Technical Report No. 220

PROCESS STUDIES WORKSHOP REPORT

Edited by

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GRASSLAND BIOME

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ABSTRACT

The Grassland Biome central laboratory held a series of three 2-day workshops approximately one month apart early in 1972 at Colorado State University, Fort Collins, to describe grassland system processes. The results of these workshops are presented in seven chapters in this report. Initial flow diagrams reporting state variable components and flow interrelationships were reported for the following: (i) Abiotic subsystems, (ii) mineral nutrient subsystems involving nitrogen and phosphorus, (iii) producer subsystems, (iv) decomposer subsystems, and (v) the consumer subsystem with diet selection and energetics. Recommendations stemming from the workshop groups are listed and discussed in the introductory section.

CHAPTER 1. INTRODUCTION

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1.1 WORKSHOP PROCEEDINGS AND GENERAL RESULTS

The seven chapters compiled in this report represent the first rough draft of output obtained from a series of three scheduled workshops held to examine rate process studies information early in 1971. In the first meeting (January 14 and 15) we established a trophic level basis for constructing box and arrow diagrams that were to later serve as models for information gathering in our process studies systems. Five subsystems in all were set up: (i) the abiotic subsystem concerned with heat and water models, (ii) the nutrient subsystem concerned with phosphorus and nitrogen models, (iii) the producer subsystem or basic plant model, (iv) a consumer subsystem with both diet selection and consumer energetics models, and (v) a decomposer subsystem. Initial relationships were constructed during this first meeting, and in the interim between the first meeting and the second meeting held one month later in February each participant was charged with locating information in his area of specialty or assignment. At the second meeting, revisions that were thought necessary in the models were first attended to, and then reports of findings related to flow rates were given by the participants. For some of the subsystem models it was evident by the second meeting that many difficulties were being encountered. Each subsystem group had passed by the common body of knowledge in their respective areas and had progressed to the "frontier." Thus, there were many gaps found in the reported literature, and it was also very difficult to rearrange the material to fit the needs for the process studies model. By the time of the third workshop held at the end of March, nearly all of the literature surveys presented here were completed, or at least pertinent literature citations were made available. The ultimate aim of identifying prime systems

needs and of obtaining experimental designs to fill these needs were only partially realized. However, the inter-system relationships as presented in Fig. 1.1 were agreed upon and in general have been adopted by the Grassland Biome for progressing toward needed program inputs. Thus, the major program requirements were identified as follows (Fig. 1.2):

A. Between producer and consumer subsystems.
   1. Consumer effect on plant growth.
      a. Consumption rates by various types of consumers such as insects, small mammals, and birds.
   2. Plant effects on consumers.
      a. Availability of labile and non-labile plant materials.
      b. Availability of reproductive parts such as flowering organs and seeds.

B. Between producer and decomposer subsystems.
   1. Dead plant material.
      a. Roots.
      b. Litter (availability of labile and non-labile materials in these compartments).
   2. Rates of root respiration.
   3. Availability of exudate from the plant, both in roots and in tops.

C. Between consumer and decomposer subsystems.
   1. Decomposition rates of animal excrement for large herbivores, insects, and small mammals.

D. Between producer and abiotic subsystems.
   1. Infiltration rates of water.
   2. Evapotranspiration indices.

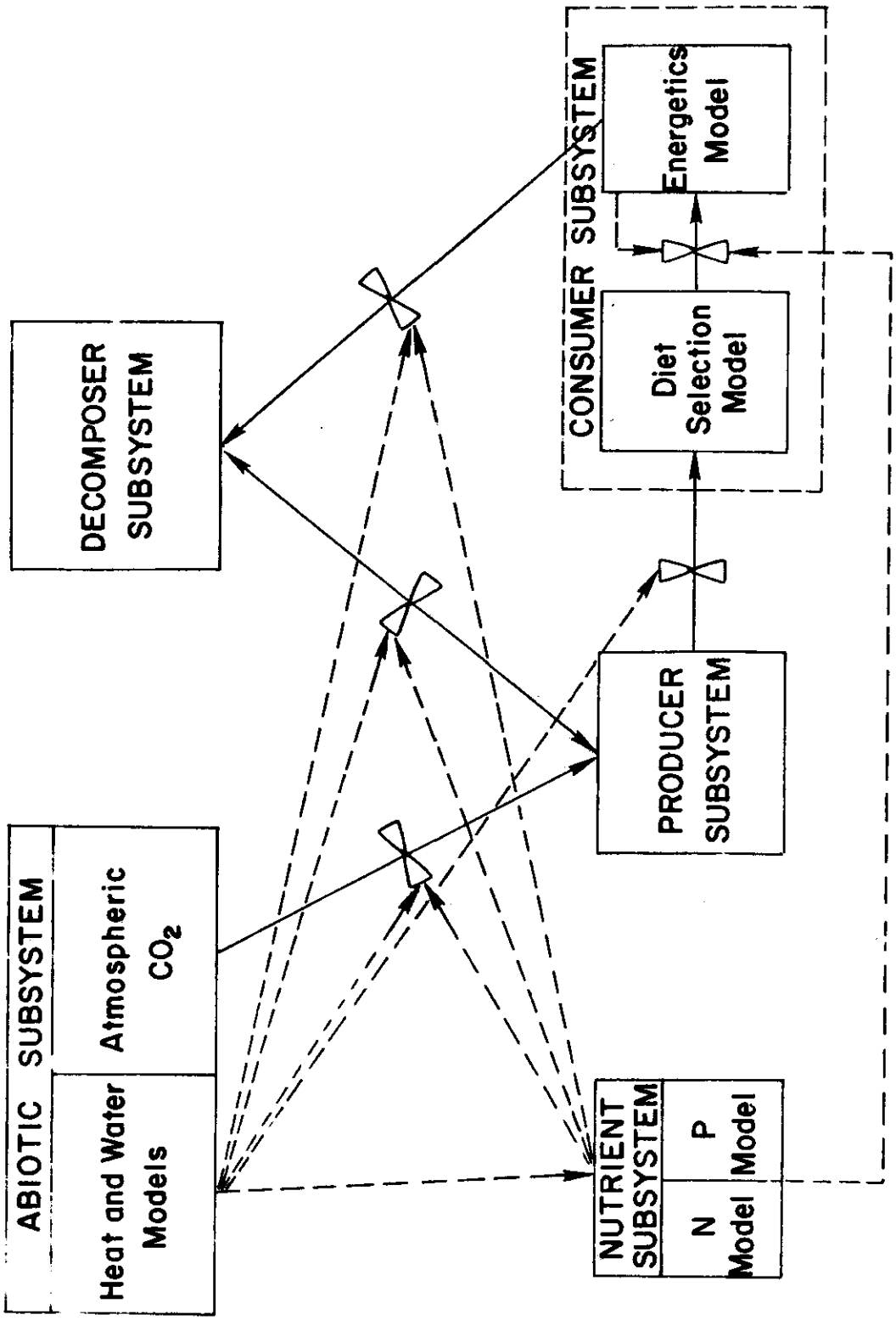

Fig. 1.1. Inter-subsystem relationships and flow and informational connections for process studies oriented programs in U.S. IBP Grassland Biome studies.

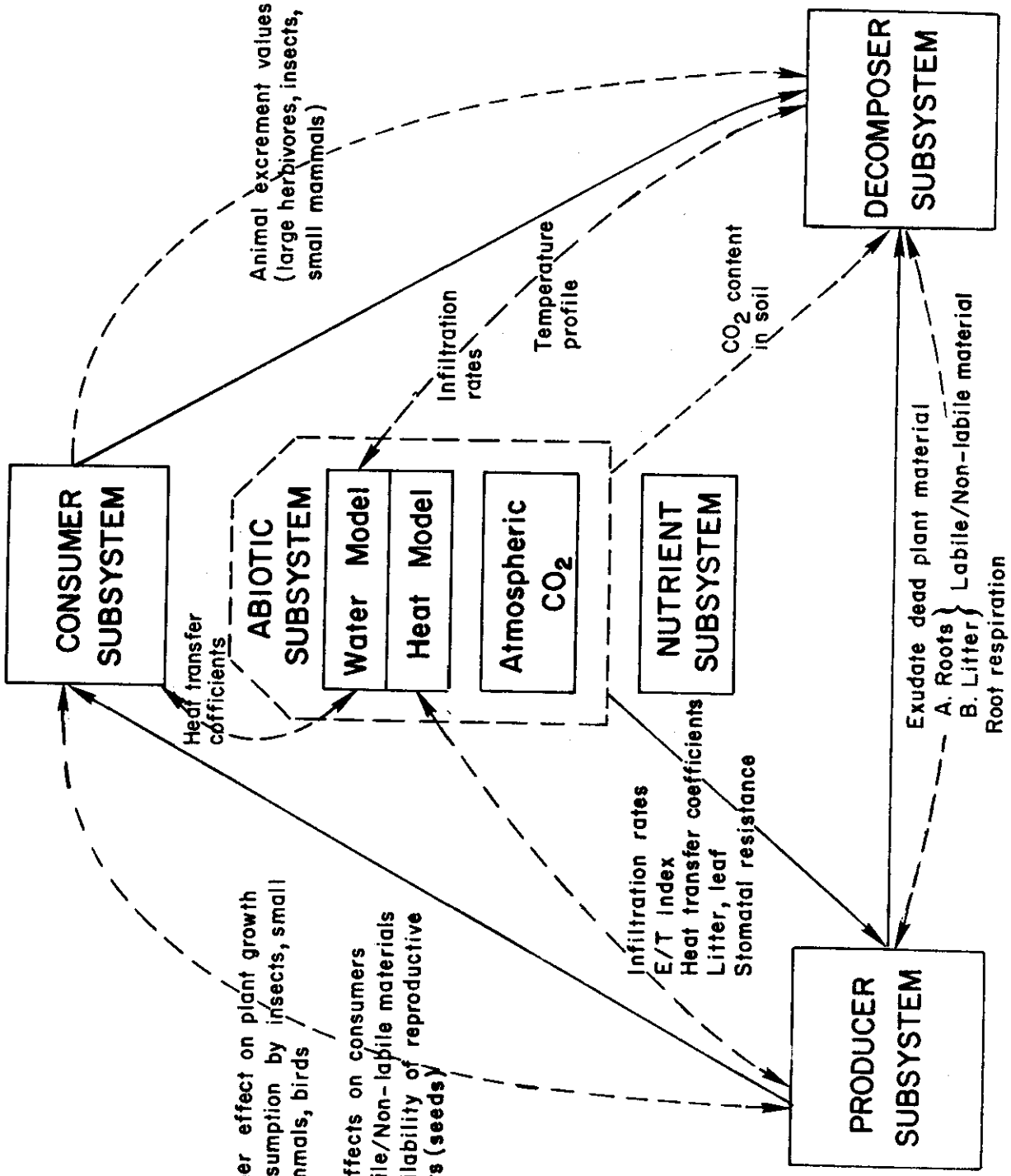

Fig. 1.2. Inter-subsystem relationships and needs in the Grassland Biome program.

3. Heat transfer coefficients for litter and leaf materials.

4. Stomatal resistance in various types of plants.

E. Between decomposer and abiotic subsystems.

1. Infiltration rates.

2. Temperature profile.

3. Carbon dioxide content in soil.

F. Between nutrient subsystem and producer subsystem (Fig. 1.3).

1. Levels of nitrogen in plant and the rate of transfer throughout the plant.

a. In roots.

b. In tops.

2. The effects of temperature and water on these transfer rates.

3. The rate of transfer of mineral solution to a live plant.

a. The root biomass must be known.

b. The top biomass must be known.

G. Between the mineral subsystem and the decomposer subsystem.

1. Detailed values of carbon to nitrogen ratios in organic and soil components.

H. Within the nutrient subsystem.

1. Transfer rate of soil organic phosphorus or nitrogen to solution phosphorus or nitrogen.

1.2 WORKSHOP GUIDELINES

In order for some uniformity to be achieved, a set of conventions were adopted for all workshop groups. Sketches were drawn as Forrester diagrams for each process (Forrester, 1961). Each compartment box was identified by

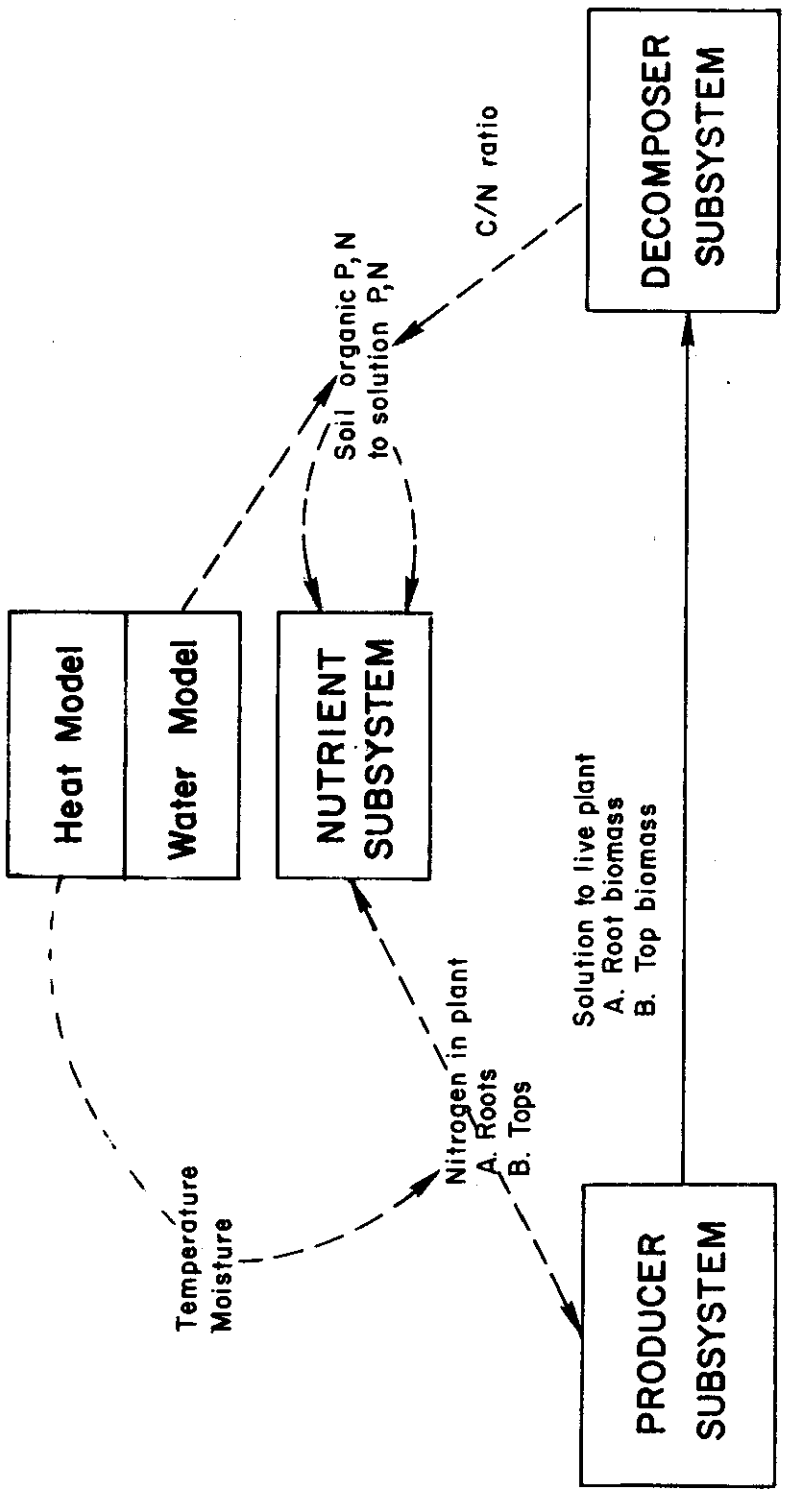

Fig. 1.3. Inter- and intra-subsystem relationships and needs involving the nutrient subsystem in the Grassland Biome program

a number, and flows between compartments were identified by names and number pairs (e.g., 101, 102). Solid lines between boxes indicate flows and dashed lines controls over the flows.

Each chapter reported here is organized around the key flows. In order that each working group could proceed with some confidence that their work would not duplicate other groups, a preliminary sketch was prepared and circulated to all participants. Compartment number assignments were as follows:

Submodel	Compartment Numbers
Heat	101 to 199
Water	201 to 299
Carbon and Energy	301 to 799
Producer	301 to 499
Decomposer	501 to 599
Consumer:	
Energetics	601 to 699
Diet Selection	701 to 799
Nitrogen	801 to 899
Phosphorus	901 to 999

Although the organization of the workshops could lead to a more easily modeled output, the main reason for adopting the conventions was prompted by a need for workshop organization rather than modeling requirements per se. Thus, in many instances, information is presented which will still require considerable reworking to become a strict mathematical or computerized model.

1.3 RECOMMENDATIONS

It is noteworthy that nearly all of the major priorities have been given to inter-subsystem information-gathering requisites. Only one intra-subsystem priority has been allocated, that of identification of soil organic phosphorus and nitrogen transfer rates to solution phosphorus and nitrogen that are in turn available for plant uptake. Unfortunately, there are no experimental designs in all instances that we can recommend to fill these gaps.

The largest single problem that confronts the biome at this particular time is that of adequately identifying belowground root biomass, rates of transfer of material into the roots, and rates of decomposition of roots after they die. Thus, initially, we have given considerable attention to programs oriented in this line of work. A further obvious major omission in this workshop is population dynamics of both plants and animals. A separate treatment of this area is recommended.

Future plans include principally carrying out recommendations put forward by the various subsystem committee members and the author-critic of each subsystem chapter. Further, it is recognized that critical thought must be given to a continuous mode of updating and reorganizing rate process studies. Principally, such reorganization will stem from results of the synthesis and integration efforts in the biome in addition to recognition of modeling needs through these iteration efforts. Our main challenge is to recognize when we have sufficient data to fulfill our information demands and to be able to pass on to other needed efforts. For the main part, this means that a more rapid turnover in certain programs may be necessary. It also may be necessary to update or validate certain

types of information, whether they be from the literature or from previous work at extant sites in the Grassland Biome. But, even though we recognize that a certain amount of flexibility is necessary to obtain the most efficient use of our funds and efforts, there are many projects that we must maintain over relatively long periods of time in order to gain the necessary information for the processes identified in the subsequent chapters. Thus, it is obvious that both strategies must be employed to make the process-oriented portion of the Grassland Biome program as efficient as possible.

1.4 ACKNOWLEDGMENTS

The material in this volume represents the collective efforts of nearly 70 participants. Reports of workshop groups are represented in separate chapters with the contributors of each workshop listed in the chapter headings.

The results from each workshop were collected by the chapter authors of this volume. As a final step these chapters were edited into the combined volume.

Each chapter received a somewhat brutal treatment by the volume editors in order to achieve an overall uniformity of editorial style and conventions. In some chapters the editors even went so far as to add supplementary material in order to make the treatment commensurate with that of other chapters. Naturally, the volume editors take full responsibility for this high-handed behavior and can only beg the indulgences and understanding of the individual contributors for the mistreatment of their ideas and information.

1.5 LITERATURE CITED

Forrester, J. W. 1961. Industrial dynamics. MIT Press, Cambridge, Massachusetts. 464 p.

CHAPTER 2. ABIOTIC SUBSYSTEMS:

HEAT AND WATER MODELS

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2.1 ABSTRACT

A synthesis of the working papers developed during the Process Studies Workshops for the heat and water abiotic subsystems is presented. The synthesis of each subsystem represents a compilation, reorganization, and editing of the original material presented. No further literature review or mathematical development is included. The workshops provided a fairly comprehensive development for heat exchange as basic physical processes, but demonstrated the need for further understanding of water cycling through the grassland ecosystem if water relationships are to be understood in the same basic physical sense.

The section concludes with the recommendations and summary comments of both the process study workshop participants and of the section author.

2.2 INTRODUCTION

This chapter, describing the heat and water abiotic subsystems discussed during the Process Studies Workshops, is divided into two parts. Section 2.3 is concerned with the heat submodel. Section 2.4 describes the water submodel.

For each subsystem the following format was attempted. First an overall general description of the models is presented relating the flows and processes between compartments (Sections 2.3 and 2.4). A detailed discussion of the individual flows including descriptions of flow rates and controls when possible then follows (Section 2.3.1 to 2.3.16 for heat and 2.4.1 to 2.4.13 for water). Sufficient information for the heat subsystem was generated by the workshops to make this presentation possible. For each flow a graphical model, a diagram illustrating system relationships, analytical expressions, and a table of controls are presented. For many flows additional information relating flow rates and controls are given. An attempt was made to make each flow description in the heat model stand alone, enabling the reader to examine the compartment transfers individually and determine the information for modeling. This required that some information or expressions be duplicated for some flows.

For the water subsystem either not enough is known about many of the processes relating the flows or this information was not given during the workshop to enable as formal a description as in the heat submodel.

These detailed discussions of the abiotic subsystem flows are then followed by summary comments and recommendations of the workshop participants (Sections 2.3.17 for heat and Sections 2.4.14 for water). Finally, concluding remarks by the section author are given.

The philosophy in synthesizing the material for this chapter was to represent the material and recommendations presented during the Process

Studies Workshops for the abiotic subsystems. The chapter author exercised editorial license in the organization and condensation of the material, in standardizing much of the notation, and either in correcting mathematical expressions or indicating suitable coordinate systems. The chapter author/editor reserved his own prejudices and recommendations until the final section. No attempt was made to fill missing descriptions of compartment flows by either resorting to the literature or independent mathematical development. The users of this report, particularly system modelers, need to decide when further development is needed and how sensitive overall model performance is to missing links. In the material that follows the Process Studies participants making the major contribution to each section has been identified. It should be recognized, however, that all participants contributed at least indirectly to each of these topics.

Finally, this chapter author/editor would like to apologize to the Process Studies Workshops participants in the abiotic system for any errors or omission in synthesizing their material.

2.3 THE HEAT SUBMODEL

(Victor Hasfurther, Larry Pochop, J. A. Smith)

A compartment flow model for the heat transfer process in the grassland ecosystem is shown schematically in Fig. 2.1. The first-order interaction of the heat model with the water, producer, and consumer models is indicated by the dotted line just below the atmosphere box (101), and the heat interaction with the decomposers and roots by the dotted line to the soil heat flow arrows. These other models provide some controls on the heat flow transfer for some compartments and, in return, heat flow partly governs the rate flows for these models. For example, LAI modifies the incoming heat flux to the soil (101–105), and evaporation of water from plants to the atmosphere is partly determined by the heat flux available.

The atmosphere acts as both a heat source and a heat sink. Deep soil layers may also act as a sink. In general, three processes are involved in the heat transfer model. These are convection, conduction, and radiation. Convection is the transfer of heat by the actual transfer of hot material from one place to another by motion of the material. In the heat model of Fig. 2.1 this transfer is accomplished through motion of air, and convection thus plays a role in the flows between the atmosphere and animals, plants, and soil [(101–102), (101–105), (101–112)]. Conduction is the transfer of heat from warm areas to cooler areas by the action of the molecular motion of warm areas in exciting neighboring molecules by contact. Heat flow by radiation is accomplished by the continued emission of energy from the surface of all bodies. This energy is called radiant energy and is in the form of electromagnetic waves. This energy is normally absorbed by a surface and is converted to heat. Radiant energy emitted by a surface, per unit time and

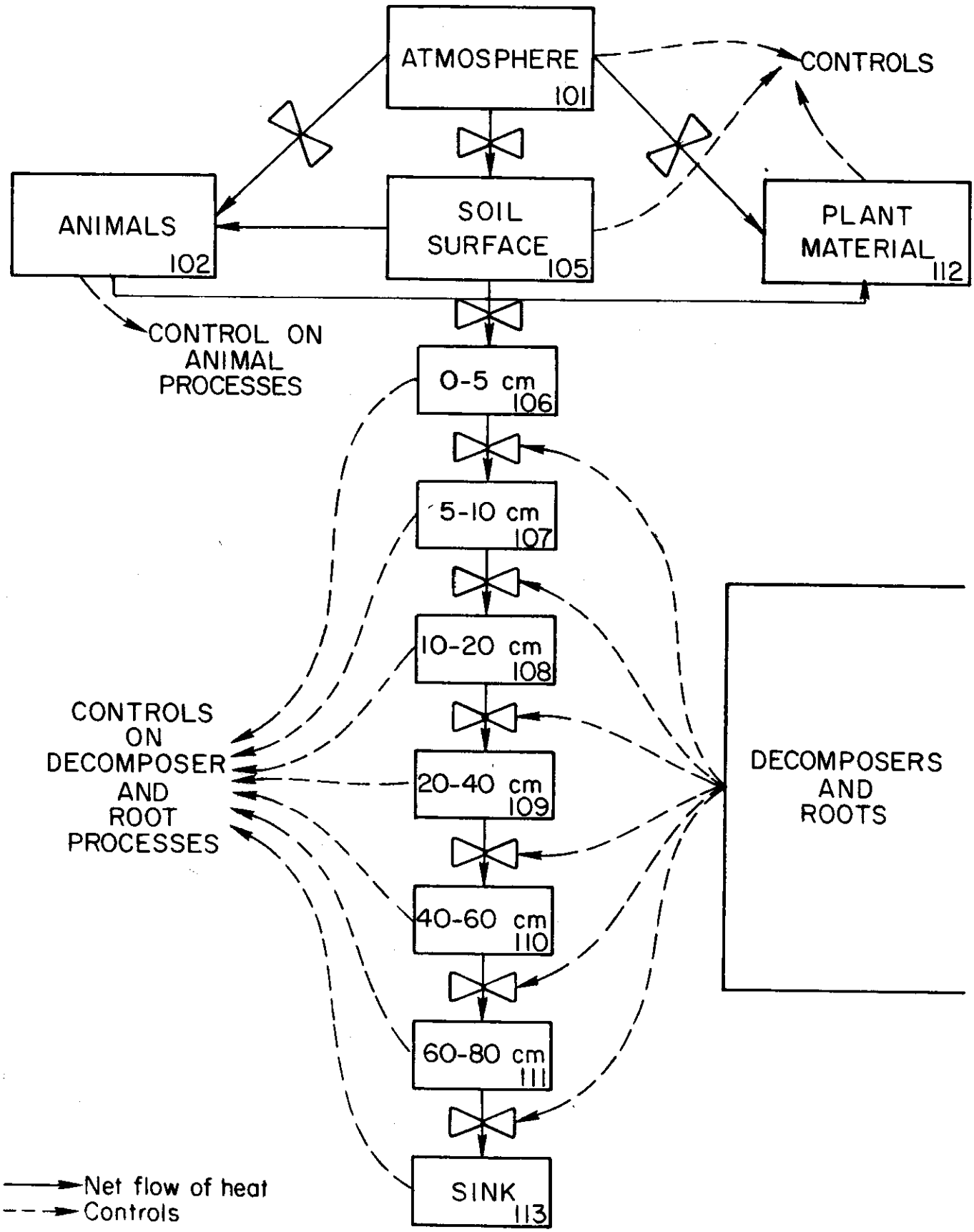


Fig. 2.1. Heat model.

per unit area, depends on the nature of the surface and on its temperature. In addition, heat transfer through vapor (101–102) which represents heat loss from lungs due to respiration and heat loss from surfaces due to evaporation, is also briefly described.

The total heat transfer between the atmosphere and an animal (101–102) involves several physical processes. The net heat exchange is dependent on the total heat load on the animal, the total heat production of the animal, and a number of physical and environmental parameters which vary in space and time. Various models for defining the heat transfer process between animals and the environment exist and show promise, with proper modification, for application to the grasslands.

The movement of heat from the atmosphere to the plant material of the grassland ecosystem (101–112) and the movement of heat from the plant material components of leaves, stems, and litter [(102–112), (112–106)], as noted above, is accomplished by the processes of radiation, convection, and conduction. It appears that radiation is the principal process involved in the transfer of heat to the leaves, stems, and litter and also to the soil surface, although the mass convective transfer of heat should not be overlooked as a source of heat input into the plant and soil components of the ecosystem. The direct movement of heat by conduction into the soil mass from leaves and stems via stem bases and roots does take place, but seems generally to have been neglected as a source of soil heat. Gates (1962) referred to the movement of heat by conduction into the soil mass from leaves and stems as negligible. The movement of heat to the soil surface both by direct thermal radiation and by reradiation from plant parts is without doubt a major source of soil heat.

Where any appreciable amount of litter exists on the soil surface, the movement of heat into the litter, the transfer of heat through the litter, and the movement of heat from the litter is principally by radiation, but convection can be expected to play a fairly important part in this transfer. The movement of heat through the litter and its transfer to the soil surface at the plane of contact between litter and soil should be primarily a function of the conduction process. But, since there could be many air spaces in the body of the litter, convection should not be overlooked.

There is little direct transfer of heat to the mineral soil from the living and dead standing biomass. However, the movement of heat through the litter, wherever there is an appreciable amount of litter, is apparently an inescapable route of heat travel from the atmosphere to the soil surface, and this phenomenon should be given major consideration in developing the heat model.

The processes 105 through 113 of the heat flow model deal with the transfer of heat from the soil surface through the soil profile. In process 101 through 105 the transfer of heat is mostly by short- and longwave radiation to the soil surface particles, but the mechanism is essentially one of heat conduction for processes 106 through 113.

On a microscopic scale, heating of the soil surface is caused during the day by short- and longwave radiation which excite the molecules on the surface by a transfer of energy to the molecules. The excited molecules then collide with neighboring molecules and a transfer of energy through a momentum exchange takes place. The result of all these collisions between the molecules at the surface with the molecules below them and so on is a change in

the energy levels of all the molecules. As a result, a transfer of heat downward during the day occurs. At night the process reverses itself somewhat so that there is a flow of heat upward as well as downward. This implies that during part of the year (summer-type days) the net transfer of energy in the form of heat is into the soil profile, but during the rest of the year (winter-type days) the net transfer of heat is out of the soil profile. The phenomena is therefore of sinusoidal type (cyclic) on a daily and a yearly basis.

On a macroscopic scale the flow of heat from the soil surface down through the soil profile is caused by a difference in temperature between the different soil layers. Heat flows in the direction of the temperature gradient (from a higher temperature level to a lower temperature level) either toward the soil surface or away from the soil surface or both. The net result is again a sinusoidal phenomena on a daily and yearly basis. At the lower soil depths, the temperature variation during a day is almost nil and changes only slightly during the entire year. However, as the soil surface is approached, the temperature variation becomes much more pronounced.

It should be noted that the transfer of heat does not occur by conduction alone. However, it is acceptable to define the effective conductivity of soils as a first approximation and formulate the heat transfer process on this basis (Nakano and Brown, 1971).

2.3.1 (101–102) Convection (Larry Pochop)

The convective heat exchange between a surface and the surrounding medium may be described by Newton's Law of Cooling. In this case the usual heat transfer coefficient includes a velocity factor (Esmay, 1969; Beckett and Vidrine, 1970).

2.3.1.1 Analytical expressions.

$$\frac{dQ}{dt} = hcv\ Acv\ (Ts - Ta) \quad (cal\ day^{-1}) \qquad (2.1)$$

2.3.1.2 Controls.

Control Description	Symbol	Units
Heat flow per unit time	$\frac{dQ}{dt}$	cal day^{-1}
Surface area of animal	Acv	m^2
Convective heat transfer coefficient	hcv	cal m^{-2} day^{-1} $°C^{-1}$
Surface temperature of animal	Ts	°C
Air temperature	Ta	°C

2.3.1.3 Flow rates. The heat transfer coefficient (hcv) can be written in terms of the dimensionless Nusselt (N_u) and Reynolds (R_e) numbers

$$N_u = \frac{hcvd}{K}$$

and

$$R_e = \frac{Vd}{\nu}$$

where

V = wind velocity cm sec^{-1}

K = thermal conductivity of air, which is 5.78×10^{-5} cal cm^{-1} sec^{-1} $°C^{-1}$ @ 0°C

ν = kinematic viscosity of air, which is 0.13 cm^2 sec^{-1} @ 0°C

d = characteristic dimension of the body in cm

Wiersma and Nelson (1967) determined

$hcv = 14.05$ kcal m^{-2} $°C^{-1}$ hr^{-1}

for a 362 kg bovine model and a wind speed of 305 cm sec^{-1} at an air temperature of 32.2°C.

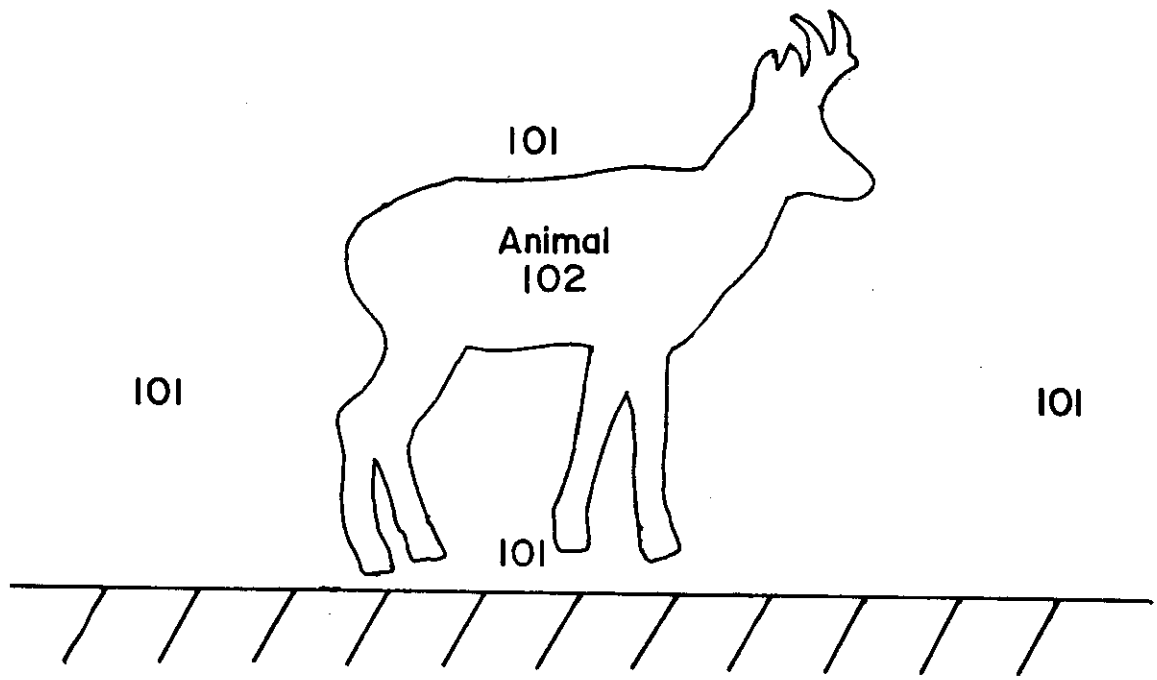
The total surface area (A_t) of dairy cattle, averaged for data from 96 purebred Holstein and Jersey cows, has been given as (Brody and Elting, 1926)

$$A_t = 0.15(\text{weight})^{0.56}$$

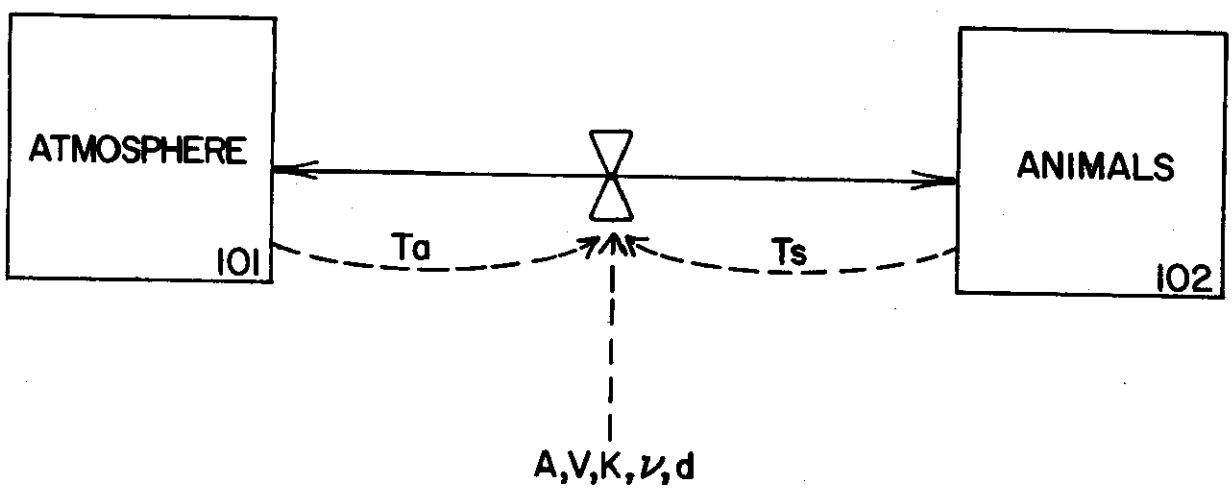
with the weight in kg.

A value for the effective surface area exposed for convection has been listed as 80% of the total body surface for swine (Esmay, 1969).

A difficult parameter to determine is the surface temperature of the animal. This temperature will be largely influenced by the environmental temperature and the amount of incident radiation. Curves depicting the average relation between surface and air temperatures have been given by Thompson, Worstell, and Brody (1952) for data from Jersey, Holstein, and Brahman cows. These curves are for animals not exposed to direct solar radiation.



A. Graphical Model



B. System Relationships

Fig. 2.2 Atmosphere-animal convection heat flow.

2.3.2 (101–102) Conduction (J. A. Smith)

The conduction exchanges between animals and the atmosphere are small compared to radiative and convective energy exchanges. Conduction exchanges may either be ignored or included with convective transfer by modifying hcv, the convective heat transfer coefficient.

2.3.2.1 Analytical expressions.

$$\frac{1}{h'cv} = \frac{Ya}{K} + \frac{1}{hcv} \qquad (2.2)$$

$$h'cv \sim \text{cal } m^{-2} \text{ day}^{-1} \text{ °C}^{-1}$$

2.3.2.2 Controls.

Control Description	Symbol	Units
Convective heat transfer	hcv	cal m^{-2} day^{-1} $°C^{-1}$
Coefficient of thermal conductivity of air	K	cal day^{-1} m^{-1} $°C^{-1}$
Height above animal at which air temperature is measured	Ya	m

2.3.3 (101–102) Radiation (Larry Pochop)

Most radiant heat transfer between animals and the environment considers itself with exchange between the animal and corresponding surfaces rather than the atmosphere (e.g., processes 102 to 105, etc.). This is especially true for the longwave components. Shortwave radiation components are usually considered to be heat loads. The radiation heat transfer may be expressed basically by the Stefan-Boltzmann Law.

2.3.3.1 Analytical expressions.

$$\frac{dQ}{dt}\ \text{radiation} = A_s S_d A_{sd} + A_s S_e A_{se} + A_l R_{li} A_{se} + E\sigma A_{se} T_s^4 \qquad (2.3)$$

(cal day^{-1})

2.3.3.2 Controls.

Control Description	Symbol	Units
Air temperature	Ta	°C
Surface temperature of animal	T_s	°K
Effective area of animal for direct shortwave radiation	A_{sd}	m^2
Effective area of animal for indirect radiation	A_{se}	m^2
Absorptivity of animal to shortwave radiation	A_s	dimensionless
Absorptivity of animal to longwave radiation	A_l	dimensionless
Direct shortwave radiation flux	S_d	cal m^{-2} day^{-1}

2.3.3.2 Controls (continued).

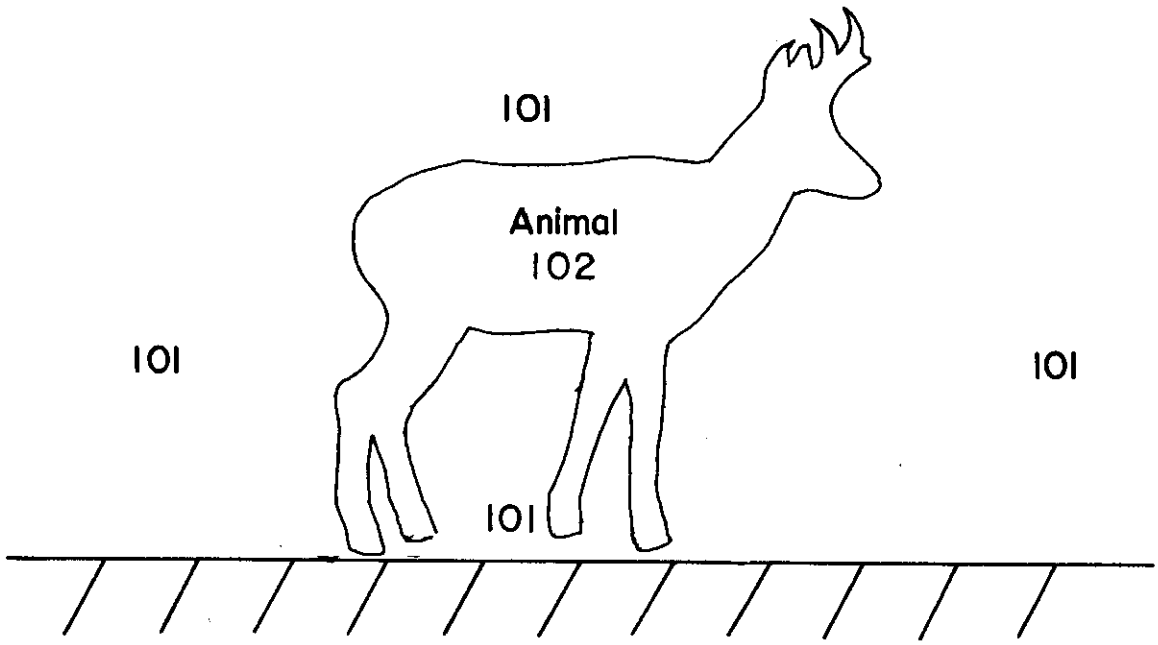
Control Description	Symbol	Units
Indirect shortwave radiation flux	S_e	cal m^{-2} day^{-1}
Incoming longwave radiation	R_{li}	cal m^{-2} day^{-1}
Emissivity of the animal surface	E	dimensionless
Stefan-Boltzmann constant	σ	cal m^{-2} day^{-1} $°K^{-4}$

2.3.3.3 Flow rates. Radiant transfer consists of four separate components as shown in equation (2.3), the first three of these being heat loads and the fourth a heat loss. The determination of each of these components requires determination of the effective area for radiation, definition of the absorptivity or emissivity characteristics of the surface, and measurement (or in some cases, estimation) of the radiation intensity or, in the case of the heat loss component, measurement of the surface temperature.

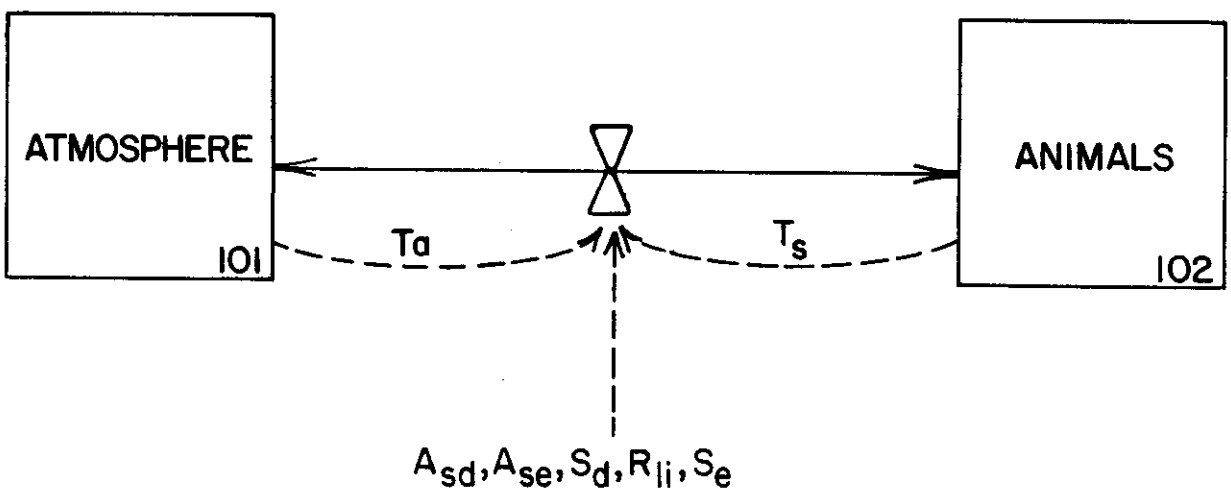
The effective area for absorption of direct solar radiation (A_{sd}) has been estimated as near 50% of the total body surface area for livestock (Johnson, 1965), while the effective area for diffuse and longwave radiation (A_{se}) has been given as 75% of the total surface area (Esmay, 1969) for swine.

The absorptivity for solar radiation (A_s) varies with the hair coat color, thus a wide range of values may be expected. Johnson (1965), for example, has listed values ranging from 0.49 for zebu to 0.89 for Black Angus, while Bond, Morrison, and Givens (1969) have reported values from 0.50 for a white animal and 0.90 to 0.95 for a dark animal. The absorption (A_l) and emissivity (E) for longwave radiation, however, approximate that of

a black body. Typical values given are 0.92 (Esmay, 1969) and 0.93 (Smith, 1964) for swine, and 0.90 to 0.95 for animals in general (Bond et al., 1969).



A. Graphical Model



B. System Relationships

Fig. 2.3. Atmosphere-animal radiative heat flow.

2.3.4 (101–102) Vapor (Larry Pochop)

Heat loss from the lungs is dependent upon the volume of air exchanged in respiration and the psychrometric conditions of the inhaled and exhaled air, more specifically the enthalpies. Evaporative heat loss from the surface is a direct function of the rate of evaporation from the surface.

2.3.4.1 Analytical expressions.

$$\frac{dQ}{dt}\ \text{latent heat} = W_a(H_e - H) + k_e A_e V^n (P_s - P_a) \quad (2.4)$$

$$(\text{cal day}^{-1})$$

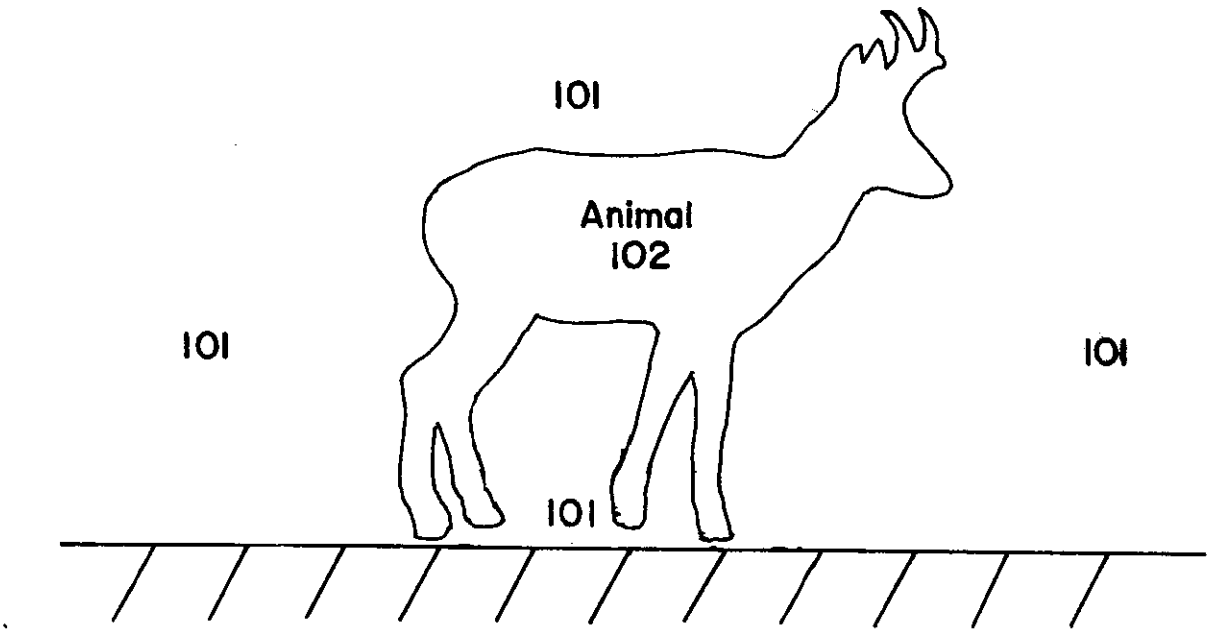
2.3.4.2 Controls.

Control Description	Symbol	Units
Weight of air breathed	W_a	g day $^{-1}$
Enthalpy of exhaled air	H_e	cal g^{-1}
Enthalpy of ambient air	H	cal g^{-1}
Wind speed	V	m day^{-1}
Exponent for velocity component	n	dimensionless
Vapor pressure of water at animal surface	P_s	millibar
Vapor pressure of air	P_a	millibar
Evaporative constant	k_e	--
Air temperature	Ta	°C
Soil surface temperature	Ts	°C
Relative humidity of atmosphere	RHa	percent
Effective area of animal for evaporation	Ae	m^2

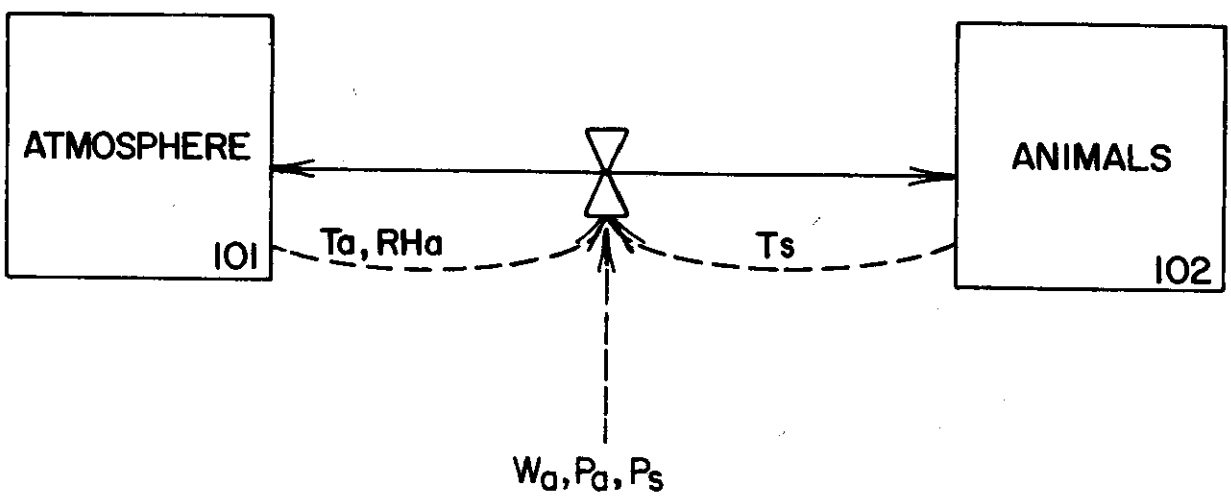
2.3.4.3 Flow rates. The volume of air exchanged in respiration depends upon the type of animal being considered, as well as upon environmental conditions, and must be selected accordingly. Values for respiration rates and volumes are usually readily available (e.g., Brody, 1945). The psychrometric conditions of the exhaled air can more easily be generalized. Smith (1964) has given an enthalpy of 448 kcal/kg air exhaled based on assumed conditions for exhaled air of 35.5°C, and 85% relative humidity for swine. Other values appearing in the literature are similar to this (e.g., Beckett and Vidrine, 1970).

Finally, neither the evaporative constant (K_e) nor the exponent (n) for the evaporative component of the latent heat transfer have been adequately determined for animals (Esmay, 1969; Johnson, 1965).

In order to develop a general model for the heat transfer process between the atmosphere and animals, several approximations may be necessary. For example, one of the problems in defining the transfer process is the estimation of the effective surface area for each component of energy exchange. Basically, the approach to defining these areas is that of determining the total surface area of the animal and then applying reductions to estimate the effective surface areas. Although estimation of these areas have been made for only a limited number of animals, large differences would not be expected in the reduction factors for different types of animals as long as the general body shapes are similar.



A. Graphical Model



B. System Relationships

Fig. 2.4. Heat exchange through vapor loss.

2.3.5 (101–105) Convection (John Nunn)

Heat flow per unit time by convection is generally noted as a single first-order differential equation involving a convection coefficient, hcv. This coefficient is a function of Nusselt, Prandtl, Grashof, and Reynolds numbers, and varies for forced and free convection situations (Gates, 1962).

2.3.5.1 Analytical expressions.

$$\frac{dQ}{dt} = hcv\ A(Ts - Ta) \qquad (2.5)$$

Free convection: $hcv = f(Nu, K, L)$

$$Nu = .71(Gr \times Pr)^{\frac{1}{4}}$$

$$Gr = 156(Ts - Ta)\ L^3\ @\ 20°C$$

Forced convection: $hcv = f(Nu, K, L)$

$$Nu = .664\ Re^{\frac{1}{2}}Pr^{\frac{1}{3}}$$

$$Re = \frac{PVL}{u}$$

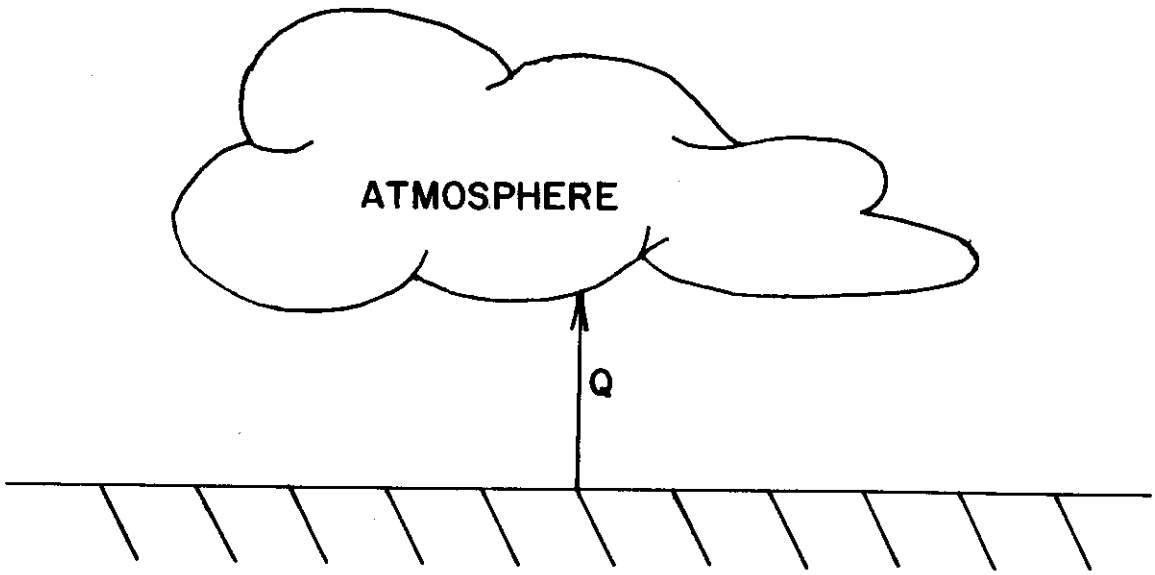
2.3.5.2 Controls.

Control Description	Symbol	Units
Grashof number	Gr	dimensionless
Prandtl number	Pr	dimensionless
Nusselt number	Nu	dimensionless
Reynolds number	Re	dimensionless
Soil surface temperature	Ts	°C

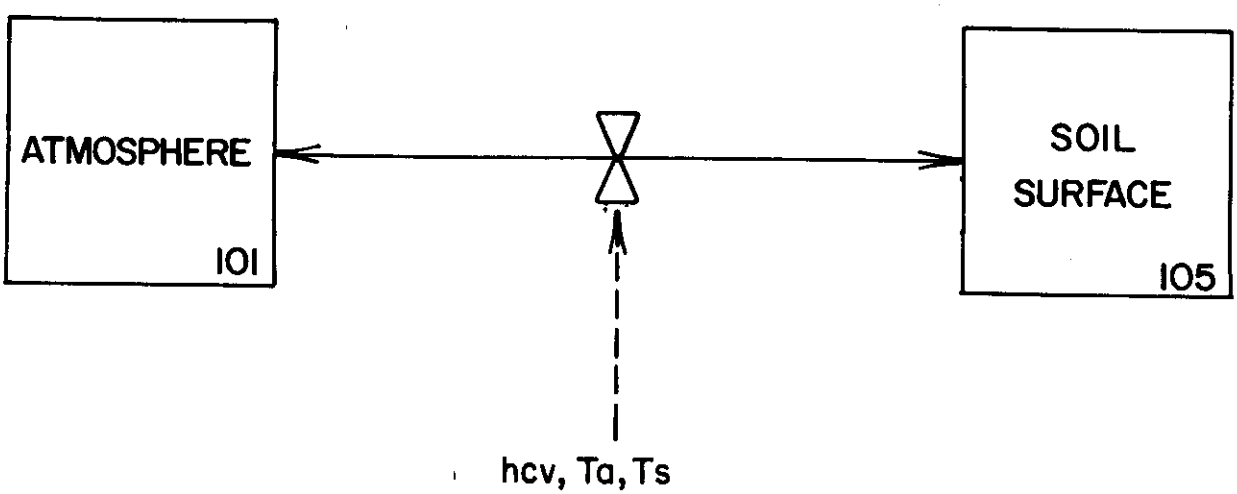
2.3.5.2 Controls (continued).

Control Description	Symbol	Units
Air temperature	Ta	°C
Surface area	A	m^2
Thermal conductivity of air	K	cal day^{-1} m^{-1} $°C^{-1}$
Characteristic dimension of object	L	m
Density of air	P	g m^{-3}
Velocity of air	V	m day^{-1}
Coefficient of viscosity	u	g day^{-1} m^{-1}
Convection coefficient	hcv	cal m^{-2} day^{-1} $°C^{-1}$

2.3.5.3 Flow rates. The qualitative dependence of convective heat flux on the temperature gradient, convective heat transfer coefficient, and wind speed is indicated in Fig. 2.6 through 2.8.



A. Graphical Model



B. System Relationships

Fig. 2.5. Convection exchange between atmosphere and soil surface.

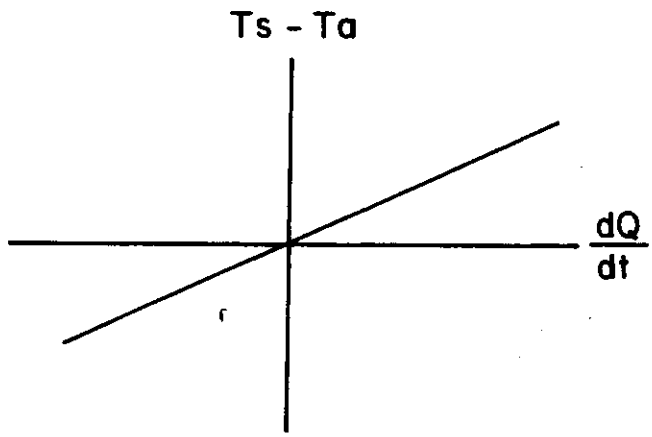


Fig. 2.6. Heat flux dependence on temperature gradient.

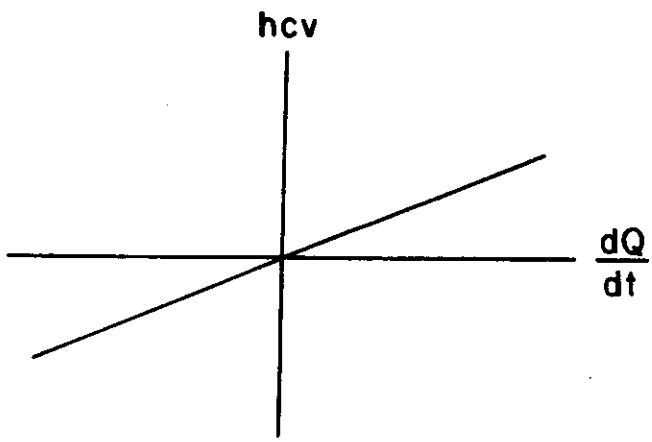


Fig. 2.7. Convective heat flux dependence on convective transfer coefficient.

