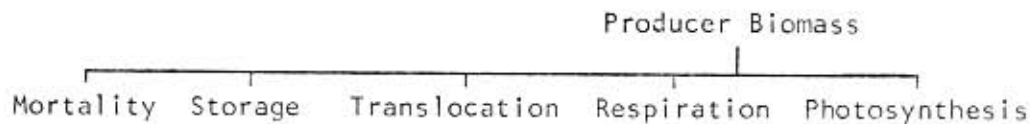
Waggoner's model (i) gives net photosynthesis as a function of respiration, nutrient status, photo-thermal status, temperature, and solar radiation. This may be hierarchically represented as shown below. (See also Fig. 3.3.1).



The photosynthesis model due to Bledsoe and Jameson (ii) may be represented as a function of soil moisture, soil nutrients, temperature, solar radiation, above- and belowground biomass and leaf area. This may be represented below, taken from Fig. 3.3.1:



The Bledsoe and Jameson herbage dynamics model (iii) gives above, below, and reproductive part herbage biomass as a function of metabolic mortality, storage, translocation, respiration and photosynthesis. This may be represented by that section of the hierarchical diagram shown below (see Figure 3.3.1).



3.4 Consumers

3.4.1 Consumer Population

The diagrammatic representation for energy flow or biomass change within the "consumer group" can be represented as a function of two general causal factors: (i) change in population numbers; (ii) weight changes or energy flow for those present members comprising the population. The following relationship exists:

$$B = N \cdot \bar{W}$$

where B is the total biomass of a population, N is the number of population members, and \bar{W} is the average weight of a population member. Moreover,

$$\dot{B} = N \cdot \dot{\bar{W}} + \bar{W} \cdot \dot{N}$$

and the rate of change of B is also related to the two mentioned variables.

Therefore, the consumer hierarchical diagram has been divided into these two

components. This discussion is concerned with the change in numbers or population dynamics aspect of the diagram. This diagram is shown in Fig. 3.4.1.1.

The causal relationships, on the left, those of change in population numbers effected by mortality, natality, and movement into and out of the system, is the most evident and well-accepted of all the causal relationships in Fig. 3.4.1.1.

The three variables affecting natality are the number of offspring produced per breeding effort per breeding animal, the number of breeding efforts, and the number or proportion of breeding animals within the population. To relate the first of these variables to specific causal factors in a general hierarchical context is difficult. There have been extensive research efforts related to the clutch size in birds, litter size in mammals, etc., but little or no significant work has been presented in the literature combining all factors into one model. Of the five factors listed relating to numbers of young produced, only one, geographic area, is not driven by the output from another compartment. Geographic position has been shown to affect the number of young produced in several populations of consumers. However, the *actual* causal factors have been widely disagreed upon; suggested factors include climatic influences, food availability, and day length. Therefore, no attempt is made to have geographic area relate to a driving function or a specific outside compartment.

A second variable that influences natality is frequency of breeding effort. Fecundity and dependence period require explanation. If the diagram was structured for only mammals, then one could speak of this factor in terms of gestation and lactation periods, but more general terminology is used here.

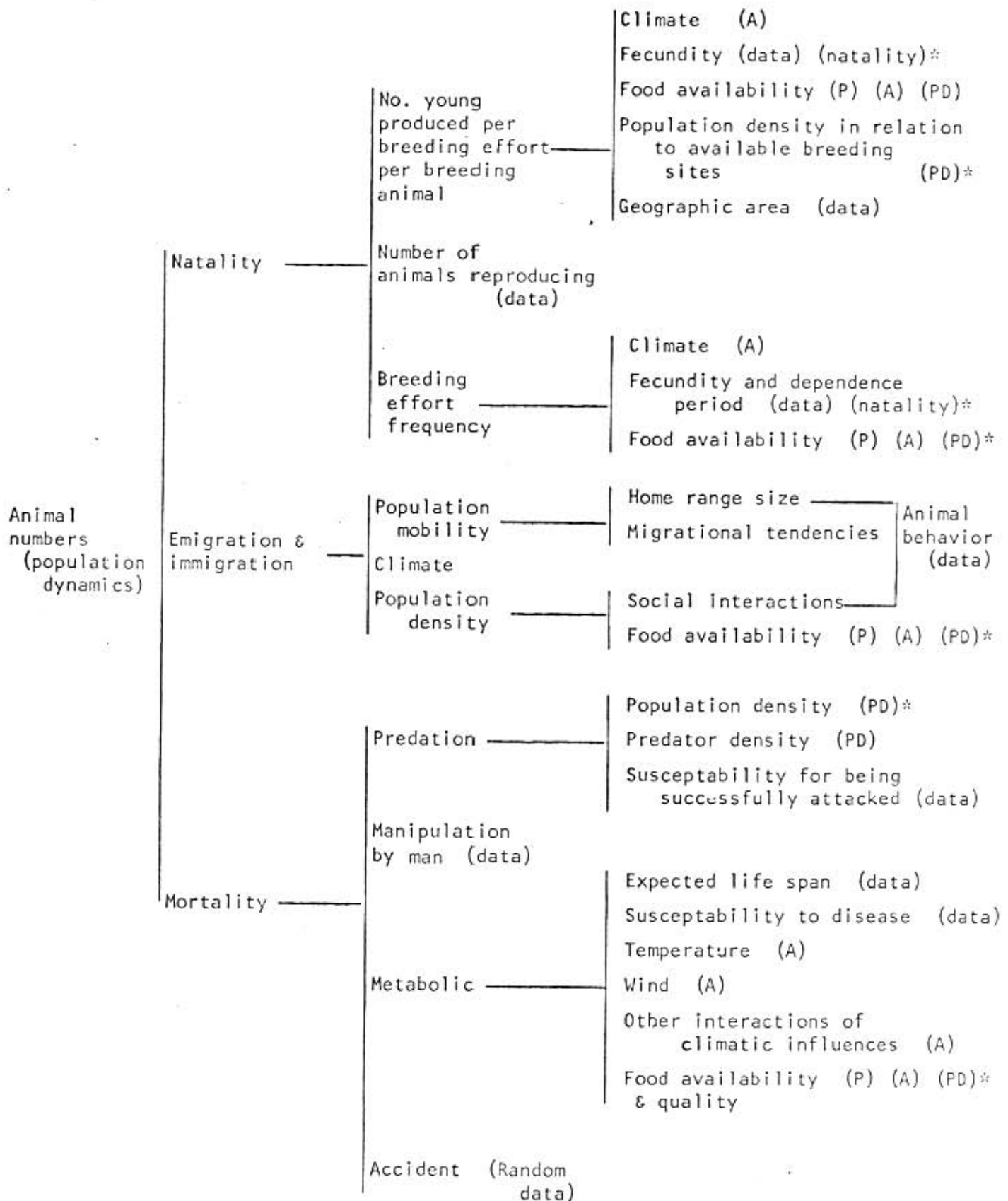


Fig. 3.4.1.1. Components of the consumer trophic level: population dynamics (tentative).

Emigration and immigration of population members into and out of the system being modelled are aspects of population density that are more closely linked to animal behavior than either mortality or natality. Consequently, in the diagram most listed factors are eventually tied to animal behavior. Even food supply can be indirectly related to behavior.

Basic knowledge concerning mortality is sparser than that about natality. The mortality factor is considered to be a function of four other factors in the hierarchical diagram. Of the four, accident can be treated initially as a purely random event, at least on an intraseasonal basis, and not subject to mechanistic modelling inputs. Predation, as it affects mortality, has been studied intensively and many dynamic models have been devised to simulate predator-prey relationships. Most of this effort has been done with insect populations. The susceptibility-of-prey-for-attack factor is meant to include all of the predator-prey-mortality interactions not covered by population densities.

The metabolic pathway of death is designed to include all causes of mortality not fitting elsewhere. Our knowledge of the interactions within this group of causal relationships is perhaps more vague than at any other place on the diagram.

The inputs into this hierarchical diagram from other such diagrams and driving functions, and the feedback loops from the output of this one, are only presented to indicate what might be possible eventually, and not what is feasible in the modelling efforts of the immediate future.

3.4.2 Consumer Weight Change of an Individual

In considering factors influencing the weight change of an individual, the total partitioning of energy has been emphasized. Consequently certain

aspects of body composition will be needed for predicting weight change from caloric change if a non-caloric estimate of biomass is desired.

The hierarchical diagram depicting the relationships of various factors which may affect the weight change of an individual consumer is largely based on mammals. The diagram is given in Fig. 3.4.2.1.

3.4.3 Net Energy and Those Factors Which Affect It

(i) Net Energy

$$\text{Net Energy} = \text{Metabolizable Energy} - (\text{Basal Metabolism} + \text{Thermoregulation} + \text{Activity} + \text{Heat Increment} + \text{Reproductive Energy})$$

Net energy is defined as that part of the metabolizable energy which is not directly catabolized and which is thus available for anabolism.

(ii) Metabolizable Energy

$$\text{Metabolizable Energy} = f(\text{Assimilation, Excretion, Secretion})$$

Metabolizable energy is the only energy input of virtually all consumers. Certain microorganisms, however, are both autotrophic and heterotrophic, and certain other organisms actively absorb heat from the environment. This latter factor is included under thermoregulation.

Assimilation refers to the amount of chemical energy which is absorbed into the animal from the environment or gut. Certain animals, however, do not have a gut. For most animals:

$$\text{Assimilation} = f(\text{Ingestion, Digestibility, Organisms, Competition})$$

$$\text{Ingestion} = f(\text{Food Availability and Preference, Digestibility, Animal History, Caloric Content of Food in Relation to Their Need})$$

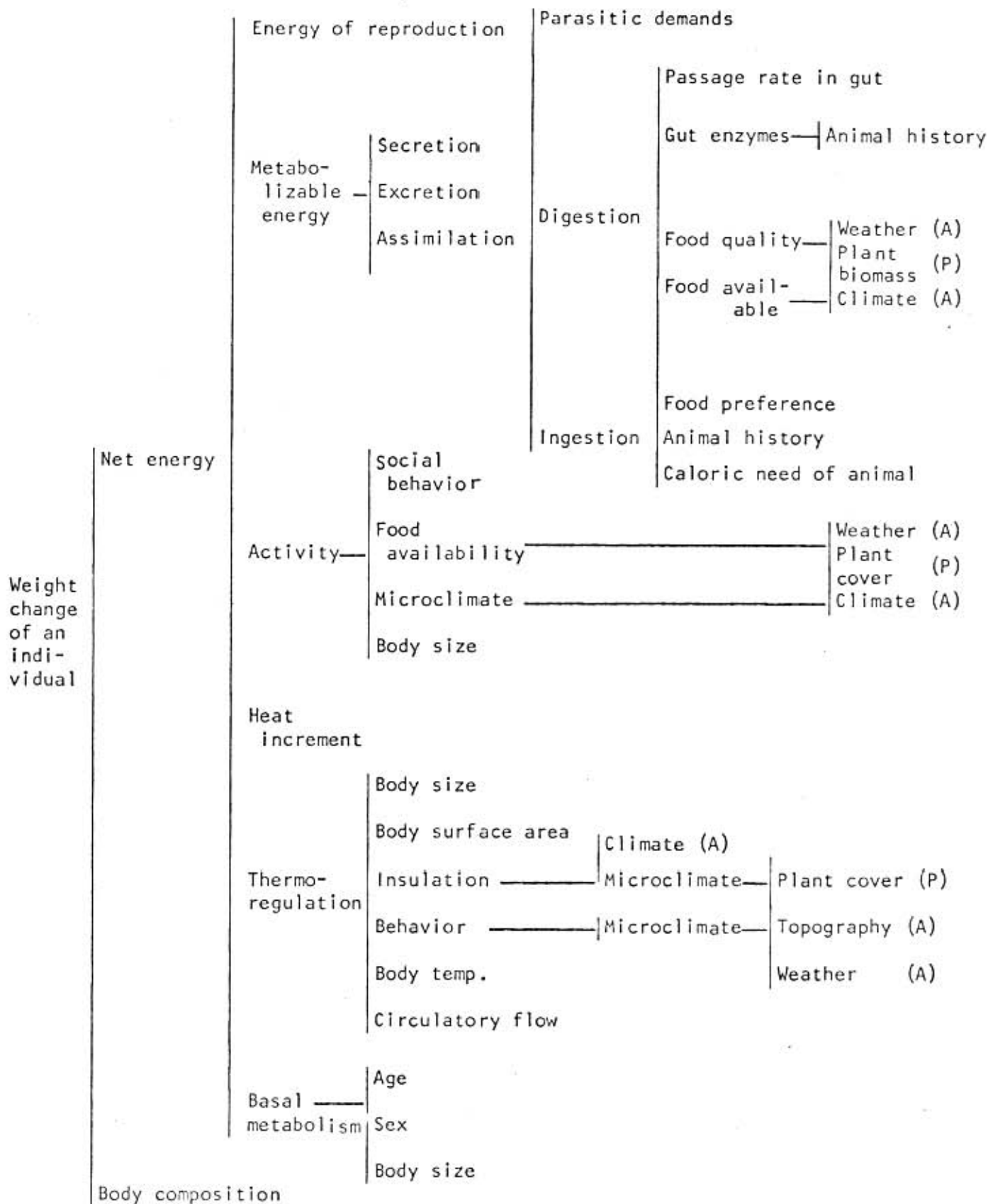


Fig. 3.4.2.1. Components of the consumer trophic level: animal energetics (tentative).

$$\text{Digestibility} = f(\text{Passage Rate, Gut Enzymes, Food Quality})$$

Organism in the gut (both parasites and symbionts) require part of the ingested energy. Many if not all contribute to the host animal by supplying heat and by converting certain nutrients from a useless to a useable form.

(iii) Basal Metabolism

$$\text{Basal Metabolism} = f(\text{Body Size, Sex, Age, } Q_{10})$$

Basal metabolism is usually defined as the metabolic rate of a fasting and resting homeotherm in a thermoneutral environment and which is neither hibernating nor aestivating. This definition is extended herein to include all animals whether they are poikilothermic (cold-blooded), hibernating, or aestivating (summer hibernating). This is rationalized on the existence of the rather continuous gradient between the homeothermic and poikilothermic extremes which are found in nature.

(iv) Thermoregulation

$$\text{Thermoregulation} = f(\text{Microclimate, Response to Microclimate, Insulation, Body Surface Area, Body Size})$$

Thermoregulation refers to physiological activity which regulates the internal temperature of a consumer. Although this factor is normally thought of as being unique to birds and mammals, it is not universal. It applies in some degree to reptiles and perhaps other "poikilotherms."

Microclimate is used as a general term to describe wind speed, relative humidity, radiation flux, and temperature at the animal's surface. Although input to Microclimate is labeled as abiotic and producer (the latter being through shelter), the necessary information may not be available from abiotic or plant models.

(v) Activity

$$\text{Activity} = f(\text{Body Size, Microclimate, Food Availability, Social Behavior})$$

Virtually all consumers are motile (some parasites excluded) and thus require energy to move. The amount of energy required will depend on the size of the animal, the prevailing microclimate, the time and effort required to feed, and on the intensity and duration of social behavior.

(vi) Reproductive Energy

All groups of animals reproduce. Many are dependent on their parents for nutrition during their early growth stages. Since offspring are new individuals, weight changes associated with zygote nutrition must not be included in net energy or possibly even metabolizable energy. Milk production can be considered as gland secretion and thus be accounted for under metabolizable energy.

