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PWNEE: A Grassland Ecosystem Model

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## ABSTRACT

The primary objective of Grassland Biome Project modelling efforts this year (1970) has been to produce a mechanistic total system model of a grassland ecosystem. The result has been a model which is mechanistic to the extent that, wherever possible, the mathematical formulations are analogous, at some level of resolution, to the functional mechanisms operating within the system.

The model is primarily designed to describe the shortgrass prairie ecosystem of the Pawnee National Grassland. It is designed as a highly modular system for two reasons:

- i.* So that individual processes or mechanisms may be changed as information becomes increasingly available, and
- ii.* So that the model can be used in situations having greater (Pawnee Site) or lesser (Comprehensive Sites) detail in data and information.

The current version of the model is in a first-pass condition, and has not been subjected to extensive scientific debugging (i.e., the mechanisms have not been closely reexamined by biologists).

The model is structured in the following way:

- i.* It is a time-dependent biomass model. No spatial aspects are taken into consideration at present.
- ii.* The primary equations to be solved make up a series of first-order differential equations. Thus, the equations for the principal system variables express the rate of change of biomass with respect to time.

- iii.* The total model is made up of trophic level submodels. Within each trophic level various functional relations describe the processes.

A set of 40 first-order differential equations has been developed to describe the abiotic, producer, consumer, and decomposer components of the ecosystem. The abiotic section involves driving forces of solar energy, air temperature, wind speed and precipitation, and driven variables of micro-climatic temperature, soil temperature, and soil moisture. The producer variables consist of biomass density of aboveground live biomass for four plant functional groups, plant standing dead, plant litter, and plant live roots. The consumer biomass is compartmentalized as animal live material, animal dead material, and animal fecal material. The animal live biomass is further subdivided into five functional groups (wild primary consumers-mammal, domestic primary consumers-mammal, secondary consumers-mammal, birds, and insects). The decomposer compartments are mediated by microbial functional groups whose activity is in turn controlled by their biotic and abiotic environment.

## ACKNOWLEDGEMENTS

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## 1. INTRODUCTION

The purpose of this report is to provide the basic mathematical documentation for a Grassland Ecosystem Model developed by the modelling group of the Grassland Biome Study of the US IBP. Its primary purpose is to communicate with persons capable of reading and understanding conventional mathematical notations. A second purpose is to communicate the model mechanisms to the general biological scientist who may not be conversant in mathematical notation. A third purpose is to indicate the directions which further research on high-resolution models of whole ecosystems will take in the Grassland Biome Study.

The purpose of the model, entitled PWNEE, MOD 1, is to mathematically represent a shortgrass prairie ecosystem, specifically at the Pawnee Site where an intensive research effort is being undertaken. In its attempt to cover all trophic levels of the ecosystem, the model involves a great deal of systems complexity. On the other hand, the mechanisms for individual processes are made as simple as possible so as to make the initial system organization job not overly complex. The primary purpose of this version of PWNEE is to stimulate discussion and feedback on all phases of this modelling approach--the biological mechanisms, the mathematical notation, the computer implementation, and this report--as a method of communicating modelling ideas.

The mechanisms in the current version of the model have not been thoroughly examined by experimental scientists; some of the mechanisms were derived from the literature or by consultation with biologists. A great many mechanisms fall into the category of "intuitive guesses" where the intuition is that of the authors of this report who are not biological scientists. The model was

implemented on the computer in a highly modular fashion, i.e., most of the processes or mechanisms were implemented as separate FORTRAN functions or subroutines. This was done to facilitate changes in future versions of the model. This also allows for a set of different mechanisms to be substituted for a particular process of the system. In this way, the same general structure may be used with high resolution mechanisms to compare with Pawnee Site data and lower resolution mechanisms to apply to Comprehensive Site data. Thus, the purpose of this first version of a complete ecosystem model is to provide a skeletal structure within which modifications may be made to eventually provide a realistic description of grassland ecosystem functioning.

In the light of the above stated purpose of this model, explanations of mechanisms contained in this report will frequently be without reference to the open literature. Wherever such a reference is appropriate, it will be included. Generally, the rationale which goes into the construction of the mechanisms of the model is sufficiently simple that it will be transparent upon study of the mechanism explanation. When faced with a plethora of possible alternative causes for a known phenomenon, the selection of a simple mechanism involving only one or a few of these causes is arbitrary. Justification of the mechanism selected over other mechanisms is of little use in this case, since it is only one of a set of equally acceptable hypotheses.

When the reader encounters mechanisms in the model which are presented without explicit written justification or literature citation, he may assume the above situation to be the case. Some of the mechanisms have been previously reported in Bledsoe and Jameson (1969). These will be indicated.



A particular problem in the writing of this report has been the diversity of the audience to which it is directed. As stated in the beginning of this section, we are primarily concerned with a documentation of mathematics. We are also concerned with a description for the non-mathematically inclined reader and a documentation of the rationale which went into the construction of the model. Later reports concerning other versions of this model could have a different purpose since the objective of higher realism will demand more detailed justification of mechanisms. As a result of our varied objectives in this report, some mathematically inclined readers may be frustrated by the detail which goes into the description of mathematics which, to them, is trivial, or they may be confused by some conventions of biological terminology. On the other hand, the biologically inclined readers may be confused by the use of nomenclature, units, and equation conventions which are common among mathematically oriented scientists. Clearly, the detailed explanation of conventions common to various scientific disciplines is beyond the scope of this report. We can only ask our readers to bear with us and, perhaps, to read selectively, skipping over sections which are either confusing or seem trivial. We have revised this manuscript repeatedly at the suggestions of proofreaders from divergent backgrounds.

The next section contains a discussion of the organization of the model and of the nomenclatural and notational conventions used. Following is a presentation of the algebraic form of the mechanisms in the driving functions, abiotic, producer, consumer, and decomposer sections of PWNEE, and a brief discussion of possible future areas of modifications for each section.

Appendix material includes: (A) a summary of algebraic and differential equations in the model; (B) a glossary of symbols used for variables and parameters in the model, including a cross reference between algebraic and computer notation; (C) a description of the computer implementation of the model including a listing of the FORTRAN code; (D) a description of input and output formats for the computer program together with a listing of parameter values used in (E), a final appendix section with a set of graphs containing results of typical computer simulation of the system.

## 2. DESCRIPTION OF THE MODEL

### 2.1 General Description

PWNEE is a system of 40 principal variables, 33 of which are represented by first order ordinary differential equations, generally nonlinear. The remaining seven are represented by algebraic equations. The equations are designed to describe the general functioning of a grassland ecosystem; the variables are somewhat arbitrarily categorized into 4 groups: abiotic, producer, consumer, and decomposer. Fig. 2.1 shows in a diagrammatic way the approximate chain of causal relations among these four groups and subdivisions within the groups. However, the reader should not attempt to draw conclusions about the operation of the model solely by reference to the diagram. The model is designed to be deterministic; however, this distinction is somewhat trivial since the parameters could be drawn randomly from empirically determined distribution functions in a series of system simulations to provide a measure of the stochastic nature of the system variables. The time resolution of the model is such that the derivatives of the principal variables will have, in some cases, significant changes over a 3 to 5 minute period. At the other end of the scale, the model should eventually depict ecosystem changes over a longer time, e.g., several years. Currently, simulations are being made only on an intra-year basis.

### 2.2 Notation and Nomenclature

In order to enhance communication about the ecosystem model, it is necessary to adopt a set of conventions concerning the names for the different variables which occur in the mathematical system description. Every discipline

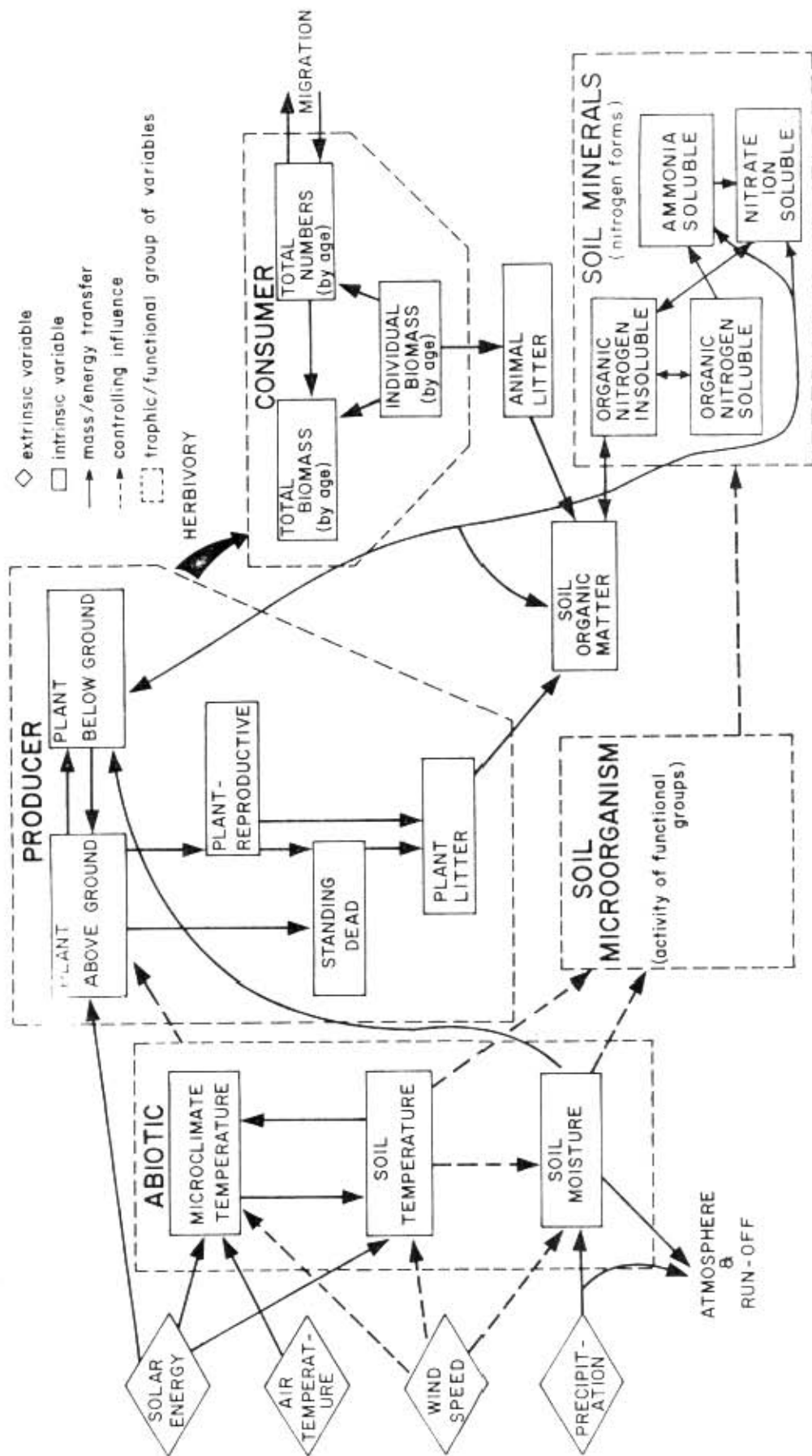


Fig. 2.1. Generalized diagram of the grassland ecosystem showing biomass, energy, and nutrient flows as represented by equations in this text. Species enumeration and process names have been omitted for clarity.

which utilizes mathematical models has, to some degree, adopted their own conventions. However, there is little agreement across disciplines and, even within disciplines the conventions are rarely well defined. This subsection describes the nomenclature which has been decided upon to be used in this report and tentatively for use in future Grassland Biome modelling reports. This nomenclature has evolved after a great deal of thought and discussion. The biological problems of the model are of greater importance than the nomenclature problems and we will allocate our time accordingly. The important aspect of the nomenclature is that a system be adopted and adhered to. Thus, we expect our nomenclature to be modified as our experience with the system increases, but we shall not be overly concerned with minor inadequacies.

Analogous to the nomenclature problem is the problem of selecting an algebraic notation for written representation of the mathematical equations which comprise PWNEE. Again, various disciplines have adopted their own conventions and we have abstracted some of these for our own use. The general criteria for selection of a notational system were: 1) that the notation must clearly discriminate among the types of variables described by the nomenclatural system; 2) that it must do as much as possible to enhance the understanding of the mathematical systems by the reader who is not familiar with the model; and 3) that it must be mathematically convenient to work with. The decision as to what distinctions are to be made among the variables was made primarily upon the basis of biological criteria rather than the type of mathematics associated with the variables. Thus, we do not

distinguish between whether the variables are defined by differential equations as opposed to algebraic equations but rather between the variables which are more or less important to the biological description of the ecosystem.

There are six general types of variables utilized in the model, defined as follows:

*Driving variables.* A driving variable is one which is necessary for the elaboration of other variables of the system, but with whose mechanistic description we are not concerned. For example, it is necessary to know the precipitation rate in order to drive the soil moisture differential equation. However, we are not concerned with the mechanisms responsible for the occurrence of precipitation. We are satisfied with a non-mechanistic description of precipitation such as would be given by a tabulation of actual values or a stochastic rainfall generator.

The algebraic notation for driving variables is a small letter "z" followed by a single subscript. See Table 2.1 for examples.

*Principal system variables.* The principal system variables (PSV's) are the primary, dependent variables of the model. These are variables such as aboveground live plant biomass or densities of small mammals which comprise the principal output of the model, i.e., a graph of the PSV's as a function of time can be thought of as the solution to the set of equations which comprise the model. The purpose of the computer program which implements the model is to produce such a set of graphs. The algebraic notation for a PSV consists of one or two English letters, possibly subscripted, the first of which is a capital and second of which is a small letter. See Table 2.1 for examples.

Table 2.1. Examples of variable notation and nomenclature used in this report.

Type of Variable	Example--name of variable	Example--symbol for variable
Driving variable	Air temperature	$z_2$
	Precipitation rate	$z_3$
Principal system variable (PSV)	Aboveground biomass density of plant group $i$	$A_i$
	Biomass density of consumer	$C_i$
Intermediate system variable (ISV)	Translocation rate above- to belowground, plant group $i$	$bt_i$
	Ingestion rate per unit body weight, $i$ th consumer group	$fc_i$
Independent variable (time)	Time from Jan. 1, seconds	$t$
	Time from Jan. 1, hours, modulo 24	$thm$
Dummy Function argument	--	$x$
		$x_1$
		$x_2$
Parameters	Threshold of positive photosynthesis response to temperature, plant group $i$ (first parameter used in formulation of $T_c$ )	$pTc_{i1}$
	Upper threshold for density of consumed material ( $j$ ) at which food consumption will be equal to $pf_{c1i}$ (second parameter used in formulation of the ISV $fc_i$ )	$pf_{c_{i2j}}$

*Intermediate system variables.* Intermediate system variables (ISV's) are the values of mathematical functions which are necessary in the calculation of the PSV's. The distinction between PSV's and ISV's is based upon the following biological (as opposed to mathematical) criterion: a PSV is decided upon a priori as a desired output variable of the model; an ISV arises a posteriori in the process of writing equations to relate the PSV's. As shown in the example in Table 2.1, ISV's are frequently rates, i.e., they usually give the change per unit time or flow of a biomass or energy density variable. Thus, they are frequently in the same units as the derivative of a principle system variable. The differential equation for the principal system variables frequently consists of a sum of terms, each term containing an ISV, a PSV, and a parameter (explained below). For example, see the first term in equation 5.1 of Appendix A.

The algebraic notation utilized for ISV's consists of two small letters, sometimes with a subscript. Table 2.1 contains some examples. The first of these two letters may not be a p, t, z, or x as these are reserved for other types of variables in the model as explained above and below.

*Independent variables.* Since this model does not have explicit spatial variability, the only independent variable is time. It is frequently convenient to have time available in different systems of units for the formulation of equations in different parts of the model. For example, in formulating a mechanism which fluctuates diurnally, such as windspeed, the time of day in hours might be useful; for a seasonal fluctuation, the time of year in months might be useful. We have utilized separate symbols to indicate time in the



various units which might be utilized for the independent variable. These are summarized in Table 2.2 together with the symbolic notation of the computer implementation described in Appendix C.

*Dummy function arguments.* In the simulation of an ecosystem model, it is frequently necessary to utilize mathematical functions purely for their mathematical, as opposed to biological, properties. For example, the usual trigonometric functions such as sine and cosine have been used. In addition, there are less common functions which are defined in the text of the model documentations. For example, we have found it necessary to utilize a function which asymptotes to zero as its' argument decreases and to one as its' argument increases, with a smooth transition in between (at  $(x_1, x_2, x_3)$ , see equation 7.18). We have called these functions intermediate system variables. When they are defined, it is necessary to have variables to use for their arguments. Conventional mathematical usage labels these arguments "dummy variables," and we will utilize a small letter "x," sometimes subscripted, as shown in Table 2.1, for a symbol. For an example of the use of a dummy variable see equation 7.18.

*Parameters.* In any mathematical model there are variables whose derivative, with respect to all other variables of the system, is zero. These are frequently termed coefficients, constants, or parameters. For various reasons, some of them arbitrary, we have decided to uniformly call such variables "parameters." The model uses a great number of parameters and we have adopted a notational system to make it somewhat easier to relate the parameters to the ISV's and PSV's with which they are associated. The parameters always begin with a small letter p and the next one or two letters correspond

Table 2.2. Symbolic notation for time in different units.

Algebraic Symbol	Description	Program Symbol
t	Time, seconds	T
td	Time, days	TD
tdm	Time, days, modulo 365	TDM
th	Time, hours	TH
thm	Time, hours, modulo 24	THM
tw	Time, weeks	TW
twm	Time, weeks, modulo 52	TWM
tm	Time, months (Julian)	TM
tmm	Time, months, modulo 12	TMM
ty	Time, years	TY

to the PSV or ISV which the parameter is used to formulate. In the event that a parameter is used in formulation of more than one PSV or ISV, this selection is arbitrary. If the system variable referred to has subscripts, they will appear as the first subscript in the parameter. Additional subscripts may appear as well. These additional subscripts may be used simply to enumerate the various parameters involved in formulation of the ISV or PSV. They might also refer to other enumerated variables of the model. The example in Table 2.1 should help to clarify the usage. The parameter  $pTc_{i1}$  is the first parameter used in the formulation of the principal system variable  $Tc$ . The subscript  $i$  indicates that it refers to the  $i$ th plant group. The parameter  $pfc_{i2j}$  is the second parameter used to formulate the intermediate system variable  $fc_i$  (food consumption rate of  $i$ th consumer); the subscript  $j$  refers to the  $j$ th group being consumed.

A uniform system of physical units facilitates the construction of an ecosystem model by avoiding the use of parameters whose sole purpose is to convert other variables to the proper system of units. We have decided to utilize centimeters for length, grams for weight, and seconds for time for nearly all of the variables of the model. When exceptions occur, they will be noted in the text. Appendix B contains a glossary of all of the system variables, together with their units, their algebraic notation, and the corresponding notation utilized in the computer implementation. The notation used in the computer implementation differs substantially from the algebraic notation, because the two have evolved at different rates during model development. Table 2.3 contains a summary of the numbers of different

Table 2.3. Number of variables of different types used in various sections of PWNEE, MOD 1.

Type of Variable	Section					Total
	Driving Variables	Abiotic	Producer	Consumer	Decomposer	
Driving	4	-	-	-	-	4
PSV	-	3	7	17	13	40
ISV	1	0	51	249	21	321
Parameters	5	2	116	217	59	340

types of variables used in the various sections of PWNEE. This should give the reader some idea of the size of the PWNEE model.

### 2.3 Parameter Values

The text will frequently show numerical values inserted in equations where a symbol for a parameter would seem more logical. This is a reflection of the fact that at the time of preparation of this manuscript, the model had not been "cleaned up" thoroughly and contained a number of relatively minor inconsistencies. The numerical values were not replaced with symbols, primarily because the computer implementation contained the same values rather than symbols for storage locations where a value could be input from a parameter card (see Appendix D). Though insertion of a symbol for a number in the text of this report is a minor task, modification of the computer program is more involved. These and other modifications are being made continuously, both to the model and its computer implementation, and will be reflected in the documentation for PWNEE, MOD 2.

In order to experiment with the computer implementations of a model, it is necessary to have values for all model parameters. Ideally, the parameter values should be chosen to make the intermediate system variables conform to empirically determined results. In point of fact, the empirical results are not available for most of the ISV's, and it is necessary to use a combination of several heuristic techniques to obtain initial estimates of parameter values. One such technique is to assume a certain percentage growth rate under optimal or normal conditions for principle system variables and adjust the parameters to provide that rate. For example, one might assume that, under optimal conditions of moisture, temperature,

sunlight, and nutrients, the warm season grasses will have a net production of 5% per day. This would dictate the value for the parameter  $pA_1$  of  $.05(\text{day})^{-1}$  or  $.058 \times 10^{-5} (\text{seconds})^{-1}$ . Parameter values for the translocation function might be calculated by making crude assumptions concerning relative above- and belowground growth rates. The justification for the assumptions are not based upon any literature or experimental values, but rather by the intuition and experience of the biological scientist or the modeller. The numerical estimates *per se* are made by a modeller (who may or may not be also a biologist), however his information comes through consultation with biological scientists. Frequently, the consultation may involve examination of data concerning similar species. As stated earlier, at the stage of model building represented by this report, the fact that the assumptions made are very crude does not affect the overall objectives of the model. Appendix D contains a set of numerical values for the parameters utilized to produce the output in Appendix E. The same parameters were utilized to produce the graphs of intermediate system variables which are found in later sections of the text. Time does not permit giving a detailed explanation of the rationale for the determination of each parameter; as model development proceeds these parameter values change so rapidly that the rationale is of little use in any event. (The fact that the parameter values are so rapidly modified during model development is one reason why they are not called constants.)

#### 2.4 Updating and Validating the Model

Since a purpose of this model is to stimulate criticism to improve future versions, it is appropriate to comment on the manner in which PWNEE might be updated. Basically, there are four types of modifications which can be made. These correspond to the steps used in producing the model originally. In order of complexity of the modification, most complex first, these areas are as follows:

- (i) addition and deletion of PSV's,
- (ii) addition and deletion of terms in the equations for the PSV's or their rates of change,
- (iii) changes in the formulation of functional curves which relate the ISV's to other system variables, and
- (iv) changes in the values of model parameters.

A change in the value of a model parameter is a very easy modification; additions and deletions of PSV's affect the model much more drastically and are more difficult to implement and document. Modifications of type two and three change the basic mathematics of the model. It is here where we expect most activity in updating the model to take place. Criticisms of any type will be useful and interesting. Only those which fall under the category of specific changes of one of the above types will result in any immediate improvement in the model. Suggestions concerning a change in basic methodology have been initiated in other project phases. The differential equation approach is supported by years of experience in other scientific disciplines and a growing literature in ecology. A great deal of thought has gone into the selection of this approach. Alternate methods are being explored as

separate projects, but we are committed to a major effort with the differential equation approach for high resolution ecosystem models.

In order to achieve a smooth and orderly transition from our initial modelling efforts into a reputable and realistic ecosystem model, it is necessary to make changes a small amount at a time. For example, biological scientists may feel that the entire range of principle system variables is fundamentally incorrect and must be changed. However, in order to avoid redoing the work which has gone into the current version of the model, we would suggest adding and deleting PSV's one at a time with constant reevaluation of model output. It is only in this way that future results can be built upon past effort and that we can profit by our mistakes as we proceed.

Validation of a whole ecosystem model is a topic beyond the scope of this report, however a few comments are in order. Ideally, validation involves comparison of all PSV's and ISV's of the model with experimental data. ISV's would be measured over the range of all environmental parameters of which they are a function (the "process studies" of the Grassland Biome), and PSV's would be monitored for a sufficient number of years to provide a wide cross section of environmental conditions. If the PSV's of the model, when graphed as a function of time, do not agree with the corresponding empirically determined values, the modeller must reformulate parts of the system and try again (assuming the system has been driven with the appropriate data). It is impractical of course to determine the complete range of all ISV's as a function of all variables and to measure all ecosystem variables corresponding to PSV's. The Grassland Biome study is endeavoring to do as much of this type of experimental measurement as possible. Fortunately, model validation is not



an absolute thing but rather a continuum. It can be defined, in a practical sense, as any technique which helps the modeller to gain confidence in the efficacy of his model as a description of reality. As defined in Bledsoe and Jameson (1969), a model is an abstraction of reality. The level of the abstraction is determined by the resolution of the model. The concept of model resolution is discussed in Grassland Biome Technical Report No. 32 (Swartzman 1970). A great many of the principle system variables of the PWNEE model have been measured in the 1970 field season. Some of those which were not measured in 1970 will be measured in 1971 and succeeding years. Consider some examples of model validation in areas where other than complete data are available. If a total predicted standing crop of all plant functional groups in the model corresponds with the total standing crop as measured in the field, this would be an aid to determining the reality of the model mechanisms, even if comparison by species or functional groups could not be done, and thus, is a method of validation. Similarly, if project scientists feel that the rate of change of a principle system variable, such as animal density, has been completely formulated to a realistic degree, they may have a great deal of confidence in the prediction of animal numbers in spite of the fact that field technique might not be adequate to provide a check. Such a situation could result from laboratory studies or literature data providing appropriate ISV information. It is true that in some areas where it is very difficult to make field measurements of model PSV's, it may be desirable to reformulate the model and redefine the principle system variables to correspond to those field values which can be measured. However, this need not always be the only alternative as pointed out above.

An objective of research in the Grassland Biome is to provide the most complete and realistic ecosystem models at several levels of resolution which are possible with the current state of ecological knowledge and experimental techniques, subject to a reasonable monetary constraint. Exactly how complete and realistic these models will be remains to be seen. We believe that they will represent a considerable enhancement of the knowledge of the functioning of grassland ecosystems. This enhancement will probably result from the integration of existing knowledge rather than from the discovery of new fundamental truths in separate subdivisions of the ecosystem.

### 3. DRIVING VARIABLES

Driving variables are those ecosystem variables which are not produced via mechanistically formulated equations but are nevertheless needed as input to the rest of the model. For example, we are not interested in a mechanistic formulation to predict air temperature (at 2 m) but we do need to know what air temperature is at any time in order to predict, say, photosynthesis rate. The driving functions of the current PWNEE model are  $z_1$ --net shortwave radiation [ $\text{cal}/(\text{cm}^2 \cdot \text{sec})$ ],  $z_2$ --air temperature at 2 m ( $^{\circ}\text{C}$ ),  $z_3$ --precipitation rate (cm/sec), and  $z_4$ --wind speed at 2 m (cm/sec). Our current notational scheme utilizes a small letter "z" with a single subscript for a driving variable.

There are three basic methods of inputting driving variables to the computer implementation of the model:

- i.* an actual record of the variables as recorded on an experimental site for some time period. The program must provide an interpolation scheme to provide information between the recorded time points since any data entered into a digital computer must be discrete. This scheme can be a simple linear interpolation if time points are close, relative to the time resolution of the model (say, every five minutes), or it must be more complex if there is a lengthy spacing between time points (say, twice a day);
- ii.* a deterministically generated variable. This might be used if data were unavailable for some needed driving variable for purposes of checking out the model. For example, one might assume a simple sinusoidal variation in air temperature or solar radiation;
- iii.* a stochastically generated variable. Here one would employ a numerical scheme which would produce a set of pseudo-random numbers

whose statistical characteristics match the characteristics of the variable as measured in the field.

The computer implementation of PWNEE, MOD 1, contains a mixture of methods (i) and (ii) to produce the needed driving variables.

PWNEE, MOD 1, utilizes the very simplest possible mechanisms to give continuous driving variables. At the time of construction of this version, the most readily available data consisted of records of daily precipitation and maximum and minimum temperatures. The wind speed and solar radiation functions contain only diurnal variability; seasonal changes are reflected only through the precipitation and air temperature variables. The reason is the priority placed on production of a whole system model as a target for discussion and framework for modification.

### 3.1 Net Shortwave Radiation

Method (ii) is utilized to give a figure for  $z_1$  [ $\text{cal}/(\text{cm}^2 \cdot \text{sec})$ ], at any time. Solar radiation is assumed to be a truncated sinusoid with a peak value given by parameter  $pz_1$  as shown by equation (3.1):

$$z_1 = \begin{cases} pz_1 \cdot \sin \left[ \frac{2\pi}{24} (\text{thm} - 6.) \right] & \text{if } 6 \leq \text{thm} \leq 18 \\ 0 & \text{otherwise} \end{cases} \quad (3.1)$$

Time of day in hours is given by thm.