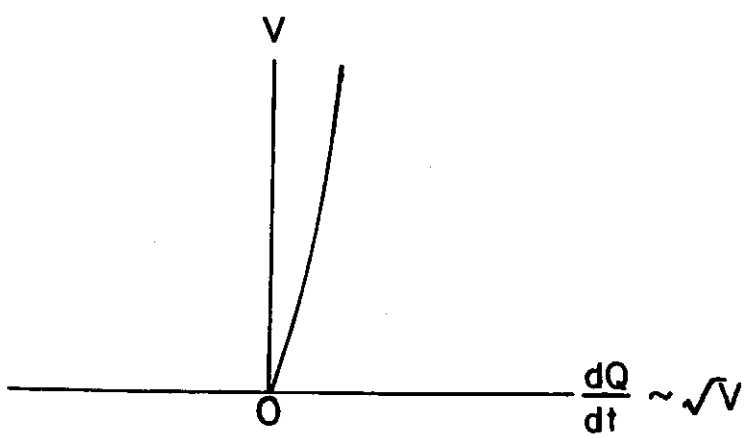


Fig. 2.8. Heat flux dependence on wind speed.

2.3.6 (101–105) Conduction (John Nunn)

The heat flow per unit time between the soil surface and the atmosphere resulting from conduction can be expressed by a single first-order differential equation equating heat flow per unit time to thermal conductivity, surface area, and vertical temperature gradients (Gates, 1962; Hartiner and Martin, 1957).

2.3.6.1 Analytical expressions.

$$\frac{dQ}{dt} = -KA\frac{dT}{dy} \quad (\text{cal day}^{-1}) \tag{2.6}$$

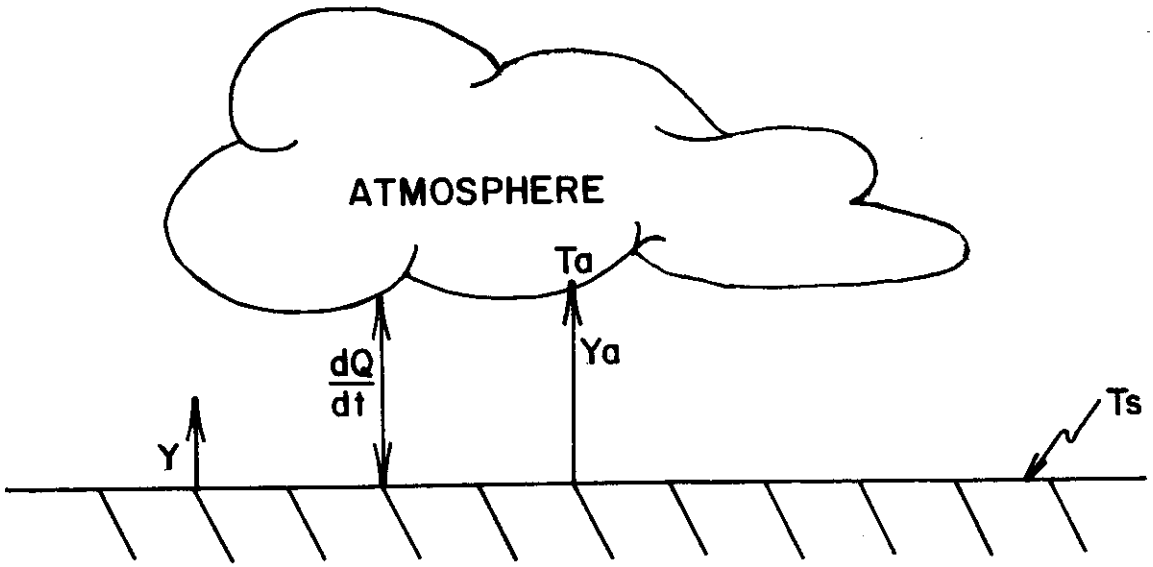
$$\frac{dT}{dy} \sim (Ta - Ts)/Ya$$

2.3.6.2 Controls.

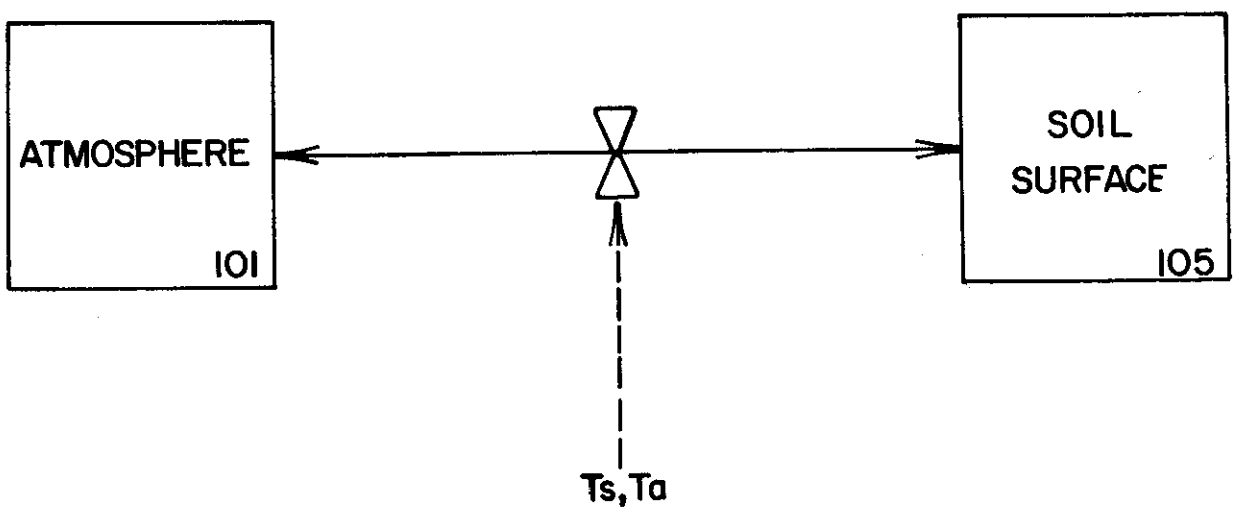
Control Description	Symbol	Units
Air temperature	Ta	°C
Soil surface temperature	Ts	°C
Coefficient of thermal conductivity of air	K	cal day^{-1} m^{-1} $°C^{-1}$
Soil surface area in contact with media	A	m^2
Height of air temperature measurement	Ya	m
Temperature gradient	$\frac{dT}{dy}$	°C m^{-1}

2.3.6.3 Flow rates. The coefficient of thermal conductivity for air, K, is normally assumed to be 6.0×10^{-5} cal sec^{-1} cm^{-1} $°C^{-1}$ for an air temperature of 20°C. In general, however, it is a function of both air temperature and water content. The temperature gradient may be adequately

approximated by examining air temperature at 200 cm. The qualitative dependence of heat conduction on this temperature gradient is indicated below.



A. Graphical Model



B. System Relationships

Fig. 2.9. Conduction transfer between atmosphere and soil.

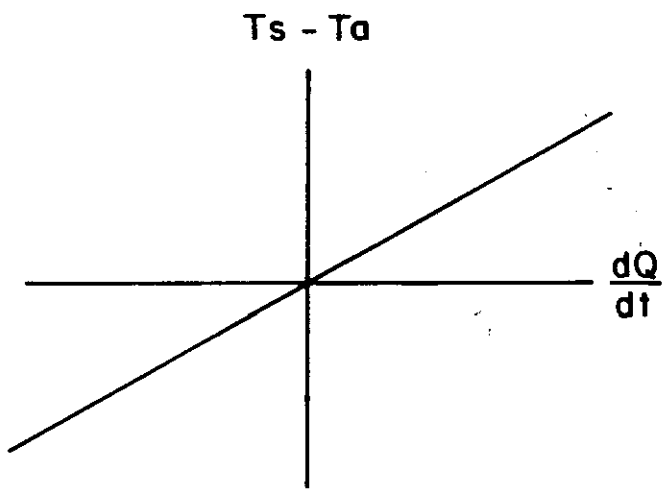


Fig. 2.10. Conductive heat flux dependence on temperature differences.

2.3.7 (101–105) Radiation (John Nunn)

The net radiation energy received by the mineral soil surface is easily expressed by the summation of its components, i.e., the net balance of longwave and shortwave radiation.

2.3.7.1 Analytical expressions.

$$Rn = R_{si} - R_{so} + R_{li} - R_{lo} \tag{2.7}$$

$$Rn = (1 - \alpha)R_{si} + R_{nl}$$

$$\frac{dQ}{dt} = Rn \qquad (cal\ day^{-1})$$

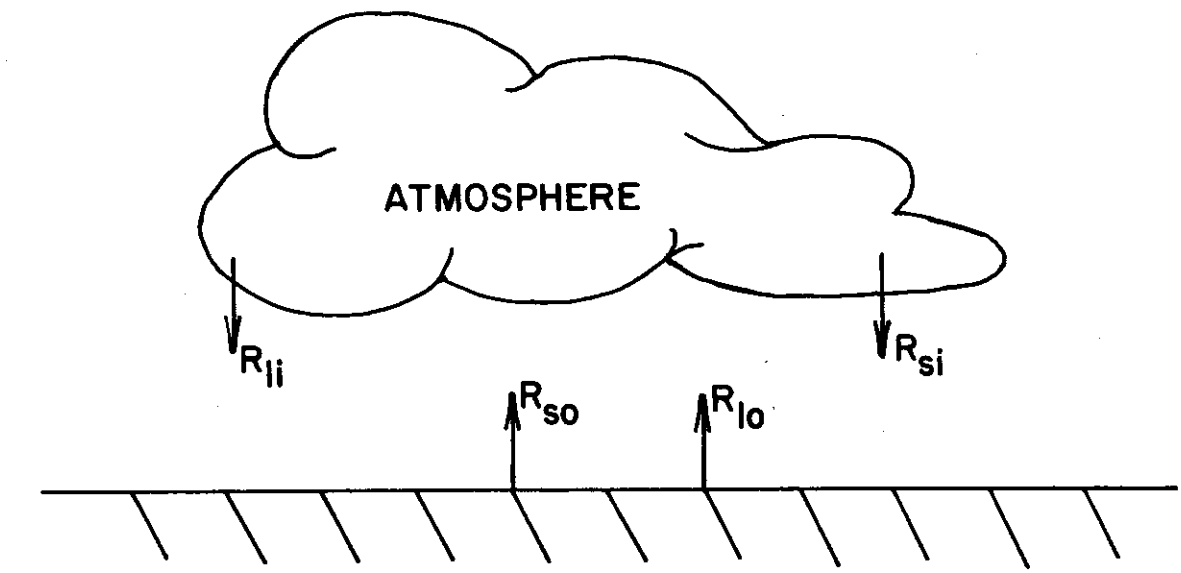
2.3.7.2 Controls.

Control Description	Symbol	Units
Surface temperature	Ts	°C
Air temperature	Ta	°C
Net radiation	Rn	cal day^{-1}
Incoming longwave radiation	R_{li}	cal day^{-1}
Outgoing longwave radiation	R_{lo}	cal day^{-1}
Incoming shortwave radiation	R_{si}	cal day^{-1}
Outgoing shortwave radiation	R_{so}	cal day^{-1}
Net longwave radiation	R_{nl}	cal day^{-1}
Albedo of soil surface	α	dimensionless

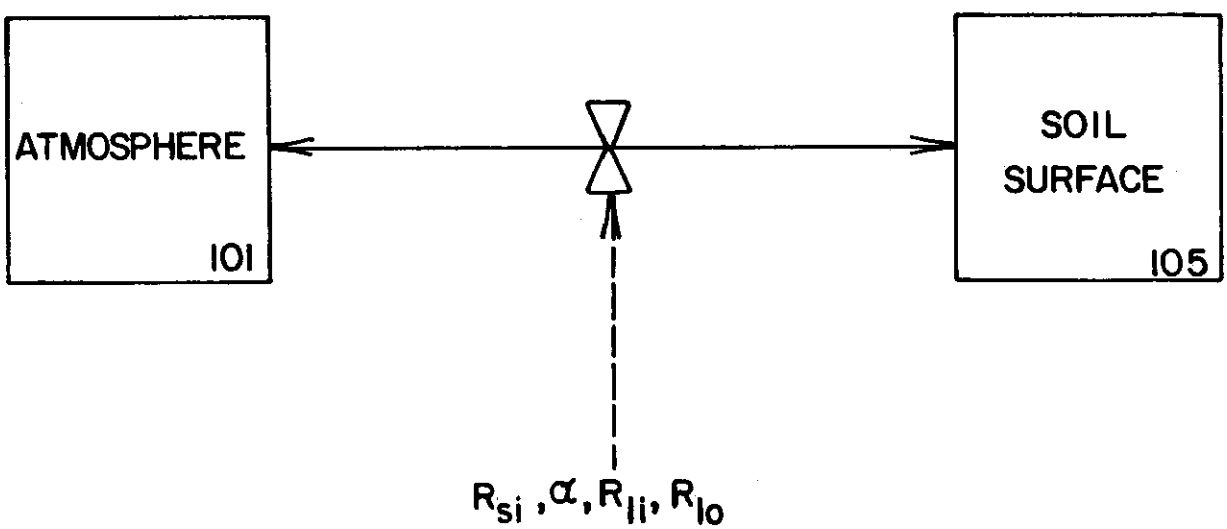
2.3.7.3 Flow rates. The net radiation accumulation to the soil surface is governed by the albedo of the surface defined to be the percent of shortwave radiation reflected by a surface (Monteith and Szeicz, 1960), net longwave radiation, and incoming shortwave radiation. Typical values of albedo for various surface types are given in Table 2.1 (Geiger, 1966). Net longwave radiation varies between 80 cal cm^{-2} day^{-1} for cloudy skies to 190 cal cm^{-2} day^{-1} for clear skies (Monteith, 1959). However, these values depend on surface temperature, surface emissivity, and atmospheric conditions. Typical values for incoming longwave radiation are 0.39 to 0.47 cal cm^{-2} min^{-1} (Robinson, 1950). Outgoing longwave radiation for grass is about 0.21 cal cm^{-2} min^{-1} (Monteith and Szeicz, 1960). The qualitative dependence of radiation flux on these various parameters are indicated in Fig. 2.12 through 2.15.

Table 2.1. Typical value of albedo.

Surface Type	Value
(Values from Geiger, 1966)	
Fresh snow	75-95%
Dense cloud cover	60-90%
Old snow	40-70%
Clean firm snow	50-65%
Light sand dunes	30-60%
Clean glacier ice	30-46%
Dirty firm snow	20-50%
Dirty glacier ice	20-30%
Sandy soil	15-40%
Meadows, fields	12-30%
Woods	5-20%
Dark cultivated soil	7-10%
(Values from Budyko, 1958)	
Coniferous forest	10-15%
Deciduous forest	15-20%



A. Graphical Model



B. System Relationships

Fig. 2.1 Atmosphere-soil radiation heat flow.

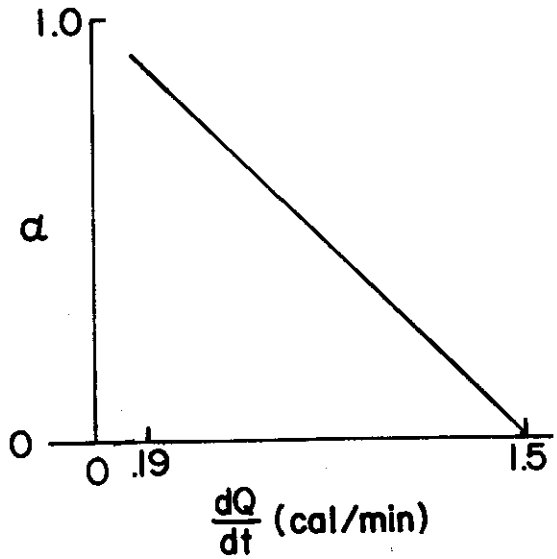


Fig. 2.12. Heat flux variation (dQ/dt) with albedo (α).

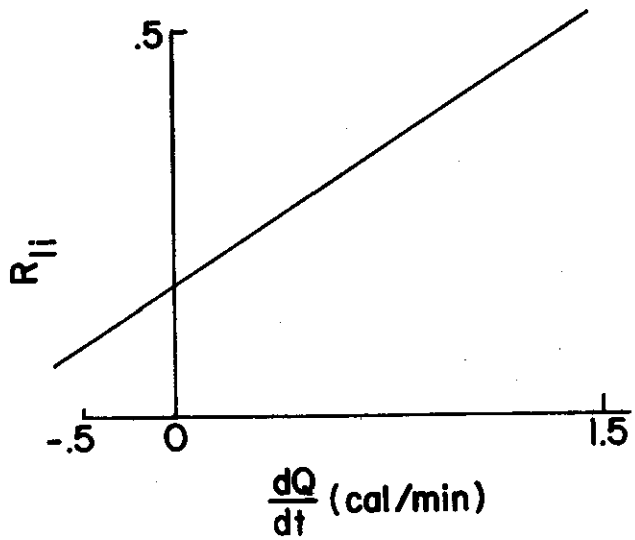


Fig. 2.13. Heat flux variation (dQ/dt) with incoming longwave radiation (R_{li}).

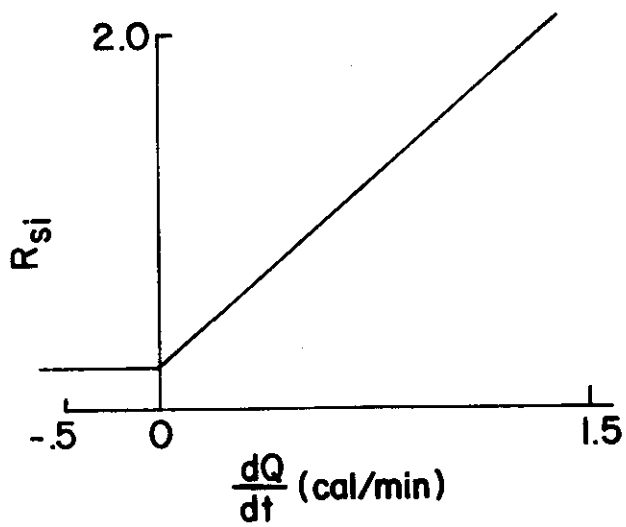


Fig. 2.14. Heat flux variation (dQ/dt) with incoming shortwave radiation (R_{si}).

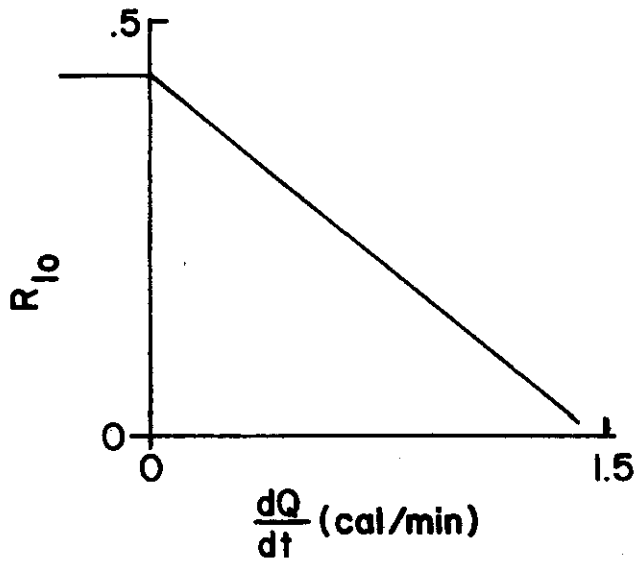


Fig. 2.15. Heat flux variation (dQ/dt) with outgoing longwave radiation (R_{lo}).

2.3.8 (101–112) Convection (John Nunn)

Heat flow per unit time by convection is generally noted as a single first-order differential equation involving a convection coefficient, hcv. This coefficient is a function of Nusselt, Prandtl, Grashot, and Reynolds numbers, and varies for forced and free convection situations (Gates, 1962).

2.3.8.1 Analytical expressions.

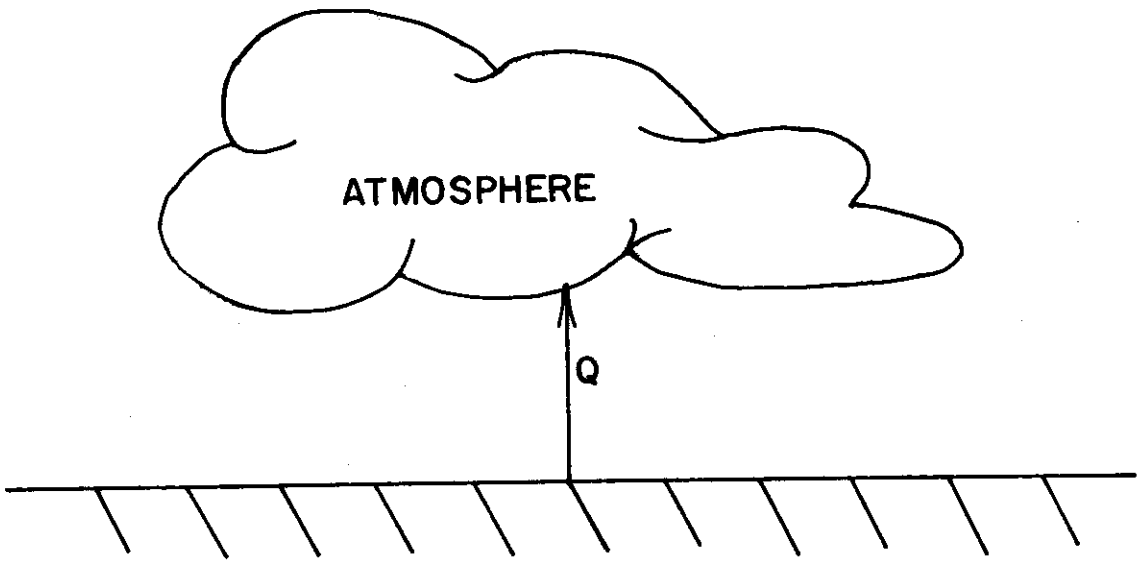
$$\frac{dQ}{dt} = hcv\ A(Ts - Ta) \qquad (2.8)$$

$$(cal\ day^{-1})$$

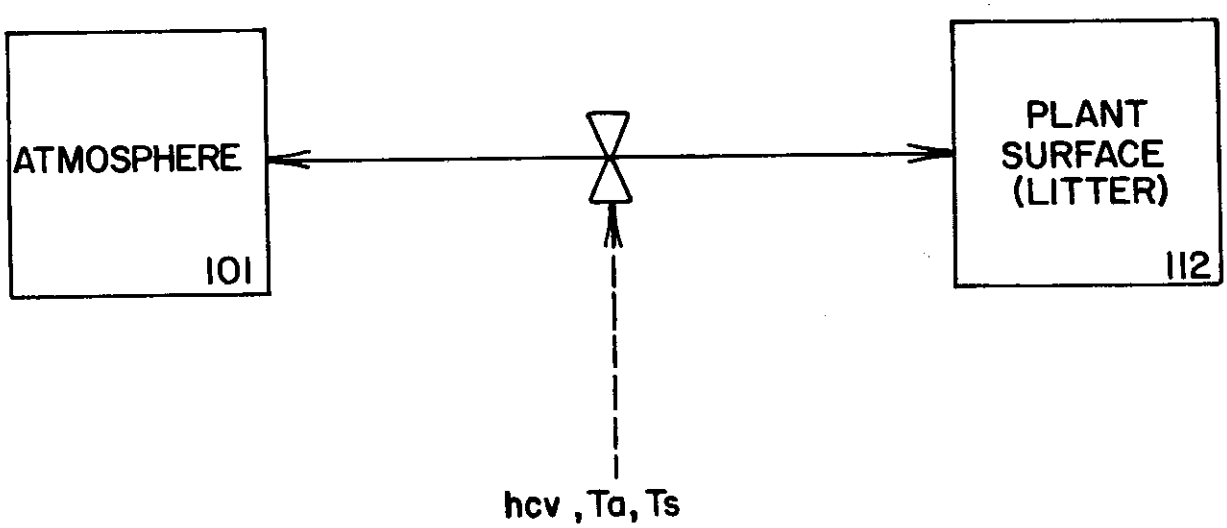
2.3.8.2 Controls.

Control Description	Symbol	Units
Prandtl number	Pr	dimensionless
Nusselt number	Nu	dimensionless
Reynolds number	Re	dimensionless
Surface area	A	m^2
Convective coefficient	hcv	cal m^{-2} day^{-1} $°C^{-1}$
Air temperature	Ta	°C
Soil surface temperature	Ts	°C

2.3.8.3 Flow rates. The same qualitative control of temperature gradient, heat transfer coefficient, and wind speed on convective heat transfer as indicated in Section 2.3.5 applies.



A. Graphical Model



B. System Relationships

Fig. 2.16. Convection exchange between atmosphere and plant surface.

2.3.9 (101–112) Conduction (John Nunn)

The heat flow per unit time between the soil surface and the atmosphere resulting from conduction can be expressed by a single first-order differential equation equating heat flow per unit time to thermal conductivity, surface area, and vertical temperature gradients (Gates, 1962; Hartiner and Martin, 1957).

2.3.9.1 Analytical expressions.

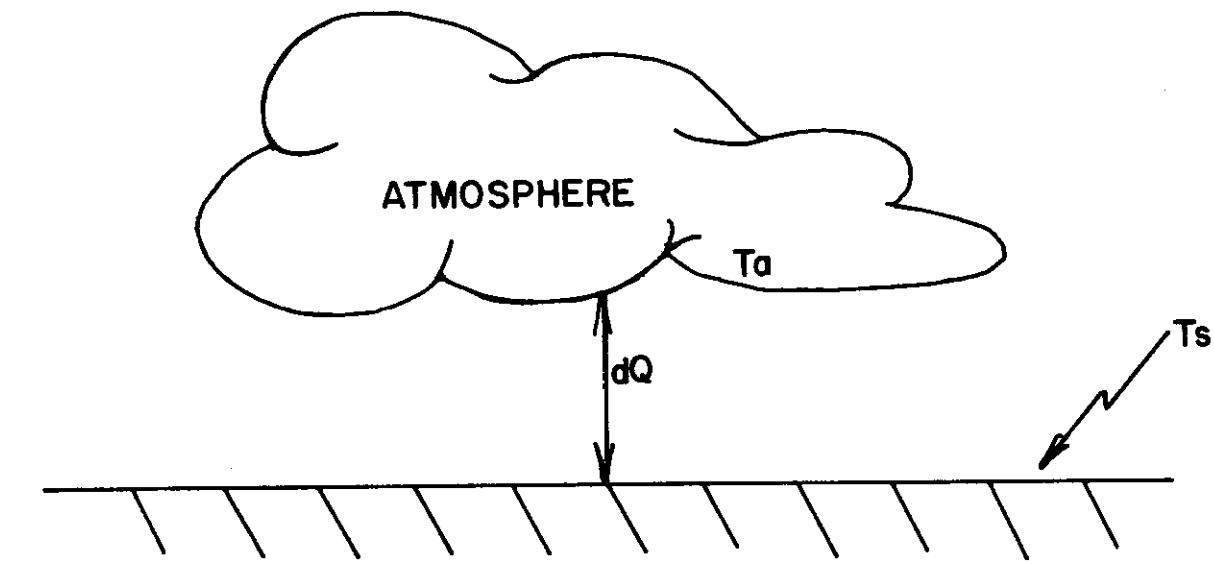
$$\frac{dQ}{dt} = -KA\frac{dT}{dy} \qquad (\text{cal day}^{-1}) \tag{2.9}$$

$$\frac{dT}{dy} \sim (Ta - Ts)/Ya$$

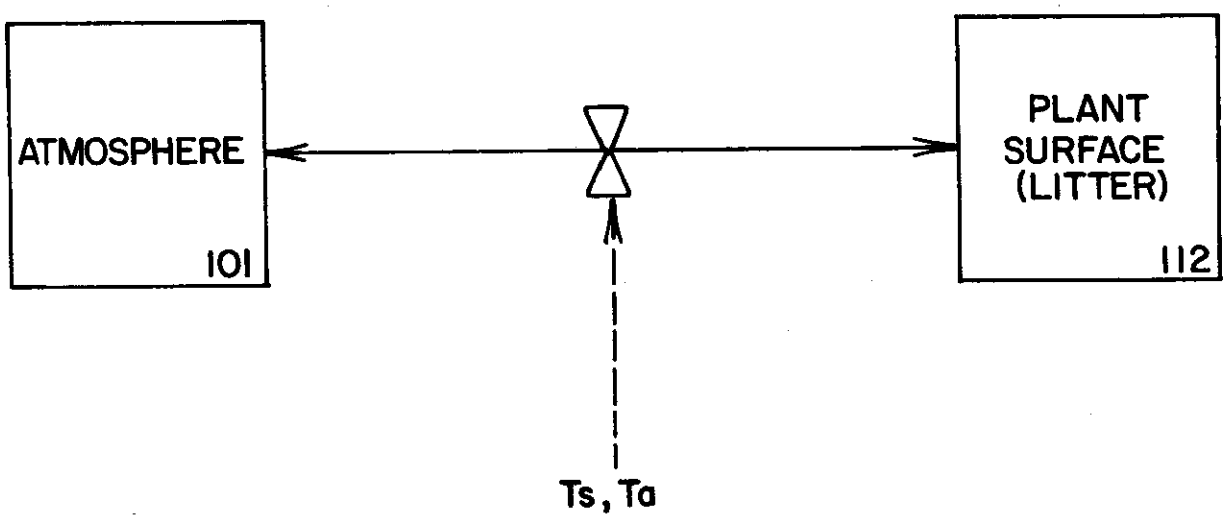
2.3.9.2 Controls.

Control Description	Symbol	Units
Air temperature	Ta	°C
Plant surface temperature	Ts	°C
Coefficient of thermal conductivity of air	K	cal day^{-1} m^{-1} $°C^{-1}$
Plant surface area in contact with media	A	m^2
Height of air temperature measurement	Ya	m
Temperature gradient	$\frac{dT}{dy}$	°C m^{-1}

2.3.9.3 Flow rates. The same considerations governing heat conduction in Section 2.3.6 apply here also. The primary difference from the soil case in rate of transfer arises from the differing area of plant surface in contact with air.



A. Graphical Model



B. System Relationships

Fig. 2.17. Conduction exchange between atmosphere and litter.

2.3.10 (101–112) Radiation (John Nunn)

The net radiation energy received by the plant surface (litter) is easily expressed by the summation of its components, i.e., the net balance of longwave and shortwave radiation.

2.3.10.1 Analytical expressions.

$$Rn = R_{si} - R_{so} + R_{li} - R_{lo} \tag{2.10}$$

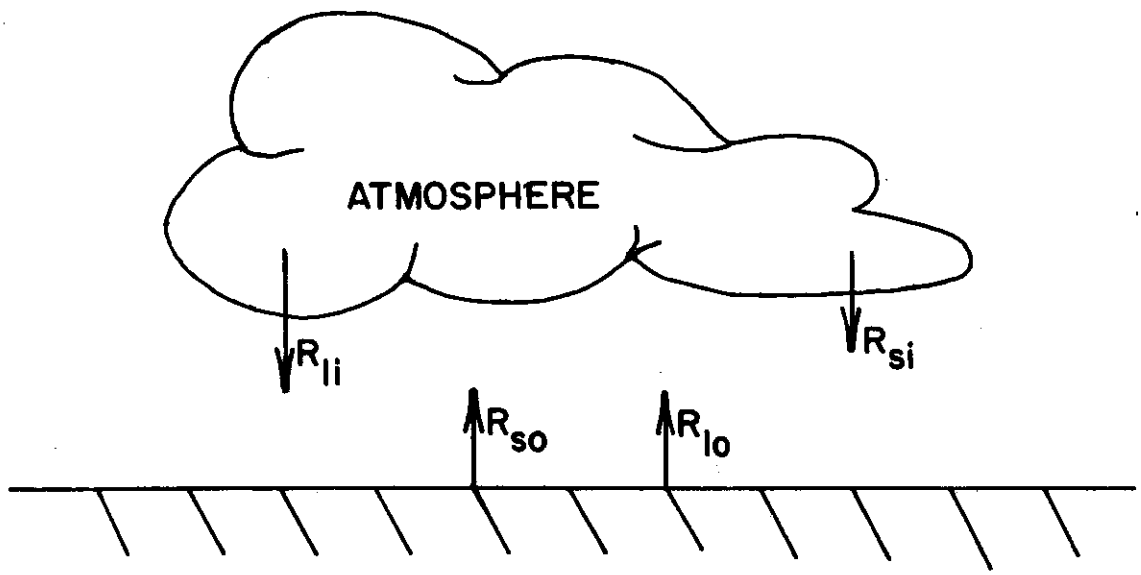
$$Rn = (1 - \alpha)R_{si} + R_{nl}$$

$$\frac{dQ}{dt} = Rn \qquad (\text{cal day}^{-1})$$

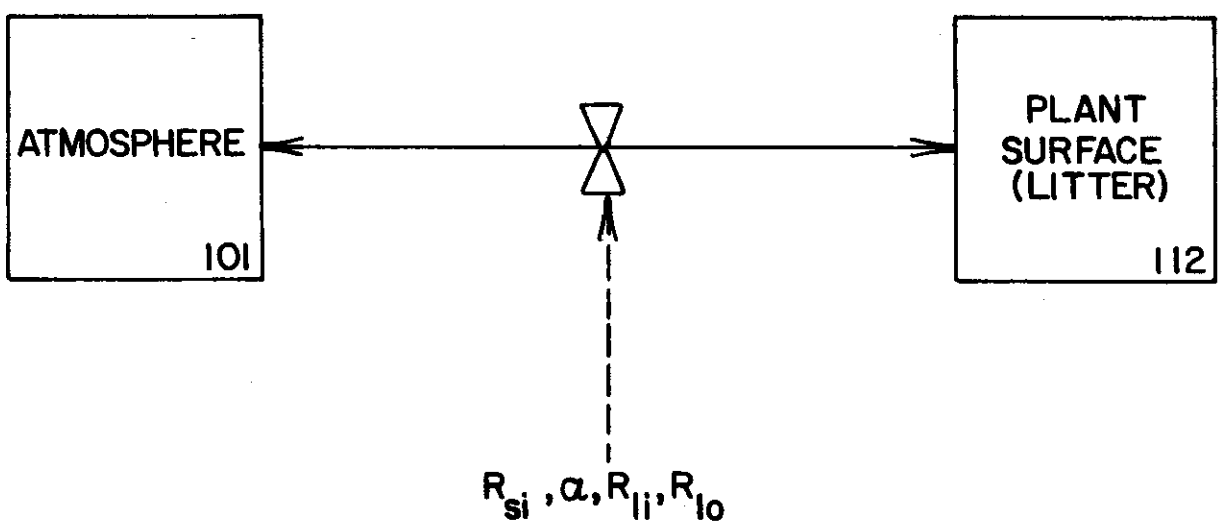
2.3.10.2 Controls.

Control Description	Symbol	Units
Surface temperature	Ts	°C
Air temperature	Ta	°C
Net radiation	Rn	cal day^{-1}
Incoming longwave radiation	R_{li}	cal day^{-1}
Outgoing longwave radiation	R_{lo}	cal day^{-1}
Incoming shortwave radiation	R_{si}	cal day^{-1}
Outgoing shortwave radiation	R_{so}	cal day^{-1}
Net longwave radiation	R_{nl}	cal day^{-1}
Albedo of plant surface	α	dimensionless

2.3.10.3 Flow rates. The discussion of flow rate given in Section 2.3.7 is also applicable here.



A. Graphical Model



B. System Relationships

Fig. 2.18. Atmosphere-soil radiation heat flow.

2.3.11 (102–105) Conduction (Larry Pochop)

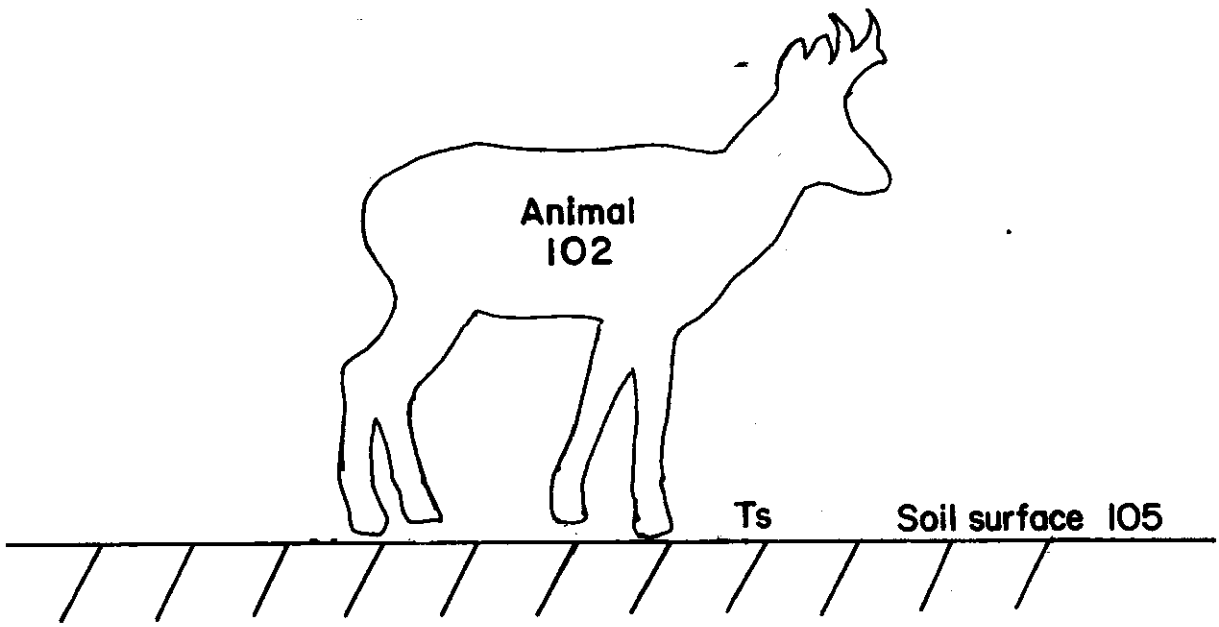
The rate of conductive heat transfer between animals and the soil surface may be expressed in terms of the Fourier equation for steady-state heat conduction. The overall conduction coefficient for this equation depends upon the thermal resistance of the soil surface and the thermal resistance of the animal surface.

2.3.11.1 Analytical expressions.

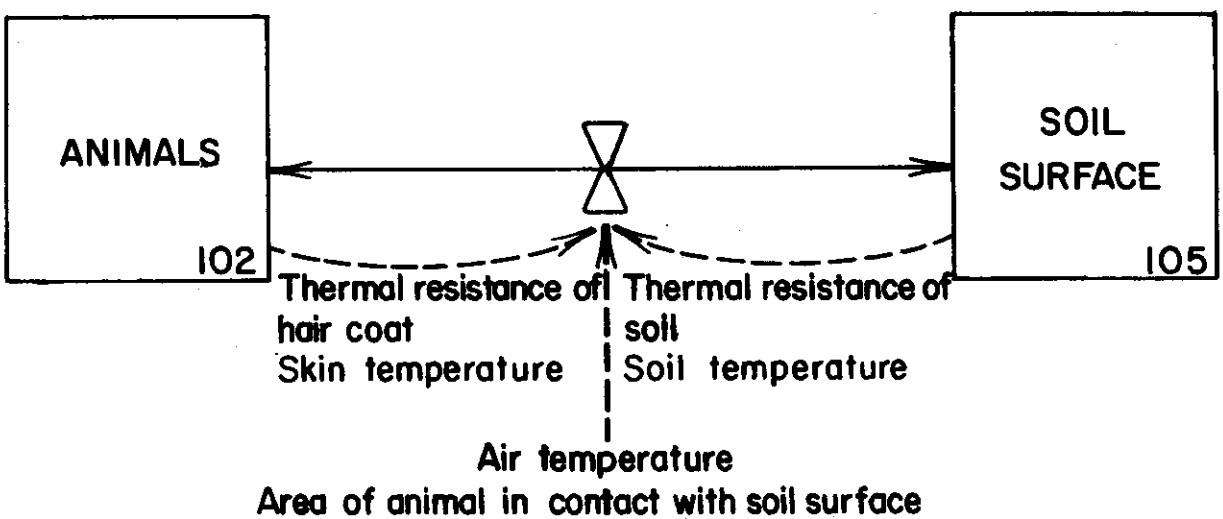
$$\frac{dQ}{dt} = Kc\ Aac(Ta - Ts) \qquad (2.11)$$

2.3.11.2 Controls.

Control Description	Symbol	Units
Surface area of animal in contact with soil	Aac	m^2
Soil temperature	Ts	°C
Surface temperature (animal)	Ta	°C
Effective thermal conductivity	Kc	cal day^{-1} m^{-2} $°C^{-1}$



A. Graphical Model



B. System Relationships

Fig. 2.19. Animal-soil conduction exchange.

2.3.12 (102–105) Radiation (Larry Pochop)

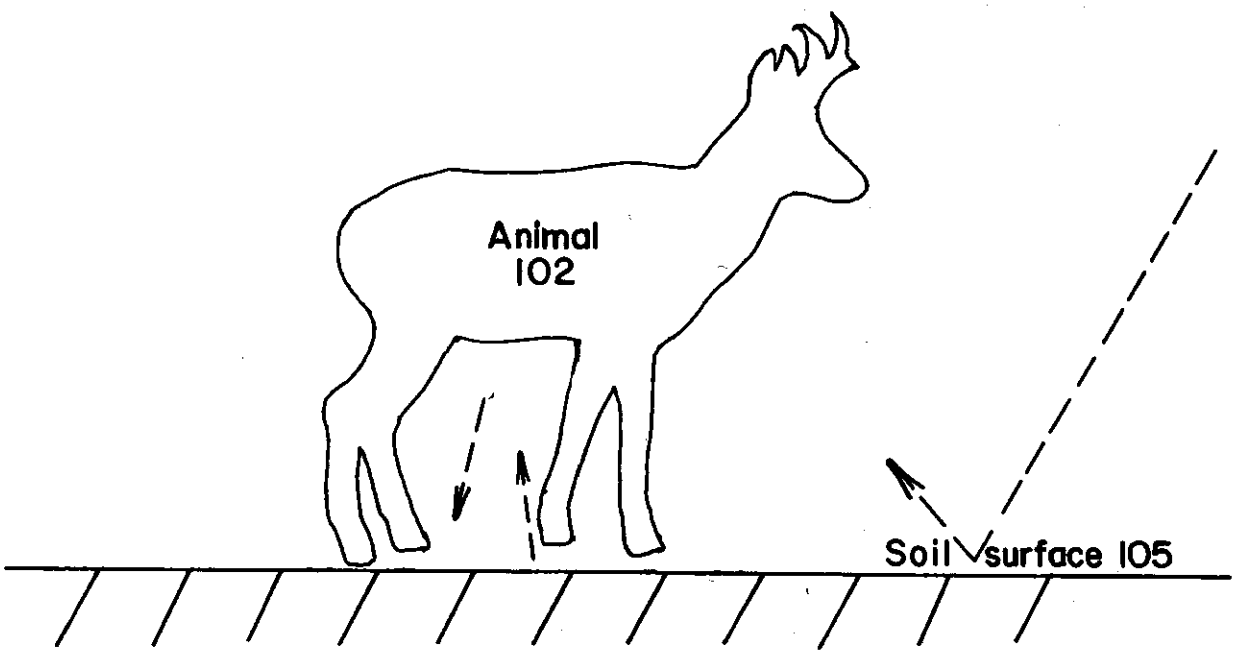
A continual radiation exchange takes place between two bodies in visual range if not separated by a radiation-absorbing medium. The net radiation exchange is proportional to the effective surface areas of the animal and soil, and the temperatures of the surfaces of each.

2.3.12.1 Analytical expressions.

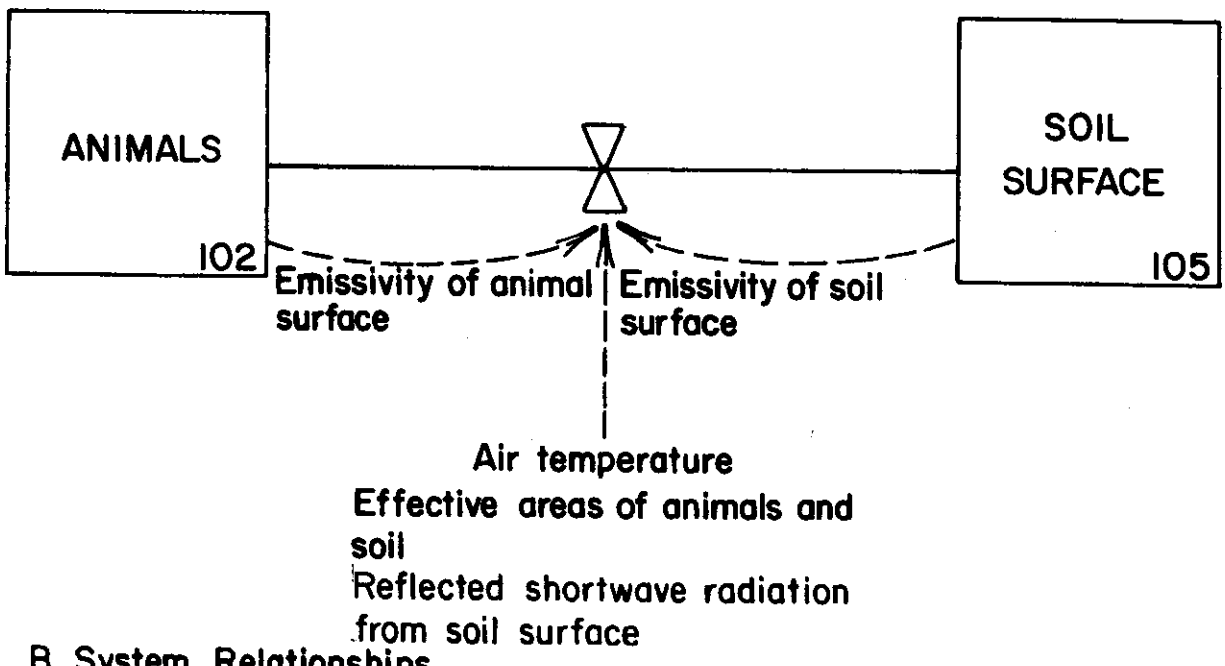
$$\frac{dQ}{dt} = \sigma A\ F_a F_e (T_1^4 - T_2^4) + as\ Sui\ As \qquad (2.12)$$

2.3.12.2 Controls.

Control Description	Symbol	Units
Surface area of soil	A	m^2
Emissivity factor of soil	F_e	dimensionless
Shape configuration factor	F_a	dimensionless
Litter temperature	T_2	°C
Surface temperature (animal)	T_1	°C
Stefan-Boltzmann constant	σ	cal m^{-2} day^{-1} $°C^{-4}$
Shortwave absorptivity of animal surface	as	dimensionless
Solar radiation reflected (soil)	Sui	cal m^{-2} day^{-1}
Effective area for shortwave absorption	As	m^2



A. Graphical Model



B. System Relationships

Fig. 2.20. Animal-soil radiation exchange.

2.3.13 (102–112) Conduction (Larry Pochop)

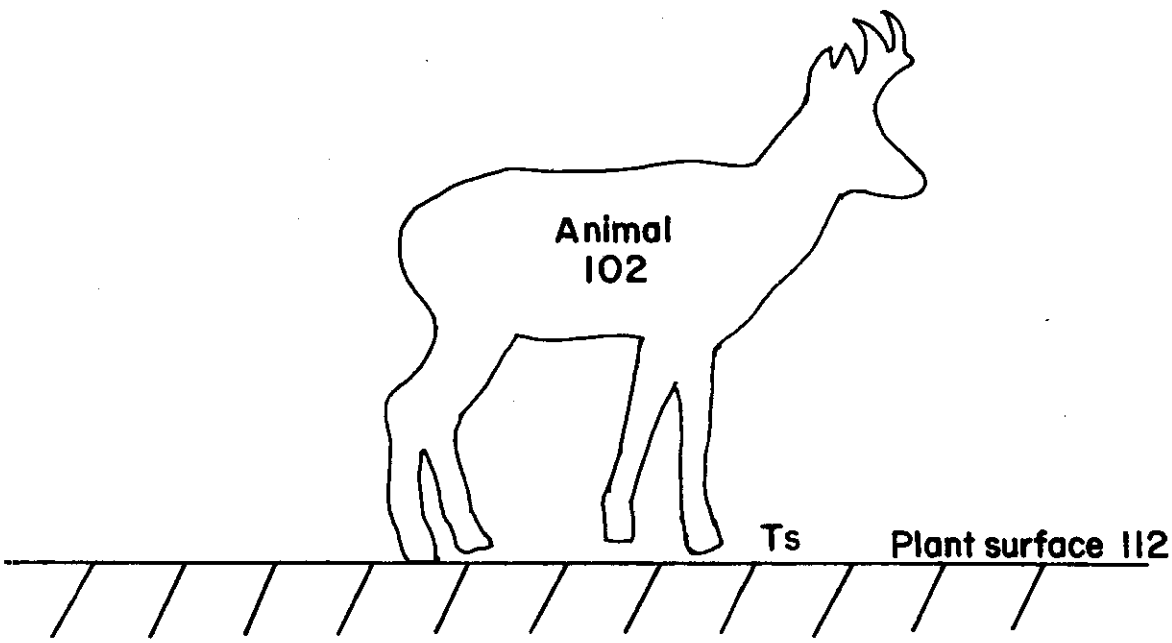
The rate of conductive heat transfer between animals and the plant surface may be expressed in terms of the Fourier equation for steady-state heat conduction. The overall conduction coefficient for this equation depends upon the thermal resistance of the plant surface and the thermal resistance of the animal surface.

2.3.13.1 Analytical expressions.

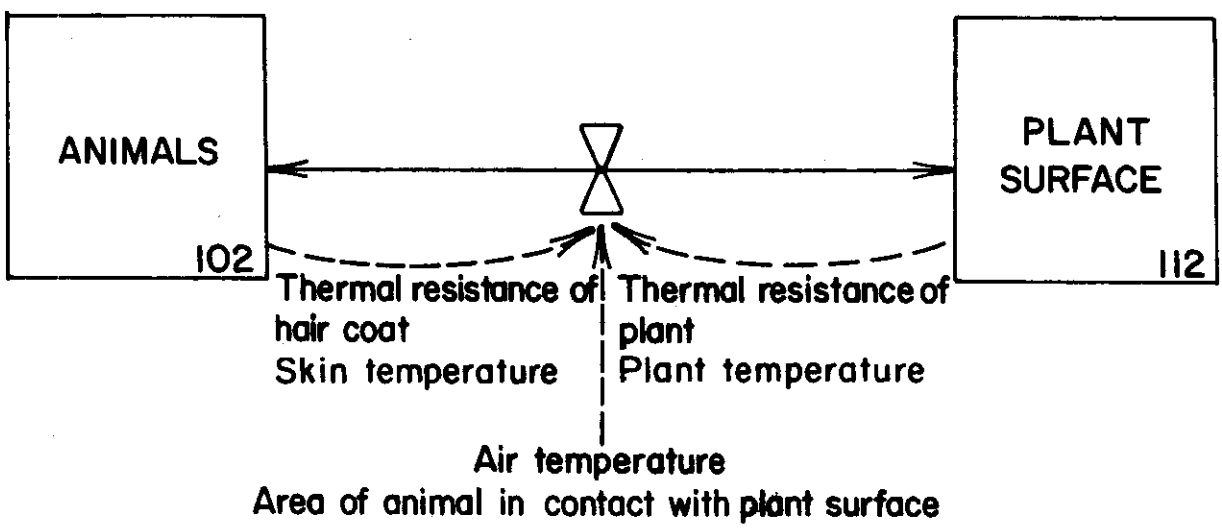
$$\frac{dQ}{dt} = -KA(Ta - Ts) \qquad (2.13)$$

2.3.13.2 Controls.

Control Description	Symbol	Units
Contact surface area of plant	A	m^2
Effective thermal conductivity	K	cal day^{-1} m^{-2} $°C^{-1}$
Surface temperature (animals)	Ta	°C
Surface temperature (plants)	Ts	°C



A. Graphical Model



B. System Relationships

Fig. 2.21. Animal-plant conduction exchange.

2.3.14 (102–112) Radiation (Larry Pochop)

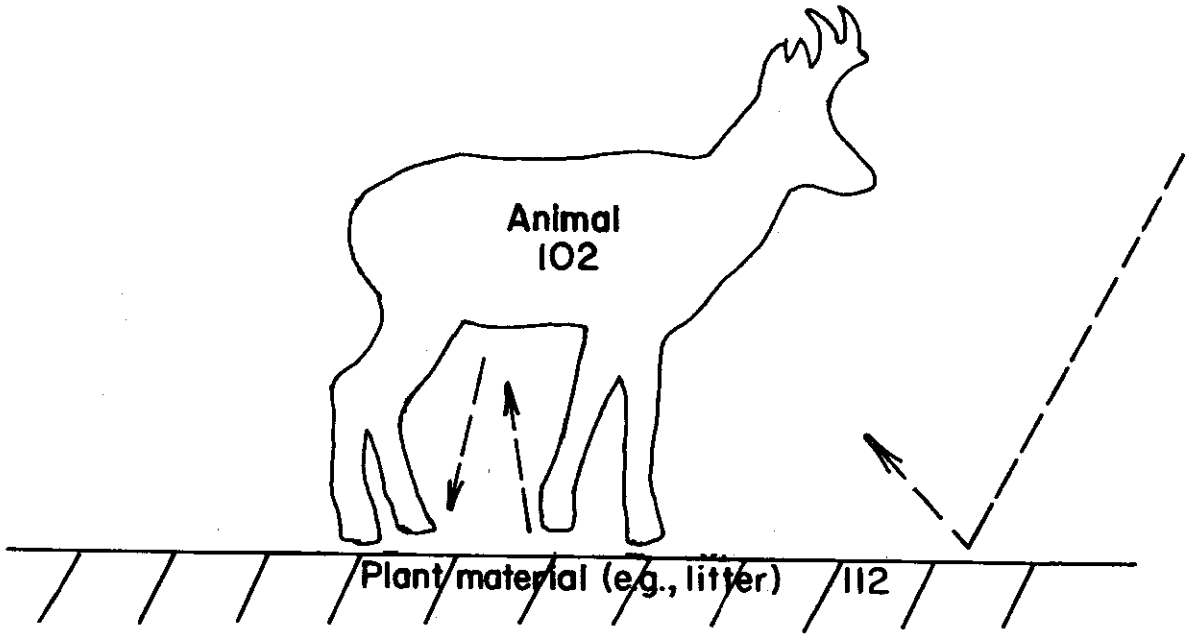
A continual radiation exchange takes place between two bodies in visual range if not separated by a radiation-absorbing medium. The net radiation exchange is proportional to the effective surface areas of the animal and plant and the temperatures of the surfaces of each.

2.3.14.1 Analytical expressions.

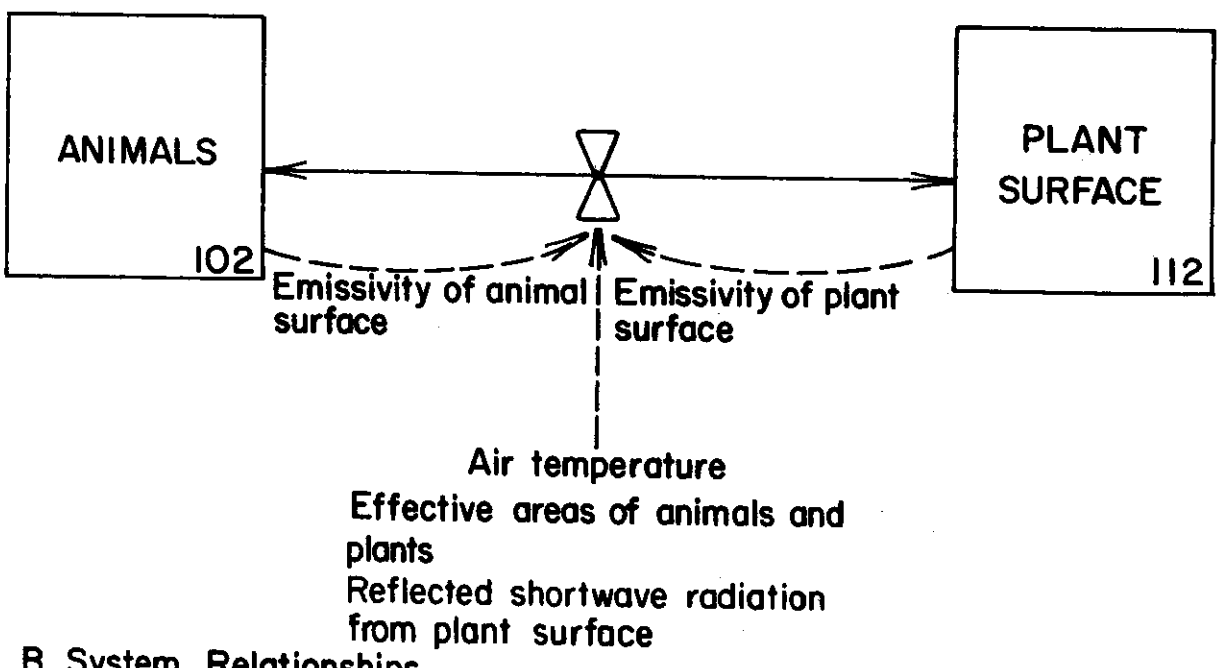
$$\frac{dQ}{dt} = \sigma A F_a F_e (T_1^4 - T_2^4) + as\ Sui\ As \qquad (2.14)$$

2.3.14.2 Controls.

Control Description	Symbol	Units
Surface area of plant material	A	m^2
Emissivity factor of plant material	F_e	dimensionless
Shape configuration factor	F_a	dimensionless
Litter temperature	T_2	°C
Surface temperature (animal)	T_1	°C
Stefan-Boltzmann constant	σ	cal m^{-2} day^{-1} $°C^{-4}$
Shortwave absorptivity of plant surface	as	dimensionless
Solar radiation reflected (plant)	Sui	cal m^{-2} day^{-1}
Effective area for shortwave absorption	As	m^2



A. Graphical Model



B. System Relationships

Fig. 2.22. Animal-plant radiation exchange.

2.3.15 (105 through 113) Conduction (Victor Hasfurther)

The mathematical model most often used to describe the heat transfer by conduction between the soil surface and the different soil layers (depths) is the one-dimensional heat flow equation (Hanks, Austin, and Ondrechan, 1971; Carson, 1961, 1963; Lee, 1970; Penrod and Stewart, 1967; Smith, Taylor, and Brown, 1968; de Vries and Peck, 1958; Wieranga, Hagan, and Gregory, 1971). This equation describes the process on a macroscopic basis. Thus, the actual transfer of heat under a macroscopic analysis is considered to be performed by solid matter (soil), water, and air. The one-dimensional heat flow equation is dependent upon the above materials as they relate to the thermal conductivity (λ) and volumetric heat capacity (C) of the different soil layers. The heat flow with time which can be found once the heat conduction equation is solved depends on the surface area of the soil under consideration (A) as well as the above quantities.

2.3.15.1 Analytical expressions.

$$\frac{\partial}{\partial Z}(\lambda \frac{\partial T}{\partial Z}) = C \frac{\partial T}{\partial t} \tag{2.15}$$

If soil profile is homogeneous,

$$\frac{\partial T}{\partial t} = \alpha \frac{\partial^2 T}{\partial Z^2}$$

where

$$\alpha = \frac{\lambda}{C}$$

solution requires two boundary condition values T_{s1}, T_{s2}.