(vii) Heat Increment

When most animals ingest, digest and assimilate food, their metabolic rates increase. Some of this increase cannot be attributed to previously listed factors and thus will be included in a separate category--heat increment.

3.4.4 Clarification of Consumer Hierarchical Diagram Ambiguities

Looking at the hierarchical diagram of Fig. 3.4.2.1 we see that certain aspects of both the producer models and the abiotic models will be required as inputs. Several generalizations can be made.

(i) Microclimate results from modification of climate and weather by the structural surroundings of the animal. Thus, topography and plants shelter an animal and thereby modify the microclimate.

(ii) Physiological response to heat loss by conduction, convection and radiation will be characterized by changes in an animal's exposed surface. Climatic change will affect the thickness of the coat. Some weather conditions may cause individual hairs to stand on end.

(iii) Maximum food availability will be determined by the producer model. Thus an animal cannot eat what has not grown. The abiotic inputs (such as snowfall) will tend to reduce the available food by making food difficult to find.

(iv) The abiotic and producer components of the environment provide an animal with a structural framework within which they live. These factors will affect the frequency of interaction between individuals (e.g., earthworms rarely encounter one another and thus have little need for elaborate social behavior). The availability of shelter, nesting sites, etc. will affect territory size and thus territorial behavior.

(v) Food quality follows a seasonal trend. Young succulent spring growth is much more nutritious and much more digestible than winter forage.

(vi) Animal history is largely the result of previous weather and food supply.

Several specific models concerning consumer population dynamics and weight change are summarized below and the diagrams are then related to hierarchical diagrams in Fig. 3.4.1.1 and 3.4.2.1. These are given in Tables 3.4.4.1 through 3.4.4.4.

The bird population dynamics model summarized in Table 3.4.4.1 gives bird population numbers and weight as a function of immigration, emigration, birth rate, death rate, assimilation efficiency, food ingestion rate, and a

Tabl 3.4.4.1. Summary of bird model with inputs estimated for the lark buntings. The model gives bird population density and weight change as outputs.

Differential Equations

1. $\dot{P}(t) = I(t) - E(t) + B(t) - M(t)$

where $B(t) = L(t-h) S(t,h) P(t-h) R(t-h)$

2. $\dot{w}(t) = e(t) F(t) - RE(t)$

Output Variables

<i>Notation</i>	<i>Definition</i>	<i>Units</i>	<i>Source</i>
$P(t)$	population density at time t	birds/100 hectares	solve equation 1
$\dot{P}(t)$	rate of change of population at time t	birds/100 hectares-week	equation 1
$w(t)$	average weight per bird at time t	grams/bird	solve equation 2
$\dot{w}(t)$	rate of change of bird weight at time t	grams/bird-week	equation 2
$W(t)$	total bird biomass density	grams/100 hectares	$W(t) = w(t) P(t)$

Input Variables

<i>Variable Notation</i>	<i>Variable</i>	<i>Value (for Lark Bunting)</i>	<i>Units</i>	<i>Source of Value</i>
$I(t)$	immigration rate at time t	(60 May 1-15 (0 otherwise	birds/100 hectares/week	observation (Ryder)
$E(t)$	emigration rate at time t	(50 after Aug. 15 (0 otherwise	birds/100 hectares/week	observation (Ryder)
$B(t)$	birth rate at time t	obtained from other variables	birds/100 hectares/week	

Table 3.4.4.1. (Continued).

$M(t)$	mortality rate at time t	(.015 $P(t)$ (before June 10 (.025 + $P(t)$ (after June 10	birds/100 hectares/week	observation estimates (Ryder, Baldwin)
$e(t)$	assimilation efficiency at time t	.7 for all time		literature
$F(t)$	food intake rate at time t	41 for all time	grams/bird/week	literature + date (Baldwin)
$RE(t)$	respiration rate at time t	(28 before June 1 (29.5 June 2-July 10 (29 July 11-30 (28 after July 30	grams/bird/week	literature + observation (Baldwin)
h	hatching period	9 days		observation (Baldwin)
$L(t - h)$	egg laying rate at time $t - h$	(1.2 June 1-21 (.4 July 10-21 (0 otherwise	eggs/breeding female/week	data (Ryder, Baldwin)
$S(t, h)$	percentage egg survival	.4		observation (Baldwin)
$R(t - h)$	percentage breeding females	.45		observation (Ryder, Baldwin)

Table 3.4.4.2. Summary of insect predation model. (see: Holling, 196:).

Model form:

- a) dependent variables -- general description, type, e. g., biomass, numbers, calories, chemical constituents (specify)

The model gives the change in mortality rate of a prey insect population due to predation.

- b) equation types -- difference, differential, algebraic

all three.

- c) general form using functional notation, e. g., $P_n = f(L, T, n, M)$

$$\dot{M}_i = f(D_i, D_j, E, C_i, C_j)$$

Variable	Definition	Type	Value Used	Source of Value
\dot{M}_i	change in mortality rate for prey population i		percentage	solution of equation
D_i	density of prey population i	1	indiv./M ²	either from output of main pop. dynamics model or data
D_j	density of predator population j	1	indiv./M ²	?
E	selected environmental factors	1	variable	abiotic model
C_i	characteristic index of prey	1	percentage	data
C_j	characteristic index of predator	1	percentage	data

1 = parameter

2 = intermediate system variable

3 = driving function or input

Table 3.4.4.3. Summary of Thermoregulation Model.

The model gives the energy needed to maintain animal thermal balance.

Model, form:

a) dependent variables -- general description, type, e.g., biomass, numbers, calories, chemical constituents (specify)

Th = Thermoregulation energy.

KCAL

Units - $\frac{\text{KCAL}}{\text{individual. day}}$

b) equation types -- difference, differential, algebraic

Algebraic.

c) general form using functional notation, e.g., $P_n = f(L, T, n, M)$

Th = F(M, I, Wt., exposed surface area)

Variable	Definition	Value Used	Source of Value
M	Microclimate - wind - air temp. - radiant energy - relative humidity	Various	Abiotic and Literature and Data
I	Insulation - thickness - resistance to heat flow	Various	Literature Data
Wt.	Metabolic weight	(live wt) ^{3/4}	Data
ESA	Exposed surface area	cm ²	Literature Data

1 = parameter

2 = intermediate system variable

3 = driving function or input

Interrelation:

state probable relation to other models for which it may be a building block, which may be blocks for it, for which does it provide driving functions, etc.

This model will feed into the net energy model and will require inputs from abiotic producer models. Producers are important as providers of shelter.

Table. 3.4.4.4. Summary of Net Energy for Production Model.
(Ruminants).

The model gives the rate of production of biomass of an individual.

Model, form:

- a) *dependent variables -- general description, type, e.g., biomass, numbers, calories, chemical constituents (specify)*

Net Energy - NE

Units - $\frac{\text{KCAL}}{\text{Day} \cdot \text{Individual}}$

- b) *equation types -- difference, differential, algebraic*

Differential and Difference - Differential

- c) *general form using functional notation, e.g., $P_n = f(L, T, n, M)$*

$NE = ME - (BM + TH + HI + A + ER)$

Variable	Definition	Type	Value Used	Source of Value
ME	Metabolizable energy	2	$\frac{\text{KCAL}}{\text{Day} \cdot \text{Individual}}$	Data
BM	Basal Metab.	2	"	Data
TH	Thermoregulation	2	"	Data & Literature
HI	Heat increment	2	"	Literature
A	Activity	2	"	Data & Literature
ER	Energy of Reproduction	2	"	Literature

1 = parameter

2 = intermediate system variable

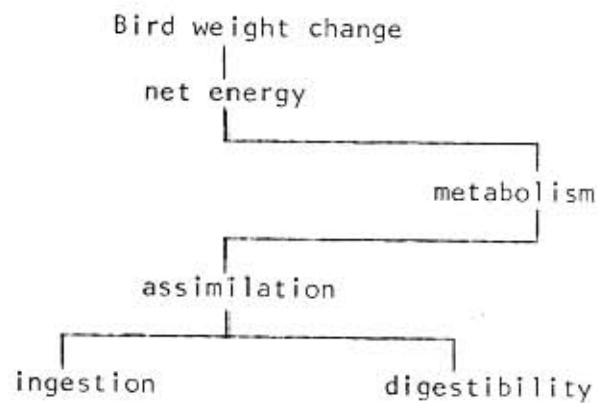
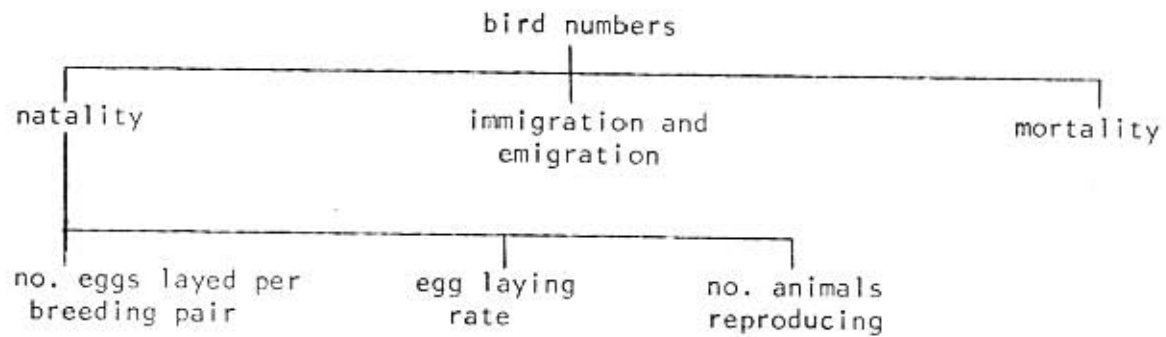
3 = driving function or input

Interrelation:

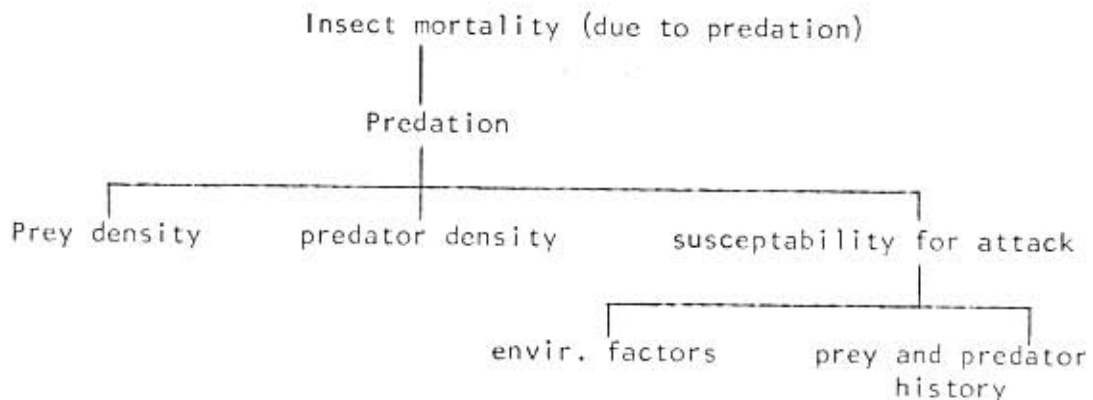
state probable relation to other models for which it may be a building block, which may be blocks for it, for which does it provide driving functions, etc.

Building block for consumer biomass model; requires models giving independent variables.

number of reproduction variables. These may be represented as the diagram below (adopted from Fig. 3.4.4.1 and 3.4.4.2):

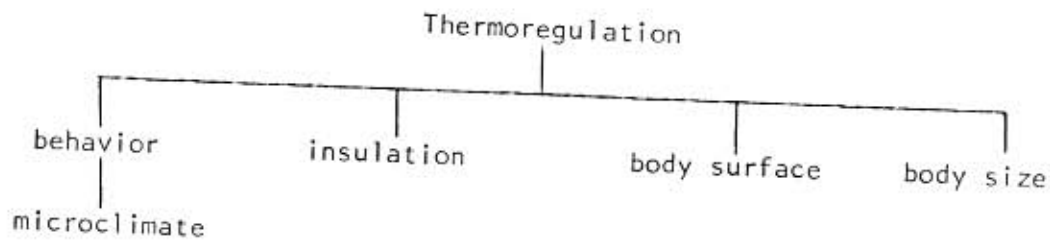


Holling's insect predation model (Table 3.4.4.2) gives the insect mortality rate due to predation as a function of prey density, environmental factors, and animal history of both predator and prey. This may be shown hierarchically below:

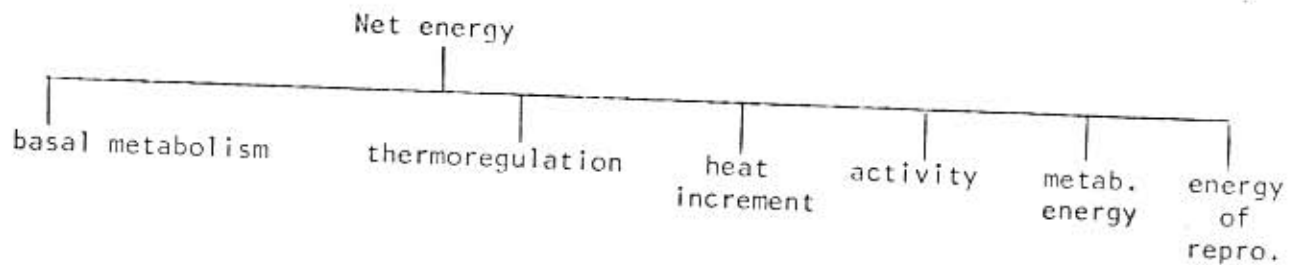


In this case the model carries beyond the resolution of hierarchical diagram 3.4.4.2 and another level of resolution had to be included (the bottom line of the diagram above).

The thermoregulation model (Table 3.4.4.3) gives thermoregulation energy cost in kcal per individual per day as a function of microclimate, insulation, metabolic weight and exposed surface area. This may be represented as in the diagram below:



The ruminant net-energy-for-production model (Table 3.4.4.4) gives net energy as a function of metabolizable energy, basal metabolism thermoregulation, heat increment, animal activity, and energy of reproduction. This may be represented hierarchically as in the diagram below:



Of the four consumer models discussed above only the first, the bird model, is currently operating in conjunction with the grassland study.

3.5 Detritus Chain

3.5.1 Microbial Hierarchical Diagram Structure

The modelling of ecosystem components whose processes are mediated mainly by microorganisms can be thought of as a system of material flows regulated by the activity of microbial functional groups (Bledsoe and Jameson 1969). For example, oxidation of ammonia, or flow from NH_4^+ to NO_2^- is mediated by the activity of *Nitrobacter* in the soil. The hierarchical diagram in Fig. 3.5.1.1 details the causative links which must be expressed mathematically to determine activity of a microorganism functional group. There are three major subheadings: microorganism presence, biomass, and proper environmental conditions.

The first factor involved in determination of microbial activity is the presence or absence of the bacterial types. If they are present in the active form, there are four possible mechanisms by which they came to be present. If present in the spore form, the environmental conditions for spore germination must be present if subsequent activity is to occur. These conditions will frequently be different from the conditions for growth.