### 3.2 Air Temperature

Method (i) is utilized here ( $z_2$ ,  $^{\circ}\text{C}$ ) and a complex interpolation scheme has been employed since the recorded temperatures consist of daily maximum and minimum. Since the time of day at which the optimal temperatures occurred was

not recorded, the assumption is made that the maximum temperature always occurs at 2:00 PM (thm = 14.0) and the minimum at 5:00 AM (thm = 5.0). If the input daily values are regarded as parameters,  $pz_{2,1,i}$  and  $pz_{2,2,i}$ ,  $i = 1, \dots, 730$  days, for maximum and minimum, respectively, for each day for two years, then the formulation is a cosine interpolation as follows:

$$z_2 = \begin{cases} (pz_{2,1,i-1} - pz_{2,2,i}) \text{cx}[(\text{thm} + 10.) \cdot \frac{\pi}{15.}] + pz_{2,2,i} & \text{if } 0 \leq \text{thm} \leq 5.0 \\ (pz_{2,1,i} - pz_{2,2,i}) (1. - \text{cx}[(\text{thm} - 5.) \frac{\pi}{9}]) + pz_{2,2,i} & \text{if } 5. < \text{thm} \leq 14. \\ (pz_{2,1,i} - pz_{2,2,i+1}) \text{cx}[(\text{thm} - 14.) \frac{\pi}{15.}] + pz_{2,2,i+1} & \text{if } 14. < \text{thm} < 24. \end{cases} \quad (3.2)$$

where

$$\text{cx}(x_1) = \frac{1}{2}[1 + \cos(x_1)] \quad (3.3)$$

and  $i = \text{td}$  gives the time index.

### 3.3 Precipitation

Method (i) is utilized to give precipitation ( $z_3$ , cm/sec) rates for any time of day. The basic data record is the amount of rainfall which occurs in any one day without any information about when during the day it occurred, so some assumptions are required. We have assumed that the daily

rainfall occurs between 3:00 AM and 8:00 AM ( $t_{hm} = 3.0$  to  $t_{hm} = 8.0$ ) during the months October through June. During the summer months, all precipitation occurs between 3:00 PM and 7:00 PM ( $t_{hm} = 15.$  to  $t_{hm} = 19.$ ) to correspond with the afternoon thunderstorm typical of the Great Plains in late summer. The following algebraic equation summarizes this mechanism:

$$z_3 = \begin{cases} 1.39 \cdot 10^{-4} p_{z_3,i} & \text{if } (6. \leq t_{mm} < 9.) \text{ and } (15. \leq t_{hm} < 17.) \\ 5.56 \cdot 10^{-5} p_{z_3,i} & \text{if } (t_{mm} < 6. \text{ or } t_{mm} \geq 9) \\ & \text{and } (3. \leq t_{hm} \leq 8.) \\ 0. & \text{otherwise} \end{cases} \quad (3.4)$$

where  $i = td$  gives the time index and  $p_{z_3,i}$  is the amount of precipitation, in cm, occurring on the  $i$ th day. The numerical constants are for conversion of precipitation rate in cm/day to the appropriate time period, either two hours or five hours.

### 3.4 Wind Speed

Method (ii) is utilized here. We assume that the wind blows constantly at 5 mph during the hours 12:00 noon to 6:00 PM ( $t_{hm} = 12.$  to  $t_{hm} = 18.$ ), at 0 mph between 9:00 PM and 9:00 AM ( $t_{hm} = 21.$  to  $t_{hm} = 9.$ ), and changes linearly in the interim periods ( $t_{hm} = 9. - 12.$  and  $t_{hm} = 18. - 21.$ ). The following equation summarizes this:

$$z_4 = \begin{cases} 447. & \text{if } 12. \leq thm < 18. \\ (thm - 9.) \cdot 149. & \text{if } 9. \leq thm < 12. \\ -(thm - 18.) \cdot 149. + 447. & \text{if } 18. \leq thm < 21. \\ 0 & \text{if } 21. \leq thm < 24. \end{cases} \quad (3.5)$$

### 3.5 Future Expansion

For air temperature and precipitation rate, near-continuous recording devices are operating on the Pawnee Site. A simple linear interpolation scheme will eventually provide a very realistic driving function for these two variables. Solar radiation and wind speed are also being continuously recorded for periods of several weeks at a time. Correlation of these data with periodic measurements of wind speed (e.g., total miles/day) and other meteorological parameters will allow generation of realistic values for  $z_1$  and  $z_4$ . This would be a combination of methods (i) and (ii) or (i) and (iii).

For simulation of locations other than the Pawnee Site, a more realistic extension of the methods described herein might be used. These would be based on analysis of data from nearby stations of the U.S. Weather Bureau and utilization of existing functions in the meteorological and climatological literature. For example, the summer thunder storm intensity might be given by the Gamma distribution function employed by Amaracho and Broadstetter (1967). This would allow the storm intensity to vary within the storm period instead of assuming a square distribution as in MOD 1.

#### 4. DRIVEN ABIOTIC VARIABLES

The abiotic section of PWNEE is relatively simple compared to other sections. This is because of the greater amount of knowledge already in existence concerning mathematical forms in this area. Rather than attempt to duplicate other research, we basically have sought to formulate mechanisms which will provide the rest of the system with needed variables. We expect that the hydrologists and agricultural engineers in the Grassland Biome study will be able to supply correct formulations in future modifications of PWNEE. The task of mathematical modelling is met with much less skepticism and much greater confidence by scientists of this area than in the biologically oriented areas. Thus, it is necessary to place a different emphasis on abiotic mechanism formulation in construction of a model designed to encourage mathematical statement of mechanisms.

The PSV's of this section are soil temperature,  $T_s$ , soil moisture,  $M_s$ , and soil surface temperature,  $T_c$ . There are no ISV's associated with the abiotic PSV's. Such obvious associated variables as soil moisture tension or nutrient status are included in later sections because of their use in formulating PSV's of those sections.

##### 4.1 Principal System Variables

The soil surface temperature,  $T_c$ , is utilized synonymously with plant canopy temperature and is used in other sections of the model as the characteristic temperature for mediating aboveground plant physiological mechanisms. In a completely mechanistic approach, the soil would be broken down into thin horizontal layers with a PSV to describe the temperature of each layer. This would be done by developing heat budget equations for each layer to give rate



of change of heat content as a function of other system variables (Whitman, 1969). For the current level of resolution of PWNEE we have regarded this as too complex and detailed an approach. We have adopted the following expedient in which  $T_c$  is formulated in an algebraic equation, in contrast to most PSV's of PWNEE.

$T_c$  is regarded as being equal to air temperature,  $z_2$ , under conditions of high wind or zero solar radiation since radiative heating due to insolation can be removed by convection under these conditions. Otherwise,  $T_c$  can rise to as much as  $10^\circ\text{C}$  (an order of magnitude estimate) above  $z_2$ . The following equation summarizes this relation:

$$T_c = \begin{cases} z_2 + 10 \cdot \left(\frac{z_1}{pz_1}\right) & \text{if } (z_4 \leq 223.5) \text{ and } (z_1 > .0002) \\ z_2 & \text{otherwise} \end{cases} \quad (4.1)$$

Notice that the breakpoint for an increase in  $T_c$  over  $z_2$  is a wind speed less than 5 mph (223.5 cm/sec).

Soil temperature,  $T_s$ , is calculated by a linear differential equation which causes a first order lag behind  $T_c$ . The time constant of the lag is  $pT_s$ . We define  $T_s$  as an average for the top 20 cm of the soil.

$$\dot{T}_s = pT_s(T_c - T_s) \quad (4.2)$$

Fig. 4.1 gives a graph of  $z_2$ ,  $T_c$  and  $T_s$  for the first few days of January as calculated in PWNEE. The temperature minima and maxima used in Appendix E were taken in 1967 near Akron, Colorado on an area of sandhills prairie (courtesy of USDA).

Soil moisture,  $M_s$ , is given in cm of water in the top 20 cm of the soil. It is characterized by a linear differential equation with precipitation rate as an input and a linear loss rate as the only driving mechanism. The rate constant for loss is  $pM_s$ .

$$\dot{M}_s = z_3 - pM_s \cdot M_s \tag{4.3}$$

The constant-coefficient linear loss term,  $pM_s \cdot M_s$ , is used to account for all sources of moisture loss from the ground. With the precipitation driving functions used, the soil never becomes saturated so it was not necessary to put a saturation limiting mechanism into the model. Bledsoe and Jameson (1969) contains a description of such a mechanism, but it was not implemented for the reason given above. Fig. 4.2 gives a graph of  $M_s$  as a function of time for precipitation data taken concomitantly with the temperature data in Fig. 4.1.

The parameter values reported in Appendix D were all order of magnitude values with the exception of  $pM_s$ . This parameter was chosen by trial and error to give soil moisture values to correspond with measurements made concomitantly with the precipitation values,  $pz_{3,i}$ ,  $i = 1, \dots, 730$ .

#### 4.2 Future Expansion

PWNEE, MOD 2, will probably separate the soil surface and canopy temperatures into two PSV's with a heat budget formulation including net radiative heating and evaporative cooling for each. The information necessary to validate such mechanisms is currently being made (on the Pawnee Site) with automated digital recording devices. A separate modelling project on prediction of soil temperature as a function of depth is being carried out independently of Grassland Biome support by the Agricultural Engineering Department of the

University of Wyoming. Improvements in the soil temperature PSV will be based on this project. A soil moisture model is being developed by the personnel responsible for the microwatershed experimental project at the Pawnee Site (Department of Watershed Resources, Colorado State University). This model would consider such phenomena as runoff, evaporation, transpiration, surface roughness, slope, and aspect.

To give a better seasonal distinction in the model, PSV's for snow depth and hail might be added. The modifications mentioned above will probably require additional driving forces such as cloud cover and dew point depression. Modifications in other sections of the model may also require elaboration of the abiotic section to provide the necessary environmental data.

## 5. PRODUCER VARIABLES

### 5.1 Principal System Variables

There are seven producer principal system variables. The first four of these are the aboveground live biomass densities of four plant functional groups representing four of the major groups on the Pawnee Site.  $Al_1$  denotes the biomass per square centimeter of warm season grasses, as typified by *Bouteloua gracilis*;  $Al_2$  denotes the biomass of cool season grasses, as typified by *Agropyron smithii*;  $Al_3$  represents forbs, as typified by *Sphaeralcea coccinea*;  $Al_4$  represents *Opuntia polyacantha*, which makes up over 95% of the cactus species. Each of the PSV's, though typified by a single plant species, stands for the total biomass in each of the four functional plant groups. These four groups make up a large percentage of the plant biomass on the experimental pastures at the Pawnee Site. They also are the groups which are most important in consideration of grazing patterns for domestic herbivores on the site.

The rates of change of each of these four producer PSV's are represented by the differential equation given below.

$$\dot{Al}_i = pAl_i \cdot hp_i \cdot Al_i - (bt_i + da_i + ha_i) \quad , \quad i = 1, \dots, 4 \quad (5.1)$$

where the processes of photosynthesis, translocation of photosynthate to belowground parts, death of aboveground parts, and harvest of aboveground parts are represented by  $hp_i$ ,  $bt_i$ ,  $da_i$ , and  $ha_i$ , respectively, for the  $i$ th plant group. All units are  $g/(cm^2 \cdot sec)$ . These ISV's vary with time depending on the states of various system variables. These relationships are discussed

below.  $pA_i$  is a conversion factor for  $CO_2$  fixation rate to photosynthate accumulation rate for species  $i$ .

The last three producer system variables are the belowground (i.e., top 20 cm of soil) live plant biomass,  $B_l$ , the biomass of plant standing dead,  $A_d$ , and the biomass of plant litter,  $L_t$ . These last three variables are totals for all plant functional groups represented because species separation was not done (1970 field season) in the collection of field data on them. The rates of change for these variables are given in the model by the following three differential equations.

$$\dot{B}_l = \sum_{i=1}^4 bt_i - (db + rb \cdot B_l + hb) \quad (5.2)$$

$$\dot{A}_d = \sum_{i=1}^4 da_i - (sa \cdot A_d + hs) \quad (5.3)$$

$$\dot{L}_t = sa \cdot A_d - (hl + hm + lc \cdot L_t) \quad (5.4)$$

There are several intermediate system variables in these equations. The respiration rate of belowground plant parts is  $rb$ ;  $hb$ ,  $hs$ , and  $hl$  are the harvest rates by macroconsumers (as opposed to microbial harvest) of belowground, aboveground standing dead, and litter biomasses, respectively. The rate of shattering of plant standing dead material is  $sa$ , and  $lc$  is the rate of leaching of plant litter into the soil. The microbial harvest rate of plant litter is  $hm$ . All these rates are given in grams per square centimeter per second [ $gm/(cm^2 \cdot sec)$ ] or  $(sec)^{-1}$  if the ISV is multiplied by a biomass density.

The mechanisms used to represent each of these processes in the model will be discussed in the following sections.

## 5.2 Intermediate System Variables

The rate of net photosynthesis in this model is based on a graph of a generalized photosynthesis function given by Gates (1968). Photosynthesis (per unit leaf area) depends, in his work, on canopy temperature and intensity of photosynthetically active radiation. Qualitative curves are given by Gates for relative net photosynthesis as a function of these two abiotic variables. Equation 5.5 is an algebraic translation of the general shape of the curves as given by Gates. Fig. 5.1 is a graph of equation 5.5. The function gives net photosynthesis, and thus may be negative under environmental conditions in which respiration exceeds gross photosynthesis. A moisture stress and nutrient stress index,  $ms_i$  and  $ns_i$ , respectively, were added to include stresses specifically due to soil moisture and nutrient deficiencies. These ISV's are discussed below. Their functional range is from zero to one. Since Gate's curve is given for a unit leaf area, the leaf area index,  $la_i$ , is used to convert to a soil surface basis. The ISV,  $cr_i$ , fractional cover, takes into account the fact that the ground is not uniformly covered with vegetation of group  $i$ .

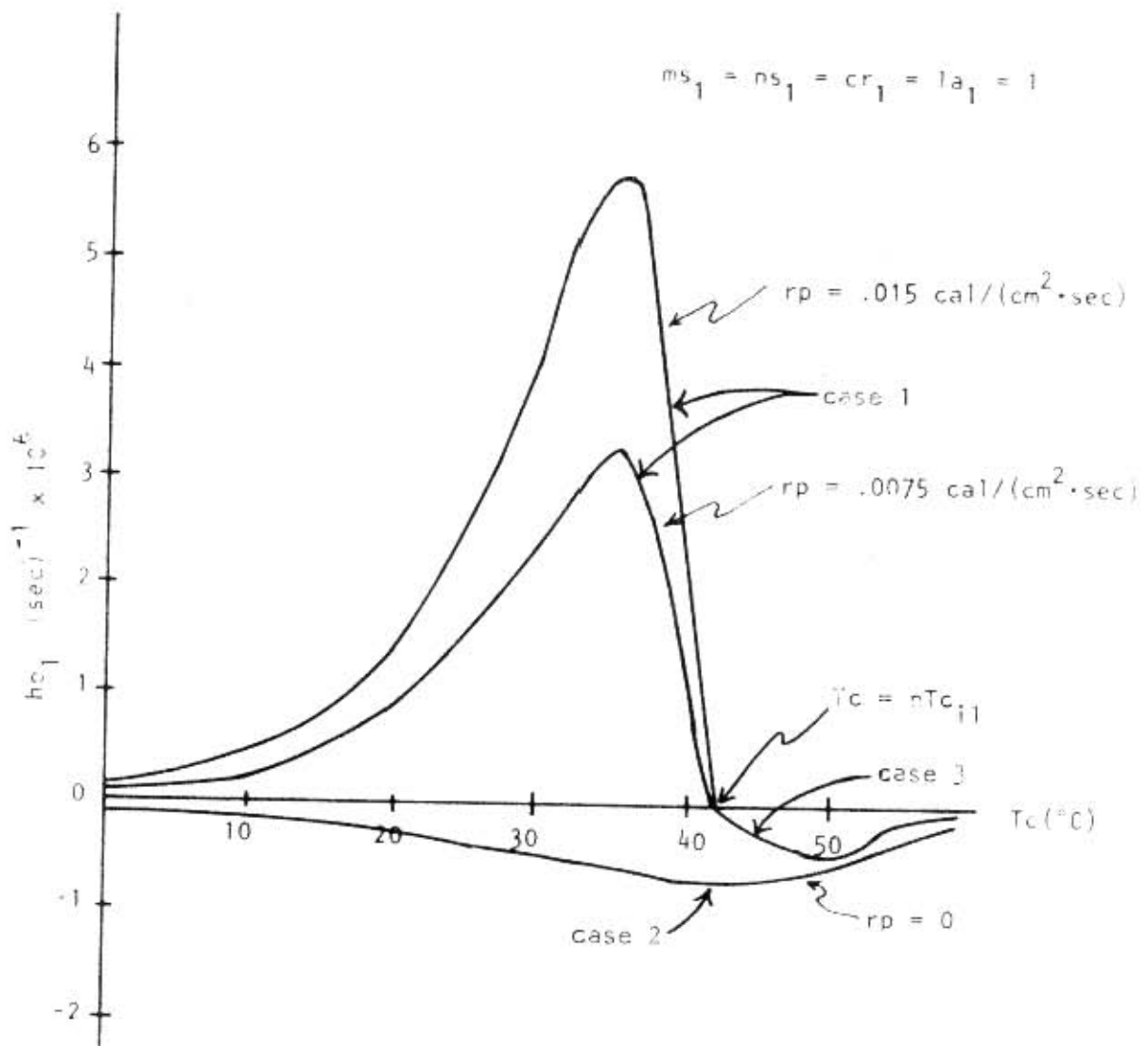


Fig. 5.1. Net photosynthesis ( $hp_1$ ) vs. canopy temperature ( $T_c$ ) for warm season grasses.

$$\begin{aligned}
 & ms_i \cdot ns_i \cdot cr_i \cdot la_i \cdot php_{i1} \left[ \frac{php_{i2} \cdot rp}{(1 + php_{i2} \cdot rp)} - \frac{php_{i2} \cdot prp_{2i}}{(1 + php_{i2} \cdot prp_{2i})} \right] \\
 & \quad \cdot [(pTc_{i1} - Tc) \exp(-php_{i3} [pTc_{i1} - Tc])] \\
 & \quad \text{if } rp > prp_{2i} \text{ and } (0 < Tc < pTc_{i1}) \quad [\text{case 1}] \\
 \hline
 & -ms_i \cdot ns_i \cdot cr_i \cdot la_i \cdot php_{i4} \left[ \frac{(prp_{2i} - rp)}{prp_{2i}} \right] \left( \frac{Tc}{pTc_{i2}} \right)^{php_{i5}} \\
 & \quad \exp \left\{ \left( \frac{php_{i5}}{php_{i6}} \right) \left[ 1 - \left( \frac{Tc}{pTc_{i2}} \right)^{php_{i6}} \right] \right\} \quad (5.5) \\
 & \quad \text{if } rp < prp_{2i} \text{ and } Tc > 0 \quad [\text{case 2}] \\
 \hline
 & -ms_i \cdot ns_i \cdot cr_i \cdot php_{i7} [(Tc - pTc_{i1}) \exp(-php_{i8} (Tc - pTc_{i1}))] \\
 & \quad \text{if } rp > prp_{2i} \text{ and } Tc > pTc_{i1} \quad [\text{case 3}] \\
 \hline
 & 0 \quad \text{if } Tc \leq 0 \quad [\text{case 4}]
 \end{aligned}$$

The four cases in equation (5.5) correspond to a categorization of the sunlight and canopy temperature status. Case 1 is for normal daytime and moderate temperatures; case 2 is for low sunlight or darkness and moderate temperatures; case 3 is for excessively high temperature with normal daylight; and case 4 is for freezing temperatures. Fig. 5.1 has the corresponding curves marked. This mechanism is also explained in Bledsoe and Jameson (1969).



The parameters in equation (5.5) consist of unit interchange and scaling coefficients and three threshold values (compensation points) for temperature and sunlight ( $prp_{2i}$ ,  $pTc_{i1}$ , and  $pTc_{i2}$ ). The compensation point for a variable is the level of that variable at which gross photosynthesis exactly equals respiration, giving a net photosynthesis rate of zero.  $Tc$  denotes canopy temperature (see above, section 4) and  $rp$  denotes photosynthetically active radiation. Percent cover and leaf area index were taken as unity for the results given in Appendix E, except for *Opuntia* where  $la_4 = .15$ .

The ISV  $rp$ , photosynthetically active radiation, is calculated solely as a function of the driving variable solar radiation,  $z_1$ . The idea is that the geometry of the grass leaves is such that a greater amount of radiation will be intercepted per unit soil surface than a horizontal plane would intercept for the solar position at other than the zenith. The driving variable  $z_1$  describes the positive portion of a sine curve during the daylight hours. However,  $rp$  will describe a curve given by a fractional power of a sine curve as shown in equation 5.6 and Fig. 5.2. This mechanism is explained in Bledsoe and Jameson (1969).

$$rp = pz_1 \cdot \left(\frac{z_1}{pz_1}\right)^{prp_1} \quad (5.6)$$

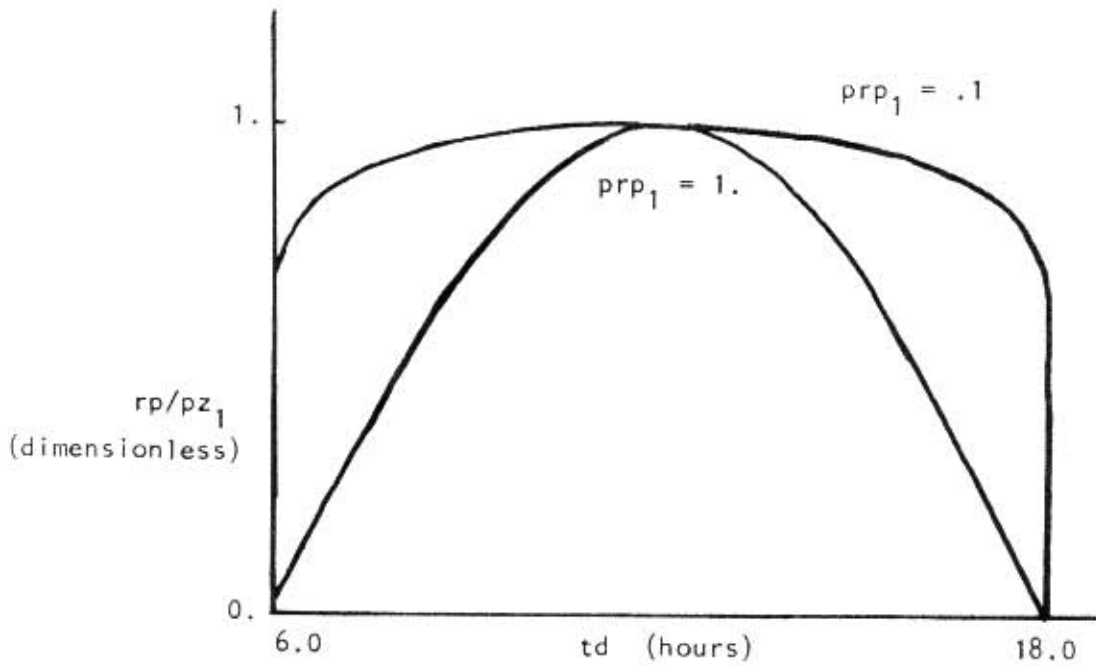


Fig. 5.2. Relative photosynthetically active radiation ( $rp/pz_1$ ) as a function of time of day ( $td$ ).

Growth response by the  $i$ th plant group to moisture stress is given by  $ms_i$ , which is a function of the soil moisture by volume,  $Ms$ . It is formulated to imitate the growth response which might be observed as a function of soil moisture tension which would vary in soils of different types with a given volume fraction of water. It is also designed to take into account differential plant tolerances to high moisture tension. The

formulation is designed to exhibit a semi-threshold response of varying degrees of sharpness. Equation 5.7 and 5.8 and Fig. 5.3 show the mechanism.

$$ms_i = at(pms_{i2}, pms_{i1}, fw) \quad (5.7)$$

where

$$fw = \frac{\left(\frac{Ms}{20}\right)}{1.4} \quad (5.8)$$

the ISV, fw, is soil moisture converted to fraction by weight (in top 20 cm of soil) assuming a bulk density of 1.4. The function (ISV) at( $x_1, x_2, x_3$ ) gives an arc tangent response to its independent variable as follows.

$$at(x_1, x_2, x_3) = \left(\frac{1}{\pi}\right) \tan^{-1}[c_1(x_3 - x_1)] + .5 \quad (5.9)$$

$$c_1 = \tan\left(.4 \cdot \frac{\pi}{x_2}\right) \quad (5.10)$$

This ISV is a mechanism for calculating an index between zero and one which is dependent upon a semi-threshold effect utilizing an arc tangent function. Notice that the function is designed so that if the first argument,  $x_1$ , is the inflection point, the second argument,  $x_2$ , is a measure of spread or the distance from the inflection point to accomplish a rise of the index from .5 to .9, then the third argument is the variable for which the index is to be computed.

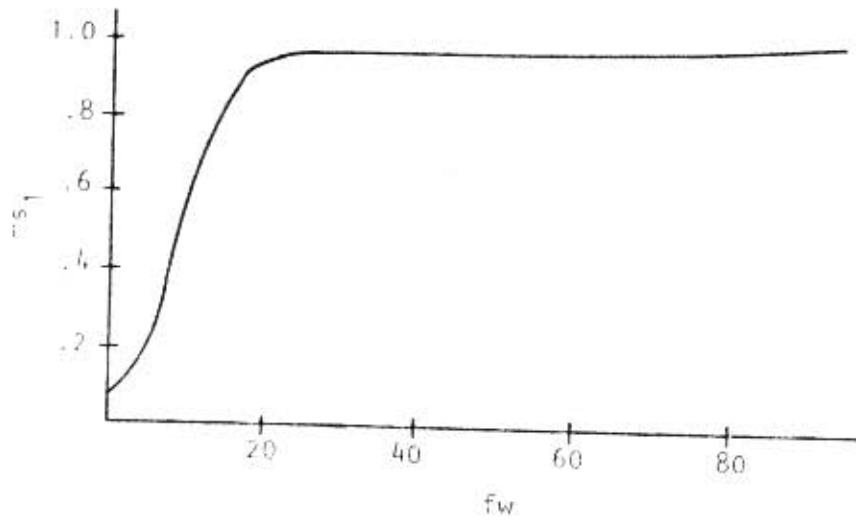


Fig. 5.3. Moisture stress index ( $ms_1$ ) for the warm season grasses as a function of percent soil moisture by weight ( $fw$ ) in the top 20 cm of soil.

The nutrient stress index,  $ns_i$ , also utilizes the arc tangent relation with a weighted sum of decomposer PSV's as its argument. Details of this ISV are given in section 7.

The respiration of belowground plant parts,  $rb$ , is assumed to be a function of soil temperature. Fig. 5.4 shows this relationship which is formulated in equation (5.10).

$$rb = \begin{cases} prb_1(44 - Ts)\exp\left\{\frac{-(44 - Ts)}{8}\right\} & \text{if } Ts \leq 44 \\ 0 & \text{otherwise} \end{cases} \quad (5.11)$$

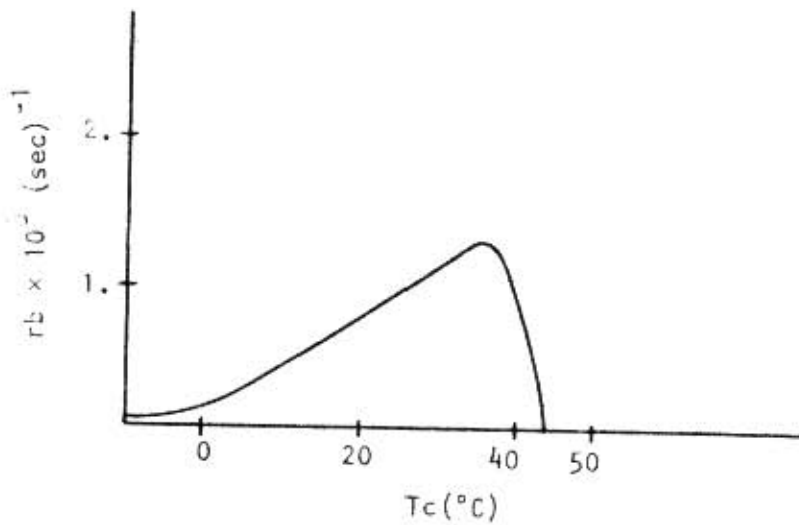


Fig. 5.4. Rate of respiration of belowground plant parts ( $r_b$ ) vs. soil temperature ( $T_c$ ).

It is assumed that  $36^\circ$  is a temperature value above which the belowground plant respiration decreases precipitously. The rate,  $r_b$ , is given in  $\text{g}/(\text{cm}^2 \cdot \text{sec})$  per  $\text{g}/\text{cm}^2$  of belowground live plant material (thus  $r_b$  has units  $\text{sec}^{-1}$ ). The maximum respiration rate under this assumption is about 5% of the mean root biomass ( $10^4 \text{ g}/\text{cm}^2$ ) per day.

The death rate of belowground plant material,  $db$ , is taken to be half the respiration rate as an initial assumption.

$$db = \frac{r_b}{2} \tag{5.12}$$

This rate is in  $\text{g}/(\text{cm}^2 \cdot \text{sec})$  per  $\text{g}/\text{cm}^2$  of belowground live plant tissue.

The ISV,  $da_i$ , death rate of aboveground parts, is calculated as a function of the moisture stress index,  $ms_i$ , and the canopy temperature,  $T_c$ , as in equation 5.11.

$$da_i = (1 - ms_i)pda_{i1} \cdot at(pda_{i3}, pda_{i2}, T_c) \cdot Al_i \quad (5.13)$$

Fig. 5.5 shows  $da_1$  as a function of canopy temperature for limiting soil moisture ( $ms_1 = 0.$ ). For higher levels of soil moisture the curve would have similar shapes but proportionally lower values.