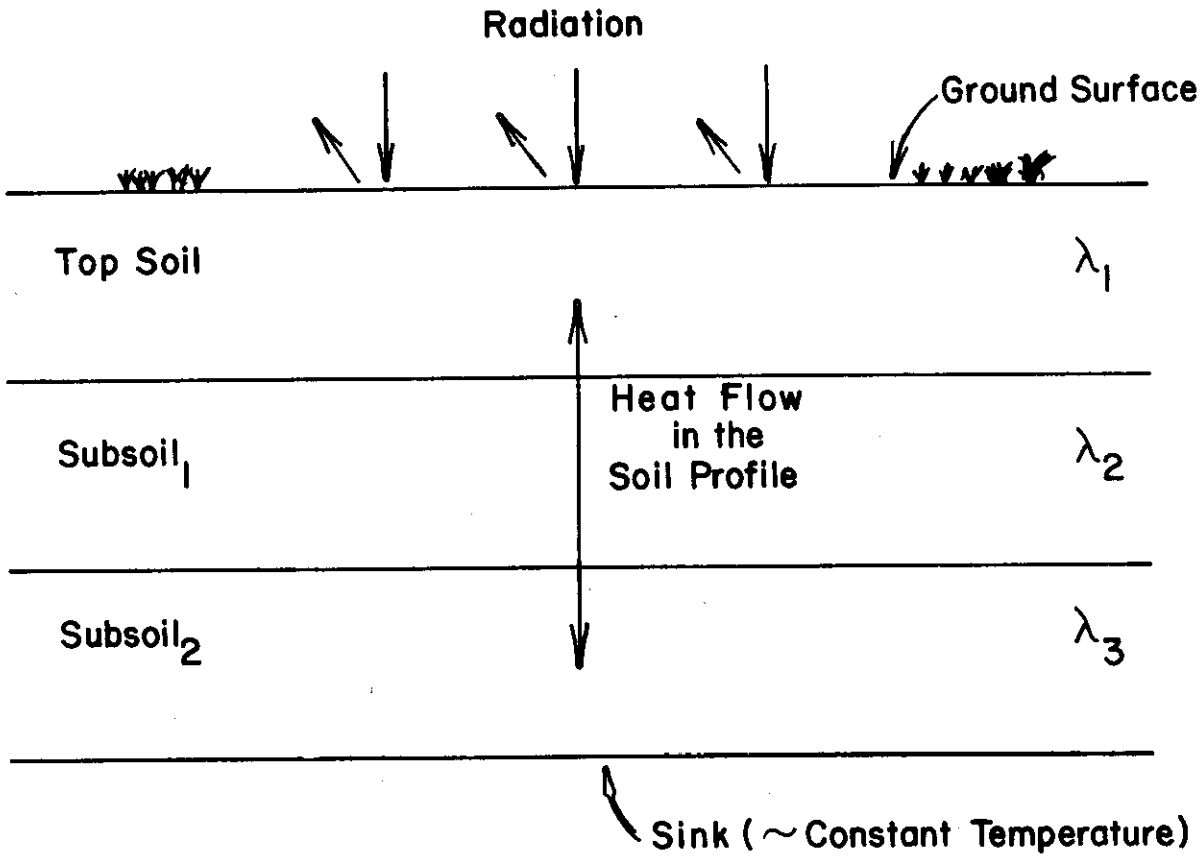
Once the above equations have been solved, the soil temperature profile as a function of t and z will be found; then the heat flux can be found by:

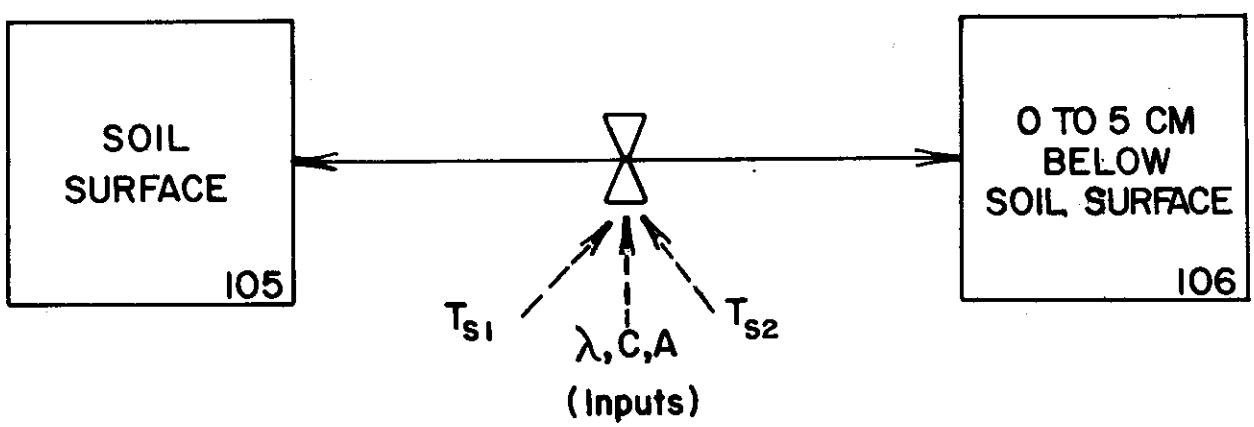
$$\frac{\partial Q}{\partial t} = -\lambda A \frac{\partial T}{\partial Z}$$

2.3.15.2 Controls.

Control Description	Symbol	Units
First soil depth temperature	T_{s1}	°C
Second soil depth temperature	T_{s2}	°C
Thermal conductivity capacity	λ	cal day^{-1} m^{-2} $°C^{-1}$
Area of soil layer	A	m^2
Volumetric heat capacity	C	cal cm^{-3} °C
Coordinate, distance from soil surface in the vertical direction	Z	cm

2.3.15.3 Flow rates. The flow of energy through the soil layers varies linearly with soil thermal conductivity. However, this quantity depends on mineral composition and structure, porosity, and water content; thus the conductivity may vary throughout the soil profile. The thickness of the organic soil layer and the latent heat of the organic and mineral constituents of the soil may also affect heat transfer through the soil. If so, they may be added as an additional term in the heat conduction equation (Nakano and Brown, 1971).





B. System Relationships

Fig. 2.23. Heat conduction through soil layers.

2.3.16 (112–106) Conduction (Larry Pochop)

The heat flow per unit time between the litter layer and soil can be expressed by a first-order differential equation relating conduction exchange to thermal conductivity, proportional surface area, and vertical temperature gradient (Gates, 1968*a*,*b*).

2.3.16.1 Analytical expressions.

$$\frac{dQ}{dt} = K A_{ls}(T_l - T_s) \qquad (\text{cal day}^{-1}) \qquad (2.16)$$

$$K = \frac{1}{R_l + R_g}$$

$$= \frac{1}{\left(\frac{1}{K_l}\right)Y_l + \left(\frac{1}{K_g}\right)Y_s}$$

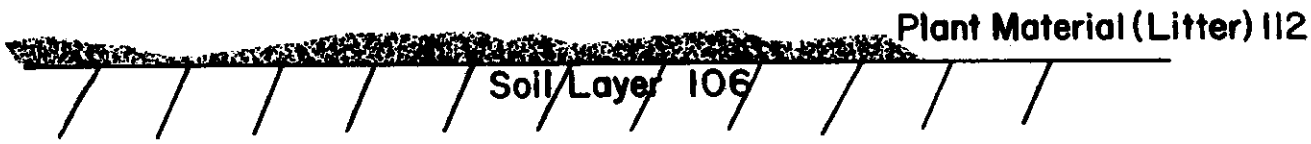
2.3.16.2 Controls.

Control Description	Symbol	Units
Area of soil layer	A	m^2
Temperature of the litter (average at a specific time)	T_l	°C
Temperature of the first soil layer (average at a specific time)	T_s	°C
Resistance of the litter	R_l	cal^{-1} day m^2 °C
Resistance of the soil	R_g	cal^{-1} day m^2 °C
Thickness of the litter from soil-litter interface to the midpoint of litter	Y_l	m
Depth of soil at which T_s is taken	Y_s	m
Thermal conductivity of the litter	K_l	cal day^{-1} m^{-1} $°C^{-1}$

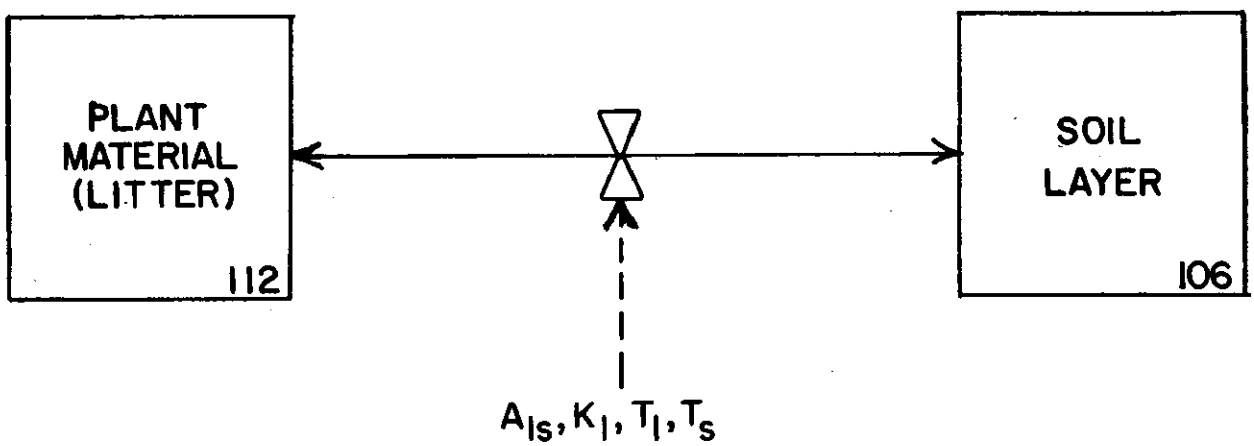
2.3.16.2 Controls (continued).

Control Description	Symbol	Units
Thermal conductivity of soil	K_g	cal day^{-1} m^{-1} $°C^{-1}$
Contact surface area between litter and soil	A_{ls}	m^2
Effective thermal conductivity of system	K	cal day^{-1} m^{-1} $°C^{-1}$

2.3.16.3 Flow rates. The principal factor producing the movement of heat from the plant material to the soil surface will be the temperature gradient between these two surfaces. The rate of flow will also strongly depend on the thermal conductivity of the litter interface. It will be necessary to study the dependence of the thermal conductivity on moisture content and temperature of the plant material.



A. Graphical Model



B. System Relationships

Fig. 2.24. Conduction exchange between litter and mineral soil surface.

2.3.17 Summary Comments and Recommendations for Heat Model (all participants and J. A. Smith)

Three major priorities for the development of the heat model emerged from the Process Studies Workshops. These were:

1. Determining the influence on heat flow by plant material, principally litter.
2. Estimating the heat transfer coefficients between compartments.
3. Modeling the net energy exchange at plant, animal, and soil surfaces.

Heat transfer processes from the atmosphere to top soil layer (101–105) were thought to be adequately described in the literature. However, additional studies would be needed to determine the thermal conductivity of air as a function of air moisture and temperature, and further analysis of existing data for the radiation transfer would be necessary.

The heat transfer process between animals and their surroundings (usually including both the atmosphere and surrounding surfaces) has been studied quite extensively, and, in fact, models depicting the process have been developed (e.g., Beckett and Vidrine, 1970; Bartlett and Gates, 1967; Smith, 1964; Esmay, 1969). A model has also been presented for poultry (Bouchillon, Reece, and Deaton, 1970). Each of these models has the characteristic of having been developed only for a specific animal and for a rather limited set of conditions. However, use of current information as discussed in this review along with measurement of appropriate environmental parameters makes it appear that general, although approximate, models for application to the grasslands are feasible. The main difficulties appear to be determining these environmental parameters.

Additional studies need to be made in order to refine the quantities to be used in the heat conduction equation. This necessarily entails finding a better method for predicting and defining the initial boundary conditions to be used in solving equations.

A link also needs to be made between the daily cyclic temperature and heat flow and the yearly cyclic effect of the same quantities if more accurate estimates of what will be happening a few days in advance is desired.

Studies on changes of thermal conductivity with changes in soil properties need to be analyzed through a model such as the one outlined in this report. Almost no work has been done in this area.

To produce a good soil heat flow model, taking into consideration the above suggested studies, approximately $100,000 to $150,000 would be needed.

2.4 THE WATER SUBMODEL

(Robert Doty, W. David Striffler, L. E. Allen, Freeman M. Smith, J. A. Smith)

The subsystem diagram for the water model is shown schematically in Fig. 2.25. The water flow model is designed to simulate the net flow of water from the atmosphere to plant material and both surface and subsurface soil layers. Physical processes composing the water cycle include precipitation, interception, evaporation, transpiration, condensation, infiltration, snowmelt, and redistribution and uptake within the soil layers. Water leaves the system through the processes of runoff, drainage, and evapotranspiration. Experimentally, net runoff appears to be zero for the Pawnee Site. Drainage occurs only if the seven soil layers simulated in the model exceed field capacity. Liquid and solid precipitation [(201–202), (201–203), and (201–206)] provide the major water input into the system. This process may be simulated stochastically using historical records of precipitation, minimum and maximum daily temperatures, relative humidity, and other weather factors. Condensation [(201–204), (201–202), and (201–206)] is assumed neglible.

Interception (201–204) refers to both the process of precipitation being caught and held on vegetation surfaces and the quantity of precipitation caught and held. When rain occurs, drops striking the leaves are spread out over the leaf surface and held on the surface. As more drops are caught, the surface becomes saturated, and additional drops striking the leaf tend to drip from the leaf margins or tips. Also during the process, a small amount of water is lost from the wet surface by evaporation. When the rain stops, a small amount of drip may continue for a short time while evaporation begins to dry the leaf surfaces. Evaporation [(201–206) and (201–204)] is a change of state from liquid form to vapor form. Heat

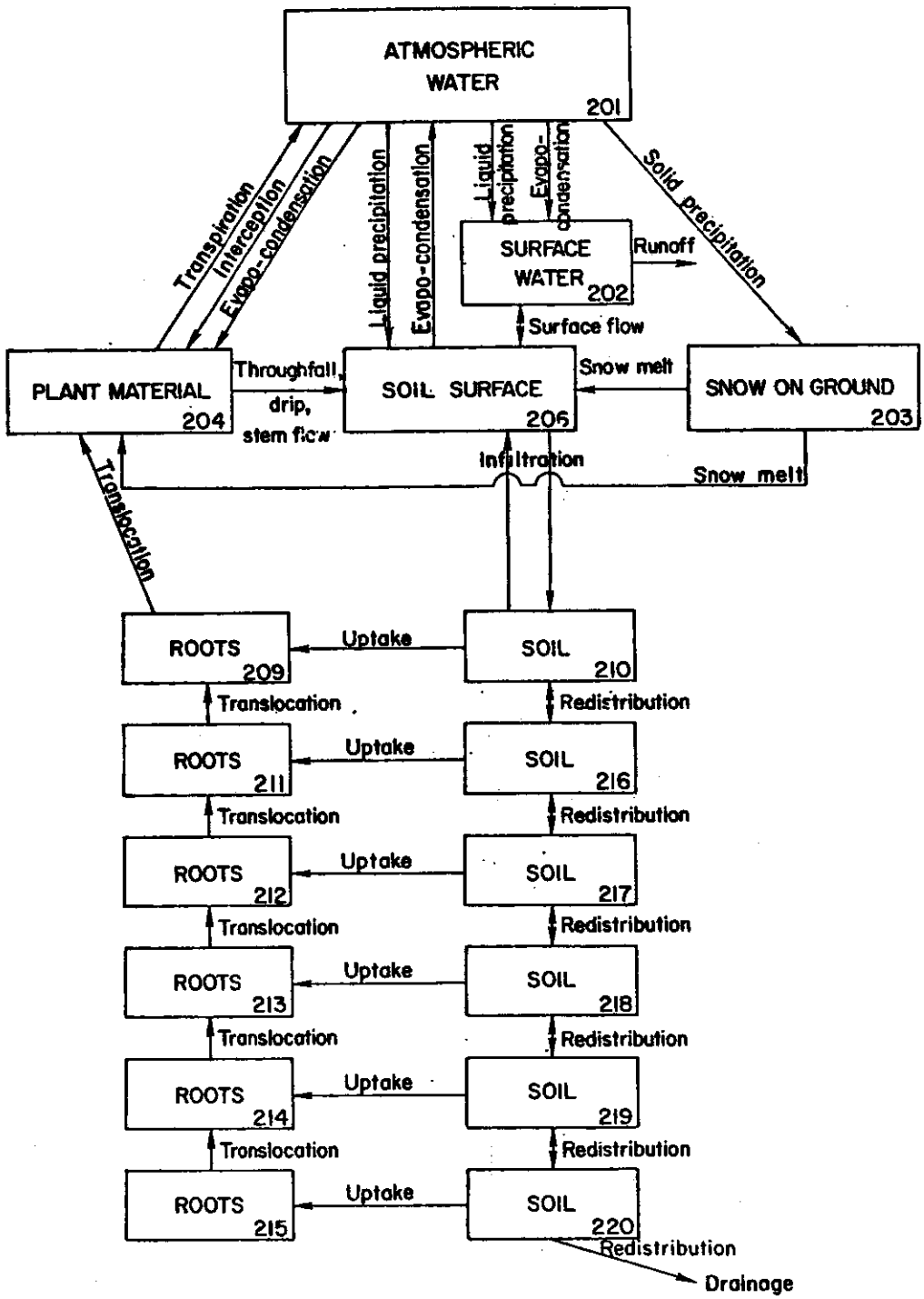


Fig. 2.25. Water model.

is added to the system in order for this process to be completed; however, under natural conditions other factors such as wind speed and vapor pressure gradients come into play and act as resistances to vapor transport. Expressions for evaporation predictions are summarized by Herbel and Pieper (1970). Transpiration (201–204) rate is estimated as the difference between total evapotranspiration and soil evaporation. All precipitation that is not intercepted by (201–204) is assumed to go directly to soil (204,206) via drip, stem flow, or throughfall.

The snowmelt process can be thought of as a mechanism for converting precipitation which occurs in a solid form (snow, sleet, etc.) to a liquid form (water) wherever it has accumulated on the surface (on the canopy, litter, or mineral soil).

This is the one-way process of moving water from 203 to 204 and from 203 to 206. Essentially a physical process, the same inputs are acting whether we go from 203 to 204, 205, or 206. These factors are air temperature, snow albedo, radiation, cloud cover, wind, dew point, liquid precipitation, slope, vegetation cover, elevation, surface evaporation, ground melt, or percolation.

The physical process of melting the snow that has accumulated on the vegetation, litter, or mineral soil is basically a heat flow problem. The end product resulting from the calories of heat added to the snowpack is melt-water. The primary driving force is the sun with several weather and site factors altering the delivery of the sun's energy to the snowpack. The absence or presence of a snowpack is simultaneously governed by the process of precipitation and the outflow of the melt process itself.

Infiltration (206–210) is the hydrologic process in which water at the soil surface enters the soil mass. Although the same laws governing infiltration also apply to soil water movement through the soil mass, the term "infiltration" refers only to the boundary phenomenon. Infiltration rate varies with time and is related to soil saturation. Usually the rate is high and decays to constant potential infiltration rate.

The redistribution [(210–216), (216–217), (217–218),...,(220–221)] of water in the soil following infiltration is a complicated process requiring complicated analytical procedures. In spite of the fact that a great deal of work has been done, most studies and analytical procedures do not account for reduction in soil water due to uptake by plants or evaporation. The redistribution of water is primarily due to gravity forces and/or soil water suction forces. The process involves the desorption of the initially wetted zone and the sorption of the dryer soil zones below the wetted zone. As redistribution proceeds, the boundary between the sorbing and desorbing layers increases in depth and the rate of redistribution decreases. Redistribution is a function of the depth of the initially wetted zone, the soil water potential gradient between the layers, and the conductivity of the soil. It is complicated by hysteresis effects, evapotranspiration losses, impeding layers, and the presence of a water table. Many analytical approaches are available.

The uptake of water [(210–209), (216–211), and (217–212)] by plants is a very complicated process involving the movement of water to the roots under the influence of soil water potential gradients which are induced by suction gradients within the roots. The rate and amount of uptake depends on many

interacting factors including atmospheric factors (evaporative demand), soil factors (soil water content, soil water potential, and conductivity), and plant factors (root density, root depth, rate of root extension, and root physiology). Because of the complexity and interactions among variables and the difficulty in measuring potential gradients between the roots and soil, most studies of uptake have been qualitative or have approached the uptake process indirectly without accounting for actual processes. In spite of this, a few analytical and theoretical models do exist, notably that of Rose and Stern (1967) which analyzes soil water withdrawal from different soil depth zones in relation to soil wetness and hydraulic properties and the rate of plant root uptake.

The uptake of water by plants is generally considered to be the result of tension gradients within the soil-plant-atmosphere continuum. The evaporative demand of the atmosphere causes water vapor to diffuse through the stoma on the plant leaves which, in turn, sets up a suction gradient within the conducting tissues of the plant down to the root system where water is taken into the roots. The amount and rate of uptake depends upon the ability of the roots to absorb water from the soil with which they are in contact and the ability of the soil to conduct water to the roots at a rate sufficient to meet transpiration requirements. Plant factors affecting intake thus include the rooting density, rooting depth, rate of root extension, and physiological plant factors. Soil factors affecting intake include hydraulic conductivity, diffusivity, soil water potentials, and soil water contents. In addition, atmospheric conditions determine the rate at which a plant must transpire and, thus, the rate at which water must be taken into the root systems.

Translocation through the root system [(204-209),...,(214-215)] is assumed to proceed as long as there is available soil water and net evaporation/transpiration.

Finally, surface flow (202-206) represents an important part of the water cycle, but no information enumerating it was presented during the Process Studies Workshops.

2.4.1 (201–202), (201–203), and (201–206) Liquid and Solid Precipitation (Robert Doty)

A host of climate and weather factors are involved in the transfer of atmospheric water (201) to the earth's surface (202 or 203) which would be very difficult to deal with in modeling the precipitation process. It may be sufficient to characterize from past records the weather patterns, precipitation extremes, and other expected fluctuations so that adequate restraints can be developed. In the model storm bursts, or hourly, daily, weekly, etc., precipitation amounts could be simulated using the above restraints to provide inputs of water into the sytstem (at 202 or 203, etc.).

Some restraints that might be necessary or useful are:

1. Maximum 5- or 10-min intensities.
2. Maximum volume for various time intervals by seasons (seasons relative to weather systems; for example, November to March frontal storms) and perhaps by rain or snow events.
3. Expected or mean volumes for various time intervals that might be modeled.
4. Probabilities of an event or of one event following another (dry days following wet, etc.).

Separating the liquid and solid components could be accomplished by a method suggested by Willen, Shumway, and Reid (1971) such that:

$$S = P\ 1.0 - (B/A)$$

where

S = proportion of precipitation occurring as snow (inches, water equivalent)

P = total daily precipitation (rain plus snow) (inches)

A = maximum - minimum temperature

B = maximum - base temperature for snowfall

Also, an additional process of redistribution of the snow on the ground by the wind may need to be developed for the snowmelt process.

2.4.2 (201–204), (201–202), and (201–206) Condensation

Formation of dew on plant and soil material was considered in the water model. Discussion of the condensation process, however, resulted in deleting the process from the model. Moisture formation on plant surfaces influences the plant in one of two ways--by reducing transpiration or by actually entering the plant through the stomata. Both can be of value to plant growth.

Absorption of water vapor through the stomata would seem to have the same resistances (in reverse) as transpiration. Koller and Samish (1964) and others have shown the relative vapor pressure gradients to be small. In addition, the gradient is toward the plant only at night when the stomata are generally closed and air motion is small. Therefore, both the internal and external resistances to vapor diffusion will be high. Specific plant species, under some conditions, can absorb water through their leaves and transfer it through the plant and even to the soil. However, the resistance is normally so high in many species that the quantity of water absorbed in an overnight period is insignificant (Slatyer, 1967).

2.4.3 (202-201) Evaporation (W. David Striffler)

Evaporation from a free water surface is controlled by the net energy input, vapor pressure deficit, and wind speed. The basic Penman (1948) equation is modified by van Bavel (1966) due to empiricism.

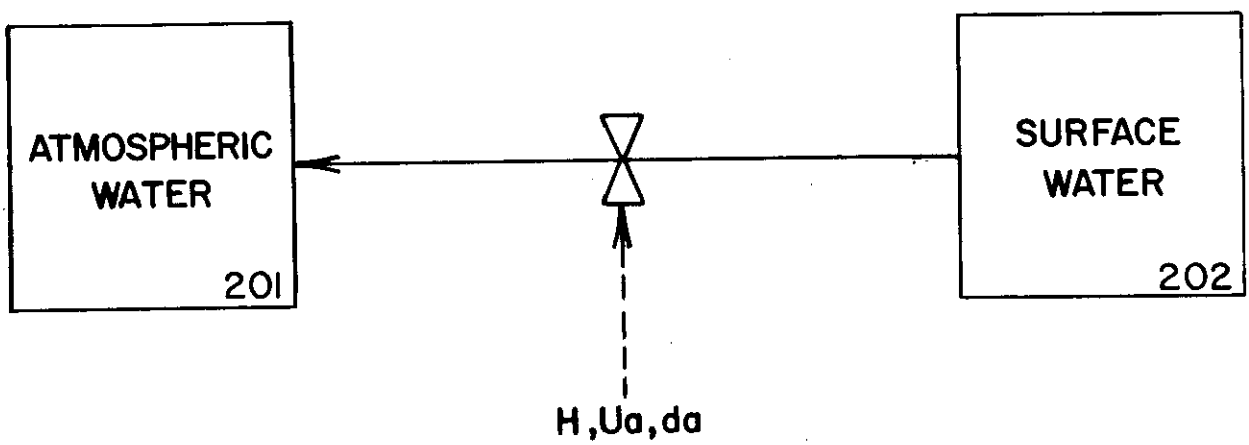
2.4.3.1 Analytical expressions.

$$E = \frac{eH + da/Ra}{e + 1.0 + Rs/Ra} \quad (m\ day^{-1}) \qquad (2.17)$$

$$Ra = \frac{[\ln Z/Zo]^2}{K^2 Ua}$$

2.4.3.2 Controls.

Control Description	Symbol	Units
Net radiation + soil heat flux in evaporation equivalents	H	m day^{-1}
Vapor pressure deficit	da	millibar
Wind speed	Ua	m day^{-1}
Aerodynamic roughness parameter	Zo	m
Height of measurement	Z	m
Von Karman's Constant	K	dimensionless = .40
Surface resistance to evaporation (determined from lysimeter)	Rs	day m^{-1}
Air resistance	Ra	day m^{-1}
Evaporation	E	m day^{-1}
Water/air molecular ratio	e	.623



System Relationships

Fig. 2.26. Evaporation between surface water and atmosphere.

2.4.4 (201-204) Interception (W. David Striffler)

Interception refers to both the process of precipitation being caught and held by the vegetative canopy and the quantity of water lost by the interception process. Two separate components must be considered: (i) the storage of water on the leaf surface and (ii) the evaporative loss of water from the leaf surface during the storm. The sum of these is the interception loss.

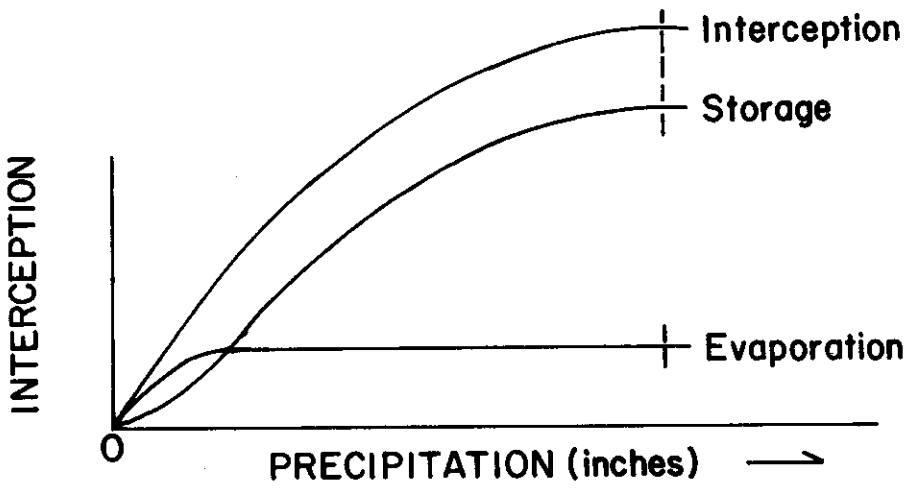
Factors affecting the total interception loss during any particular storm include the rainfall intensity and amount, the total surface area of the foliage, and the roughness or wetability of the leaf surface and the surface tension forces.

2.4.4.1 Analytical expressions.

$$I = (S + REt)(1 - e^{-cP}) \quad (m) \tag{2.18}$$

2.4.4.2 Controls.

Control Description	Symbol	Units
Interception losses	I	m
Surface storage on canopy	S	m
Surface ratio of interception surface ratio to projected area	R	dimensionless
Evaporation rate during storm	E	$m\ hr^{-1}$
Storm duration	t	hr
Total storm rainfall	P	m
Constant	c	m^{-1}



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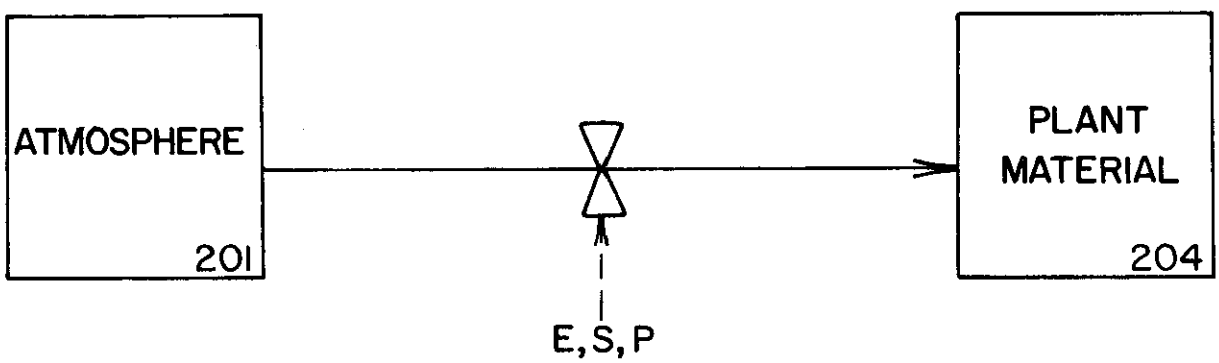


B. System Relationships

Fig. 2.27. Interception by plant material.

2.4.5 (204-201) Transpiration (W. David Striffler and J. A. Smith)

Total water flux to the atmosphere [evapotranspiration (ET)] is equal to water loss as transpiration (Et) plus soil evaporation (Es). Soil evaporation may be estimated by considering the energy balance at the surface. If the potential evapotranspiration rate and soil evaporation are known, the transpiration rate can be determined by considering the various resistances to vapor transfer.

2.4.5.1 Analytical expressions.

$$ET = Et + Es \tag{2.19}$$

$$Et = (Eo - Es)/[1 + (\gamma/(\gamma + s))(rc/ra)] \quad \text{(langleys day}^{-1}\text{)}$$

$$Es = Rn - G - H$$

$$ra = \frac{[\ln Z/Zo]^2}{K^2 Ua}$$

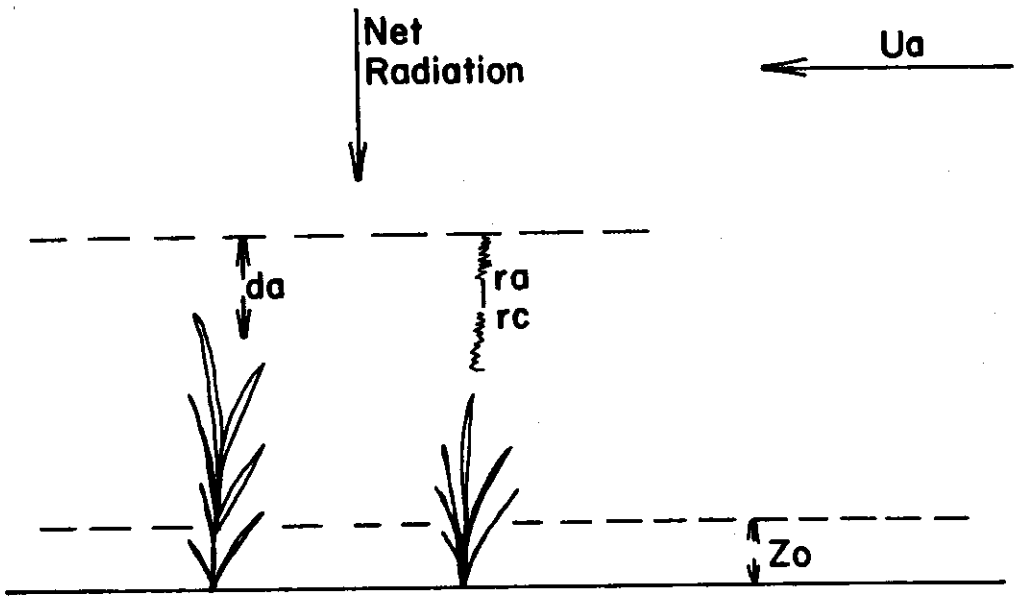
(van Bavel, 1966), (Brun, Kanemasu, and Powers, 1972), (Block, Tanner, and Gardner, 1970)

2.4.5.2 Controls.

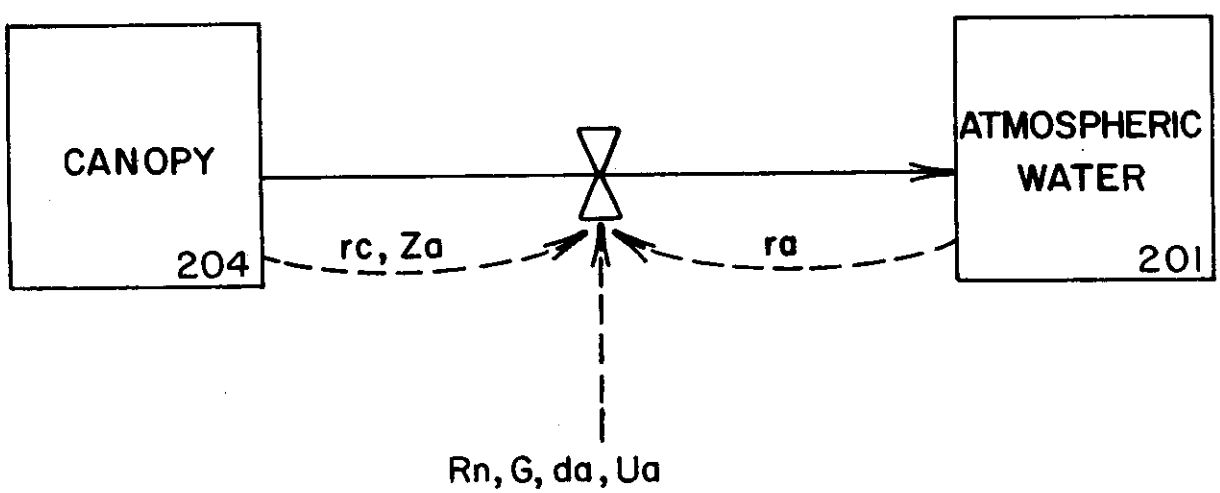
Control Description	Symbol	Units
Sensible heat flux	H	langleys day^{-1}
Net radiation	Rn	langleys day^{-1}
Psychometric constant	γ	millibar $°K^{-1}$
Soil heat flux	G	langleys day^{-1}
Slope of saturation vapor pressure curve	s	millibar $°K^{-1}$
Vapor pressure deficit	da	millibar

2.4.5.2 Controls (continued).

Control Description	Symbol	Units
Von Karman's constant	K	0.40
Wind speed	Ua	m day^{-1}
Height of measurement	Z	m
Aerodynamic roughness	Zo	m
Potential evaporation	Eo	langleys day^{-1}
Transpiration	Et	langleys day^{-1}
Diffusion resistance	ra	sec cm^{-1}
Soil evaporation	Es	langleys day^{-1}
Transpiration resistance (function of leaf area index and stomatal resistance)	rc	sec cm^{-1}



A. Graphical Model



B. System Relationships

Fig. 2.28. Transpiration exchange between canopy and atmosphere.

2.4.6 (201–206) and (201–204) Evaporation (W. David Striffler)

The water loss from the canopy and mineral surface is approached by defining the actual evaporation instead of the potential evaporation due to the rare occasion of saturated conditions. Vapor pressure gradients, wind speed, resistance coefficients, and energy supply are used in determining the net water loss.

2.4.6.1 Analytical expressions.

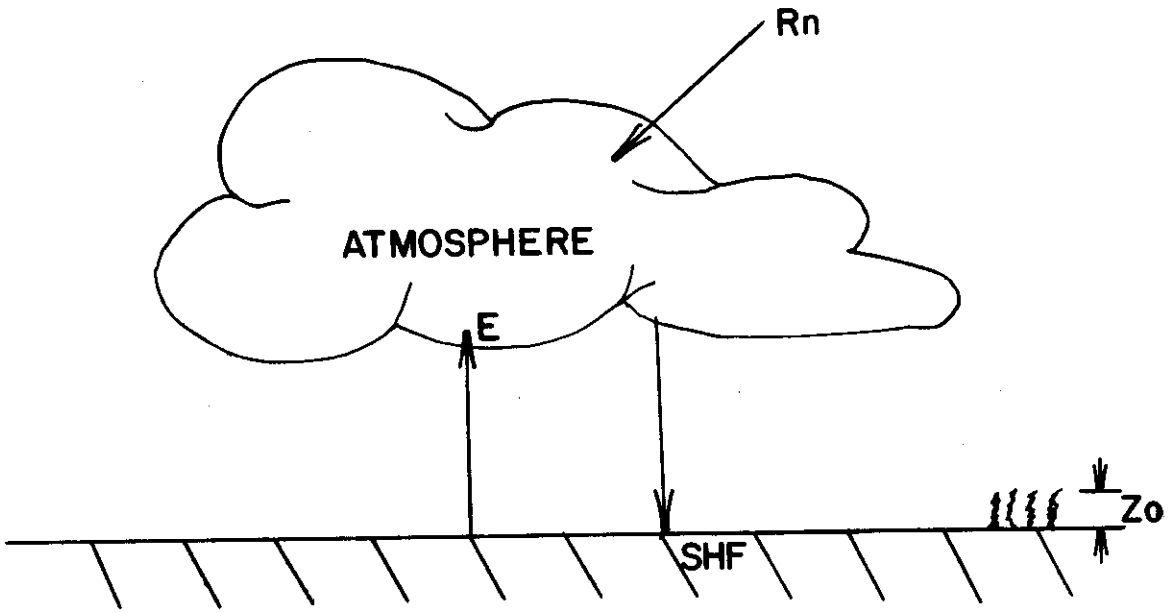
$$E = \frac{eH + da/Ra}{e + 1 + Rs/Ra} \qquad (2.20)$$

$$Ra = \frac{[\ln Z/Zo]^2}{K^2 Ua} \quad (m\ day^{-1})$$

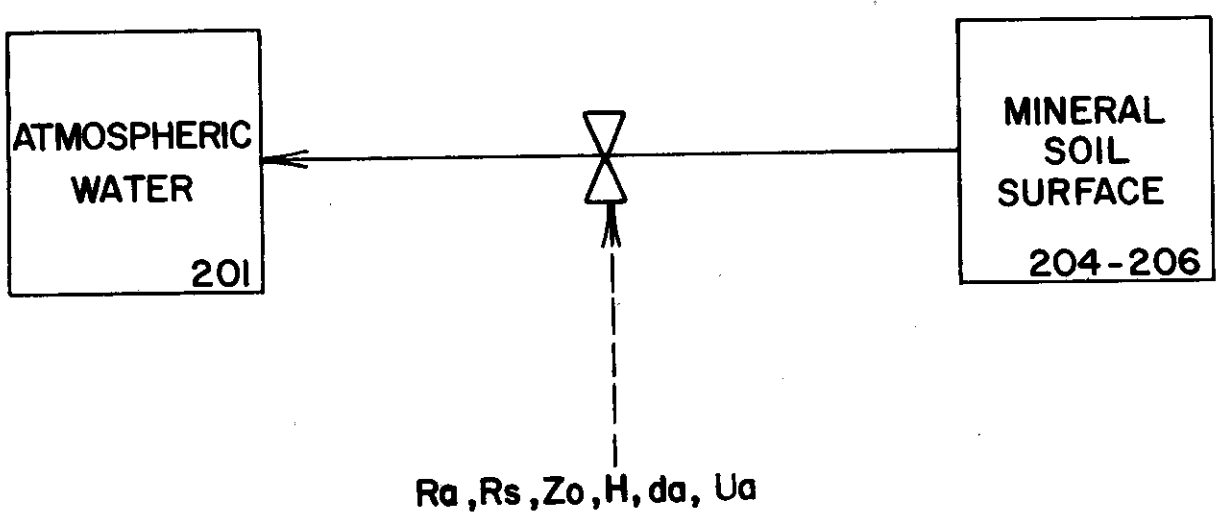
2.4.6.2 Controls.

Control Description	Symbol	Units
Net radiation + soil heat flux in evaporation equivalents	H	m day^{-1}
Vapor pressure deficit	da	millibar
Wind speed	Ua	m day^{-1}
Water/air molecular ratio	e	.623
Aerodynamic roughness parameter	Zo	m
Height of measurement	Z	m
Von Karman's Constant	K	0.40
Surface resistance to evaporation (residual calculated through use of lysimeter)	Rs	day m^{-1}
Air resistance	Ra	day m^{-1}
Evaporation	E	m day^{-1}
Net radiation	R_n	langleys day^{-1}
Sensible heat flux	SHF	langleys day^{-1}

2.4.6.3 Flow rates. The qualitative dependence of evaporation on wind speed, vapor pressure deficit, net radiation flux, and barometric pressure is indicated in Fig. 2.30 through 2.33.



A. Graphical Model



B. System Relationships

Fig. 2.29. Evaporation exchange between surface and temperature.

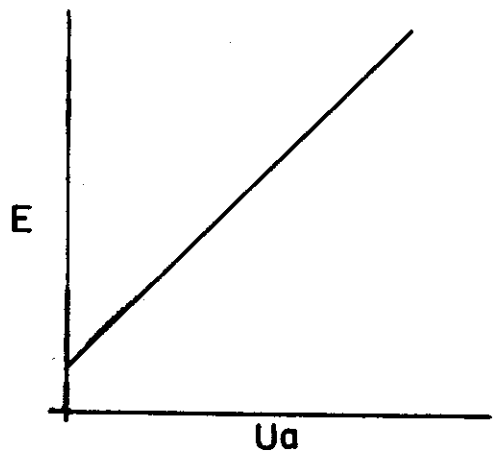


Fig. 2.30. Dependence of evaporation (E) on wind speed (Ua).

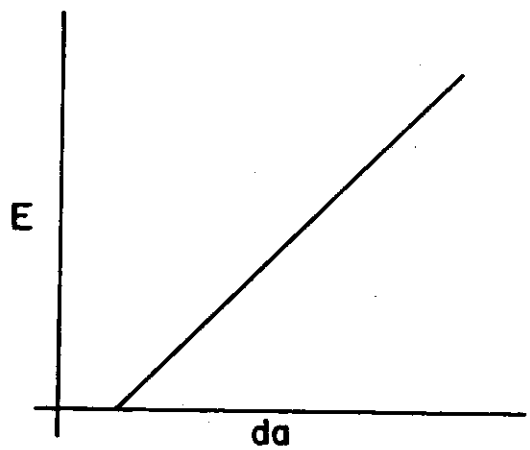


Fig. 2.31. Dependence of evaporat. (E) on vapor pressure deficit (da).

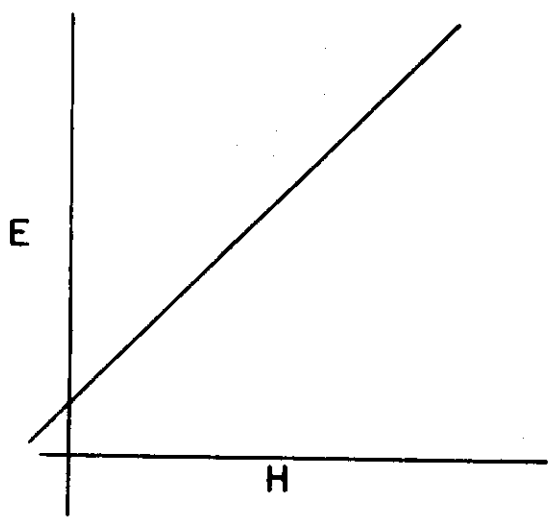


Fig. 2.32. Dependence of evaporation (E) on net radiation (H).

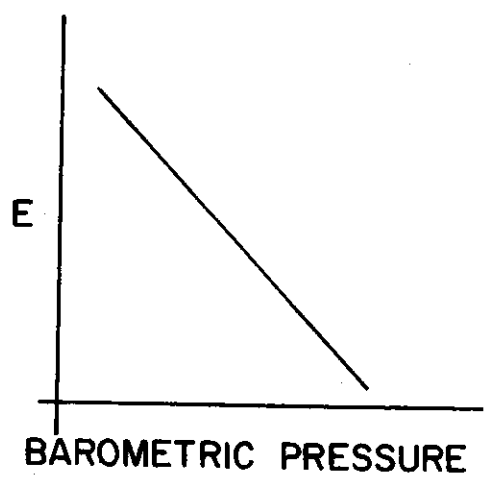


Fig. 2.33. Dependence of evaporation (E) on barometric pressure.

2.4.7 (202--206) Surface Flow

No information was presented on this process during the workshops.

2.4.8 (203–206) and (203–204) Snowmelt (Robert Doty and L. E. Allen)

In the past, many snowmelt models have been developed. Some are quite rudimentary, some are highly empirical, but lately some have become more refined by making better use of the physical factors which determine the melt rate. These factors include air temperature, snow albedo, radiation, cloud cover, wind, dew point, liquid precipitation, slope, vegetation cover, elevation, surface evaporation, ground melt, or percolation. The heat budget approach is basic to most where the snowpack is thought of as a heat reservoir. The sun is the driving force adding heat with some additions from the soil and some addition from precipitation. Such a model takes into account the various factors regulating the flow of heat into and out of the snowpack. Once this heat balance reaches the point where the pack is at 0°C, additional heat is converted to a volume of water melted. Consequently, the end product (output) is kept in the units of the water model.

At the same time that the heat balance is monitored the quantity of water equivalents in the snowpack must be observed. Inflow of water as snow or rain is accounted for in the precipitation process, and outflow as melt water is calculated from the snowmelt heat budget.

Recently, two different models have been published which are basically heat flow models. Neither have been applied to the grasslands, but appear applicable since they utilize the important physical processes which should apply at any location. Factors due to vegetation are also included, although in a somewhat gross way, which would benefit the transfer of the model to the grassland.

The two models are discussed separately here primarily because the first is a heat flow model which is then converted to meltwater equivalents, while the second converts heat flow internally to meltwater equivalents. In this discussion the units used are those of the original authors and will have to be converted to the units used in the final model.

The model developed by Willen, Shumway, and Reid (1971) relates snowmelt to the factors of radiation, albedo, cover density, air temperature, and snow surface temperature. Since factors of aspect, elevation, wind, and other topographic factors are not included, their effect must be related to the above along with some assumptions about the site to be remodeled.

The model is expressed as:

$$\text{Snowmelt } (\text{cal/cm}^2) = R_{sw}(1.0 - A) + C(ST_a^4 - ST_s^4) + (1.0 - C)(0.757\ ST_a^4 - ST_s^4) \quad (2.21)$$

where:

R_{sw} = total daily shortwave radiation, cal cm^{-2}

A = albedo of the snow, decimal fraction

C = cover density, decimal fraction

S = Stefan-Boltzmann constant, 1.17×10^{-7} cal cm^{-2}, $^{\circ}K^{-4}$

Ta = Air temperature, absolute (°C + 273.16)

Ts = Snow temperature, absolute

0.757 = coefficient of longwave back radiation

Once the precipitation model determines that a snowpack has begun to develop, the output from this model is added algebraically to the heat capacity of the snowpack until it reaches °C whereupon the pack is considered

to be isothermal and additions beyond that point contribute to melt, and the output is computed as volumes of water.

The second model by Hendrick and Filgate (1971) considers the same factors plus some topographic conditions which affect radiation plus wind, water vapor in the air, and rainfall on the snow. With some modification of the U.S. Army Corps of Engineers (1960) equation, the following equation was developed:

$$M = C(1 - F)(1 - 0.7N)(0.0025\ Ic)(0.2[T'_x] + 1) - 0.84(1 - N)(1 - F) + 0.0084\ v(1 - 0.8\ F)(0.1\ T'_x + 0.78\ T'_d) + T'_a(0.025 + 0.007\ R) \quad (2.22)$$

where

M = Snowmelt (inches day^{-1})

C = exposure to shortwave radiation relative to an open horizontal surface, a function of slope aspect and topography

F = forest canopy closure, decimal fraction

N = average daily cloud cover, decimal fraction

Ic = clear sky radiation for the particular date and latitude (langleys day^{-1})

T'_x = maximum daily temperature minus 32°F (°F)

T'_a = mean daily air temperature 10 ft above the snow surface minus the temperature of the snow surface (°F)

T'_d = mean daily dew point of the air 10 ft above the snow surface minus snow surface temperature (°F)

v = mean daily wind speed (mph) at 50 ft above the snow surface

R = daily rainfall (inches)

In both models no provisions for heat from the ground or surface evaporation are made. The two are somewhat offsetting and are assumed to be

negligible under forested conditions. The need to include them in the grassland model should be investigated.

The snowmelt models as developed by Willen et al. (1971) and Hendrick and Filgate (1971) do not account for water lost from the snowpack due to the processes of evaporation or sublimation or due to gains from condensation. Generally, they are taken to be minor in areas of deep snowpacks at high elevations. However, for the grassland situation their importance may require greater consideration. The literature listed here gives some idea of the extent to which snow evaporation, condensation, or sublimation have been studied, but problems still exist in fully evaluating them. A primary problem is separating losses or gains due to these processes from changes due to wind movement of snow particles when wind speeds exceed threshold values for the snow. The threshold values themselves vary greatly. Doty and Johnston (1969) give a fair measure of evaporation losses or condensation gains in the open as long as the wind did not exceed 7 mph. Data obtained was fitted to an equation with measurements of wind speed, relative humidity, and air temperature as follows:

$$E = 0.00335 + 0.966\ Wa' - 0.00523\ RH + 1.99 \times 10^{-5} Ta' \qquad (2.23)$$

where

E = average evaporation for an 8-hr day

Wa' = represents average wind at 1 m after the transformation

$$\left[\frac{-|Wa - 313|^{2.7}}{.5468 \times 10^{7}}\right] \text{ where } Wa' = .006 + .07 \exp$$

RH = average relative humidity at 1 m

Ta' = represents average temperature at 1 m after the transformation

$$Ta' = (Ta + 1)^2$$

An experimental design to consider this problem further must be able to measure evaporation and condensation from the snow surface in the presence of winds throughout the expected range of wind speeds. This might be applied to an ice surface, but that would not reflect some of the characteristics of a natural snow surface.

The second problem not taken into account in the two proposed snowmelt models is the effect of vegetation in or under the snowpack on the rate of melt and the movement of water through the pack. The bulk of snowpack research done has not dealt with vegetation of this type as has been done on trees or shrubs which produce a canopy over the snow. Some work has been done on the effects of stubble (Smika and Whitfield, 1966) and of sagebrush (Hutchison, 1965) on the snowpack. This work only scratches the surface, however. Again an important factor is the wind in its role of redistributing snow on the ground.

2.4.9 (204–206) Drip, Stem Flow, Throughfall (W. David Striffler and J. A. Smith)

All precipitation that is not intercepted by (201–204) is assumed to go directly to the soil.

2.4.10 (204–209), (209–211), (211–212),...,(214–215) Translocation (W. David Striffler and J. A. Smith)

Translocation through the root system proceeds according to the availability of soil water at the particular root layers and the evaporative demand of the atmosphere (201 204).

2.4.11 (206–210) Infiltration

Infiltration has been studied and modeled since the beginning of the 20th century. There have been two parallel paths of investigation--one being the empirical and the other the theoretical.

A word model of the process involves the concept of potential infiltration, also known as the "infiltration capacity." Potential infiltration is defined as the maximum rate at which water can enter the soil for the given condition of the soil. If the input rate to the soil is less than the potential infiltration rate, the infiltration rate is equal to the input rate. If the input rate is greater than the potential infiltration rate, the infiltration rate equals the potential rate.

For an unsaturated soil the infiltration rate is initially high, but decays to a constant rate with the passage of time. This general nature of the process led early empirical studies directly to models of exponential-like decay. Early theoretical studies dwelled on physical aspects of air-water interfaces.

In the ultimate sense, the infiltration process is controlled only by the physical factors of the soil-air-water system. However, the physical factors are modified by virtually all trophic levels of the ecosystem. For example, soil structure is an extremely important factor which is modified externally (near the surface) by the activities of consumers and internally by the activities of decomposers.

At the surface the character and amount of aboveground vegetation (producers) exerts pronounced effects on infiltration. Equally important is the influence of belowground root biomass both on decomposer activity and on soil structure directly.

The input to the infiltration process is the supply rate of water delivered to the soil surface. Usually this is thought of as the rain rate; however, the rate of snowmelt or the rate of overland flow can also be inputs to the infiltration process.

There are two outputs of the infiltration process. One is the infiltration rate, i.e., the rate that water enters the soil. The other is the "excess rain rate" which is the rate at which water that does not infiltrate becomes available for overland flow. The excess rain rate is also called lateral outflow (or inflow to an adjacent area).

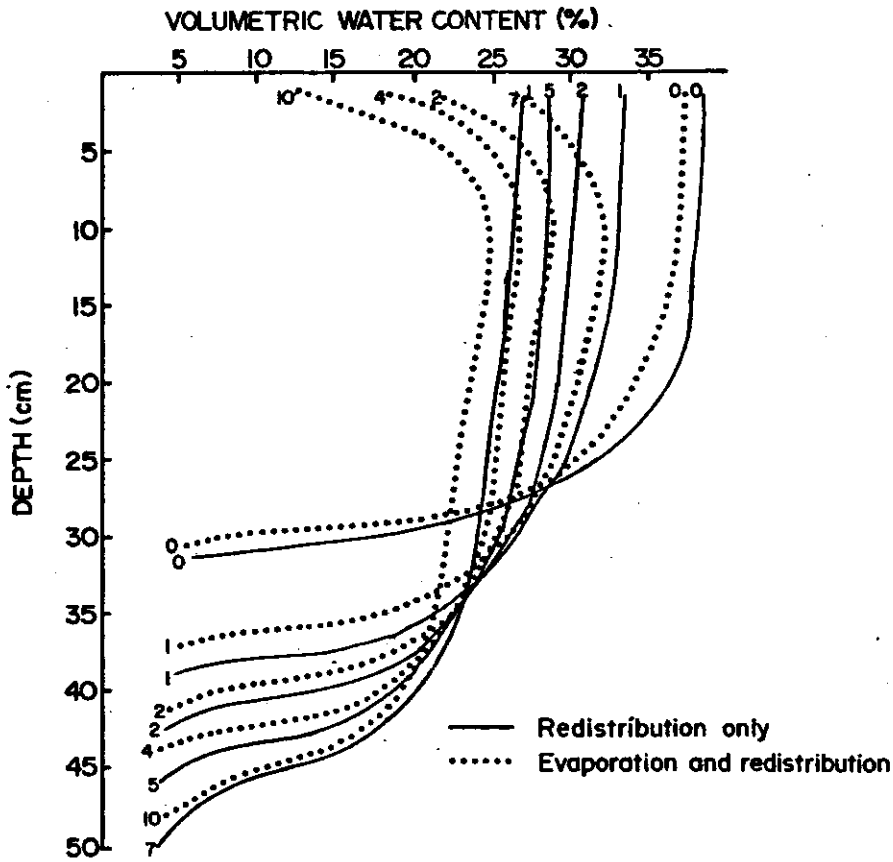
The dimensions of both inputs and outputs of the infiltration process are lt^{-1}. Any convenient units with these dimensions are appropriate.

2.4.12 (210–216), (216–217), (217–218),...,(220–221) (W. David Striffler)
Redistribution of Soil Water

Water received on a soil surface infiltrates into the soil, wetting the surface layer to near saturation. The depth (Z) of the layer depends upon the amount of water infiltrated (F) and the porosity (P) of the soil. When infiltration stops, the water held in the soil continues to percolate. The soil layer wetted to near saturation does not retain its full water content, but will redistribute water under the influence of gravity and/or suction (ψ) gradients in the soil. The soil profile can thus be divided into a desorbing zone and a sorbing zone. The depth of the interface between these zones gradually increases with time as redistribution proceeds. The initial desorbing zone at time equals zero is equal to the initially wetted zone at the end of infiltration. The rate of redistribution will determine the amount of water at various depths at various times following infiltration. The rate and duration of downward flow also determines the effective water holding capacity of the soil.

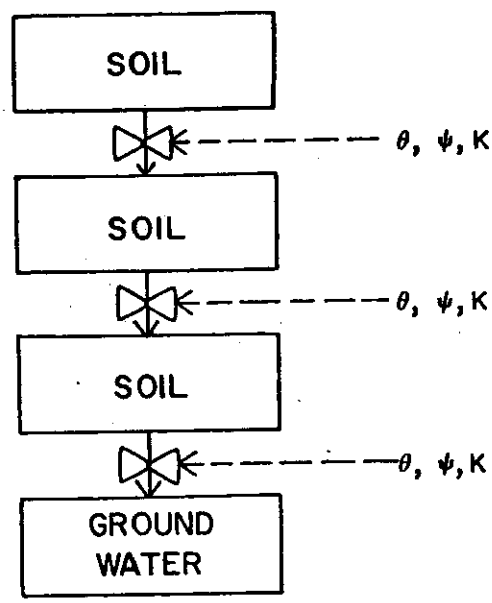
The initial rate of redistribution depends on the initial wetting depth, the relative dryness of the lower layers, and the hydraulic conductivity (K). If the wetting depth is small and if lower layers are dry, then suction gradients are strong and redistribution is rapid. If the wetting depth is great and underlying soil is wet, suction gradients are small and redistribution is by gravity. Redistribution rates generally decrease with time as the suction gradients decrease and as the wetted zone desorbs.

The redistribution process involves hysteresis. The relationship between wetness (θ) and suction (ψ) is not unique, but depends on whether the soil is sorbing or desorbing. For any point in the soil profile, a family of scanning



A. Graphical Model

Successive moisture profiles of soil columns following an irrigation of 100 mm. Profiles are designated according to number of days after irrigation (from Gardner, Hillel, and Benyamini, 1970).



B. System Relationships

Fig. 2.34. Redistribution of soil water through soil layers.

curves ($d\theta/d\psi$ curves) can occur between the sorbing curve and the desorbing curve depending upon the state of the soil. This hysteresis effect greatly complicates the analysis of the redistribution process.

2.4.12.1 Analytical expressions.

Vertical flow equation (Hillel, 1971):

$$\frac{\partial \theta}{\partial t} = -\frac{\partial}{\partial Z}\left(K\frac{\partial \psi}{\partial Z} + K\right) \tag{2.24}$$

Redistribution involving hysteresis (Miller and Klute, 1967):

$$\left(\frac{d\theta}{d\psi}\right)_h \frac{\partial \psi}{\partial t} = -\frac{\partial}{\partial Z}\left[K_h\ (\psi)\ \frac{\partial \psi}{\partial Z}\right] - \frac{\partial K_h(\psi)}{\partial Z}$$

Eliminating ψ (Rubin, 1967):

$$\frac{\partial \theta}{\partial t} = -\frac{\partial}{\partial Z}\left(\frac{K}{C}\frac{\partial \theta}{\partial Z} + K\right)$$

based on the assumption that in the relationship of conductivity to wetness, hysteresis can be neglected.

2.4.12.2 Controls.

Control Description	Symbol	Units
Soil wetness	θ	mm^{-1}
Time	t	sec; day; hr
Soil depth	Z	m
Conductivity	K, K_h	$cm\ sec^{-1}$
Differential water capacity	C	cm^{-1}
Diffusivity = $\frac{K}{D}$	D	$cm^2\ sec^{-1}$
Soil water potential	ψ	cm

2.4.12.3 Flow rates. The rate of distribution determines the amount of water in the soil at any depth at various times following infiltration. Soil physical properties affecting redistribution include soil texture, type of clay minerals, organic matter content, depth of wetting, antecedent moisture contents, impeding layers, presence of a water table, and evapotranspiration withdrawals.

Fig. 2.35 through 2.37 illustrate changing moisture profile with time under varying conditions.

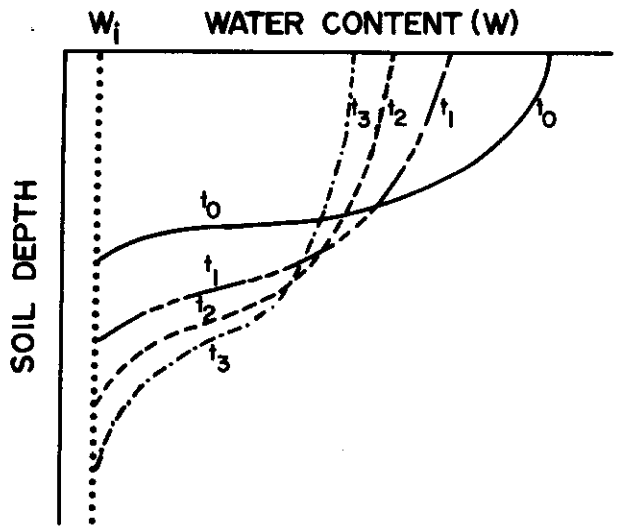


Fig. 2.35. The changing moisture profile in a medium-textured soil during redistribution following an irrigation. The moisture profiles shown are for 0, 1, 4, and 14 days after the irrigation. W_i is preirrigation soil wetness (after Hillel, 1971).