Given the presence of the organism in active form, the environment must be favorable for metabolic activity to occur. The environment is arbitrarily divided into abiotic and organic segments. The factors under these headings were taken from Brock (1966) and are, in their general form, well known to microbiologists. The sources of these factors will be other models, literature or experimentally measured values (DATA), variable factors representing man's manipulations of the ecosystem (HI), or factors determined by the model itself in feedback loops (indicated by asterisks).

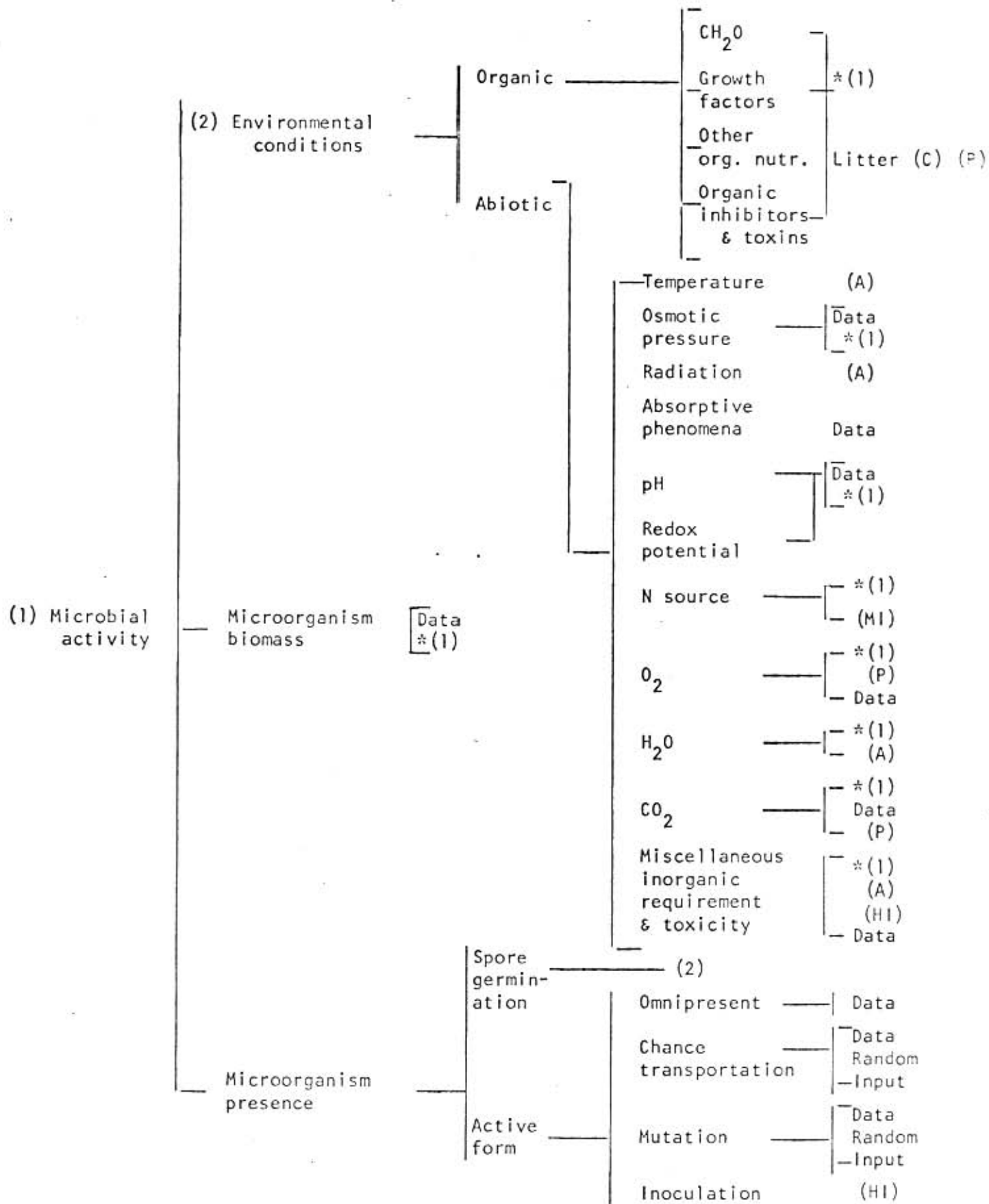


Fig. 3.5.1.1. Schematic of activities in the detritus compartment (tentative).

The organic and abiotic factors indicated as coming from the producer and consumer diagrams will be provided via a connection to some existing variable of those diagrams. For example, the carbohydrate (CH_2O) component will exist in a variety of forms (e.g., cellulose, chitin, cellobiose) but all will come largely from plant and animal litter. Finally, microbial biomass will affect activity and rate of change of biomass. This factor will be determined from experimental measurement for initial conditions and will be denoted by feedbacks.

3.5.2 Detritus Chain Models

Four models concerned with the detritus chain are summarized in Tables 3.5.2.1 through 3.5.2.4. The three models concerning the microbial element can be directly related to the hierarchical diagram in Fig. 3.5.1.1. The soil nutrient model does not directly relate to any one of the hierarchical diagrams. This points out that the analogy between models and hierarchical diagrams does not always hold. The diagrams may be seen as guidelines for model development but not as *rules*.

3.6 Abiotic: Climatic

The abiotic elements were divided up into climatic and soil subgroups. In the climatic subgroup most of the systems are not amenable to a hierarchical diagram, except for the net radiation.

Table 3.5.2.1 Summary of principal Soil Nutrients Model

Model form

a) dependent variables -- general description, type, e.g., biomass, numbers, calories, chemical constituents (specify)

The model describes the concentrations of the principal soil nutrients, i.e., nitrogen forms, phosphorus, cellulose, plant proteins, etc. May be partitioned to be descriptive of various soil depths. Rate of change is proportional to activity of a microbial form in some cases.

b) equation types -- difference, differential, algebraic

10-20 Differential Equations per soil layer

c) general form using functional notation, e.g., $P_n = f(L, T, n, M)$

$$\dot{N}_i = f(M_1 \dots M_n, N_i, T_3, S_m, I_i)$$

System variables:

Variable	Definition	Type	Value Used	Source of Value
$N_i, i=1 \dots m$	Concentration of i th soil Nutrient,	4	-	-
M_i	Active biomass of i th microbial form	4	-	-
T_3	Soil temperature	3	-	Abiotic model
S_m	Soil moisture	3	-	" "
I_i	Sum of inputs and outputs of i th Nutrient form due to all non-soil processes	2	-	Plant and animal models, external manipulations (fertilizer, etc.)

1 = parameter

2 = intermediate system variable

3 = driving function or input

4 = principal system variable

Interrelation:

state probable relation to other models for which it may be a building block, which may be blocks for it, for which does it provide driving functions, etc.

Closely related to soil microbe model.

Table 3.5.2.2. Summary of Soil Microbe Model I

Model, form:

- a) *dependent variables -- general description, type, e.g., biomass, numbers, calories, chemical constituents (specify)*

The model describes the biomass of active microbial forms associated with transfers of soil organic nutrients. Generally a logistic or exponential DE with variable parameters.

- b) *equation types -- difference, differential, algebraic*

10-20 differential equations

- c) *general form using functional notation, e.g., $P_n = f(L, T, n, M)$*

$$\dot{M}_i = f_i(T_3, S_m, N_1 \dots N_m, T_{x_1} \dots T_{x_p}, M_1 \dots M_n, B_i)$$

$i = 1, \dots, n$ microbial forms

$$\dot{T}_{x_i} = f(M_i, N_1 \dots N_m)$$

System variables:

<i>Variable</i>	<i>Definition</i>	<i>Type</i>	<i>Source of Value</i>
$M_i, i=1, \dots, n$	Active biomass of i th microbial form	4	--
T_3	Soil temp.	3	Abiotic model
S_m	Soil moisture	3	--
$N_i, i=1, m$	Concentration of i th form at soil organic or inorganic nutrient	3	Nutrient cycling model
$T_{x_i}, i=1 \dots p$	Metabolic byproducts	2	Soil toxicity model
B_i	Boolean variable giving switch on growth conditions for i th microbial form	2	Soil microbe II model

1 = parameter

2 = intermediate system variable

3 = driving function or input

4 = principal system variable

Interrelation:

state probable relation to other models for which it may be a building block, which may be blocks for it, for which does it provide driving functions, etc.

Closely related to soil nutrient cycling model

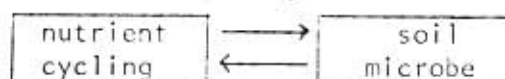


Table 3.5.2.3. Summary of Soil Microbe Model II

Model, form:

a) *dependent variables -- general description, type, e.g., biomass, numbers, calories, chemical constituents (specify)*

The model gives Boolean variables giving yes or no answer (0 or 1) to question "Are environmental conditions correct for activity of this organism?" and "Is this organism present in the soil?"

b) *equation types -- difference, differential, algebraic*

Boolean -- one set of logical formulae for each microbial form

c) *general form using functional notation, e.g., $P_n = f(L, T, n, M)$*

$$B_i = \begin{cases} \text{true if } (k_{i1} \leq Z_1 \leq k_{i2}) \vee (k_{i3} \leq Z_2 \leq k_{i4}) \vee \dots \\ \text{false else} \end{cases}$$

Variable	Definition	Type	Source of Value
B_i	0 or 1 depending on conditions for activity of i th microbial form	2	--
$k_{ij}, j=1, \dots, q$	Parameter specifying environmental tolerances	1	literature, field measurement
Z_1	Environmental variable specifying condition important to growth of same micro organism-- usually same as T_{xi} , T_3 , S_m , etc.	3	generated by various models

1 = parameter

2 = intermediate system variable

3 = driving function or input

Interrelation:

state probable relation to other models for which it may be a building block, which may be blocks for it, for which does it provide driving functions, etc.

Provides input for soil microbe I model

Table 3.5.2.4. Summary of Soil Toxicity Model.

Model, form:

- a) dependent variables -- general description, type, e.g., biomass, numbers, calories, chemical constituents (specify)

The model gives concentrations of materials in the soil which might be toxic to any other life form -- excludes substances which are included in principle soil nutrient model

- b) equation types -- difference, differential, algebraic

10-15 differential equations

- c) general form using functional notation, e.g., $P_n = f(L, T, n, M)$

$$T_{x_i} = f(M_1, M_2 \dots M_n, V_{B1} \dots V_{BP}, I_1 \dots I_q)$$

Variable	Definition	Type	Source of Value
T_{x_i}	Concentration of ith soil toxin	2	--
M_j	See soil Microbe I model	4	--
V_{B_j}	j species of plant, below ground biomass	4	Plant model
I_j	External input due to man's manipulation, etc.	3	Model controls

1 = parameter

3 = driving function or input

2 = intermediate system variable

4 = principle system variable

Interrelation:

state probable relation to other models for which it may be a building block, which may be blocks for it, for which does it provide driving functions, etc.

Provides input for soil microbe I & II models.

3.6.1 Net Shortwave Radiation Hierarchical Diagram

In this diagram the net radiation is represented as being determined by the incoming solar radiation, absorption in the air, and reflection in both the air and the ground. These in turn are affected by topographic and climatic conditions as is outlined in Fig. 3.6.1.1. We see here inputs from the producer element via cover and microclimate and from human control through the passage of particulate matter into the atmosphere.

3.6.2 The Climatic Subsystem

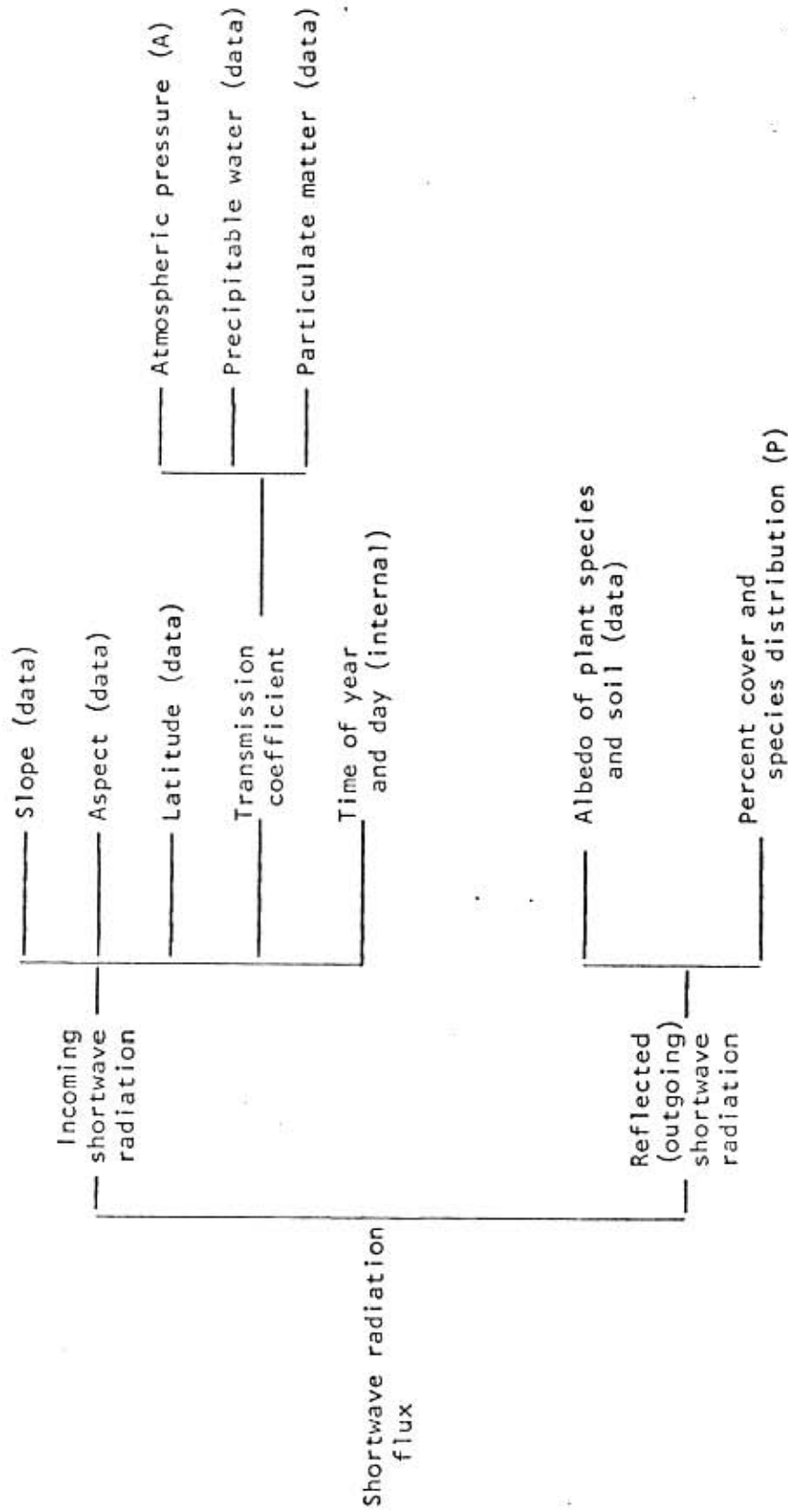
The precipitation submodel is envisioned as the central element of the climatic model because sufficient record of precipitation exists to permit the development of a statistical model which will accurately represent natural conditions, and because many of the other climatic elements to be modelled show a dichotomous response to wet vs. dry conditions. The determination, therefore, of whether it rained on a given day or not will control directly the functions or computational procedures to be used by the other submodels, the solar radiation model excepted.