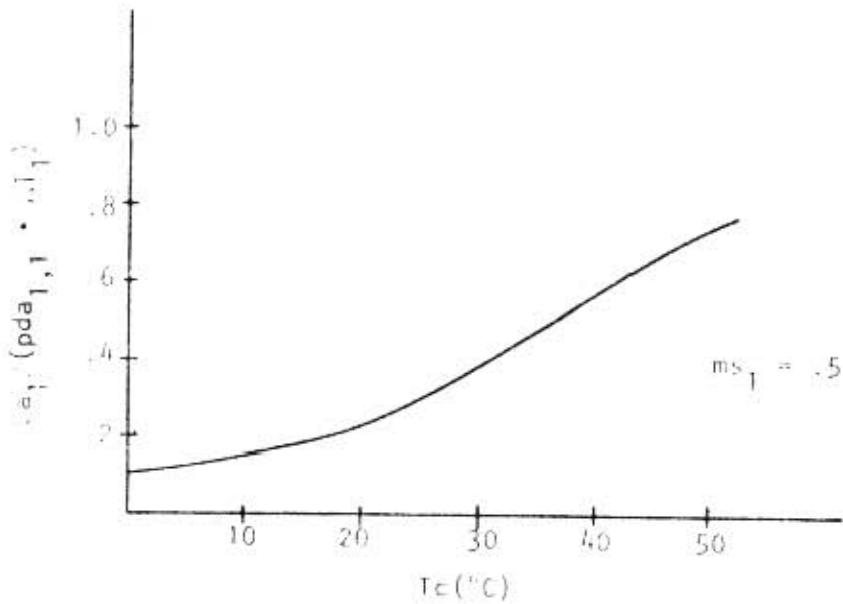


Fig. 5.5. Death rate of warm season grasses ( $Al_1$ ) as a function of canopy temperature ( $T_c$ ).

The translocation from above- to belowground plant parts,  $bt_i$ , is given in this model as a function of both the above- and belowground plant biomasses. The total specific aboveground plant biomass is denoted by  $ab$ , and is equal to the sum over  $i$  of  $A1_i$ . Then the translocation rate in  $g/(cm^2 \cdot sec)$  is given in equation (5.13).

$$bt_i = ms_i \cdot \begin{cases} 0. & \text{if } Ts \leq 0 \\ \text{-----} \\ \max[0., (pbt_{i1} - pbt_{i2} \cdot bl_i) A1_i] & \text{if } (A1_i > pbt_{i3}) \text{ and } (Ts > 0) \\ \text{-----} \\ -\min[0., pbt_{i4}(bl_i - pbt_{i5})] & \text{if } (A1_i \leq pbt_{i3}) \text{ and } (Ts > 0) \end{cases} \quad (5.14)$$

where

$$bl_i = B1 \cdot \frac{A1_i}{ab} \quad (5.15)$$

and

$$ab = \sum_{i=1}^4 A1_i \quad (5.16)$$

This appears graphed in Fig. 5.6. The ISV  $bl_i$  is a device for estimation of the belowground biomass plant group. Since only the total belowground plant biomass is known ( $B1$ ), it is assumed that the belowground plant parts are in the same ratio as aboveground parts.

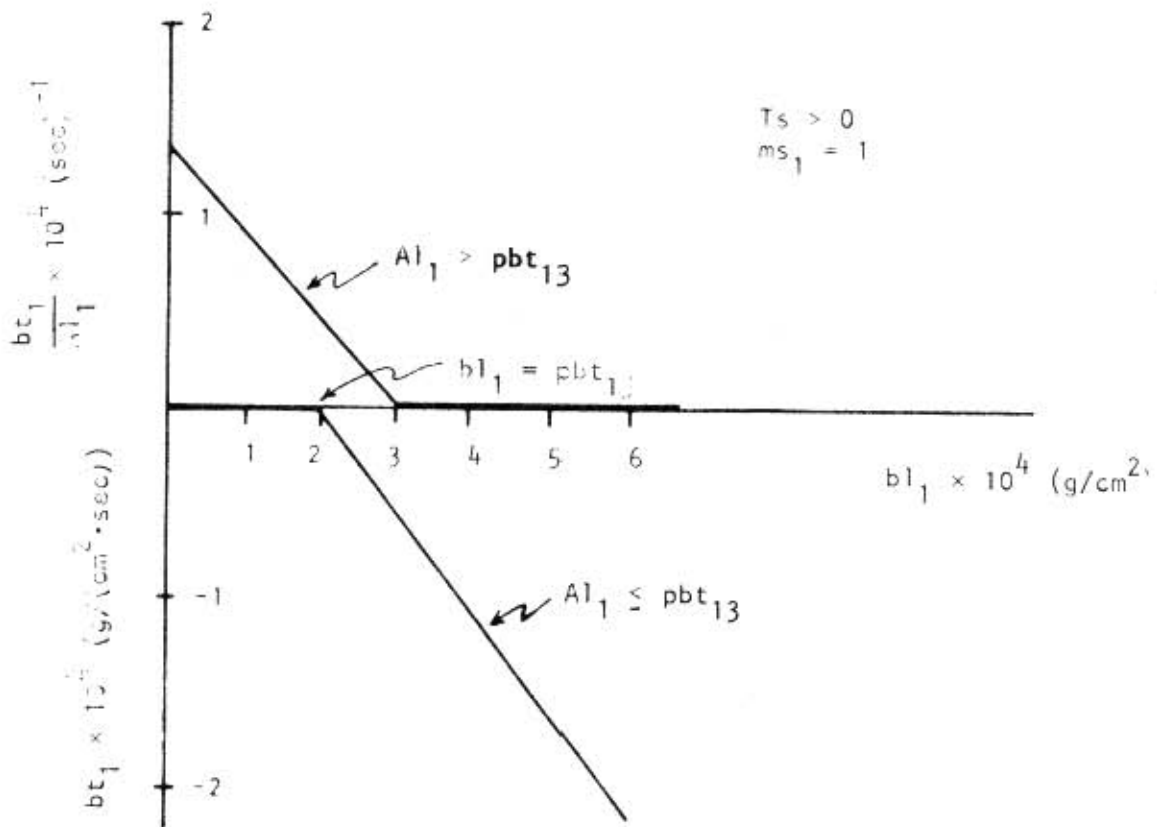


Fig. 5.6. Translocation ( $bt_i$ ) of photosynthate from aboveground to below-ground plant parts for warm season grasses. In this graph,  $pbt_{i1}$ ,  $pbt_{i5}$  have values  $1.3 \times 10^{-4}$ ,  $.43 \times 10^{-4}$ ,  $3.0 \times 10^{-4}$ ,  $.27 \times 10^{-4}$ , and  $2 \times 10^{-4}$ , respectively.

The shatter rate,  $sa$ , is given as a piecewise linear function of wind speed. For wind speed less than 5 mph (223.5 cm/sec) the shatter rate is constant at  $.005(\text{sec})^{-1}$ . Above this wind speed the shatter rate increases linearly.



$$sa = \begin{cases} .005 & \text{if } z_4 \leq 223.5 \text{ cm/sec} \\ (.005 + 2.21 \cdot 10^{-4} \cdot z_4) & \text{if } z_4 > 223.5 \end{cases} \quad (5.17)$$

The values used are based on an assumed shatter rate of .5% per day with a 5 mph wind. The shatter rate is graphed in Fig. 5.7.

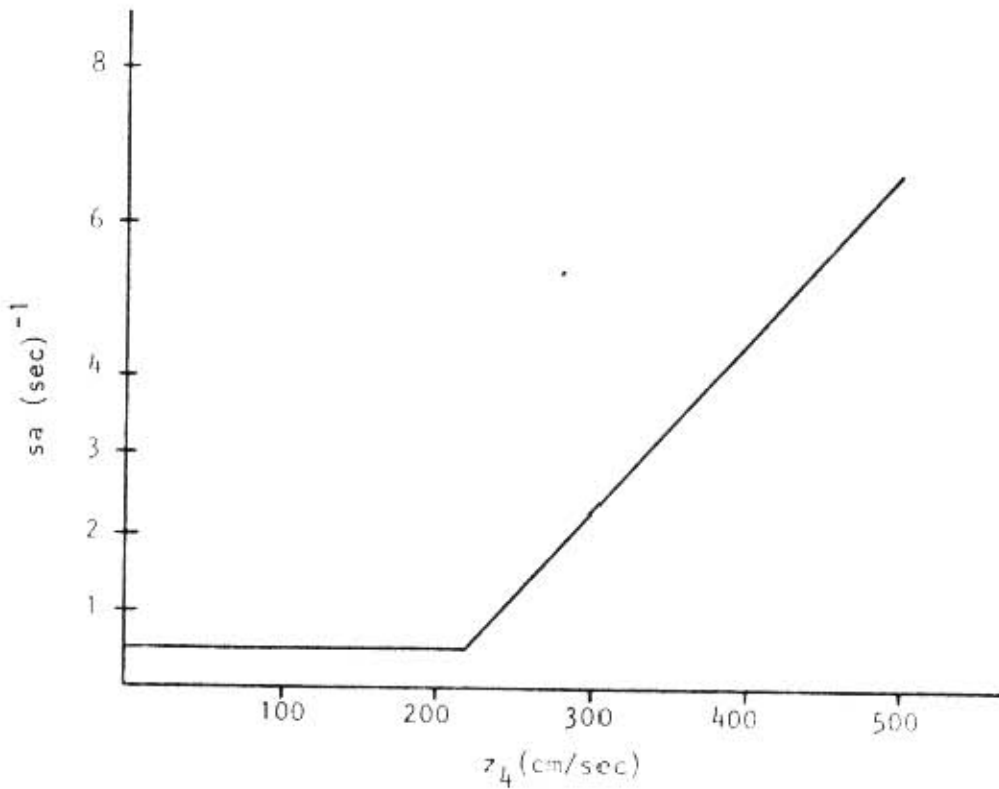


Fig. 5.7. Shatter rate of standing dead plant material ( $sa$ ) as a function of wind speed.

The leaching rate,  $l_c$ , is assumed to depend on the precipitation rate.

$$l_c = .035 \cdot z_2 \quad (5.18)$$

where  $z_2$  is the precipitation rate in  $g/(cm^2 \cdot sec)$ . A graph of  $l_c$  vs.  $z_2$  appears in Fig. 5.8. (A rainfall rate of  $5 \times 10^{-5}$  cm/sec corresponds to a rain of about 1 cm/day.)

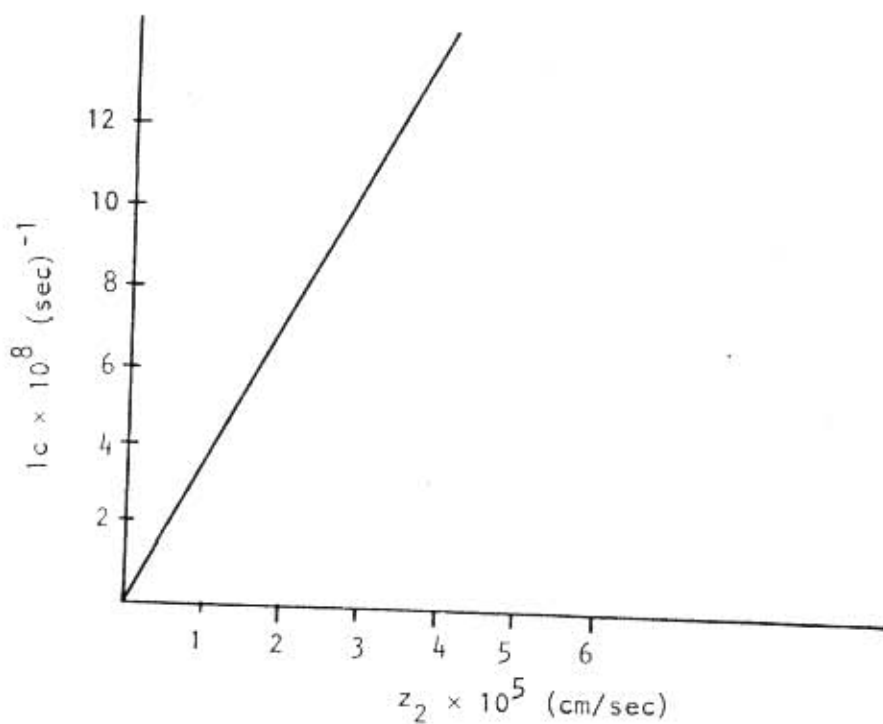


Fig. 5.8. Leaching rate of plant litter,  $l_c$ , into soil organic matter as a function of precipitation ( $z_2$ ). The leaching rate with .5 cm rain in a day would be about .5% per day of the total litter biomass. Harder rains would give proportionately more leaching.

Appendix B contains a summary of parameter definitions; Appendix E contains typical solution curves; parameter values are given in Appendix D.

### 5.3 Future Expansion

The possible areas for modification and expansion are so numerous that only a cursory catalog of the most obvious will be attempted. The first modifications will probably involve redefinition of the PSV's so that the major plant species have their own functional group. The belowground and dead biomasses will probably also be subdivided by functional group. A dead root compartment might be added. Separate PSV's for reproductive parts of plants might be added. Additional ISV's will include a microbial harvest term to account for in situ decay from each PSV, a trampling loss term for all above-ground biomasses, and a shattering term for live plants.

Modifications of the formulation of ISV's might include addition of the photosynthesis rate as an argument of the translocation function, as indicated by an experimental project in the Botany Department of the University of Wyoming. Belowground respiration might be made a function of other soil variables than temperature; photosynthesis might be broken into gross photosynthesis minus respiration; an actual soil moisture tension ISV might be added; shatter rates might be made to depend on snow cover and storm intensities; leaf area index should be made a function of solar angle and biomass density with concomitant changes in photosynthetically active radiation; aboveground death rate might be modified to consider phenological data; leaching rates should consider the previous occurrences of rainfall; nutrient and moisture stress indices should be formulated to give more specific responses than a simple reduction in rate of occurrence of physiological

functions; nutrient stress should give differential responses for shortage to different nutrient forms; allowances should be made for soil toxicities, such as salinity. Obviously, this list could be extended. The modification plan, as explained in section 2, will involve the gradual inclusion of the above factors rather than an attempt to rewrite the entire section and include everything. The decision as to what changes to make first will be a difficult one and the choice will necessarily be arbitrary sometimes.

For a longer view, the model will need to be a spatial rather than point system. The ISV,  $cr_i$ , percent cover of the  $i$ th plant group contains the beginnings of this extension. Currently,  $cr_i$  has a constant value and properly should be renamed as a parameter. Changing  $cr_i$  to a PSV and representing it by a differential equation will allow spatial growth of plant groups. Constraints can be placed on the sum of the  $cr_i$  values so that they do not exceed 100% cover. Some mechanisms of this type can be found in Clymer and Bledsoe (1970). The spatial model can be made more realistic by superimposing it on the plant communities of a fine scale vegetation map of an experimental area. Such maps have been and are being produced for various areas at the Pawnee Site by members of the Range Management Department of the University of Wyoming.

## 6. CONSUMER VARIABLES

### 6.1 Principal System Variables

The biomass density of seven functional groups is represented in the consumer section of the total ecosystem model. Associated with each of the first five functional groups (live material) is the name of a representative species in that group, as shown in Table 6.1.

The units for variables in the consumer section differ slightly from other sections of the model in that a "day" rather than a "second" is the basic time unit. The computer implementation allows for this by multiplying all derivatives calculated by the number of days/second  $(.864 \cdot 10^5)^{-1}$ . Similarly, harvest rates calculated in other program sections and supplied to the consumer section are multiplied by  $.864 \cdot 10^5$ .

Let

$N_i$  = density of individuals in group  $i$   $(\text{cm}^2)^{-1}$

$W_i$  = average weight of an individual in group  $i$  (g)

$C_i$  = biomass density of group  $i$   $(\text{g}/\text{cm}^2)$

Then in order to compute the biomass of the first five functional groups, representing live biomass, at any time, differential equations are solved for  $N_i$  and  $W_i$ . Then the algebraic formulation in equation (6.1) gives total biomass densities.

$$C_i = N_i W_i; \quad i = 1, \dots, 5 \quad (6.1)$$

Table 6.1. Consumer functional groups.

Functional Group	Representative Species	Population Numbers	Avg. Weight	Biomass
Primary consumer-- wild	Black-tailed jackrabbit	$N_1$	$W_1$	$C_1$
Primary consumer-- domestic	Cow	$N_2$	$W_2$	$C_2$
Secondary consumer	Coyote	$N_3$	$W_3$	$C_3$
Omnivore-- migratory	Lark bunting	$N_4$	$W_4$	$C_4$
Insect	Grasshopper	$N_5$	$W_5$	$C_5$
Total animal feces	--	--	--	Fe
Total animal dead material	--	--	--	Cd

The differential equation for the rate of change of animal density with respect to time is written in the following form:

$$\dot{N}_i = N_i [nb_i - nd_i] - \frac{ha_{i+7}}{W_i} + im_i - em_i; \quad i = 1, \dots, 5 \quad (6.2)$$

where

$nb_i$  = instantaneous birth rate of consumer group  $i$  (day)<sup>-1</sup>

$nd_i$  = instantaneous natural mortality rate of consumer group  $i$  (day)<sup>-1</sup>

$ha_{i+7}$  = harvest rate (g/(cm<sup>2</sup>·day)) of consumer group  $i$  (in terms of biomass density)

$im_i$  = immigration rate of consumer group  $i$  (cm<sup>2</sup>·day)<sup>-1</sup>

$em_i$  = emigration rate of consumer group  $i$  (cm<sup>2</sup>·day)<sup>-1</sup>

Thus, the number of individuals in consumer group  $i$  is increased by birth and immigration and is decreased by natural mortality, harvest (predation), and emigration. In this model, all of the above mentioned rates are assumed to be functions of time only and are not influenced by such factors as the numbers of individuals in other consumer functional groups or the biomass composition of the various primary producer functional groups. This simplification was for the priority reasons mentioned in other sections and at the beginning of the report.

The differential equation for the rate of change of the average weight of an individual in consumer group  $i$  is written in the following form:

$$\dot{W}_i = W_i \cdot as_i \cdot fc_i - re_i; \quad i = 1, \dots, 5 \quad (6.3)$$

where

$as_i$  = assimilation efficiency of the food ingested by an individual  
in consumer group  $i$

$fc_i$  = food intake rate (day)<sup>-1</sup> for an individual in consumer group  $i$

$re_i$  = respiration rate (g/day) for an individual in consumer group  $i$

The differential equation for the rate of change of the biomass of animal feces with respect to time is written in the following form:

$$\dot{F}_e = \left[ \sum_{i=1}^5 C_i (1 - as_i) fc_i \right] - ha_{13} \quad (6.4)$$

where

$ha_{13}$  = harvest rate (g/(cm<sup>2</sup>·day)) of animal feces.

Thus, the animal feces compartment is simply an accumulation of material ingested but not assimilated by the five consumer groups.

The differential equation for the rate of change of animal dead material with respect to time is written as

$$\dot{C}_d = \left[ \sum_{i=1}^5 C_i \cdot nd_i \right] - ha_{14} \quad (6.5)$$

where

$ha_{14}$  = harvest rate (g/(cm<sup>2</sup>·day)) of animal dead material.

Thus, the animal dead compartment is simply an accumulation of the biomass of the animals dying from natural causes (non-predation) in the five consumer groups.



## 6.2 Intermediate System Variables

*Birth, death, immigration, emigration.* The instantaneous birth rates ( $nb_i$ ), natural mortality rates ( $nd_i$ ), immigration rates ( $im_i$ ), and emigration rates ( $em_i$ ) are determined for the first five consumer groups in the following manner. Note that immigration and emigration are modelled only in consumer group 4 (birds), i.e.,  $im_i = em_i = 0$  for  $i = 1, \dots, 5$ , except  $i \neq 4$ .

- i. The percent of functional group 1 (primary consumer--wild) reproducing during the year decreases linearly from 100% at day 58 (start of the breeding season for a 365-day year) to 10% at the end of the breeding season. This mechanism is to lump all restrictions on breeding (e.g., sex ratio, fecundity) into a single factor. The instantaneous natural mortality rate is restricted so that a net increase in the population size occurs from day 58 to day 210, and a net decrease in the population size occurs after day 210. The reason for changing (decreasing) the proportion of the population reproducing during the breeding season is that young individuals recruited into the population due to birth do not reproduce.

Thus,

$$nb_1 = \begin{cases} 0 & \text{if } (tdm < 58) \text{ or } (tdm > 252) \\ .007[1 - .0046(tdm - 58)] & \text{if } 58 \leq tdm \leq 252 \end{cases} \quad (6.6)$$

$$nd_1 = .0022 \quad (6.7)$$

- ii. Consumer group 2 (primary consumer--domestic) is kept at a fixed density, as if stocking rates were not changed and animals neither died nor gave birth on the range.

$$nb_2 = nd_2 = 0 \quad (6.8)$$

- iii. Due to a lack of information on secondary consumer population dynamics, consumer group 3 is kept at a fixed density, representing an estimated average value.

$$nb_3 = nd_3 = 0 \quad (6.9)$$

- iv. The birth, natural mortality, immigration, and emigration rates of consumer group 4 (birds) mimic those simulated by Swartzman (1969) for lark buntings in Technical Report No. 3. Thus, hatching occurs during weeks 23, 24, 27, and 28. Birds immigrate at a rate of 26 birds/100 ha/day during weeks 17 and 18 (days 113 through 126) and emigrate at a rate of 21 birds/100 ha/day after week 31 (day 218).

Thus,

$$nb_4 = \begin{cases} .0308 & \text{if } 155 \leq tdm \leq 168 \\ .0102 & \text{if } 190 \leq tdm \leq 203 \\ 0 & \text{otherwise} \end{cases} \quad (6.10)$$

$$nd_4 = \begin{cases} .0021 & \text{if } tdm \leq 154 \\ .0035 & \text{if } tdm > 154 \end{cases} \quad (6.11)$$

$$im_4 = \begin{cases} .26 \cdot 10^{-8} & \text{if } 113 \leq tdm \leq 126 \\ 0 & \text{otherwise} \end{cases} \quad (6.12)$$

$$em_4 = \begin{cases} .21 \cdot 10^{-8} & \text{if } 218 \leq tdm \leq 235 \\ 0 & \text{otherwise} \end{cases} \quad (6.13)$$

- v. The percent of consumer group 5 (insects) reproducing during the year decreases linearly from 100% at day 162 (start of the breeding season) to 10% at day 224 (end of the breeding season). Natural mortality occurs at a constant instantaneous rate from day 162 to 259. The instantaneous natural mortality rate is restricted so that a net increase in the population size occurs from day 162 to day 208, and a net decrease in the population size occurs after day 208 and until day 259. This information was modified from preliminary reports of grasshopper population data taken by Biology Department personnel at the University of Colorado, Colorado Springs campus.

Thus,

$$nb_5 = \begin{cases} .0214[1 - .0145(tdm - 162)] & \text{if } 162 \leq tdm \leq 224 \\ 0 & \text{otherwise} \end{cases} \quad (6.14)$$

$$nd_5 = \begin{cases} .0071 & \text{if } 162 \leq tdm \leq 259 \\ 0 & \text{otherwise} \end{cases} \quad (6.15)$$

*Enumeration of food sources.* In order for computations of the above rates to be made, all possible sources of food for any consumer group must be enumerated. These sources of food are referred to as consumed groups and are listed in Table 6.2.

The first seven consumed groups refer to the seven principal system variables in the producer section of the model, and the last five consumed groups refer to the first five principal system variables in the consumer section of the model. Let  $cb_j$  = biomass of consumed group  $j$ ;  $j = 1, \dots, 12$ . Thus,  $cb_8 = C_1$ ,  $cb_5 = B1$ , etc.

In general, when a variable or parameter must be subscripted doubly to refer both to a consumer group and a consumed group, the first subscript will denote the consumer and the second will denote the consumed group.

*Food intake rates.* Ingestion involves calculation of two basic quantities relating to the quantity and quality of food eaten. The two basic ISV's are food intake,  $fc_i$ , and food preference,  $fp_{ij}$ , where  $i$  indicates the consumer group and  $j$  indicates the consumed group. We will treat these two interrelated quantities next.

The food intake rate ( $fc_i$ ) for consumer group  $i$ , at any time, is controlled by two factors:

- i. The average weight ( $w_i$ ) of an individual in that group, and
- ii. The amount of available food.

Let

$pfc_{i1}$  = food intake rate (day)<sup>-1</sup> for consumer group  $i$  under  
ideal food availability conditions

Table 6.2. Numbering of biomass PSV's for purposes of consumer section.

Index (j) of Consumed Group	Functional Name	PSV
1	Warm season grass	Al <sub>1</sub>
2	Cool season grass	Al <sub>2</sub>
3	Forb	Al <sub>3</sub>
4	Cactus	Al <sub>4</sub>
5	Belowground plant parts	Bl
6	Standing dead (plant)	Ad
7	Litter	Lt
-----		
8	Primary consumer--wild	C <sub>1</sub>
9	Primary consumer--domestic	C <sub>2</sub>
10	Secondary consumer	C <sub>3</sub>
11	Bird	C <sub>4</sub>
12	Insect	C <sub>5</sub>

$mp_i$  = index of most preferred food source for consumer group  
i under ideal food availability conditions

The former is an input parameter to the model; the latter is a model ISV which is explained below.  $mp_i$  is used to indicate an element of the array  $[cb_j]$ ; thus it must be equated to a subscript.

The food intake rate ( $fc_i$ ) for consumer group i, at a particular time, will be less than  $pfc_{i1}$  if any of the following conditions occur:

- i. The average weight of an individual in consumer group i ( $w_i$ ) is above a threshold weight ( $pdl_{i1}$ ) for that group. Thus, if an individual gets too heavy, it consumes less food than normal and its weight is consequently reduced to within a specified range.
- ii. The biomass of the most preferred source of food (consumed group k) under ideal food availability conditions, ( $cb_k$ ), drops below a threshold ( $pb_{1k}$ ). Thus, the biomass of the most preferred source of food has a direct effect on the amount of food consumed by a particular consumer group. The food intake rate for consumer group i ( $fc_i$ ) will be greater than  $pfc_{i1}$  if the average weight ( $w_i$ ) of an individual in consumer group i is below a second threshold weight ( $pwl_i$ ) for that group, and more food is available for consumption. Thus, if an individual gets too light, it will consume more food, if available, than normal and its weight will increase to within a specified range.

Thus, if

$$\begin{aligned} k &= \text{most preferred source of food for consumer species } i \\ &= mp_i \end{aligned}$$

$$d1_i = \begin{cases} pfc_{i1} \left( \frac{pdl_{i1}}{W_i} \right); & W_i > pdl_{i1} \\ pfc_{i1}; & pdl_{i2} \leq W_i \leq pdl_{i1} \\ pfc_{i1} \left( \frac{pdl_{i2}}{W_i} \right); & W_i < pdl_{i2} \end{cases} \quad (6.16)$$

= dummy food intake variable

$$fc_i = \begin{cases} d1_i; & cb_k > pfc_{i2k} \\ d1_i \left( \frac{cb_k}{pfc_{i2k}} \right); & pfc_{i3k} \leq cb_k \leq pfc_{i2k} \\ d1_i \left( \frac{pfc_{i3k}}{pfc_{i2k}} \right); & cb_k < pfc_{i3k} \end{cases} \quad (6.17)$$

$pfc_{i3k}$  is a threshold which is explained in the next section.

The selection of the qualitative aspects of the diet, or functional groups consumed, are described below.

Let

$pfp_{ij}$  = amount of the diet of consumer species  $i$  made up of consumed species  $j$  under ideal food availability conditions

Then

$k = j$  such that  $pmp_{ij} = \max\{pmp_{ij}; j = 1, \dots, 12\}$

Then

i. If the biomass of any consumed species  $j$  ( $cb_j$ ) is below a fixed

threshold ( $pf_{i3k}$ ), that consumed species is eliminated from the diet of all consumer species.

- ii. If the biomass of the most preferred source of food ( $k$ ) is below a fixed threshold ( $pf_{i2k}$ ), then the amount of the diet of consumer species  $i$  made up of consumed species  $k$  is reduced from what it would be under ideal food availability conditions.

Thus,

$$d_{ik}^2 = \begin{cases} pfp_{ik}; & cb_k > pf_{i2k} \\ pfp_{ik} \left( \frac{cb_k}{pf_{i3k}} \right); & pf_{i3k} \leq cb_k \leq pf_{i2k} \\ 0; & cb_k < pf_{i3k} \end{cases} \quad (6.18)$$

= dummy food preference factor

$$d_{ij}^2 = \begin{cases} pfp_{ij}; & cb_j \geq pf_{i3j} \\ 0; & cb_j < pf_{i3j} \end{cases} \quad j \neq k \quad (6.19)$$

Finally, we normalize the proportions of consumed material,

$$fp_{ij} = \frac{d_{ij}^2}{\sum_{j=1}^n d_{ij}^2}, \quad (6.20)$$



So that

$$\sum_{j=1}^{12} fp_{ij} = 1.0. \tag{6.21}$$

The use of  $fp_{ij}$  in formulating differential equations for the PSV's comes in calculating the harvest ISV's. If  $ha_j$  is the harvest of the  $j$ th biomass group, then we have

$$ha_j = \sum_{i=1}^5 hp_{ij} \tag{6.22}$$

$$\text{where } hp_{ij} = fc_i \cdot fp_{ij} \cdot C_i \tag{6.23}$$

Table 6.3 gives typical values for  $hp_{ij}$  corresponding to the simulation run explained in section 6.3.