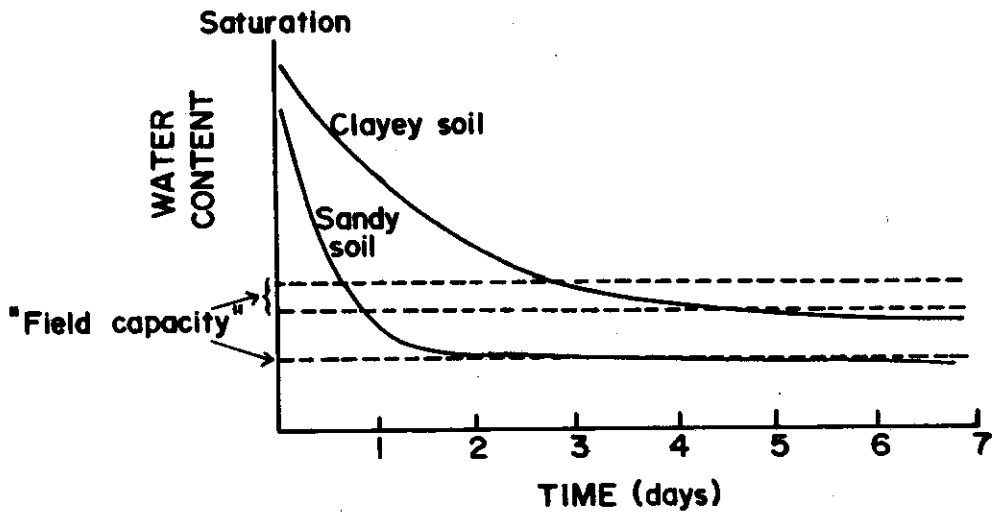


Fig. 2.36. The monotonic decrease of soil wetness with time, in the initially wetted zone, during redistribution (after Hillel, 1971).

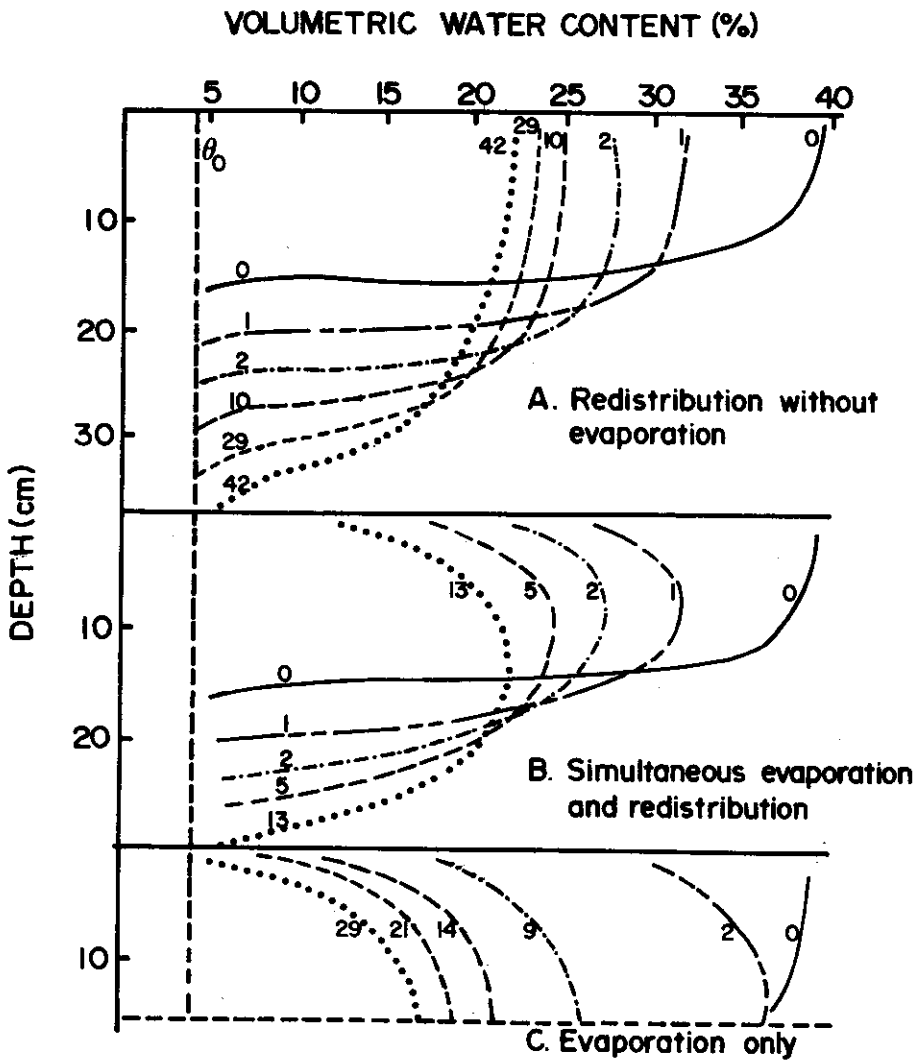


Fig. 2.37. Successive moisture profiles of soil columns following an irrigation of 50 mm. Profiles are designated according to number of days after irrigation (after Gardner, Hillel, and Benyamini, 1970).

2.4.13 (210–209), (216–211), (217–212),... (W. David Striffler)
Uptake of Soil Water by Plants

Two basic conditions must prevail for water to be taken into a root system. First, the plant must require water to satisfy transpiration losses; second, water must be available to the roots. The soil-plant-atmosphere continuum (SPAC) is generally considered as a series of interdependent processes. Atmospheric water demand is the driving force which causes vapor to diffuse from the leaf stomata. Loss of water from the stomatal pores causes a water deficit in the mesophyll cells, which then take in water from the xylem elements, which, in turn, transmit the water deficit down through the plant to the root system. In this manner, a water potential gradient is established from the atmosphere to the plant leaves, from the leaves to the roots, and from the roots to the soil. If water is available in the soil, uptake occurs and water moves along the potential gradient. If water is not available or available at a rate slower than the demand, the internal water deficit will increase until wilting occurs. A number of variables affect the rate and amount of uptake. First, the water demand or evaporativity of the atmosphere varies with solar radiation, air temperature, humidity, and wind. Thus, the demand on the root system will vary according to the same factors. Second, the water available to the root system depends on a number of plant factors and soil factors. Plant factors include the density and depth of the root system, the rate of extension of the root system, and the physiological condition of the root system. Soil factors include those which affect the movement of water to the root system. These include soil water content (θ), soil water potential (ψ), hydraulic conductivity (K), and diffusivity (D). These factors are, in turn, related to texture, structure, organic content, etc.

2.4.13.1 Analytical expressions. The water balance equation for a given depth of soil and a given period of time from Rose and Stern (1967) is:

$$\int_{t_1}^{t_2} (i - \nu_Z - q_e)\, dt - \int_0^Z \int_{t_1}^{t_2} \frac{\partial \theta}{\partial t}\, dzdt = \int_0^Z \int_{t_1}^{t_2} r_z\, dzdt \qquad (2.25)$$

The average rate of uptake by roots is:

$$\bar{r}_z = \int_{t_1}^{t_2} rz\, dt/(t_2 - t_1)$$

The pattern of soil water uptake with depth can be determined by repeated calculations for successive small increments of t and z. Total or cumulative water uptake is:

$$R_z = \int_0^Z r_z\, dz$$

The driving variable is evaporative demand (PE).

2.4.13.2 Controls.

Control Description	Symbol	Units
Rate of water supply (rainfall)	i	$m\ sec^{-1}$
Vertical flux of water at depth Z	ν_Z	$m\ sec^{-1}$
Evaporation rate from soil surface	q_e	$m\ sec^{-1}$
Soil water content	θ	$m\ m^{-1}$
Rate of decrease of soil wetness due to water uptake (measured?)	r_z	$m\ sec^{-1}$

2.4.13.2 Controls (continued).

Control Description	Symbol	Units
Total decrease of soil wetness	R_z	m
Soil water potential	ψ	bars
Evaporative demand	PE	bars
Hydraulic conductivity	K	cm sec^{-1}
Soil depth	Z	m
Time intervals	t_1, t_2	sec
Root density		
Root depth		m

2.4.13.3 Flow rates. Fig. 2.38 through 2.42 indicate the dependence of water uptake on soil type, root density, etc.

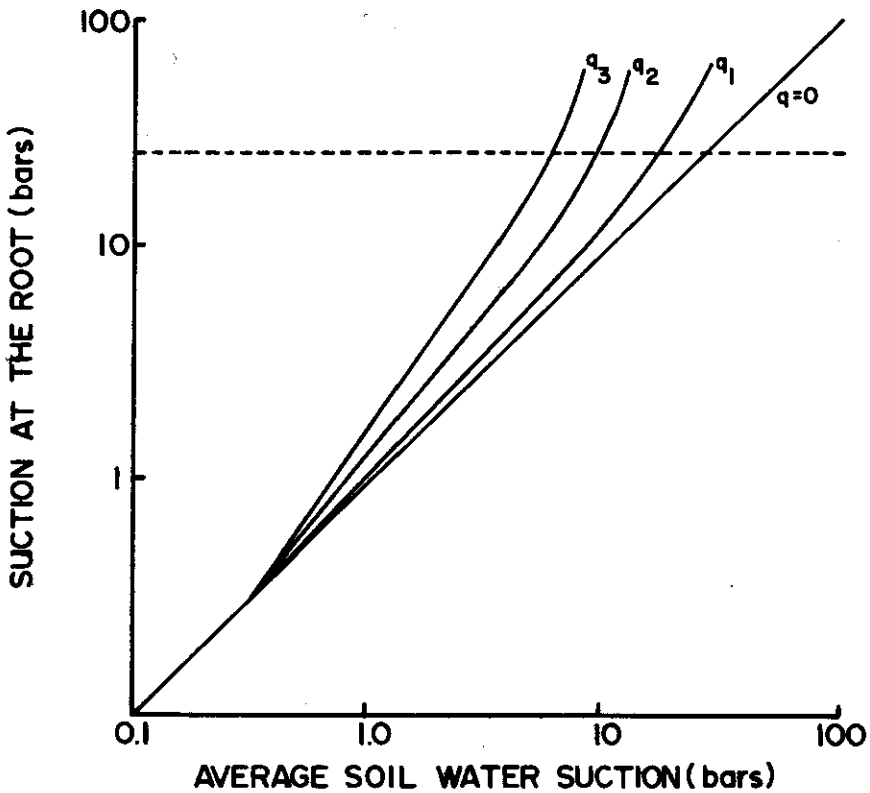


Fig. 2.38. The relation of suction at the root to the average soil water suction for different uptake rates ($q_1 < q_2 < q_3$). The dashed line indicates an approximate value of critical suction at which the plant wilts. The soil water suction at which wilting occurs is seen to depend upon the uptake, and hence the transpiration rate (after Gardner, 1960).

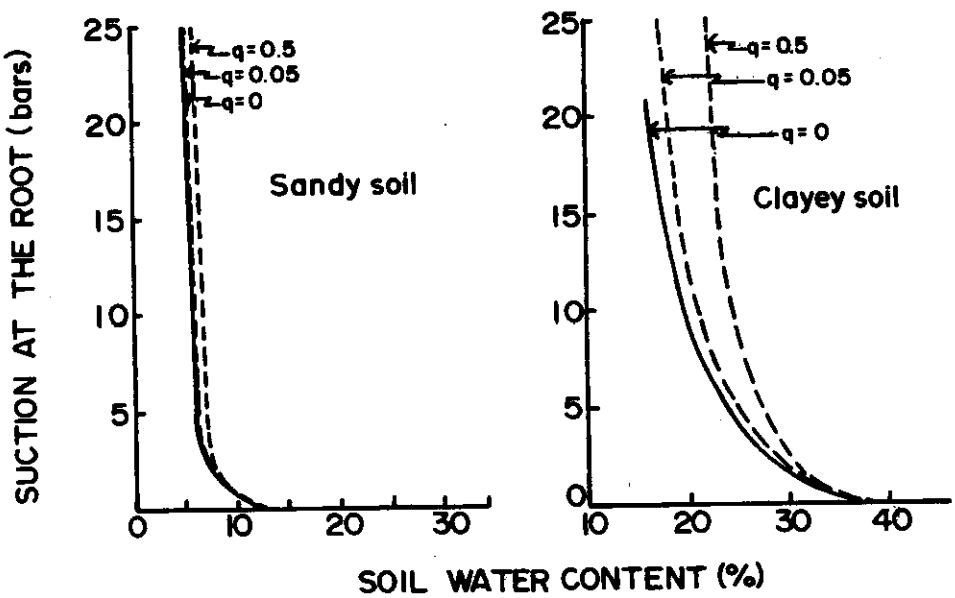


Fig. 2.39. Relation of water suction at the root to average soil water content, at various water uptake rates and for two different types of soil (after Gardner, 1960).

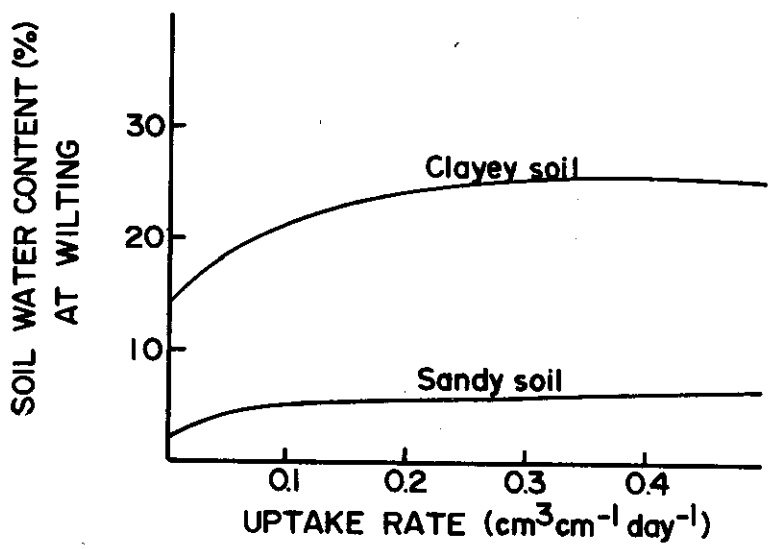


Fig. 2.40. Relation of soil wetness at wilting to the root uptake flux (after Hillel, 1971).

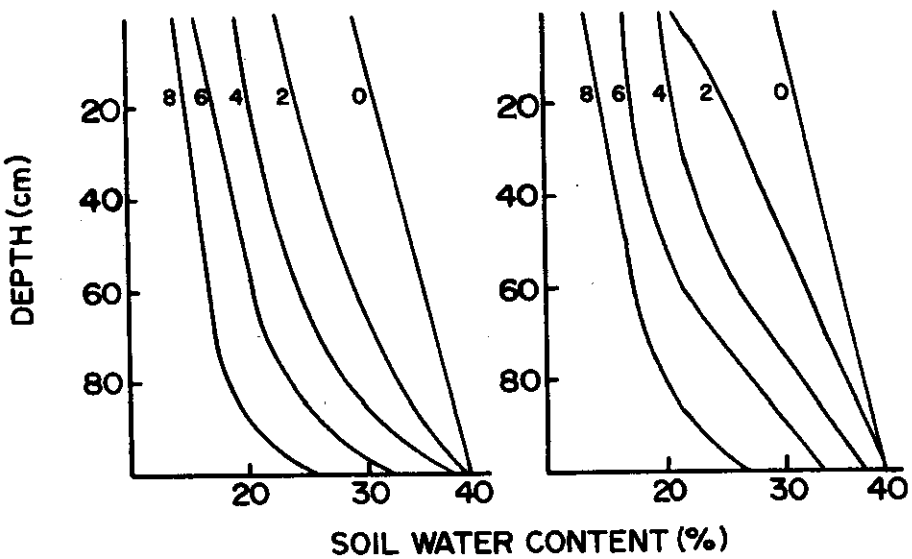


Fig. 2.41. Soil water profiles 0, 2, 4, 6, and 8 days after the start of transpiration. At right: for a system with root density decreasing logarithmically with depth. At left: root density decreasing linearly with depth (after Gardner, 1964).

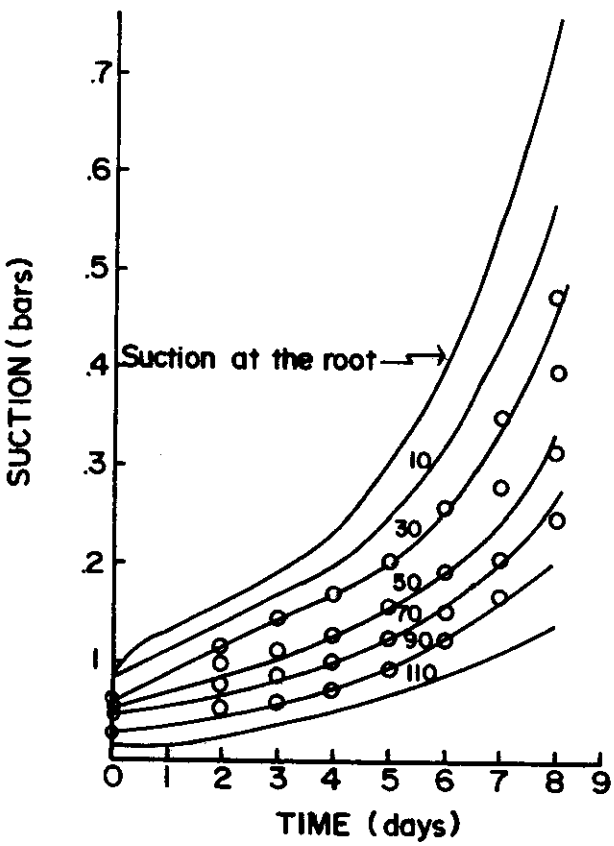


Fig. 2.42. The increase of average soil water suction with time in different depths in a field of alfalfa. The numbers by the curves represent different depths (cm) within the rooting zone (after Ogata, Richards, and Gardner, 1960).

2.4.14 Summary Comments and Recommendations for Water Model (all participants and J. A. Smith

Three major priorities for the development of the water model emerged from the Process Studies Workshops. These were:

1. Determining resistance of the plant leaves or canopy to allow separation of transpiration and evaporation.
2. Determining the biotic control relations for infiltration and water uptake.
3. Modeling water content of the litter layer. The amount of water content in the litter layer is also an important parameter in determining the thermal conductivity of this plant material.

The process of evaporation from a saturated mineral soil surface was thought to be adequately described in the literature if the necessary parameters were all described. However, further analysis for arid lands with limited instrumentation was thought necessary.

In addition, specific recommendations for the processes of uptake, redistribution, interception, and snowmelt are given below.

Several studies exist which report interception by grass and litter. Most studies give quantitative losses without deriving equations or relating losses to driving variables or state variables. From the few relationships derived, it appears that interception losses on a shortgrass prairie would be very small and of minor importance in the water balance studies. However, the importance to plants may be of significance.

Reasonable estimates of interception losses can probably be made with current data collection efforts. However, to obtain accurate estimates, a study of interception losses should be undertaken.

Specifically, a study of storage capacities of the shortgrass vegetation would improve the estimate, while measurements of interception losses for specific events and over the various developmental stages of vegetation and grazing treatments would be much more meaningful.

A complete study of interception could be accomplished for about $10,000. This would include one GRA, plus expenses for supplies and travel.

Designing an experiment to answer the questions about wind, vegetation, evaporation, sublimation, and effects on snowmelt is difficult because of the apparent lack of instrumentation capable of isolating and measuring inputs that are physically or biologically meaningful. Even with a compromise which integrates some variables to obtain a net effect it is difficult. The close interrelationship of wind, evaporation-condensation, and the presence of vegetation does suggest that both problems could be studied together assuming proper attention is given to all of the variables present. A possible outline of important considerations follows:

Study Design

I. Objectives.
   - A. To study evaporation from or condensation to the snow surface with special consideration to wind effects.
   - B. To study vegetation in or under the snowpack as it might affect snowmelt or movement of meltwater.
   - C. To study changes in the pack as a result of wind redistribution.

II. Major variables to consider.
   - A. Wind: alteration of vapor gradients as well as snow-particle movement.
   - B. Radiation: resulting heat inputs and distribution.

C. Water in air: vapor gradients as well as precipitation forms, rates, durations, etc.

D. Vegetation: by species or type, characteristics which may alter snow distribution or the heat balance.

III. Instrumentation possibilities.

A. Field weighing lysimeter with provisions for measuring snow moved from the plot by wind, or

B. Wind tunnel-controlled environment system.

Instrumentation suggested may appear exaggerated and expensive, but many years have been spent working on these problems with inadequate instrumentation.

A tremendous literature on soil water movement exists covering a large number of analytical approaches. Most approaches are based on laboratory studies of soil column drainage although a number of field studies do exist and may be adaptable to Pawnee conditions. A complicating factor in most analytical approaches is that evapotranspiration losses during the redistribution process are not considered.

A test of one or more analytical approaches against measured soil water contents would be a valuable addition to our understanding of soil water processes on grassland sites. Such a study could be done on the stress plots where known amounts of water are applied periodically and the redistribution measured. Redistribution following natural events is being measured to some extent on the microwatersheds. Some slight addition to the existing instrumentation would be necessary to adequately evaluate moisture changes with time. It sould be feasible to evaluate the effect of evapotranspiration losses on redistribution in this manner.

This study could probably be done for about $10,000. Costs would include a GRA, some principal investigator time, instruments, supplies, and transportation.

The process of soil water uptake is conceptually well defined. Most literature studies, however, report soil water depletion as a function of time, potential gradients, or other limiting factors rather than defining the uptake process. This is due to the difficulty of measuring potential gradients from the root surface to the soil and the complexity of the process. It is, however, possible to determine average uptake rates and define average soil condition. It would be easier to treat the uptake, translocation, and transpiration processes as a continuum and model it as a single process.

A study of transpiration rates of grassland vegetation and related uptake of water from the soil would be a valuable addition to the current IBP producer and abiotic process studies. Plant stresses, including leaf water potential and root water potential, could be measured and related to soil water potentials and atmospheric potential. Transpiration can be calculated if the various resistances in the pathway can be determined. This would be a feasible way of separating soil evaporation and transpiration losses. (These studies should cost about $15,000).

2.5 CONCLUSIONS

(J. A. Smith)

The Process Studies Workshops gathered together the necessary background material for preliminary modeling of the abiotic processes. An initial model for heat containing 16 processes distributed among 7 net flows is indicated. Approximately four controls per process directly appear. However, these controls themselves may be dependent upon other time-varying parameters. Similarly, a model for water exhibiting 14 processes distributed among 8 net flows is indicated.

Sufficient information is either given in the review or indicated in the literature to develop a model to determine the sensitivity of the abiotic flows to input parameters. This information would partially answer the questions of how often and over what spatial extent either driving variables or control parameters need to be determined.

The overall level of sophistication for the heat and water models appears to be the same for the individual processes. Much of the "science," i.e., potential difficulties, appears hidden in such parameters as thermal conductivities. However, a detailed analysis of the variation of these quantities during the Process Studies Workshops and without preliminary modeling of the whole abiotic flow would have produced a very unbalanced model. Some processes would be very well determined but depend on quantities modeled only grossly. A modest approach as indicated by the participants seems warranted.

A basic question in the heat model arises, however, that needs to be examined more closely. This is the decision of whether the temperature profile between boundary surfaces needs to be modeled to determine the temperature gradient and then the one-dimensional heat flow equation solved or whether a linear approximation to the gradient is sufficient. The

Process Studies participants suggested a temperature profile modeling approach only for the soil layers. If this approach is warranted in this case, perhaps it is also necessary for conductive flow between the atmosphere and litter. Air temperature is cyclic; and if litter temperature lags behind it, the linear approximation may not be sufficient. Since it is easier to continuously monitor surface and medium temperatures than to measure heat flux, and since it is fairly easy to incorporate cyclic variations in the two-dimensioal temperature equations, this approach may be more realistic.

Finally, in modeling the heat and water flows, an effort will be required to more closely integrate coupling between them. For example, feedback from the transpiration/evaporative processes in the water model to the heat budget of plant material needs to be indicated more strongly in the heat model.

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CHAPTER 3. NUTRIENT SUBSYSTEM: PHOSPHORUS AND NITROGEN MODELS

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3.1 ABSTRACT

Detailed nutrient flow models are being developed for both nitrogen and phosphorus. State variables for the phosphorus model include soil solution P (1), labile soil P (2), soil mineral P (3), live root P (4), dead root P (5), plant top P (6), animal P (7), litter P (8), and soil organic P (9). State variables in the nitrogen model are atmospheric source and sink (0), soil nitrate N (1), soil ammonium N (2), N in soil minerals (3), live root N (4), dead root N (5), plant top N (6), animal N (7), litter N (8), and soil organic N (9). The similarities evident in the state variables reflect the biological similarity of the nutrients. Mechanisms used to simulate root uptake, translocation, and mineralization of organic forms are similar but not identical. In other sections mechanisms may be quite different.

Important features of both systems include (i) plant uptake controlled by temperature, water, and the amount of nutrient present in the soil solution phase, (ii) translocation controlled by the root and top concentrations and by the phenological stage, and (iii) available producer and decomposer processes controlled by nutrient concentrations in live and dead plant material.

These models are expected to be useful for examining both the intra-seasonal dynamics of nutrient flow and long-term effects of management practices. While neither model is presently complete, an operational version of the phosphorus model is available.

3.2 INTRODUCTION

Nutrient flow models are developed in this section for nitrogen and phosphorus. These models are expected to be useful for examining intraseasonal dynamics of nutrient flow as well as long-term effects of management practices. Incorporation of these models as modules in the overall ecosystem model will allow us to examine the interaction of nutrient flows with other parts of the system and, in particular, to determine the conditions under which nutrient supply imposes constraints on overall system performance.

A major portion of the phosphorus model is operational at present; and although the performance of sections of the nitrogen model describing certain key flows have been tested against reference data, the total model is not yet operational. The nitrogen and phosphorus models are similar in several important aspects, reflecting the similarity of the biological roles of nitrogen and phosphorus. In several instances, the same state variables are used in both models and similar flow mechanisms are assumed.

In some sections the model is fairly detailed, and well-documented mechanisms are utilized such as the equilibrium between solution and labile phosphorus and the nutrient uptake equations. In others, such as partitioning of nutrients between live and dead roots or rates of mineralization of soil organic nitrogen and phosphorus, rough estimates are used in the absence of more reliable data on these processes. A major feature of both the nitrogen and phosphorus submodels is the convergence of the major flow on the soluble pools of the nutrients on the soil solution.

Thus, the model reflects the dependence of the system on soil water supply, not only as it affects plant growth but also as it controls chemical and biological processes within the soil system.

3.3 NITROGEN SUBMODEL

The following state variables are represented in the nitrogen submodel:

800	Atmospheric source and sink	
801	Soil nitrate nitrogen (NO_3^-)	g/m^3
802	Soil ammonium nitrogen (NH_4^+)	g/m^3
803	Nitrogen in soil minerals	g/m^3
804	Live root nitrogen	g/m^3
805	Dead root nitrogen	g/m^3
806	Nitrogen in plant tops	g/m^2
807	Nitrogen in herbivores	g/m^2
808	Nitrogen in litter	g/m^2
809	Nitrogen in soil organic matter	g/m^3

The state variables and flows as they are represented in the present version of the model are shown in Fig. 3.1. The state variables representing belowground pools of nitrogen are each divided into four depths. Depth divisions used are 0 to 2.5 cm, 2.5 to 7.5 cm, 7.5 to 12.5 cm, and 12.5 to 17.5 cm.

The nitrate nitrogen pool is considered to be mobile and will move with soil water. Thus, a transfer will occur between depths within this state variable. At present, no similar transfers between depths are being considered for the remaining state variables.

It is recognized that some additional flows are present in nature. For instance, nitrogen in the NH_4^+ form may be utilized directly by plant roots. However, the flows as represented should give a fairly realistic representation of nitrogen movement in the ecosystem. Additional flows may be represented in later versions of the model.

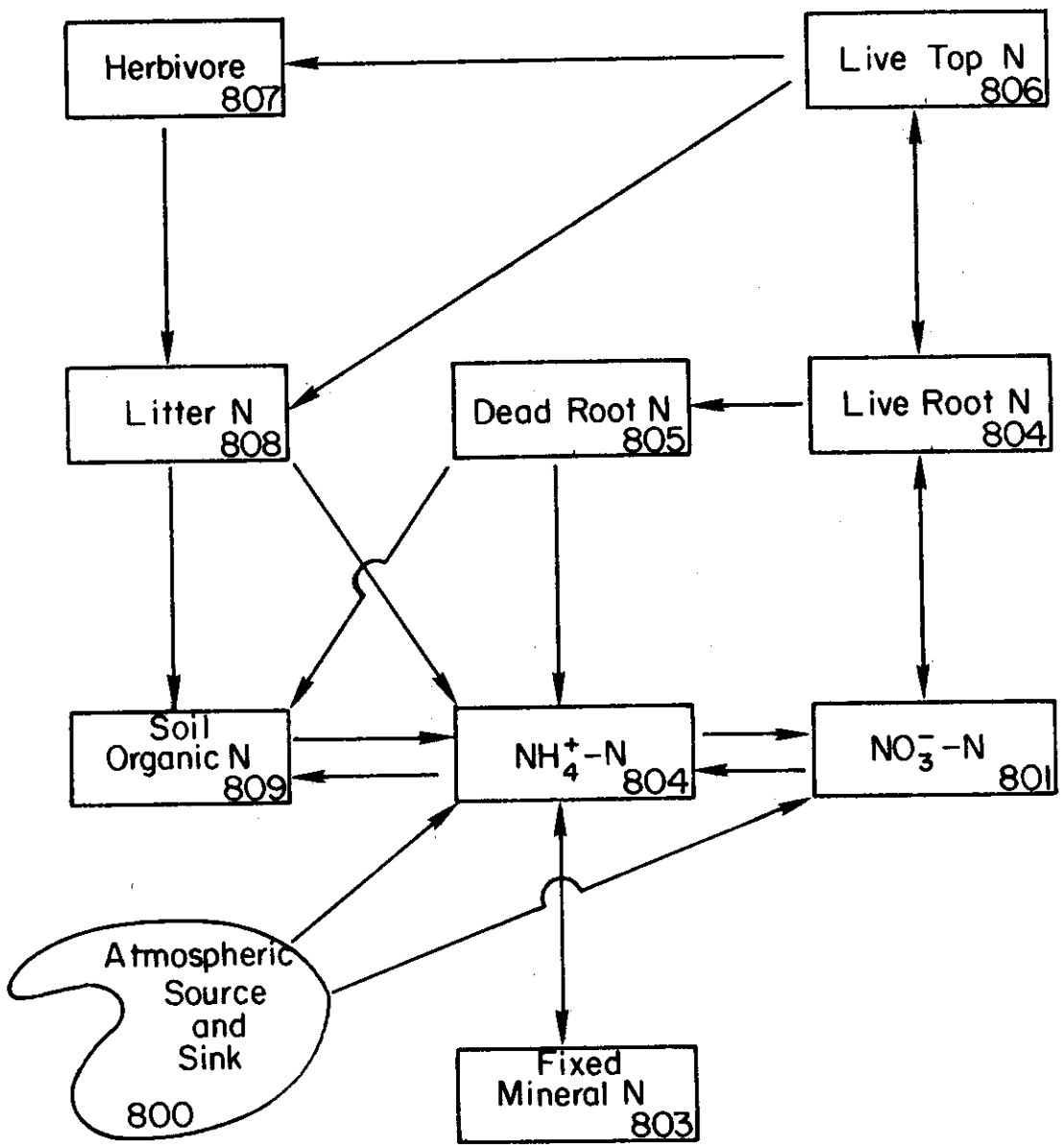

Fig. 3.1. State variables and flows to be considered in the nitrogen model.

At present, some of the more important flows have been considered in a rather detailed fashion; others are being represented in a less detailed manner while still others are not yet being considered.

3.3.1 (800-802), (800-801) Movement of Nitrogen From Atmospheric Sink to Soil NH_4^+ and NO_3^-

These flows represent nitrogen fixation and the NH_4^+ and NO_3^- contained in the rainfall. At present, rainfall nitrogen is calculated by assuming an input of 0.006 g nitrate nitrogen (NO_3^--N) and 0.006 g ammonium nitrogen (NH_4^+-N)/m^2/mm precipitation. Under Pawnee Site conditions, this would represent a total of about 0.4 g N/m^2 annually. Nitrogen fixation is not at present included, but will be represented by a function dependent on legume density, phenological stage, temperature, and soil water.

Movement of nitrogen from nitrate nitrogen to the atmospheric sink (denitrification) is assumed to be zero.

3.3.2 (809-802) Movement of Nitrogen From Soil Organic Matter to Soil NH_4^+

This system encompasses the processes known as "mineralization" and the reverse processes referred to as "immobilization." At present, it is handled simply as a net transfer from organic matter to NH_4^+. The movement is calculated to achieve a net flow of .02 (organic nitrogen) annually at depths of 0 to 10 cm. At 10 to 30 cm the total annual flow is .01 (organic nitrogen) while in the 30 to 100 cm layer the total flow is .0025 (organic nitrogen). The time the flow occurs is regulated by the soil temperature and water.

3.3.3 (802-803) Movement of Nitrogen From Soil Mineral Lattices to the Soil NH_4^+ Pool

This process involves fixation in or release from inaccessible sites in the mineral lattices. It is disregarded in the present version of the model.

3.3.4 (802-801) Oxidation of NH_4^+ Nitrogen to NO_3^-

This nitrification process has been considered in detail. While biologically it is essentially only a one-way process, a small reverse flow is included in the model to increase stability and to allow the equilibrium NH_4^+ concentration to be regulated by the NO_3^- level. The basic forward rate (802-801) is considered to be a function of the amount of NH_4^+ present. The relationship presently used for the forward rate is

$$\text{Rate} = \text{antilog}\ [-.00250\ (NH_4^+) - 0.3590] + 0.025 \qquad (3.1)$$

where rate is expressed in units of day^{-1} and NH_4^+ in grams per cubic meter. This gives a basic forward rate of 0.025/day at high NH_4^+ levels, increasing to about 0.046 at very low NH_4^+. Thus, at concentrations below 25 g N/m^3, over 40% of the NH_4^+ present is oxidized per day.

3.3.4.1 Adjustments. The above rates are applicable at soil water field capacity levels (0.33 bars) and 25°C. The rates are subject to adjustments for water and temperature as shown in Fig. 3.2 and 3.3. The flow is then calculated by

$$\text{Flow} = \text{rate} \times (NH_4^+) \times \text{temperature coefficient} \times \text{water coefficient} \qquad (3.2)$$

where flow is in grams per day per cubic meter, rate has units of day^{-1}, NH_4^+ is in grams per cubic meter, and the temperature and water coefficients are dimensionless.

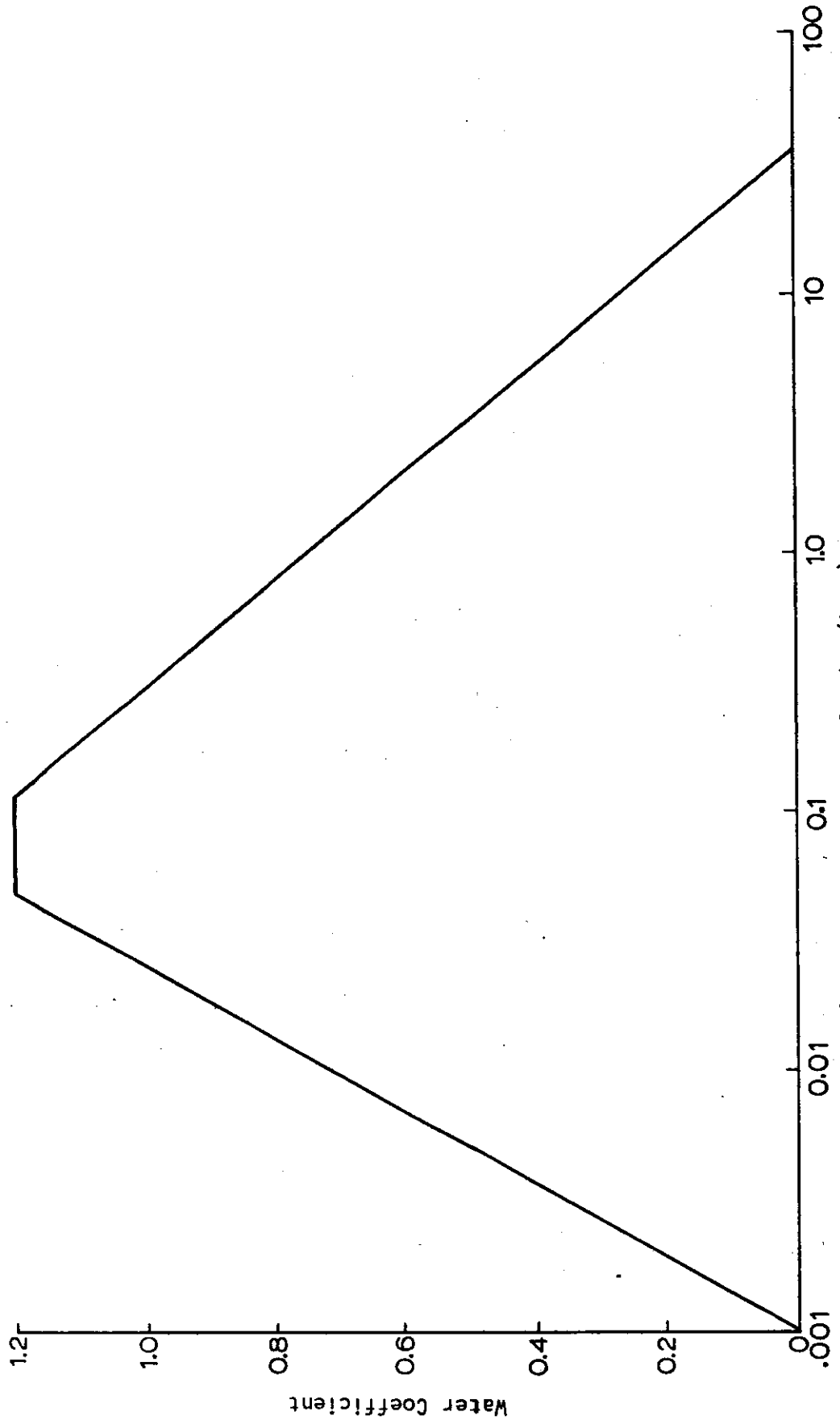

Fig. 3.2. Water adjustment for nitrification rate.

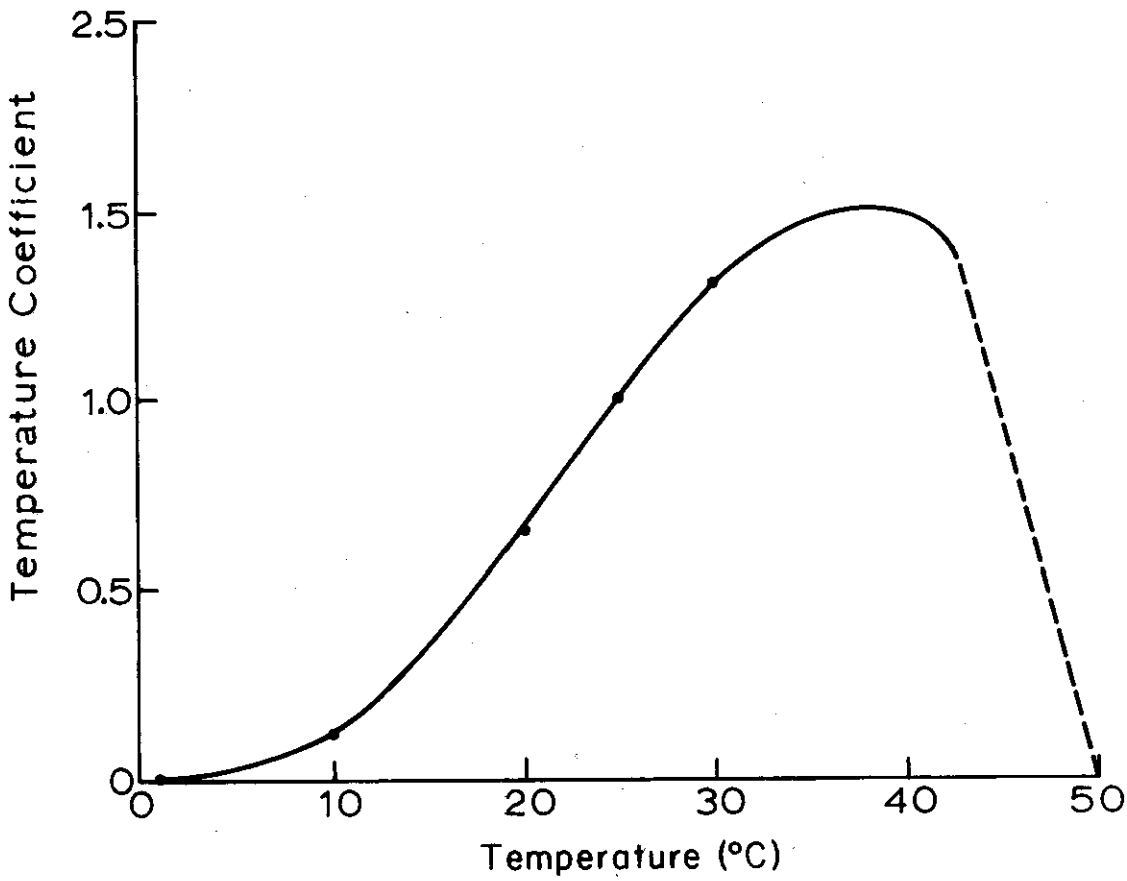

Fig. 3.3. Basic temperature adjustment for use in nitrogen model.

3.3.4.2 Reverse rate. The reverse rate presently in use is described by the relationship

$$\log \text{rate} = -1.2 - 0.4 \log (NO_3^-) \tag{3.3}$$

where NO_3^- represents the concentration of nitrate N in grams per cubic meter and rate is in units of day^{-1}. This is subject to the same temperature and water limitation as the forward rate.

3.3.5 (801-804) Uptake of Nitrogen by Live Roots

At the present time nitrogen uptake is assumed to occur entirely from the nitrate nitrogen pool. This is described as the sum of two processes by the following relationships

$$\text{Total uptake} = \frac{U_{A_{max}}}{1 + \frac{K_A}{NO_3^- \text{ conc}}} + \frac{U_{B_{max}}}{1 + \frac{K_B}{NO_3^- \text{ conc}}} \tag{3.4}$$

Most plant nutrient uptake rates can be described by this bype of relationship and it has been adopted for both the nitrogen and phosphorus sections of the model. Dimensions of the various terms and constants chosen for the initial stages of the model are:

Total uptake = µg N/g root/day

$U_{A_{max}}$ = 980 µg N/g root/day and is the uptake at infinite N concentration

$U_{B_{max}}$ = 210 µg N/g root/day and is the uptake at infinite N concentration

K_A = 84 g N/m^3 and is the concentration at which the uptake is $\frac{1}{2} U_{max}$

K_B = 4.8 g N/m^3 and is the concentration at which the uptake is $\frac{1}{2} U_{max}$

In this type of relationship the rate of uptake at low concentrations is controlled by $U_{B_{max}}$ and K_B, while the uptake at high concentrations is controlled largely by the $U_{A_{max}}$ and K_A values. While it may not be necessary to describe the N uptake as a sum of two processes, this relationship is consistent with the essentials of observed uptake rates, i.e., at 0 concentration uptake is 0; the uptake increases rapidly with small increases in concentration and continues to increase at a diminishing rate up to relatively high NO_3^- concentrations. Using the constants above, a maximum uptake of 1190 µg N/g root/day could be attained if soil nitrate nitrogen were infinitely high.

3.3.4.3 Adjustments. The uptake of nitrogen is also subject to temperature and water coefficients. The temperature coefficient is the same as that shown in Fig. 3.3 and used for the nitrification rate. Water adjustment is shown in Fig. 3.4.

3.3.6 (804-801) Nitrogen Flow From Live Root to Soil Solution

The nitrogen uptake rates described above would result in continued nitrogen accumulation in the roots at the same rates regardless of the level present in the roots. In order to provide a more realistic picture, a hypothetical "back flow" is included. This back flow is calculated as a fraction of the root uptake (801-804), with net uptake considered to be the sum of the forward and backward flows. The ratio of forward to reverse flow rates is shown in Fig. 3.5. The maximum N concentration attained is a function of soil NO_3^- (801), resulting in a family of curves.

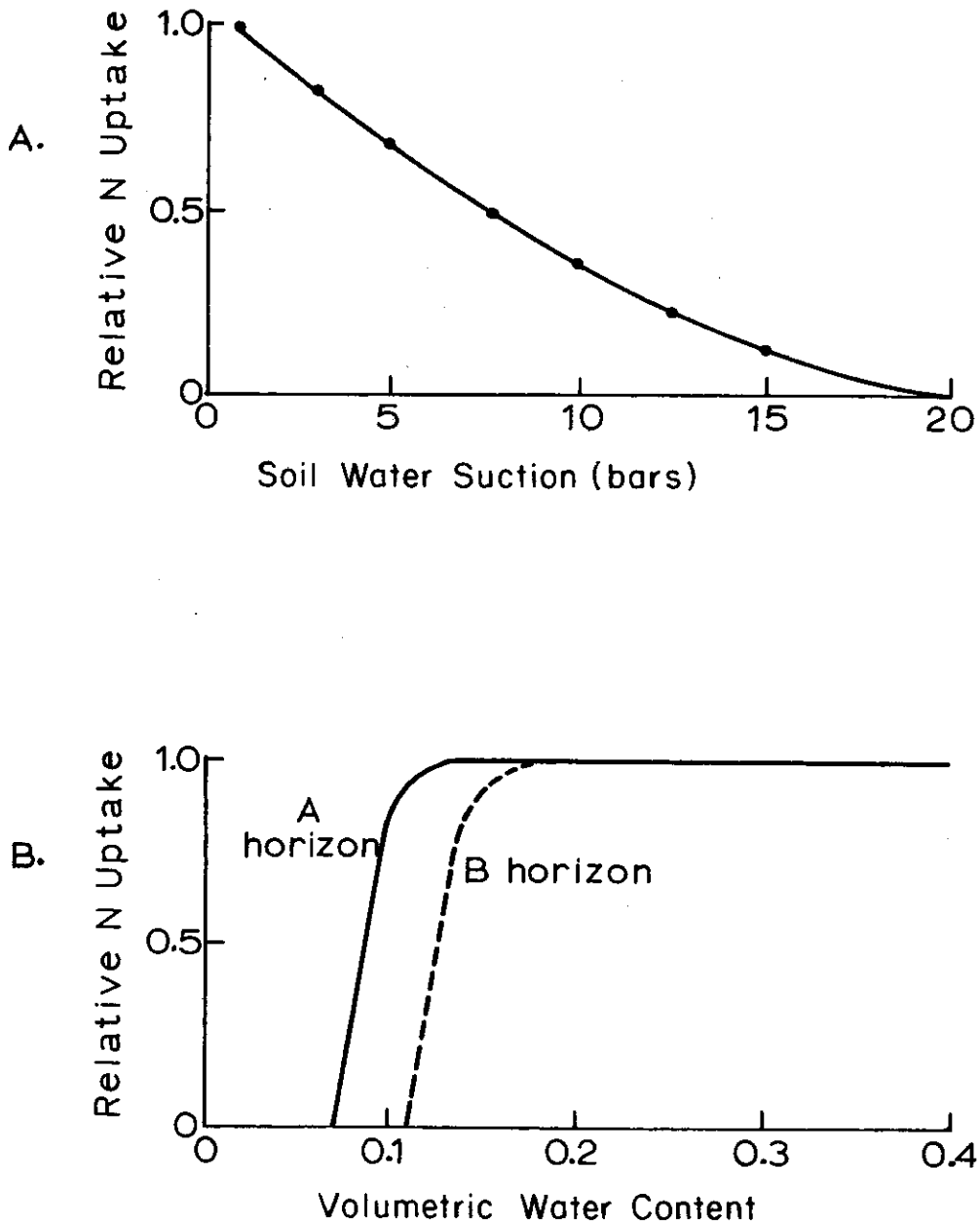

Fig. 3.4. Water adjustments for N uptake.
A. General relationship based on soil water suction.
B. Relationship for Ascalon sandy loam from the Pawnee Site as a function of volumetric water content.

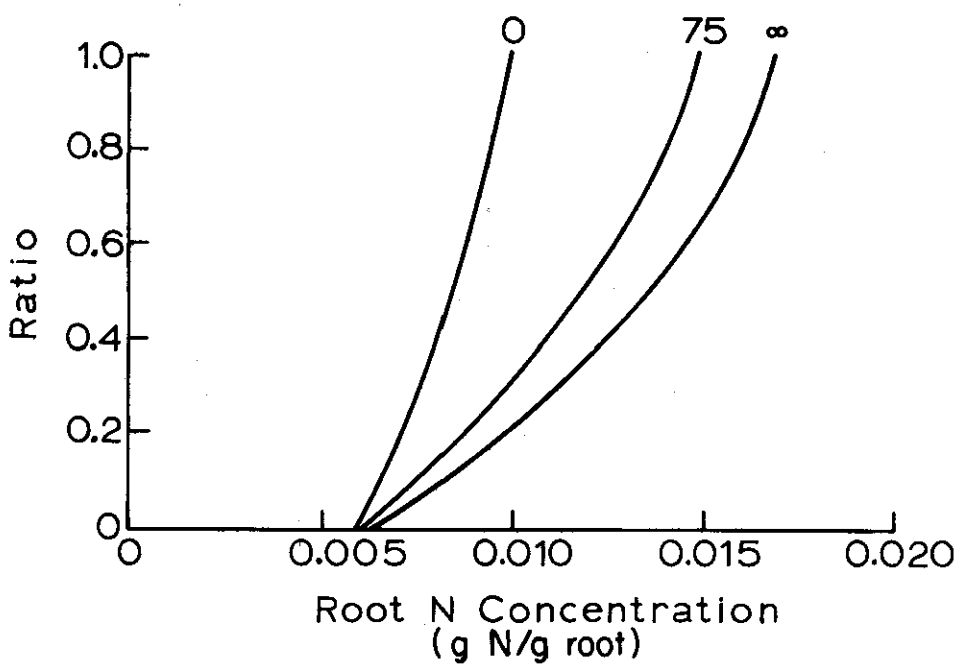

Fig. 3.5. Relative N flow from live root to soil solution. The ratio is the fraction of the N uptake rate. The three curves show ratios at different soil NO_3^- levels ($\mu g/cm^3$).

3.3.7 (804-806) Translocation of Nitrogen From Live Roots to Tops

The translocation is controlled by maintaining an equilibrium between nitrogen concentration in roots and tops. The ratio of the equilibrium nitrogen concentration in the tops to that in the roots varies from 3.0 to 1.0, depending on the phenological stage as shown in Fig. 3.6. In order to preserve realistic root nitrogen concentration (above 0.6%) in the roots, it is necessary to provide a mechanism whereby top biomass accumulation can be controlled by top nitrogen concentration. The nitrogen concentration at which maximum biomass accumulation occurs will vary from approximately 3.0% early in the season to 1.5% at the later phenological stages. This mechanism provides for flow in either direction and under conditions of adequate nitrogen level in the plant tops would result in movement from tops to roots in the later stages of growth.

3.3.8 (804-805) Live Root Nitrogen to Dead Root Nitrogen

This transfer is a function of root death rate and live root nitrogen concentration. Modeling of this flow requires more precise determinations of root death rates than are presently available. For the initial phases, an annual rate of 25% is assumed.

3.3.9 (805-809), (805-802) Flow of Nitrogen From Dead Roots to Soil Organic Matter and NH_4^+

Quantitative description of these flows have not yet been developed. However, rates will depend on C/N ratios in the roots at time of death. Relative amounts partitioned to each pathway will likewise depend on C/N ratios.

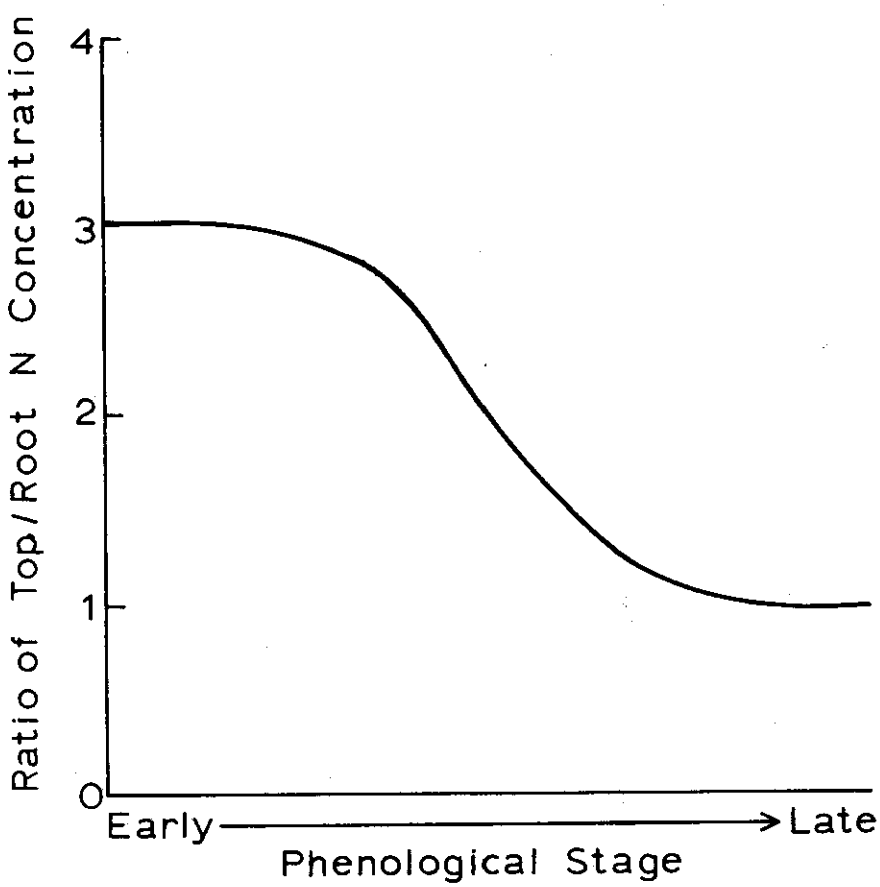

Fig. 3.6. Ratios of equilibrium N concentrations of tops to roots as a function of phenological stage.

3.3.10 (806-807), (807-808), (806-808), (808-802), (808-809) Other Flows

No quantitative descriptions have been developed for the remaining flows to date. In general, they will depend largely on litter accumulation and decomposition rates from producer and decomposer models and on flows occurring through consumers.

3.4 PHOSPHORUS SUBMODEL

The following state variables are represented in the phosphorus submodel:

901	Soil solution P	g/m^3
902	Soil labile P	g/m^3
903	Soil primary mineral and precipitated P	g/m^3
904	Live root P	g/m^3
905	Dead root P	g/m^3
906	Plant top P	g/m^2
907	Animal P	g/m^2
908	Litter P	g/m^2
909	Soil organic P	g/m^3

The state variables and flows (processes) as represented in the model are shown in Fig. 3.7. The five most important processes controlling phosphorus cycling in semiarid grasslands are listed below:

Flow	Process Description
901-902	Solubility of phosphorus in the soil solution
901-904	Phosphorus uptake by plant roots
904-906	Phosphorus translocation from plant roots to tops
905-909	Dead plant root decomposition
909-901	Mineralization of soil organic P

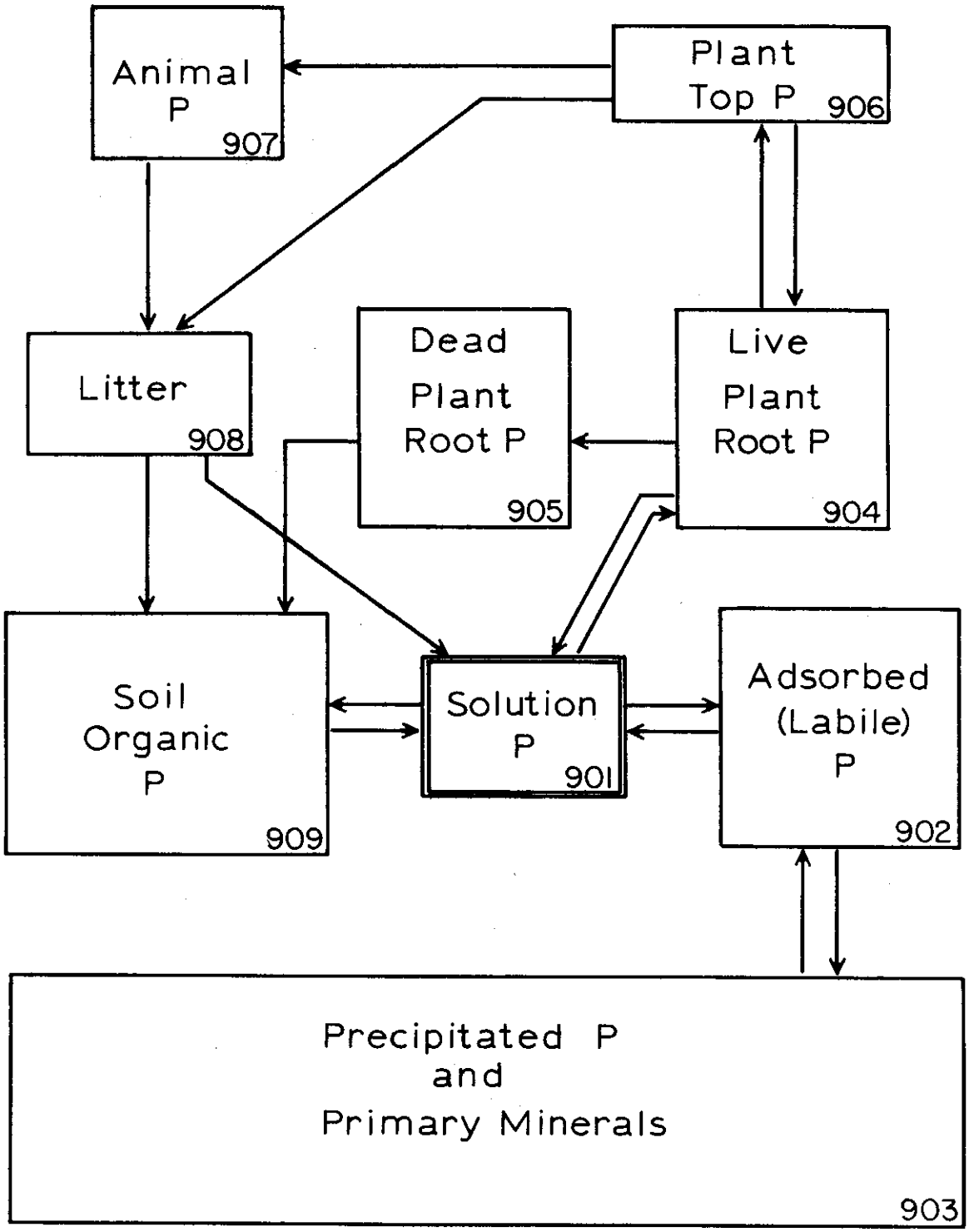

Fig. 3.7. State variables and flows in the phosphorus submodel.

The principles controlling some of these processes are well established, and much valuable information is available in the literature for documentation of flow rates in general. Detailed studies will be required to establish rate constants for application to specific systems.

3.4.1 (901-902), (902-901) Phosphorus Solution and Adsorption

Phosphorus solubilities in calcareous soils are characterized by a very rapid equilibrium between phosphorus in solution and a labile pool composed of soluble calcium phosphates and monolayers of phosphate adsorbed on clay minerals and calcium carbonate (Cole and Olsen, 1959*a*,*b*).

$$\text{Solution P} \left(\frac{901}{d\theta}\right) \underset{C21}{\overset{C12}{\rightleftharpoons}} \text{Labile P} \qquad (3.5)$$

The rate of solution of labile phosphorus (C21) has been determined by anion resin techniques (Olsen and Watanabe, 1966). Values for various calcareous soils for this constant range from 0.4 to 2.0 per day. The phosphorus concentration in solution at a given depth of soil is given by the relationship

$$\frac{\text{Solution P}}{d\theta} = \text{P concentration}$$

where θ is the volumetric water content and d is the increment of depth in the soil profile. Phosphorus concentration in solution is related to the size of the labile pool by the expression

$$\frac{\text{Labile P (902)}}{\text{P conc} \left(\frac{901}{d\theta}\right)} = \frac{C21}{C12} \qquad (3.6)$$

Ratios of the labile pool to phosphorus concentrations at equilibrium are highly correlated with total soil surface area and range from 100 on sandy soils to approximately 200 on heavily textured soils (Olsen and Watanabe, 1963).