(i) Precipitation Model

Determine if rain occurred on a given day using a Markov chain. Different relationships will be developed for each period of about 20 days. The lag will be one day.

If it rained on a given day, determine the amount. This will be accomplished by random selection of a storm size from a frequency distribution of storm sizes for the appropriate season. The frequency distributions will be developed from existing data.

Distribute the rain from this point estimate of storm size over the site. This will be accomplished using the data from the Intensive Network of "pasture gauges." The method of distribution is not yet established.



(P) Producer model
(A) Abiotic model

Fig. 3.6.1.1. Hierarchical diagram of shortwave radiation model (tentative).

(ii) Temperature Model

Determine departure from normal maximum and minimum temperatures using a Markov chain. Different relationships will be developed for wet and dry days and for different periods of the year; the length of these periods is not yet established.

From the maximum and minimum temperatures, develop temperature regime for the dry days based on average diurnal fluctuation for the season.

Establish concurrently a vertical temperature profile within the leaf zone, by a method not yet established.

(iii) Cloud Cover Model

Select at random a percent cloud cover for the day from a frequency distribution developed from existing data. The possibility of modelling diurnal fluctuations in cloud cover depends on the nature of the existing data. Different frequency distributions will be developed for different seasons and for wet and dry days.

(iv) Wind Model

Randomly select wind speed for a day from a frequency distribution for the appropriate season and wet or dry condition.

Randomly select a wind direction from a frequency distribution for the appropriate season, wet or dry condition, and wind speed class (e.g., 0-10, 10-20 mph, etc.).

Develop diurnal fluctuation from this point-in-time estimate using a function representing average diurnal fluctuation for the season.

(v) Relative Humidity

Randomly select a relative humidity from a frequency distribution for the appropriate season, percent cloud cover and wet or dry condition.

The opportunity for modelling diurnal fluctuation in relative humidity depends on the nature of the existing data but should be possible.

(vi) Solar Radiation

Solar radiation will be modelled mechanistically. Solar radiation reaching the earth depends on time of day and year, latitude, slope, aspect, cloud cover, and particulate matter in the atmosphere.

(vii) Atmospheric Pressure

Randomly select an atmospheric pressure for the day from a frequency distribution of atmospheric pressures for the appropriate season and wet or dry condition.

A shortwave radiation model developed from Fig. 3.6.1.1 gives the net shortwave radiation as a function of incoming radiation, albedo of the surface, and all the other environmental factors given in Fig. 3.6.1.1. Such a model may be seen as enclosing all the elements of the figure. It is summarized in Table 3.6.2.1.

3.7 Abiotic: Edaphic

3.7.1 Soil Water Hierarchical Diagram

Characteristically, runoff from grasslands is infrequent, although overland flow and re-infiltration are common. Runoff refers to the water that is removed from the area by streamflow. Therefore, soil water dynamics is central to our approach rather than runoff in the conventional case.

The hierarchical arrangement of Fig. 3.7.1.1 is a virtual listing of the input and output to the soil water, and major processes through which this occurs, the primary variables and factors affecting these processes, and the secondary and suspected variables and factors influencing the primary

Table 3.6.2.1. Summary Shortwave Radiation Model

32

Model form:

a) dependent variables -- general description, type, e.g., biomass, numbers, calories, chemical constituents (specify)

The model gives the shortwave radiation (SWR) absorbed by soil or plant cover. Cal. CM^{-2} time $^{-1}$

b) equation types -- difference, differential, algebraic

Algebraic

c) general form using functional notation, e.g., $P_n = f(L, T, n, M)$

$\text{SWR} = F(\text{INC}, \text{AL}, \text{TY}, \text{TD}, \text{TC}, \text{LA}, \text{AS}, \text{SL}, \text{AP}, \text{PW}, \text{PM})$

Variable	Definition	Type	Source of Value
INC	Incoming S-W radiation	2	
AL	Albedo of surface	1	Data
TY	Time of year	3	Internal
TD	Time of day	3	Internal
TC	Transmission coefficient	2	
LA	Latitude	1	Data
AS	Aspect	1	Data
SL	Slope	1	Data
AP	Atmospheric pressure	3	Pressure model
PW	Precipitable H_2O in atmosphere	3	Data & relative humidity & cloud model
PM	Particulate matter in atmosphere	3	Data

1 = parameter

2 = intermediate system variable

3 = driving function or input

Interrelation:

state probable relation to other models for which it may be a building block, which may be blocks for it, for which does it provide driving functions, etc.

Provides driving function to producer and consumer models.

Cloud cover & precipitation models provide inputs to it.

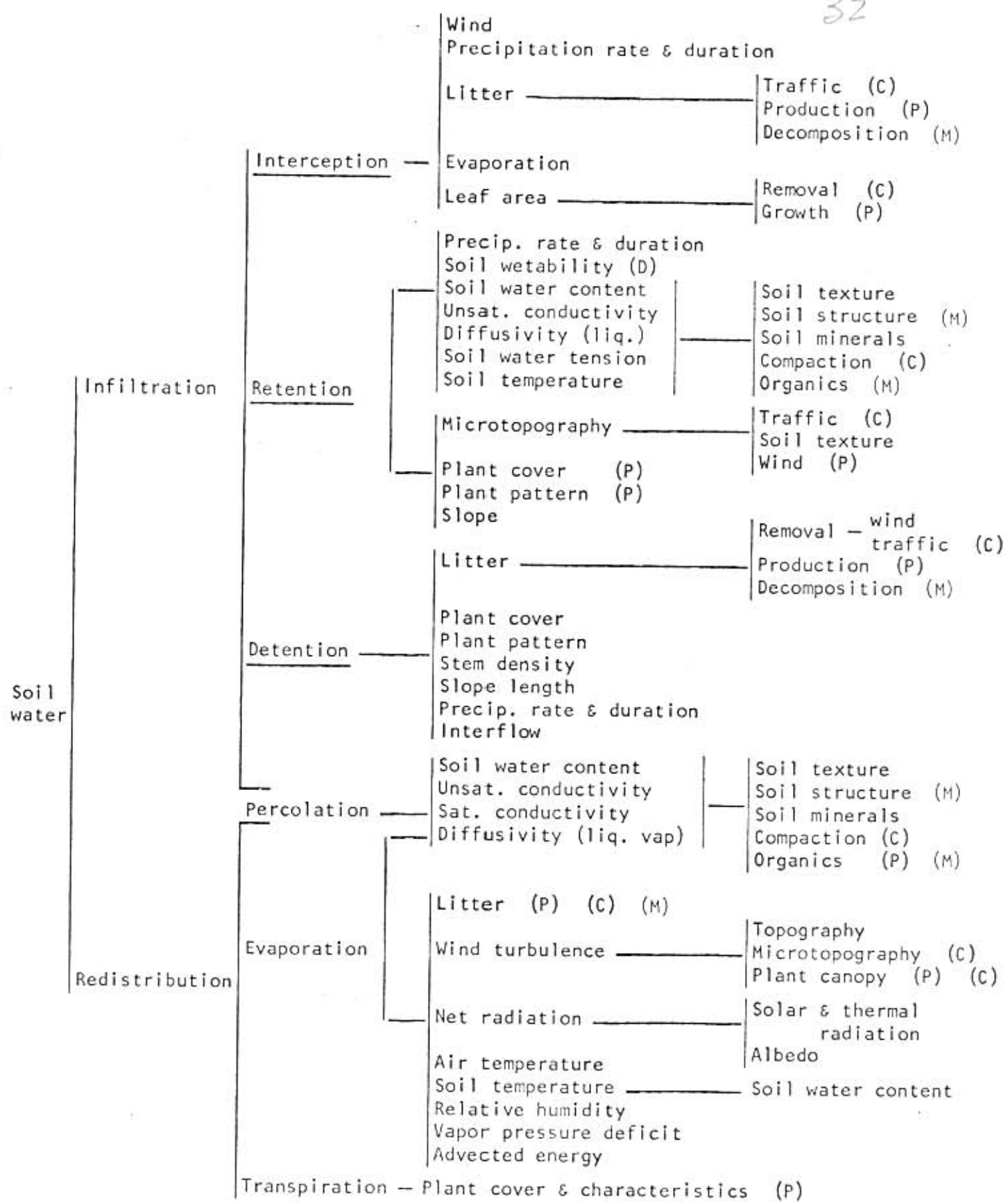


Fig. 3.7.1.1. Schematic of dynamics of soil water in the grassland (tentative).

ones. Physically, the major processes are both intradependent and interdependent and must be treated as a true system. This cannot be conveniently illustrated by the more artificial hierarchical system. However, the diagram will display the relations of the soil water model to the producer, consumer, and decomposer models.

The hydrologic cycle is relatively easy to describe in qualitative terms and the major processes and factors affecting these processes are well known. The state of the art in hydrologic modelling is quite advanced as far as modelling the abiotic processes (strictly physical), and the real challenge in modelling these processes is in the effects of the plant, animal, and decomposer on the behavior of water in ecosystems.

The left half of Fig. 3.7.1.1 represents the input of water to the soil, and the right half represents the output of water from the soil. One major distinction between the input and output processes is the time scale. Input occurs in a matter of minutes or hours, at the most, and output proceeds in terms of days or weeks.

The only input pathway to the soil-water system occurs through infiltration, which is the movement of water through the *soil surface* into the soil mass as distinguished from percolation, which is the movement of water through the *soil mass*. However, the two processes must be considered simultaneously since either process limits the other. To discuss the entire soil-water recharge system, we will begin with interception, the process controlling the net rainfall available for infiltration. Next are retention and detention, the two processes characteristic of the *surface* phenomena. Finally there is percolation, the process characteristic of the soil mass.

For all processes, one of the models (if any) will be presented that are now available from the literature. Functional notation is given for models not yet developed, i.e., those representing the biotic influences on the soil recharge processes.

Interception is the process through which the rainfall amount (and the rainfall energy) is reduced before reaching the soil surface. The amount of rainfall that does not reach the soil is a function of the storage capacity of the leaves and litter (intercepting area x water film thickness), the leaf area index, the total ground cover, the rainfall rate and duration, the evaporation rate during the storm, the wind during the storm, and the duration of inter- and intrastorm pauses. The storage capacity of a plant and litter canopy represents the threshold that must be exceeded (assuming a lumped system) before infiltration begins. Wind (the mechanical process) and evaporation, restore the storage capacity. The duration of inter- and intrastorm pauses provide the time for storage recovery through evaporation.

3.7.2 Soil Water Models

Of the factors discussed, only the rainfall amount, the storage capacity, the leaf area index, and the evaporation rate during a storm have been included in mathematical model for interception.

$$I = S(1 - e^{-CP}) + REt$$

or

$$I = (S + REt)(1 - e^{-CP})$$

are alternate equations used to represent interception, where

I = interception in inches depth over the projected area of the canopy

S = storage capacity of the vegetation over the projected area of the canopy

C = a fitted constant

P = gross precipitation

R = leaf area index

E = evaporation rate in inches per hour during the storm

t = storm duration in hours

The information required for these models must be obtained experimentally. The necessary biotic models that must be developed have to do with the changes in S , R , and C . For example, S is a function of leaf and litter area, which in turn depends on growth, litter production, forage removal, and litter decomposition:

$$S = f(\text{leaf area, litter})$$

The same functional representation could be used for R and C .

Retention and detention are two soil surface processes affecting the length of time available for water to infiltrate into the soil. Retention storage is the quasi-static amount of surface depression storage represented by the micro depressions of the soil surface. If infiltration is temporarily neglected, retention storage is simply the threshold that must be exceeded before overland flow begins. The measurement of retention storage is tedious and subject to great variation. For most purposes it has been calculated as a residual from analysis of plot hydrographs. As such, there are no developed models for retention storage.

The importance of retention storage is apparent if we consider whether animal traffic can change this basic threshold. If this is plausible, it would appear that retention storage (RS) could be represented as:

$$RS = f(\text{animal traffic} \times \text{soil mechanical properties})$$

Animal traffic (force and frequency of compaction) would interact with soil properties such as clay content. For example, clay soil when moist would compact, reducing relief and micro depressions.

Detention is the process through which flowing water is retarded by the friction of the surface. Detention storage or the amount of dynamic storage as water flows over a surface is usually represented

$$De = \frac{.000818 i^{3/5} N^{3/5} L^{8/5}}{S^{3/10}}$$

where De is surface detention in (ft^3/ft), i is the supply rate (inches/hour), N is the Manning roughness coefficient, L is the slope length (ft) and S is the slope (ft/ft).

The slope and slope length are available from field measurements, but the roughness coefficient must be fit from data. No analytic expression is known for roughness. For our purposes, it would appear that the resistance and flow caused by stem density and litter, and sinuosity caused by plant pattern basal area and microchannels, would be an important coupling between detention storage and plant and animals. Here, roughness would be a function such as:

$$n = f(\text{stem density, basal area, litter, microchannels})$$

Such a model would depend on herbage production and rate of removal, plus the animal traffic imposed during grazing. The development would require a regression approach.

Infiltration and percolation are deterministically described by the same equation:

$$\frac{\partial \theta}{\partial t} = \frac{\partial}{\partial Z} \left(D \frac{\partial \theta}{\partial Z} \right) - \frac{\partial \kappa}{\partial Z}$$

where θ is the volumetric water content of the soil, t is time, Z is the vertical direction, D is the liquid diffusivity and κ is the hydraulic conductivity. In this model, κ and D are the factors through which biotic influences are effected. κ and D are functions of soil physical properties that can be altered through compaction, and microbial activity. Compaction primarily reduces the porosity, however microbial activity may enhance porosity through the promotion of water stable soil aggregates. In an opposite effect, microbial activity may cause non-wetability and scaling of the soil surface.

Each of the edaphic models described above could be represented on the functional relations in the hierarchical diagram for soil moisture in Fig. 3.7.1.1. The four models; interception, retention, detention and evaporation--are denoted in the figure by underlining the left most elements in the hierarchy involved and italicizing the right most elements.

4. INTERRELATIONSHIPS BETWEEN MODELS

A series of 28 models, forcing functions, and indices may be formulated from the hierarchical diagrams in Section 3 which form a 'whole system' model for a grassland ecosystem. These models are tabulated in Table 4.1 with the model outputs on the left-hand side and model inputs (driving forces) on the right-hand side of the page.

Table 4.2 is a matrix showing the interconnections between the models of Table 4.1. The outputs are listed on the left-hand side of the matrix, while the model inputs are listed along the top of the matrix.

An element s_{ij} may either be a blank--denoting no relationship between model i and model j --an x denoting that an output of model j feeds directly into model i , or an s denoting that an output of model j feeds as an input into model i , but that the output of j must first be modified before it can be used directly in model i . An f in element s_{ii} (a diagonal element of the matrix) denotes that the output of i feeds back into itself as an input.

The matrix of Table 4.2 shows relationships among models of Table 4.1 by connecting lines between the proper model inputs and outputs.