Example

We shall calculate food preference and food consumption variables for consumer group 1 (Black-tailed jackrabbit) as an example.

i.  $pf_{c_1} = .200\text{g/g body weight/day}$

j	pfp(1,j)
1	.05
2	.12
3	.70
4	.07
5	0.0
6	.059
7	.001
8	0.0
9	0.0
10	0.0
11	0.0
12	0.0

Table 6.3. Typical harvest rate values using parameters of Table 6.5  
[g/(cm<sup>2</sup>·day)].

hp <sub>ij</sub>	j											
	1	2	3	4	5	6	7	8	9	10	11	12
1	.134E-5	.321E-5	-	.187E-5	-	.158E-5	.241E-7	-	-	-	-	-
2	.132E-5	.132E-5	-	.783E-7	-	.156E-6	.232E-7	-	-	-	-	-
i 3	-	-	-	-	-	-	-	.153E-8	-	-	.900E-10	.180E-8
4	-	-	-	-	-	-	-	-	-	-	-	.378E-9
5	.271E-5	.648E-5	-	.377E-5	-	.319E-5	.486E-7	-	-	-	-	-
ha <sub>j</sub>	.537E-5	.110E-4	-	.572E-5	-	.493E-5	.959E-7	.153E-8	-	-	.900E-10	.218E-8

Equating this notation to the notation of the producer section of the model:

$$ha_5 = hb$$

$$ha_6 = hs$$

$$ha_7 = hl$$

ii.  $k = 3$

Thus, under ideal food availability conditions, forbs make up 70% of the diet of black-tailed jackrabbits and are the most preferred source of food for that species.

iii. Assume  $W_1 = 75. \leq pd_{i2} = 100.$

Since the jackrabbit population is underweight, on the average, each individual will consume a larger than normal amount. Thus,

$$d_{1,1} = pfc_{11} \left( \frac{pd_{i2}}{W_1} \right) = (.200) \left( \frac{100.}{75.} \right) \\ = .267 \text{ g/g body weight/day}$$

iv. The only source of food  $j$  whose biomass is below  $pfc_{i3j}$  is consumed species 3. Thus,  $d_{2,1,3}$  is set equal to zero.

$j$	$d_{2,1j}$
1	.05
2	.12
3	0.0
4	.07
5	0.0
6	.059
7	.001
8	0.0
9	0.0
10	0.0
11	0.0
12	0.0

v.  $cb_3 = .100E-3 \leq pfc_{1,3,3} = .200E-3$

Since the primary source of food for black-tailed jackrabbits is

below both critical thresholds, the amount of food consumed by jackrabbits must now be reduced. Thus,

$$fc_1 = d1_1 \left( \frac{pfc_{i3,3}}{pfc_{i2,3}} \right) = (.267) \left( \frac{.200E-3}{.500E-3} \right)$$
$$= .107 \text{ g/g body weight/day}$$

Therefore, food consumption is ultimately reduced due to the inadequate supply of the primary source of food.

vi. The actual dietary composition is now computed.

j	$f_{p1j}$
1	.167
2	.400
3	0.0
4	.233
5	0.0
6	.197
7	.003
8	0.0
9	0.0
10	0.0
11	0.0
12	0.0

#### *Assimilation*

Each consumed group (j) is assumed to have a constant assimilation efficiency ( $pas_j$ ) regardless of the consumer group (as given in Table 6.2). Thus, for any consumer group, i, the assimilation efficiency ( $as_i$ ) of the food ingested at any time is simply the sum of the products of

the assimilation efficiencies of the consumed groups and the fraction of the diet made up of the consumed groups at that time.

Thus,

$$as_i = \sum_{j=1}^{12} pas_j \cdot fp_{ij}; \quad i = 1, \dots, 5 \quad (6.24)$$

Once the assimilation efficiencies have been computed, the food consumption rates can be calculated as

$$as_i \cdot fc_i \cdot W_i \quad .$$

Typical values are given in Table 6.4.

#### *Respiration*

The respiration equations are written in the following form:

$$re_i = pre_{i1} \cdot (W_i)^{pre_{i2}}, \quad i = 1, \dots, 5 \quad (6.25)$$

The form of the equation is mechanistic to the extent that it is thought that the rate of respiration (basal metabolism) for an animal is approximately proportional to the surface area of that animal. The parameters for the respiration equations are given below in Table 6.5.

An estimate of  $pre_{1,2}$  was taken from Hansen and Cavender (1970), of  $pre_{2,2}$  from Kleiber (1961), of  $pre_{4,2}$  from Swartzman (1970), and of  $pre_{5,2}$  from Wiegert (1965). The value of  $pre_{3,2}$  was guessed.

Table 6.4. Typical values of assimilation and intake rates.

$i$	$as_i$	$as_i \cdot fc_i \cdot W_i = \text{intake}$
1	.382	3.07
2	.389	5630
3	.938	1690
4	.776	3.72
5	.382	0.012

Table 6.5. Typical values for respiration parameters.

$i$	$pre_{i1}$	$pre_{i2}$
1	0.54	0.67
2	2.10	0.75
3	3.80	0.67
4	0.28	0.75
5	0.13	0.84

The given values of  $pre_{i1}$  were determined so that under optimal food availability conditions

- i. An individual in consumer group 1 will increase from 100 g to 125 g in 30 days,
- ii. An individual in consumer group 2 (cow) will increase from 400 lb. (181,200 g) to 500 lb. (226,500 g) in 30 days,
- iii. An individual in consumer group 3 will increase from 20 lb. (9,060 g) to 25 lb. (11,325 g) in 30 days,
- iv. An individual in consumer group 4 will increase from 30 g to 35 g in 30 days, and
- v. An individual in consumer group 5 will increase from .30 g to .35 g in 30 days.

### 6.3 Summary and Example

The consumer section of the model was simulated independently of the model by providing a record of forb aboveground biomass ( $Al_3$  or  $cb_3$ ) as an artificial driving variable. The graph of this driver is shown in Fig. 6.1(a). Table 6.6 summarizes the initial conditions and parameter values used in the simulation. It was designed to allow investigation of the consumer response to a limiting food supply. Accordingly, the food preference factors ( $pf_{ij}$ ) were arranged so that forbs are the most preferred food source for all the herbivorous consumers. Table 6.7 shows the rate of change of the individual average weights ( $w_i$ ,  $i = 1, \dots, 5$ ) for the initial conditions of the simulation. For the parameter and initial conditions



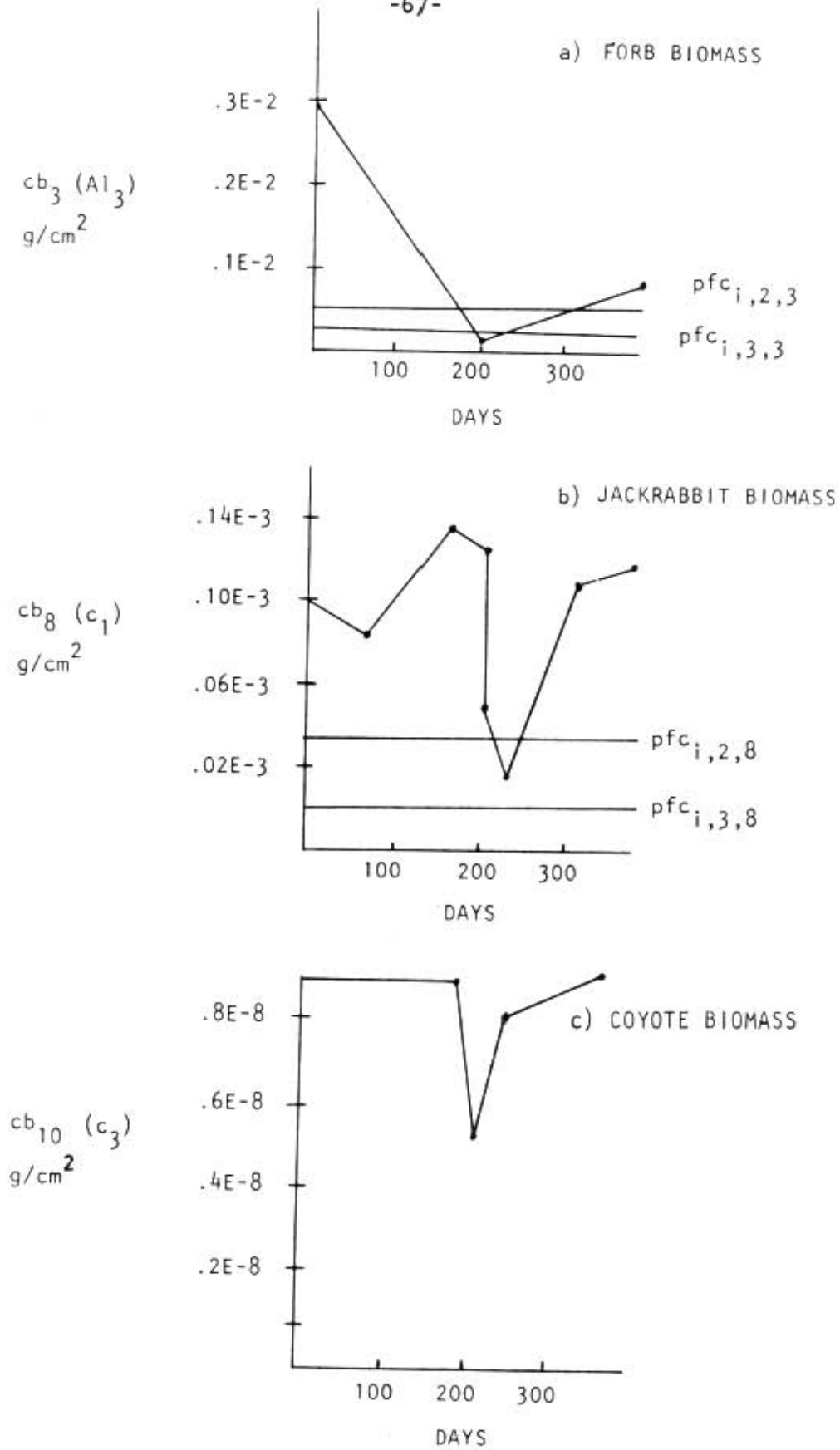
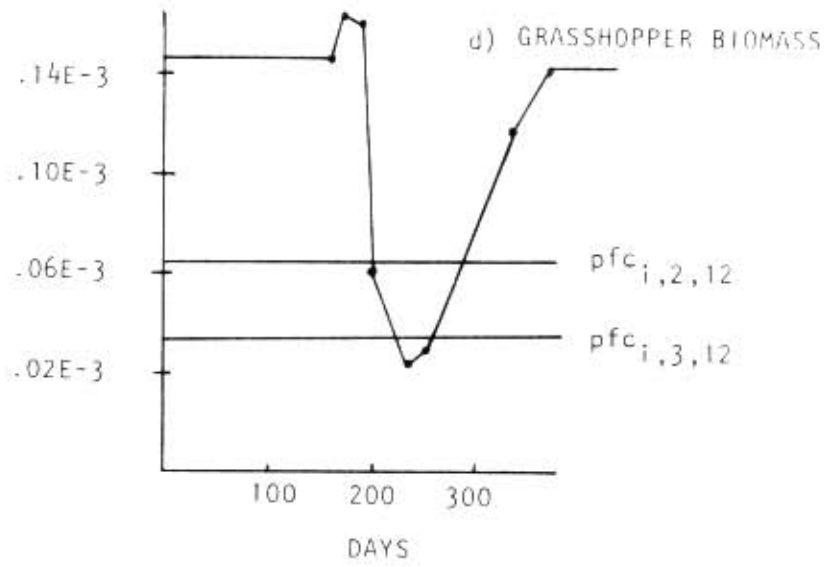


Fig. 6.1. Results of 365 day simulation of consumer submodel. a) Forb artificial driving function, b) through e) biomass densities of consumers.

$cb_{12} (c_5)$   
 $g/cm^2$



$cb_{11} (c_4)$   
 $g/cm^2$

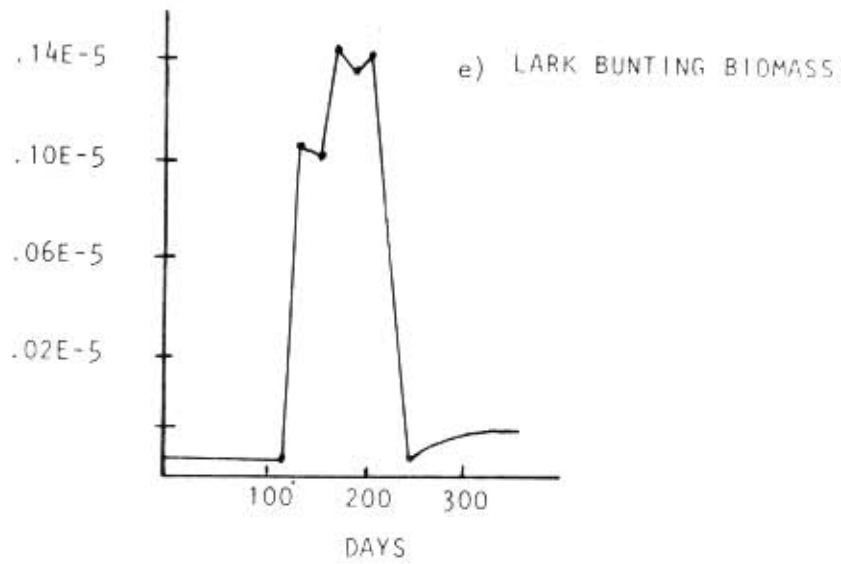


Fig. 6.1. (cont.)

Table 6.6. Parameter, PSV, and ISV values for a sample solution with dummy producer values ( $t_d = 0$ ).

Consumed Species $i$	Initial Conditions			Parameter Values		
	$N_i$ #/cm <sup>2</sup>	$W_i$ g/ind.	$C_i$ g/cm <sup>2</sup>	$pwu_i$ g/ind.	$pwl_i$ g/ind.	$pfc_i$ g/g/day
1	.100E-5	.750E+2	.750E-4	.100E+3	.100E+3	.200
2	.200E-9	.181E+6	.362E-4	.181E+6	.181E+6	.200
3	.100E-11	.900E+4	.900E-8	.900E+4	.900E+4	.200
4	.100E-9	.300E+2	.300E-8	.300E+2	.300E+2	.160
5	.500E-9	.300	.150E-3	.300	.300	.270

Consumed Species $j$	Parameter and ISV Values			
	$cb_j$ g/cm <sup>2</sup>	$pfc_{i,3,j}$ g/cm <sup>2</sup>	$pfc_{i,2,j}$ g/cm <sup>2</sup>	$pas_j$
1	.300E-2	.100E-2	.200E-2	.300
2	.100E-2	.100E-3	.200E-3	.500
3	.100E-3	.200E-3	.500E-3	.700
4	.300E-2	.100E-2	.200E-2	.350
5	.600E-1	.141E-1	.282E-1	.000
6	.100E-1	.230E-2	.470E-2	.250
7	.500E-2	.120E-2	.240E-2	.200
8	.750E-4	.125E-4	.250E-4	.950
9	.362E-4	0	1.0	.000
10	.900E-8	0	1.0	.000
11	.300E-8	.270E-6	.540E-6	.900
12	.150E-3	.280E-4	.750E-4	.850

Table 6.6. (Continued)

$pf_{ij}$  - Food Preference Under Ideal Food Availability

---

Species $i$	$j$											
	1	2	3	4	5	6	7	8	9	10	11	12
1	.05	.12	.70	.07	-	.059	.001	-	-	-	-	-
2	.25	.25	.45	.015	-	.03	.005	-	-	-	-	-
3	-	-	-	-	-	-	-	.85	-	-	.05	.10
4	-	.175	.175	-	-	-	-	-	-	-	-	.65
5	.05	.12	.70	.07	-	.059	.001	-	-	-	-	-

---

Computed Values

---

$i$	Primary Source of Food	Food Consumption Rates
	$mp_i$	$fc_i$ (g/g body weight/day)
1	3	.107
2	3	.080
3	8	.200
4	12	.160
5	3	.108

---

Table 6.6. (Continued)

Food Preference -  $fp_{ij}$ ;  $j = 1, \dots, 12$ ;  $i = 1, \dots, 5$

Consumer Species $i$	$j$											
	1	2	3	4	5	6	7	8	9	10	11	12
1	.167	.400	-	.233	-	.197	.003	-	-	-	-	-
2	.455	.455	-	.027	-	.055	.008	-	-	-	-	-
3	-	-	-	-	-	-	-	.850	-	-	.050	.100
4	-	.212	-	-	-	-	-	-	-	-	-	.788
5	.167	.400	-	.233	-	.197	.003	-	-	-	-	-

given in Table 6.6, we get the following values (Table 6.7) for the change in the average weight of an individual in consumer group  $i$ ;  $i = 1, \dots, 5$ . Thus, the consumer groups whose primary source of food is not available lose weight while the other two consumer groups remain fairly constant.

A one-year (365 day) run of the consumer submodel was made. The producer variables  $\{cb_1, \dots, cb_7\}$  are the driving forces for the run. All producer variables with the exception of  $cb_3$  (forbs) are kept at constant biomass values, above all critical thresholds, throughout the run. The forb biomass decreases linearly from  $0.003 \text{ g/cm}^2$  at time 0 to  $0.0002 \text{ g/cm}^2$  at time 200, and then increases linearly to  $0.0007 \text{ g/cm}^2$  at time 365. Thus,

$$(i) \quad cb_3 < pfc_{i,2,3} \quad 175 \leq t \leq 310$$

$$(ii) \quad cb_3 < pfc_{i,3,3} \quad 193 \leq t \leq 210$$

Plots of the biomasses of jackrabbits  $cb_8$ , coyotes  $cb_{10}$ , grasshoppers  $cb_{12}$ , and lark buntings  $cb_{11}$  are made against time in Fig. 6.1. It should be noted that, under ideal food availability conditions, the primary source of food for jackrabbits and grasshoppers is forbs, and that the primary sources of food for coyotes and lark buntings are jackrabbits and grasshoppers, respectively. Thus, the forb biomass is the primary controlling factor on the whole system. It is interesting to note that as soon as the forb biomass ( $cb_3$ ) drops below  $pfc_{i,2,3}$ , both the jackrabbit and grasshopper biomasses drop. When forbs are completely removed from the diets of jackrabbits and grasshoppers ( $cb_3 < pfc_{i,2,3}$ ), those consumer biomasses decrease at a more rapid rate. As soon as forbs are added back into the diets of jackrabbits and grasshoppers ( $cb_3 > pfc_{i,3,3}$ ), those consumer biomasses start to increase again. In a similar manner the coyote (secondary consumer) starts to decrease as soon

Table 6.7. Rates of change of individual weights for consumer simulation run with producer driving variable.

$i$	$f_{n_i}$ (g assimilated/ individual/day)	$r_{e_i}$ (g respired/ individual/day)	$\dot{w}_i$ (g/individual/ day)
1	.307E+1	.974E+1	-.667E+1
2	.563E+4	.184E+5	-.128E+5
3	.169E+4	.169E+4	.000
4	.372E+1	.366E+1	.006E+1
5	.012	.047	-.035

as the jackrabbit biomass  $cb_8$  drops below  $pfc_{i,2,8}$ , and the lark bunting biomass starts to decrease as soon as the grasshopper biomass ( $cb_{12}$ ) drops below  $pfc_{i,2,12}$ . The lark buntings never completely recover because of the fact that their emigration starts during the period of rapid decline in biomass. Table 6.7 summarizes the harvest rates which occurred during the simulation.

#### 6.4 Future Expansion

Expansion of the PSV's of this section will probably involve association of the variables with particular species rather than broad functional groups. This can certainly be done for small mammals and lagomorphs. Arthropods may remain grouped to some extent, e.g., grasshoppers and sapsuckers as two separate PSV's. Division of PSV's for certain of the consumers into sex and/or age classes will also be desirable. At first these would be only a simple yearling/adult or nymph/adult dichotomy but will be extended in future versions.

The basic ISV's, e.g., respiration, birth rate, etc., will probably remain as such, however, their formulation will be heavily modified. One serious fault of the model which goes across all consumers is the failure to provide mechanisms individually for the functional groups, i.e., the same general form of food preference or respiration function should not be applied across the board to all consumers with variations only in parameter values. Within the specific mechanisms of the model, here are a few areas to be investigated further.

The birth and natural mortality functions need to be tied into the biological and abiotic environment. This is an area where field data is extremely difficult to procure, however, every effort will be made to find



sources of reliable information. It is expected that laboratory studies on such subjects as insect egg mortalities may be useful here. Stochasticization of the model (by the method mentioned in section 2.1) to simulate the random character of the population may be a useful alternative when birth and death functions are measurable with variability but no relation to environmental variables is possible. The introduction of density-dependent mechanisms for the birth and death functions is justified only when a specific case can be made based on literature or field data or as a hypothesis to be tested. We expect to have a library of such hypotheses available for substitution in PWNEE, MOD 2. Cattle stocking rates should also be entered as a driving variable for domestic herbivores.

The integro-differential equation approach to animal population dynamics (Bledsoe and Jameson 1969) is the most desired formulation from a standpoint of resolution. This mechanism, however, needs considerably more work as a separate model before it will be ready for inclusion in a whole system model. Both the methods of numerical analysis for the integral equations and the formulation of the required ISV's need further research.

The mechanisms of PWNEE concerned with the quality (i.e., dietary items) and quantity of food ingested are mathematically the most complex in the model. The basic fault of the current formulation is the failure to allow animals to shift their diet readily since ingestion rate is dependent only on the "most preferred species" rather than on total food availability. This single item could be corrected by a fairly simple "patch" to the model, however, we plan to take a broader look at the system. In particular, the array of possible food items should be extended to include additional items

such as belowground plant parts, carrion, and feces, as well as supplemental food (as a driving variable) supplied by man. Bledsoe and Jameson (1969) contains a more complex mechanism for food choice based on a time varying dietary composition which can be keyed to plant conditions such as succulence and phenological state. Similarly, assimilation rates will be keyed to plant digestibility functions which will themselves be partially determined by environmental variables. A more complex mechanism involving digestive interactions among dietary items is also a candidate for inclusion.

The respiration function needs to be broadened so that a separate mechanism can be included for different animal types such as poikilotherms vs. homiotherms. The introduction of an "activity cycle" (Bledsoe and Jameson 1969) for animals will allow a variable respiration rate depending upon animal activity as well as the external environment. This mechanism would also affect ingestion rates. The activity cycle would be basically diurnal with a seasonal variation imposed to allow for extra metabolic levels such as lactation, gestation, egg production, etc.

## 7. DECOMPOSER VARIABLES

The decomposer section of the PWNEE model consists of three groups of variables interfaced to the rest of the system. These three groups can be described as variables giving characteristics of the soil ( $So_i$ ,  $i = 1, \dots, 3$ ), variables giving the density per unit area of soil nitrogen in various forms ( $Mn_i$ ,  $i = 1, \dots, 4$ ), and variables giving an index to the activity per unit area of soil surface of various soil microorganisms ( $Mc_i$ ,  $i = 1, \dots, 6$ ). The general philosophy is that transformations among the nitrogen variables and some of the soil characteristic variables are regulated by the activity level of microbial populations which are, in turn, dependent on the substrate levels and the abiotic soil characteristics (temperature and soil moisture). Fig. 7.1 gives the names of the variables in the decomposer section and schematically depicts their interrelation.

### 7.1 Principal System Variables

There are six microbial functional types which comprise the PSV's symbolized by  $Mc_i$  as follows:  $i = 1$ , protein decomposer;  $i = 2$ , deaminifier;  $i = 3$ , nitrifier;  $i = 4$ , denitrifier;  $i = 5$ , nitrogen fixer; and  $i = 6$ , cellulose decomposer. The change in activity of each microbial type is determined fundamentally by a logistic equation whose variable coefficients are determined by the substrate levels for the particular microbe and by the abiotic variables, soil temperature ( $T_s$ ), and soil moisture ( $M_s$ ). The differential equation is given below:

$$Mc_i = dv_i \cdot \frac{Mc_i (mu_i - Mc_i)}{mu_i} \quad (7.1)$$

where  $dv_i$  and  $mu_i$  are functions of other PSV's.

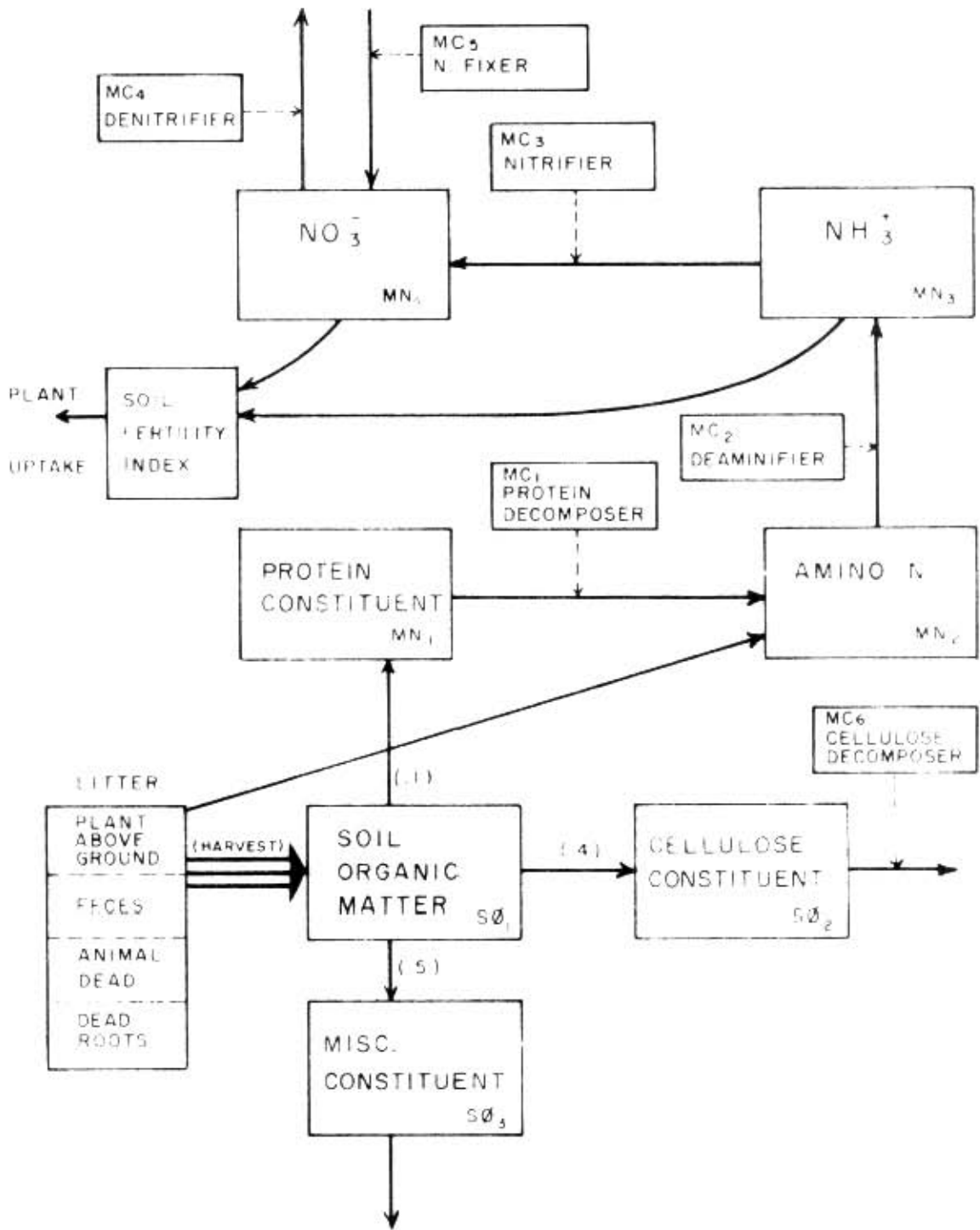


Fig. 7.1. Diagrammatic representation of decomposer section relations.