The ratios of labile phosphorus to phosphorus concentration and the rate of solution of labile phosphorus (C21) determine the value for the rate of adsorption. Thus, for a reference soil (Apishapa), the ratio of soil labile phosphorus to phosphorus concentration in solution is 140, the rate of release of labile phosphorus (C21) 1.24 day^{-1}, and the value of C12 is calculated to be 173 day^{-1}. Corresponding values for soils at the various site locations may be established by procedures described in the above references. Some additional solubility studies will be needed to establish temperature coefficients for this equilibrium reaction.

3.4.2 (901-904) Phosphorus Uptake by Plant Roots

Phosphate uptake processes involve a complex interaction between phosphorus concentration in solution, diffusion characteristics of the soil medium, soil water tension, and metabolic processes in the roots themselves. Phosphorus uptake by plant roots operates under steady state conditions, and the relationship to phosphorus concentration may be described by Michaelis Menton type kinetics with two uptake processes operating simultaneously.

$$\text{Total uptake} = \frac{U_{A_{max}}}{1 + \frac{K_A}{P\ conc}} + \frac{U_{B_{max}}}{1 + \frac{K_B}{P\ conc}} \qquad (3.7)$$

Uptake by the first mechanism dominates in the higher concentrations while uptake by the second mechanism is predominant at lower phosphorus concentrations. The rate constants in equation 3.7 include the diffusion characterisitcs of the particular soil medium. In a more rigorous treatment these may be treated separately (Olsen and Kemper, 1968).

Phosphorus uptake by plant roots responds to variations in soil water stress as well as the phosphorus concentrations in solution. Thickness of moisture films, diffusion path length, degree of hydration, and elongation of the roots appear to be the factors involved. Uptake of phosphorus in a given soil is a linear function of the volumetric water content, as shown in Fig. 3.8 for four reference soils (Watanabe, Olsen, and Danielson, 1960).

The temperature coefficients for uptake by the two uptake reactions indicates that both represent chemical reactions (Carter and Lathwell, 1967). The temperature coefficients shown in Fig. 3.3 for nitrogen processes is also used in the corresponding phosphorus uptake calculations.

Root uptake processes are energetically driven so that concentrations in the cytoplasm may exceed those in the external solution by 50-fold or more. However, with adequate phosphorus supply plant roots do not continue to absorb phosphorus in great excess of their requirements. Beyond certain limits of phosphorus concentrations in the cytoplasm, the limiting membrane (plasmalemma) becomes leaky and there is a return flow to the soil solution. This flow is simulated in a manner similar to that described for nitrogen in section 3.3.6.

Metabolic control of phosphorus processes involves supply of carbohydrates to the roots and interactions with supply of other nutrients. There is considerable evidence that microrhizal fungi in association with

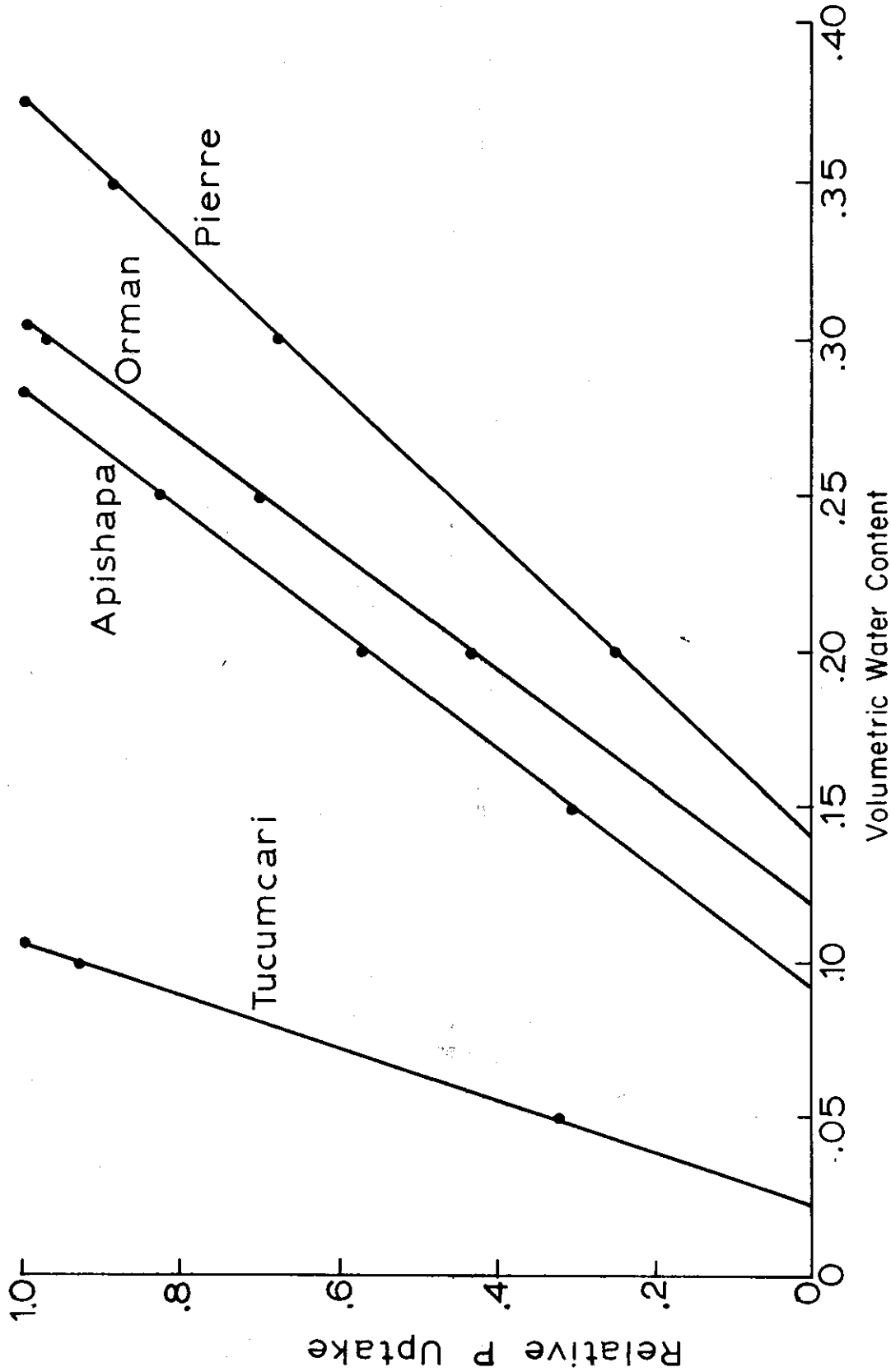

Fig. 3.8. The effect of volumetric water content on the relative rates of P uptake for four reference soils.

plant roots may facilitate uptake of phosphorus under conditions of low phosphorus supply. However, no attempt will be made to model this process with the limited information available at the present.

3.4.3 (904-906) Phosphorus Translocation From Roots to Tops

The dynamics of phosphorus transport within plants are, to a large extent, controlled by the activities of newly developing (meristematic) tissues within the plant. This results in a complex pattern of flow of nutrients into developing leaves in early stages of growth and then export, at later stages of development, under the stress of demand from the newly developing tissues. Any modeling of translocation from roots to tops must of necessity represent a gross oversimplification of phosphorus transport processes among developing tissues during the growth cycle. However, various limiting factors may be described:

1. Minimum level of phosphorus must be maintained in a given tissue to maintain physiological processes within that tissue.
2. Excess amounts of phosphorus above this level are rather freely transported to other tissues.
3. The level of phosphorus concentration in a given tissue at a given time represents the ratio between rates of accumulation of dry matter and net accumulation of phosphorus. In general, phosphorus accumulation by plant tops precedes the period of maximum dry matter accumulation. Phosphorus concentrations rise during early stages of growth and then decline throughout later stages as dry matter accumulation dilutes phosphorus supplies. There is evidence that in perennial grasses phosphorus is conserved in later stages of growth by transport back to root tissues for storage.

For modeling purposes, phosphorus concentration in the roots is used as a driving variable for supply of phosphorus in the tops, as regulated by phenological stage of the plants. Thus, phosphorus translocation reaches its peak at early phenological stages. Timing of phenological stages as supplied by the producer model is a function of climatic conditions for a particular season. This allows for the adjustment of seasonal trends in phosphorus translocation. Thus, cool season grasses will arrive at a given phenological stage considerably earlier than warm season grasses, and phosphorus translocation is paced by these predictions. There is a need for considerably more information to quantify these relations.

3.4.4 (905-909) Dead Roots Decomposition

A high proportion of total plant phosphorus is contained within root biomass of grassland ecosystems. No accurate data are yet available on the proportion of live to dead roots, but an estimate of one-third live to dead is being used in present versions of the model. The rate of decomposition of dead roots is assumed at 25% per year, pending more reliable predictions from the decomposer submodel. As dead roots decompose, the carbon to phosphorus ratio narrows from 600 to 1 in dead roots to 100 to 1 in the soil organic phosphorus fraction.

3.4.5 (909-901) Mineralization of Soil Organic Phosphorus

As soil organic phosphorus is mineralized, it enters the solution pool as inorganic phosphorus and is transferred to the labile pool or is absorbed directly into plant roots. Rates of mineralization are controlled by temperature, soil water, and supply of other nutrients, particularly nitrogen. A maximum mineralization rate of 1% per year is being used in

the present version, but in the future, values for the rate of mineralization from the nitrogen submodel will be used to predict rates of phosphorus mineralization.

3.4.6 (904-905), (906-907), (906-908), (907-908), (908-909), (908-901), (902-903) Other Flows

No quantitative descriptions have been developed for the remaining flows to date.

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CHAPTER 4. PRODUCER SUBSYSTEM

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4.1 ABSTRACT

In many ecosystem components it has been historically possible to make repetitive measurements of the state variable in the system. With this experience relevant flow relationships developed from these state variable measurements. In the producer subsystem of grasslands the same background is not available. Since it is not possible to conveniently measure the weight of the same plant at times t and t+1, plant sampling has been accompanied by plant destruction, and this lack of background information is an important limitation to producer process studies.

Here, two levels of effort are outlined: an elementary and admittedly incomplete level and a more comprehensive level. Major aboveground transfers of plant material can be accounted for with rather simple procedures as outlined in the elementary approach. Accounting of major belowground processes at this level, however, is a formidable obstacle. A simple matter of priorities would indicate that the elementary approach be used on aboveground plant parts until the ability to handle the belowground processes has been brought into line. Simpler approaches are to be favored until progress can be made with more comprehensive approaches.

A comprehensive view would insist that belowground transfers be documented as well as the aboveground. Major difficulties appear in such studies as root respiration, but possible approaches are outlined.

To reduce the function of the producer subsystem to a set of physical laws requires a careful analysis of the biochemistry of the system. Except in the case of photosynthesis, background information is so scanty that a meaningful discourse at this level is not possible at this time.

4.2 INTRODUCTION

It is extremely helpful in any process study to first have a gross overview of the results of the processes. We are able, for example, to measure soil water at time t and time t+1, and with a measurement of precipitation we are able to infer that the difference is the result of evapotranspiration. We can give an animal a measured amount of feed and infer that any change in weight is accounted for by intake minus losses. For decomposer activity we can measure the difference in sample material such as litter bags, and since there is no input infer that the losses are due to decomposition.

In the producer subsystem the same background is not available. Historically, we have not been able to measure the weight of the same plant at times t and t+1, let alone infer the gains and losses. Plant sampling has been accompanied by plant destruction, and the dearth of background information is a decided detriment to producer process studies.

Since we have a background of elementary studies in the other subsystems and can now proceed in somewhat more detail, it would not be too illogical to presume that the same elementary background will be necessary in the producer subsystem. It is also true that such elementary studies would be of little or no interest to many present-day scientists. Although it may be possible to omit the elementary and proceed to the biochemical, there is no a priori reason to expect that it will be a successful leap.

To hedge, we will outline two levels of effort, the elementary and incomplete approach and a more comprehensive approach.

The producer section is outlined in Fig. 4.1 and 4.2 for one species. Subsequent species may be assigned the following blocks of numbers (Table 4.1).

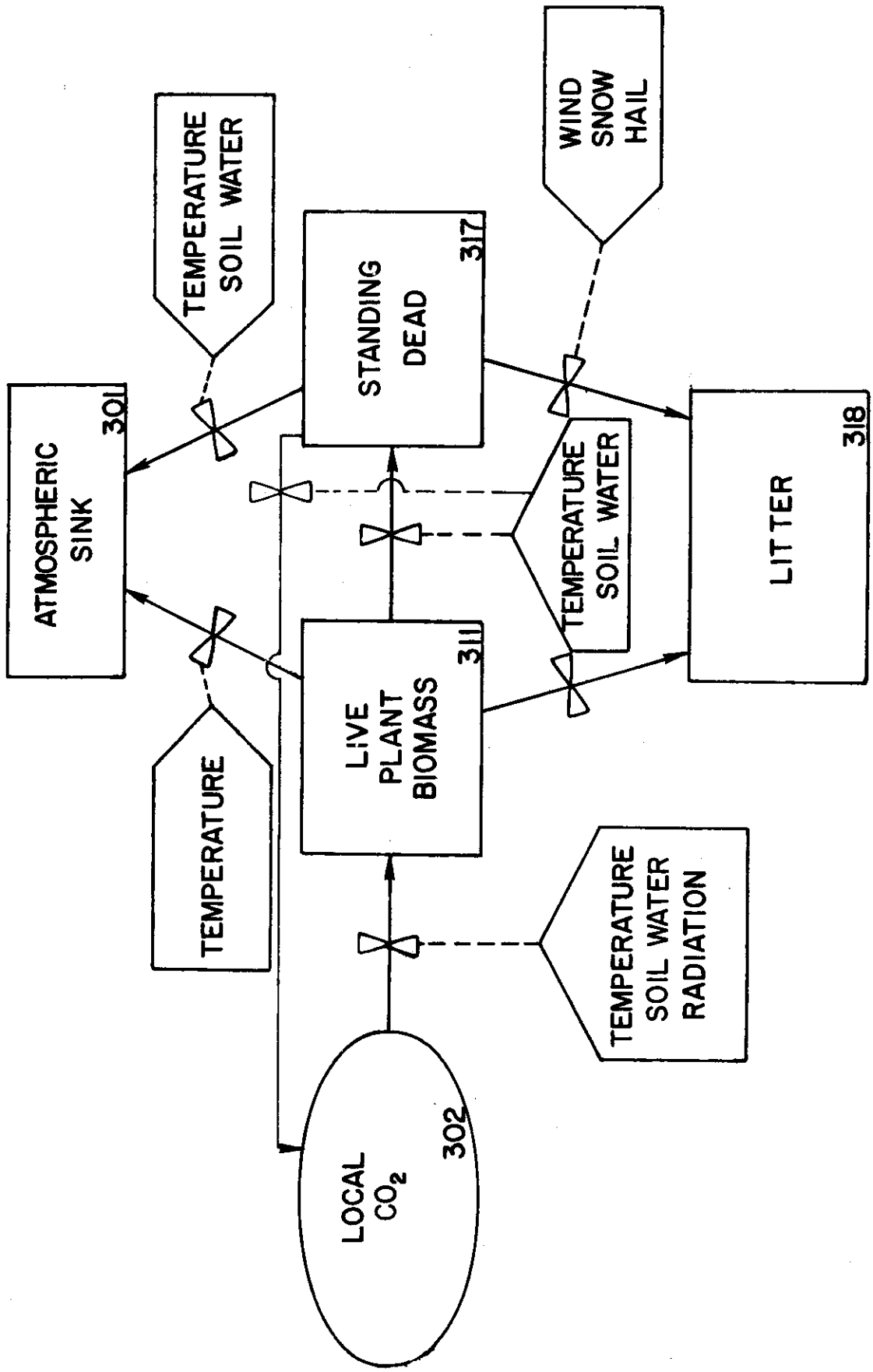

Fig. 4.1. Elementary diagram of the producer subsystem.

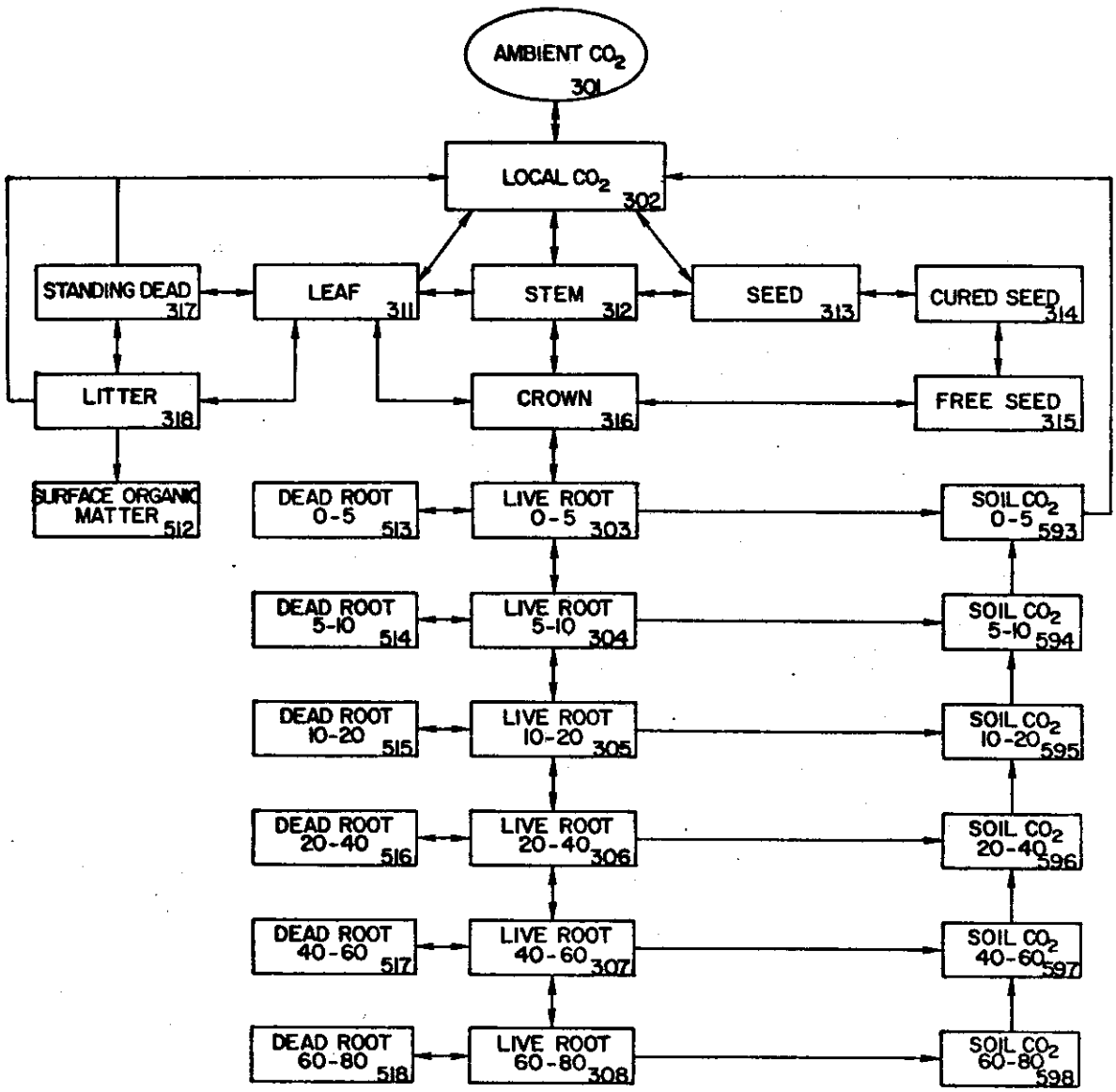

Fig. 4.2. Detailed producer section for one species. The compartments beginning with the number 5 and compartments 303 to 308 are the same for all species.

Table 4.1. Scheme for designating state variable components for a series of plant species.

Species	Leaf	Stem	Seed	Cured Seed	Free Seed	Crown	Standing Dead	Litter
1	311	312	313	314	315	316	317	318
2	321	322	323	324	325	326	327	328
3	331	332	333	334	335	336	337	338
4	341	342	343	344	345	346	347	348
5	351	352	353	354	355	356	357	358
6	361	362	363	364	365	366	367	368
7	371	372	373	374	375	376	377	378
8	381	382	383	384	385	386	387	388
9	391	392	393	394	395	396	397	398
10	401	402	403	404	405	406	407	408
11	411	412	413	414	415	416	417	418
12	421	422	423	424	425	426	427	428
13	431	432	433	434	435	436	437	438
14	441	442	443	444	445	446	447	448
15	451	452	453	454	455	456	457	458
16	461	462	463	464	465	466	467	468
17	471	472	473	474	475	476	477	478
18	481	482	483	484	485	486	487	488
19	491	492	493	494	495	496	497	498

4.3 AN ELEMENTARY APPROACH

The elementary approach logically would utilize only existing and proven techniques and would thus omit any processes for which techniques are uncertain or missing.

Since root measurements provide several difficulties for which the answers are not readily apparent, the elementary approach would simply negate the fact, with inputs and outputs, that roots are a functional part of the plant. This does not mean that root distribution cannot be used as a soil profile descriptor nor that roots should not be used as a control variable for aboveground flows. It does mean, however, that until some very difficult problems of translocation and root respiration are worked out, a simple approach should be followed. The same difficulties do not appear in woody plants since repetitive measurement techniques have been utilized by many previous workers, especially forest researchers.

The elementary approach would have a box-and-arrow diagram similar to Fig. 4.1.

4.3.1 (317-318) Standing Dead to Litter

Accumulation of litter from standing dead, which should be the same as losses of standing dead to litter, can be determined by collecting the litter additions from previously cleared plots. This would be an important process to identify as it is necessary in interpreting other losses of standing dead. Several investigators in the Grassland Biome and elsewhere have conducted such experiments. The technique is very simple, a number of plots are cleared of all litter. At intervals thereafter the plots are cleared again, and the new accumulation of litter is weighed.

Primary control variables are wind, snow, and hail. Although these are intuitively obvious, data have not been reported.

4.3.2 (317, 327, 337, 357-302) Standing Dead to Atmosphere

Total losses of standing dead include those into the atmosphere as well as into the soil (see Fig. 4.3). Nyhan (1972) investigated the total loss of standing dead material by suspending nylon bags containing dead herbaceous material in a vertical position just over the soil. Loss rates were determined by repetitive weighing of the bags, but the author felt that this preliminary effort needed further development to produce reliable results. The gross estimates of these flows should be corrected for losses to litter discussed in flow (317-318) (Fig. 4.2).

If an in situ, nondestructive method of sampling intact plants were available, it would be preferable to the nylon bag technique. Fortunately, the beta attenuation technique is both suitable and reliable (Mitchell, 1972). The capacitance technique, which depends on water, is not suitable for determining dry forage (Uresk and Sims, 1969), nor is the multispectral technique which depends on chlorophyll and cell turgor. The beta attenuation technique, however, depends primarily on molecular mass and is just as suitable for dry forage as for growing forage. Results of such studies have not been reported in the literature.

Control variables are shown in the diagram as temperature and soil water. The term "soil water" probably can be used as an expression of vapor pressure near the ground and, thus, an index of water content of the standing dead vegetation.

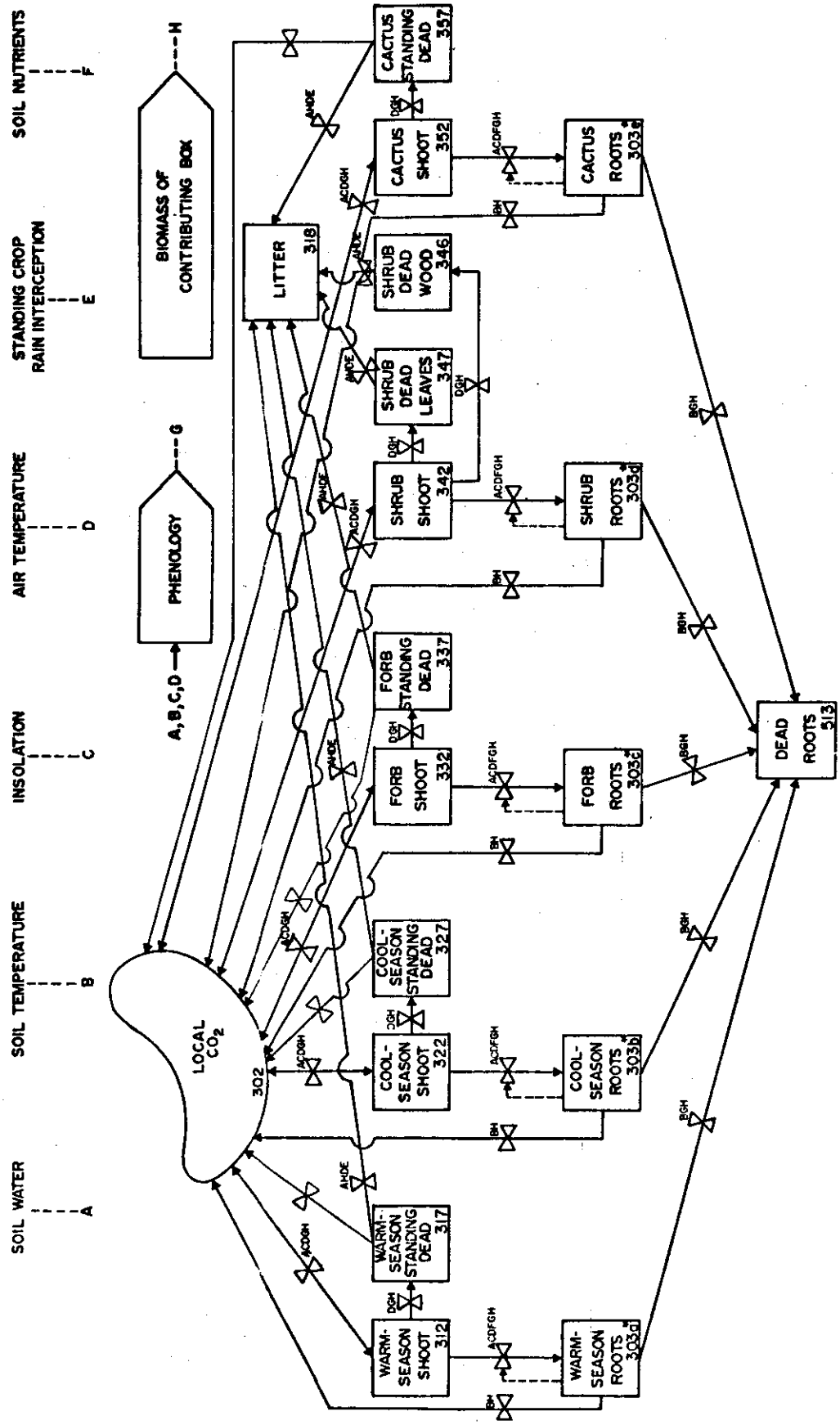

Fig. 4.3. Diagram of several plant species, each with one root compartment.

4.3.3 (311-318) Standing Live to Litter

Ordinarily this flow would be minimal and could probably be ignored although effects of hail, trampling, etc., could be treated.

4.3.4 (311-317) Standing Live to Standing Dead

The change from live vegetation (311) to dead (317) is not a process of translocation, but rather one of aging or phenology. It becomes nearly impossible to determine whether or not a given plant leaf should be considered live or dead based on color or other characteristics. Such a broad zone of indecision exists that no clear-cut distinction can be made.

An alternative to the impasse is to assume that all except the very youngest and oldest leaves have some attributes of being both living and dead. In later sections on the comprehensive approach these live and dead characteristics will be referred to as labile and non-labile, and suggestions on separate accounting will be made.

Indices of live and dead, which can include plant pigments, nitrogen, phosphorus, soluble carbohydrates, and water, will show what proportion of live and dead material must be present to achieve the nutrient analyses of specific samples. Thus, the "flow rate" can be inferred.

Temperature and soil water are listed as control variables for this flow. Leaf water tension would be a more specific expression of the effect of these variables.

4.3.5 (302-311) Net Aboveground Accumulation

In the elementary approach this flow has been left until last because it is the least satisfying; the other flows were "one-way" flows associated with identifiable processes, but this flow is a sum of several concurrent

processes. We may assign the name "net aboveground accumulation" to the process.

Flow (302-311), if measured during a time of active growth, is approximately net photosynthesis less translocation. During periods of senescence or death, flow (311-317) is an additional loss, but this could be avoided experimentally by working with plants on plots from which all standing dead material has been removed.

A major flaw in this approach is the lack of information about translocation. We are not able to infer a translocation rate from root dynamics (Bartos, 1971), since root changes are due to more than translocation, nor do direct measurements of translocation reported in the literature provide much insight.

In spite of the shortcomings, it seems necessary to proceed with the elementary approach because of lack of proven techniques for more detailed studies. More detailed procedures will be discussed in later sections.

The measurement of accumulation requires a nondestructive, repetitive measurement. Techniques which are primarily related to biomass are visual estimates, height measurements, and beta attenuation.

Visual estimates have long been a useful procedure in aboveground biomass sampling, but have seldom been used in rate studies. A skilled observer can often account for 75% of the variance between plots, but this is probably inadequate for rate determinations. Repeatability of measurements on the same plot with this technique is probably not better than independent measurements.

Plant height measurements provide some help, particularly for more upright plant habits. The use of plant heights to estimate weight has long

been useful (Canfield, 1944), but again it has not been applied to rate determinations. Hickey (1961) used both plant height and clump diameter and accounted for 80% of the variation between plots. Repeatability of height measurements on the same plants would appear to be much better than independent measurements, and height measurements probably are an acceptable index of aboveground accumulation.

The beta attenuation procedure, as reported by Mitchell (1972), is much superior to either the visual estimates or height measurements. Coefficients of variation in Mitchell's work were greater than 0.91. The equipment consists of a radioactive source, a G-M tube, and a counter; thus no significant equipment difficulties appear. Repeat measurements with beta attenuation could be incorporated as a standard vegetation measurement technique to give both rates of aboveground accumulation and improved state variable sampling.

Several control variables for this process include both plant activity indicators and environmental factors. Dye (1972) found that radiation, temperature, and soil water content were determinants of carbon fixation, and the same factors probably would be found to be suitable control variables for net accumulation.

On the other hand, Brougham (1960) found that leaf area index and chlorophyll were suitable control variables, and Uresk (1971) presented data which showed a high correlation between plant nitrogen (state variable 806, see Fig. 3.1) and relative growth rate (Flow 302-311). Nitrogen and chlorophyll are part of a highly correlated set of internal plant status indicators which includes turgor, leaf water tension, protein, phosphorus, and many plant pigments. The entire milieu is probably incorrectly

controlled by root uptake rates, which in turn are controlled by the plant-soil water balance.

Thus, several good leads for measurement of control variables can be inferred. Preferably, a nondestructive measure which could be used in conjunction with a nondestructive biomass determination could be adopted. A very promising technique is the use of multispectral scanning which indicates chlorophyll (at 0.68 μ), leaf turgor (at 0.78 μ), and leaf area (by the total absorption and reflectance at these wavelengths). Multispectral scanning has been used for estimating biomass correctly (Pearson and Miller, 1971), but is a better indicator of live rather than total vegetation which indicates that it would be an even better index of plant status. Beta attenuation, on the other hand, is a better indicator of plant dry weight than of wetness (Mitchell, 1972) which indicates that it is more reliable for plant biomass.

If nondestructive measurements of plant status are not available, a sample of plant material coupled with determination of radiation, temperature, and soil water, should provide adequate control variables. Plant water content (state variable 204, see Fig. 2.25), nitrogen (state variable 806), total pigments, and phosphorus (state variable 906, see Fig. 3.7) should provide the necessary information and also supply linkages to the water, nitrogen, and phosphorus models.

4.3.6 Seeds and Stems

Transfer of carbon to and from seeds and stems are not reported here (see Table 4.1 for species listing of all possible flows from leaf to stems and leaf to seeds). Stems, much more so than leaves, can be followed by height measurements. Seeds can be determined by harvest procedures. Tracer

studies of these translocation processes have been reported in the literature and further use of these techniques probably will not be necessary for the Grassland Biome.

4.3.7 Apologies for the Elementary Approach

The approach outlined above has many disadvantages from the standpoint of comprehensiveness, but has the distinct advantage of very high success probability. The chief shortcomings are the lack of translocation measurements and disregard of belowground plant material as a functional part of the system which, on the grassland, is several times the magnitude of the aboveground material.

4.4 A COMPREHENSIVE APPROACH

A more comprehensive level of investigation is outlined in Fig. 4.2 and 4.3. Although the level of detail has not been greatly expanded from the elementary approach, a great deal of difficulty has been added. Particularly, the determination of downward translocation which has been investigated somewhat (e.g., Knievel and Schmer, 1971) and root respiration which has not been reported are formidable obstacles. The problem is compounded when several species are involved, especially when we are not even able to distinguish to which species a root belongs.

4.4.1 (302-311) Photosynthesis

The discussion of this section was prepared largely by A. J. Dye.

Photosynthesis is generally considered to be the diffusion of carbon dioxide from the immediate surroundings of stomata to the substomatal cavity and subsequent fixation. These two steps will be discussed separately.

4.4.1.1 Diffusion of carbon dioxide. The diffusion step involves the movement of CO_2 molecules through the stomata from the surrounding atmosphere into the area of mesophyll tissue for absorption and fixation (Fig. 4.4). Time required for diffusion depends partly on wind speed and partly on the surface geometry (mainly size and shape of the leaf).

The controls for the movement of CO_2 into the photosynthetic tissue are primarily wind speed and total diffusive resistance of the plant to such movement. Simply, the carbon cannot diffuse through stomata unless they are open. If stress situations induce closure of stomata through transpirational stress or unfavorable temperatures, then essentially no CO_2 can diffuse into the tissue for fixation.

Diffusive resistance is normally measured in seconds per centimeter. One source (Zelitch, 1971) lists the following equation as an approximation for air boundary layer resistance:

$$Ra = k\sqrt{\frac{\text{leaf width (cm)}}{\text{wind speed (cm/sec)}}} \qquad (4.1)$$

where k is a constant approximately equal to 1.3 $\text{sec}^{\frac{1}{2}}/\text{cm}$. The general range of Ra is from 0.1 to 2.0 sec/cm. Probably Ra seldom limits photosynthetic rates since its value is very small compared with the total diffusive resistance of 4 to 20 sec/cm.

Stomatal resistance is probably the key to the control of CO_2 diffusion into the tissue. Zelitch also lists an equation for calculating the stomatal resistance:

$$Rs = \frac{1}{nD}\left(\frac{d}{\pi ab} + \frac{1}{2\sqrt{ab}}\right) \qquad (4.2)$$

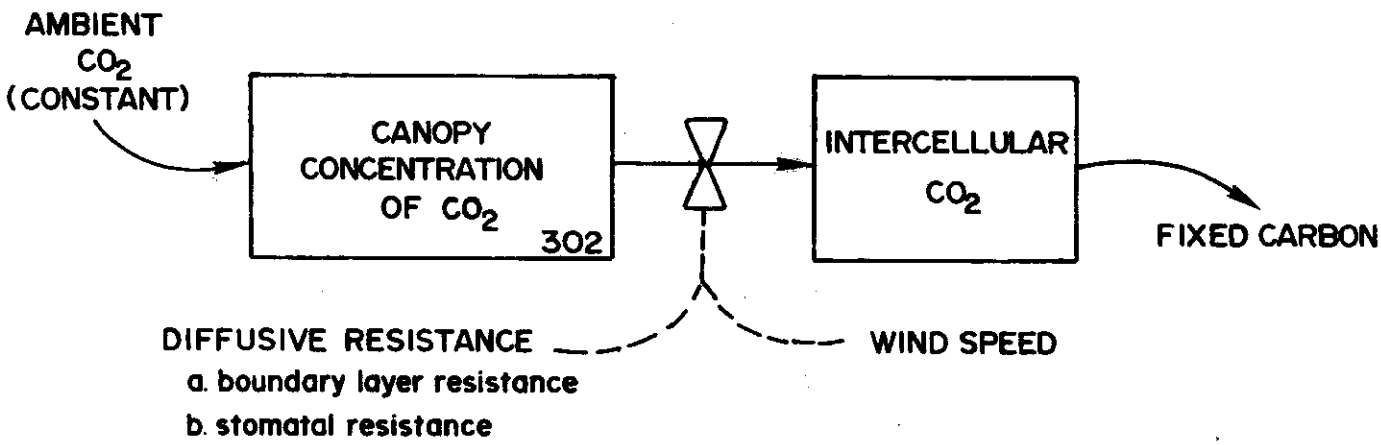

Fig. 4.4. Diffusion step of photosynthesis.

where n = number of stomata per cm^2

D = coefficient of diffusion

d = stomatal depth

a = semiwidth of stomata (radius of circle)

b = semilength of aperture

The stomatal resistance may be a magnitude larger than boundary layer resistance. General range observed for Rs is 0.7 to 12.0 sec/cm.

4.4.1.2 Fixation rates. The actual rates of fixation by chloroplasts are determined to a large extent by the amount of incoming energy (Fig. 4.5). This portion of the producer subsystem will be concerned with the various rates of fixation and the controls governing such rates.

There is an exponential decline in carbon fixed as the soil water content decreases from near field capacity toward the permanent wilting point.

Solar radiation is probably a limiting factor of photosynthesis of blue grama. Bjorkman et al. (1972) reported on a C_4 dicotyledon which exhibited a linear rate of fixation up to peak radiation intensities of about 1.4 langleys/min. Blue grama fixes CO_2 through the same type of pathway, yet plants which fix carbon through the Calvin pathway may have photosynthesis light saturated at 50% of full sunlight intensity.

Zelitch (1971) presented some examples of the effect of temperature on net photosynthesis. Most species of the C_3 category do not have a pronounced temperature optimum at high irradiances between 10° and 35°C. High photorespiration is a characteristic of these species, and as the leaf warms the increased photorespiration may mask any large increase in gross photosynthesis. Yet species with low photorespiration, such as blue

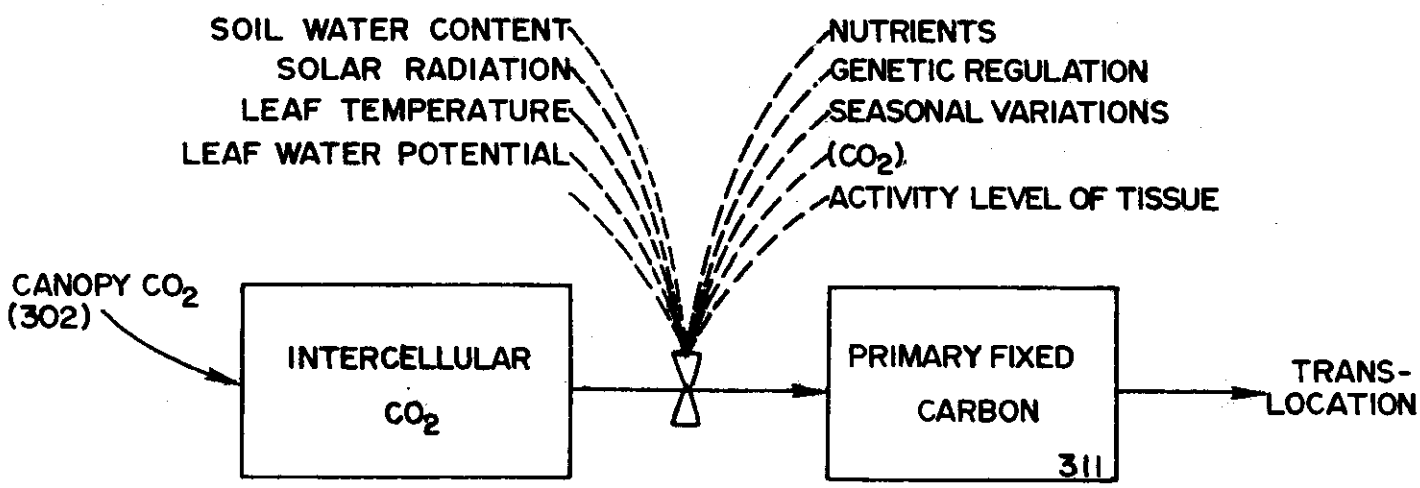

Fig. 4.5. Fixation step of photosynthesis.

grama, may double fixation rates for a 10° rise between 15° and 25°C. Optimum temperatures for low photorespiring species range from 25° to 35°C while 20° to 25°C is a more typical range for C_3 plants (Table 4.2).

Perhaps some index of leaf water content should be included as a control for the transfer of carbon dioxide from the canopy atmosphere into the substomatal cavity. At any rate, net photosynthesis is dependent upon diffusion of CO_2 through open stomata, and a sufficient decrease in leaf water content will close stomata and reduce photosynthesis. Boyer (1970*a*,*b*) reported 50% inhibition of CO_2 assimilation with -14 bars of leaf water potential in corn.

Nevins and Loomis (1970) reported on the photosynthetic rates and nitrogen nutrition of sugar beets (*Beta vulgaris* L.). There was a reduced rate of carbon fixation when the nitrogen levels were inadequate.

Genetic regulation is included as a control simply to put some realistic bounds on rates of fixation according to the pathway of carbon fixation. Low photorespiring plants might exhibit as much as 100% higher rates of fixation than plants with high levels of photorespiration.

The intrinsic responses through some type of preconditioning effect necessitate the inclusion of some index to indicate seasonal variations in abiotic conditions. Phillips and McWilliam (1971) reported on photosynthesis of saltbush (*Atriplex numularia*) and they observed a change in photosynthetic rates dependent upon the day/night temperature at which the plants were grown. The maximum rates of photosynthesis changed as well as the optimum temperatures for the different day/night temperature regimes.

Net photosynthesis increases almost linearly with CO_2 concentration increases up to about 300 ppm and at high irradiance levels. Maize (corn)

Table 4.2. Water use efficiency (increase in dry wt (mg) per g water consumed) in C_3 and C_4 grass species at different temperatures for growth. Values are means for three C_3 species and four C_4 species, respectively. (After Downes, 1969).

Temperature (°C)	C_4 Species	C_3 Species	C_4/C_3
20°	4.0	2.4	1.7
25°	3.1	1.7	1.8
30°	3.6	1.1	3.3
35°	2.3	0.2	11.5

leaves in full sunlight exhibited 50% greater photosynthetic rates at 500 ppm than at 300 ppm of CO_2. Current studies (Dye, Brown, and Trlica, 1972) indicate that blue grama vegetation exhibits an essentially constant rate of fixation up to 190 ppm of CO_2.

Bull (1971) indicated that photosynthetic rates declined in the older leaves of both young and mature plants of sugarcane (C_4 plant). He attributed the decrease to the increased stomatal resistance. After severe drought the maximum photosynthetic rates were similar to those of C_3 plants.

4.4.1.3 Prediction of CO_2 uptake from irradiance, soil water, and temperature. On the Pawnee Site several environmental factors were monitored simultaneously under natural field conditions in an attempt to determine the relationship between photosynthesis of blue grama and the environment (Dye, 1972). Although photosynthetic rates are certainly affected by irradiance, temperature, soil water, nutrients, tissue activity, genetic regulation, and numerous other variables, examination of the results indicated that only two or three of the environmental factors probably exerted a large control over the photosynthetic rates of blue grama (Fig. 4.6, 4.7, 4.8). Photosynthesis can be expressed as some function of irradiance, soil water, and temperature with sufficient accuracy for present ecological use, and such an approach seems to offer a reasonable starting place to develop an empirical relationship for predictive purposes. Appropriate functions for photosynthesis and respiration for other important species of the shortgrass ecosystem need to be developed.

There are two fairly common forms of expressing photosynthesis as a function of irradiance. One is the logarithmic relation:

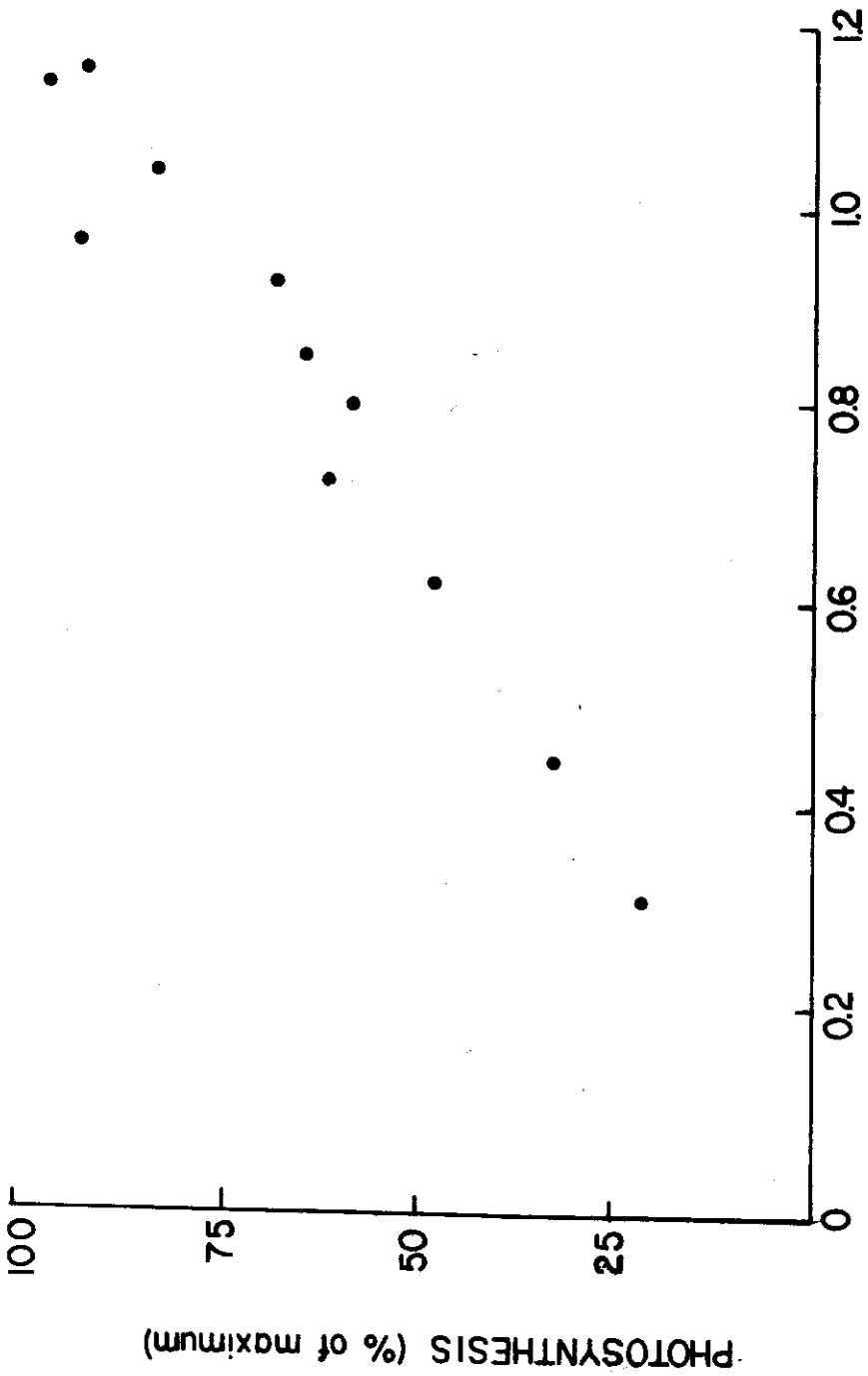

Fig. 4.6. Photosynthesis of blue grama (percent of the maximum uptake rate observed at each sampling period) as a function of irradiance. Points above 0.7 langley min^{-1} were observed at 36 ±1°C; those below 0.7 langley have temperature noted.

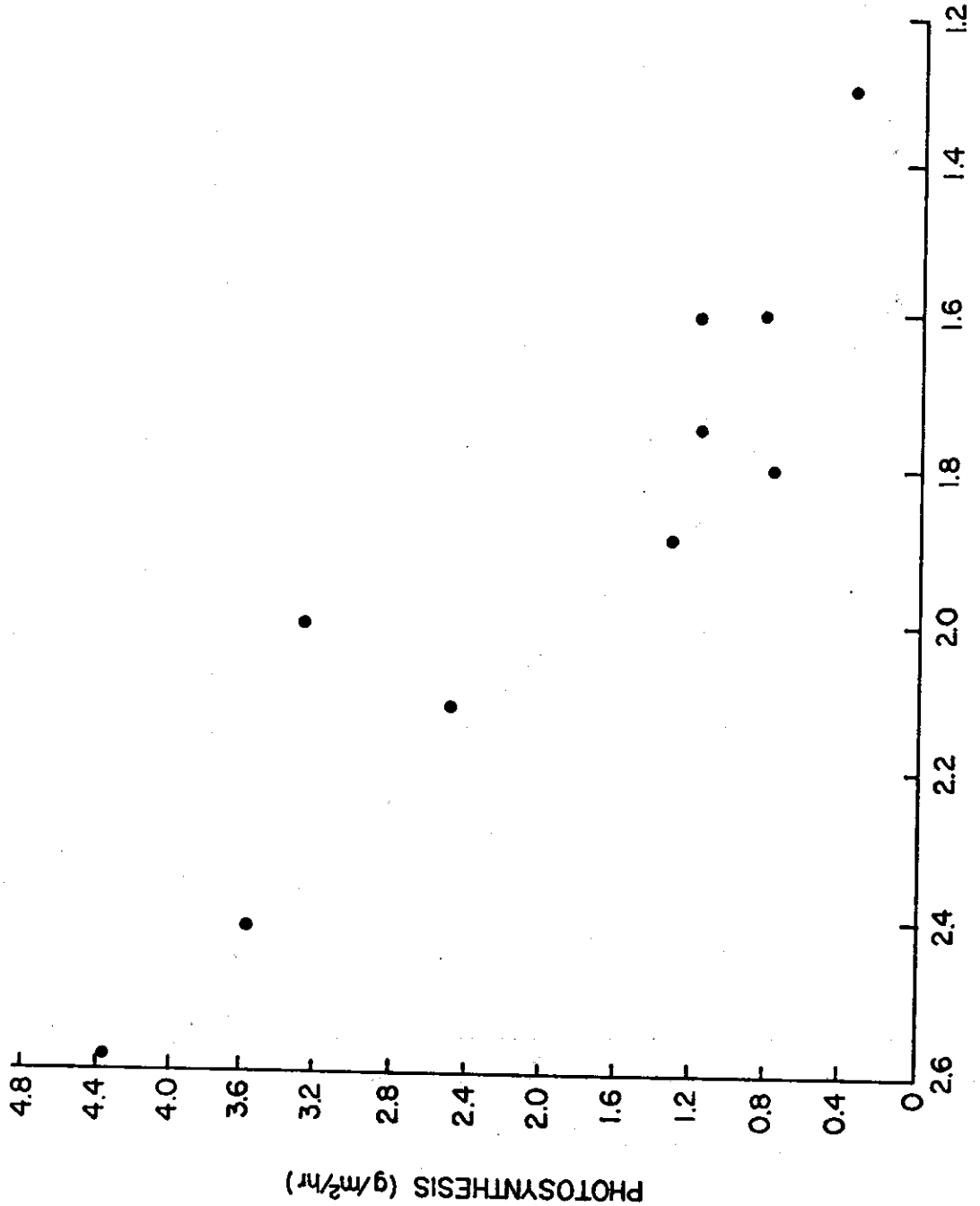

Fig. 4.7. Net photosynthesis (g CO_2/m^2 leaf area/hr^1) of blue grama sods as a function of soil water content in the upper 22 cm. Time period was mid-June through July 14, 1971.

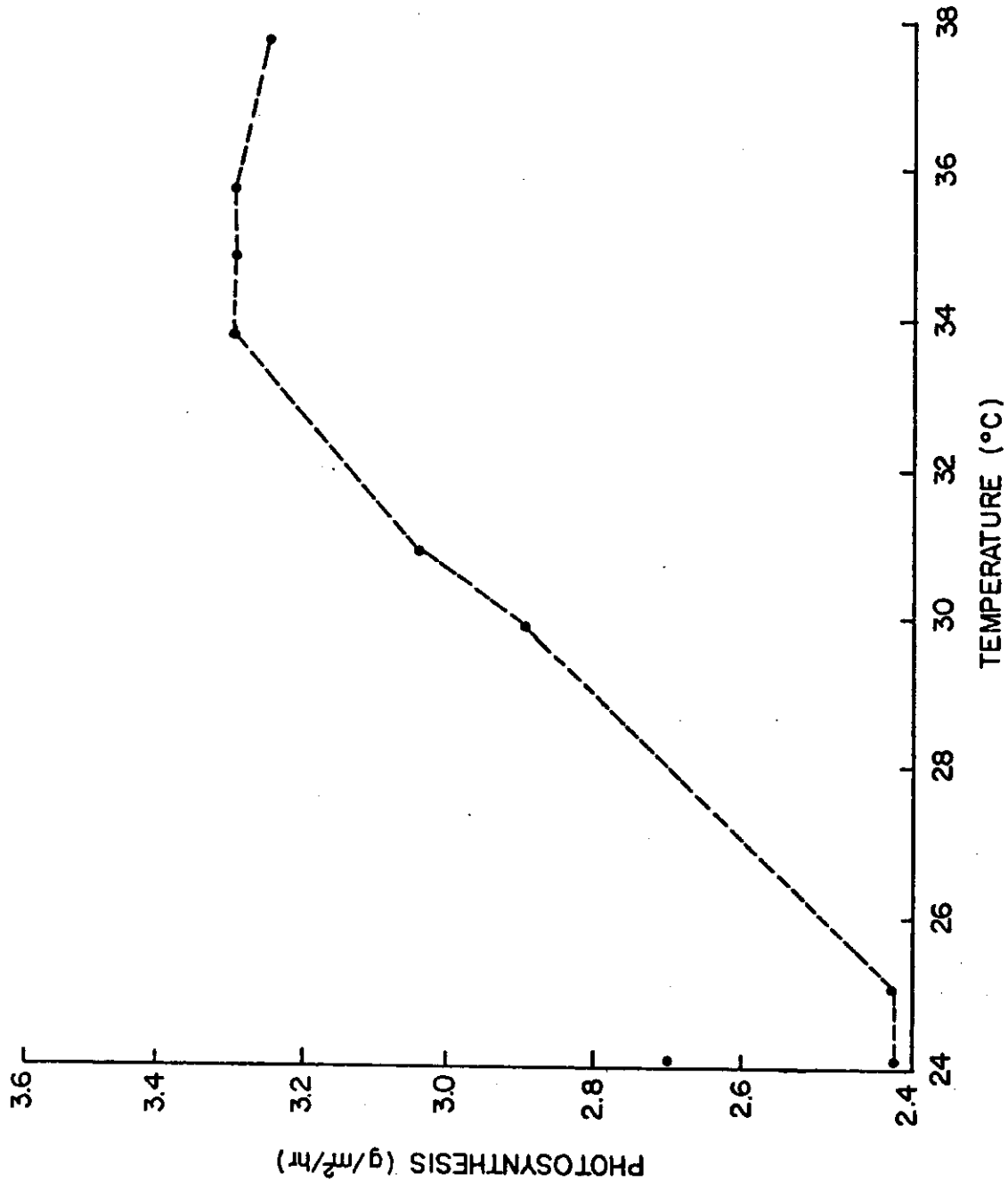

Fig. 4.8. Net photosynthesis (g CO_2/m^2 leaf area/hr^{-1}) of blue grama sods as a function of air temperature. Irradiance level is 1.2 langleys/min^{-1}, and soil water content is 4.0 cm.

$$P_s = b_0 + b_1 \ln R \tag{4.3}$$

where

P_s = photosynthetic rate (mg CO_2 per unit of leaf area or weight)

R = irradiance (often langleys/min)

b_0 and b_1 = constants

Blackman and Wilson (1951) found this equation to describe the response of several herbaceous species. The relationship between photosynthesis and irradiance has also been described by the equation (Botkin, 1969) for rectangular hyperbolae:

$$P_s = \frac{k\, P_{max}\, (R - R_o)}{1 + k\, (R - R_o)} \tag{4.4}$$

where

P_s = photosynthetic rate

R = irradiance

R_o = irradiance level at the compensation point (where $P_s = 0$)

P_{max} = maximum photosynthetic rate observed

k = a constant

The temperature response curve for photosynthesis is generally of the minimum-optimum-maximum type. Conceptually, an equation of the form

$$P_s = a + bT + cT^2 \tag{4.5}$$

would describe the stimulating and depressing effects of low and high temperatures (T) through the coefficients a, b, and c.

Maximum CO_2 uptake rates for 10 days from June 15 to July 14 were chosen with common levels of irradiance and temperature for regression

against soil water content. On any given day, most of the variation in the CO_2 uptake rate could be accounted for by variations in temperature and irradiance, but to account for the average day-to-day decrease in assimilation rates an additional variable such as some index of soil water availability had to be included. Soil water content proved to be the best parameter to use on the basis of the variation (R^2). Multiple regression analysis indicates that the best relationship to describe the observed responses is

$$P_s = b_0 \, R^{b_1} \, T^{b_2} \, SW^{b_3} \qquad (4.6)$$

where

P_s = photosynthetic rate (mg CO_2/m of leaf area per hr)

R = measure of irradiance

T = air temperature within the vegetation canopy

SW = soil water content measured at 15 cm

b_0, b_1, b_2, b_3 = constants

All variables were linearly transformed and analyses were carried out in the logarithmic plane. The coefficient of determination (R^2) was 85% for the 10 values of maximum CO_2 uptake rates. Since the irradiance and temperature levels were within a relatively narrow range, the standardized coefficient for soil water content (0.62) indicated that it was the most important of the three independent variables. The standardized coefficient for irradiance was 0.40, and -0.08 for temperature.

The next attempt was to determine if such an equation could be used to describe the variations in CO_2 uptake rates throughout the growing season with a wide range in irradiance, temperature, and soil water content. The

same analysis was carried out with 3-min averages (n = 630) of photosynthetic rates from natural blue grama sods. With these data, the following relation was obtained:

$$P_s = .289\ R^{1.6}\ T^{-0.2}\ SW^{3.2} \qquad (4.7)$$

where the terms are defined as in equation 4.6. The coefficient of determination (R^2) was 74%, and the standardized coefficients were irradiance, 0.70; soil water, 0.53; and temperature, -0.09. This indicated that, over the range of soil water content (2.5 cm to 1.3 cm) from a relatively wet condition to severely limiting conditions, the irradiance was probably the most important variable in determining CO_2 uptake rates.

This empirical equation indicates that photosynthesis is inversely related to temperature; the evidence presented previously indicates a parabolic effect. The extremely high relationship between temperature and irradiance precludes a clear statistical separation between temperature and irradiance effects, and the irradiance term in this equation probably represents both the irradiance effect and the positive effect of temperature.

The soil water term is a rising exponential term. Obviously, this would not be the case for high values of soil water; the data used here may have been the lower part of a sigmoid curve.

4.4.2 (311, 491-312, 492), (312, 492-303) Translocation

The following discussion on translocation is taken from Schmer and Knievel (1972) (see also Table 4.1).

4.4.2.1 Carbohydrate movement from the leaf. Following a buildup of assimilates in the photosynthetic tissue of a leaf, there seems to be a

movement of only a certain amount and kind of substances into the conducting phloem tissue. Sugars, usually sucrose (but in some plants stachyose or other carbohydrates), generally constitute the bulk of organic material moving through the phloem. A considerable number of nitrogenous compounds and steroids are also known to be translocated (Biddulph and Cory, 1965; Clauss, Mortimer, and Gorham, 1964; Mittler, 1953; Mortimer, 1965; Trip, Nelson, and Krotkow, 1965; Webb and Burley, 1962, 1964; Zimmermann, 1958). Generally, this movement of assimilates into the conducting tissue occurs against a concentration gradient (Bieleski, 1966; Phillis and Mason, 1933; Roeckl, 1949). Also, energy is required for the transfer of assimilates from photosynthetic to conducting tissue (Ullrich, 1962; Ziegler, 1956). A reason for a reduction in light intensity reducing not only the photosynthetic rate but also the proportion of assimilates moved from leaves (Hartt, Kortschak, and Burr, 1964; Hartt and Kortschak, 1967) may be related to an alteration in the products of photosynthesis, but part of the effect may be that the energy required to transfer the assimilates from leaf to conducting tissue may have also dropped. Limiting the rate of photosynthesis by reducing the carbon dioxide concentration, however, has been shown to increase the transfer of assimilates to conducting tissue (Nelson, 1963). Although this effect may be related to a failure to divert carbon into leaf storage products during low rates of carbon dioxide fixation, there is also the possibility that because less energy is used for carbon dioxide fixation, more energy is available for transfer.