The resolution of these models might be increased by following the hierarchical diagrams given in Section 3 over to the next level, thus introducing more causal links into the model. Table 4.1 does not represent models that are now running. Several of these appear in Section 3. The models of Table 4.1 are mainly for future development. Table 4.2 should be seen mainly as a planning tool to direct the modelling effort in the near future. For example, the plant pattern model takes on new importance when viewed in the light of Table 4.2, since it is noticed that the plant pattern model is required as an input to nine other models--far above the average.

Table 4.1. Submodel outputs and inputs.

1. Net shortwave radiation

1.

Incoming shortwave radiation
Plant and soil albedo
Plant cover
Atmospheric pressure
Particulate matter
Relative humidity

2. Soil water

2.

Soil evaporation rate

Soil percolation rate

Soil diffusivity

Soil water

Precipitation interception rate

Wind profile

Litter

Evaporation rate

Leaf area

Soil water retention

Precipitation rate and duration

Soil water

Soil properties

Wind profile

Plant cover

Soil temperature

Topography

Soil water detention

Litter

Plant cover

Topography

Precipitation rate and duration

Transpiration rate

Table 4.1. (Continued)

3. Temperature profile	3. Net shortwave radiation Photosynthesis Transpiration rate Soil radiation absorption Soil conduction loss Vapor pressure deficit
4. Soil temperature profile	4. Soil evaporation rate Soil water content Soil energy conduction rate Soil energy Soil energy absorption rate Relative soil thickness
5. Plant biomass Aboveground biomass Belowground biomass Reproductive part biomass Litter biomass	5. Photosynthesis Translocation Metabolic death rate Harvest (ingestion) Respiration Soil temperature Air temperature
6. Photosynthesis rate	6. Net shortwave radiation Total plant biomass Air temperature Plant morphology Plant cover Leaf moisture status Leaf nutrient status
7. Plant transpiration rate	7. Soil water Plant cover Soil physical properties Wind velocity Evaporation rate Plant morphology
8. Three-dimensional plant pattern	8. Ingestion Animal activity Wind profile Plant pattern*

Table 4.1. (Continued)

9. Humus biomass	9. Animal litter Plant litter Humus biomass*
10. Soil organic material	10. Soil organic material* Microbial activity Humus biomass
11. Soil nutrient density Soil nutrients (N, P, etc.)	11. Soil nutrients* Humus biomass
12. Microbial activity	12. Soil temperature Soil moisture Soil albedo Incoming shortwave radiation Soil nutrients Microbial presence
13. Animal population and age distribution	13. Climate Animal history Producer biomass Producer pattern Animal population Social behavior Predation and parasitism
14. Animal activity	14. Microclimate Body size and weight Producer biomass Producer pattern Animal behavior
15. Plant respiration	15. Photosynthesis rate Translocation rate Photo-thermal status Nutrient status Water status

Table 4.1. (Continued)

16. Soil evaporation rate	16. Soil water Plant cover Wind profile Net shortwave radiation Litter Air temperature Soil temperature Vapor pressure deficit Soil properties
17. Animal biomass Average biomass per individual Litter biomass	17. Ingestion Metabolic requirements Animal activity
18. Plant translocation rate	18. Plant phenology Nutrient status Water status Photo-thermal status Respiration Photosynthesis
19. Plant metabolic death rate	19. Plant morphology Pathology Nutrient status Water status Photo-thermal status
20. Animal investion (harvest)	20. Producer biomass Producer pattern and composition Animal food preference, history, and caloric needs
21. Net precipitation	
22. Vapor pressure deficit	
23. Soil texture and other properties	
24. Atmospheric pressure	
25. Wind profile	

Table 4.1. (Continued)

-
- 26. Topographic pattern
 - 27. Plant morphology
 - 28. Animal history and physiology
-

* = feedback

Table 4.2. Matrix of interconnections between models of Table 4.1.

Outputs/Inputs	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1. Net shortwave radiation	.							x																				
2. Soil water		f		x	x		x	x								x	x											
3. Temperature profile			.			x																						
4. Soil temperature profile		x		f																								
5. Plant biomass			x	x	.	x																						
6. Photosynthetic rate	x	s	x		x	.		x			s																	
7. Plant transpiration rate		x					.	x																				
8. 3D plant pattern					x			f																				
9. Humus biomass									f																			
10. Soil organic material									x																			
11. Soil nutrient density									f																			
12. Microbial activity	x	x		x					x																			
13. Animal population and age distribution	s				x			x					f															
14. Animal activity	s				x			x																				
15. Plant respiration	s	s	s			x																						
16. Soil evaporation	x	x	x	x				x																				
17. Animal biomass																												
18. Plant translocation	s	s	s			x																						
19. Plant metabolic death	s	s	s																									
20. Animal ingestion					x			x																				

f = feeds to itself

s = slave model required

x = output j to input i

Reasoning like this should be used in placing a model's relative importance into proper perspective.

5. CONCEPTUAL INTERRELATIONSHIPS OF MODELS

5.0 Introduction

The aim of an integrated research study is the detailed analysis of whole ecosystems. From a modelling standpoint this means construction of whole ecosystem models. The models listed in Section 4 are primarily for small parts of the ecosystem and do not accomplish in themselves this goal. This section concerns the synthesis of multi-trophic level models from these process and component models and by other methods. We view these methods as being applicable either to interbiome or intrabiome models. Thus a model can be regarded at any time as an end-point in itself, or as a building block in a still larger hierarchy.

We have envisaged the building of whole ecosystem models as delimited by two extremes. The first of these (Type 1) is the technique of building a model from the ground up, i.e., listing a set of relevant dependent variables and proceeding to derive the quantitative relations among the variables. In a whole ecosystem model the variables chosen must be in some way descriptive of the entire ecosystem. The other method (Type 2) consists of interfacing existing models for small parts of the ecosystem into a coherent whole ecosystem model. Any intermediate between these two extremes can also be utilized. Generally, some combination of the two is used based on previous knowledge of the system.

5.1 Whole Systems Models Built From the Ground Up (Type 1)

The primary advantage of this approach is that it is relatively rapid to construct a set of mathematical equations which can be construed as a whole ecosystem model. Such a system for the grasslands might consist of from 10 to

20 principal dependent variables. The disadvantage, of course, of this method is that it is very difficult to attack the complexity of an entire ecosystem by looking at the entire thing at once. Such a model is of extremely low resolution and low precision. However, if carefully done, it can be of some use in guiding future modelling strategy.

Sometimes a whole system model developed for a very specific purpose rather than for the general display of ecological attributes can be constructed in this way. The grazing model of Goodall (1969) was developed in this way. The antelope model reported by Van Dyne (1969b) is another example of a whole system model constructed from the ground up.

Intermediate between the two types of whole system models discussed above is the model of Bledsoe and Jameson (1969). This model was originally conceived as a whole system model and at the stage of development recorded in Bledsoe and Jameson was divided into parts corresponding roughly to trophic levels with an individual attack made on each part. The equations of Bledsoe and Jameson are designed to be interfaced among each other. However, they are still fragmentary and have a number of parts omitted. At the current time these parts are being developed and programmed independently for later interfacing as the second type of whole system model.

5.2 Whole System Models Constructed by Interfacing of Submodels (Type 2)

A whole system model of this type can be as complex as one desires and its resolution is generally a reflection of the amount of time and the number of people from different disciplines that have been involved in its construction. If an adequate library of submodels is in existence and if the submodels are

of similar type, e.g., all differential equation models with common variable definitions and notational conventions, then the construction of a whole system model is relatively simple. As a matter of practice it is rarely the case that the submodels are sufficiently similar that their interfacing is simply a matter of placing computer subroutines together in the same computer program.

A preliminary step in submodel interfacing can be seen in the examples of Section 4 of this report. Submodels can be thought of as having certain outputs and inputs or driving functions. In the construction of the whole system model the driving functions of one submodel become the outputs of another submodel. Some of the submodel driving functions become driving functions for the whole system. This accomplishes merely the conceptual phase of interfacing. An equally difficult task is that of casting the submodels into the same computer code conventions and the construction of an actual simulation program.

In the case of the Grassland Biome, all of the submodels are developed by a well integrated group officed in the same locale and who have the opportunity for day-to-day interaction. Development of submodels proceeds along previously agreed upon guidelines to assure that the interfacing difficulties will be minimal. One might proceed to develop a whole system model by using, for example, the photosynthesis model of Waggoner (1969b) as a part of a larger herbage dynamics model, feeding this to a wild ruminant consumption model and interfacing this with a Leslie (1945, 1948) type population dynamics approach. Miscellaneous small models might be used to fill in the gaps and to provide such things as decomposer function. It can be fairly well predicted that, in this case, one would have an extremely difficult time in the construction of a whole system model whose output bore any resemblance to the real system.

The conclusion is that there are two ingredients essential for the development of whole ecosystem models which have a high degree of realism and precision. The first of these is the requisite interaction time between modellers for construction via the submodel interface approach. The second is the requirement that the submodels be developed according to a common mathematical framework. As a consequence of this it is desirable that the developers of submodels be located at essentially the same site; if this is not possible, it is essential that the necessary interaction be provided via frequent travel and discussion sessions.

5.3 Increasing the Realism and Precision of the Model

Once a model for the whole system has been constructed and programmed and is giving fairly reasonable output, there are a number of possible modifications to enhance the usefulness of the model for different purposes.

The first of these modifications is in the area of stochasticization. Variables observed in nature nearly always have a random component. This may be due to inherent variation in the variable, inherent variation in the method of measurement or, usually, both. For some purposes it is desirable to have a whole system model whose output variables lack this random character, i.e., it is frequently desirable to predict only the central tendency of the variables. Such purposes as testing of sampling methods, determination of statistical ecosystem attributes, or use of the model as a driving function for another model, or the addition of random factors can be useful. There are two basic ways to stochasticize a model.

The first method is the addition of stochastic driving variables. The driving variables of a model are those input variables which, though generated by a physical process are not considered as variables which the model simulates

in a mechanistic fashion. For the grassland ecosystem we consider such things as air temperature, solar radiation, and precipitation in this category. Given a deterministic grassland model a set of output variables can be derived, for example, for a given rainfall regime in a given year. On the other hand, one may not wish to specify a particular exact distribution of precipitation but merely the statistical parameters of that distribution. If one is interested in the statistical distribution of the output variables of the model, it is necessary to make stochastic simulation runs in which the input rainfall is chosen according to random methods in many computed simulation runs. In this way statistical characteristics of the output variables can be built up.

The second method for adding a random character to a model is by making the constants or parameters utilized in the model variable with time (within the simulation) by drawing values for them from a set of random numbers having certain statistical characteristics. Of course, a deterministic model can be considered as a degenerate random model in which the distribution function for the parameters has zero variance. A model with non-stochastic driving functions, but stochastic parameters, has the characteristic that when it is run successively with the same input it will not give the same output. Thus it is difficult to draw conclusions about the range of variables from a single run given a set of driving functions. It is necessary to make repeated simulation runs in order to determine the true model characteristics.

If the model is to be used as a general management tool it needs to be cast in the form of a management game which can be used by natural resource managers. The management game is nothing more than an ecosystem model

implemented on a computer with input and output easily regulated and understood by persons other than those who built the model. The input variables should be manipulatable characteristics of an ecosystem; the output should be interpretable in terms of management goals. Additionally, a management game should have concise and accurate statements of the assumptions on which the model is based and a thorough documentation of the model's general characteristics. This is essential if the results of the model are to be used intelligently by natural resource managers for realistic determination of the effects of management decisions.

Another method of enhancing the value of an ecosystem model is in the case when one has well-defined management objectives which involve the optimization (minimization or maximization) of certain model characteristics. Frequently this optimization will involve constraining some input parameters to include realistic considerations, often dictated by economics. One approach to optimization of variables is, of course, the trial-and-error method in which case the modeller or game user attempts different sets of driving functions and parameter manipulations and picks out that set which gives output as close as possible to the desired output. For large models this is not a practical approach, and it is desirable to formulate the model in such a way that a simulation can be called for internally in the computer by an optimization procedure. The procedure will, by evaluating numerically the first and second derivatives of output variables, move in a systematic fashion toward a set of driving functions and parameters which will

yield the desired optimum result. There are a number of such optimization routines available for various computers, and it is a relatively easy job to convert a given computer code to the form necessary to be used by these routines (Bledsoe and Van Dyne 1969). In constructing the code for the original model and management game it is desirable to keep the optimization use in mind and plan the code accordingly. Another consideration is that of computer time. An optimization procedure will involve many computer runs of the individual model which may already take a fair amount of computer time. An optimization technique can then be quite costly. Thus, programming techniques which minimize computer time must be utilized.

5.4 Notational Conventions for Model Development

In July of 1969 a meeting of modelling personnel from the various biomes was held in Madison, Wisconsin, under the auspices of the *Analysis of Ecosystems* program. One of the tacit conclusions of this meeting was the need for a uniform set of definitions of terms used in ecological modelling. There was a plethora of such terms in use, generally with different meanings, by different investigators. It seems to us in the Grassland Biome that any structure for modelling terminology must be kept flexible and simple in order to be usable. Following is a definition of some terms presently used in Grassland Biome modelling, and an example of two differential equations with the appropriate terminology for their variables. By a variable, we mean a symbol representative of some set of elements, e.g., the real numbers. The above Sections 3 and 4 adhere in general to these definitions. It is hoped that the up-and-coming meeting at the Pawnee Site of modellers from all the biomes can devote some time to consideration of these and other definitions.

The proposal for the present 16 months of operation contains some terminology (Table 6.45.1, p. 145) which overlaps with that presented below. To clarify the situation, we should state that the symbols (q_1 through q_9 and s_1 through s_4) used to represent *processes* and *control functions* are not intended to be variables in the mathematical sense. They are, rather, functions or sets of functions. On the other hand, the components of the vectors \underline{V} , \underline{E} , and \underline{P} are variables and fall under the following set of definitions. Originally we felt that the term component or compartment should be reserved for a variable measured in units of mass or energy density and other ecosystem variables were parameters or properties (e.g., pH). Now we prefer to make our definitions of variables purely in terms of their mathematical rather than their contextual connotations. The phrases in parentheses below have been used by other authors to denote similar although not always identical concepts.

Principal system variables (Dependent variables, Components, Compartment variables)

These are variables of principal interest to the modeller. In order to keep track of them in a simulation the modeller would have them output at convenient time intervals. In our modelling to date each variable has usually been expressed as a first-order ordinary differential equation with its first derivative on the left-hand side of the equation expressed as a function of other variables, usually intermediate system variables and driving variables.

Parameters (Coefficients, Constants)

These are variables whose values do not change during the course of a simulation. Of course, the values may change between one simulation run and another as the modeller alters the values to discover the effect

on model output. Any mathematical model must have some variables of this type. One method of refining a model is to convert a parameter to an *intermediate system variable* in which case its value is no longer constant during a single simulation run.

Intermediate system variables (Intermediate functions, Slave models)

These are variables necessary to the statement of the equations for the *principal system variables* of the model. They are specified to vary as a function of other *principal system variables*, *driving functions*, or conceivably, other *intermediate system variables*. The functional definition of *intermediate system variables* will generally include some *parameters*.

Driving variables (Driving functions, Model inputs, Inputs)

Driving variables frequently describe variables which are of principal interest to the modeller. However, they are created by physical mechanisms which he, for some reason, has no desire to model. For example, precipitation is a variable of principal interest in the Grassland Biome. However, we will not concern ourselves with a mechanistic model for the generation of the precipitation variables.