There are three soil characteristics ( $So_i$ ) which are currently being utilized as follows:  $i = 1$ , soil organic matter total;  $i = 2$ , cellulose in soil organic matter; and  $i = 3$ , miscellaneous soil organic matter constituents. The first variable,  $So_1$ , is an algebraic sum of the other two soil variables and  $Mn_1$  which is the soil insoluble organic nitrogen constituent (protein).

$$So_1 = So_2 + So_3 + Mn_1 \quad (7.2)$$

The philosophy of operation is that input into the soil organic matter compartment is via a microbial or physical harvest process from four other compartments of the ecosystem: dead animals (ha), animal feces (hf), belowground plant parts (db), and plant litter (hm). In each case the harvest rate is calculated as an intermediate system variable in subroutine ISV and each of the harvested variables has a variable exponential decay rate given by products of parameters and ISV's. The sum of all these harvests is characterized by a distribution of constituents given by array  $pSo_{1i}$ ,  $i = 1, \dots, 3$ . For example, if the total detritus is characterized as being 10% protein and 40% cellulose, the remainder going to the  $So_3$  compartment, then  $pSo_{1,1} = .1$ ,  $pSo_{1,2} = .4$ , and  $pSo_{1,3} = .5$ . Notice that

$$\sum_{i=1}^3 pSo_{1i} = 1.0 \quad (7.3)$$

The cellulose content of soil organic matter is characterized by the following differential equation:

$$\dot{So}_2 = pSo_{1,2}(hm + db + hf + ha) - pSo_{2,1} \cdot Mc_6 \cdot So_2 \quad (7.4)$$

which indicates an inflow proportional to the sum of the harvest variables, the proportion being given by the second element in the array  $pSo_{1i}$ . The loss is characterized by a decay rate,  $pSo_{2,1}$ , and is proportional both to the contents of the compartment and to the population level of the sixth microbial type which is responsible for cellulose decomposition.

The third soil characteristic variable, miscellaneous constituents, can be described by the following differential equation:

$$\dot{So}_3 = pSo_{1,3}(hm + db + hf + ha) - pSo_{3,1} \cdot So_3 \quad (7.5)$$

The input rate is again proportional to the sum of harvest variables; the decay rate is proportional to the contents of the compartment, with constant of proportionality  $pSo_{3,1}$ . Since there is no microbial type associated with this catchall soil compartment, it is characterized by a constant exponential loss rate.

The four species of soil nitrogen are as follows:  $Mn_1$ , insoluble organic nitrogen (protein);  $Mn_2$ , soluble organic nitrogen (amino nitrogen);  $Mn_3$ , soluble ammonia ion; and  $Mn_4$ , soluble nitrate ion. There is a differential equation for each of these variables which is characterized by a loss rate for each variable proportional to the contents of the compartment (amount of substrate) and the size of the microbial population responsible for transformation to the next nitrogen form. The  $i$ th nitrate species has a parameter associated with the loss,  $pMn_{i,1}$ . The following differential equations describe the nitrate variables:

$$\dot{Mn}_1 = pSo_{1,1}(hm + db + hf + ha) - pMn_{1,1} \cdot Mc_1 \cdot Mn_1, \quad (7.6)$$

$$\dot{Mn}_2 = pMn_{1,1} \cdot Mc_1 \cdot Mn_1 + lc \cdot Lt - pMn_{2,1} \cdot Mc_2 \cdot Mn_2, \quad (7.7)$$

$$\dot{Mn}_3 = pMn_{2,1} \cdot Mc_2 \cdot Mn_2 - pMn_{3,1} \cdot Mc_3 \cdot Mn_3 - au(Mn_3, pt), \quad (7.8)$$

$$\dot{Mn}_4 = pMn_{3,1} \cdot Mc_3 \cdot Mn_3 + nf(Mc_5) - dn(Mn_4, Mc_4) - nu(Mn_4, pt). \quad (7.9)$$

## 7.2 Intermediate System Variables

For a given substrate level the relation of  $dv_i$  and  $mu_i$  to soil temperature and moisture is shown in Fig. 7.2. The algebraic formulation of  $dv_i$  and  $mu_i$  is given below:

$$dv_i = pMc_{i8} \cdot op(pMc_{i1}, pMc_{i2}, Ts) \cdot op(pMc_{i3}, pMc_{i4}, Ms) \cdot sb(pMc_{i5}, pMc_{i6}, d3_i) \quad (7.10)$$

$$mu_i = pMc_{i7} \cdot op(pMc_{i1}, pMc_{i2}, Ts) \cdot op(pMc_{i3}, pMc_{i4}, Ms) \cdot sb(pMc_{i5}, pMc_{i6}, d3_i) \quad (7.11)$$

where  $d3_i$  is equated to the PSV which is the substrate for the  $i$ th microbial type. Thus,

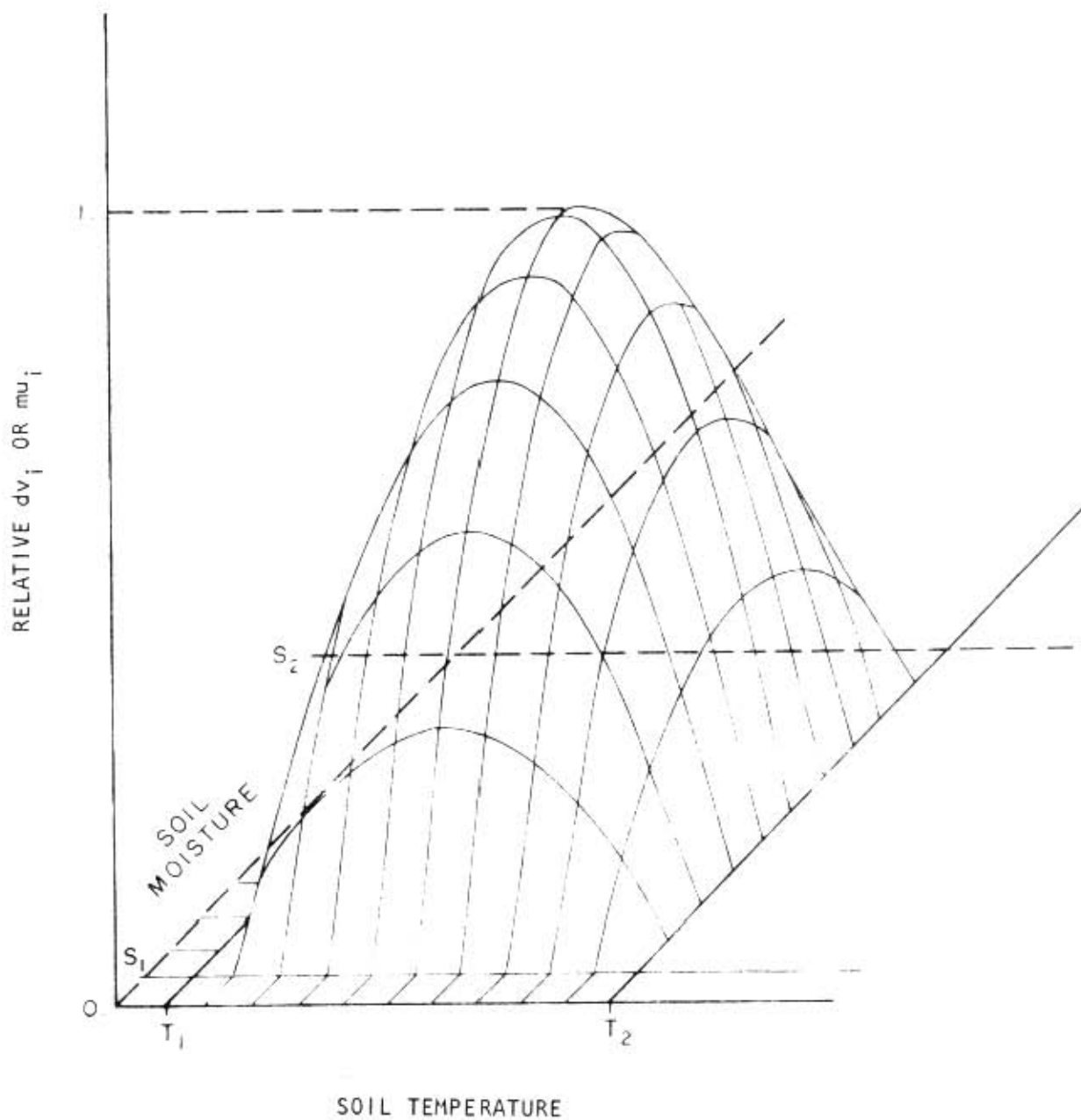


Fig. 7.2.  $dv_i$  and  $\mu_i$  graphed as a function of temperature and soil moisture for a given substrate level.



$$\left. \begin{aligned} d3_1 &= Mn_1 \\ d3_2 &= Mn_2 \\ d3_3 &= Mn_3 \\ d3_4 &= Mn_4 \\ d3_5 &= So_1 \\ d3_6 &= So_1 \end{aligned} \right\} \quad (7.12)$$

The other ISV in equations (7.10) and (7.11) are defined below:

$$op(x_1, x_2, x_3) = \frac{-4 \cdot (x_3 - x_1)(x_3 - x_2)}{(x_2 - x_1)^2} \quad (7.13)$$

and

$$sb(x_1, x_2, x_3) = \begin{cases} .001 & \text{if } x_3 \leq x_2 \\ \left\{ \begin{aligned} 1. & \text{if } x_1 = 0 \\ (x_3 - x_2) \cdot x_1 & \text{if } x_1 \neq 0 \end{aligned} \right\} & \text{if } x_3 > x_2 \end{cases} \quad (7.14)$$

Equation (7.13) gives a relation of any biological variable (equated to  $op$ ) to an experimental gradient ( $x_3$ ) in which the variable has an optimum for some value of the gradient and is essentially zero for much larger or much smaller values.  $x_1$  and  $x_2$  are the upper and lower bounds at which the biological variable is zero; halfway between  $x_1$  and  $x_2$  the variable reaches its optimum. The function is normalized to one, i.e.,  $\max(op) = 1$ . Equation (7.14) gives a relation of a biological variable (equated to  $sb$ ) to an environmental gradient

( $x_3$ ) in which the variable rises linearly with the gradient after it passes a threshold value given by  $x_2$ . The slope of the rise is  $x_1$ . Fig. 7.3 shows the graph.

The differential equations for the four nitrate variables (equations 7.6 through 7.9) each contain one or more decay rates with positive or negative signs of the form

$$pMn_{i1} \cdot Mc_i \cdot Mn_i$$

There are two major inputs to the set of nitrogen variables, one given by the first term in equation (7.6), due primarily to death of plant roots, and the second given by the second term of equation (7.7), a leaching function,  $lc$ . The leach rate is described in the producer section as a loss of soluble nitrogen from the plant litter compartment due to rainfall.

In addition to the inputs and decay rates described above there is a loss from total soil nitrogen due to plant uptake as given by ISV's  $au(Mn_3, pt)$  and  $nu(Mn_4, pt)$ . These functions give the rate of uptake by plants of ammonia and soluble nitrate, respectively. The uptake is proportional to the photosynthesis occurring at the time if photosynthesis is positive. The ionic uptake will be zero if photosynthesis is negative or zero. The ISV giving the total positive photosynthesis is  $pt$ . The theory here is that whenever a positive aboveground growth increment occurs a proportional amount of mineral nitrogen (nitrate or ammonia) must be removed from the soil. The proportionality constants are  $pnu_1$  and  $pau_1$ , respectively. The uptake rate is proportional to the amount of ions present as well. The parameters  $pnu_1$  and  $pau_1$  are also indicative of the plants "preference" for one ionic species over another. The rate constant for ammonia will be several times larger than the

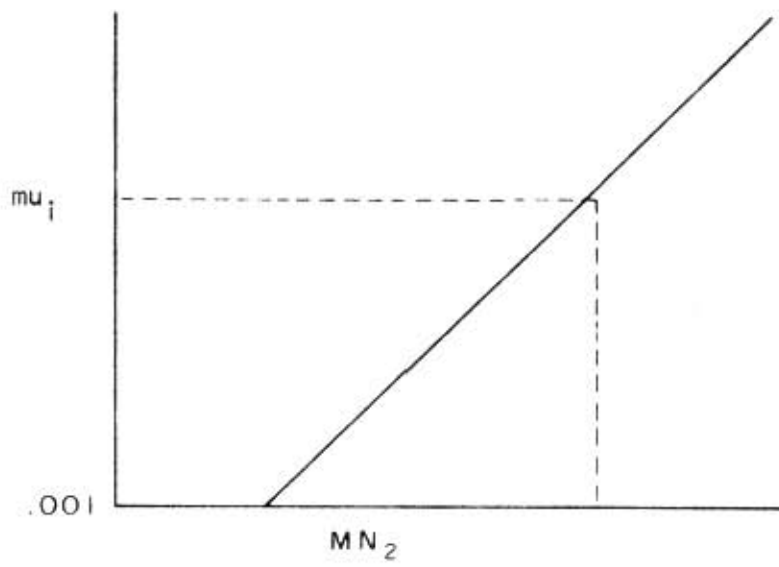


Fig. 7.3.  $\mu_i$  graphed as a function of the substrate level for optimum temperature and soil moisture.

rate constant for nitrate..

There is a further addition and loss to the nitrogen system given by nitrogen fixation (nf) and denitrification (dn). Nitrogen fixation occurs at a rate proportional to the population of nitrogen fixers ( $M_{c_5}$ ); the constant of proportionality is parameter pnf. Denitrification is proportional to the amount of soil nitrate and the population of denitrifying bacteria ( $M_{n_4}$ ) and is characterized by a rate constant pdn. The relations for the five ISV's used in the differential equations for nitrogen PSV's are summarized below:

$$lc = 34.5 \cdot Z_2 \quad (7.15)$$

$$au = pau \cdot Mn_3 \cdot pt \quad (7.16)$$

$$nu = pnu \cdot Mn_4 \cdot pt \quad (7.17)$$

$$nf = pnf \cdot Mc_5 \quad (7.18)$$

$$dn = pdn \cdot Mn_4 \cdot Mc_4 \quad (7.19)$$

Interaction between the decomposer and the producer section is given by a "nutrient availability index,"  $ns_i$ , for the  $i$ th plant group. This is an index of the relative soil fertility for each of the producer functional groups. The mechanism is designed to involve calculation of a weighted average amount of nitrogen available. The weights are given by pnu and pau; the resulting calculation is passed through a semi-threshold function of the arc tangent type (ISV, at, defined in producer section). The mathematics is described below:

$$ns_i = at(pns_{i1}, pns_{i2}, c_2)$$

$$c_2 = \frac{pau \cdot Mn_3 + pnu \cdot Mn_4}{pau + pnu}$$

Fig. 7.4 graphs  $ns_1$  as a function of  $c_2$ , the weighted average nitrogen availability.

### 7.3 Future Expansion

The decomposer section of PWNEE, MOD 1, conforms in its general formulation to the ideas of soil scientists and microbiologists about microbially mediated processes in the soil (see, for example, Bartholemew and Clark 1965). The difficulty lies in the fact that most of the transformations have been studied in the laboratory under idealized environmental conditions in isolated cultures rather than complete soil ecosystems. The measurement of PSV's and the calculation of rates for the processes described above is largely beyond the technology of soil science at this time. Since PWNEE, MOD 1, was formulated, the microbiologists, soil scientists, and modellers of the Grassland Biome have come up with a restructured decomposer model designed to emphasize variables which can be experimentally attacked. The model is in the conceptual stages, however it is sufficiently far advanced that 1971 experimental studies are being designed around it. The mathematical version of this model will appear in PWNEE, MOD 2; its principal features are described below.

The nitrogen section emphasizes that a certain fraction of nitrogen in the soil must be of a "fast turnover" type which appears yearly as plant protein and returns to the soil via translocation to and death of roots and via rainwater leaching. The relative magnitudes of these processes and their

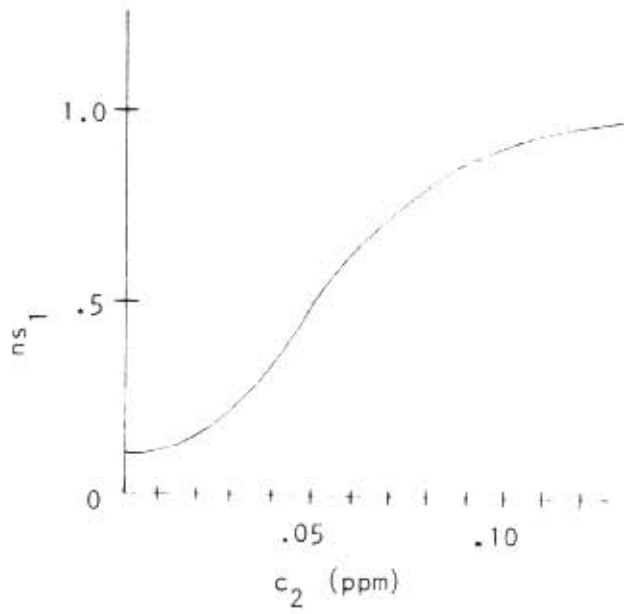


Fig. 7.4. Nutrient stress index  $ns_1$  as a function of weighted average nitrogen availability  $c_2$ .

dynamics are under experimental study. Studies of gaseous nitrogen input and losses are also planned.

A practical, conceptual carbon cycle in the soil is one focal point for 1971 decomposer studies. Studies will emphasize the carbon input to the soil from root death and the loss via  $\text{CO}_2$  evolution. Dynamics of these processes will be studied under various commonly occurring environmental conditions in the soil. The model will contain a fractionation of soil organic matter, as in MOD 1, with loss rates from the fractions as determined by experiment. The inputs to the various fractions will be via a modification of the mechanism explained in section 7.2. Each input will be characterized by a composition vector giving the proportion, e.g., of dead roots, in each organic matter fraction. This vector may be allowed to vary throughout the season depending upon laboratory analysis of 1971 root samples.

The decomposer model will probably be limited in MOD 2 to carbon and nitrogen, pending experimental plans to measure and analyze dynamics of other nutrients such as phosphorus.

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Appendix A. List of all the equations from all the sections.

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$$z_1 = \begin{cases} pz_1 \cdot \sin \left[ \frac{2\pi}{24} (\text{thm} - 6.) \right] & \text{if } 6 \leq \text{thm} \leq 18 \\ 0 & \text{otherwise} \end{cases} \quad (3.1)$$

$$z_2 = \begin{cases} (pz_{2,1,i-1} - pz_{2,2,i}) \text{cx} \left[ (\text{thm} + 10.) \cdot \frac{\pi}{15.} \right] + pz_{2,2,i} & \text{if } 0 \leq \text{thm} \leq 5.0 \\ (pz_{2,1,i} - pz_{2,2,i}) (1. - \text{cx} \left[ (\text{thm} - 5.) \frac{\pi}{9} \right]) + pz_{2,2,i} & \text{if } 5. < \text{thm} \leq 14. \\ (pz_{2,1,i} - pz_{2,2,i+1}) \text{cx} \left[ (\text{thm} - 14.) \frac{\pi}{15.} \right] + pz_{2,2,i+1} & \text{if } 14. < \text{thm} < 24. \end{cases} \quad (3.2)$$

$$\text{cx}(x_1) = \frac{1}{2} [1 + \cos(x_1)] \quad (3.3)$$

## Appendix A. (Continued)

$$z_3 = \begin{cases} 1.39 \cdot 10^{-4} p_{z_3,i} & \text{if } (6. \leq t_{mm} < 9.) \text{ and } (15. \leq t_{hm} < 17.) \\ 5.56 \cdot 10^{-5} p_{z_3,i} & \text{if } (t_{mm} < 6. \text{ or } t_{mm} \geq 9) \\ & \text{and } (3. \leq t_{hm} \leq 8.) \\ 0. & \text{otherwise} \end{cases} \quad (3.4)$$

$$z_4 = \begin{cases} 447. & \text{if } 12. \leq t_{hm} < 18. \\ (t_{hm} - 9.) \cdot 149. & \text{if } 9. \leq t_{hm} < 12. \\ -(t_{hm} - 18.) \cdot 149. + 447. & \text{if } 18. \leq t_{hm} < 21. \\ 0 & \text{if } 21. \leq t_{hm} < 24. \end{cases} \quad (3.5)$$

$$T_c = \begin{cases} z_2 + 10. \left( \frac{z_1}{p_{z_1}} \right) & \text{if } (z_4 \leq 223.5) \text{ and } (z_1 > .0002) \\ z_2 & \text{otherwise} \end{cases} \quad (4.1)$$

## Appendix A. (Continued)

$$\dot{T}_s = pT_s(T_c - T_s) \quad (4.2)$$

$$\dot{M}_s = z_3 - pM_s \cdot M_s \quad (4.3)$$

$$A\dot{i}_i = pA_i \cdot hp_i \cdot A_i - (bt_i + da_i + ha_i) \quad , \quad i = 1, \dots, 4 \quad (5.1)$$

$$B\dot{i} = \sum_{i=1}^4 bt_i - (db + rb \cdot B_i + hb) \quad (5.2)$$

$$A\dot{d} = \sum_{i=1}^4 da_i - (sa \cdot A_d + hs) \quad (5.3)$$

$$L\dot{t} = sa \cdot A_d - (hl + hm + lc \cdot L_t) \quad (5.4)$$

## Appendix A. (Continued)

$$ms_i \cdot ns_i \cdot cr_i \cdot la_i \cdot php_{i1} \left[ \frac{php_{i2} \cdot rp}{(1 + php_{i2} \cdot rp)} - \frac{php_{i2} \cdot prp_{2i}}{(1 + php_{i2} \cdot prp_{2i})} \right]$$

$$[(pTc_{i1} - Tc) \exp(-php_{i3} [pTc_{i1} - Tc])]$$

$$\text{if } rp > prp_{2i} \text{ and } (0 < Tc < pTc_{i1}) \quad [\text{case 1}]$$

$$-ms_i \cdot ns_i \cdot cr_i \cdot la_i \cdot php_{i4} \left[ \frac{(prp_{2i} - rp)}{prp_{2i}} \right] \left( \frac{Tc}{pTc_{i2}} \right)^{php_{i5}}$$

$$hp = \left\{ \exp \left\{ \left( \frac{php_{i5}}{php_{i6}} \right) \left[ 1 - \left( \frac{Tc}{pTc_{i2}} \right)^{php_{i6}} \right] \right\} \right. \quad (5.5)$$

$$\text{if } rp < prp_{2i} \text{ and } Tc > 0 \quad [\text{case 2}]$$

$$-ms_i \cdot ns_i \cdot cr_i \cdot php_{i7} [(Tc - pTc_{i1}) \exp(-php_{i8} (Tc - pTc_{i1}))]$$

$$\text{if } rp > prp_{2i} \text{ and } Tc > pTc_{i1} \quad [\text{case 3}]$$

$$0 \quad \text{if } Tc \leq 0 \quad [\text{case 4}]$$

$$rp = pz_1 \cdot \left( \frac{z_1}{pz_1} \right)^{prp_1} \quad (5.6)$$

## Appendix A. (Continued)

$$ms_i = at(pms_{i2}, pms_{i1}, fw) \quad (5.7)$$

$$fw = \frac{\left(\frac{Ms}{20}\right)}{1.4} \quad (5.8)$$

$$at(x_1, x_2, x_3) = \left(\frac{1}{\pi}\right) \tan^{-1}[c_1(x_3 - x_1)] + .5 \quad (5.9)$$

$$c_1 = \tan\left(.4 \cdot \frac{\pi}{x_2}\right) \quad (5.10)$$

$$rb = \begin{cases} prb_1(44 - Ts) \exp\left(\frac{-(44 - Ts)}{8}\right) & \text{if } Ts \leq 44 \\ 0 & \text{otherwise} \end{cases} \quad (5.11)$$

$$db = \frac{rb}{2} \quad (5.12)$$

$$da_i = (1 - ms_i) pda_{i1} \cdot at(pda_{i3}, pda_{i2}, Tc) \cdot Al_i \quad (5.13)$$

## Appendix A. (Continued)

$$bt_i = ms_i \cdot \begin{cases} 0. & \text{if } Ts \leq 0 \\ \text{-----} \\ \max[0., (pbt_{i1} - pbt_{i2} \cdot bl_i) Al_i] & \\ & \text{if } (Al_i > pbt_{i3}) \text{ and } (Ts > 0) \\ \text{-----} \\ -\min[0., pbt_{i4}(bl_i - pbt_{i5})] & \\ & \text{if } (Al_i \leq pbt_{i3}) \text{ and } (Ts > 0) \end{cases} \quad (5.14)$$

$$bl_i = Bl \cdot \frac{Al_i}{ab} \quad (5.15)$$

$$ab = \sum_{i=1}^4 Al_i \quad (5.16)$$

$$sa = \begin{cases} .005 & \text{if } z_4 \leq 223.5 \text{ cm/sec} \\ (.005 + 2.21 \cdot 10^{-4} \cdot z_4) & \text{if } z_4 > 223.5 \end{cases} \quad (5.17)$$

## Appendix A. (Continued)

$$1c = .035 \cdot z_2 \quad (5.18)$$

$$C_i = N_i W_i; \quad i = 1, \dots, 5 \quad (6.1)$$

$$\dot{N}_i = N_i [nb_i - nd_i] - \frac{ha_{i+7}}{W_i} + im_i - em_i; \quad i = 1, \dots, 5 \quad (6.2)$$

$$\dot{W}_i = W_i \cdot as_i \cdot fc_i - re_i; \quad i = 1, \dots, 5 \quad (6.3)$$

$$\dot{F}e = \left[ \sum_{i=1}^5 C_i (1 - as_i) fc_i \right] - ha_{13} \quad (6.4)$$

$$\dot{C}d = \left[ \sum_{i=1}^5 C_i \cdot nd_i \right] - ha_{14} \quad (6.5)$$

## Appendix A. (Continued)

$$nb_1 = \begin{cases} 0 & \text{if } (tdm < 58) \text{ or } (tdm > 252) \\ .007[1 - .0046(tdm - 58)] & \text{if } 58 \leq tdm \leq 252 \end{cases} \quad (6.6)$$

$$nd_1 = .0022 \quad (6.7)$$

$$nb_2 = nd_2 = 0 \quad (6.8)$$

$$nb_3 = nd_3 = 0 \quad (6.9)$$

$$nb_4 = \begin{cases} .0308 & \text{if } 155 \leq tdm \leq 168 \\ .0102 & \text{if } 190 \leq tdm \leq 203 \\ 0 & \text{otherwise} \end{cases} \quad (6.10)$$

$$nd_4 = \begin{cases} .0021 & \text{if } tdm \leq 154 \\ .0035 & \text{if } tdm > 154 \end{cases} \quad (6.11)$$

$$im_4 = \begin{cases} .26 \cdot 10^{-8} & \text{if } 113 \leq tdm \leq 126 \\ 0 & \text{otherwise} \end{cases} \quad (6.12)$$



## Appendix A. (Continued)

$$em_4 = \begin{cases} .21 \cdot 10^{-8} & \text{if } 218 \leq tdm \leq 235 \\ 0 & \text{otherwise} \end{cases} \quad (6.13)$$

$$nb_5 = \begin{cases} .0214[1 - .0145(tdm - 162)] & \text{if } 162 \leq tdm \leq 224 \\ 0 & \text{otherwise} \end{cases} \quad (6.14)$$

$$nd_5 = \begin{cases} .0071 & \text{if } 162 \leq tdm \leq 259 \\ 0 & \text{otherwise} \end{cases} \quad (6.15)$$

$$dl_i = \begin{cases} pfc_{i1} \left( \frac{pdl_{i1}}{w_i} \right); w_i > pdl_{i1} \\ pfc_{i1}; pdl_{i2} \leq w_i \leq pdl_{i1} \\ pfc_{i1} \left( \frac{pdl_{i2}}{w_i} \right); w_i < pdl_{i2} \end{cases} \quad (6.16)$$

= dummy food intake variable

Appendix A. (Continued)

$$f_{c_i} = \begin{cases} d1_i ; cb_k > pfc_{i2k} \\ d1_i \left( \frac{cb_k}{pb_{1k}} \right) ; pfc_{i3k} \leq cb_k \leq pfc_{i2k} \\ d1_i \left( \frac{pfc_{i3k}}{pfc_{i2k}} \right) ; cb_k < pfc_{i3k} \end{cases} \quad (6.17)$$

$$d2_{ik} = \begin{cases} pfp_{ik} ; cb_k > pfc_{i2k} \\ pfp_{ik} \left( \frac{cb_k}{pfc_{i3k}} \right) ; pfc_{i3k} \leq cb_k \leq pfc_{i2k} \\ 0 ; cb_k < pfc_{i3k} \end{cases} \quad (6.18)$$

= dummy food preference factor

$$d2_{ij} = \begin{cases} pfp_{ij} ; cb_j \geq pfc_{i3j} \\ 0 ; cb_j < pfc_{i3j} \end{cases} \quad j \neq k \quad (6.19)$$

## Appendix A. (Continued)

$$fp_{ij} = \frac{d2_{ij}}{\sum_{j=1}^{12} d2_{ij}}, \quad (6.20)$$

$$\sum_{j=1}^{12} fp_{ij} = 1.0. \quad (6.21)$$

$$ha_j = \sum_{i=1}^5 hp_{ij} \quad (6.22)$$

$$hp_{ij} = fc_i \cdot fp_{ij} \cdot C_i \quad (6.23)$$

$$as_i = \sum_{j=1}^{12} pas_j \cdot fp_{ij}; \quad i = 1, \dots, 5 \quad (6.24)$$

$$re_i = pre_{i1} \cdot (W_i)^{pre_{i2}}, \quad i = 1, \dots, 5 \quad (6.25)$$

## Appendix A. (Continued)

$$Mc_i = dv_1 \cdot \frac{Mc_i (mu_i - Mc_i)}{mu_i} \quad (7.1)$$

$$So_1 = So_2 + So_3 + Mn_1 \quad (7.2)$$

$$\sum_{i=1}^3 pSo_{1,i} = 1.0 \quad (7.3)$$

$$\dot{So}_2 = pSo_{1,2} (hm + db + hf + ha) - pSo_{2,1} \cdot Mc_6 \cdot So_2 \quad (7.4)$$

$$\dot{So}_3 = pSo_{1,3} (hm + db + hf + ha) - pSo_{3,1} \cdot So_3 \quad (7.5)$$

$$\dot{Mn}_1 = pSo_{1,1} (hm + db + hf + ha) - pMn_{1,1} \cdot Mc_1 \cdot Mn_1 \quad (7.6)$$

$$\dot{Mn}_2 = pMn_{1,1} \cdot Mc_1 \cdot Mn_1 + lc \cdot Lt - pMn_{2,1} \cdot Mc_2 \cdot Mn_2 \quad (7.7)$$

## Appendix A. (Continued)

$$\dot{Mn}_3 = pMn_{2,1} \cdot Mc_2 \cdot Mn_2 - pMn_{3,1} \cdot Mc_3 \cdot Mn_3 - au(Mn_3, pt), \quad (7.8)$$

$$\dot{Mn}_4 = pMn_{3,1} \cdot Mc_3 \cdot Mn_3 + nf(Mc_5) - dn(Mn_4, Mc_4) - nu(Mn_4, pt). \quad (7.9)$$

$$dv_i = pMc_{i8} \cdot op(pMc_{i1}, pMc_{i2}, Ts) \cdot op(pMc_{i3}, pMc_{i4}, Ms) \cdot sb(pMc_{i5}, pMc_{i6}, d3_i) \quad (7.10)$$

$$mu_i = pMc_{i7} \cdot op(pMc_{i1}, pMc_{i2}, Ts) \cdot op(pMc_{i3}, pMc_{i4}, Ms) \cdot sb(pMc_{i5}, pMc_{i6}, d3_i) \quad (7.11)$$

$$\left. \begin{aligned} d3_1 &= Mn_1 \\ d3_2 &= Mn_2 \\ d3_3 &= Mn_3 \\ d3_4 &= Mn_4 \\ d3_5 &= So_1 \\ d3_6 &= So_1 \end{aligned} \right\} \quad (7.12)$$

Appendix A. (Continued) .

$$op(x_1, x_2, x_3) = \frac{-2 \cdot (x_3 - x_1)(x_3 - x_2)}{(x_2 - x_1)} \quad (7.13)$$

$$sb(x_1, x_2, x_3) = \begin{cases} .001 & \text{if } x_3 \leq x_2 \\ \left\{ \begin{array}{l} 1. & \text{if } x_1 = 0 \\ (x_3 - x_2) \cdot x_1 & \text{if } x_1 \neq 0 \end{array} \right\} & \text{if } x_3 > x_2 \end{cases} \quad (7.14)$$

$$lc = 34.5 \cdot Z_2 \quad (7.15)$$

$$au = pau \cdot Mn_3 \cdot pt \quad (7.16)$$

$$nu = pnu \cdot Mn_4 \cdot pt \quad (7.17)$$

$$nf = pnf \cdot Mc_5 \quad (7.18)$$

$$dn = pdn \cdot Mn_4 \cdot Mc_4 \quad (7.19)$$

Appendix B. Glossary of PSV's, ISV's, and parameters. A dash in the units column indicates a variable which is a pure number.