Pristupa (1964) demonstrated the movement of assimilates from the photosynthetic tissue into the conducting vessels of small vascular bundles,

and within 3 hr into the phloem of large bundles, with a series of micro-autoradiographs of cereal leaves treated with $^{14}CO_2$. The rate of movement of assimilates out of the leaf can vary. For example, in tobacco 46% of the carbon assimilated at any one time may have left the leaf in 3 hr (Clauss et al., 1964) and 68% in 96 hr. Porter and Bird (1962) found a much slower initial loss of assimilates from a tobacco leaf that had been kept in darkness for 48 hr prior to the assimilation of $^{14}CO_2$. Joy (1964) found that about 50% of the carbon assimilated was translocated from the leaf of a sugar beet within 24 hr and about 70% in 3 days; however, Mortimer (1965) showed that up to 60% of the assimilated carbon could be exported within 4 hr. The movement from the leaf of labeled carbon assimilated during grain development in wheat may be almost complete in 24 hr, or it may take several days (Lupton, 1966). It has been reported that only 20% of the assimilated carbon was exported from a tomato leaf 24 hr after assimilation (Khan and Sagar, 1966). Less than 30% of the assimilates moved out of a pine seedling branch in 3 days (Balatinecz, Forward, and Bidwell, 1966); however, there probably was actively growing tissue within the branch itself which could explain the slow movement.

Although a general translocation pattern seems to exist with an initial rapid transfer of assimilates from the leaf which is followed by a slower movement (Clauss et al., 1964), it is not always clear from published data as to the cause of the great variations of assimilate transfer from a fully grown leaf. It is dependent not only upon factors within the leaf but also upon the ability of other parts of the plant to use or store the available assimilates (Hansen, 1967; Hew, Nelson, and Krotkov, 1967; King, Wardlaw,

and Evans, 1967). Where leaf area is large relative to the growth requirements for carbohydrates, the demand for assimilates per unit leaf area will be small. Removal of the upper part of a leaf in *Lolium temulentum* L., thus reducing leaf area relative to growth, stimulated the transfer of carbohydrates from the remaining basal area (Evans and Wardlaw, 1964). However, in sugarcane the opposite effect was obtained from removal of the upper part of a leaf blade. A reduction in flow of assimilates from the remainder of the leaf was incurred (Hartt et al., 1964). Another factor in the modification of carbohydrate movement from the leaf may be the ability of a leaf to temporarily store excess carbohydrates (Mortimer, 1965).

Very young leaves obtain their carbohydrates as exports from older leaves. Not until they reach one-third to one-half of the maximum leaf area is their assimilation of carbohydrates high enough to meet the growth requirements and is the export of assimilates started (Forde, 1965; Webb and Gorham, 1964). Leaves have been shown to be most active in exporting assimilates soon after reaching their maximum size, and the rate of export declines steadily with age (Clauss et al., 1964; Vyvyan, 1924).

4.4.2.2 Assimilate distribution in relation to leaf position. There is a pattern of assimilate distribution in most plants that shows a relation to leaf position. The lower leaves act as the main source of assimilates for the shoot apex. The intermediate leaves may transport assimilates in either direction. This pattern has been shown to occur in many plants and even grasses and cereals (Evans and Wardlaw, 1964; Williams, 1964). When considering the direction of movement of assimilates, it must be remembered that a living plant is not a static organism and that the position of the leaf relative to the shoot is forever changing. Thus, a typical pattern of

distribution of assimilates has been shown for wheat (Doodson, Manners, and Myers, 1964) and the perennial grass, timothy, (Williams, 1964). This pattern indicates that, initially, a young leaf exports to the adjacent shoot apex, but as development advances and more leaves separate this leaf from the shoot apex an increasingly greater proportion of the assimilates move to the roots. One exception to this general pattern is the observation by Khan and Sagar (1966) that in tomato plants ^{14}C assimilated by the lower leaves moved upward to the shoot apex, while assimilates from the upper leaves moved downward. The upward movement from the lower leaves might be explained by a redistribution of assimilates that first moved downward and then subsequently moved back to the shoot apex through the xylem (Winter and Mortimer, 1967). Also, Bonnemain (1965) has demonstrated that the vascular traces of a tomato leaf unite with the other vascular traces only at the node below the point of insertion of the leaf. Therefore, the assimilates have to travel through one internode downward before moving up to the shoot apex. In the work by Khan and Sagar (1966) the flow of assimilates from the upper leaves was very slow so that, at the time of harvest, it would have appeared that many of the assimilates were still traveling that passage through the internode and actually appeared to be moving downward.

4.4.2.3 Assimilate demand. During early growth a leaf will require carbohydrates from other parts of the plant. Once the leaf is fully developed, it is no longer capable of importing assimilates, even when placed in darkness (Aronoff, 1955; Doodson et al., 1964; Rabideau and Burr, 1945; Williams, 1964). Some exceptions occur and appear to involve the redistribution of leaf assimilates back through the xylem (Eschrich, 1966;

Williams, 1964), or occur when movement into the leaf has been stimulated by the addition of growth substances (Booth et al., 1962).

Movement of assimilates away from the site of assimilation may continue even when the leaves are detached or isolated by ringing. However, this movement is greatly enhanced by growing tissues and storage organs (Aronoff, 1955; Hartt, 1962; Hartt and Kortschak, 1964; Humphries, 1963). Tissues differ in their demand for assimilates, and there are a number of mechanisms that can cause these differences. First, there is the ability to deplete the supply of carbohydrates and, thus, create a concentration gradient in favor of movement to a certain organ. Consequently, either the intensity of metabolism and the active unloading of the vein system (Geiger, 1966) or the number of sites of utilization and the size of a growing organ may be important. Distance from the site of assimilation to the organ may be important in developing and maintaining a concentration gradient. Secondly, growth substances moving out from the organ may either suppress the development of alternate sites of assimilate utilization or alternately stimulate translocation of assimilates through the vascular system to the sites of utilization (Booth et al., 1962; Davies and Wareing, 1965; Hew et al., 1967; Muller and Leopold, 1966; Seth and Wareing, 1967).

It has been suggested (Wardlaw, 1968) that flowers are a weak sink and fruits a strong sink in grapes. Regrowth of corn following removal of the cob (Loomis, 1945) suggests that fruits develop at the expense of vegetative growth (Leonard, 1962). Dominance of reproductive over vegetative organs has been illustrated several times by the pattern of assimilate distribution or changes in pattern following leaf or fruit removal (Bonnemain, 1965; Hansen, 1967; Khan and Sagar, 1966; Wardlaw, 1965), whereas in trees heavy

seed production may be associated with decreased secondary thickening (Kozlowski and Keller, 1966). Although in cereals there may be some movement of assimilates from the ear to the developing stem during the initial stages of grain development, this movement seems to stop as stem development stops and an increased movement of assimilates to the grain is noticed (Buttrose and May, 1965). This same restriction in movement is evident in pods of bean plants; however, up to half of the assimilates could be exported from a green pod if this was the only portion of the plant illuminated (Wanner and Bachofen, 1961). The exported assimilates are then moved to other pods of the plant. The sugar beet (Geiger, 1966) also appears to dominate vegetative growth in a manner similar to fruits.

Growth of established shoots appears to have priority over root and bud growth where conditions simulate assimilate deficiency (Evans and Wardlaw, 1964). In *Pinus*, Nelson (1964) observed that translocation of assimilates to the roots under low light intensities was less than under high light intensities. Roots and buds appear to be parts of the plants that are low in priority for assimilates compared to other organs in a plant and only receive assimilates in excess of the requirements of other parts.

The relative abilities of roots and buds to obtain assimilates depend on many conditions. Roots on intact shoots growing under low light conditions will continue to grow slowly, although bud development is almost totally inhibited. However, if the shoot apex is removed, as often occurs with severe defoliation of pasture species, the buds are released from apical dominance and then grow at the expense of the root system (Milthorpe and Davidson, 1966).

Within the shoot there may be competition for assimilates between the shoot apex, leaves at different stages of development, and expanding stem tissue. The apex, because of its small size, will not have a large demand for assimilates, but the intensity of this demand may be high. The actual apex, if relatively inactive, might be expected to show retarded development during periods of general assimilate deficiency. Friend, Helson, and Fisher (1962) working with wheat found that differences in light intensity had only slight effects on the development of the apex.

A leaf at the stage of most rapid development seems to retard the growth of the next youngest leaf above it (Vyvyan, 1924). Stem expansion could occur at the same time leaf expansion is occurring and may compete with young leaves for assimilates. However, studies of this phenomenon have not been undertaken to show its importance. Competition between the stem and developing ear for assimilates in cereals has been shown by Friend (1965) when he found that both stem height and ear length increased with increasing light intensity up to 2,500 footcandles.

Although storage organs actively accumulate assimilates, the leaves, stem, and roots have some capabilities for holding excess carbohydrates such as starch, oligosaccharides, or simple sugars. Temporary storage of assimilates in the stem of cereals, at the time of anthesis, is followed by a redistribution of these materials to the ear and new shoots (Stoy, 1965).

4.4.2.4 Environmental factors affecting carbohydrate distribution. After considering the previous factors, it should be evident that the environment can control the distribution of assimilates in one or more ways. Environmental factors may affect assimilate distribution by causing

changes in the rate of growth of developing organs (which also may be influenced by hormonal levels, by alterations in photosynthetic levels, and by outflow of assimilates from leaves) or by directly affecting movement of assimilates. Also, changes in plant development, e.g., from leaf production to flower and fruit formation, will add to the above effects.

Temperature. With shifts in temperature there is often a marked change in the development pattern of plants, much of which is presumably caused by direct growth rate change of the developing organs. The accumulation of soluble carbohydrates at low temperatures suggests that growth rates are affected more by temperature than are photosynthetic rates (Evans and Wardlaw, 1964); however, the differences in response may be due somewhat to a limitation of photosynthesis at higher temperatures through an inadequate supply of carbon dioxide (Gaastra, 1963). Reduced growth due to low temperatures has been shown to reduce the rate of assimilate translocation (Hartt, 1965*a*; Vernon and Aronoff, 1952; Whittle, 1964); however, since translocation itself is a metabolic process it may be directly affected by temperature. For example, where the photosynthetic rate does not fall with low temperatures but shoot growth declines, more assimilates will become available for the growth of roots and buds. Therefore, the change in distribution of assimilates with falling temperature is not necessarily associated with differences in the optimum temperature for growth of different plant organs. Friend (1966) found the optimum temperature for growth of attached roots in wheat to be about 15°C, while that for isolated roots in a sterile culture was 25°C. Translocation of assimilates from the leaves of sugarcane was found to be more dependent on root than shoot temperature (Burr et al., 1958). Part of this effect could be related to the

production of tillers from the base of the sugarcane plant where temperatures will be close to those of the root system. Also, any change in temperature may affect nutrient uptake.

Although there is evidence to infer that movement of assimilates through conducting tissue is associated with metabolically active cells and may be dependent upon temperature, there is no conclusive evidence that reduced translocation is ever the primary cause of limiting growth under conditions of low temperatures. There is little indication from most work that the optimum temperature for translocation differs from that for growth. Hsia, Waon, and Wang (1963) concluded from their work on wheat, in which they lowered the temperature on the ear, stem, and flag leaf separately, that the effect of temperature on the distribution of assimilates from the flag leaf was primarily dependent on the growth of the ear and to a lesser extent on the function of the leaf. Lowering the temperature of the stem from 20° down to 8°C had no observable effect on assimilate distribution. The effect of temperature on the regions of growth and assimilate movement out of the leaf was assumed to be related to the energy requirements of these processes (Geiger, 1966; Ullrich, 1962). The failure of Hsia et al. (1963) to find any direct effect of temperature on translocation is not in accordance with the results of several other workers who have shown that local stem or petiole temperatures from 0° to 5°C inhibited the movement of applied ^{32}P and of ^{14}C assimilates (Swanson and Whitney, 1953; Webb, 1967; Webb and Gorham, 1965).

The effect of temperature on translocation may be transient as shown by the work of Swanson and Geiger (1967) on sugar beets. Whittle (1964) has suggested that the recovery of translocation under low temperatures

could be related to a buildup of sugars in the supply regions of the plant, and hence the development of a steeper sugar concentration gradient through the cooled zone. However, Ford and Peel (1966) concluded from their work on the relation between temperature and movement of ^{14}C through a willow stem to an aphid colony that lateral movement out of the sieve tubes is metabolic and dependent on temperature, whereas longitudinal movement down the length of the sieve tubes is independent of temperature. Perhaps temperature effects on cell-membrane permeability and lateral release of assimilates could explain some of the effects of temperature on translocation. It is apparent that this aspect still needs clarification not only in relation to the effects of temperature on the pattern of assimilate distribution but also in relation to the mechanism of translocation. However, it seems likely that the primary effect of temperature on assimilate distribution is associated with growth rather than sugar conduction, as the shifts in distribution of assimilates with reduced temperature are the reverse of the changes normally associated with a decrease in assimilate supply.

Light. Even though the pattern of assimilate movement is influenced by the relative ability of different organs to "attract" the available carbohydrate, it is also influenced by the rate of assimilate production in photosynthesis, which is regulated by the duration of light intensity. Root and bud growth are inhibited to a greater extent than shoot growth by a reduction in light. Nelson et al. (1961) observed reduced movement of ^{14}C assimilates from the needles to roots in conifers grown under low light.

Although root growth is more restricted than shoot growth under low light, there are some instances where it has been shown that, of the

assimilates leaving a leaf, the proportion moving to the root system is greater in the dark than in the light (Nelson, 1964; Nelson and Gorham, 1957). Thrower (1964) has shown that a reduction in the rate of photosynthesis of an expanding soybean leaf, due either to darkening or a reduction in the supply of carbon dioxide, results in a smaller demand and reduced import of assimilates into the growing leaf. Such an effect could explain the observed differences in assimilate distribution pattern between light and dark. Translocation of assimilates to the growing organs throughout a normal 24-hr cycle may occur largely in the dark period or largely in the light period (Mason and Maskell, 1928). However, under low light conditions with less accumulation of carbohydrates in leaves and stems, translocation during the dark period is likely to become far less important than during the light period. Therefore, by reducing movement of assimilates during darkness, the overall effect would be to increase the relative proportion of assimilates reaching the shoot.

Movement of assimilates out of a leaf, as mentioned earlier, is influenced by light energy. Therefore, not only is the rate of photosynthesis reduced under low light but also the proportion of assimilated carbon leaving the leaf. Hartt and Kortschak (1964) and Hartt (1965*b*) have suggested that there is a light process involved in translocation in a sugarcane leaf, with a maximum response at low intensities (approximately 100 footcandles). However, Shan'gina (1965), working with tomatoes, has found that a decrease in light intensity from about 3,600 down to 900 footcandles, which has only a small effect on leaf photosynthetic rate, results in a slower outflow of assimilates and an increase in leaf polysaccharides. This response of translocation to decreasing light intensities,

at higher levels than those reported by Hartt (1965*b*), suggests that either sugarcane leaves respond in a different manner than leaves of other species or the response may have been affected by detaching the sugarcane leaves.

Day length, through changes in plant development, will have a considerable indirect effect on the distribution of assimilates. Nelson (1963) noted that movement of assimilates in larch was affected by day length through effects on root and shoot development. Perhaps the more conspicuous effects of day length are related to the change from vegetative to floral development, and probably the greater translocation of assimilates in long-day plants under long days and short-day plants under short days is the result of this developmental process.

Water. Gates (1955*a*) has already pointed out that the effect of water stress on growth and therefore on the distribution of photosynthetic assimilates is not fully understood. Elongation growth commonly shows an early response to water stress, whereas photosynthesis and the accumulation of assimilates continues for some time after stress is evident in the elongation of the plant (Iljin, 1957). The observation by Slayter (1957) that dry weight accumulation ceased earlier than stem elongation in tomato plants is an exception. Other forms of growth are not so easily altered by stress as is elongation. For example, grain development in cereals may be unaffected by a stress that causes wilting of the leaves (Asana, Saini, and Ray, 1958). The response to water stress depends on the organs involved. Iljin (1957) suggested that cells, such as those found in seeds, buds, and storage organs, which generally lack vacuoles and are filled with food reserves will be the most resistant to desiccation. It is resistance to desiccation rather than the ability of an organ to function with a low

water content that appears to give an organ the ability to withstand water stress.

There are often marked alterations in the pattern of assimilate distribution when plants are subject to water stress. These alterations may be the direct result of reduced growth rates or of reduced photosynthetic rates, although there is some evidence for a more direct effect of stress on the conduction of assimilates.

The observation by Hartt (1967) of an increase in the sugar content of the stem when sugarcane plants are under water stress seems to fit Iljin's (1957) theory, i.e., "reduced growth under stress results in the accumulation of sugars." Hartt favors a direct cause-and-effect explanation in which sugar accumulation is the result of a reduced velocity of movement through the conducting system. This is somewhat similar to a view expressed earlier by Gates (1955*a*,*b*) who suggested that changes in the weight ratios of different plant organs when under stress were due to a modification of translocation. Roberts (1964) observed that water stress increased the upward movement of assimilates in yellow poplar. Also, during grain development of wheat, a water stress that caused reduced photosynthetic activity in the leaves resulted in an increased movement of assimilates from the lower leaves to the ear (Wardlaw, 1967). This is similar to translocation that occurs when assimilation is reduced under low light intensities.

The work of Plaut and Reinhold (1965) on the movement of applied sucrose in bean plants under water stress has been interpreted as showing that water stress directly alters translocation. Certainly, changes in xylem tension affect pressures within the sieve tubes of the phloem, as Peel and Weatherley (1962, 1963) demonstrated by measuring the exudation

of phloem sap through aphid stylets. However, where growing organs are not subject to the same stress as the rest of the plant, as with the ear of wheat during grain development, velocity of movement of labeled assimilates through the conducting tissue was found to be relatively insensitive to stress (Webb and Burley, 1964). This is evidence, in part, for the suggestion by Nelson (1963) that water stress affects the movement of assimilates into but not through the conducting tissue. There is ample evidence that there is a reduction in the rate of movement of assimilates out of the photosynthetic tissue during water stress (Hartt, 1967; Plaut and Reinhold, 1965; Roberts, 1964; Wardlaw, 1967; Wiebe and Wihrheim, 1962). The close interaction between growth and translocation makes it difficult to assess the relative importance of these processes in determining the pattern of distribution of assimilates in plants under water stress. In the few instances where growth has been eliminated as a factor it appears that translocation is relatively insensitive to stress. Also, the observation by McWilliam (1968) of a significant movement of assimilates from stem to roots and buds in the perennial grass (*Phalaris tuberosa* L.O.) when the plants are dormant due to a restricted water supply suggests that the transport system is insensitive to desiccation.

4.4.3 (303-543) and (303-513) Root Respiration and Decomposition

The information presented in this section was prepared by Singh (unpublished) (4.4.3.1) and Singh and Coleman (1972) (4.4.3.2).

4.4.3.1 The model. A variable portion of the pool of labile carbon compounds present in the rhizomes and roots undergoes respiratory metabolism to release energy for the support of live processes (Fig. 4.9, 4.10). Thus, the labile carbon content forms the source of input for the process.

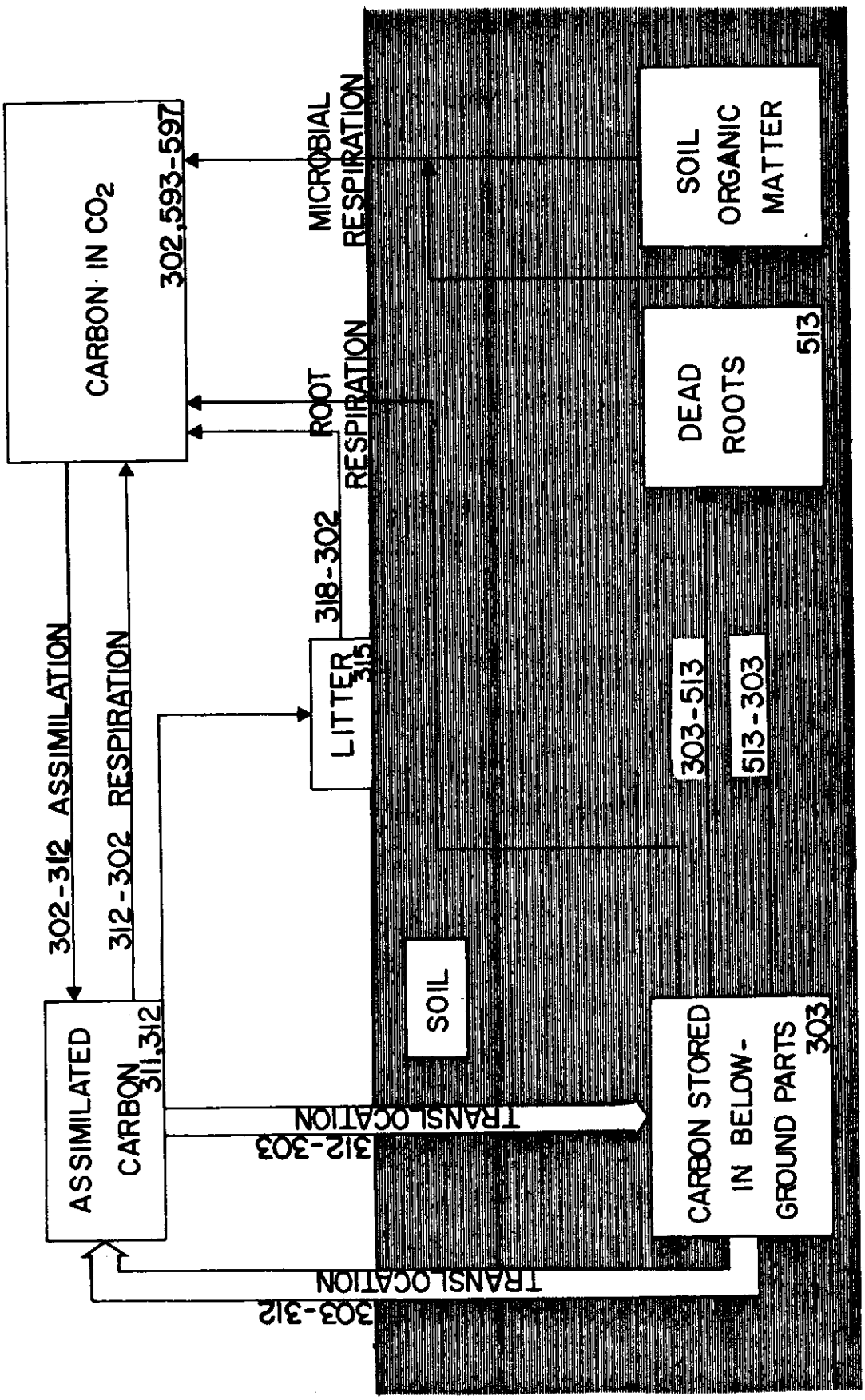

Fig. 4.9. Transfer of carbon in various compartments of plant-soil-air system.

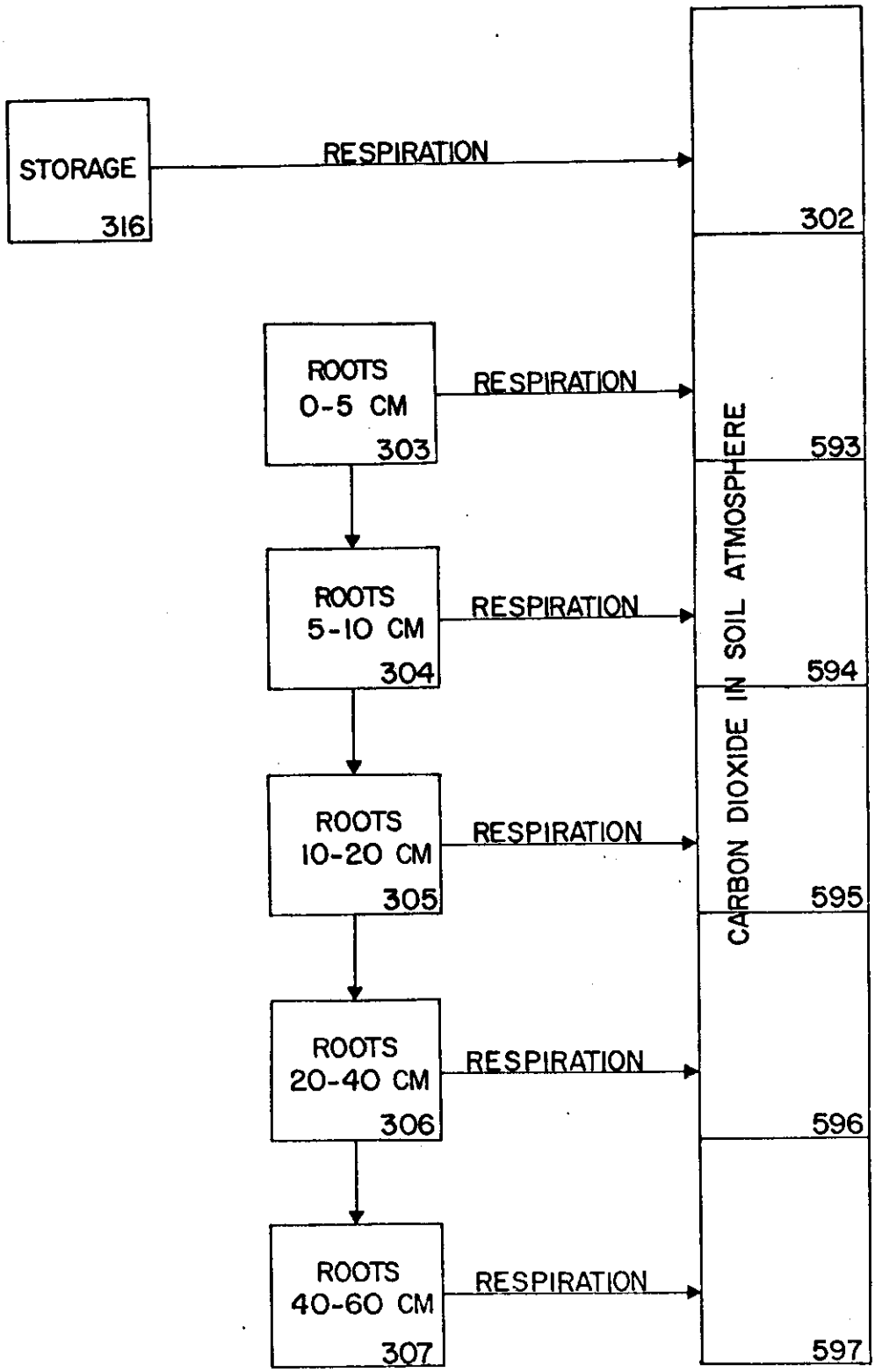

Fig. 4.10. Respiratory carbon loss from belowground parts.

As a result of this process of breakdown of organic compounds, carbon is released as carbon dioxide to the soil atmosphere. Since this phenomenon is essential for life, respiration is a continuous process. However, its rate is governed by factors such as the amount of metabolizable carbon compounds (hence the amount of live matter), the age of the tissue, the phenologic shape of the plants, the moisture content of the tissue, the soil water, the soil temperature, and the soil aeration (Fig. 4.11).

Because of the paucity of literature it is practically impossible to present graphical models of this process which would be applicable to a grassland ecosystem. In order to give some sort of insight which could be used in developing future process studies, however, certain graphs indicating the relationship of root respiration with different factors which have been pulled out from literature or have been conceptually drawn are presented in this section.

Age of the tissue. Data reported by Brown and Broadbent (1950) and many other workers (see Yemm, 1965) indicate that small undifferentiated cells of the meristem have a low rate of respiration per cell while the cells of the elongating zone may exhibit 5 to 10 times greater respiratory activity as compared to meristematic cells. Beyond this, the cells of the differentiating zone maintain a high and fairly constant level of respiration, but as the cells mature there is a gradual decline in the rate which, perhaps, would ultimately level off to a reasonably steady rate. These points are illustrated in Fig. 4.12.

Because of such observations it would seem that the rate of CO_2 production by root mass at different depths would depend on the proportion of new and old growth.

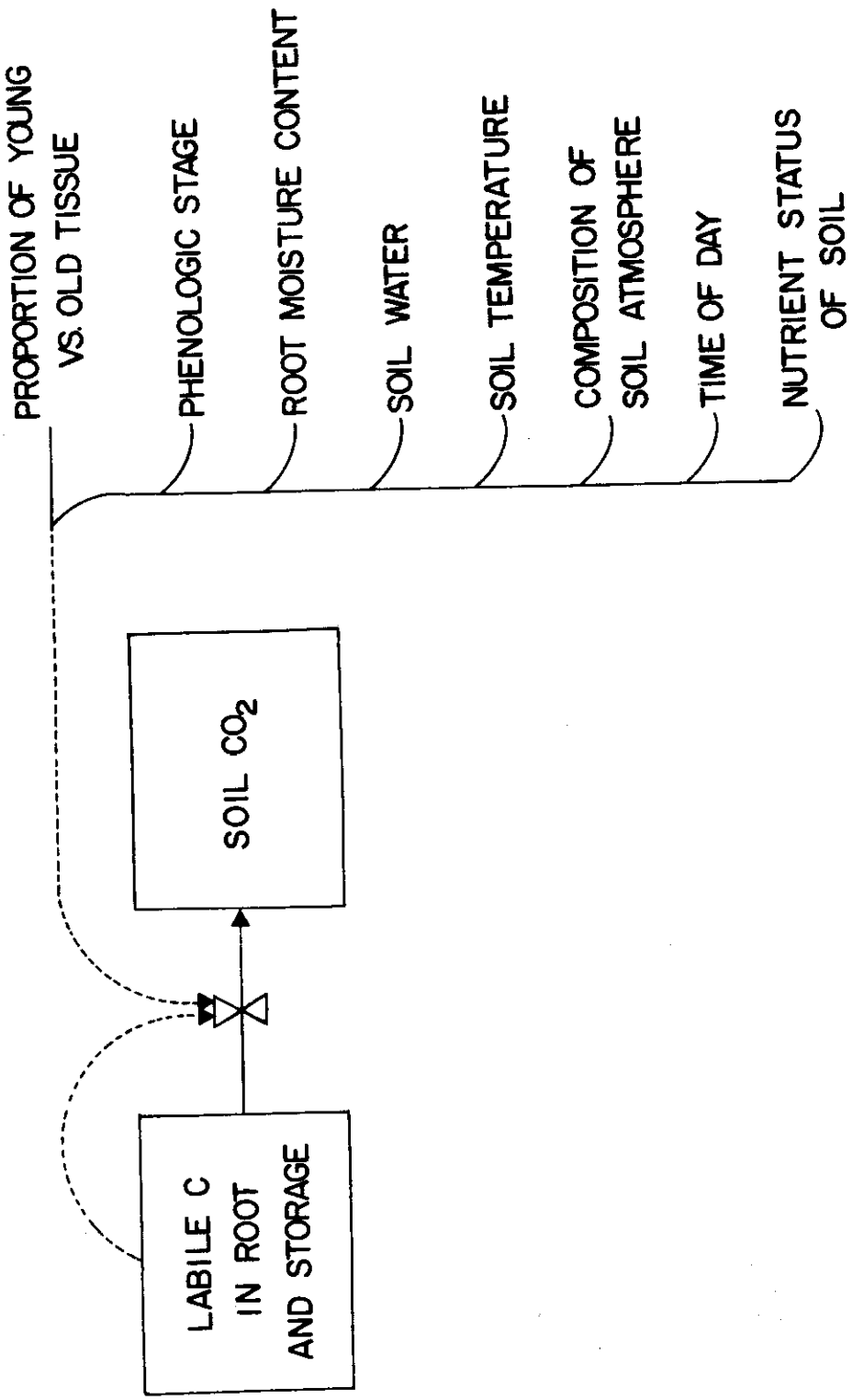

Fig. 4.11. Controls for the process.

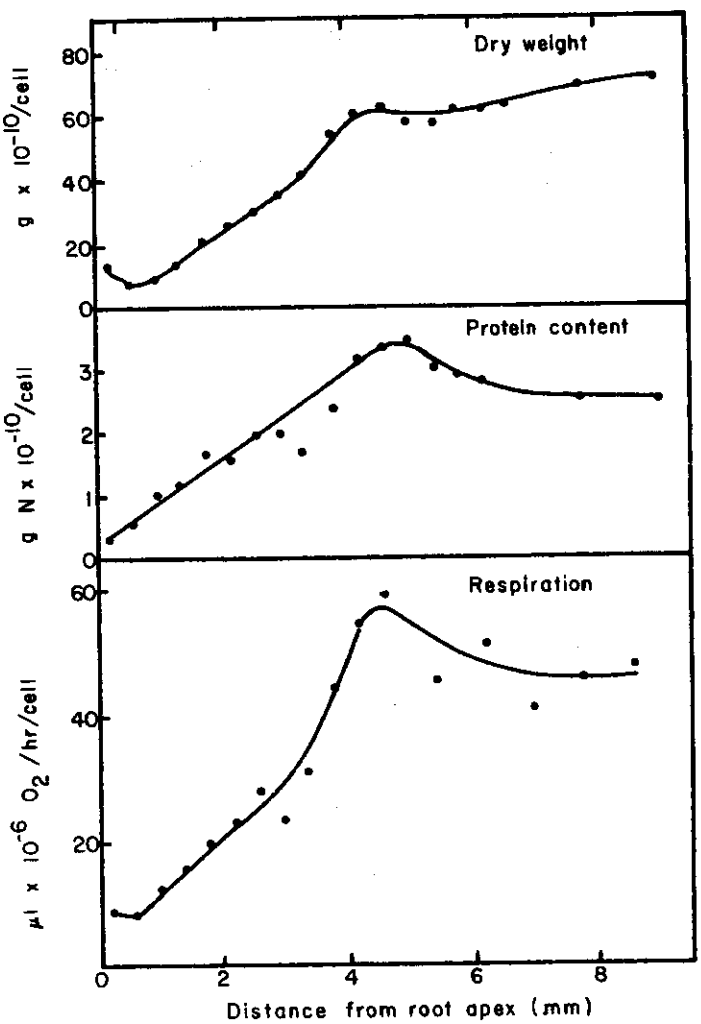

Fig. 4.12. Cellular respiration and development in the growing point of pea roots (Brown and Broadbent, 1950); after Yemm (1965).

Phenology of the plant. Stoklasa and Ernest (1905), working with barley, wheat, rye, and oats, surmised greater CO_2 production per gram dry matter by the tender roots of young plants. They reported maximum CO_2 production when the plants were 70 to 80 days old. These authors also found that CO_2 is a principal component of root secretions.

Lau (1906) found that root respiration has a marked effect upon the carbon dioxide production by the soil which increased with the growth of the plant and reached a maximum at the blooming period.

Bizzell and Lyon (1918) compared the CO_2 content of the soil atmosphere of bare and cropped (oat) soil at different times between June and September. They also reported the greatest amount of CO_2 during the blooming period of the plant. A typical response curve obtained by these authors is illustrated in Fig. 4.13.

Quantity of live roots. Harris and van Bavel (1957) reported that root respiration per plant is primarily determined by the weight of the root system. Crapo and Coleman (1972) studying the broom sedge old-field community in South Carolina concluded, "The spatial contribution of root respiration in the field remains unknown, but presumably is in proportion to the biomass present." For any one sampling date it could be assumed that the rate of respiration per square meter holds a positively linear relation with the root biomass present (Fig. 4.14). However, it should be borne in mind that the same quantity of root mass may respire at different rates under varying sets of environmental factors.

Root moisture. Coleman (1973) attributed 2 to 3 mg CO_2/25 hr/5-cm deep, 25-cm^2 soil core to roots with moisture indices of less than 100. Crapo and Coleman (1972) found similar data with unrinsed roots of

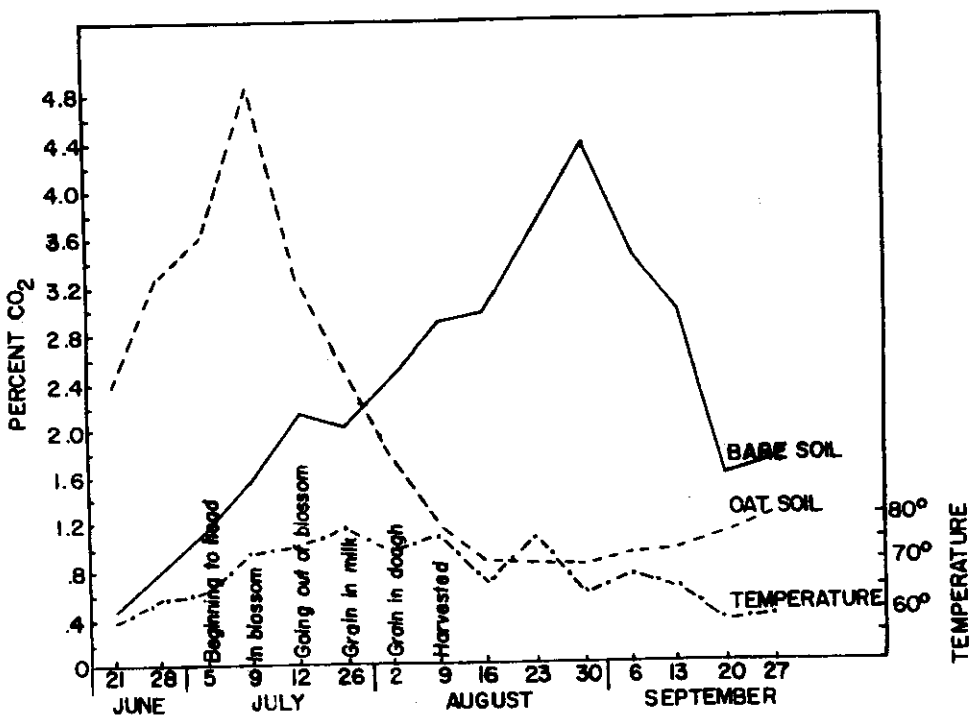

Fig. 4.13. Diagram showing carbon dioxide in air from unlimed Dunkirk clay loam, cropped and bare, with the mean atmospheric temperature for the week preceding each analysis (after Bizzell and Lyon, 1918).

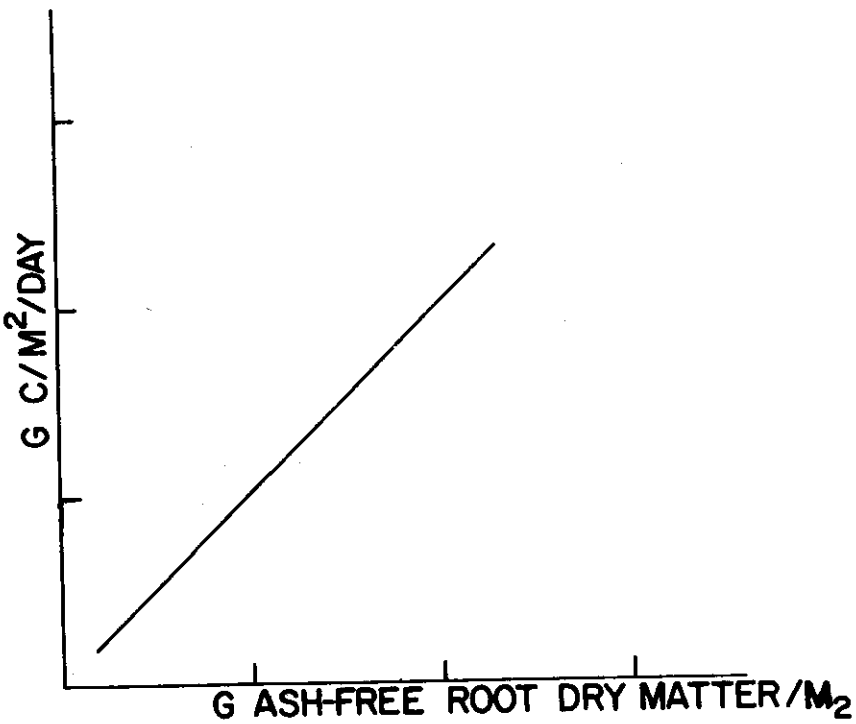

Fig. 4.14. Relation of root respiration and ash-free dry matter.

Andropogon which had moisture indices up to 211, but reported a pronounced increase in respiration rates for rinsed roots with moisture indices of 184 to 667. Moisture index in these studies was calculated according to the following expression:

$$\text{Moisture index} = \frac{H_2O \text{ wt}}{\text{Dry wt}} + 100 \qquad (4.8)$$

Crapo and Coleman (1972) also reported a direct correlation between CO_2 production by *Andropogon* roots and their moisture content, with 57% of the variation accounted for by variation in root moisture content (Fig. 4.15).

Soil water. Wiant (1967*a*) recorded a sharp decrease in soil CO_2 production at low soil water regimes. Coleman (1973) obtained a pronounced increase in the total CO_2 production during the month of August and attributed this to an increase in soil temperature or soil water content stimulating the metabolic rates of all soil organisms including the roots of green plants. Working on a shortgrass prairie, Clark and Coleman (1972) recorded a several-fold increase in CO_2 production by intact soil cores following precipitation in September. Perhaps soil water influences the rate by increasing the turgidity of the root tissue. Nishikawa (1956) felt that respiration substrate in rice seedlings grown on a higher N level of nutrition is consumed more rapidly under flooding due to enhanced respiration.

Indirectly, a very high level of soil water may adversely influence the root respiration by diminishing soil aeration. In the absence of more clear-cut studies, it may be assumed that root respiration follows a sigmoid curve with increasing soil water (Fig. 4.16).

Soil temperature. Soil temperature has been found to have a profound influence on soil respiration (the term includes microbial respiration in

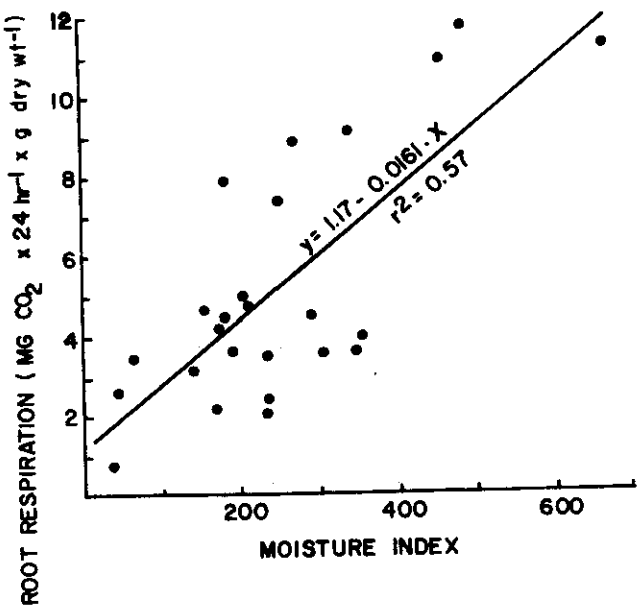

Fig. 4.15. Regression of root respiration against moisture index (after Crapo and Coleman, 1972).

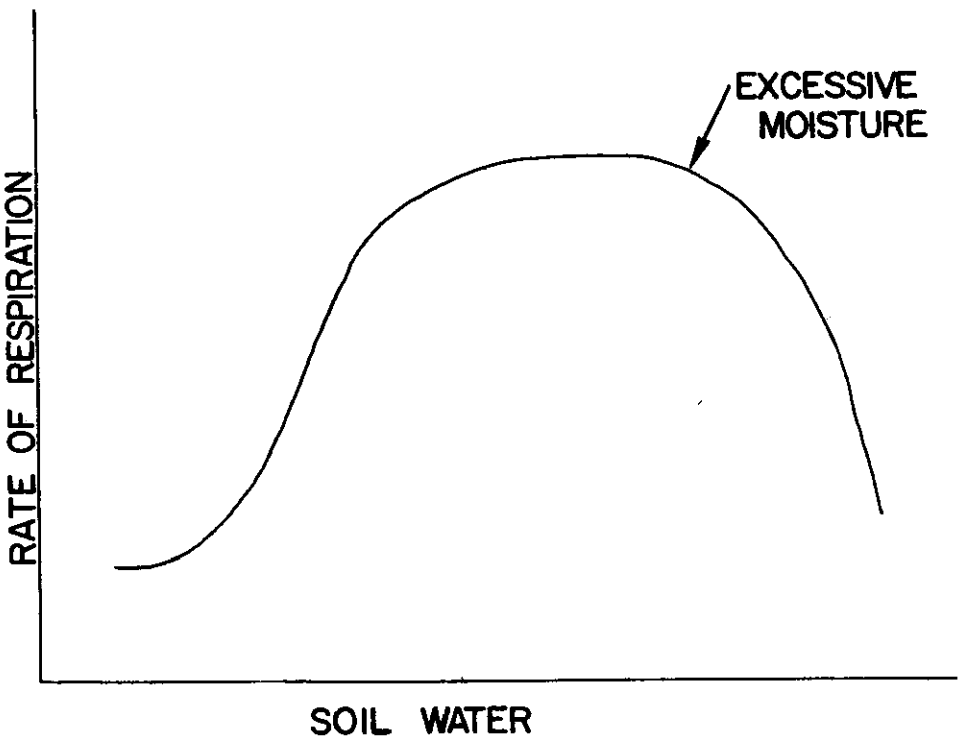

Fig. 4.16. Relation of root respiration to soil water.

addition to root respiration). Lundegårdh (1921) recorded a rapid rise in the rate of soil respiration up to 60°C, and in a later study he cited soil respiration data which followed a Q_{10} of approximately 2 between 10° and 20°C (Lundegårdh, 1927). Koepf (1953) reported a Q_{10} of about 2 between 10° and 40°C, the value decreasing sharply at higher temperatures. At temperatures of 0°C or below, soil respiration has been reported to be very low or comes to a virtual standstill (Féher and Sommer, 1928). However, it may be pointed out that even if the temperature of the surface soil is near or at 0°C, the subsoil may be warm enough to permit considerable root respiration.

Bunt and Rovira (1954) found increased oxygen uptake and carbon dioxide evolution with increasing temperatures above 50°C. These authors rightly attributed this increased activity at higher temperatures to chemical oxidation in soil.

Wiant (1967*b*) found almost a logarithmic increase in CO_2 production from soils under white pine, spruce, hemlock, and oak between 20° and 40°C, following a Q_{10} of about 2 (Fig. 4.17). At 50°C and above, CO_2 production declined markedly.

Berry and Norris (1949) reported interesting interaction between temperature and oxygen concentrations (Fig. 4.18). These authors found that the highest rate of respiration in onion root tips was not attained until 50% oxygen was supplied, and at lower values the occurrence of high respiratory quotient values indicated anaerobic respiration. At 15° and 20°C, the roots were oxygen saturated at 20% oxygen. However, at any given oxygen concentration, rate of respiration increased up to 30°C, with a little decline at 35°C.

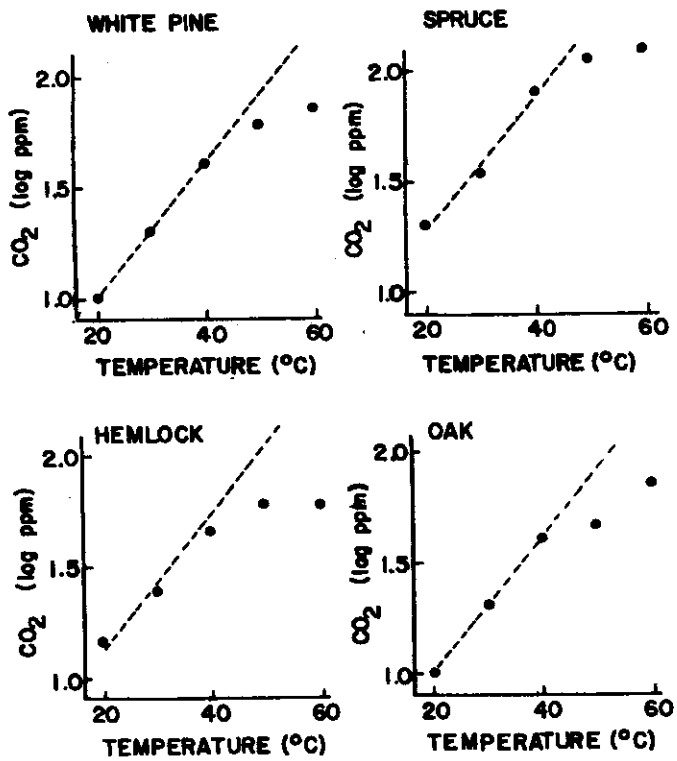

Fig. 4.17. Log of carbon dioxide production for soil samples at various temperatures. The broken line represents a Q of 2.0 (after Wiant, 1967*b*).

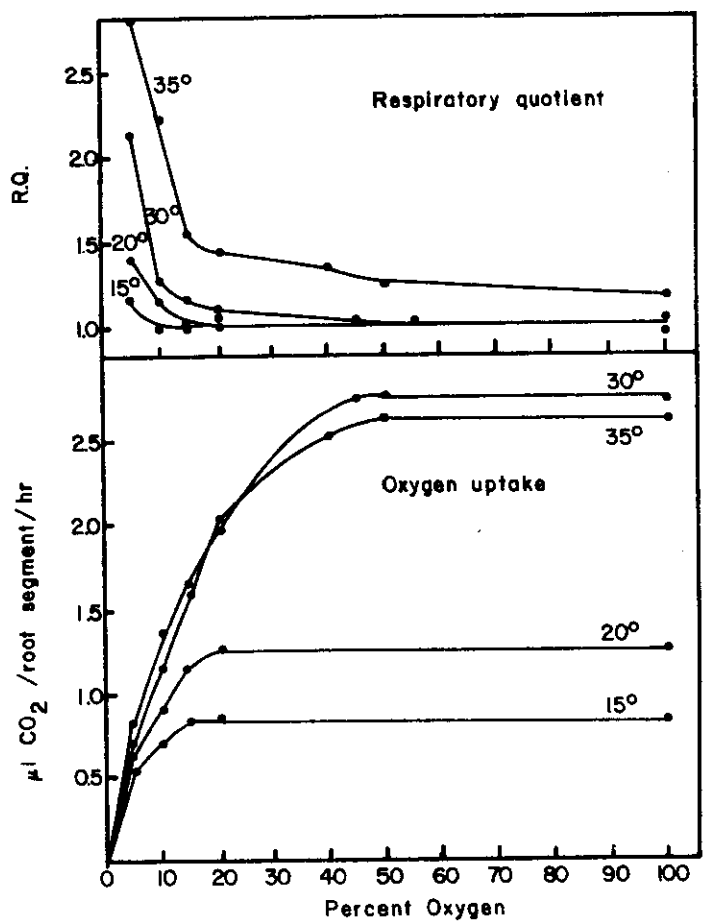

Fig. 4.18. The influence of temperature and oxygen concentration on the respiration of onion root tips. The apical segment (0 to 5 mm) was cut from 2-day-old roots for manometric measurements of oxygen uptake and carbon dioxide production (Berry and Norris, 1949); after Yemm (1965).

The influence of temperature may also be related to the sucrose content of storage organs. Working with "King Edward" potatoes, Barker (1936) reported an increase in total sugar from .2% (fresh weight) at 10°C to 6.7% at -1°C. At 10°C sucrose is about one-fifth of the total sugar, at -1°C it is about one-third, and at +1°C it represents one-half to two-thirds of the total sugar. Rate of respiration showed a hyperbolic relation to the concentration of sucrose (Fig. 4.19). The inset in this figure shows a direct relation between the reciprocals of respiration and sucrose concentration.

Oxygen and carbon dioxide concentration. Harris and van Bavel (1957) raised tobacco plants in sand and flushed various gases through the cultures. The rates of root respiration measured under different aeration treatments are given in Table 4.3. The results illustrate the inhibitory influence of the increase in CO_2 relative to oxygen concentration in the root atmosphere. Since maximum CO_2 production is obtained during the active growth period (McKinley, 1931) and since root growth in many species (e.g., tomato, tobacco, soybean) ceases at .5% oxygen concentration and increases until the ambient level of O_2 concentration is reached (Hopkins, Specht, and Hendricks, 1950), it may be fair to assume at or below .5% O_2 in soil atmosphere that root respiration will be reduced to near zero. Interaction of O_2 concentration and temperature has already been discussed.

The concentrations of oxygen and carbon dioxide in the soil atmosphere vary throughout the year. Two examples of this seasonal variation are presented in Fig. 4.20 and 4.21 (Furr and Aldrich, 1943; Boynton and Compton, 1944, respectively).

Time of the day. Harris and van Bavel (1957) measured the root respiration of tobacco, corn, and cotton plants at different times in the day.

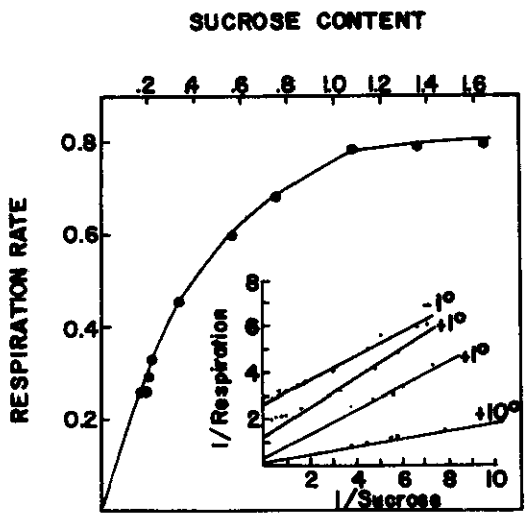

Fig. 4.19. The relation between respiration rate and sucrose content of "King Edward" potato tubers during sweetening at -1°C. *Inset*: The reciprocal of respiration rate plotted against the reciprocal of the sugar concentration in potatoes sweetening at -1°C and +1°C, and desweetening at 10°C. For the sake of clarity, the top graph has been raised by two units and the second graph by one unit (Barker, 1936); after Forward (1965).

Table 4.3. Root respiration of tobacco plants as affected by the composition of root atmosphere.

Treatment			CO_2/g root/24 hr (mg)
N_2 (%)	O_2 (%)	CO_2 (%)	
80	20	0	397
80	15	5	408
80	10	10	387
80	5	15	287
80	0	20	83

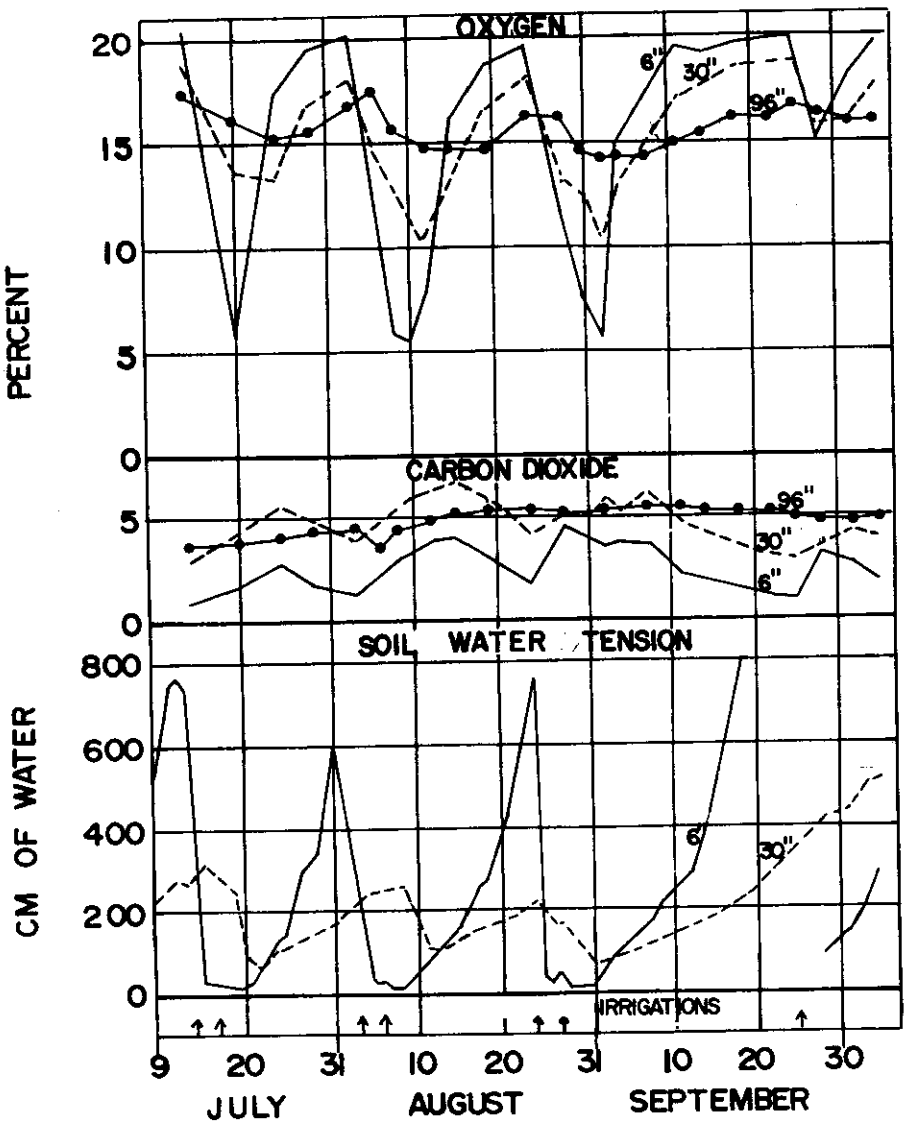

Fig. 4.20. The percentages of oxygen and carbon dioxide in soil-air samples from depths of 0.30 and 96 inches, and the soil water tension at depths of 6 and 30 inches in an infrequently irrigated plot (after Furr and Aldrich, 1943).

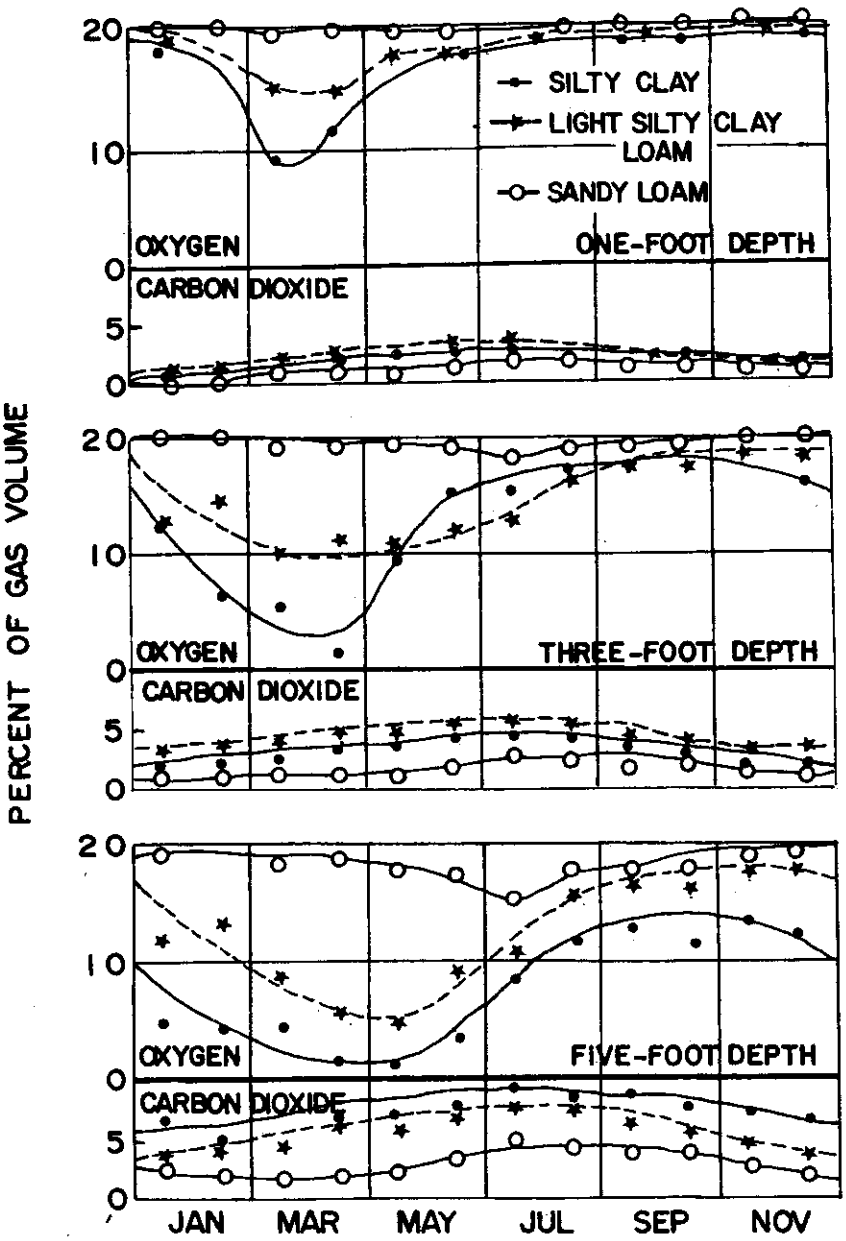

Fig. 4.21. Normal seasonal changes of oxygen and carbon dioxide percentages in gas from different depths in a silty clay, a light silty clay loam, and a sandy loam subsoil (after Boynton and Compton, 1944).