The combined set of driving variables and parameter values may be thought of as the specifications necessary for a model simulation run, once the mathematical form of the model has been determined. In the above terminology, the components of V and P (Table 6.45.1 of the 1969-70 proposal) are *principal system variables* and those of E are *driving variables*. The variables involved in the components of Q and S would be *intermediate* or *principal system variables*. It would be necessary to have a model described in greater detail to be certain.

The following example, intended to describe a microbial population-mineral nutrient interaction, serves to illustrate the above definitions.

$$\dot{N} = r N (N_{\max} - N) / N_{\max}$$

$$\dot{V} = -k_1 N V + I(t)$$

$$N_{\max} = k_2 + k_3 V + k_4 V^2$$

$$r = k_5 + k_6 T + k_7 T^2$$

where:

N = microbial population density ($1/\text{cm}^2$)

V = concentration of nutrient mineral

T = temperature of growth medium

$I(t)$ = external input rate of nutrient mineral

N_{\max} = function giving maximum population size for a given nutrient concentration

r = function giving population growth rate for a given temperature

k_1 through k_7 = parameters

In this example N and V are *principal system variables*. T , temperature, which is a function of time (t) and $I(t)$ are the *driving functions* for the system. N_{\max} and r are *intermediate system variables* which help to describe the interaction of the *principal system variables*. k_1 through k_7 are model *parameters*. Values for these variables would normally be determined by using analytic techniques with measured field data. Alternatively, they might be constructed utilizing graphs or verbal descriptions available in the scientific literature.

6. MODELS AND EXPERIMENTS

Good models and good experiments are intimately related. For an experiment to be considered from an ecosystem point of view we must first have at least crude models of the system. The first models need not be sets of mathematical equations, but should provide at least an outline of how various pieces of information fit together.

Models provide several aids to experimentation. These may be (i) a general outline and research guide, (ii) a means of specifying measurements and evaluating techniques, and (iii) a means of evaluating individual experiments for their contribution to the overall effort. In return, experiments aid in providing data to test the models, which, in effect, test our understanding of the system.

6.1 Design and Redesign

Initial models should attempt to utilize all pertinent existing information, and preferably should be developed to a considerable extent before much experimentation is initiated. Very few models will completely exploit all existing information, however, and experimentation should not be delayed until the last gram of usefulness is gleaned from the first models; instead, experimentation should be outlined as soon as major gaps in information become apparent.

The model description should specify constants and variables for which values are needed. For concurrent model-experiment development, these values must be already available or can be reliably determined using existing techniques. Some constants and variables cannot be evaluated properly because of technical limitations; others may be considered to be of too little importance to be included in a first-run model. In either case, any necessary simplifying assumptions should be explicitly stated.

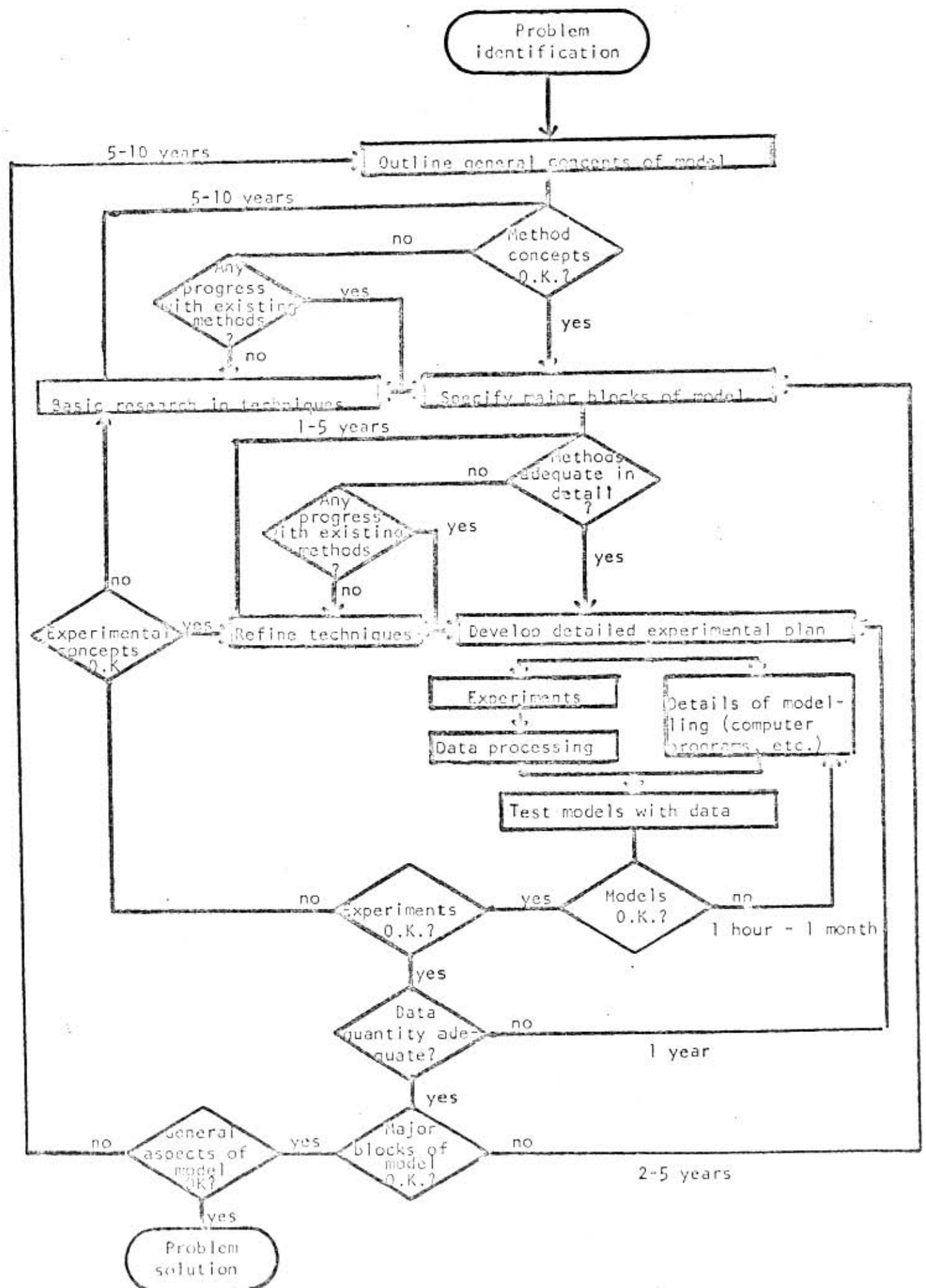
Following the initial round of model design and experimentation, the models should be first tested with the data gathered by experimentation, then redesigned to guide the second round of experimentation. *Rapid turnaround* in redesign is absolutely necessary in order to avoid wasted time in the experimental effort and also to maintain the interest of the experimental group.

Details of the modelling effort can parallel the experimental effort, but preferably the modelling effort should be several cycles ahead of the experimental effort. Such lead time in modelling is desirable in order to guide the general planning effort of experimentation.

Such "look-ahead" modelling also provides the necessary lead time for basic studies in techniques which will be required for future experimentation. Initial models may be satisfied with small amounts of data collected by slow and tedious techniques, but in order for the models to become really useful, new techniques which can supply prodigious quantities of data may have to be developed. This lead time should be anticipated so that details of the modelling-experimental effort will not be delayed (Fig. 6.1.1).

Conversely, testing of the initial experimental efforts must not be delayed because of lag time in modelling. At least rough models must be operational to test each experimental cycle. Modelling teams must resist the temptation to be too refined in initial attempts, just as the experimentalist must resist the temptation to become too refined in experimental techniques. Adequate refinement will come only with several cycles of the modelling-experimental effort, but lack of either testable models or gross knowledge of the system can lead to much waste and inefficiency. Research in components and

Fig. 6.1.1 Flow chart of modelling-experimental effort showing approximate time requirements in ecosystem research.



processes can be guided by component and processes models. Conduct of research in *ecosystems*, however, requires ecosystem models. No matter how crude, perhaps total system models must precede detailed component and process models, and models must be available for testing each turnaround of experimental effort.

6.2 A Simplified Example

As an example of application of modelling to grassland ecosystems, let us consider the following greatly simplified model. Grassland ecosystems are commonly characterized by herbage species whose growth rate is variable, depending upon climatic conditions and herbivores which feed on the herbage. A useful model could consider $j = 1, \dots, m$ herbage species, $i = 1, \dots, n$ herbivores, and $k = 1, \dots, s$ time periods (beginning at $t_1, t_2, \dots, t_k, t_{k+1}, \dots, t_{sm}$) with manipulation of the system possible at the beginning of each period. Change in herbage biomass can be expressed by:

$$\dot{W}_{jk} = P_{jk} W_{jk} - R_{a,jk} W_{a,jk} - R_{b,jk} W_{b,jk},$$

where

\dot{W}_{jk} = biomass change of the j th species during the k th period

P_{jk} = photosynthetic rate per unit biomass of the j th species during the k th period

$W_{a,jk}$ and $W_{b,jk}$ = biomass of the aboveground and belowground portions, respectively, of the j th species at the beginning of the k th period.

$R_{a,jk}$ and $R_{b,jk}$ = the respiration rate per unit biomass of the aboveground and belowground portion, respectively, of the j th species during the k th period.

W_{jk} = biomass of j th species at the beginning of k th interval = $W_{a,jk} + W_{b,jk}$

Therefore

$$W_{j,k+1} = W_{jk} + \int_{t_k}^{t_{k+1}} \dot{W}_{jk} dt,$$

This model assumes that an equilibrium always exists between W_a and W_b , so translocation between the aboveground and belowground parts is not considered.

Photosynthesis and respiration are, of course, not constant, but can be approximately represented for each species as:

$$P = f(T_2, S_w),$$

$$R_a = f(T_2),$$

$$R_b = f(T_3),$$

where T_2 is a characteristic temperature of air surrounding the plant leaves, T_3 a characteristic belowground temperature, and S_w the soil moisture.

Photosynthesis (P) reaches a zero value at a temperature higher than does respiration (R_a and R_b), while respiration continues at low temperatures when photosynthesis has effectively ceased. Appropriate functions for each species need to be developed.

We know from past experience that during a growth phase without harvest

$$P_{jk} W_{a,jk} \gg R_{a,jk} W_{a,jk} + R_{b,jk} W_{b,jk},$$

and a net increase in P_{kj} results. If, however, $W_{a,jk}$ is reduced by harvest, both the total photosynthesis and aboveground respiration are reduced. If photosynthesis remains greater than the sum of aboveground and belowground respiration, biomass accumulation continues, but if W_a is reduced sufficiently then

$$P_{jk} W_{a,jk} < R_{a,jk} W_{a,jk} + R_{b,jk} W_{b,jk},$$

and plant biomass will begin to metabolically decrease.

Since photosynthesis requires light, we must consider the interception of solar radiation by plants. Solar radiation energy striking a flat plane is zero at sunrise and reaches a maximum at high noon; thus solar radiation reaching a flat surface can be expressed as a sine function of the time of day. Grass blades, however, are not a flat plane, but are arranged more or less perpendicular to the setting and rising sun. Instead of a simple sine function, the solar radiation striking a grass blade approximates a square wave. For a simple model, then, photosynthesis can be assumed to proceed at a constant level during daylight and return to zero at night.

To utilize existing temperature data, which is primarily recorded for 150 cm height, we will express T_1 as

$$T_1 = \alpha \cos \frac{2\pi d}{365} + \beta \sin \frac{2\pi d}{365} + \gamma \cos \frac{2\pi s}{24} + \delta \sin \frac{2\pi s}{24} + \epsilon ,$$

where

d = time of the year in days

s = time of day in hours

α and β = constants of time lag of annual temperature regime

γ and δ = constants of time lag of daily temperature regime

ϵ = departure of temperature from normal.

A simple model could consider temperature departures from the mean as random. A more refined model would consider that the departure of temperature from the mean for any day depends upon the departure the day before, i.e., warm days tend to follow warm days and cold days tend to follow cold days. As an additional refinement we could consider that temperatures are also correlated with precipitation.

T_2 , the temperature in the leaf zone, and T_3 , the temperature in the root zone, can be expressed as functions of T_1 .

$$T_2 = f(T_1)$$

$$T_3 = f(T_1)$$

Precipitation is, of course, highly variable, but wet days tend to follow wet days and dry days tend to follow dry days. The probabilities of precipitation following wet days and precipitation following dry days can be determined from an analysis of previous records and can be expressed as a function of season. The amount of precipitation on any given wet day can be determined by a random number drawn from a population the same as a storm size-class distribution of the area under study.

$$P_p = \begin{cases} 0 & \text{if } \epsilon' < P_{\text{prob}} \\ \epsilon'' & \text{if } \epsilon' \geq P_{\text{prob}} \end{cases}$$

where

P_p = the amount of precipitation

$P_{\text{prob}}(t)$ = the probability of precipitation occurrence

ϵ' = a random number from a uniformly distributed population

$\epsilon''(k)$ = A random number from a population representing the storm size-class distribution for the k th period.

Thus the uncertainty which is characteristic of grassland ecosystems is introduced through the random selection of temperature departures from the seasonal norm, presence or absence of precipitation, and storm size-class.

Soil moisture is a function of precipitation and evapotranspiration:

$$\dot{S}_w = P_p - E_t ,$$

where \dot{S}_w is the change in soil moisture, P_p the moisture added by infiltration, and E_t the evapotranspiration. In this simple model we have assumed that no runoff occurs unless S_w exceeds S_a . Evapotranspiration in turn is a function of temperature and soil moisture between the precipitation events,

$$E_t = f(S_w, T_3),$$

where the evapotranspiration function is determined empirically. Recurring precipitation events and subsequent evapotranspiration give a fluctuating soil moisture situation with many peaks followed by drying. Soil moisture between precipitation events might be a simple exponential decay,

$$S_w = S_m + S_a e^{-gt},$$

where S_m is the minimum soil moisture, $S_m + S_a$ is the maximum available soil moisture, g is a computed constant which varies with soil moisture and the temperature T_3 , and t is elapsed time following a precipitation event.

Thus far we have shown development of a model of plant production as determined by probabilistic rainfall events and temperature. In grassland ecosystems, however, portions of the aboveground biomass are removed by grazing. Thus we have an array of herbage available for grazing W_a . Harvest of this resource, however, has an influence on the biomass accumulation of the plants.

$$\dot{W}_{jk} = P_{jk} W_{a,jk} - R_{a,jk} - R_{b,jk} W_{b,jk} - \sum_{i=1}^n H_{i,jk},$$

where $H_{i,jk}$ is the harvest rate of aboveground plant material by the i th herbivore from the j th plant species during the k th period.

Let us next visualize a community of carnivores which periodically harvest animals that live on herbage. The harvest occurs at specified times

of the year. The herbivores, of course, cannot eat more herbage than is available; i.e.,

$$\int_{t_k}^{t_{k+1}} \sum_{i=1}^n H_{ijk} \leq W_{jk} ,$$

Each herbivore is able to digest a certain fraction of the plants eaten, and in turn convert this digested material to body weight.

$$\dot{A}_{ik} = B_{ik} D_{ik} \sum_{j=1}^m H_{ijk} - F_{ik} ,$$

where \dot{A}_{ik} is the weight gain rate of the i th herbivore species during the k th time interval as a result of consuming herbage, D_{ik} is the digestibility of the diet of the i th herbivore, B_{ik} is a conversion factor empirically determined for each species which converts digestible feed intake to weight gain, and F_{ik} is the maintenance requirements rate of the i th herbivore for the k th period.