Algebraic	FORTTRAN	Description	Units
DRIVING VARIABLES			
<i>PSV's</i>			
$z_1$	IC	Shortwave radiation	cal/(cm <sup>2</sup> ·sec)
$z_2$	T1	Air temperature	°C
$z_3$	PP	Precipitation	cm/sec
$z_4$	WS	Wind speed	cm/sec
<i>ISV's</i>			
$cx(x_1)$	COSX	Cosine function translated to vary between 0 and 1	--
<i>Parameters</i>			
$pz_1$	SC	Peak solar radiation rate	cal/(cm <sup>2</sup> ·sec)
$pz_{2,1,i}$	TMX(TD)	Maximum daily air temperature, <i>ith</i> day	°C
$pz_{2,2,i}$	TMN(TD)	Minimum daily air temperature, <i>ith</i> day	°C
$pz_{3,i}$	PRECIP(I)	Amount of precipitation on <i>ith</i> day	cm
$pTs$	STLAG	Rate constant for soil temperature lag	(sec) <sup>-1</sup>
ABIOTIC VARIABLES			
<i>PSV's</i>			
$Tc$	T2	Soil surface temperature (synonymous with canopy temperature)	°C
$Ts$	T3	Soil temperature for top 20 cm	°C

## Appendix B. (Continued).

Algebraic	FORTTRAN	Description	Unit
Ms	SM	Soil moisture, total in top 20 cm	cm
<i>Parameters</i>			
pTs	STLAG	Rate constant associated with soil temperature lag	(sec) <sup>-1</sup>
pMs	SMLAG	Rate constant associated with soil moisture loss rate	(sec) <sup>-1</sup>
PRODUCER VARIABLES			
<i>PSV's</i>			
Al <sub>i</sub> , i = 1, 4	VA(I)	Aboveground biomass of live plant material; i = 1-warm season grass, i = 2-cool season grass, i = 3-forbs, i = 4- <i>Opuntia</i>	g/cm <sup>2</sup>
B1	VB	Belowground live plant parts, total of all species	g/cm <sup>2</sup>
Ad	VS	Biomass of standing dead plants, total	g/cm <sup>2</sup>
Lt	VL	Biomass of aboveground plant litter, total	g/cm <sup>2</sup>
<i>ISV's</i>			
hp <sub>i</sub>	PHOTO(I)	Net photosynthesis rate in net g of CO <sub>2</sub> fixed per unit plant green tissue, species i	(sec) <sup>-1</sup>
bt <sub>i</sub>	TB(VA,I)	Net translocation rate for <i>i</i> th species	g/(sec·cm <sup>2</sup> )



## Appendix B. (Continued).

Algebraic	FORTTRAN	Description	Unit
fw	PSM	Percent soil moisture by weight in top 20 cm of soil	--
da <sub>i</sub>	AGD(I)	Death rate of aboveground plant parts, <i>i</i> th plant group	g/(cm <sup>2</sup> ·sec)
ha <sub>i</sub>	HA(I)	Harvest rate of aboveground plant parts, <i>i</i> th plant group	g/(cm <sup>2</sup> ·sec)
db	BGD(RB)	Death rate of belowground plant parts	g/(cm <sup>2</sup> ·sec)
rb	RB(T3)	Respiration rate of belowground plant parts per unit of plant tissue (weight)	(sec) <sup>-1</sup>
hb	HB	Harvest rate of belowground plant parts, all harvesters	g/(cm <sup>2</sup> ·sec)
sa	SHATR(WS)	Shattering rate of standing dead per unit of standing dead tissue	(sec) <sup>-1</sup>
hs	HS	Harvest rate of standing dead vegetation, macrofauna	g/(cm <sup>2</sup> ·sec)
hl	HL	Harvest rate of plant litter by macrofauna	g/(cm <sup>2</sup> ·sec)
hm	HM	Harvest rate of plant litter by microfauna	g/(cm <sup>2</sup> ·sec)
lc	LEACH(PP)	Leaching rate of plant litter into soil by rainwater, per unit of plant litter	(sec) <sup>-1</sup>
ms <sub>i</sub>	MOIS(I)	Moisture stress index for <i>i</i> th plant species (number between 0 and 1)	--
ns <sub>i</sub>	ETE(I)	Nutrient stress index for <i>i</i> th plant species (number between 0 and 1)	--
rp	PHAR(IC)	That part of net solar radiation effective for photosynthesis, includes geometry of leaves but not leaf area index	cal/(cm <sup>2</sup> ·sec)

## Appendix B. (Continued).

Algebraic	FORTTRAN	Description	Unit
$cr_i$	CR(I)	Percent cover of $i$ th plant species	--
$la_i$	L(I)	Leaf area index of $i$ th plant group	--
at	ATANX	Mathematical function related to arc tangent	--
ab	TVA	Total aboveground biomass	$g/cm^2$
$bl_i$	VBI	Prorated amount of total belowground biomass in plant group $i$	$g/cm^2$
<i>Parameters</i>			
$pAl_i$	EPSI(I)	Conversion factor for photosynthesis function-- converts $CO_2$ fixation rate to photosynthate accumulation, $i$ th plant group	--
$php_{i1}$	K1(I)	Peak photosynthesis rate under optimum temperature, sunlight, moisture and nutrient conditions, per unit of leaf area, $i$ th plant group	$(sec)^{-1}$
$php_{i2}$	K3(I)	Parameter associated with sunlight response of photosynthesis curve, $i$ th plant group	--
$php_{i3}$	K2(I)	Parameter associated with temperature response of photosynthesis curve during normal daylight and moderate temperatures, $i$ th plant group	$(^{\circ}C)^{-1}$
$prp_{2i}$	SC(I)	Threshold of positive photosynthesis response to sunlight, $i$ th plant group	$cal/(cm^2 \cdot sec)$

## Appendix B. (Continued).

Algebraic	FORTTRAN	Description	Unit
$pTc_{i1}$	T20(1)	Threshold of positive photosynthesis response to temperature, <i>ith</i> plant group	$^{\circ}C$
$php_{i4}$	K6(1)	Peak photosynthesis (respiration) rate under conditions of zero sunlight and optimum temperature, moisture, and nutrients, <i>ith</i> plant group	$(sec)^{-1}$
$pTc_{i2}$	T21(1)	Parameter associated with temperature response (position of peak) of photosynthesis curve during limiting sunlight, <i>ith</i> plant group	$^{\circ}C$
$php_{i5}$	K7(1)	Parameter associated with temperature response (spread of curve for moderate temperature) of photosynthesis curve during limiting sunlight, <i>ith</i> plant group	--
$php_{i6}$	K8(1)	Parameter associated with temperature response (spread of curve for high temperature) of photosynthesis curve during limiting sunlight, <i>ith</i> plant group	--
$php_{i7}$	K4(1)	Peak photosynthesis (respiration) rate under conditions of optimum sunlight, moisture, and nutrient and high temperatures, <i>ith</i> plant group	$(sec)^{-1}$
$php_{i8}$	K5(1)	Parameter associated with temperature response (spread) of photosynthesis curve during normal sunlight, moisture and nutrients but high temperatures, <i>ith</i> plant group	$(^{\circ}C)^{-1}$

## Appendix B. (Continued).

Algebraic	FORTTRAN	Description	Unit
$pms_{i1}$	PMS1(I)	Parameter determining sharpness of threshold response of growth to soil moisture	--
$pms_{i2}$	PMS2(I)	Parameter determining location of threshold response of growth to soil moisture	--
$pns_{i1}$	PNS1(I)	Parameter related to spread of semi-threshold relation for nutrient stress index ( $ns_i$ ) for $i$ th plant group	$cm^2/g$
$prb_1$	PRB1	Parameter relating to peak respiration rate of below-ground plant parts	$(sec)^{-1}$
$pda_{i1}$	PDA1(I)	Parameter associated with maximum aboveground death rate	$sec^{-1}$
$pda_{i2}$	PDA2(I)	Parameter associated with response of aboveground death rate (spread of curve) to temperature	$(^{\circ}C)^{-1}$
$pda_{i3}$	PDA3(I)	Parameter associated with response of aboveground death rate (location of inflection) to soil temperature	$^{\circ}C$
$pbt_{i1}$	TBMX(I)	Parameter giving maximum translocation for high aboveground biomass	$sec^{-1}$
$pbt_{i2}$	TBSLP1(I)	Parameter associated with rate of change of translocation rate with increasing belowground biomass for high aboveground biomass	$cm^2/(g \cdot sec)$
$pbt_{i3}$	VABRK(I)	Threshold for change of sign of translocation function as aboveground biomass changes	$g/cm^2$

## Appendix B. (Continued).

Algebraic	FORTTRAN	Description	Unit
$pbt_{i4}$	TBSLP2(I)	Parameter associated with rate of change of translocation rate with increasing belowground biomass for low aboveground biomass	(sec) <sup>-1</sup>
$pbt_{i5}$	VBBRK(I)	Parameter giving value of belowground biomass below which zero translocation occurs if aboveground biomass is low	g/cm <sup>2</sup>

## CONSUMER VARIABLES

<i>PSV's</i>			
$N_i$	PN(I)	Density of animals in group $i$	(cm <sup>2</sup> ) <sup>-1</sup>
$W_i$	W(I)	Average weight of individual in group $i$	g
$C_i$	C(I)	Live biomass density of group $i$ , $i = 1,5$	g/cm <sup>2</sup>
Fe	SH	Density of animal feces	g/cm <sup>2</sup>
Cd	AD	Density of animal dead	g/cm <sup>2</sup>
<i>ISV's</i>			
$nb_i$	B(I)	Instantaneous birth rate of $ith$ animal group	(days) <sup>-1</sup>
$nd_i$	D(I)	Instantaneous death rate of $ith$ animal group	(days) <sup>-1</sup>
$ha_i$	HA(I)	Harvest rate of $ith$ animal group by macro-consumers	g/day
$im_i$	XIM(I)	Immigration rate of $ith$ animal group	(day) <sup>-1</sup>
$em_i$	EM(I)	Emigration rate of $ith$ animal group	(day) <sup>-1</sup>

## Appendix B. (Continued).

Algebraic	FORTTRAN	Description	Unit
$as_i$	EFF(I)	Assimilation efficiency of $i$ th animal group <u>(Ingestion-egestion)</u> Ingestion	--
$fc_i$	AF(I)	Ingestion rate, $i$ th animal group, per unit body weight	(day) <sup>-1</sup>
$re_i$	RE(I)	Respiration rate of $i$ th animal group	g/day
$ha_{13}$ (=hf)	HSB	Harvest rate (by microbes) of animal feces	g/(day·cm <sup>2</sup> )
$ha_{14}$ (=ha)	HAD	Harvest rate (by microbes) of animal dead	g/(day·cm <sup>2</sup> )
$cb_j$	XC(J)	Biomass density of $j$ th consumed species, Table 6.2 gives meaning of subscript	g/cm <sup>2</sup>
$d1_i$	YF(I)	Dummy variables used in calculation of $fc_i$	--
$d2_{ij}$	YK(I,J)	Dummy variable used in calculation of $fp_{ij}$	--
$fp_{ij}$	AK(I,J)	Proportion of the diet of consumer group $i$ made up of consumed species $j$ under actual food availability conditions	--
$fc_i$	XINT(I)	Food consumption rate of animal group $i$ , per individual	g/day
$hp_{ij}$	HC(I,J)	Harvest rate on total biomass basis of consumed group $j$ by consumer group $i$	g/cm <sup>2</sup> ·day)
<i>Parameters</i>			
$pf_{c_{i1}}$	XF(I)	Food intake rate for $i$ th animal group under ideal food or availability conditions	g/day

## Appendix B. (Continued).

Algebraic	FORTTRAN	Description	Unit
$pd1_{i1}$	TWU(I)	Upper threshold for consumer weights at which food consumption is equal to $pfc_{i1}$	g
$pd1_{i2}$	TWL(I)	Lower threshold for consumer weights at which food consumption is equal to $pfc_{i1}$	g
$pfc_{i2j}$	TT(J)	Upper threshold for density of consumed material (k) at which food consumption will be equal to $pfc_{i1}$ (program does not allow variation over animal group, i)	$g/cm^2$
$pfc_{i3j}$	THO(J)	Lower threshold for density of consumed material (k) at which food consumption will be a constant function of $pfc_{i1}$ (program does not allow variation over animal group, i)	$g/cm^2$
$pmp_{ij}$	XK(I,J)	Relative amount of the diet of consumer species i made of consumed species j under ideal food availability conditions	--
$pas_j$	EF(J)	Efficiency of assimilation of $jth$ consumed biomass group	--
$pre_{i1}$	K1(I)	Coefficient of respiration function	g/day
$pre_{i2}$	K2(I)	Exponent of respiration function	--
DECOMPOSER VARIABLES			
<i>PSV's</i>			
$Mc_i$	MC(I)	Index of activity of $ith$ microbial type, $i = 1, \dots, 6$	$(cm^2)^{-1}$

## Appendix B. (Continued).

Algebraic	FORTTRAN	Description	Unit
$Mn_i$	MN(I)	Density of <i>ith</i> nitrogen form in the soil, $i = 1, \dots, 4$	$g/cm^2$
$So_i$	SO(I)	Density of <i>ith</i> soil constituent, $i = 1, \dots, 3$	$g/cm^2$
<i>ISV's</i>			
$dv_i$	DIV(I)	Reproduction rate of <i>ith</i> microbial type	$(sec)^{-1}$
$mu_i$	MCMAX(I)	Maximum value of $Mc_i$	$(cm^2)^{-1}$
$lc$	LEACH(PP)	Rate of leaching of soluble organic nitrate from plant litter	$(sec)^{-1}$
$au$	AMUP	Rate of uptake of ammonia nitrogen by plants	$g/(cm^2 \cdot sec)$
$nf$	NFIX	Rate of fixation of gaseous nitrogen from the atmosphere	$g/(cm^2 \cdot sec)$
$dn$	DENIT	Rate of loss of nitrate by denitrification	$g/(cm^2 \cdot sec)$
$nu$	NITUP	Rate of uptake of nitrate by plants	$g/(cm^2 \cdot sec)$
$op$	PARAB	Mathematical function giving parabolic curve	--
$sb$	SBSTR	Mathematical function giving a piecewise linear curve	--
$tp$	TPN	Sum of positive photosynthesis rates	$(sec)^{-1}$
$at$	ATANX	Mathematical function giving shifted arc tangent curve	--
$d3_i$	--	Dummy variable equated to PSV forming the substrate for the <i>ith</i> microbial type	$gm/cm^2$



## Appendix B. (Continued).

Algebraic	FORTTRAN	Description	Unit
<i>Parameters</i>			
$pMc_{i,1}$	MT1(1)	Minimum temperature for microbial functioning	$^{\circ}C$
$pMc_{i,2}$	MT2(1)	Maximum temperature for microbial functioning	$^{\circ}C$
$pMc_{i,3}$	MM1(1)	Minimum soil moisture for microbial functioning	cm
$pMc_{i,4}$	MM2(1)	Maximum soil moisture for microbial functioning	cm
$pMc_{i,5}$	SLD(1)	Rate of increase of microbial exponential growth factor ( $dv_j$ ) per unit of substrate density, $Mn_j$ , $j = 1, \dots, 3$	$cm^2/(sec \cdot g)$
$pMc_{i,6}$	VMND(1)	Level of substrate, $Mn_j$ , $j = 1, \dots, 3$ , below which $dv_j$ if zero	$g/cm^2$
$pMc_{i,7}$	MCMAXS(1)	Absolute maximum population of $i$ th microbial group	$(cm^2)^{-1}$
$pMc_{i,8}$	DIVS(1)	Absolute maximum exponential growth factor for $i$ th microbial group	$(sec)^{-1}$
$pSO_{1,i}$	SOMDIS(1)	Fraction of total soil organic matter in the $i$ th type, $i = 1$ -protein, $i = 2$ -cellulose, $i = 3$ -miscellaneous, $i = 4$ -not used	--
$pMu_{i,1}$	DECRATE(1)	Parameter associated with loss rate from $i$ th nitrogen form	$cm^2/sec$
pau	NPREF(3)	Parameter associated with ammonia uptake rate by plants	$cm^2/g$
pnu	NPREF(4)	Parameter associated with nitrate uptake rate by plants	$cm^2/g$
pnf	NFIXR	Parameter associated with nitrogen fixation rate by soil microorganisms	$g/sec$

## Appendix B. (Continued).

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Algebraic	FORTTRAN	Description	Unit
pdn	DENITR	Parameter associated with denitrification rate by soil microorganisms	cm <sup>2</sup> /g
pnx <sub>i1</sub>	PNX1(I)	Parameter related to location of threshold in nutrient index (nx)	g/cm <sup>2</sup>
pnx <sub>i2</sub>	PNX2(I)	Parameter related to rate of response of nutrient index to changes in soil nitrogen densities	cm <sup>2</sup> /g

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## Appendix C. Description of Program Organization and Code Listing

ODE is the name of a program described basically in Grassland Biome Technical Report No. 46<sup>1/</sup> designed to numerically integrate a set of differential equations. The user writes a FORTRAN subroutine to provide the derivatives given the state of the system. The computer implementation of PWNEE, MOD1 was constructed by modifying ODE; however, the basic structure remains as described in Technical Report No. 46. The following diagrams show the structure of ODE and the subprograms which calculate the derivatives of the PSV's. DER is the name of the main subroutine for derivative calculation; it operates by calling other subprograms for specific calculations. The program is implemented under the SCOPE 3.16 Executive system of the Control Data 6400 computer. The FORTRAN RUN compiler of that system is utilized; however, the program is basically ASA FORTRAN IV compatible.

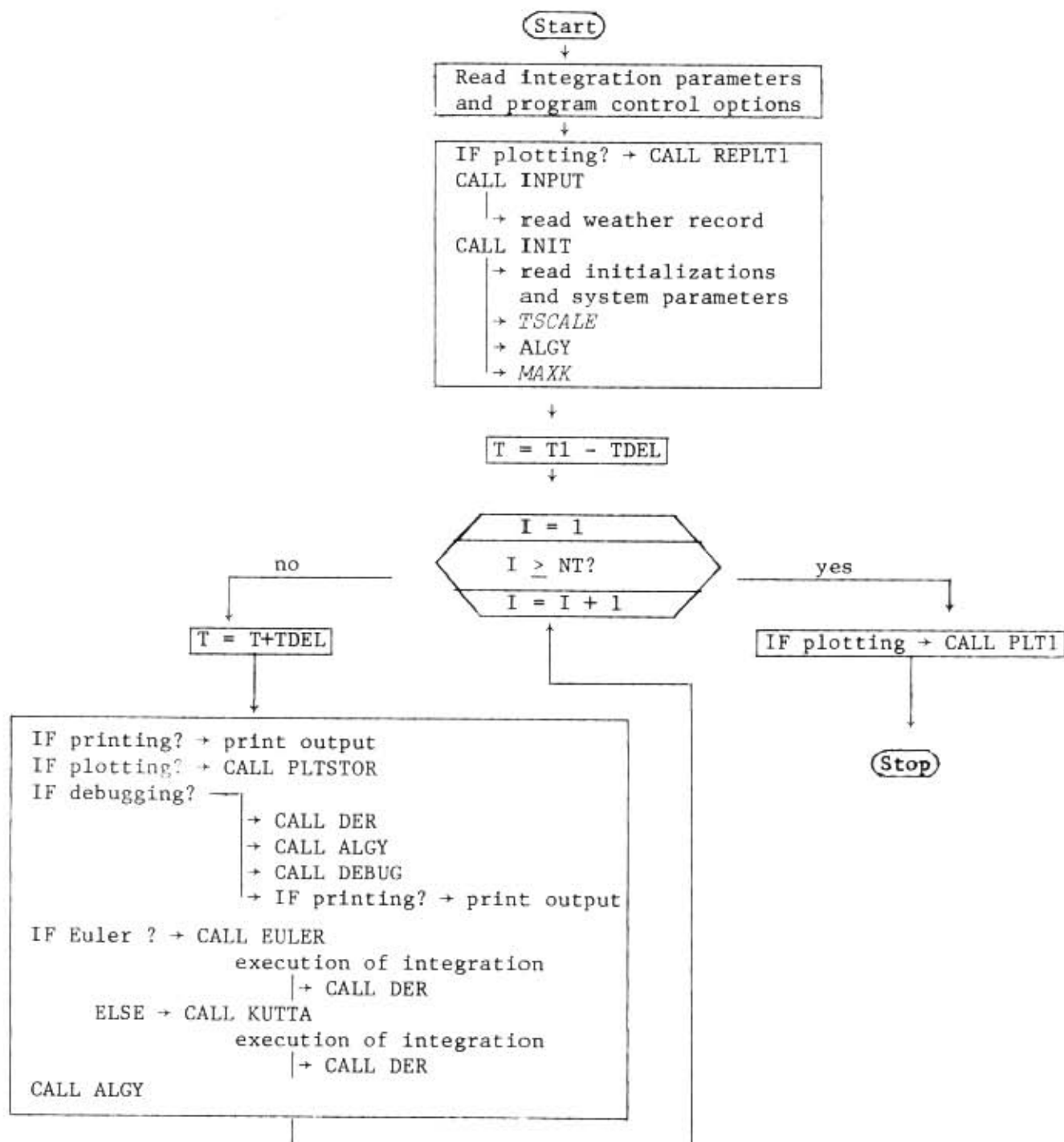
The code contains numerous coding inefficiencies of which we are aware. In our haste to concentrate on the biological mechanisms, we have ignored these but expect to correct them in future program versions, to be recorded from scratch rather than by modification of this program. As a result of these inefficiencies and incomplete analysis of the integration step sizes required, approximately 40 minutes are required for execution over a 140 day growing season with approximately 5% maximum overall error. We expect this to reduce to about 10 minutes when inefficiencies were corrected.

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<sup>1/</sup> Bledsoe, L. J. 1970. ODE: Numerical analysis for ordinary differential equations. U.S. IBP Grassland Biome Tech. Rep. No. 46. 42 p.

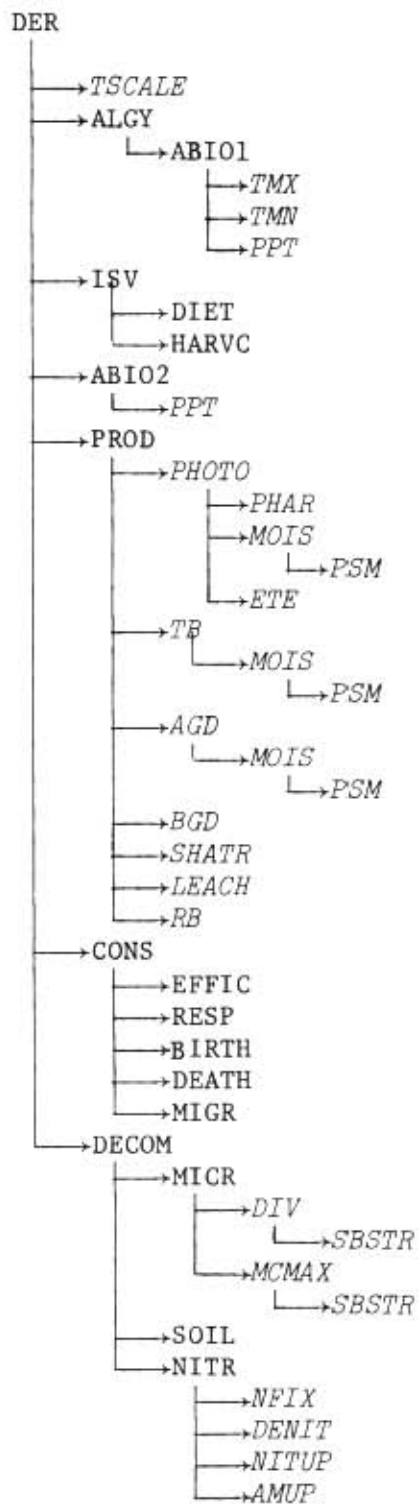
Calling sequence of subroutines (Roman) and functions (italics).

I. Main program and integration loop (Program ODE).



Note: Evaluation of derivatives needed for integration is implemented by the CALLs to DER and proceeding as follows.

## II. Derivative evaluation.



III. Description of subprograms. All subprograms whose function is not described by Technical Report No. 46 are briefly identified below.

Subprogram Name	Purpose
INPUT	Reads parameters associated with driving functions from system file WXDATA.
INIT	Reads parameters of model from file INPUT.
<i>TSCALE</i>	Calculates the independent variable in various time units from the basic time variable in seconds.
ALGY	Calculates all PSV's defined by algebraic, as opposed to differential, equations.
<i>MAXK</i>	Finds index of maximum number in array.
DER	Basic subroutine to convert PSV's from formal parameters to COMMON block L1 and calls derivative finding routines.
ABI01	Finds values for driving functions by calling other routines.
<i>TMX</i>	Looks up daily maximum temperature in parameter array.
<i>TMN</i>	Looks up daily minimum temperature in parameter array.
<i>PPT</i>	Looks up daily precipitation in parameter array.
ISV	Calculates values of certain ISV's needed in more than one model section (e.g., harvest rates).
DIET	Calculates food intake rates for consumers.
HARVC	Calculates harvest rates.
ABI02	Main routine for finding derivatives of abiotic PSV's.
PROD	Main routine for finding derivatives of producer PSV's.
<i>PHOTO</i>	Finds photosynthesis rate.
<i>PHAR</i>	Finds photosynthetically active radiation level.
<i>MOIS</i>	Finds moisture stress index.