They found the maximum rate of respiration was reached regularly at 4 PM and the minimum between 2 and 10 AM (Fig. 4.22). This, however, may be a response to the variation in temperature.

Nutrient status of the soil. There are many studies reporting a higher rate of respiration for plants grown on a high nitrogen nutrient level. Nishikawa (1956) found that rice seedlings grown on a high N level showed higher respiration rates than those grown on a low N level. However, there seems to be no report for the influence of nitrogen on the respiration of roots alone.

4.4.3.2 Experimental methodology. Coleman (1973) has attempted to separate root respiration from total soil respiration, and Singh and Coleman (1972) have outlined the scope of the problem as given in this section.

Fig. 4.9 depicts the major processes involved in the maintenance and turnover of this huge belowground carbon reserve. A part of the carbon assimilated through photosynthesis is transferred belowground for the new growth of roots and storage. This is the ultimate source of input. From the roots, carbon is lost through respiration, death, and decay. The exudates and dead roots provide input to soil organic matter and ultimately lose carbon as carbon dioxide through microbial decomposition. A certain amount of carbon is translocated out from the root reserve as initial input for regrowth of aboveground plant parts. The turnover rate of carbon in subterranean parts is governed by the processes (303-593 [Fig. 4.2]), (303-513), and (513-303), and the turnover of soil organic matter is governed by the rate of processes (303-513), (513-303), and microbial respiration of detached soil organic matter. Although the processes described above and represented diagrammatically in Fig. 4.9 are well

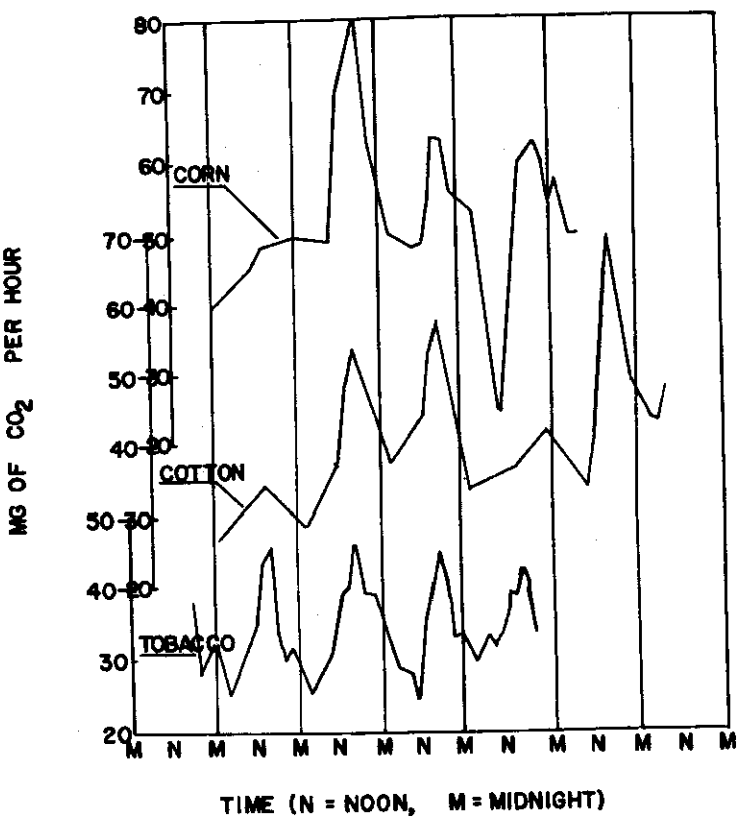

Fig. 4.22. Daily fluctuations in the carbon dioxide released by the roots of corn, cotton, and tobacco plants expressed in milligrams of CO_2 per hour: November 4 to 20 for tobacco, February 8 to March 12 for corn, February 28 to March 5 for cotton. Note that at the lowest rate for tobacco, pots were irrigated with a freshly prepared batch of nutrient solution which was 10°F cooler than the temperature of the greenhouse. Respiration was probably reduced by the cooling effect (after Harris and van Bavel, 1957).

recognized, information on transfer parameters and residence time of carbon in different compartments of the plant-soil system is generally wanting. Attention has either been focused on the global carbon dioxide cycle (Revelle and Suess, 1956; Plass, 1955; Moller, 1963; Revelle, 1965) or on turnover of soil organic matter (Russell, 1964; Jenkinson, 1966). Individual studies on soil respiration have helped in getting some idea of total soil metabolism (MacFadyen, 1970; Odum, 1971) although it has not been possible to partition the carbon output into that originating from root respiration or soil-fauna respiration and that originating from microbial respiration. Clark and Coleman (1972) recently tried to partition the CO_2 evolved due to root respiration and CO_2 output due to microbial action for a grassland ecosystem with some success.

Information on the rate, magnitude, and period of accumulation of carbon in belowground parts and release of this carbon to soil and ultimately to air as CO_2 is also scanty. Field evaluations through harvest of root systems suffer from a lack of information on periods of greatest root growth and mortality (Dahlman and Kucera, 1965; Sims and Singh, 1971). Stucky (1941) and Brown (1943) observed active root development during the early growing season followed by disintegration and decomposition later in the summer. Dahlman and Kucera (1969) reported a similar trend for a tallgrass prairie using ^{14}C. Bartos (1971), on the other hand, working on a shortgrass prairie at the Pawnee Site, hypothesized active root growth during the middle of the growing season preceded by active decomposition.

In an elaborate study using ^{14}C, Dahlman and Kucera (1969) have determined that the root system in a tallgrass prairie undergoes an average

turnover approximately once every 4 years, and maximum transfer of radiocarbon from roots to the soil occurs during late summer of the year, following incorporation by the roots. But nowhere in the literature is any information available on approximate short-term decay rate of the root system from which daily decay rate could be extrapolated.

Recent studies by Samtsevich (1965) have indicated a significant amount of organic matter deposited in soil as root exudates. He calculated an input of about 350 g/m^2 in a winter wheat crop and claimed it would be higher for perennial grasses.

The use of litter bags for studying decomposition of litter has become very popular in recent years (Crossley and Hoglund, 1962). Modification of this technique for root material employing labeled roots will perhaps yield reliable parameter values.

Two major approaches have been used in the determination of root respiration: (i) measurement of total CO_2 evolution (soil respiration) or oxygen uptake by the soil and estimation of the contribution of roots to this quantity and (ii) measurement of the respiration of intact roots or sections of roots under standardized laboratory conditions, i.e., direct measurement of the root respiration.

4.4.3.3 Soil respiration. "The soil respiration is the total of all soil processes in which carbon dioxide is produced" (Lundegårdh, 1927). It includes three biological processes, viz, microbial respiration, soil-fauna respiration, and root respiration, and one non-biological process, viz, chemical oxidation which is particularly pronounced at high temperatures (Bunt and Rovira, 1954).

Principal methods used by different workers for measuring soil respiration are summarized below:

Laboratory measurements.

1. The soil sample, undisturbed as far as possible, is collected, brought to the laboratory, and its CO_2 content is evaluated (Leather, 1915).
2. The soil sample is incubated for varying periods of time with sufficient moisture in air-tight flasks at constant temperature(s); the CO_2 produced is then drawn in and absorbed in a suitable alkali (Lundegårdh, 1922).
3. Carbon dioxide-free air is passed over the soil sample contained in a flask, and the CO_2 evolved by the sample is measured by alkali absorption (Stoklasa and Ernest, 1905; Waksman and Starkey, 1924).
4. Marsh (1928) modified the preceding method in such a way as to pass the air through the soil as well as over it.
5. Wiant (1967*a*) used essentially the same method, but the CO_2 was evaluated with the help of an infrared gas analyzer, and the sample jars and a copper coil for incoming air were placed in a controlled temperature bath. The air was moved across the samples at a rate of 1 liter/min.
6. Chase and Gray (1957) used a Warburg respirometer for evaluation of the respiratory activity of soil samples.

Field measurements.

1. The "enrichment" method involves an isolation chamber set out on the surface of the soil for a definite period of time. Then a

sample of air enriched in CO_2 is removed from it, and the CO_2 content of the sample is determined (Lundegårdh, 1927).

2. Lundegårdh (1927) also used a brass tube to extract air from desired soil depth and analyzed it for CO_2 concentration.
3. Wallis and Wilde (1957) extracted air from the soil through glass funnels or metal cylinders with the help of a battery-operated pump, trapping the CO_2 in a normal solution of sodium hydroxide. The quantity of CO_2 extracted from the soil at different intervals provides an estimate of CO_2 production.
4. Russell and Appleyard (1915) and Bizzell and Lyon (1918) collected samples of air from the drainage tubes at the bottoms of large lysimeter tanks and the CO_2 was absorbed in an alkali. Repeated observations at different time intervals yielded the estimate of CO_2 production.
5. The "air current" method is air drawn from the outside through an isolation chamber, covering a fixed area of soil continuously at a definite rate. The CO_2 is determined quantitatively in the air coming from the chamber (Humfeld, 1930).
6. The "foil" method involves circular discs of aluminium foil pressed and molded on the soil surface with an intake tube in the center. A control flow is mounted above the foil so that by the use of a valve the CO_2 can be monitored from under the foil and above the foil in alternating sequences, the difference being the contribution of the soil under these conditions (Odum et al., 1970).
7. Odum et al. (1970) improved the isolation chamber air current method by installing a hot-wire anemometer within the chamber.

By doing so, they were able to control the speed of airflow within the chamber equal to that outside.

8. The "absorption" method is an alkali solution of known strength placed into a vessel, immediately before beginning the determination, inside the isolation chamber to absorb the CO_2 evolved for a definite period of time (Lundegårdh, 1921). Lieth and Ouellette (1962) and Monteith, Szeicz, and Yabuki (1964) used the same method with slight modifications.
9. A major improvement in the above method was suggested by Witkamp (1963, 1966*a*). He used open-ended cylinders which could be left in the soil for long periods in order that the effects of disturbance might be reduced. These cylinders were then capped by an airtight cover for a short while (an hour or two) during which CO_2 derived from the soil is absorbed in alkali and its quantity is estimated by titration. Crapo and Coleman (1972) also used this method.

4.4.3.4 Partitioning of soil respiration attempts at estimating root respiration. Lundegårdh (1927) compared the CO_2 production from bare soil with that from the same soil covered with oats and reported that root respiration forms about 30% of the total soil respiration.

Russell and Appleyard (1915) and Bizzell and Lyon (1918) used lysimeter tanks to grow different crop plants and compared the CO_2 production from cropped soil and bare soil. The difference gives an estimate of root respiration.

Wiant (1967*b*) used paired plots measuring 50 cm on each side. From one of the plots of each pair, all visible roots to a depth of 30 cm were

extracted. The other plot served as control. A bottomless quart can was inserted 2 cm into the soil in each plot, and air was drawn by the air-current method. Carbon dioxide was analyzed using an infrared gas analyzer. This method yielded an estimate of root respiration as 50% of the total soil respiration.

Witkamp and Frank (1969) tried to partition CO_2 evolution from litter, humus, and mineral soil and assessed the contribution of root respiration by relating root distribution to CO_2 production in the profile. Air was drawn at a rate of ~1 cm/min from just above the forest floor through each of six clear plastic boxes (36 × 20 cm, 15 cm high) and was analyzed for CO_2 in an infrared gas analyzer. Two channels drew surface air; two boxes contained litter only; two boxes contained litter and humus; two boxes had their bottoms cut out so as to receive CO_2 evolving from the entire profile. All layers inside the boxes retained their natural position and depth. The boxes were sunk into the floor so that their litter was level with the outside litter. They estimated contribution of roots to be 50% of the total soil respiration.

Odum et al. (1970) used plastic bags to wrap exposed surface roots of a number of rain forest components, with air entering one side and being drawn out the other side into the gas analyzer. These rates together with the amount of root biomass were used to compute total soil respiration.

Odum and Jordan (1970) used "giant plastic cylinders" to measure the metabolism of the forest floor. These authors estimated the contribution of roots to the total forest floor respiration by subtracting from the latter the rates of log-, fruit-, and leaf-fall.

The estimates of soil respiration obtained through the isolation chamber, the enrichment method, or the absorption method suffer from the fact that the values do not represent actual CO_2 production. Smith and Brown (1931, 1932) have illustrated that "soil respiration is not a simple diffusion of carbon dioxide through the soil and evolution at the surface but that it is also a function of the diffusion velocity, adsorption, utilization, solution, and combination." The laboratory methods and air-current methods summarized above again suffer from modification of temperature and other physical factors. As far as assessing the contribution of roots to the total soil respiration is concerned, the value of 50% is often accepted (MacFadyen, 1970) and the other 50% is attributed to microbial respiration, although Fehér (1933) stated that the contribution of roots is often negligible while Turpin (1920) attributed more than 66% of total soil respiration to roots. However, under relatively dry conditions when the top soil gets considerably drier than the subsoil, roots may be contributing substantially more than 50% because under such conditions microbial respiration will be greatly reduced for the want of moisture, while roots will be receiving their moisture supply from deeper layers.

4.4.3.5 Direct measurement of root respiration. Three major types of experiments are recorded in the literature:

1. One experiment used intact roots. Harris and van Bavel (1957) grew tobacco, corn, and cotton plants in pots containing quartz sand. These pots were completely sealed from the atmosphere, and different gas mixtures were passed through the medium. Composition of incoming and outgoing gasses was determined by CO_2 meters as well as alkali absorption. Since the plants are grown in sand cultures, the rates of root respiration

obtained may not be comparable to those growing in natural conditions. Seedlings of corn raised in plant culture units, which were sealed to exclude plant tops, absorbed the CO_2 produced by roots alone in sodium hydroxide (Crapo and Bowmer, submitted). These experiments were conducted at constant temperatures as well as in a growth chamber simulating spring conditions. Measurements were made from intact as well as decapitated plants. The authors, however, could not estimate the respiration rate on a unit, dry weight basis because of the difficulty in removing the sand particles from the roots.

2. Crapo and Coleman (1972) obtained root samples for respiration studies by digging up clumps of *Andropogon* and gently shaking off the soil. Roots were kept in plastic bags to retard desiccation while transporting the samples to the laboratory. Carbon dioxide evolution was determined 1 hr to 2 hr after samples were taken for 20 to 24 hr. Respiration rates were measured at a constant temperature of 20°C by alkali absorption. Roots were then dried to a constant weight at 100°C. Clark and Coleman (1972) measured total soil respiration from intact soil cores, separated the roots, rhizomes (crowns), and soil, and measured the CO_2 production by each component. The sum total of respiration of these components by far exceeded the respiration of the intact soil core. Evidently, disturbance stimulates the rate.

3. Thin sections of various lengths of roots have been used for specific experiments under standardized laboratory conditions, depending upon the objective of the experiments. Such experiments have been extensively reviewed in physiology texts (Yemm, 1965; Forward, 1965), but the

rates obtained can hardly be said to be representative of rates under natural conditions.

In Table 4.4 a sample of values reported for total soil respiration for various habitats is given. Contribution of roots has also been calculated on the basis of 50% value.

The following estimates indicate the variation in root respiration obtained on a dry weight basis for different species.

Author	Species	mg CO_2/g/day
Harris and van Bavel (1957)	Tobacco	210 to 400
	Cotton	488
	Corn	197
Crapo and Coleman (1972)	*Andropogon*	2 to 11.5

Clark and Coleman (1972) measured respiration of rhizomes (crowns) and roots collected from the grassland at the Pawnee Site in August and September and obtained the following estimates:

Part of Plant	August	September
	(mg CO_2/g/day)	
Rhizomes (crowns)	4.73	7.27
Roots	1.38	2.92

Clark and Coleman have also calculated the percentage contribution of crowns, roots, and soil to total soil for the top 2.5 cm of profile as below:

Table 4.4. Estimates of soil respiration and the contribution of roots in various habitats (g $C/m^2/hr$).

Author	Habitat	Soil Respiration	Root Respiration
Lundegårdh (1927)	Forest	.351 to .702	.75 to .351
	Forest	.66	.33
	Swamp	.084	.042
	Meadow	.099	.049
Humfeld (1930)	Soybean field	.15	.075
	Soybean field	.16	.080
	Cornfield	.17	.085
	Cornfield	.18	.09
Walter and Haber (1957)	Temperate soil	.03 to .11	.015 to .055
Medina (1966)	Venezuelan soil		
Wallis and Wilde (1957)	Oak forest	2.33 to 1.38	1.16 to .69
	Pine forest	1.11 to 1.08	0.55 to .52
	Grassland	2.64 to 1.83	1.32 to .91
	Birch	.936	.468
Golley, Odum, and Wilson (1962)	Luquillo forest	.24	.12
Voigt (1962)	Forest	.04 to .20	.02 to .1
Reiners (1968)	Minnesota forest	0 to .28	0 to .14
Witkamp (1966*b*)	Pine forest	1×10^{-3} to 1.2×10^{-3}	5×10^{-4} to 6×10^{-4}
	Oak forest	1×10^{-3} to 1.3×10^{-3}	5×10^{-4} to 6.5×10^{-4}
	Maple forest	1.2×10^{-3} to 1.3×10^{-3}	5×10^{-4} to 6.5×10^{-4}
Witkamp and Frank (1969)	Forest floor	.01	.005
Clark and Coleman (1972)	Grassland	.012 to .18	.006 to .09
Odum and Jordan (1970)	Rain forest		.36
Odum et al. (1970)	Rain forest		.34

Month	Percent Contribution to Total		
	Crowns	Roots	Soil
August	60.2	12.3	27.5
September	62.8	7.7	29.5

Regarding CO_2 production depthwise, data collected at the Pawnee Site (Clark and Coleman, 1972) indicate that three-fourths of the daily rate of CO_2 evolution is accounted for by the top 5 cm of soil profile. The 5- to 10-cm segment of the profile yielded an additional 10% of daily output, leaving 15% to be accounted for by deeper layers. However, removal of the top 5 cm or top 20 cm of the profile in a dry soil had only negligible effect (about 10%) on CO_2 production.

From the foregoing, it would be apparent that data reported in literature can hardly be used for inclusion in a model for a shortgrass prairie ecosystem. The best line of approach for obtaining reliable and realistic transfer parameter values seems to be in the use of ^{14}C.

Bartos (1971) and Bartos and Jameson (1972) have shown that roots are simultaneously undergoing accumulative and loss processes. The total of these processes as indicated by the data shows root growth beyond the probable downward translocation from the tops. If the total root flux does exceed the downward translocation, processes other than translocation and respiration are of major importance; at the present time, we have no clear idea what these processes may be, but they are being investigated to some degree (Christensen, personal communication).

Thus with the necessary addition of belowground biomass, we immediately reach what appears to be an impasse in techniques. It appears quite obvious that this area should receive a major emphasis before proceeding further. Paradoxically, however, considerable investigation has been done in more detailed areas, especially photosynthesis, and these will be briefly sketched in the next section.

4.4.4 Labile, Non-labile Compounds

During the course of the process workshop it became apparent that a complete treatment of the producer compartments should encompass a view of labile vs. non-labile compounds. Only the labile compounds are available for most of the reactions of sections 4.4.1, 4.4.2, and 4.4.3. The non-labile compounds are generally subject only to decomposition. The following discussion on this problem was prepared by M. J. Trlica and M. Y. Buwai.

4.4.4.1 Review of literature. Despite the importance of this area, literature is generally lacking for grassland vegetation. There has been considerable work, however, on carbohydrate reserves or the more readily available carbohydrates in various storage organs within perennial vegetation. Several studies have been conducted to determine how the various parameters affect carbohydrate reserves in storage organs, but there have been relatively few studies which have not only addressed themselves to the labile or readily available carbohydrates but also concerned themselves with the non-labile or structural carbohydrates.

In this section, pertinent literature is reviewed concerning the status of carbohydrates within various organs of the plant and factors which influence change of status of carbohydrates. Labile carbohydrates

include the simple sugars as glucose and fructose, oligosaccharides, and polysaccharides such as fructosans and starches. Non-labile carbohydrates will include the structural carbohydrates such as the larger chained polysaccharides, cellulose, lignin, hemicellulose, and pentosans. Although the labile carbohydrates are not truly mobile carbohydrates, they can be considered as a readily available source of energy for either plant functioning, herbivory, or decomposition. Units of measurement include grams of carbon in the various forms of carbohydrates, or grams of various fractions of the carbohydrates. Outputs would also be in grams of carbon or grams of carbon for the changed status of carbohydrate.

Numerous studies have shown that carbohydrate reserves or readily available carbohydrates are affected by stage of phenology, grazing, and other biotic and abiotic factors of the environment. In general, most of these studies have shown that carbohydrate reserves follow a U- or V-shaped curve throughout an annual cycle. However, most of these studies have not concerned themselves with the non-labile carbohydrate fractions simultaneously. In general, the carbohydrate reserve cycle is at the low point during early or rapid growth in the spring and attains the highest level of reserves during maturity or quiescence. Researchers have pointed out that carbohydrate reserves in the storage organs appear to be inversely related to growth rate of aboveground organs. They have also indicated that these reserves are used as a substrate of energy in times of stress; i.e., carbohydrate reserves located in storage organs are used to initiate new growth following defoliation, drought, burning, etc. However, this assumption has not been shown to be correct in all instances. Few studies to date have been made which have utilized radioactive carbon and have

traced carbon in storage organs to the new growth following the stress situation.

The readily available carbohydrate fraction in plants usually varies from approximately 25% to near 1 to 5% of the total carbohydrates within the plant. In contrast, the structural carbohydrates (cellulose, hemicellulose, lignin, and pentosans) may comprise the bulk of the carbohydrates within the various plant organs. It does appear, however, that the readily available or labile carbohydrates vary more in nature than do the structural carbohydrates.

Sullivan and Sprague (1949) showed that carbohydrates in perennial ryegrass stubble were affected by temperature. It appeared that the structural carbohydrates, such as cellulose, pentosan, and lignin, were higher under the warmer temperatures than under cooler temperatures. In contrast, the nonstructural or labile carbohydrates such as sucrose and fructosan were higher under the cooler temperatures. Sullivan and Sprague's (1943) data showed that the carbohydrate fractions also varied with stage of growth. Again, the labile components such as glucose, fructose, and sucrose were less than 5% whereas lignin, pentosan, and cellulose components ranged from above 10% to about 35% of the carbohydrate fraction. Sullivan and Sprague's (1943) data showed that little change in the structural carbohydrate roots of ryegrass were found if plants were put in either a light or dark environment. However, under the darkness environment, total soluble carbohydrates decreased to nearly 0%, whereas there was an increase in total soluble carbohydrates under the lighted environment. New data did indicate that both the labile and non-labile components were more affected by light and darkness in stubble of perennial ryegrass.

Burton, Jackson, and Knox (1959) showed that not only did light affect the status of carbohydrates in herbage of grasses but also the fertility level affected the labile and non-labile components within herbage of coastal Bermuda grass. The total available carbohydrates (TAC) were reduced by high applications of nitrogen fertilization.

Fructosans and sucrose content in roots and stubble of orchard grass were shown by Sullivan and Sprague (1953) to be influenced by rate of nitrogen fertilization. They found that all treatments of nitrogen fertilization decreased fructosans and sucrose after hay cutting.

Adegbola and McKell (1966) studied the effects of nitrogen fertilization on reducing sugars and sucrose contents of leaves, stems, stolons, rhizomes, and roots of coastal Bermuda grass (*Cynodon dactylon*). They found that heavier rates of nitrogen fertilization caused increases in reducing sugars within the leaves of coastal Bermuda grass, but had less influence on reducing sugars in stems, rhizomes, stolons, and roots. However, sucrose content of all these organs was generally highest in plants receiving no additional nitrogen. Nitrogen fertilization had less effect on fructosans in leaves, stems, and stolons, but had more of an effect on fructosan content of rhizomes and roots. Green and Beard (1969) found that increasing rates of nitrogen fertilization had little effect on sucrose, glucose, and fructose content in leaves of several grasses. However, oligosaccharides were decreased by increasing rates of nitrogen fertilization.

Norman (1937) showed that cellulose and lignin increased in herbage of ryegrass during the growing season, whereas fructose contents decreased in the herbage. However, McCarty (1935) found hemicellulose in herbage changed

very little during the course of the growing season, and the readily available carbohydrates tended to increase slightly during the growing season. He noted only small changes in both labile and non-labile carbohydrates in root and stem bases of *Elymus ambiguus* and *Muhlenbergia gracilis* during the course of the growing season. Neither of the studies included data throughout the yearly cycle for any of the plant organs studied.

Total carbohydrates in alfalfa roots were found by Leukel (1927) to be higher than total carbohydrates in aboveground plant organs. Labile carbohydrates increased in roots during May, June, and July, whereas they decreased in aboveground plant organs during the same period.

Ruelke and Smith (1956) showed that total available carbohydrates decreased from November through March in various species of clover. It appeared that decreases in total available carbohydrates during this period were closely associated with decreases in starch content during the same period. Hemicellulose components remained relatively constant throughout the sampling period. Bailey (1964), however, found that hemicellulose and cellulose did vary from May through October in herbage of white clover. Again, neither of these studies indicated carbohydrate fractions in various plant organs over a yearly cycle.

Several studies have indicated that the structural carbohydrates such as lignin, cellulose, hemicellulose, and pentosans tend to increase with intensity or frequency of grazing (Cook and Harris, 1968). As grazing becomes more extensive, these structural carbohydrates are bound to increase in diets of grazing herbivores, unless the grazing stimulates renewed growth activity of the plants. Cook and Harris (1952) found that lignin content of

foraging sheep's diets increased with advanced stages of phenological development of cheatgrass (*Bromus tectorum*). However, he observed little increase in lignin, cellulose, and other carbohydrates in sheep's diets of crested wheatgrass (*Agropyron cristatum*) over the same time period.

Hyder and Sneva (1959) found that removing the reproductive structures of crested wheatgrass increased the total available carbohydrates within the roots.

McIlvanie (1942) studied the total labile carbohydrates in roots of bluebunch wheatgrass (*Agropyron spicatum*) throughout an annual growth cycle. His study indicated that total labile carbohydrates were not very well correlated with changes in reducing sugars, sucrose, and reserve polysaccharides. His study pointed out the difficulties in correlating total labile carbohydrates with any of the various labile carbohydrate fractions. Therefore, it may be to some advantage to study all the labile fractions as one component rather than study a single labile fraction, such as one of the reducing sugars, and use this as an indicator for all labile carbohydrates.

McCarty and Price (1942) studied the effects of intensity and frequency of clipping a wheatgrass (*Agropyron elongatum*). He found that the various carbohydrate fractions, labile and non-labile, were more influenced by season of defoliation than by intensity of defoliation. It appeared that the hemicellulose fraction increased under clipping treatments, whereas the labile carbohydrates decreased in roots and stem bases under the various clipping treatments.

Changes in carbohydrate fractions in stems, leaves, and whole plants of lucerne were studied by Hirst, Mackenzie, and Wylam (1959). Their

studies showed that stems were consistently higher in total hexose than either leaves or whole plants, that leaves were lower in sucrose but higher in glucosans, and that leaves were consistently lower in cellulose and lignin than stems. Glucose and fructose were generally higher in stems than in leaves. Flowers were higher in glucose, and seeds were highest in fructose and sucrose. There was little difference between years except at the end of one season when plants became almost void of hexose.

Benedict and Brown (1944) studied the effects of nitrogen on various carbohydrate fractions of *Agropyron smithii* and *Bouteloua gracilis*. They found that top growth was higher in starch in the minus nitrogen treatment, while roots were higher in starch in the plus nitrogen treatment. Hemicellulose showed little variation between dates and treatments. Greatest increase in sucrose occurred in roots, while that for starch occurred in tops. Between harvesting dates, roots of plants in minus nitrogen solution showed greatest decreases in sucrose.

From the literature review of the various carbohydrate fractions located in labile and non-labile pools, it can clearly be seen that although research results are available for perennial and other grassland vegetation, it is truly fragmentary. Very few studies have included the various plant organs such as stems, leaves, roots, and storage organs throughout a yearly cycle. Although we do have the knowledge and the methodology for determining various carbohydrate fractions, it appears that very few studies have been done to date on these various carbohydrates within the plant system.

4.5 CONCLUSIONS

Major aboveground transfers of plant material can be accounted for with rather simple procedures as outlined in the elementary approach. Accounting of major belowground processes, however, is a formidable obstacle. A simple matter of priorities would indicate that the elementary approach be used on aboveground plant parts until the ability to handle the belowground processes has been brought into line. Science in general has not demonstrated an ability to progress other than incrementally, and we have no reason to expect to do so in this case.

It does appear, however, that filling the gaps with the elementary approach will not be a very time-consuming nor expensive endeavor, and we should be prepared to move into more comprehensive approaches. The processes outlined in the latter part of this chapter suggest promising avenues for this comprehensive research.

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CHAPTER 5. DECOMPOSER SUBSYSTEM

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5.1 ABSTRACT

The decomposer subsystem is responsible for the major portion of mineralization processes which occur in grasslands, and the biomass in this ecosystem is found predominantly below the soil surface. The model of these processes depicts the flow of organic materials from primary production and herbivore activities to the decomposers. Materials which become available for use by the decomposers include a range of intermediary substrates which are produced by both abiotic and biotic processes. Once these intermediate substrates are available, the decomposers transform them to mineralized products subject to a series of abiotic and biotic controls.

To a certain degree, the approach follows that of the producer section. The initial section describes carbon dioxide evolution. The CO_2 arises from decomposition, which is treated in two sections. An elementary section describes procedures which can be utilized in elucidating some of the overall characteristics of the subsystem. A more comprehensive section describes viewpoints which will allow a more in depth approach to the decomposer area. In general, the elementary approach utilizes the concept of simple approximations to substrate changes; the comprehensive approach uses a more detailed look at individual substrates.

5.2 CARBON DIOXIDE EVOLUTION[1/]

Soil respiration has long been an index of biological activity in the soil (Boussingault and Levy, 1853; Möller, 1879; Wollny, 1831). Although measurements of either CO_2 evolution or O_2 consumption are relatively inexpensive and simple, CO_2 evolution is usually the measurement of choice for characterizing the total biological activity of the soil. Organisms having active decarboxylases can liberate CO_2 without concomitant uptake of O_2. In anaerobic microsites, CO_2 is liberated without O_2 being consumed. Other conditions variously affect both CO_2 and O_2 values. Even in completely aerobic environments, the respiratory quotient (RQ) varies with the C/O ratio of the substrate, the environmental conditions, and the types of organisms involved. Nonbiological production of CO_2 or consumption of O_2 may occur because of chemical decarboxylation, chemical oxidation, or by the release of gases by soil materials or the soil solution.

Nevertheless, measurements of soil respiration are widely accepted as being the most productive approach for studying biological activity and the carbon and energy flows within the soil. The diverse array of technical journals concerned with plant ecology and soil science quite regularly carry contributions concerning soil respiration. Over the years, many hundreds of references have accumulated; however, no attempt will be made to review the extensive literature at this time. Literature prior to the last decade has been nicely reviewed by Domsch (1962). Numerous additional papers have appeared in the last decade (e.g., Crapo and Coleman, 1972; Ino and Monsi, 1969; Kucera and Kirkham, 1971; Lieth and Ouellette, 1962; Van Cleave and Sprague, 1971; Wiant, 1967*a*,*b*; Witkamp and Frank, 1969). The flows under

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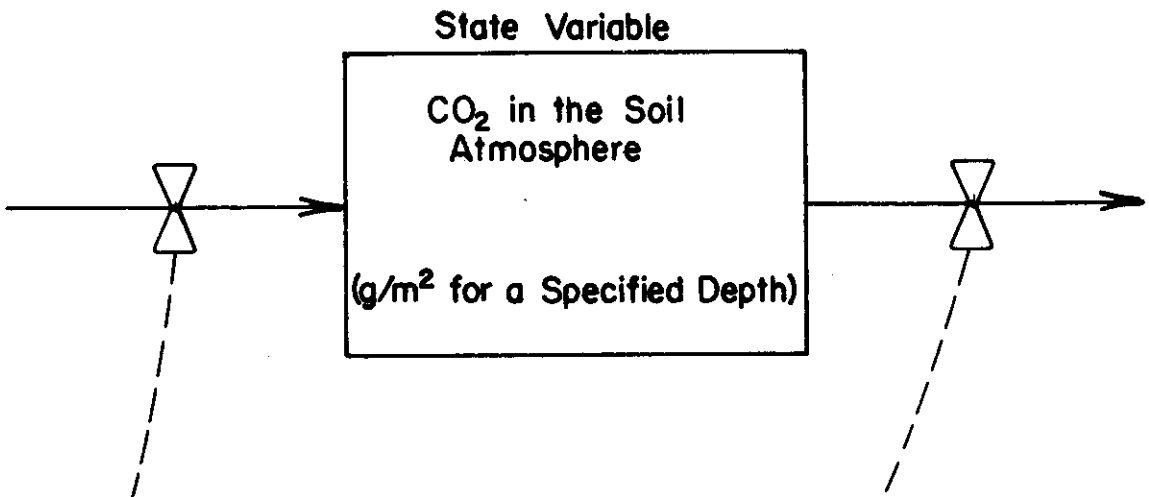
[1/] This section was prepared by Francis E. Clark.

consideration are (593, 598-302) and (302-593, 598). These flows are actually the results of several flows which are summarized in Fig. 5.1. In the foregoing, flow 593-598 represents the CO_2 contents of six separate depths of the soil profile, and 302 represents the local CO_2 content in the atmosphere immediately above the soil surface (see Fig. 4.1). The depth and relative profile positions of 593 through 598 are shown in Fig. 5.2.

The problem in the narrowest sense is simply to take known inputs of CO_2 arising from the respiratory activities of the soil biota and plant roots, together with releases from abiotic sources, and to describe the movement of this CO_2 to the soil surface. The problem is primarily one of soil physics and not of soil biology. Fig. 5.1 lists some processes that affect the movement of CO_2 within and from the soil atmosphere. Diffusion and pressure gradient flows are abiotic phenomena, and so are those concerning the release of CO_2 from the soil matrix or the soil solution. Reassimilation of gaseous CO_2 into the living tissues of organisms is a biological process, but one which, in heterotrophs, does not approach the magnitude of their respiratory output of CO_2. In the chemotrophs at population densities commonly occurring in soil, CO_2 assimilation, even though it is the sole cellular carbon source, is sufficiently negligible that it can be ignored.

The process of gaseous diffusion in soil is subject to many controls. Fortunately, the basic equation is already known (Crank, 1956). It is Fick's first law of diffusion and is based on the hypothesis that the rate of transfer of a diffusing substance through a unit area section is proportional to the concentration gradient measured normal to the section. It is usually written



Examples of rate processes controlling inputs:

Live root respiration.

Soil biota respiration (includes all subterranean decomposers and feeders).

Abiotic releases of CO_2 from storage compartments (soil solution, buffers, etc.)

Examples of rate processes controlling outputs:

Gaseous diffusion to the epigeal atmosphere.

Pressure gradient flows from the soil pores.

Reassimilation of CO_2 into living tissue.

Abiotic fixations.

Fig. 5.1. Basic representation of CO_2 state variable in soil and processes affecting inputs and outputs of CO_2.

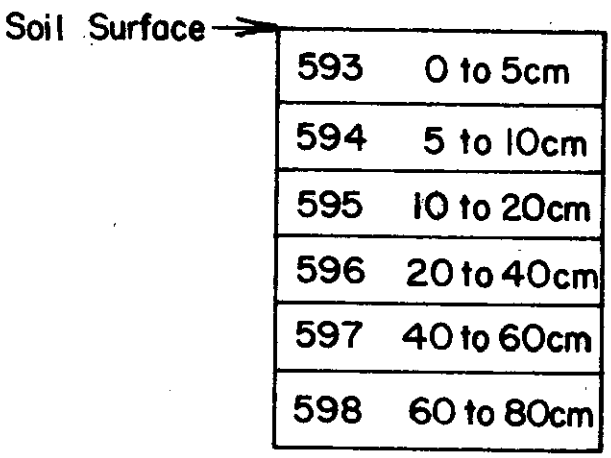


Fig. 5.2. Profile depths for the state variables 593 through 598.

$$F = -D \frac{\partial C}{\partial X} \qquad (5.1)$$

where

F = the rate of transfer per unit area of section

C = the concentration of the diffusing substance

X = the space coordinate measured normal to the section

D = the diffusion coefficient

Obviously in order to solve for F in the field soil system, the diffusion coefficient or at least some reasonable approximation thereof must be determined. The diffusion coefficient is highly dependent on soil porosity, structure, aggregate size, and soil water.

Investigations of gaseous diffusions in soil usually have used oxygen as the experimental gas (Lemon and Erickson, 1952; Penman, 1940; Poel, 1960; Raney, 1950; Taylor and Abrahams, 1953; Taylor, 1950), and much of the concern has been with proper techniques of measurement. Nevertheless, certain generalizations have emerged. Diffusion rates show significant correlations with soil water, aggregate size, and soil depth. Exemplification can be made from data of Lemon and Erickson (1952) as reproduced in Fig. 5.3 and 5.4. The dashed curves in Fig. 5.4 show the relationship between diffusion rate and porosity at each depth for three different aggregate sizes. Above a porosity of 20%, the curves approach linearity, while below 20% there is a rapid drop in rate with decreasing porosity. Penman (1940) and Taylor (1950) have also shown that diffusion is a linear function of porosity in the normal range of porosities found in soil. Raney (1950) found that below 22% porosity, there was a curvilinear relationship, possibly due to the closing of the connecting channels between pores. Smith and Brown (1933)

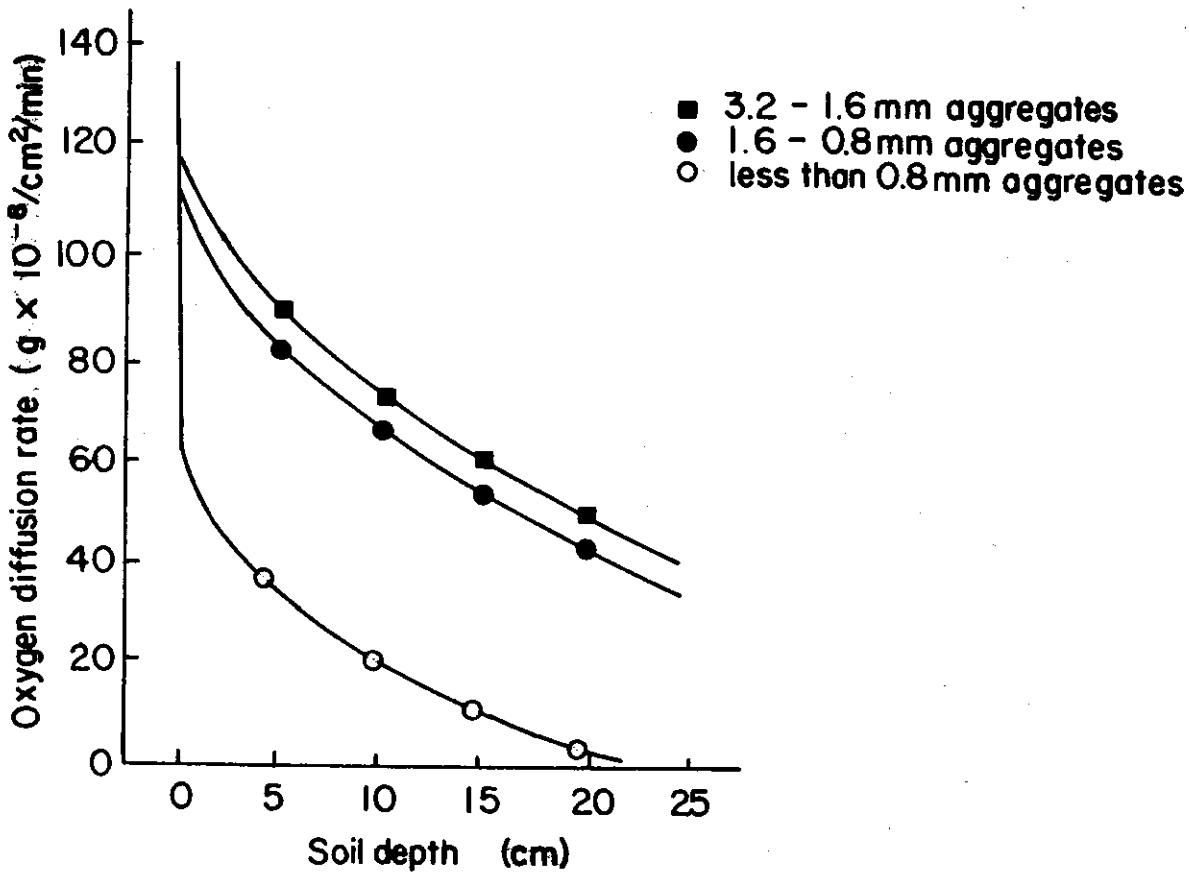


Fig. 5.3. Relation between soil depth and oxygen diffusion. (Redrawn from Lemon and Erickson, 1952).

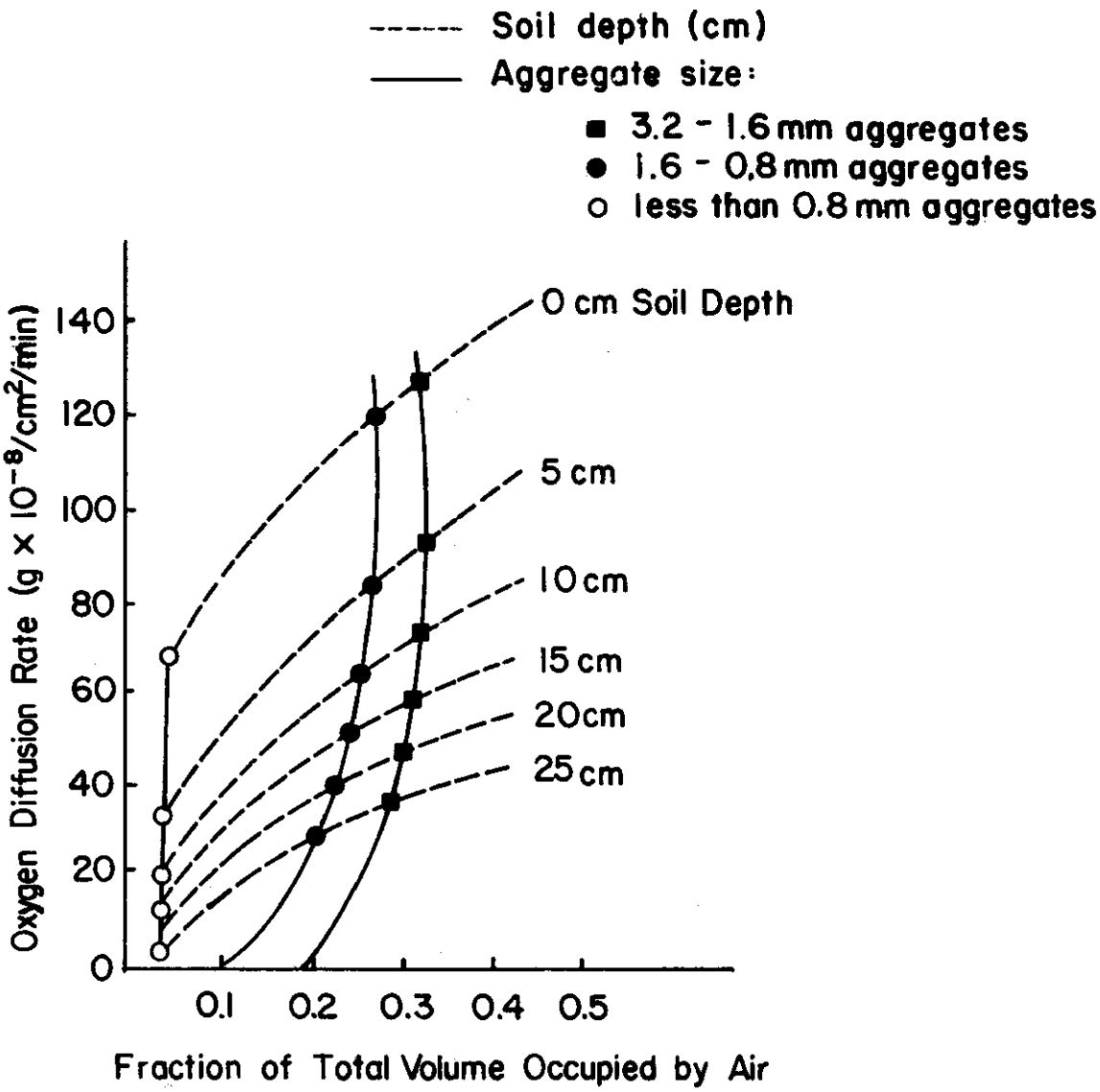


Fig. 5.4. Relation between porosity and oxygen diffusion as affected by soil depth and aggregate size. (Redrawn from Lemon and Erickson, 1952).

found the regression equation for the correlation between rates of diffusion and porosity to be

$$D \times 10^7 = 2.297 \times \text{porosity} + 1.402 \qquad (5.2)$$

The regression coefficient indicated an average increase of 2.297×10^{-9} cm^3 of CO_2 for each percent increase in pore space.

The influence of soil water on diffusion can be expected to be pronounced inasmuch as thickness of moisture films directly affects pore size and the continuity of channels between pores. There is extensive literature on relationships between soil water and the amounts of CO_2 evolved from soil, but such outflow information involves not only rates of diffusion but also the rate of production in soil. Quite frequently, increased soil water has meant more favorable conditions for microbial activity, and total CO_2 output has gone up despite the fact that conditions for gaseous diffusion have become less favorable.

Another complicating factor is that of storage of CO_2 in the profile, and this is still further confounded by the air fluxes that occur with barometric changes. Respiratory CO_2 formed in the soil does not necessarily diffuse uniformly toward the surface. It diffuses from high to low concentration. If there is a high rate of production of CO_2 in the upper profile and less respiratory activity deeper, then CO_2 diffuses downward as well as upward. This leads to temporary storage of CO_2 in the deeper profile. At such times, measuring CO_2 evolution at the soil surface does not accurately reflect the rate of CO_2 production in the soil. Later, as the soil respiration activity slows, the concentration of CO_2 in the deeper profile exceeds that in the upper profile, and diffusion upward occurs. At such times, measurement

of CO_2 output at the surface overestimates the actual rate of CO_2 production in the soil. This storage problem is complicated by changes in barometric pressure. A rising barometer causes downward airflow into the soil, while a falling barometer accelerates release of gases from the soil.

Fig. 5.5 illustrates the extent to which CO_2 concentrations vary in the soil profile during a growing season. There is much information of this type on record for various soils but not for soils currently being studied in the Grassland Biome program.

The above presentation has been more in the nature of a reconnaissance than an in depth survey of the topic of soil respiration. Even so, certain points are quite evident. There is a wealth of information in the literature that should provide the mathematical formulae needed for modeling. There needs to be a laborious gleaning of the literature for pertinent information, and this should be done by a mathematician, preferably by someone qualified in modeling and also in physics.

Once the general framework or first approximations are established, there undoubtedly will be a need for certain additional information on the Grassland Biome soils currently under study. Although some porosity and bulk density data may already be available on these soils, it is probable that further experimental work will be needed in order to define the diffusion coefficients for a range of soil water values at differing depths of the soil profile. Inasmuch as CO_2 production occurs simultaneously with diffusion processes in the soil, the modeling of soil respiration must also deal with the input or respiration processes as well. Further work involving field measurements of soil respiration will need to be undertaken.

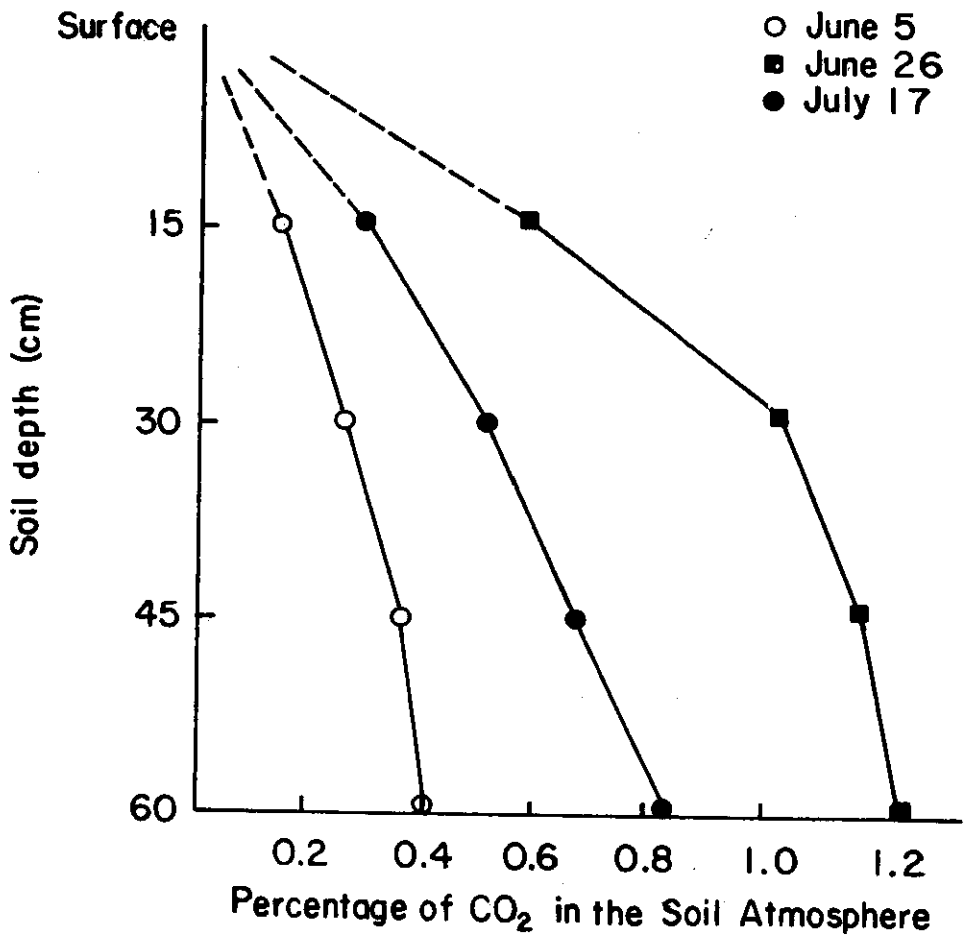


Fig. 5.5. CO_2 percentages in the soil atmosphere at four profile depths on three dates of sampling.

Contents of CO_2 in the soil atmosphere at various profile depths will also need to be determined. Such measurements can provide meaningful validation data for modeling the flows (593, 598-302). The experimental approach might involve establishment of capillary-type access tubes into successive depths of the soil profile, collection of soil air samples by means of hypodermic syringes, and determination of CO_2 contents in the samples by means of gas chromatography.

Finally, since it can be assumed that at least half of the respired carbon dioxide arises from carbon compounds in the dead root compartment, more information will be needed on root turnover and organic matter decomposition. Isotopic studies in this area should prove fruitful.

5.3 DECOMPOSITION: AN ELEMENTARY APPROACH[2/]

This section provides a statement of dead root decay (flow 513-520) and decay of other organic material. Expected decay rates of these materials are presented. Both sources yield CO_2 as a major product, and the evolution of CO_2 from the soil to the atmosphere is discussed.

Dead roots serve as a major source of ephemeral organic carbon within the soil. Ideally, this category should include such short-lived components as root hairs and the mucilaginous root caps on sheaths. Accurate estimation of input from these two categories is very scarce. Samtsevich (1965) calculated an input of 350 g/m^2 in a winter wheat crop and claimed it would be higher for perennial grasses.

There is considerable variability in decay between species, and younger roots with the lower C:N ratios decay faster than old ones (Weaver,

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2/ This section was inserted by the editors to indicate the possibilities for some simpler studies. It does not necessarily represent the views of either of the authors nor other microbiologists.

1947; Dahlman and Kucera, 1965). Weaver found 45% survival of *Bouteloua gracilis* roots after 3 years. Dahlman and Kucera measured approximately 25% replacement of entire root mass on Missouri tallgrass prairie (per annum), but Bartos (1972) has estimated that these values are too low. Weaver (1947) found 33% of killed roots lost compared to live roots. Thus, dead root structural tissue inputs are at least 25% per year, and much of the rise and fall occurs in the spring-summer-early fall 6- to 8-month period.

The root decomposition process is influenced by root mass, soil temperature, soil water, and root age. The major outputs of this process are carbon dioxide and secondary decomposition products. The root decomposition process can be represented as shown in Fig. 5.6.

Root decomposition is donor-controlled because a certain percentage is lost each year. Root mass fluctuations over the growing season are shown in Fig. 5.7. The concurrent growth and decomposition processes must be considered; if the difference between minimum and maximum values are assumed to be due to decomposition alone, the rate will be greatly underestimated.

Soil temperature is a limiting factor for root decomposition. There is a certain range over which dead roots decompose, and if these extremes are exceeded then decomposition ceases.

Soil water plays an important role in root decomposition since decomposers are more active under moist conditions (Pilat, 1969). Rodin and Bazilevich (1967) indicate that during dry years the decomposition process is much slower and there may be more root mass during dry years than in wet years.

Age of roots are important in this root decomposition process. Young roots decompose more rapidly than older roots (Fig. 5.8). Studies have shown that grass roots live no longer than 5 years, and most live less than 2 years.

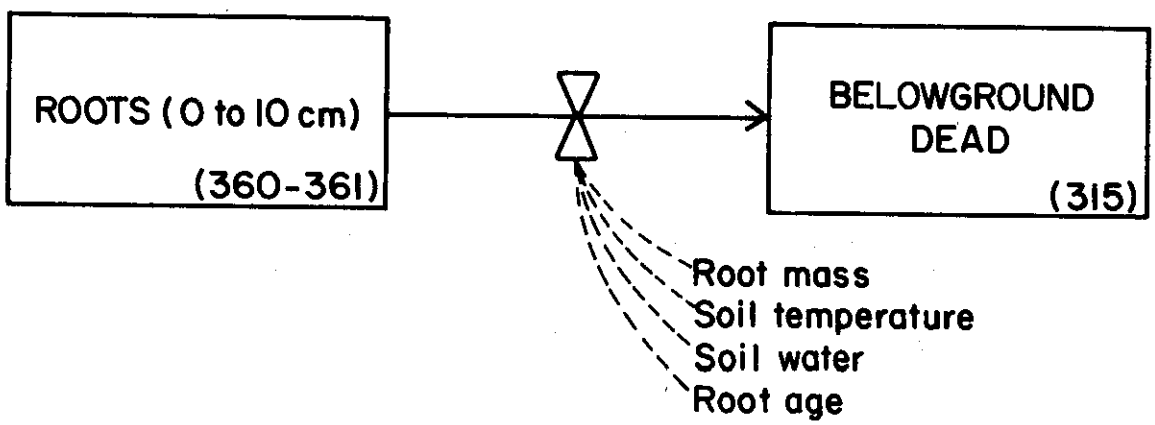

Fig. 5.6. Basic root decomposition model and control variables.

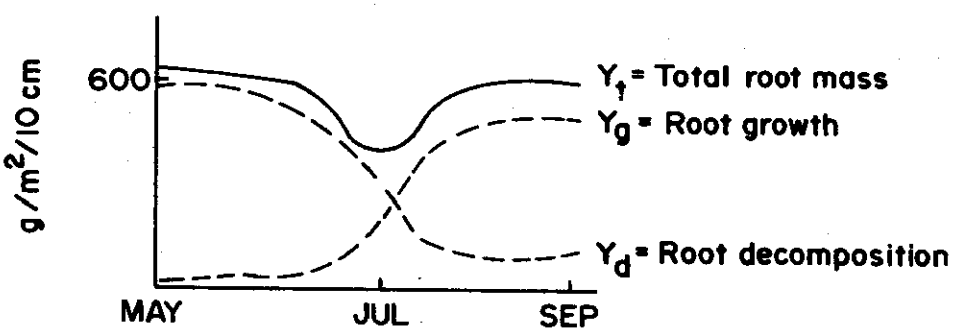

Fig. 5.7. Time curve of root growth and decomposition (from Bartos, 1972).

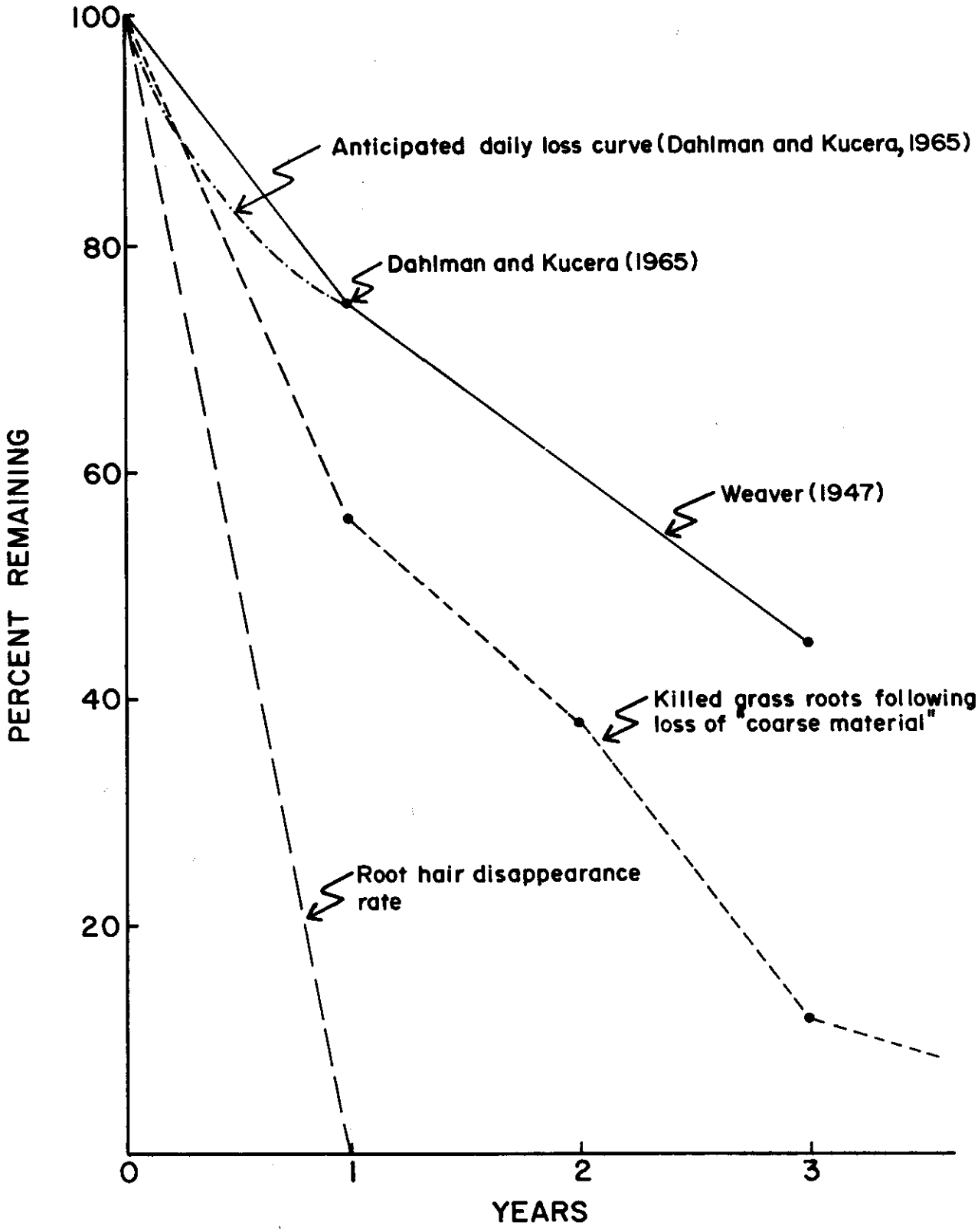

Fig. 5.8. Root decomposition rates.

Weaver (1947) worked with decomposition of blue grama roots and reported root losses of 67% in 2 years. Earlier, Weaver and Zink (1946) used a banding technique to determine the length of time that roots lived. After three growing seasons, only 45% of the blue grama roots were alive. Stoddart (1935) found that grass roots live at least 1 year, and many live in excess of 2 years.