Thus the weight per herbivore species at the end of the k th time period is

$$A_{ik+1} = A_{oik} + \int_{t_k}^{t_{k+1}} \dot{A}_{ik} dt ,$$

where A_{oik} is the initial weight at the beginning of the k th period. The weight of herbivores harvested at the end of each period (A_c) is shown by

$$A_{ci} = [A_{ik+1} - A_{oik+1}] ,$$

where A_{ik+1} is the total amount of the i th animal product present at the end of the k th period, and A_{oik+1} is the weights passed on to the next period (the average weight of the herbivores left after harvest).

If the value or preference for each herbivore species by the carnivore group can be specified, then we want to maximize

$$Q_{\max} = y = \sum_{i=1}^n C_i \cdot A c_i ,$$

where C_i is the relative value per unit of animal product of the i th herbivore. Non-harvested animals would have a zero C_i unless they are retained in the system for some purpose other than harvest.

The maximization technique required is a recursive optimization. It must take into account the effect of herbage harvest by animals on herbage availability, and the effect, in turn, of herbage availability on weight gains of the animals. Although having more animals will give more gains, having more animals will also reduce herbage production and consequently result in fewer weight gains.

Thus far we have considered our grassland ecosystem at one geographic location. If we allow several locations (such as where there are nomadic grazing units) we must add another dimension and another subscript to all variables. Free ranging animals may voluntarily move to another location when any component of their diet becomes limiting. The optimization may show that some sort of intermittent herbivory is optimal, or, depending on the relationships of photosynthetic tissue to respiring tissue, it may show that continuous herbivory is optimal.

Many modifications could be made to add realistic complexity to the model. There is practically no limit to the amount of complexity which can be included; there is, however, a point where additional complexity is not necessary in order for the original objectives of the model to be met. Some of the simplifying assumptions which have been made are:

1. Markovian properties of temperature ignored.
2. Soil moisture and air moisture not considered in computing T_2 and T_3 .
3. Relationship between T_1 and P_p ignored.
4. Wind and changes in solar radiation ignored.
5. Soil moisture, soil temperature, and air temperature considered to have a uniform vertical distribution.
6. Rates of precipitation and limits on infiltration not considered.
7. Horizontal movement of water, dissolved solids, and particulate matter ignored.
8. Soil nutrients not considered.
9. Square wave assumed for photosynthesis.
10. Photosynthetic rate and respiratory rates assumed constant for all portions of aboveground and belowground biomass.
11. Translocation between aboveground and belowground plant parts not explicitly expressed.
12. Decay of detritus ignored.
13. Plant competition, plant reproduction and animal reproduction ignored explicitly, but corrected with periodic biomass determinations.
14. Animal weight gains a constant for digestible dry matter intake.
15. Herbage unused in one period carried over to a new period with full nutritive value. Carry-over feed should be set to zero at onset of rapid herbage growth, and only new growth considered. New growth may actually be a function of W_b rather than W_a .
16. Animal death loss not specified but included in animal weight gains.
17. All animals are considered to be either herbivores feeding on aboveground plant parts or top carnivores, no omnivores are considered.
18. Animal migrations and other movement ignored.

Variables and constants included in this simplified model can be either determined by repeated census, compiled from previous records, determined as random events, estimated as rate constants based on process studies, or computed as slave variables from other variables (Table 6.2.1).

In the Table 6.2.1 all items are specified as to their present availability. Those with an information status of 1 need no "look-ahead" to proceed with experimentation. Those with a status of 2 need perhaps a one year look ahead. With a status of 3 the planning period should be two to five years, and for a status of 4, five to ten years. It is very important, however, that at least some information be available for each constant or variable to be included in the model, even though we may be dissatisfied with the amount and precision of the data from existing techniques.

Table 6.2.1. Variables and constants used in simplified model.

Notation	Status ^{1/}	Description
1. <i>Needing measurement at each period:</i>		
$W_{a_{jk}}$	2	Weight of the aboveground edible portions of the jth species at the kth period.
$W_{b_{jk}}$	4	Weight of the belowground or non-edible portions of the jth species at the kth period.
S_w	3	Soil moisture
A_{oik}	1-5	Initial amount of the ith herbivore at the kth period
2. <i>Compiled from previous records:</i>		
T_1	1	Normal air temperature at 150 cm
$\alpha, \beta, \gamma, \delta$	1	Parameters describing time lag in normal temperature
P_{prob}	1	Probability of precipitation occurrence
3. <i>Determined as random events:</i>		
ϵ	1	Departure of temperature from the norm
ϵ'	1	Probability of precipitation occurrence
ϵ''	1	Precipitation amount
4. <i>Determined by experimentation:</i>		
C_i	1-5	Carnivores preference for the ith herbivore
P_{jk}	2	Photosynthetic rate per unit of biomass of the jth species for the kth period, a function of T_2 and S_w
$R_{a_{jk}}$	2	Respiration rate of the aboveground parts of the jth species for the kth period, a function of T_2
$R_{b_{jk}}$	3	Respiration rate of the belowground parts of the jth species for the kth period, a function of T_3
T_2	1	Temperature in the leaf zone, a function of T_1
T_3	1	Temperature in the root zone, a function of T_1

Table 6.2.1 (continued)

Notation	Status ^{1/}	Description
g	2	Soil drying rate, a function of S_w and T_3
S_d	1	Minimum soil moisture (wilting point)
S_a	1	Maximum possible soil moisture (field capacity)
H_{ijk}	2	Preference of the i th herbivore for the j th plant during the k th period
B_{ik}	1	Body weight gain per unit intake of digestible herbage for the i th herbivore, k th period
D_{ik}	2	Digestibility by the i th herbivore of the j th plant species for k th period
F_{ik}	1	Maintenance requirement of the i th herbivore for the k th period
5. "Slave" variables, computed from other variables:		
A_{ik}		Weight of the i th herbivore for the k th period, computed from B_{ik} , D_{ik} , H_{ijk} , F_{ik}
S_w		Soil moisture computed from P_p , S_d , S_a , and g
Ac_i		Harvest of the i th herbivore, computed from A_{ik} and $A_{oi,k+1}$
Y		Sum of harvested herbivores (Ac_i) weighted by appropriate value functions (C_i)

^{1/} Information status

1. Adequate amount and kind of information can be obtained by existing techniques.
2. Proper kind of information can be obtained by existing techniques, and basic techniques apparently are immediately available for developing methods for collecting adequate amounts of data.
3. Proper kind of information can be obtained by existing techniques. New techniques for obtaining an adequate amount of information are available in concept, but need much developing.
4. Information can be obtained with difficulty, and no new concepts are promising.
5. Information cannot be obtained with sufficient accuracy within reasonable financial limits. (Note: none of these variables should be in the model.)

6.3 Evaluation of Experimental Projects and Models

A primary objective of the Grassland Biome program is an increased insight into the mechanisms involved in the structure and function of grassland ecosystems. Our approach involves the construction of a hierarchy of mathematical structures, certain subsets of which may be called models. These models require for their construction certain specific bits of information about specific natural phenomena which, for the most part, either exist in the scientific literature or must be determined by experimental measurement. In view of the cost in dollars and scientific manpower for these experiments and the limited availability of these resources, it is desirable to attempt to formulate some objective allocation scheme.

Any resource allocation must be based on the ultimate value of the project goal and its subdivisions (separate models). Since it is difficult to objectively measure the value of the individual models, we must settle for a subjective measure based on certain guidelines, as follows:

(i) The value of a model is relative only to another model and has no interpretation in absolute units such as dollars or Ph.D.-man-hours.

(ii) A model for a whole ecosystem or a multi-trophic level or multi-component model is more valuable than a model for a process or small part of an ecosystem.

(iii) A mechanistic model (at any level) is more valuable than a curve fitting model.

We shall let W_j be the relative value or importance of the j th model. Given that the necessary experimental data are available, a particular model will have a certain probability of completion or success. We define this probability as M_j for the j th model and emphasize that M_j is conditional upon

completion of the required experimental work. M_j is not a certainty (i.e., $M_j \neq 1$.) since there are other random events, e.g., availability of analysts and programmers, or probability that the experimental data can be successfully interpreted in terms of the model, upon which success of a model is dependent. Notice that the set of probabilities M_j is based upon events which are not independent, i.e., the successful conclusion of the k th model would require the success of models i and j if model k is a superset containing i and j .

Suppose that the i th subcontracted experimental project has probability E_i of successful completion. Let S_{ij} be defined as follows

$$S_{ij} = \begin{cases} 1 & \text{if the } i\text{th project will contribute data necessary} \\ & \text{for the } j\text{th model} \\ 0 & \text{otherwise} \end{cases}$$

We shall assume that the probabilities E_i are based upon independent events. Then the absolute probability, P_j , of successful completion of the j th model is

$$P_j = M_j \prod_{\substack{i=1 \\ S_{ij} \neq 0}}^n E_i$$

where n is the number of projects. A measure of the value of the i th project, V_i , is

$$V_i = \sum_{j=1}^m S_{ij} P_j W_j$$

where m is the total number of models. Based on this measure we can provide a provisional estimate of the dollar value of each experimental project, S_i , under the restriction that the total amount of money available to the experimental aspects of the program is $\sum_{i=1}^n S_i$.

$$S_i = V_i \frac{\sum_{i=1}^n S_i}{\sum_{i=1}^n V_i}$$

6.3.1 An Example

Suppose that we have three models of minimal, intermediate and maximal resolution for each of four subdivisions of the Pawnee Site grassland. Suppose that we also have three Pawnee Site whole ecosystem models with varying degrees of resolution, and two generalized grassland ecosystem models for purposes of comparing sites, thus $m = 17$. For experimental projects suppose we have the following hypothetical experiments:

Abiotic

Gross meteorology	1
Soil physical	2
Soil chemistry	3

Producer

Standing crop, aboveground	4
Standing crop, belowground	5
Plant physiology and phenology	6

Consumer

Wild

Animal biomass and numbers	7
Animal diets and consumption	8

Domestic

Consumption per animal unit	9
Biomass per animal unit	10

Decomposer

Activity of soil microorganisms	11
Activity of soil fauna	12
Dead organic soil constituents	13
Aboveground dead material	14

Using the guidelines listed above and supposing that the research manager assigning probabilities is cognizant of such factors as an experimental scientist's past performance, difficulties in making measurements of certain types, difficulties in interpreting data, etc., we can construct the following hypothetical matrix (Table 6.3.1).

The model weights are assigned on an intuitive basis taking into consideration such things as possible uses for the model in solving economic and environmental problems, etc., the resulting relative values (V_i) are normalized in the $V_i/\Sigma V_i$ column, to sum to 1.0 total value for the whole experimental project. Since there are 14 experimental subprojects, comparison of $V_i/\Sigma V_i$ with $1/14 = .0714$ will indicate whether the project is more or less valuable under the above scheme than under an assumption of equal value for all subprojects. Using the non-parametric Chi-square test on the V_i 's we get a statistic of $48.9 = \sum_{i=1}^{14} (V_i - 542/14)^2 / (542/14)$ which exceeds the 99th percentile critical value (27.69) with 13 degrees of freedom. This indicates that the model gives results significantly different from the assumption of equal project values. The ranking of the 14 experiments according to value (1 = most valuable) shows that the method results are not out of line with what one would expect, i.e., aboveground herbage measurement is the most important project and soil fauna the least important. (The weights and probabilities were assigned only once before calculations were made and were not readjusted to give "more reasonable" results for purposes of this presentation.)

Table 6.3.1. An example of a procedure for quantitatively interrelating experimental projects and mathematical modelling activities in a cost-effectiveness analysis.

Experiments	Models	Pawnee			General grass-land		Abiotic			Producer			Consumer			Decomposer		
		1	2	3	1	2	1	2	3	1	2	3	1	2	3	1	2	3
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
	E_{ij}																	
1	.999	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
2	.99	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0
3	.98	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
4	.95	1	1	1	1	1	0	0	1	1	1	1	0	0	0	0	0	0
5	.90	0	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0
6	.98	0	1	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0
7	.80	0	1	1	0	1	0	0	0	0	0	0	1	1	1	0	0	0
8	.90	0	1	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0
9	.98	1	1	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0
10	.99	1	1	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0
11	.80	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1
12	.85	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
13	.93	0	1	1	0	1	0	1	1	0	0	0	0	0	0	1	1	1
14	.95	1	1	1	1	1	0	0	1	0	0	0	0	0	0	1	1	1
M_{ij}		.90	.85	.75	.90	.85	.99	.95	.90	.99	.90	.85	.99	.90	.80	.90	.80	.70
W_{ij}		5	20	50	10	20	1	2	3	2	5	10	1	4	8	4	6	8
P_{ij}		.79	.46	.28	.79	.48	.99	.87	.65	.93	.75	.71	.77	.63	.56	.64	.48	.42

i	V_i	$V_i/\Sigma V_i$	Rank	Experiment
1	49.33	.0909	5	Abiotic - Gross meteorology
2	36.49	.0673	10	Abiotic - Soil physical
3	25.15	.0464	13	Abiotic - Soil chemistry
4	59.31	.1093	1	Producer - Standing crop, aboveground
5	36.00	.0664	11	Producer - Standing crop, belowground
6	47.46	.0875	6	Producer - Plant physiology and phenology
7	40.57	.0748	8	Consumer - Wild animal biomass and numbers
8	39.80	.0734	9	Consumer - Wild animal diets and consumption
9	52.42	.0966	3	Consumer - Domestic consumption per animal unit
10	52.42	.0966	4	Consumer - Domestic biomass per animal unit
11	32.00	.0590	12	Decomposer - Activity of soil microorganisms
12	20.24	.0373	14	Decomposer - Activity of soil fauna
13	45.29	.0835	7	Decomposer - Dead organic soil constituents
14	55.40	.1021	2	Decomposer - Aboveground dead material

$$\Sigma V_i = 542.55$$

$$\chi^2 = 48.876 = \sum_{i=1}^{14} \frac{(V_i - \frac{542.55}{14})^2}{542.55/14}$$

6.3.2 Deficiencies of the Method

The method includes several assumptions which might be questioned. Perhaps modifications can be devised to circumvent some of these deficiencies:

- (i) Models are assumed to be discrete objects when in fact a high resolution model might develop in small steps from a lower resolution form.
- (ii) A model is assumed to be possible only when all of the necessary data are available. In fact, failure of a specific project would mean modification of sections of the model receiving data from that project so that the whole model would still be possible. In this case the χ^2 test mentioned above could not be employed.
- (iii) It is unlikely that an entire experimental project would fail. More likely is the case that certain types of data out of the several collected by any one experiment would become unavailable.
- (iv) The model probabilities do not take into account the interdependence of different models. Thus Pawnee model 2 might be constructed by interfacing the four trophic level models at the 2 stage. A modification of the formula for P_j might be able to take this into account, but more detailed model interrelations would have to be specified.