Subprogram Name	Purpose
PSM	Finds fraction by weight of soil moisture from amount by volume in centimeters.
ETE	Finds nutrient stress index.
TB	Finds plant translocation rate.
AGD	Finds death rate of aboveground live biomass.
BGD	Finds death rate of belowground live biomass.
SHATR	Finds rate of transfer of standing dead plants to litter.
LEACH	Finds rate of leaching of organic material from plant litter.
RB	Finds respiration rate of belowground live plant biomass.
CONS	Main routine for finding derivatives of consumer PSV's.
EFFIC	Finds assimilation rates for consumers.
RESP	Finds respiration rates for consumers.
BIRTH	Finds birth rates for consumers.
DEATH	Finds death rates for consumers.
MIGR	Finds emigration and immigration rates for consumers.
DECOM	Main routine for calculated derivatives of decomposer variables.
MICR	Finds derivatives of microbial density PSV's.
DIV	Finds exponential reproduction coefficients for microbes.
MCMAX	Finds maximum population density for microbes.
SOIL	Finds derivatives of soil characteristic variables.
NITR	Finds derivatives of nitrogen concentration variables.
NFIX	Finds nitrogen fixation rate.
DENIT	Finds denitrification rate.
NITUP	Finds nitrate ion uptake rate by plants.
AMUP	Finds ammonia ion uptake rate by plants.

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Subprogram Name	Purpose
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The following subprograms are used purely for their mathematical, as opposed to biological, properties.

<i>SUM</i>	Adds elements of an array.
<i>ATANX</i>	Gives a double asymptote function based on the arc tangent curve.
<i>PARAB</i>	Gives an inverted (negative second derivative) symmetric paraboloid function normalized to a peak value of one.
<i>SBSTR</i>	Gives a piecewise linear function.
<i>COSX</i>	Gives cosine function normalized to vary between zero and one.

---



IV. Program listing.

```

PROGRAM ONE
1 (INPUT,OUTPUT,WXDATA,TAPF5=INPUT,TAPF6=OUTPUT,TAPF1=WXDATA,
1PWNDRG,TAPER=PWNDRG)
DIMENSION V(50),VP(50),ID(8),FC(8)
DIMENSION NCM(4),XX1(100),XX2(100),XX3(100),XX4(100),YY1(100),
- YY2(100),YY3(100),YY4(100)
COMMON/5/ADRG(4)
EXTERNAL DER
READ (5,1300) ID
1 READ(5,1300) FC
DECODE (5,100,FC) N1
IF (N1 ) 2,11,4
4 DECODE (50,100,FC) NCOM,NP,NT,T1,TDDEL,ACC,DEL,ITER
READ(5,1300)DR,DEFSOLV,PLOT,CHK,WRIT
2 WRITE (6,200) ID,DR,TT,T1,TDDEL,NT
IF (PLOT,FO,10RPLOT ) CALL RDPLT1(NNN,MMM,NCM,TSTFP,NX1,NX2,
- NX3,NX4,XX1,XXU,YYL,YYU)
WRITE (6,210) NCOM,NP,ACC,DEL,ITER
READ (5,300) (V(I),I=1,NCM)
300 FORMAT(7F10,6)
WRITE (6,3002) DR,DEFSOLV,PLOT,CHK,WRIT
3002 FORMAT(* SYSTEM OPTIONS -- *5R10//)
IF (N1 .LT.0) GO TO 3
NT=ISECDAY(NT) & T1=SECDAY(T1) & TDDEL=SECDAY(TDDEL)
CALL INPUT (NP)
3 T=T1-TDEL
CALL INIT(T,V)
IF (CHK,FO,10RCHKOUT )CALL CHKOUT
WRITE(6,2000)
2000 FORMAT(1H1)
WRITE (6,600)
DO 20 I=1,NT
T=T+TDEL & T2=T+TDEL
T3=TSCALE(T)
IF (WRIT,NF,10RNOWRIT ) WRITE (6,800) T3,(V(J),J=1,NCM),ADRG
I4=T3*100.
T3=FLOAT(I4)/100.
IF (PLOT,FO,10RPLOT ) CALL PLTSTOR(NNN,NCM,T3,NCM,V,TSTEP,
- XX1,XX2,XX3,XX4,YY1,YY2,YY3,YY4,NX1,NX2,NX3,NX4,XXL,XXU,
- YYL,YYU,ADRG)
IF (DR,NF,10HDEBUG ) GO TO 8
CALL DER(T,V,VP) & CALL ALGY(T,V) & CALL DEBUG(T,V,VP)
IF (WRIT,NF,10RNOWRIT ) WRITE (6,900) (VP(J),J=1,NCM)
8 IF (DEFSOLV,FO,10HEULER ) 5,6
5 CALL EULER(T,T2,V,NCM,DEL) & GO TO 7
6 CALL KUTTA(T,T2,V,NCM,DEL,ACC,ITER,DER)
7 CALL ALGY(T2,V)
IF (WRIT,NF,10RNOWRIT ) WRITE(6,1100)
20 CONTINUE
ENDEIF 8
IF (PLOT,NF,10RPLOT ) GO TO 1
WRITE(6,3000) (NCM(I),I=1,NNN)
3000 FORMAT(1H1,*PLOT OF VARIABLES NO.:#,4I5)
CALL PLT1(IFRR,TEMP,NNN,MMM,XXL,XXU,YYL,YYU,XX1,NX1,YY1,XX2,NX2,
- YY2,XX3,NX3,YY3,XX4,NX4,YY4)
IF (IFRR,NF,0) WRITE(6,3001) IERR
3001 FORMAT(1H0,15,* POINTS WERE NOT PLOTTED *)

```



















```

LOGICAL FUNCTION MID(A,B,C)
MID= .FALSE.
IF ((A.LE.C).AND.(B.GE.C)) MID=.TRUE.
RETURN
END

```

```

PWNEE
PWNEE
PWNEE
PWNEE
PWNEE

```

```

FUNCTION COSX(Y)
COSX=(COS(Y)+1.)*.5
RETURN
END

```

```

PWNEE
PWNEE
PWNEE
PWNEE

```

```

FUNCTION ATANX(X1,X2,X3)
GIVES SHIFTED ARC TANGENT RESPONSE TO ARGUMENT X3
X1 GIVES LOCATION OF INFLECTION POINT
X2 GIVES SPREAD WIDTH. .5 -.9
3.077... = TAN(.4*PI). .318... = 1./PI
C1=3.077683537*(1./X2)
ATANX=.3183098861*ATAN(C1*(X3-X1))+.5
RETURN
END

```

```

PWNEE
PWNEE
PWNEE
PWNEE
PWNEE
PWNEE
PWNEE
PWNEE

```

FUNCTION TSCALE(X)	PWNFE
COMMON/L3/T,TD,TDMOD,TH,THMOD,TMMOD,TWMOD,TY	PWNFF
DIMENSION XMO(13)	PWNFE
HANDLES SYSTEM TIME SCALING	PWNFE
DATA (XMO(I),I=1,13)/0.,31.,59.,90.,120.,151.,181.,212.,243.,	PWNFE
1273.,304.,334.,365./	PWNFE
Y=X & TD=Y*.1157407407E-4 & T=X	PWNFE
TDMOD=AMOD(TD,365.)&TH=Y*.2777777778E-3	PWNFF
THMOD=AMOD(TH,24.)	PWNFF
DO 10 I=1,12	PWNFE
IF (TDMOD.LT.XMO(I)) GO TO 1	PWNFE
1 CONTINUE	PWNFE
M=12 & I=13 & GO TO 2	PWNFE
1 M=I-1	PWNFF
2 N=(XMO(I)-XMO(I-1))*1.0001	PWNFF
S1=(T-XMO(M))*86400.)	PWNFE
TMMOD=(M-1.)+S1/(N*86400.)	PWNFE
TMMOD=AMOD(TMMOD,12.)	PWNFE
TWMOD=TDMOD*.1428571429	PWNFE
TY=TD*.2739726027E-02	PWNFE
TSCALE=TD	PWNFE
RETURN	PWNFE
END	PWNFE







```

SUBROUTINE PROD
C GIVES DIFFERENTIAL EQUATIONS FOR PRIMARY SYSTEM VARIABLES IN THE PROD
C PRODUCER COMPARTMENT PROD
COMMON/L1/T2,T3,SM,VA(4),VR,VS,VL,C(6),PN(6),W(6),AD,SH,MN(4), PROD
1MC(6),SO(4) PROD
COMMON/L2/DT2,DT3,DSM,DVA(4),DVR,DVS,DVL,DC(6),DPN(6),DW(6),DAD, PROD
1DSH,DMN(4),DMC(6),DSO(4) PROD
COMMON/L3/T,TD,TDMOD,TH,THMOD,TMMOD,TWMOD,TY PROD
COMMON/L4/HA(12),HAD,HSH,HB,HS,HL,HM PROD
COMMON/PROD1/T20(4),T21(4),CP(4),K1(4),K2(4),K3(4),K4(4),K5(4), PROD
1K6(4),K7(4),K8(4),FTE(4),L(4),SC(4),FPSI(4) PROD
COMMON/L5/T1,PP,IC,WS PROD
REAL IC PROD
REAL K1,K2,K3,K4,K5,K6,K7,K8,L PROD
C SUPPLIES RATES OF CHANGE IN PRODUCER COMPARTMENT FOR INPUT TO OTHER CO PROD
REAL LFACH PROD
TAGD=TTR=0. PROD
DO 12 I=1,4 PROD
C COMPUTE RATE OF CHANGE OF ABOVE GROUND BIOMASS BY SPECIES PROD
DVA(I)=FPSI(I)*PHOTO(I)-(TR(VA,I) +AGD(I)+HA(I)) PROD
TTR=TTR+TR(VA,I) PROD
12 TAGD=TAGD+AGD(I) PROD
C COMPUTES RATE OF CHANGE OF BELOW GROUND BIOMASS PROD
D1=RR(T3) PROD
DVR=TTR-(RGD(D1)+D1*VR+HR) PROD
C COMPUTES RATE OF CHANGE OF PLANT STANDING DEAD PROD
DVS=TAGD-(SHATR(WS)*VS+HS) PROD
C COMPUTES RATE OF CHANGE OF PLANT LITTER PROD
DVL=SHATR(WS)*VS-(HL+HM+LFACH(PP)*VL) PROD
RETURN PROD
END PROD

```

```

FUNCTION PHOTO(I)
C COMPUTES NET PHOTOSYNTHESIS AS A FUNCTION OF CANOPY TEMPERATURE,
C PHOTOSYNTHETICALLY ACTIVE RADIATION, SOIL MOISTURE, AND SOIL
C NUTRIENT STATUS.
COMMON/L1/T2,T3,SM,VA(4),VB,VS,VL,C(6),PN(6),W(6),AD,SH,MN(4),
IMC(6),S0(4)
COMMON/PR0D1/T20(4),T21(4),CR(4),K1(4),K2(4),K3(4),K4(4),K5(4),
1K6(4),K7(4),K8(4),ETE(4),L(4),SC(4),EPSI(4)
COMMON/L5/T1,PP,IC,WS
REAL IC
REAL K1,K2,K3,K4,K5,K6,K7,K8,L
REAL MOIS
S=PHAR(IC)
PHOTO=0.
IF(T2.LT.0.) RETURN
IF(T2.LT.T20(I).AND.S.GT.SC(I)) GO TO 10
IF(T2.GE.T20(I).AND.S.GT.SC(I)) GO TO 11
C NET PHOTOSYN. ABOVE COM TEMP. AND BELOW COMP. NET RADIATION
PHOTO=-CR(I)*VA(I)*K6(I)*((SC(I)-S)/SC(I))*((T2/T21(I))
1**K7(I))*EXP((K7(I)/K8(I))*(1.-(T2/T21(I))**K8(I)))*MOIS(I)*ETE(I)
PHOTO=PHOTO*L(I)
RETURN
C FORMULA FOR NET PHOTOSYNTHESIS BELOW COMPENSATION TEMPERATURE
10 D2=S/(1.+K3(I)*S)
D3=SC(I)/(1.+K3(I)*SC(I))
D4=T20(I)-T2
D5=EXP(-K2(I)*(T20(I)-T2))
PHOTO =CR(I)*VA(I)*L(I)*MOIS(I)*ETE(I)*(D2-D3)*D4*D5
PHOTO=PHOTO*K1(I)
RETURN
C NET PHOTOSYNTHESIS ABOVE COMPENSATION TEMP. AND COMP. NET RADIATION
11 PHOTO =-CR(I)*VA(I)*K4(I)* (T2-T20(I))*EXP(-K5(I)*(T2-T20(I)))*
1MOIS(I)*ETE(I)
RETURN
END

```





FUNCTION RGD(R)

C FOR A FIRST PASS DEATH RATE OF BELOW GROUND PARTS WILL BE HALF THE RES  
 COMMON/L1/T2,T3,SM,VA(4),VB,VS,VL,C(6),PN(6),W(6),AD,SH,MN(4),  
 IMC(6),SO(4)  
 RGD=(R\*VR)/2.  
 RETURN  
 END

PROD  
 PROD  
 PROD  
 PROD  
 PROD  
 PROD

FUNCTION AGD(T)

C DEATH RATE OF ABOVE GROUND PARTS BY SPECIES  
 C WILTING BEGINS AT 35 DEG. CENT. FOR ALL SPECIES IN FIRST PASS MODULE  
 COMMON/L1/T2,T3,SM,VA(4),VB,VS,VL,C(6),PN(6),W(6),AD,SH,MN(4),  
 IMC(6),SO(4)  
 REAL MOIS  
 AGD=VA(T)\*(1.-MOIS(T))\*ATANX(35.,42.1600484521,T2)\*.43E-8  
 RETURN  
 END

PROD  
 PROD  
 PROD  
 PROD  
 PROD  
 PROD  
 PROD

REAL FUNCTION MOIS(I)

C COMPUTES PERCENTAGE OF SOIL MOISTURE CAPACITY IN TOP 20 CM OF SOIL  
 C ASSUME MOISTURE STRESS IS AN ARCTANGENT FUNCTION OF THE PERCENTAGE  
 C OF SOIL MOISTURE CAPACITY IN THE TOP 20 CM OF THE SOIL  
 COMMON/L1/T2,T3,SM,VA(4),VB,VS,VL,C(6),PN(6),W(6),AD,SH,MN(4),  
 IMC(6),SO(4)  
 COMMON/PR003/PH1,RR2,RR3,PM01(4),PM02(4)  
 PM01(T)=3.077683537/PM01(T)  
 MOIS=ATANX(PM01(T),PM02(T),PSM(SM))  
 RETURN  
 END

PROD  
 PROD  
 PROD  
 PROD  
 PROD  
 PROD  
 PROD  
 PROD  
 PROD  
 PROD

FUNCTION SHATR(WS)

C COMPUTES SHATR RATE OF STANDING DEAD AS A FUNCTION OF WIND SPEED  
 IF(WS.LE.223.5)SHATR=.005  
 IF(WS.GT.223.5)SHATR=.005+(2.2148E-04)\*WS  
 SHATR=SHATR\*1.1574074074E-5  
 RETURN  
 END

PROD  
 PROD  
 PROD  
 PROD  
 PROD  
 PROD

REAL FUNCTION LEACH(RP)

C COMPUTES DIRECT LEACHING OF LITTER AS A FUNCTION OF RAINFALL  
 C ASSUME LEACHING IS A LINEAR FUNCTIN OF RAINFALL  
 LEACH=.03448\*RP  
 RETURN  
 END

PROD  
 PROD  
 PROD  
 PROD  
 PROD

```

SUBROUTINE CONS
COMMON/L1/T2,T3,SM,VA(4),VR,VS,VL,C(6),PN(6),W(6),AD,SH,MN(4),
1MC(6),SO(4)
COMMON/L2/DT2,DT3,DSM,DVA(4),DVR,DVS,DVL,DC(6),DPN(6),DW(6),DAD,
1DSH,DMN(4),DMC(6),DSO(4)
COMMON/L3/T,TD,TDMOD,TH,THMOD,TMMOD,TWMOD,TY
COMMON/L4/HA(12),HAD,HS,HR,HS,HL,HM
COMMON/CONS/XF(5),XK(5,12),TH0(12),TT(12),EF(12),MJ(5),TWU(5),TWL(
15),AF(5),AK(5,12),HC(5,12),XC(12),B(5),RE(5),D(5),XIM(5),EM(5),EFF
2(5),XINT(5)
CONS
C
C CONSUMED SPECIES 1 = BUJR
CONS
C CONSUMED SPECIES 2 = AGSM
CONS
C CONSUMED SPECIES 3 = CA
CONS
C CONSUMED SPECIES 4 = OPPD
CONS
C CONSUMED SPECIES 5 = REFLOW GROUND PARTS
CONS
C CONSUMED SPECIES 6 = STANDING DEAD
CONS
C CONSUMED SPECIES 7 = LITTER
CONS
C CONSUMED SPECIES 8 = CONSUMER SPECIES 1 = JACK RABBIT
CONS
C CONSUMED SPECIES 9 = CONSUMER SPECIES 2 = COW
CONS
C CONSUMED SPECIES 10= CONSUMER SPECIES 2 = COYOTE
CONS
C CONSUMED SPECIES 11= CONSUMER SPECIES 3 = LARK BUNTING
CONS
C CONSUMED SPECIES 12= CONSUMER SPECIES 5 = GRASSHOPPER
CONS
C XF(I)=FOOD CONSUMPTION RATE FOR CONSUMER SPECIES I UNDER IDEAL
CONS
C FOOD AVAILABILITY CONDITIONS (G/G/DAY)
CONS
C AF(I)=ACTUAL FOOD CONSUMPTION RATE FOR CONSUMER SPECIES I
CONS
C XK(I,J)=AMOUNT OF DIET OF CONSUMER SPECIES I MADE UP OF CONSUMED
CONS
C SPECIES J UNDER IDEAL FOOD AVAILABILITY CONDITIONS
CONS
C AK(I,J)=ACTUAL AMOUNT OF DIET OF CONSUMER SPECIES I MADE UP OF
CONS
C CONSUMED SPECIES J
CONS
C TH0(J)=THRESHOLD DENSITY BELOW WHICH CONSUMED SPECIES J CEASES
CONS
C TO BE CONSUMED
CONS
C MJ(I)=MOST PREFERRED FOOD SOURCE FOR CONSUMER SPECIES I
CONS
C
CONS
C CALL FFFIC
CONS
C CALL RESP
CONS
C CALL BIRTH
CONS
C CALL DEATH
CONS
C CALL MIGR
CONS
C DO 300K=1,5
CONS
300 XINT(K)=W(K)*EFF(K)*AF(K)
CONS
C DO 100I=1,5
CONS
C II=I+7
CONS
C
CONS
C HA(J), J=1,12, IS COMPUTED IN SUBROUTINE HARVC
CONS
C AF(I), I=1,5, IS COMPUTED IN SUBROUTINE DIET
CONS
C FFF(I) IS COMPUTED IN FUNCTION SUBROUTINE FFF(I)
CONS
C RF(I), I=1,5, IS COMPUTED IN SUBROUTINE RESP
CONS
C
CONS
C DW(I)=W(I)*EFF(I)*AF(I)-RF(I)
CONS
101 DPN(I)=PN(I)*(B(I)-D(I))-HA(II)/W(I)+XIM(I)-EM(I)
CONS
100 CONTINUE
CONS
C
CONS
C MUST GET DEAD ANIMAL BMASS (DAD) AND ANIMAL FECES FOR ALL
CONS
C CONSUMER SPECIES
CONS
C
C DSH=0.
CONS

```

```
      DAD=0.  
      DO 200 I=1,5  
      II=I+7  
200   DSH=DSH+XC(II)*(1.-FFF(I))*AF(I)  
      DAD=DAD+XC(II)*D(I)  
      DSH=DSH-HSH  
      DAD=DAD-HAD  
      RETURN  
      END
```

```
CONS  
CONS  
CONS  
CONS  
CONS  
CONS  
CONS  
CONS  
CONS
```





SUBROUTINE EFFIC

CONS

THIS SUBROUTINE COMPUTES THE ASSIMILATION EFFICIENCY FOR THE FOOD  
CONSUMED BY THE CONSUMER SPECIES

CONS

CONS

CONS

CONS

FF(J)=ASSIMILATION EFFICIENCY OF CONSUMED SPECIES J, J=1,12

CONS

CONS

COMMON/CONS/XF(5),XK(5,12),TH0(12),TT(12),EF(12),MJ(5),TWU(5),TWL(15),AF(5),AK(5,12),HC(5,12),XC(12),R(5),RE(5),D(5),XIM(5),FM(5),EFF2(5),XINT(5)

CONS

CONS

CONS

DIMENSION XF(12)

CONS

DO10 I=1,5

CONS

DO1J=1,12

CONS

XF(J)=FF(J)\*AK(I,J)

CONS

FFF(I)=SUM(XF,12)

CONS

CONTINUE

CONS

RETURN

CONS

END

CONS

FUNCTION MAXK(I)

CONS

FOR ANY CONSUMER SPECIES I, THIS SUBROUTINE COMPUTES THE MOST  
PREFERRED CONSUMED SPECIES J

CONS

CONS

CONS

CONS

COMMON/CONS/XF(5),XK(5,12),TH0(12),TT(12),EF(12),MJ(5),TWU(5),TWL(15),AF(5),AK(5,12),HC(5,12),XC(12),R(5),RE(5),D(5),XIM(5),EM(5),EFF2(5),XINT(5)

CONS

CONS

CONS

XX=XK(I,1)

CONS

MAXK=1

CONS

DO10 J=2,12

CONS

YMX=AMAX1(XX,XK(I,J))

CONS

IF(YMX.LE.XX)GO TO 10

CONS

MAXK=J

CONS

XX=YMX

CONS

CONTINUE

CONS

RETURN

CONS

END

CONS

FUNCTION SUM(Y,N)

CONS

DIMENSION Y(1)

CONS

SUM=0.

CONS

DO1J=1,N

CONS

SUM=SUM +Y(J)

CONS

RETURN

CONS

END

CONS

```

SUBROUTINE RESP                                     CONS
                                                    CONS
THIS SUBROUTINE COMPUTES THE RESPIRATION RATE (G/IND/DAY) FOR THE  CONS
CONSUMER SPECIES                                     CONS
                                                    CONS
COMMON/L1/T2,T3,SM,VA(4),VB,VS,VL,C(6),PN(6),W(6),AD,SH,MN(4),  CONS
IMC(6),SO(4)                                        CONS
COMMON/CONS/XF(5),XK(5,12),TH0(12),TT(12),EF(12),MJ(5),TWU(5),TWL(  CONS
15),AF(5),AK(5,12),HC(5,12),XC(12),B(5),RE(5),D(5),XIM(5),EM(5),EFF  CONS
2(5),XINT(5)                                        CONS
COMMON/CONS2/RE1(5),RE2(5)                         CONS
DO 10 I=1,5                                         CONS
RE(I)=0.                                            CONS
10 IF(W(I).GT.0.) RE(I)=RE1(I)*W(I)**RE2(I)        CONS
RETURN                                              CONS
END                                                CONS

SUBROUTINE BIRTH                                     CONS
COMMON/CONS/XF(5),XK(5,12),TH0(12),TT(12),EF(12),MJ(5),TWU(5),TWL(  CONS
15),AF(5),AK(5,12),HC(5,12),XC(12),B(5),RE(5),D(5),XIM(5),EM(5),EFF  CONS
2(5),XINT(5)                                        CONS
COMMON/I3/T,TD,TDMOD,TH,THMOD,TMMOD,TWMOD,TY       CONS
THIS SUBROUTINE COMPUTES DAILY INSTANTANEOUS BIRTH RATES FOR  CONS
CONSUMER SPECIES                                     CONS
DO 1 I=1,5                                         CONS
R(I)=0.                                            CONS
IF(TDMOD.LE.252..AND.TDMOD.GE.58.) R(1)=.007*(1.-.0046*(TDMOD-58.))  CONS
IF(TDMOD.LE.168..AND.TDMOD.GE.155.) R(4)=.0308    CONS
IF(TDMOD.LE.203..AND.TDMOD.GE.190.) R(4)=.0102    CONS
IF(TDMOD.LE.224..AND.TDMOD.GE.162.) R(5)=.0214*(1.-.0145*(TDMOD-162  CONS
1.))                                               CONS
RETURN                                              CONS
END                                                CONS

SUBROUTINE DEATH                                     CONS
COMMON/CONS/XF(5),XK(5,12),TH0(12),TT(12),EF(12),MJ(5),TWU(5),TWL(  CONS
15),AF(5),AK(5,12),HC(5,12),XC(12),B(5),RE(5),D(5),XIM(5),EM(5),EFF  CONS
2(5),XINT(5)                                        CONS
COMMON/I3/T,TD,TDMOD,TH,THMOD,TMMOD,TWMOD,TY       CONS
THIS SUBROUTINE COMPUTES THE INSTANTANEOUS DAILY NATURAL MORTALITY  CONS
RATES FOR THE CONSUMER SPECIES.                   CONS
D(1)=.0022                                         CONS
D(2)=0.                                            CONS
D(3)=0.                                            CONS
D(4)=.0035                                         CONS
D(5)=0.                                            CONS
IF(TDMOD.LE.154.) D(4)=.0021                     CONS
IF(TDMOD.LE.259..AND.TDMOD.GE.162.) D(5)=.0071   CONS
RETURN                                              CONS
END                                                CONS

```







```

FUNCTION DENIT(NITR)
COMMON/1/T2,T3,SM,VA(4),VB,VS,VL,C(6),PN(6),W(6),AD,SH,MN(4),
1MC(6),SO(4)
REAL MN,MC
COMMON/DECOM1/DIVS(6),MCMAXS(6),MT1(6),MT2(6),MM1(6),MM2(6),
1SLD(6),SLMX(6),VMND(6),VMNMX(6),SRMN(6),SOMDIS(4),DECRATE(6),
2SOMDEC,NFIXR,DENITR,NPREF(4)
REAL MT1,MCMAXS,MT2,MM1,MM2,NFIXR,NPREF
REAL NITR
DENIT=DENITR*NITR*MC(4)
RETURN
END

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REAL FUNCTION NITUP(DUM)
COMMON/1/T2,T3,SM,V(4),VP,VS,VL,C(6),PN(6),W(6),AD,SH,MN(4),
1MC(6),SO(4)
COMMON/DECOM1/DIVS(6),MCMAXS(6),MT1(6),MT2(6),MM1(6),MM2(6),
1SLD(6),SLMX(6),VMND(6),VMNMX(6),SRMN(6),SOMDIS(4),DECRATE(6),
2SOMDEC,NFIXR,DENITR,NPREF(4)
REAL MT1,MCMAXS,MT2,MM1,MM2,NFIXR,NPREF
COMMON/DECOM2/TPN
REAL MN
NITUP=NPREF(4)*MN(4)*TPN
RETURN
END

```

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```

FUNCTION AMUP(DUM)
COMMON/1/T2,T3,SM,V(4),VP,VS,VL,C(6),PN(6),W(6),AD,SH,MN(4),
1MC(6),SO(4)
COMMON/DECOM1/DIVS(6),MCMAXS(6),MT1(6),MT2(6),MM1(6),MM2(6),
1SLD(6),SLMX(6),VMND(6),VMNMX(6),SRMN(6),SOMDIS(4),DECRATE(6),
2SOMDEC,NFIXR,DENITR,NPREF(4)
REAL MT1,MCMAXS,MT2,MM1,MM2,NFIXR,NPREF
COMMON/DECOM2/TPN
REAL MN
AMUP=NPREF(3)*MN(3)*TPN
RETURN
END

```

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```

FUNCTION DIV(I)
COMMON/L1/T2,T3,SM,VA(4),VR,VS,VL,C(6),PN(6),W(6),AD,SH,MN(4),
]MC(6),SO(4)
REAL MN,MC
COMMON/DECOM1/DIVS(6),MCMAXS(6),MT1(6),MT2(6),MM1(6),MM2(6),
]SLD(6),SLMX(6),VMND(6),VMNMX(6),SBMN(6),SOMDIS(4),DECRATE(6),
]SOMDEC,NFIXR,DENITR,NPREF(4)
REAL MT1,MCMAXS,MT2,MM1,MM2,NFIXR,NPREF
I=SRMN(I)
DIV=DIVS(I)*PARAR(MT1(I),MT2(I),T3)*PARAR(MM1(I),MM2(I),SM)*
]SRSTR(SLD(I),VMND(I),MN(J))
RETURN
END

```

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```

REAL FUNCTION MCMAX(K)
COMMON/L1/T2,T3,SM,VA(4),VR,VS,VL,C(6),PN(6),W(6),AD,SH,MN(4),
]MC(6),SO(4)
REAL MN,MC
COMMON/DECOM1/DIVS(6),MCMAXS(6),MT1(6),MT2(6),MM1(6),MM2(6),
]SLD(6),SLMX(6),VMND(6),VMNMX(6),SBMN(6),SOMDIS(4),DECRATE(6),
]SOMDEC,NFIXR,DENITR,NPREF(4)
REAL MT1,MCMAXS,MT2,MM1,MM2,NFIXR,NPREF
T=K $ I=SRMN(I)
MCMAX=MCMAXS(I)*PARAR(MT1(I),MT2(I),T3)*PARAR(MM1(I),MM2(I),SM)*
]SRSTR(SLMX(I),VMNMX(I),MN(J))
IF (MCMAX,LT,2.F+8) MCMAX=2.F+8
RETURN
END

```

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```

FUNCTION PARAR(X1,X2,X)
LOGICAL MTI
PARAR=0.
IF (.N.MID(X1,X2,X)) RETURN
C1=X2-X1
PARAR=-4.*(X-X1)*(X-X2)/(C1*C1)
RETURN
END