6.4. Some Possible Extensions and Generalizations

The presently evaluated models do not exhaust the possibilities of those applicable to the study of grassland ecosystems. The major thrust above has been towards models depicting the intraseasonal dynamics of ecosystems or else the static relationships within the ecosystem. Another block of studies could be outlined for broader ecological phenomena.

6.4.1 Regional Grassland Models

Throughout the great plains from Mandan, North Dakota on the north to Spur, Texas on the south, long-term intensity of grazing studies have been conducted. In each of these studies treatments have been applied for many years including heavy, moderate, and light grazing. These intensities vary from area to area, but they are relatively well defined. Superimposed over this time span widely fluctuating climatic conditions have occurred in some places including three major droughts in this century. Records of the climate and of general animal production are available from these studies. Additionally, in some investigations, records have been made throughout on some qualitative characteristics of the plant communities. But in recent years in most of these investigations more detailed data are available on plant cover and plant production (at least end-of-season standing crop) of important groups and species. Additional measurements are available in different studies, but the above data could be used possibly in the following way.

A system of "operators" could be defined including above average, average, and below-average climatic conditions for a given year, and "heavy, moderate, and light grazing". These two sets of operators, generating nine combinations, would give a specific expected response when applied to the three conditions (perhaps good, medium, and poor) of vegetation composition. Perhaps one could devise a scheme in which he could start with vegetation composition being identical for the three grazing treatments, apply the known climatic fluctuations over the past and the known stocking intensities, and see if changing vegetation composition sequences could be developed to match those now existing. If this is possible, then these "operators" would have some validity and predictions could be made into the future. Extensions would allow using probabilistic climatic inputs

and management decisions as far as grazing intensity. In fact, it would seem possible to construe the problem within a dynamic programming or a recursive programming context.

6.4.2 Comparative Plant-climate Relations

Another type of grassland ecology model which has been proposed is that of a spatial analysis of end-of-season geography of standing crops. Considerable volumes of data are available, especially within the Data Bank of the Soil Conservation Service, on soil types, climatic zones, and end-of-season herbage standing crops, at least for major species or groups. Analyses could be made of these data to derive mean and variance herbage yields over a variety of climatic sequences for a given location. Then a study would be made of these mean and variance values as a function of longitude, latitude, and associated edaphic and climatic variables.

The value of these two types of analyses would be that they could be used and coupled with the above-mentioned dynamic analyses to obtain a broader picture of the temporal-spatial relationships for the grassland regions of North America as a whole, with many implications for man's use of the land. This would have a considerable value for continued management of the remaining grasslands in North America. It would also have spin-off and implications for the future management of grassland regions of the world where the plough has not yet struck. It is important to note that there are still many areas in underdeveloped countries where nomadism is a way of life, admittedly for relatively few people, but for very large regions of the globe.

6.4.3 World-wide Grassland Models

With a hierarchy of intensities of models and a hierarchy of types we should be able to make syntheses of the results of grassland studies throughout the world independent of their complexity.

Many of the above models have been explained in the context of the most detailed types of IBP Grassland studies. We foresee or are aware of, for example, those of the magnitude of the Pawnee and Matador studies. It is still uncertain, but there appear to be studies in the USSR and possibly in some middle-European countries, as well as in Japan, of approximately equivalent intensity. It may therefore be possible to make comparative models for grassland ecosystems in several places in the world which would have at least many segments of the detail outlined in Section 3 of this report.

However, a much broader group of worldwide IBP Grassland studies would focus on fewer measurements per site, perhaps comparable to the series of studies in the Comprehensive Network program in the US IBP. Probably there would be in the order of two dozen such studies throughout the world, counting the network in North America. It is important to derive "condensed models" which consider only these proven major features of the grassland system in their equations. Data required for such models should be subject to rapid and economical collection.

6.4.4 Interbiome Models

One additional level of ecosystem modelling should be of value towards development of ecological theory, that is the 4-or-5 compartment model involving whole trophic levels. Therefore, comparisons could be made between different kinds of ecosystems such as deserts, grasslands, tundra, and various kinds of forests.

REFERENCES

- Amundson, N. R. 1966. Mathematical methods in chemical engineering-matrices and their application. Prentice Hall, Inc., Englewood Cliffs, New Jersey. 269 p.
- Analysis of structure and function of grassland ecosystems: A progress report and continuation proposal. 1969. Colorado State Univ., Fort Collins. 700 p.
- Ashby, W. R. 1963. An introduction to cybernetics. John Wiley & Sons, Inc., New York. 295 p.
- Barclay, G. W. 1958. Techniques of population analysis. John Wiley & Sons, Inc., New York. 311 p.
- Bartlett, M. S. 1960. Stochastic population models in ecology and epidemiology. John Wiley & Sons, New York. 90 p.
- Bartlett, M. S. 1970. Two-dimensional nearest neighbor systems, and their ecological applications. To be published in G. P. Patil, E. C. Pielou, and W. E. Waters [ed.] International Symposia on Statistical Ecology, Penn. State Univ. Press. (In press)
- Batschelet, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. Amer. Inst. Biol. Sci. Monogr. 57 p.
- Beer, S. 1968. Management science, the business use of operations research. Doubleday and Co., Garden City, New York.
- Bellman, R. 1960. Introduction to matrix analysis. McGraw-Hill Book Company, New York. 363 p.
- Benyon, P. R. 1968. A review of numerical methods for digital simulation. Simulation 11:219-238.
- Bledsoe, L. J. 1969. Compartment models and their use in the simulation of secondary succession. M. S. Thesis. Colo. State Univ., Fort Collins. 112 p.

- Bledsoe, L. J. and D. A. Jameson. 1969. Model structure of a grassland ecosystem, p. 410-437. In Dix, R. L. and R. G. Beidleman [ed.] The grassland ecosystem: a preliminary synthesis. Range Sci. Dep., Sci. Ser. No. 2. Colorado State Univ. 437 p.
- Bledsoe, L. J. and G. M. Van Dyne. 1969. Evaluation of a digital computer method for analysis of compartmental models of ecological systems. Oak Ridge National Lab. TM-2414. 60 p.
- Bledsoe, L. J. and G. M. Van Dyne. 1970. A compartmental model simulation of secondary succession. Chapter VIII in Patten, B. C. [ed.] Systems analysis and simulation in ecology. Academic Press Inc., New York. (In press)
- Brock, Thomas D. 1966. Principles of microbial ecology. Prentice-Hall Inc., Englewood Cliffs, New Jersey. 306 p.
- Bryson, R. A. 1957. The annual march of precipitation in Arizona, New Mexico, and northwestern Mexico. Univ. Arizona Inst. Atmos. Phys. Tech. Rep. on Meteorol. and Climatol. of Arid Reg. 6.
- Budagovski, A. I. and Y. K. Ross. 1967. Principles of the quantitative theory of photosynthesis by crop stands, p. 37-43. In A. A. Nichiporovich [ed.] Photosynthesis of productive systems. Israel Program for Scientific Translations, Jerusalem.
- Calhoun, J. B. and J. V. Casby. 1958. Calculation of home range and density of small mammals. Public Health Monogr. No. 55, U. S. Dep. Health, Education, and Welfare. 24 p.
- Clark, P. J. and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35:445-453.

- Dice, L. R. and P. J. Clark. 1953. The statistical concept of home range as applied to the recapture radius of the deermouse (*Peromyscus*). Contributions from the Lab. of Vertebrate Biology, Univ. Mich., Ann Arbor. No. 62. 15 p.
- Dobzhansky, T. and S. Wright. 1943. Genetics of natural populations. X. Dispersion rates in *Drosophila pseudoobscura*. Genetics 28:304-340.
- Dobzhansky, T. and S. Wright. 1947. Genetics of natural populations. XV. Rate of diffusion of a mutant gene through a population of *Drosophila pseudoobscura*. Genetics 32:303-324.
- Forest Service, USDA. 1969. Forest insect population dynamics. (Proc. Forest Insect Population Dynamics Workshop, Westhaven, Conn., 23-27 January, 1967). USDA Forest Service Res. Paper NE-125. 126 p.
- Francis, R. 1970. Simulation and estimation of movement in a stratified population subject to recruitment and emigration. Unpub. Ph.D. Thesis, Univ. of Washington.
- Gates, D. M. 1968. Toward understanding ecosystems, p. 1-35. In J. B. Cragg [ed.] Advances in ecological research. Vol. 5, Academic Press, New York.
- Goodall, D. W. 1969. Simulating the grazing situation. In F. Heinmets [ed.] Concepts and models of biomathematics: simulation techniques and methods. Marcel Dekker, Inc.
- Haug, P. 1970. Succession on old fields: a review. M. S. Thesis, Colo. State Univ., Fort Collins. 400+ p.
- Holgate, P. 1970. Random walk models for animal behavior. To be published in G. P. Patil, E. C. Pielou, and W. E. Waters [ed.] International Symposia on Statistical Ecology, Penn. State Univ. Press. (In press)

- Holling, C. S. 1961. Principles of insect predation. *Ann. Rev. Entomology* 6:163-182.
- Jameson, D. A. 1969. A paper presented at Ford Foundation Workshop, Albuquerque, New Mexico.
- Jennrich, R. I. and F. B. Turner. 1969. Measurement of non-circular home range. *J. Theoret. Biol.* 22:227-237.
- Keyfitz, N. 1968. Introduction to the mathematics of populations. Addison-Wesley Publ. Co., Reading, Mass. 450 p.
- Kleiber, M. 1961. The fire of life -- an introduction to animal energetics. John Wiley & Sons, Inc., New York. 454 p.
- Leak, W. B. 1968. Birch regeneration--a stochastic model. USDA Forest Service Res. Note NE-85. 7 p.
- Leslie, P. H. 1945. The use of matrices in certain population mathematics. *Biometrika* 33:183-212.
- Leslie, P. H. 1948. Some further notes on the use of matrices in population mathematics. *Biometrika* 35:213-215.
- Margalef, R. 1968. Perspectives in ecological theory. Univ. of Chicago, Chicago, Illinois. 411 p.
- Martel, Y. and L. J. Bledsoe. 1970. A process model for the turnover of carbon in a grassland ecosystem. Paper presented at IBP/PT Grasslands working group meeting, Saskatoon, Saskatchewan. Sept. 1969.
- Munroe, E. G. 1963. Principles of biogeography. Referred to by Watt, K. E. F. in *Annual Review of Entomology*, Vol. 7, 1962. p. 243-259.
- Odum, H. T. and R. T. Pinkerton. 1955. Time's speed regulator: the optimum efficiency for maximum power output in physical and biological systems. *Amer. Sci.* 43:331-343.

- Odum, H. T. 1960. Ecological potential and analog circuits for the ecosystem. *Amer. Sci.* 48:1-8.
- Odum, H. T. 1962. The use of a network energy simulator to synthesize systems and develop analogous theory: the ecosystem example. *Proc. Cullowage Conf. on training in biomathematics.* p. 291-297.
- Odum, H. T. 1966. Biological circuits and the marine systems of Texas, p. 99-157. In Olson, T. A. and F. J. Burgess [ed.] *Pollution and marine ecology.* Interscience Publ., John Wiley & Sons, New York.
- Odum, H. T. 1967. Energetics of world food production, p. 55-94. In *The world food problem, Vol. 3.* U. S. Government Printing Office. Washington, D. C.
- Odum, H. T. 1969. An energy circuit language for ecological and social systems: its physical basis. *Prog. Rep. to AEC on Contract At-(40-1)-3666.* Appendix I. Univ. Ill. Car. mimeo. 94 p.
- Odum, H. T. 1971. *Environment, power, and society.* Wiley Interscience, New York. 331 p.
- Olson, J. S. and S. Christofolini. 1965. Succession of Oak Ridge vegetation, p. 76-77. In *Oak Ridge National Laboratory Report ORNL-3849.*
- Olson, J. S. and V. R. R. Uppuluri. 1966. Ecosystem maintenance and transformation models as Markov processes with absorbing barriers, p. 104-105. In *Health Physics Division, Ann. Prog. Rep., Oak Ridge Nat. Lab. ORNL 4007.*
- Patil, G. P. 1968. A dictionary and bibliography of the classical and contagious discrete distributions. Ms., Department of Mathematics, Pennsylvania State Univ., University Park. 16802.

- Paulik, G. J. 1969. Development of a comprehensive simulation model of the fish resources of the great lakes. Paper presented at the Fourth Water Resources Conference: Systems analysis for Great Lakes Water Resources, Ohio State Univ., Columbus, Ohio, October 16-17, 1969.
- Pielou, E. C. 1969. An introduction to mathematical ecology. John Wiley & Sons, Inc. 290 p.
- Preston, F. W. 1966. The mathematical representation of migration. *Ecology* 47:375-392.
- Sabbagh, M. E. and R. A. Bryson. 1962. Aspects of the precipitation climatology of Canada investigated by the method of harmonic analysis, p. 250-265. *In* B. J. L. Berry and D. F. Marble [ed.] Spatial analysis: a reader in statistical geography. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.
- Siniff, D. B. and C. R. Jessen. 1969. A simulation model of animal movement patterns, p. 185-219. *In* J. B. Cragg [ed.] Advances in ecological research. Vol. 6, Academic Press, New York.
- Trucco, E. 1965. Mathematical models for cellular systems. Von Foerster - Part 1. *Bull. Math. Biophys.* 27:285-304.
- Usher, M. B. 1966. A matrix approach to the management of renewable resources, with special reference to selective forests. *J. Appl. Ecol.* 3:355-367.
- Usher, M. B. 1969. A matrix approach to the management of renewable resources, with special reference to selective forests--two extensions. *J. Appl. Ecol.* 6:347-348.
- Van Dyne, G. M. 1969a. Some mathematical models of grassland ecosystems, p. 3-26. *In* Dix, R. L. and R. G. Beidleman [ed.] The Grassland ecosystem: a preliminary synthesis. Range Sci. Dep., Sci. Ser. No. 2. Colo. State Univ. 437 p.

- Van Dyne, G. M. 1969b. Grasslands management, research, and training viewed in a systems context. Range Sci. Dep., Sci. Ser. No. 3, Colo. State Univ. 50 p.
- Von Foerster, H. 1959. Some remarks on changing populations in the genetics of cellular proliferation, p. 382-407. In F. Stohlman, Jr. [ed.] The kinetics of cellular proliferation. Grune and Stratton, New York.
- Von Foerster, H. 1961. Mitotic indices of dividing and differentiating cells. Electrical Engineering Res. Lab., Eng. Exp. Sta., Univ. Illinois, Urbana. U. S. Public Health Grant C-4044, Rep. No. 3.
- Waggoner, P. E. 1969a. Computer, forest, and fungus. Conn. Agr. Exp. Sta., Frontiers in Plant Science, (Fall). 6-7 p.
- Waggoner, P. E. 1969b. Predicting the effect upon net photosynthesis of changes in leaf metabolism in physics. Crop Sci. 9:315-321.
- Watt, K. E. F. 1968. Ecology and resource management: a quantitative approach. McGraw-Hill Book Co., New York. 450 p.
- Watts, D. G. and D. L. Loucks. 1969. Models for describing exchanges within ecosystems. Institute for Environmental Studies, Univ. Wisconsin, Madison. 18 p.
- Widder, David. 1947. Advanced calculus. Prentice-Hall, Englewood Cliffs, New Jersey.