```

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```

FUNCTION SRSTR(SL,VMN,V)
SRSTR=.001
IF (V,LE,VMN) RETURN
SRSTR=1.
IF (SL,EQ,0.) RETURN
SRSTR=(V-VMN)*SL
RETURN
END

```

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```

SUBROUTINE PLT1(JFRR,TFMP,N,M,XL,XU,YL,YU,X1,NOX1,Y1,X2,NOX2,Y2, PLOT
IX3,NOX3,Y3,X4,NOX4,Y4) PLOT
DIMENSION X1(1),Y1(1),X2(1),Y2(1),MASK(10),PLATE(11),STAMP(5) PLOT
1,X3(1),Y3(1),X4(1),Y4(1) PLOT
DIMENSION KIT(44),KITE(11),TSCAL(11) PLOT
DIMENSION SCAL(11) PLOT
INTEGER PLATE,STAMP PLOT
C INITIALIZATION OF STAMPER AND MASKER PLOT
MASK(10)=0000000000000000000077B PLOT
MASK(1)=7700000000000000000000R PLOT
MASK(2)=0077000000000000000000R PLOT
DO2 I=1,7 PLOT
2 MASK(-I+10)=64*MASK(-I+11) PLOT
STAMP(1)=10H***** PLOT
STAMP(2)=10H0000000000 PLOT
STAMP(3)=10HXXXXXXXXXX PLOT
STAMP(4)=10HHHHHHHHHH PLOT
STAMP(5)=10HRRRRRRRRRR PLOT
DO 200 I=1,44 PLOT
KIT(I)=10H, PLOT
IF(I.GT.11) GO TO 200 PLOT
KITE(I)=10HV PLOT
TSCAL(I)=10H0123456789 PLOT
200 CONTINUE PLOT
MPIATE=10H PLOT
MP=10H+ PLOT
SINCY=(YU-YL)/100, PLOT
SINCX=(XU-XL)/(10.*M) PLOT
HINCY=(YU-YL)/10, PLOT
IEF=10*M+1 PLOT
DO1 I=1,11 PLOT
1 SCAL(I)=YL+(I-1)*HINCY PLOT
IFRR=0 PLOT
PRINT2000,SCAL PLOT
PRINT 3000,(KIT(K),K=1,44),(KITE(K),K=1,11),(TSCAL(K),K=1,11) PLOT
DO 100 LCTR=1,IEF PLOT
C INITIALIZE PLATE (ERASE PREVIOUS STAMPINGS) PLOT
NCTR=MOD(LCTR-1,10) PLOT
IF(NCTR)5,3,5 PLOT
3 DO 6 K=1,11 PLOT
6 PLATE(K)=MP PLOT
GO TO 11 PLOT
5 DO 4 K=1,11 PLOT
4 PLATE(K)=MPLATE PLOT
C SEARCH PROCESS BEGINS FOR THE X1 ARRAY PLOT
11 CALL SUBPLT(X1,Y1,1,NOX1,LCTR,PLATE,MASK,STAMP,IEFR,SINCX,SINCY,XL PLOT
1,YL,XU,YU) PLOT
IF(N-1)99,101,21 PLOT
21 CALL SUBPLT(X2,Y2,2,NOX2,LCTR,PLATE,MASK,STAMP,IEFR,SINCX,SINCY,XL PLOT
1,YL,XU,YU) PLOT
IF(N-2)99,101,31 PLOT
31 CALL SUBPLT(X3,Y3,3,NOX3,LCTR,PLATE,MASK,STAMP,IEFR,SINCX,SINCY,XL PLOT
1,YL,XU,YU) PLOT
IF(N-3)99,101,41 PLOT
41 CALL SUBPLT(X4,Y4,4,NOX4,LCTR,PLATE,MASK,STAMP,IEFR,SINCX,SINCY,XL PLOT
1,YL,XU,YU) PLOT
101 IF(NCTR)106,105,106 PLOT
PLOT

```





```

SUBROUTINE SUBPLT(TX, TY, NN, NOX, LCTR, PLATE, MASK, STAMP, JFRR, SINCX, SI PLOT
INCY, XL, YL, XU, YU) PLOT
INTEGER PLATE, STAMP PLOT
DIMENSION TX(1), TY(1), MASK(10), PLATE(11), STAMP(5), IPW(101), IPC(101 PLOT
1), IPP(5), ISYM(101) PLOT
IF(NN-1)99,30,21 PLOT
30 ISTD=0 PLOT
IF(LCTR-1)99,31,21 PLOT
31 DO 6 ISTR=1,5 PLOT
6 IPP(ISTR)=1 PLOT
21 ID=IPP(NN) PLOT
IF(ID-NOX)3,3,2 PLOT
3 ICPTR=ID PLOT
DO 1 IPTR=ICPTR,NOX PLOT
IF((TX(IPTR).LT.XL).OR.(TX(IPTR).GT.XU)) GO TO 101 PLOT
TX=(TX(IPTR)-XL)/SINCX+1.5 PLOT
8 IF(IX-LCTR) 1+ 10* 1 PLOT
10 IF((TY(IPTR).LT.YL).OR.(TY(IPTR).GT.YU)) GO TO 101 PLOT
TY=(TY(IPTR)-YL)/SINCX+1.5 PLOT
11 IPWY=1+(TY-1)/10 PLOT
IPWC=IY + 10 -(10*IPWY) PLOT
IF(ISTD)57,57,58 PLOT
58 DO 12 KK=1,ISTD PLOT
IF(IPWY - IPW(KK))12,13,12 PLOT
13 IF(IPWC-IPC(KK))12,14,12 PLOT
14 IF(ISYM(KK)-NN)15,9,15 PLOT
12 CONTINUE PLOT
57 PLATE(IPWY)=(PLATE(IPWY).AND..NOT.MASK(IPWC)).OR.(STAMP(NN).AND.MA PLOT
ISK(IPWC)) PLOT
ISTD=ISTD*1 PLOT
IPW(ISTD)=IPWY PLOT
IPC(ISTD)=IPWC PLOT
ISYM(ISTD)=NN PLOT
GO TO 9 PLOT
101 JFRR=JFRR+1 PLOT
GO TO 9 PLOT
15 PLATE(IPWY)=(PLATE(IPWY).AND..NOT.MASK(IPWC)).OR.(STAMP( 5).AND.MA PLOT
ISK(IPWC)) PLOT
9 IF(IPTR-ID)17,17,1 PLOT
9 IF(IPTR-ID)35,17,1 PLOT
17 ID=ID+1 PLOT
1 CONTINUE PLOT
IPP(NN)=ID PLOT
2 RETURN PLOT
99 PRINT 35 PLOT
35 FORMAT( 34HITROUBLE IN SUBPLT WITH NN OR LCTR) PLOT
CALL EXIT PLOT
END PLOT

```

## Appendix D. Description of Program Input/Output Format and Parameter Values

Following is a description and listing of the data cards read by the program. The main program (ODE) reads in the first three cards and the group of cards labeled INIT 1 through INIT 7. The remaining data cards are read by subroutine INIT, and the labels in columns 73 through 80 refer to the name of the labeled common block into which the values on the card are stored.

A typical sample of printed output appears on the next page. Specific items are described below.

Item No.	Description
1	These are integration parameters used in both the Euler and Kutta methods. The first is the relative accuracy desired when integrating by the Kutta method. The second is a fraction which, when multiplied by the time increment, is the integration step size. The third is the maximum number of halvings of the integration step size in the Kutta method.
2	These are system options. Here requested are: the debugging options which outputs on an external storage devise (unit no. 8) the PSV's and their derivatives and most ISV's, integration by a fifth order Runge-Kutta method, no plotting, no calls to subroutine CHKOUT, and printer output requested.
3	This is a sampling every 20 days of the weather record used as driving variables.
4	This is an echo check of the parameter values read into each labeled common block.
5	This is a sample of simulation printed output for two days. Printed is the time in days at the left followed by the values of the PSV's from left to right, followed by their corresponding derivatives.

DE SOLUTION  
 PANEE MODEL MOD 1 -- ARJO. PROO. CONS. DECOM -- DECK SETUP 1/25/71

TIME STARTS AT 140.500, INCREMENTS BY 1.00000 FOR 100 STEPS

46 EQUATIONS, 730 CONSTANTS  
 KUTTA PARAMETERS ARE .01000  
 SYSTEM OPTIONS -- DERUG KUTTA .10000 NOCHECK WRIT

DRIVING FUNCTION  
 TMIN, TMAX, PPT

1	-16.11	-1.567	0.
21	-6.667	13.89	0.
41	-11.67	11.11	0.
61	-8.333	2.222	0.
81	-6.667	10.56	0.
101	-5.556	23.33	0.
121	6.111	23.89	0.
141	4.444	20.56	0.
161	8.889	18.89	0.
181	12.22	27.22	0.
201	13.89	31.11	0.
221	11.11	17.78	0.
241	6.111	18.33	0.
261	8.889	25.56	0.
281	1.111	7.778	0.
301	-1.667	22.78	0.
321	-16.67	-3.889	0.
341	-12.78	-1.111	0.
361	-17.78	-5.556	0.
381	-9.444	12.22	0.
401	-5.000	11.67	0.
421	-5.556	15.56	0.
441	-2.222	15.56	0.
461	0.	22.78	0.
481	-5.000	11.11	0.
501	6.111	13.89	0.
521	6.667	32.22	0.
541	7.778	17.78	0.
561	15.00	32.22	0.
581	12.78	31.11	0.
601	12.22	24.44	0.
621	5.667	24.33	0.
641	2.778	26.11	0.
661	1.111	12.22	0.
681	-2.222	11.67	0.
701	-5.556	15.56	0.
721	-4.444	12.22	0.

②

①

③

SYSTEM PARAMETERS

BIOTIC  
COMMON ARI01  
SC.PHEXP.STI.AG.SMI.A5  
1.50000E-02 .25000 6.41667E-04 4.01000E-07

PARMICEP

COMMON PARM01  
T20(4).T21(4).K3(4).K3(4).K3(4).K5(4).K6(4).K7(4).K8(4).ETE(4).L(4).SC(4).EPSI(4)  
42.000 34.000 74.000 50.000 .20100 .21100 .18300 1.0000 1.0000  
1.0000 1.0000 3.34000E-04 2.05500E-04 2.23000E-04 5.70300E-05 .16667 .25000 .10000  
59.000 54.900 54.900 54.900 1.42860E-05 1.66670E-05 1.66670E-05 1.20000E-05 2.32558E-02  
2.32555E-02 1.66667E-02 6.94000E-07 4.94000E-07 8.94000E-07 6.02000E-07 .40000 .40000  
.50000 .50000 1.00000 1.00000 1.00000 1.00000 1.00000 1.00000 1.00000  
1.0000 .15000 1.70000E-03 1.70000E-03 1.70000E-03 1.70000E-03 .50000 .50000  
1.0000 1.0000 .80000

COMMON HARV1

TOLTT1.TOLTT2.TUMULT.TMXLT  
1.00000E-02 2.00000E-04 0. 6.00000E+01

COMMON PARM02

VAROK.VAROK.TRSI(1).TRMX.TMSLP2  
5.00000E-04 2.00000E-04 2.00000E-05 1.00000E-04  
5.00000E-04 1.00000E-04 1.00000E-04 3.00000E-04  
7.00000E-08 5.00000E-04 1.00000E-07 7.00000E-08  
1.14000E-04 1.16000E-04 4.00000E-06 4.00000E-06  
2.32000E-05 1.16000E-04 4.00000E-04 1.33000E-04

COMMON PARM03

HR1.PH2.PH3  
1.01574E-04 4.40000E+01 4.00000E+00  
PMO1(4).PMO2(4)  
5.00000E+01 2.50000E+01 1.00000E+01 1.66667E+01  
4.00000E-02 1.40000E-01 3.00000E-01 1.80000E-01

COMMON COMS2

DEF1(5).DEF2(5)  
5.40000E-01 2.10000E+00 3.40000E+00 2.80000E-01 1.32000E-01  
5.70000E-01 7.50000E-01 4.70000E-01 7.50000E-01 8.40000E-01

COMMON COMS1

KE 20000 20000 20000 20000 15000 15000  
KX 5.00000E-02 1.2000 7.00000E-02 0.27000  
0. 0. 0. 0. 0. 0.  
KX 25000 25000 25000 25000 1.50000E-07 0.  
0. 0. 0. 0. 0. 0.  
KX 45000 45000 45000 45000 5.00000E-02 10000  
0. 0. 0. 0. 0. 0.  
KX 17500 17500 17500 17500 0.65000  
0. 0. 0. 0. 0. 0.  
TT 2.00000E-03 2.00000E-04 5.00000E-04 2.00000E-03 2.82000E-02 4.70000E-03 2.40000E-03  
2.50000E-05 1.0000 1.0000 5.40000E-07 7.50000E-05  
T-0 1.00000E-03 1.00000E-04 2.00000E-04 1.00000E-03 1.41000E-02 2.30000E-03 1.20000E-03  
1.25000E-05 0. 0. 0. 0. 0. 0. 0.  
T-1 100.00 100.00 100.00 1.41000E+05 9000.0 9000.0 30.000 30.000 .30000



5  
TIME VARIABLE VALUES

140	0.	0.	-12.500	20.000	1.0000	3.00000E-04	1.00000E-04	1.00000E-05	3.00000E-04	8.00000E-02
	3.00000E-03	3.00000E-03	3.4441E-05	5.20360E-05	8.99330E-09	0.	1.18780E-04	0.	9.95610E-07	2.00000E-10
	1.00000E-12	0.	5.00000E-04	0.	83.814	2.60180E+05	8993.3	35.280	0.	0.
	4.02840E-07	3.34720E-05	1.43000E-05	1.43000E-05	1.43000E-05	2.00000E+11	2.00000E+11	2.00000E+11	2.00000E+11	2.00000E+11
	2.00000E+11	2.00000E+11	1.4000	28000	1.1200	0.	-12.500	0.	0.	0.
DERIVATIVE	0.	0.	0.	-8.52831E-05	-4.01000E-07	4.63579E-07	2.91845E-07	5.08629E-08	-1.80341E-10	-1.08102E-06
	-3.61040E-09	3.52544E-09	0.	0.	0.	0.	0.	0.	2.47001E-14	0.
	0.	0.	-1.06843E-19	0.	-8.29247E-05	-20150	-3.39313E-05	-3.81509E-06	-3.00637E-07	0.
	2.12478E-12	1.81047E-10	-4.91790E-10	-3.48062E-09	-5.60198E-14	3.97540E-09	0.	0.	0.	0.
	0.	0.	0.	-4.63102E-07	-3.54620E-08	0.	0.	0.	0.	0.

141	141.50	4.6435	18.931	16.578	.96595	5.07645E-04	5.54754E-04	5.440198E-05	2.84945E-04	6.42323E-02
	2.88028E-03	3.10461E-03	7.67697E-05	4.86734E-05	8.99055E-09	0.	1.06663E-04	0.	9.97730E-07	2.00000E-10
	1.00000E-12	0.	5.00000E-04	0.	76.944	2.43367E+05	8990.5	34.964	0.	0.
	5.79912E-07	4.92165E-05	1.12733E-07	1.27265E-07	1.27265E-07	5.64203E-05	2.00000E+11	2.00000E+11	2.00000E+11	2.00000E+11
	2.00000E+11	2.00000E+11	1.4000	24272	1.1169	0.	18.931	0.	1.50000E-02	447.00
DERIVATIVE	0.	0.	0.	1.50945E-04	-3.87345E-07	-3.37237E-10	-3.56952E-10	-2.65241E-11	-1.68353E-10	-1.63631E-07
	-3.67434E-09	3.39774E-09	0.	0.	0.	0.	0.	0.	2.43809E-14	0.
	0.	0.	-1.14991E-19	0.	-7.61600E-05	-18781	-2.99081E-05	-3.49978E-06	-2.61161E-07	0.
	1.95478E-12	1.41161E-10	-2.47275E-11	-3.50763E-12	-4.04087E-12	3.53598E-11	0.	0.	0.	0.
	0.	0.	0.	-4.01433E-07	-3.53635E-08	0.	0.	0.	0.	0.

142	142.50	4.7254	18.040	7.6923	1.8485	1.04426E-03	5.22515E-04	5.15804E-05	2.675557E-04	5.39368E-02
	2.77395E-03	3.11244E-03	7.04433E-05	4.53861E-05	8.98912E-09	0.	9.58772E-05	0.	9.99823E-07	2.00000E-10
	1.00000E-12	0.	5.00000E-04	0.	70.506	2.26930E+05	8988.1	34.675	0.	0.
	7.43106E-07	6.26041E-05	3.54047E-10	3.59514E-10	3.83179E-10	-9.03116E-09	-5.60943E-06	-3.15770E-16	1.27888E+11	0.
	1.26554E+11	3.26937E+11	1.4000	20874	1.1139	8.0440	0.	1.50000E-02	447.00	0.

(Output discontinued for lack of space)

## Description of Input Data Format

Card Group	Card Nos.	Columns	Format	Variable Names	Description
Blank	1	1-80	A810	-	Heading for simulation
Blank	2	1- 5	15	NCOM	No. of PSV's
Blank	2	6-10	15	NP	No. of constants for weather record
Blank	2	11-15	15	NT	No. of print steps
Blank	2	16-25	F10.3	T1	Starting time
Blank	2	26-35	F10.3	TDEL	Time step for printing
Blank	2	36-45	F10.3	ACC	Relative accuracy of integration
Blank	2	46-55	F10.3	DEL	DEL*TDEL is step size for integration
Blank	2	56-60	15	ITER	Maximum no. of halvings of integration step size
Blank	3	1-10	A10	DB	Debugging option
Blank	3	11-20	A10	DESOLV	Method of integration
Blank	3	21-30	A10	PLOT	Printer plotting option (requires additional data cards)
Blank	3	31-40	A10	CHK	Subroutine CHKOUT call option
Blank	3	41-50	A10	WRIT	Printed output option
INIT	1-7	--	E10.6	V(1)	Initial values of PSV's (NCOM in number)
ABI01	1	--	--	--	Parameter values for common block
PROD1	1-9	--	--	--	Parameter values for common block
HARV1	1	--	--	--	Parameter values for common block
PROD2	1-3				Parameter values for common block
PROD3	1-3				Parameter values for common block
CONS2	1-2				Parameter values for common block
CONS1	1-9,A-0				Parameter values for common block
DECOM1					Parameter values for common block

Subroutine INPUT is called where daily minimum temperature, daily maximum temperature, and daily precipitation is read in from an external storage device (unit no. 1). NP days of weather information are read.



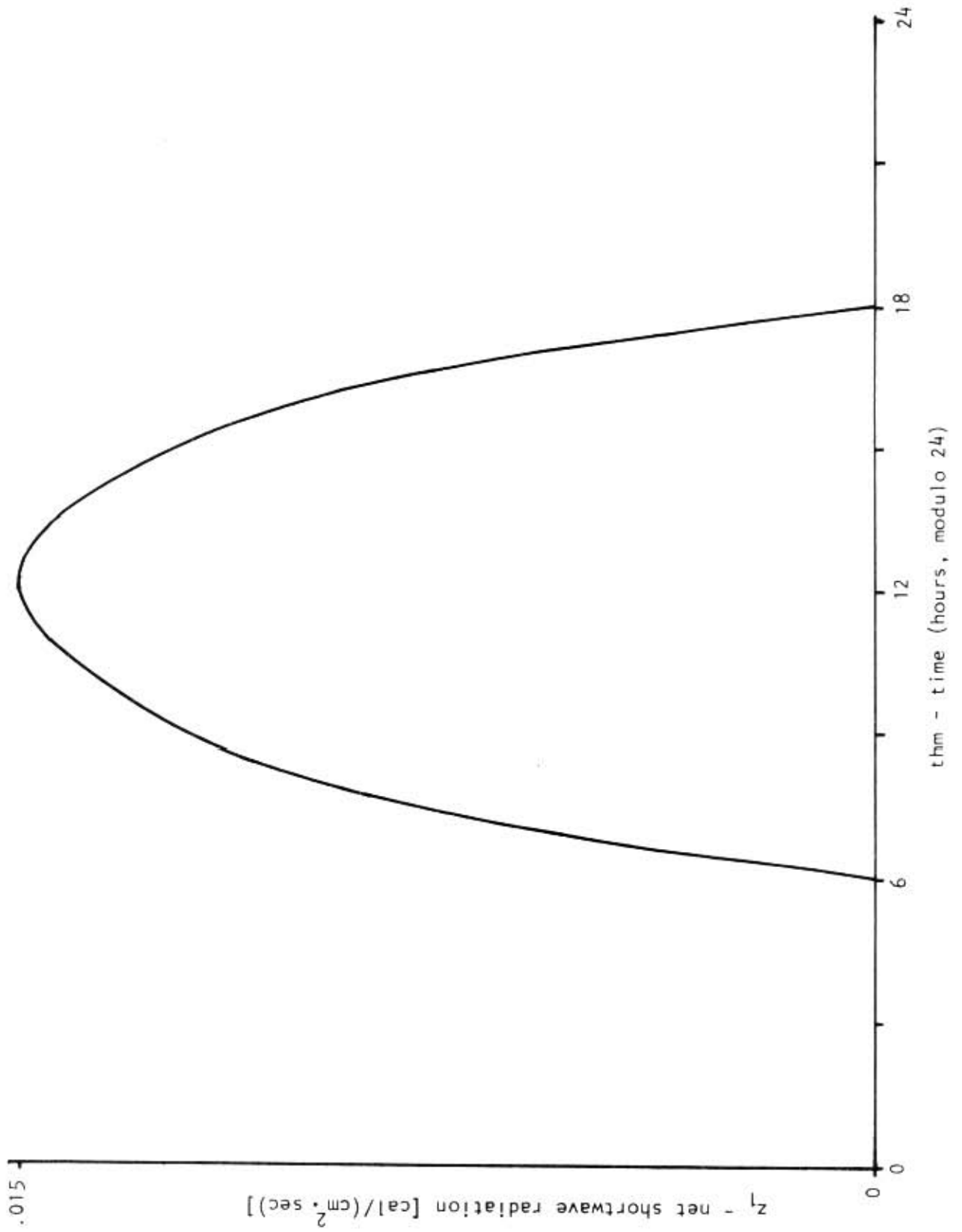


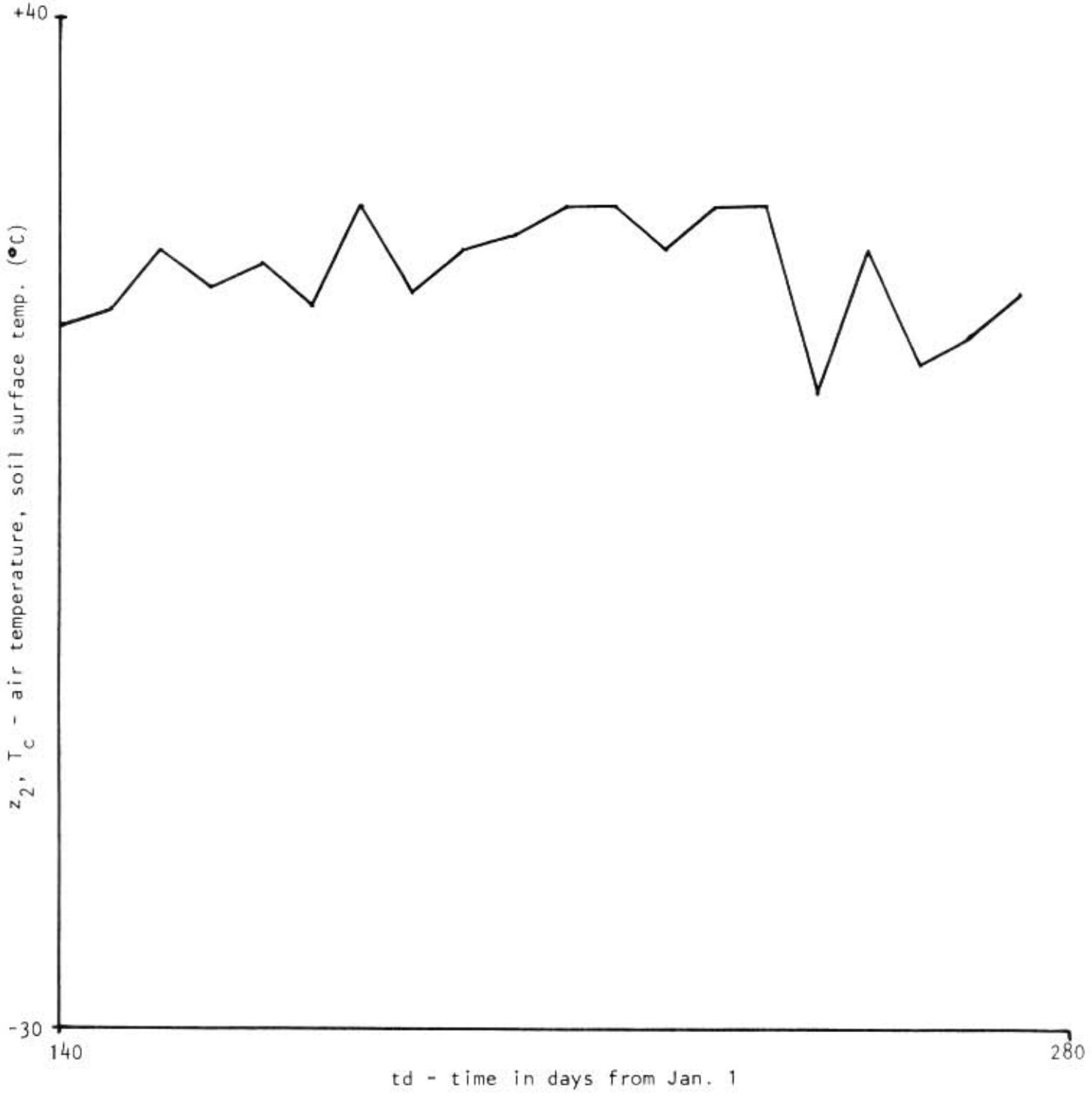
.0002	.0005							CONS 1 A
.001	.002							CONS 1 B
.0141	.0282							CONS 1 C
.0023	.0047							CONS 1 D
.0012	.0024							CONS 1 E
.125E-4	.25E-4							CONS 1 F
0.	1.0							CONS 1 G
0.	1.0							CONS 1 H
2.7E-7	5.4E-7							CONS 1 I
.38E-4	.75E-4							CONS 1 J
.1E+3	.1E+3							CONS 1 K
.181E+6	.181E+6							CONS 1 L
.9E+4	.9E+4							CONS 1 M
.3E+2	.3E+2							CONS 1 N
.3	.3							CONS 1 O
.577E-3	.577E-3	.577E-3	.577E-3	.577E-3	.577E-3	.577E-3	DIVS	DECOM1 1
2.E+11	2.F+11	2.F+11	2.F+11	2.F+11	2.F+11	2.F+11	MCMAXS	DECOM1 2
5.	5.	5.	5.	5.	5.	5.	MT1	DECOM1 3
43.	43.	43.	43.	43.	43.	43.	MT2	DECOM1 4
1.	1.	1.	1.	1.	1.	1.	MM1	DECOM1 5
12.	12.	12.	12.	12.	12.	12.	MM2	DECOM1 6
0.	0.	0.	0.	0.	0.	0.	SL0	DECOM1 7
7.77E+4	7.77E+4	7.77E+4	7.77E+4	7.77E+4	7.77E+4	7.77E+4	SLMX	DECOM1 8
0.	0.	0.	0.	0.	0.	0.	VMN0	DECOM1 9
.143E-5	.143E-5	.143E-5	.143E-5	.143E-5	.143E-5	.143E-5	VMNMX	DECOM110
1.	2.	3.	4.	11.	12.	12.	SBMN	DECOM111
1.73E-16	1.39E-15	1.39E-15	0.	0.	8.27E-18	8.27E-18	DECRATE	DECOM112
.05	.3	.7	0.	0.			SOMDIS	DECOM113
0.	0.	20.	1.				NPRFF	DECOM114
3.17E-8	0.	0.					MISC	DECOM115
END OF RUN								

## Appendix E. Numerical Solutions of Model Differential Equations

Following are graphs of the principal system variables and driving variables as a function of time for the period 140 through 280 days. The input driving variables were derived from 1967 records of daily precipitation, minimum and maximum temperature of the Akron, Colorado Experiment Station, operated by the Agricultural Research Service of the USDA. Model output was recorded daily at 12:00 noon, thus those features of the model which occur only at times other than 12:00 noon, e.g., rain, can not be observed in these graphs. For some of the driving variables ( $z_1$ ,  $z_3$ , and  $z_4$ ), a graph of related parameters or daily variation has been provided. Parameter values are given in Appendix D.

Since neither the functional forms nor the parameter values have been extensively modified from their original formulations for this set of output, the reader may expect to find anomalous results in these graphs. The variables of the decomposer section were not graphed because the values stayed essentially constant during the simulation.





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