Other substrates for decomposition come from the dead remains of bacteria, fungi, and small invertebrates which are constantly being deposited. In addition, a small percent of the total organic matter is microbial polysaccharide in origin. The relative amounts of these various materials are largely unknown, but the microbial portion is undoubtedly much larger. Thus, fungal filaments are left for secondary decomposers (various bacteria) when they die, so that the chitin and other structural polysaccharides are, in turn, broken down. Bacteria, estimated to turn over only a few times per year, may amount to from 400 to 800 kg/ha dry weight. This converts to 40 to 80 g/m^2, which may turn over four to five times per year. Thus, it is an important fraction of biomass when compared with any other biomass category.

The bulk of various substrates goes directly into CO_2, but a small percent of decomposition, via microbial living mass, proceeds to convert substrates into humic compounds. Important components are carbohydrate by-products of microbial reactions. The decomposition of these products is controlled by soil water and temperature as is the case for root decomposition changing substrate composition caused by both different decay rates and recombination into more resistant compounds.

Much of the literature on decomposition of substrates in the grassland has been reviewed by Clark and Paul (1970). Relative rates of various

substrates are shown in Fig. 5.9. These individual substrates supposedly could be aggregated into a total decomposition picture. Resynthesis into humic compounds must be considered; however, neglect of resynthesis into more sensitive compounds results in overall decomposition rates which are not consistent with field results (Clark and Paul, 1970).

Thus, substrate, soil water, and temperature are relevant variables in a decomposition study. Nyhan (1972) investigated these effects in the laboratory and found reasonable agreement with field results. In Nyhan's work, time was used as a surrogate variable for substrate composition changes; more resistant compounds were more predominant in later stages of decomposition and thus decomposition rates slowed. The soil water effect was independent of time and temperature effects (Fig. 5.10), i.e., the same shape to the response curve held for the various times and temperature conditions in the study. Temperature effects, on the other hand, were different at different times in the study (Fig. 5.10 and 5.11). Thus, it can be expected that a study of decomposition as a function of temperature includes the differential rates from various substrates, but all of the substrates in Nyhan's study apparently reacted in much the same way to soil water changes.

Although the only environmental factors included in Nyhan's study were soil water and temperature, he was able to account for over 85% of the sample variance. The difficult question appears to be an appropriate exponent of substrate composition. Nyhan (1972) used the surrogate of time. Martel and Paul (1970) devised an equation which was the sum of four exponents to express substrate change. Anway et al. (1972) used the sum of two exponents and achieved satisfactory results. A simplified view of substrate composition and dynamics similar to those mentioned is necessary for the elementary approach to be used; otherwise, the more comprehensive approach of section 5.4 will be required.

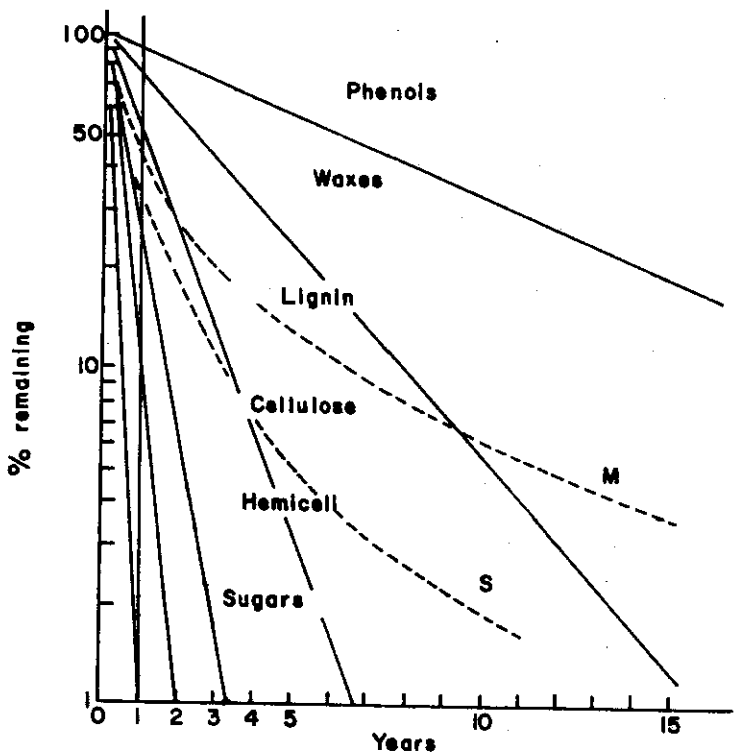

Fig. 5.9. The decomposition curves of various groups of constituents if their decomposition could be represented by a logarithmic function (the straight lines from the point 100%). The line S shows the summation curve obtained by annual summation of the residual values of the separate components. The line M gives an approximation, based on some analyses, of the probable course of the decomposition in the moor-type at Hackfort (from Minderman, 1968).

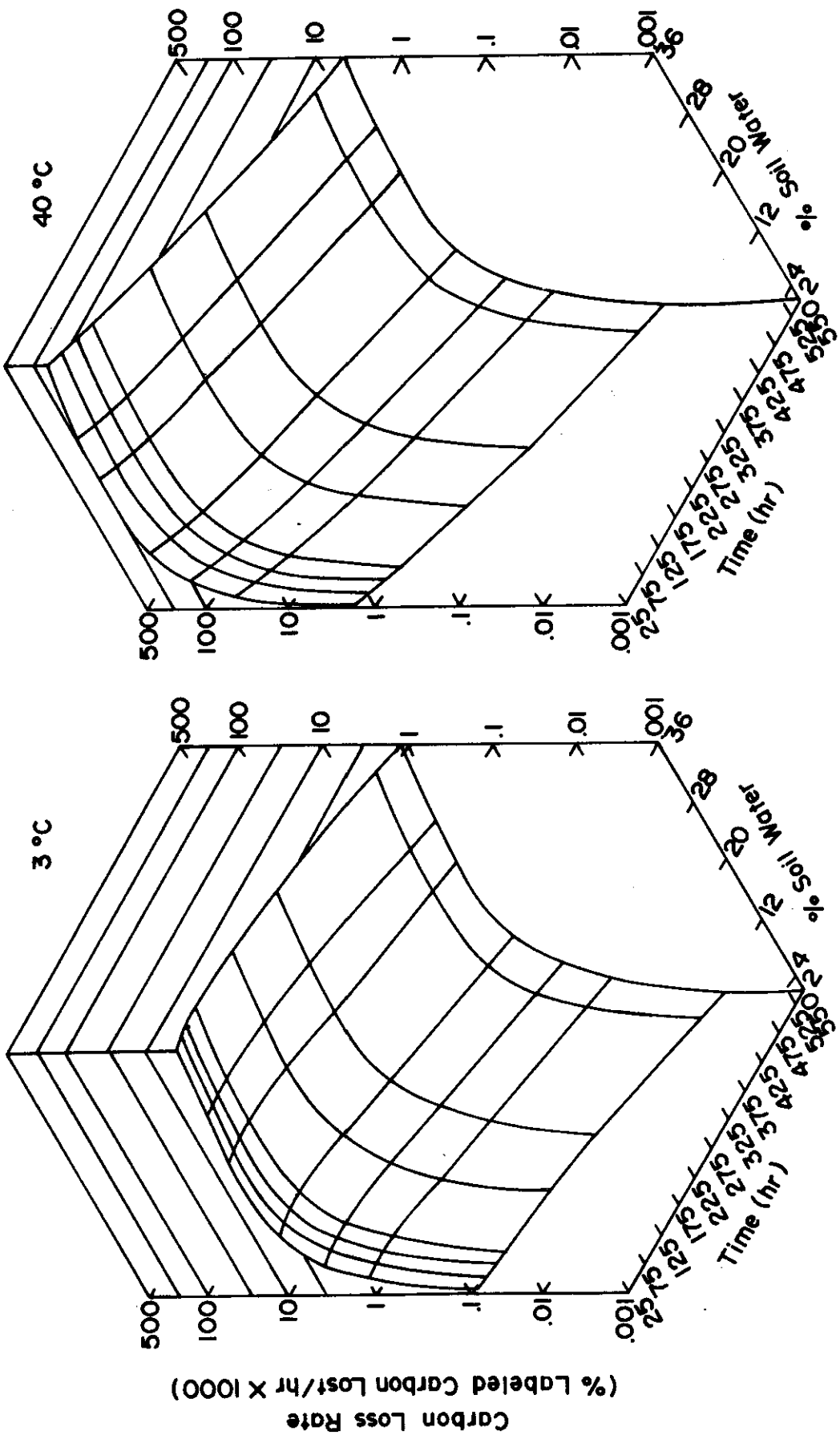

Fig. 5.10. Relationship of carbon loss rate of blue grama to percent water and time for soil incubated at 3°C and 40°C in the laboratory (from Nyhan, 1972).

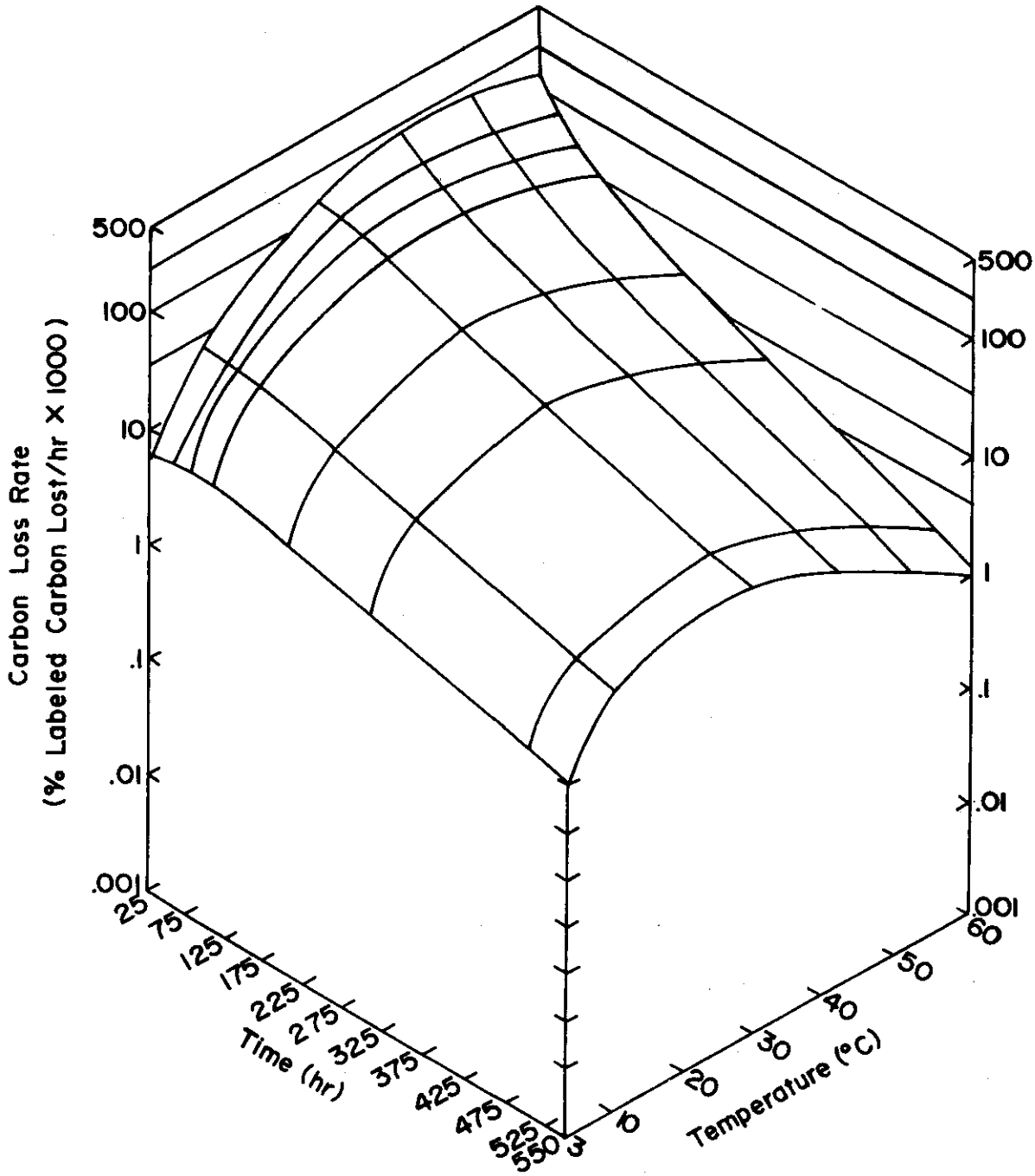

Fig. 5.11. Relationship of carbon loss rate of blue grama to temperature and time for soil incubated in the laboratory at 10% water content (from Nyhan, 1972).

5.4 A COMPREHENSIVE APPROACH[3/]

If a more detailed view of the substrates is desired than the approximations used in section 5.3, a diagram as given in Fig. 5.12 and 5.13 for aboveground and belowground portions, respectively, can be used. The division between aboveground and belowground systems has been placed at the point where plant material is or is not in intimate contact with humus or soil mineral components. This division reflects the observation that microbial biomass and decomposable plant and animal remains, which are above the soil surface, will be more subject to varied temperature and drying effects than those below the surface. These latter effects can inhibit microbial decomposition processes on the surface more readily than similar processes in a more stable temperature and moisture environment in the soil profile.

The role of moisture events in transportation of plant and animal soluble remains (leachates) to the belowground portions of the model must also be recognized. Thus the major portion of decomposer activity and biomass can be expected to function in conjunction with the belowground portion of the model.

The belowground decomposer model (Fig. 5.13) presents the major concepts which were developed in the workshop. Organic matter that is potentially available to the microorganisms can be placed in four major compartments: (i) litter-mulch (318,540), which has become an integral portion of the soil; (ii) humic compounds (532), which are available as a carbon source on a limited basis; (iii) animal excrement and residues (615); and (iv) dead

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3/ This section was prepared by Donald A. Klein.

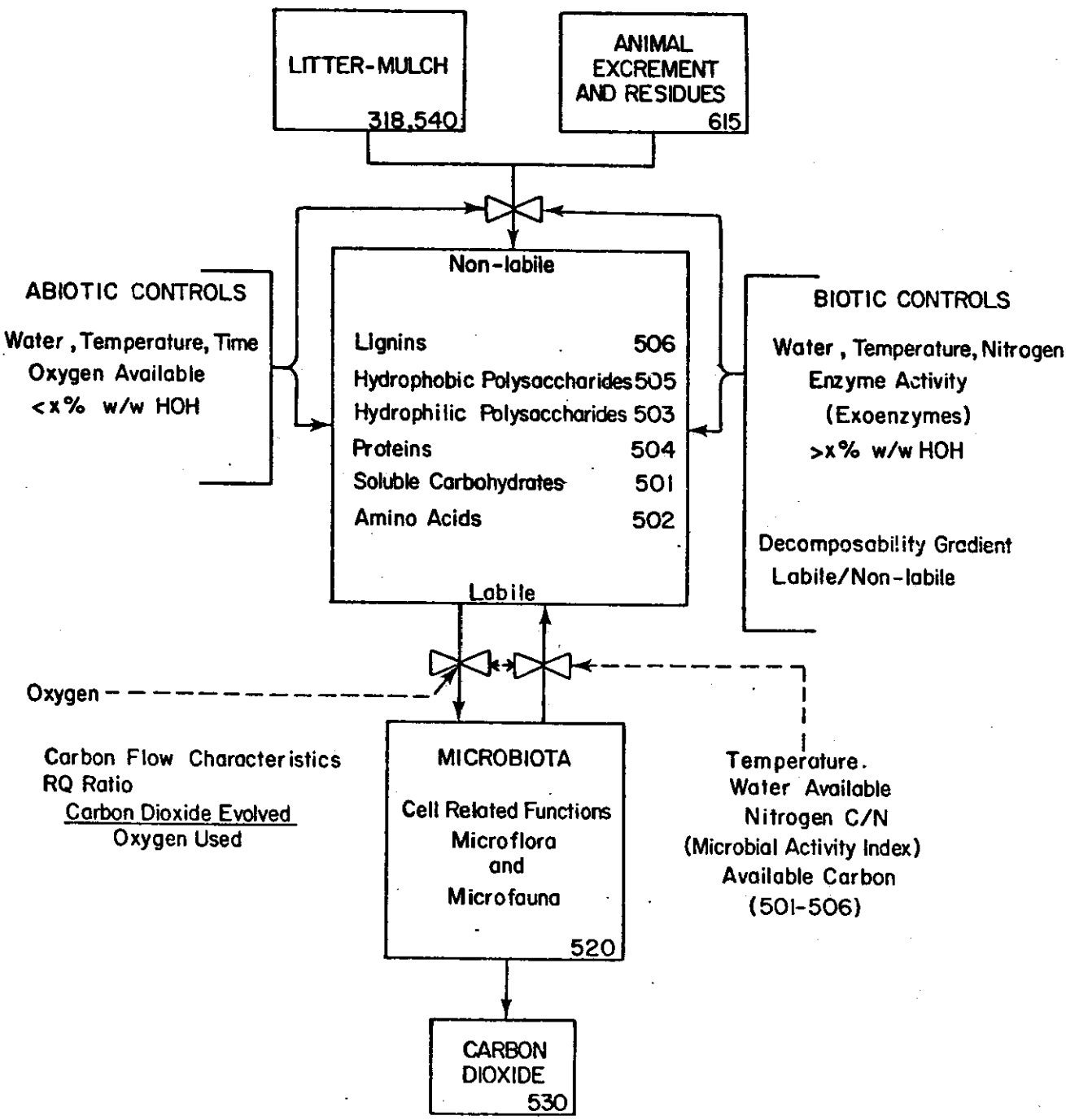


Fig. 5.12. Decomposer subsystem (aboveground model).

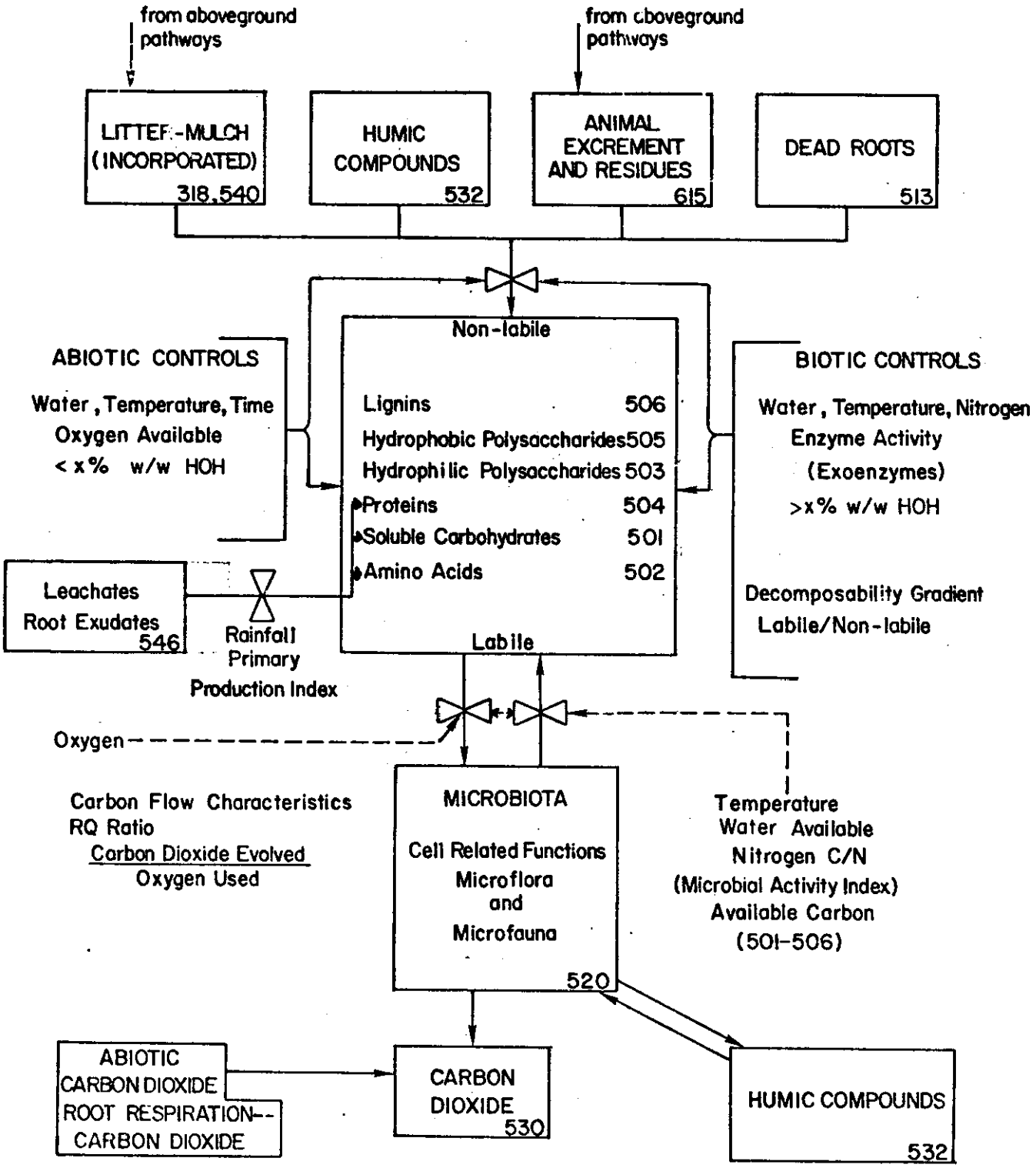


Fig. 5.13. Decomposer subsystem (belowground model).

roots (513). These last two are available both during the active plant growth phase and following the spring and early summer primary production activity.

Flows of carbon from these substrate pools are guided by both biotic and abiotic processes and result in the accumulation of compounds of varying availability as microbial substrates, such as labile types (soluble carbohydrates 501, amino acids 502, and proteins 504) and more non-labile components (hydrophilic polysaccharides 503, hydrophobic polysaccharides 505, and lignin materials 506).

Flows between the original substrates and the individual components are considered to be governed by biotic and abiotic controls. The biotic controls are based on the presence and activity of hydrolytic exoenzymes which are produced by the microbes and which can function independently of the microbes in the release of substrate constituents for microbial use. This enzymatic hydrolysis is a progressive process with initial attack resulting in the exposure of long-chained polymers such as starch (hydrophilic polysaccharide), cellulose (hydrophobic polysaccharide), and lignins. Only with subsequent exoenzyme activity which results in the liberation of soluble carbohydrates, amino acids, and aromatic substrate constituents are the materials in a soluble form that can be utilized by microorganisms. These processes, once the enzymes have been formed, do not require active microbial respiration. As these hydrolytic enzymes function only at suitable temperature and water levels in the soil environment, the model has been developed to predict that, below certain temperature and moisture limits, rates of hydrolytic activity will be decreased, resulting in a cessation of carbon transfer from original substrate boxes to the intermediary pools and from less to more labile forms within this group of intermediary materials.

Assuming plant photosynthesis, translocation, and respiration processes are active, root exudates (540) will be released directly to the labile carbon compound intermediary pool and become available for direct microbial utilization under proper moisture and temperature conditions. Certain plant leachate materials derived from the aboveground portion of the model are also available for microbial action.

In addition to enzymatic processes for release of carbon compounds for microbial use, the model also depicts the role of abiotic controls for release of substrate carbon to the soluble carbohydrate (501) and amino acid (502) pools under drying conditions in the soil system. These abiotic nutrient release steps are postulated to occur under conditions where soil water levels have decreased below a given level (<x% w/w water). Drying allows oxygen penetration in the soil system, resulting in a catalytic oxidative release of utilizable fragments. This process also has a time function to depict the progressive increase of substrate availability with time under a given set of dry conditions.

With a rainfall event, oxygen penetration will begin to be limited and the flow of nutrients through the system will shift to the biotic-enzymatic-basal processes, and the microbiota (520) which are capable of dissimilating the substrates to microbial cells (520), carbon dioxide (530), and humic compounds (532) will be able to function. The microbial compartment (520) functions are controlled by temperature and moisture variables as abiotic factors. In addition, the primary nutrient controlling activity is the amount of available carbon from the boxes 501 through 506, assuming the abiotic conditions are conducive for microbial activity. Nitrogen is not assumed to be limiting, up to a certain specific carbon flux rate and the C/N ratio

of the available substrates. Nitrogen available for microbial use in carbon compound dissimilation can be derived from amino acids (502), proteins (504), soil humus (532), and inorganic nitrogen pools, including rainwater additions. If the carbon being pulsed through the system does not have sufficient nitrogen, or if the rates of carbon flow are sufficient to exhaust the available nitrogen reserves, then this may lead to a limitation of microbial activity.

The notation of a microbial activity index for the microbiotic variable (520) reflects the observation that microbial biomass and numbers are not meaningful parameters, either to express minimal maintenance rates of carbon flow or to relate these parameters to carbon flow. Measure of microbial numbers, as expressed by plating enumeration procedures or other procedures, may be applicable for development of this activity index.

Carbon flowing through the system is considered to be transformed to microbial cells (520), carbon dioxide (530), and humic compounds (532). Upon addition of a pulse of carbon a transient increase in microbial biomass can occur. With depletion of the exogenous carbon, microbial cell materials will revert to the intermediary substrate pools until a new steady-state microbial equilibrium is reached between the microbiotic compartment (520) and carbon flow to carbon dioxide (530).

Carbon dioxide evolution to compartment 530 represents the major output parameter of the system. Combined with an ancillary measure of oxygen utilization in relation to the amount of carbon which is passed through the system, an RQ relating volumes of carbon dioxide evolved to oxygen volume used provides information on the classes of substrates being used. Based on general physiological assumptions, a higher RQ would indicate a greater

use of carbohydrates, and shifts to lower RQ values would indicate a reversal to use of amino acid level materials and to a more stressed or nutrient-limited condition in the soil environment.

In addition to the microbial evolution of carbon dioxide as noted in section 5.3.2, flows to this compartment from abiotic carbon dioxide release and root respiration processes must be considered in apportioning resultant carbon dioxide to its actual sources. Although they are not an integral portion of the decomposer subsystem, their contributions should be considered.

In total, the decomposer model thus depicts material flow by both biotic and abiotic processes to pools of intermediate compounds of varying lability. For microbial utilization, these intermediate pools then pass through the microbiotic compartment subject to temperature, moisture, and C/N ratio constraints, resulting in carbon dioxide production, accumulation of microbial cells, and reversion of cellular materials to further labile components following the active growth phase. Arbitrary indices of microbial activity, respiration quotients, and essentially instantaneous fluxes of carbon through the components 501 to 506 will provide information on the decomposability index (labile vs. non-labile components).

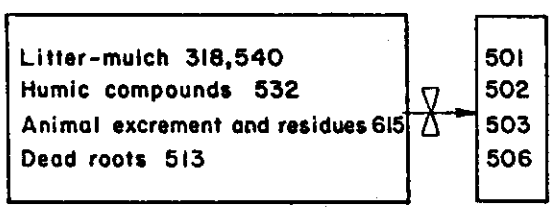
Connecting points to other carbon flux sources are indicated and should allow consideration of abiotic carbon flow and root respiration in the aboveground portion of the decomposer system.

In evaluating the available literature on carbon flow and energetics of the decomposer compartment, a series of papers should be noted which, in large part, provide general reviews of this area. These would include Clark (1969), Clark and Paul (1970), Gray and Williams (1971), MacFadyen (1970), and Reuss (1971). These reviews cover the areas of soil decomposer energetics,

and the contribution of Clark and Paul (1970) is specifically concerned with the microfloral activities in grassland ecosystems. Reviews of the soil fauna are also available and would include contributions of Coleman (1970), Heal (1970), Paris (1969), and Rapoport (1970). An especially pertinent review of plant leachates and their function in relating aboveground and belowground decomposer activities is given by Tukey (1970).

The available literature on decomposer dynamics, in general, and for grassland ecosystems in particular, is less than satisfactory from a process development standpoint. Either studies are related to static laboratory conditions where sample history and season are not considered, or field studies are carried out with the available information which is insufficient to allow correlation of results with specific environmental variables such as temperature, moisture, or seasonal conditions. Based on the present state of knowledge, the following is available as an initial summary of the major flows in the model.

5.4.1 Substrate Flows to Intermediate Pools



Satchell (1970) completed a study of approaches which must be used to allow evaluation of energy inputs from the initial compartments in this model. This includes a major separation of aboveground and belowground production and an estimation of rates of aboveground biomass consumption and

removal from the site by herbivores. The problem of evaluating dead root contributions to energy flux in the system has been reviewed by Dahlman and Kucera (1965), and current estimates give approximately 100 g/(m^2 × year), assuming that 25% of the root biomass is turned over each year.

Floate (1970) provided information using CO_2 evolution techniques to give the rates of decomposition for four plant materials and for the feces of sheep having been fed these materials. The rates of fecal decomposition were found to be approximately one-half that of the complete plants over the experimental period used (Fig. 5.14).

Estimates of total productivity for a particular ecosystem, which may vary from year to year, depend on the level of primary productivity which drives the system, and this information should be available from the producer subsystem.

A ratio of distribution for biomass dissimilation which may be applicable to the partitioning and availability of materials is given by Gray and Williams (1971) for a grazed meadow community [kg dry matter/(m^2 × year)]:

Primary products		1.17
Respiration		0.12
Net primary production		
	Total	1.05
	Eaten	0.39
	Decomposed	0.66
Mean stock		1.00

Figures of partitioning of this type may be applicable to the determination of initial pools of materials which will become available for use by the decomposer compartment.

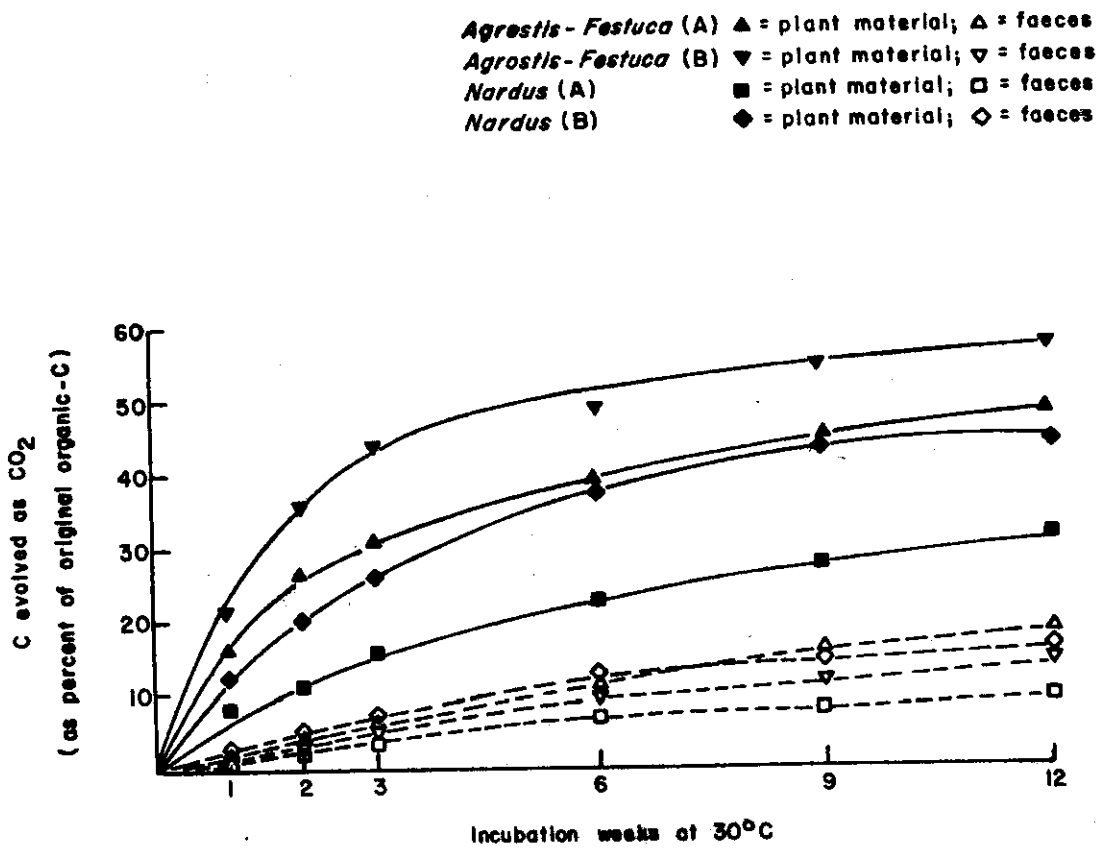


Fig. 5.14. Evolution of CO_2 from plant materials and sheep faeces incubated for 12 weeks at 30°C (from Floate, 1970).

By use of producer subsection information on plant composition, it will be possible to supply data on levels and changes in primary producer substrates which are available to the decomposer compartment over a seasonal basis. It is important to note that these constituent materials are not available for microbial use until biotic and abiotic processes have transformed them to more suitable forms, involving both commutation and release of substructural components.

5.4.2 Biotic Controls on Flows From Substrate Materials

This model is divided on the assumption that the flow of carbon through the system will be subject to exoenzyme activity (extracellular enzymes produced by microbes, plant roots, and microfauna) which aids in breaking down substrate components to microbially utilizable monomeric units. Production of enzymes by microbes has been reviewed by Skujins (1967), and the wide range of enzyme types which are produced has been described. Unfortunately, no rate or seasonal fluctuation data is given in this review. Krasilnikov (1958) has described the types of hydrolytic enzymes which can be liberated from roots and the relative levels of these enzymes which are present in the soil environment.

Sorenson (1969) has carried on a series of experiments on hemicellulose and glucose addition effects on activities of the respective enzymes in the soil system (Table 5.1) as summarized by Clark and Paul (1970). These studies indicate that enzyme levels will respond to specific organic additions. Under proper moisture and temperature conditions these enzymes should continue to be active in the soil system.

Skujins (1967) has studied the enzymatic activities of free enzymes in soil and has shown that soil colloids can adsorb enzymes which result from

Table 5.1. Effects of carbohydrate additions on hemicellulose activity and amino acid pools in soil.

Carbohydrates Added	Period of Decomposition (days)	Carbohydrate (C) Recovered in Amino Acids (% of added C)	Hemicellulose Activity (relative units)
Hemicellulose	6	7.8	1.03
	12	8.7	1.00
	30	8.1	0.92
	90	6.0	0.85
	700	3.1	0.18
Glucose	6	5.0	0.06
	12	5.0	0.06
	30	7.2	0.08
	90	6.0	0.08
	300	3.5	0.07

three sources: (i) active and dying microbes, (ii) plant roots, and (iii) soil animals. Generally the data reviewed by Skujins indicate that enzymatic activities cannot be correlated with soil microbial populations except under conditions of active microbial proliferation. An increased level of soil enzyme activities in the rhizosphere has been noted.

As the free enzymes in soil are in large part hydrolytic, their activity can be expected to diminish upon soil drying; thus comes the concept of a threshold moisture level below which hydrolysis processes will not proceed at maximal rates.

5.4.3 Abiotic Controls on Nutrient Flows To and Between Pools

During dry periods in the grassland ecosystem when the activity of hydrolytic exoenzymes can be expected to be minimal, the model also depicts that abiotic oxidative processes can release nutrients to more microbially available forms. Birch (1959) found that during successive wetting and drying events, a constant portion of the residual soil organic matter will be transformed to a state where microbial utilization can occur once soil water is present at a sufficient level.

The magnitude of decomposition rates which would occur upon subsequent wetting was found to be a direct function of the time the soils were held in a dried state as shown in Table 5.2.

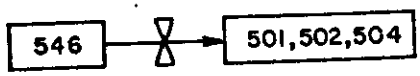
The rate of carbon mineralization was suggested to be a direct logarithmic function where carbon release would approach a limit asymptotically. This release of labile carbon during dry periods in a grassland soil should be amenable to treatment with log function nutrient release modeling. Although drying will cause a reduction in viable microbial populations (Klein, 1972; Soulides and Anderson, 1961), this effect cannot be expected to cause

Table 5.2. Effect of drying time on mineral nitrogen levels and carbon mineralization in soils of varying organic matter levels.

Soil %C	Weeks Drying				
	0	3	6	9	12
	mg mineral N/100 g soil (dry basis)				
7.0	27.4	40.6	47.7	50.9	53.7
6.0	22.1	29.8	30.5	34.8	--
5.0	18.5	24.4	26.1	--	--
	mg C mineralized/100 g soil (dry basis)				
7.0	58.3	92.0	121.6	137.7	146.3
6.0	57.3	79.1	83.7	98.4	--
5.0	55.9	72.9	86.4	--	--

major decreases in microbial populations; Sussmann (1965) has estimated that 1000 years might be required to render a dry soil sterile.

5.4.4 Root Exudate and Leachate Effects on Intermediate Pool Levels



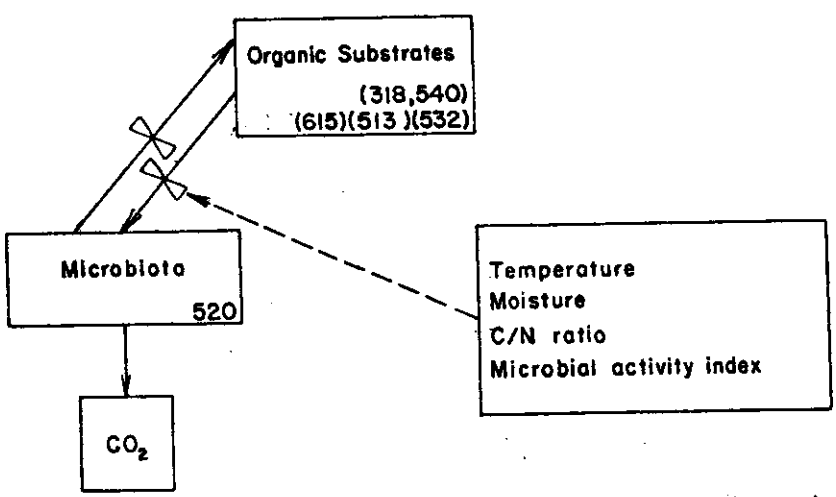
A major source of nutrient intermediate pools can consist of lower weight materials which are derived from root exudates and leached aboveground plant materials. Harmsen and Jager (1963) showed that during a 6-week period following germination of vetch, 1.6 to 2.9 mg of carbon were excreted per 100 mg of dry root material, equivalent to 3 to 6% of the root biomass. Clark (1969) has discussed additional papers which indicated that this range of exudate release may represent general levels. In general, these components represent readily available microbial carbon and energy sources, and correlation with primary productivity as related to root biomass should provide information on seasonal availability of material from these sources.

Another major source of readily available microbial carbon sources will be plant leachates derived from both living and dead aboveground plant biomass. Tukey (1970), in a recent review, indicated that carbohydrates represent the major organic materials which can be removed from plants and that up to 6% of young bean leaves dry weight could be removed in a 24-hr leaching period. Age of the plant material has major effects on the extent of leaching, with younger plants being more hydrophobic and resistant to leaching. Seaman (1971) found that samples of blue grama can lose up to 11.6% of dry weight during five successive 30-min extractions. Of the total weight, 5.2% and 8.4% could be removed in ½- and 1-hr extraction events, respectively. Similar results were obtained by Clark (1970)

where a "standard" prairie hay was found to contain 10.5% soluble carbon. Brown and Frederick (1968), studying a Sudan grass residue, found that 18% of the dry matter and 28% of the original nitrogen were water soluble under room temperature conditions. These results would indicate that plant leaching during relatively short-term moisture events can provide a major source of microbial nutrients. In the study of Seaman, no nitrogen-containing compounds could be found in leachates from the dried blue grama. By estimating rainfall duration and aboveground biomass on a seasonal basis, it should be possible to make meaningful estimations of carbon flow into these labile carbon pools from plant leachate sources.

Litter also has been reported to be a major source of microbial nutrients. Nykvist (1964) has noted that straw leachates contain sugar, amino acids, and aliphatic acids. Grabert and Matschke (1970) noted that lucerne grass cold-water extracts had higher C/N ratios than hot-water extracts, indicating that cold-water extractions will release materials which have more carbohydrate-like characteristics.

5.4.5 Microbial Activity Index and Controls on Carbon Flow



Based on general ecological concepts, flow of carbon through the microbiotic compartment (520) should be able to be related to either numbers, biomass,

or an activity constant, if approaches used for higher systems might be applicable (Fig. 5.7). Unfortunately, present understanding of this compartment does not allow such treatment of this system.

Clark (1969), Clark and Paul (1970), and Gray and Williams (1971) stressed the problem of relating known carbon flow requirements for maintenance of estimated microbial biomass with the markedly lower carbon flows which are observed in the soil ecosystem. Gray and Williams (1971) suggested that constitutive dormancy and exogenous dormancy (physical factors, inhibitors, and lack of nutrients) should be considered. In addition, Ensign (1970) noted that during starvation of *Arthrobacter* loss of biomass can occur without having concomitant decreases in viability. Inactivity may be caused also by decreases in soil water levels or temperature. Griffin (1963) noted that the soil water threshold for microbial activity can vary with the soil structure. A water content of 10% w/w can allow microbial growth in a sandy soil, whereas in loam and clay soils a similar water content may not allow growth, due to the higher suction pressures required to obtain water in the latter environments.

Temperatures below 5°C or above 30°C are known to severely limit activity of the predominant mesophilic populations (Gray and Williams, 1971), and the variables of oxygen tension and carbon dioxide content of the soil atmosphere are influenced by both temperature and soil water level considerations (Stotzky and Goos, 1965). Greenwood and Goodman (1964) found that microbial respiration can become limited at 2 to 6 $\times$ 10^{-6} M oxygen concentrations.

In addition to these physical factors, the activity of the microbial compartment can be influenced by the phenological stage and C/N ratio of the available substrates (Pinck, Allison, and Sherman, 1950). Copley and

Reuss (1972) and Reuss and Copley (1971) noted that nitrogen fixation rates in unamended grassland soils are minimal and that rainwater can supply sufficient nitrogen to meet the needs of the ecosystem. This would indicate that if the system is not subjected to excessive carbon flows, then the C/N ratio considerations should have only minimal effects on the activities of the microbiota compartment.

The possible effects of pH in the microbial environment must also be considered. Grassland soils are generally in the pH range of 6.8 to 7.5, and local shifts in pH in various microenvironments can be predicted to approach 0.5 pH units or more (McLaren and Skujins, 1963; Gray and Williams, 1971). As the normal pH growth range of most conventional mesophiles can be expected to exceed the range of 6 to 8, pH effects on activity would be expected to be minimal in the grassland ecosystem.

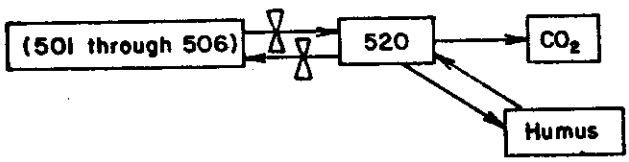
The effects of decreased oxygen levels in the grassland soil can be postulated to be minimal, as any waterlogging of the system will only be a transient occurrence.

Many estimates of the microbial biomass which will be subject to these environmental variables have been made, and these figures have been summarized and discussed by Clark (1969) and Clark and Paul (1970). Unfortunately, no suggestions are given on relating these figures to known changes in overall soil carbon flow rates. Apparently the flow rates are largely independent of microbial biomass or population estimates.

These considerations lead to the possibility of considering development of an arbitrary index of microbial activity which relates rates of oxygen uptake or carbon flow to an essentially less variable microbial potential. As viable count estimations are available which show the numerical responses

of the predominant microbial flow to carbon flow and abiotic variables (Clark and Paul, 1970; Klein, 1972; Krasilnikov, 1958, page 150), these can be related to carbon flow and oxygen uptake rates to yield an activity index which will be compatible with modeling requirements.

5.4.6 Substrate Composition Controls of Carbon Flow Rates Through the Decomposer Compartment



A large body of information is available which relates the chemical composition of substrates to availability as a source of carbon and energy for the microbiota compartment. These studies have been summarized by Clark and Paul (1970) and Gray and Williams (1971), and only major points require further discussion.

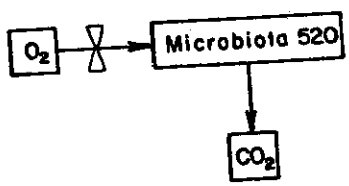
The gradation of microbial availability of substrate classes has led to the development of a labile/non-labile ratio concept based on the study of Minderman (1968) (Fig. 5.9). This is based on the observation that degradation rates of individual components may be expressed exponentially, whereas overall degradation rates of a combined material may exhibit nonlinear characteristics when graphed on an exponential scale. Clark and Paul (1970) have suggested that substrate constituents can be separated into three major forms based on their resistance to microbial degradations.

It would appear that a knowledge of substrate composition on a seasonal basis, as well as an estimation of amounts of material which may be passed through the ecosystem, will allow development of a meaningful concept of

lability vs. non-lability. The ELM decomposer model (Anway et al., 1972) currently includes this concept.

Although the role of the humus fraction in carbon flow in soil systems has received much attention, application of these data to the grassland ecosystems will require caution. Information on humus fraction characteristics and degradation rates have been given by Clark and Paul (1970) and Gray and Williams (1971). With the assumption that the humus content of the grassland will remain essentially constant over an annual basis, an intermediary level model could be developed which might assume this constant arbitrary value. Use of standard assays over a seasonal basis for extractable humic materials should provide needed information on this point.

5.4.7 Carbon Dioxide Evolution and Measures of Overall Decomposer Activity in the Soil Environment



A summary of the decomposer subsystem usually includes an attempt to relate overall productivity of the system to soil respiration. In some instances, these data have given good correlations, assuming that an annual steady-state system is maintained. Using this approach, MacFadyen (1968) showed correlations between net primary production and soil respiration, which are of potential interest (Table 5.3).

The postulate was made that for certain ecosystems, primary productivity should equal respiration (and vice versa), assuming that steady state biomass levels are maintained. It may be possible that this approach to relating net

Table 5.3. Correlations between primary productivity and soil respiration in varied soil ecosystems (from MacFadyen, 1968).

Vegetation Type	Net Primary Productivity (kcal/m^2/year)	Soil Respiration (kcal/m^2/year)
Temperate range	900 to 6400	--
Rough grazing	3300	--
Pteridium	4050	4500
Managed grassland	4200	4500
Woodland	1100 to 6400	6900 to 10000

primary productivity to required soil respiration may be applicable to the grassland system.

An additional approach to understanding the dynamics of carbon flow and microbial activity in the grassland ecosystem has been suggested by Klein (1972). By correlating oxygen uptake and carbon dioxide evolution in the grassland environment as related to time, a picture of carbon flow and microbial energetics can be derived (Fig. 5.15). Under these conditions, the spring maximal growth period allows optimal carbon flow based primarily on carbohydrate-level materials. After the dry season has started, carbon flow can be observed to occur independent of microbial respiration, indicating abiotic carbon release.

Addition of simulated rainfall events indicates that two phases of carbon flow exist, the first based on biotic processes and the second on abiotic release of microbially utilizable components. A balance point appears to exist where rainfall events will not allow major microbial respiration or concomitant carbon dioxide release.

Stotzky (1960) has suggested that "the RQ may provide an indication of the types of metabolic intermediates being utilized at a specific time and/or the type of populations using these materials." The use of either parameter without consideration of the other was suggested by this author to provide only limited information on the functioning of the system. Studies of Rixon and Bridge (1968) confirm this viewpoint.

This concept is especially critical when considering the problem of abiotic carbon dioxide release from soil systems. Without concomitant oxygen uptake and carbon dioxide evolution measurements, it is not possible

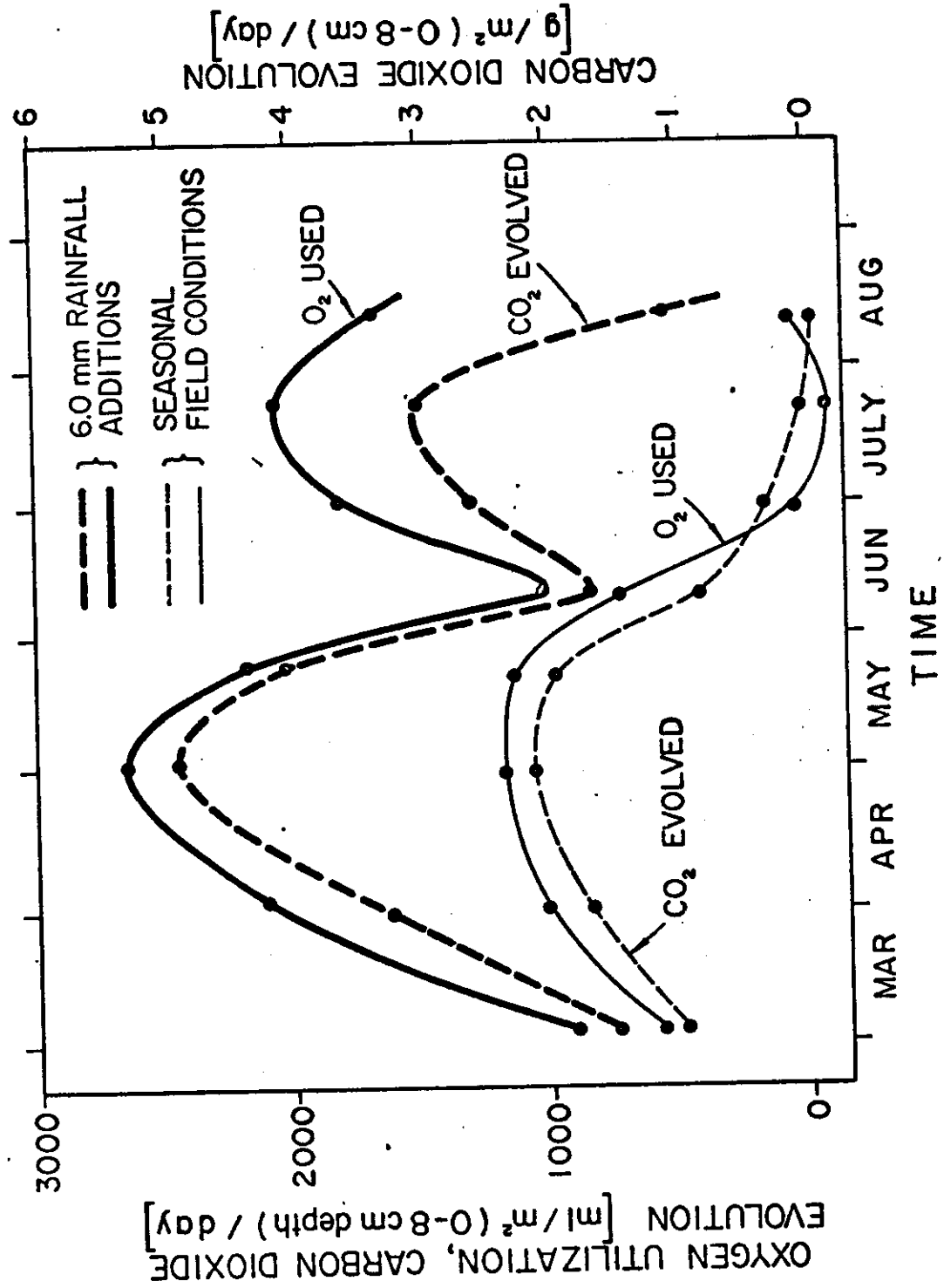


Fig. 5.15. Carbon dioxide evolution and oxygen utilization in unamended and moistened Pawnee Grassland soil.

to ascertain when periods of strict abiotic carbon release are occurring. Abiotic release of carbon dioxide has been postulated to occur as a result of chemical decarboxylations or release from soil carbonate pools (Chase and Gray, 1953, 1957), and in the arid grassland environment these processes may provide a major source of carbon dioxide flow.

Methods to differentiate between abiotic and biotic carbon flow in grassland soils will provide needed information regarding decomposer functions in this ecosystem, with the assumption that depiction of carbon flow energetics is the major function of this subsystem.

5.5 SUMMARY COMMENTS AND RECOMMENDATIONS

Development of a meaningful model for the decomposer subsystem has been limited in the past by efforts of modelers to develop models without sufficient relationships to field data and, on the other hand, by the tendency of soil microbiologists to suggest approaches to the modeling problem which are not sufficiently related to modeling requirements and which would reflect a meaningful priority rating of experimental approaches.

It is hoped that the flow diagrams presented here will meet the requirements of this subsystem. The major points which were developed included an increased use of the carbon-flow energetics relationship and an increased appreciation of the role of seasonal factors in the decomposer compartment functions.

A model which is related to a simple soil water and temperature coefficient treatment of this system is sufficient to meet elementary requirements, but the role of seasonal factors in controlling levels and

classes of carbon compounds which flow through the subsystem must be considered for a fuller development.

Recommendations which can be derived from this section include the following:

1. Studies of decomposer activities should be accompanied by soil water and temperature measurements.
2. Concurrent studies of root growth are required so that root decomposition can be distinguished from root growth.
3. Information on degradation rates for a broad series of complex substrates should be given emphasis if a simple approximation of substrates does not give adequate results.

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CHAPTER 6. CONSUMER SUBSYSTEM:

DIET-SELECTION MODEL

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6.1 ABSTRACT

Diet selection is considered as an ecosystem process which connects consumers to their food sources. From a flow modeling concept the process is simple, i.e., only the food intake flows from food to consumer are considered. The complexity occurs, however, in the controls over this flow. Implications and effects of selecting particular kinds of foods on consumer morphology and behavior, on the state of consumer populations, and on the structured producer communities are proposed.

Two alternative *strategies* of diet selection are the maximization of net energy gain and the balancing of the diet with nutrient and energy requirements. The actual *tactics* of diet selection vary from one consumer group to another.

The diet selection model, as developed in the Process Studies Workshop, is presented in terms of primary controls (*food preference*, *food density*, and *consumer selectivity*) and the secondary controls which influence the primary controls. The operation of this preliminary model regulates the rates of flow of various foods to consumers. Recommendations for future investigations of the diet selection process are based upon this model.

6.2 INTRODUCTION

In nature, animals are confronted with a variety of potential food sources. By selecting some and rejecting others, they influence the rate of flow of energy and specific nutrients from food sources into animal biomass. Thus the process of diet selection influences both the structure and state of consumer populations and determines which food categories will remain in the environment and which will be selectively removed.

The process of diet selection varies according to the degree of selectivity of different consumers; some species are totally selective, eating only specific foods or food parts (i.e., host-specific insects), while others are highly unselective, ingesting all available items (filter-feeders). This degree of selectivity may be, in turn, related to the size of the individual consumer, to the size of the consumer population, and to intrapopulation spacing behavior. Among African ungulates, the small animals are generally more selective in their feeding than the large ones (Gwynne and Bell, 1968), the reason being that sufficient energy to maintain a large biomass cannot be obtained by very selective feeding. Jarman (unpublished) implied that highly selective feeding is a more conservative, "safer" strategy, but does not permit exploitation of resources which may be very abundant at some times. Thus in ungulates, high selectivity (specialization?) appears to be related to stable food supplies and relatively small size, whereas low selectivity may accompany large size and relatively unstable food sources. Furthermore, Jarman (unpublished) showed that small, selective feeding antelope tend toward small territorial groupings, while large unselective feeders generally form large, mobile herds.

The population processes of consumers are also related to the diet selection process. Individual birth rates, death rates, growth rates, maturation rates, fattening, lactation, etc., may all be determined by the quantity and quality of food consumed. In turn, these determine the size, structure, and secondary production of the consumer population as a whole. Considerable attention has been directed toward food selection, food quality, and population processes in North American deer (Klein, 1970) and in the Red Grouse (*Lagopus lagopus*) (Miller, Jenkins, and Watson, 1966; Jenkins, Watson, and Miller, 1967; Miller, Watson, and Jenkins, 1970). Ellis (1970) showed a direct relationship between the kinds of food available in the environment and fawn survival in pronghorns.

The selective removal of specific food species by consumers has important implications for the structure of the ecosystem. It has been suggested that domestic herbivores, through selective grazing, have altered the structure of the plant community in the Great Basin of North America, leading to a reduction in native grasses and a proliferation of shrubs (Stoddart and Smith, 1955). In East Africa there is concern that elephants, by consumptive tree destruction, are rapidly converting forest and tree-savanna areas to scrub forest and grassland communities. Bell (1970) suggests that various grazing ungulates alter the structure (though not the species composition) of their savanna grazing lands in such a way that it becomes unsuitable for them but appropriate for another species, leading to an annual grazing succession involving several ungulate species. These examples emphasize that it is not only the *quantity* (caloric value) of food removed by consumers but also the kind or *quality* of food removed which influences the structure and function of the ecosystem; hence the need

to understand diet selection--the process regulating the *quality* of food removed from the ecosystem.

6.3 OPERATION OF THE DIET SELECTION PROCESS

Ecosystem processes are operations by which energy and/or materials are transferred from one ecosystem compartment to another. The diet selection process determines rates of transfer from food compartments (animal or plant) into consumer compartments. It is essentially a behavioral process whereby the consumer evaluates what foods are available against some criteria of need, preference, desirability, utility, past experience, etc., and on the average, chooses certain kinds of foods over other kinds. The operation of the process can be resolved by determining (i) the advantages of choosing certain kinds of foods over others (the *strategy* of diet selection) and (ii) the actual procedures by which the selection is made (the *tactics* of the diet selection).

Hypotheses concerning the *strategy* of food selection fall into two major categories: (i) the energy maximization hypothesis and (ii) the nutritional balance hypothesis. The first proposes that food selection is based on the maximization of *net energy gain* in foraging activities and that those food items which implement this maximization strategy will be selected. The second hypothesis includes the concept of nutrient content of foods as well as energy value; it proposes that consumers select those foods which will most readily meet their *nutrient* and *energy requirements*.

The energy maximization hypothesis has been favored where insectivores or carnivores have been considered, whereas those concerned with herbivores tend to favor the nutritional balance hypothesis. This dichotomy is related

to the fact that insectivores and carnivores, by consuming animal material, ingest a diet which is *relatively* constant in nutrient and energy composition and which is of uniform high quality, regardless of the particular items consumed. Therefore, if enough is eaten to meet the energy needs of the animal, nutrient demands will also be satisfied. This hypothesis leads to the consideration of characteristics such as the size of each food item and the amount of energy expended in obtaining (capturing, subduing, etc.) the food. Where herbivores are considered, the energy expended in obtaining food is not usually a prime consideration. However, because of the range in nutrient and energy composition of potential dietary items, differences in the *quality* of food items are of prime importance. Here the diet must provide not only a positive energy balance but also satisfaction of nutritional needs. This leads to consideration of such food characteristics as phenology, nutrient content, cellulose, nitrogen and lignin content, etc. For considerations of the energy maximization hypothesis, see Emlen (1966) and Schoener (1971); for the nutrient balance hypothesis, see Katz (1937).

The *tactics* of food selection and the variables controlling those tactics are the major subject of the rest of this paper. However, there are a number of previous hypotheses purporting to explain how particular animals may actually go about choosing one food item over another. A few of these are:

1. That search images are formed based on the frequency of contact with particular prey types (Tinbergen, 1960).
2. That birds continuously sample a variety of habitats to assess food density, but spend most foraging time in places where food acquisition is most profitable (Royama, 1970; MacClean, 1972).

3. That the Redshank (*Tringa totanus*) selects large prey over small prey when both are available (Goss-Custard, 1970; personal communication).
4. That deer select their food primarily on the basis of smell and secondarily on taste (Longhurst et al., 1968).
5. That animals learn by trial and error what are the most appropriate foods (Harris et al., 1933).

These divergent hypotheses suggest that the mechanisms of diet selection may vary among different consumers and under different food conditions; thus the need is for a general model of the diet selection process, applicable to a wide variety of consumers and food conditions.

6.4 THE DIET SELECTION MODEL

The purpose of the Process Studies Workshop was to develop a group of first-pass models which represent the state of knowledge about particular processes, which succeed in establishing connections among ecosystems processes, and which offer insight regarding directions for future process-oriented research.

In dealing with the diet selection process, different kinds of problems were encountered from those inherent in other ecosystem processes. In the first place, diet selection is essentially a behavioral process rather than a physical or physiological one. Secondly, although the model included only a single rate process (that governing transfer of particular food items from food compartments to consumer compartments), the model rapidly became quite complex due to the number of variables exerting some control over the process. Finally, a major problem was the difference in the relative

food selectivity exerted by different species. The objective, which was to develop a general model applicable to any consumer, was constrained by species-specific empirical data and a body of theory generally applicable to specific classes of consumers (i.e., grazers or predators). Realizing these problems and constraints, an attempt was made to isolate those primary controls of the diet selection process which are universal in occurence, to identify that set of secondary control variables which most frequently influence diet selection, to determine the connections between the diet selection process and other ecosystem processes, and from these controls and connections to develop a model which would mimic the general operation of the diet selection process for all consumers.

6.4.1 Structure of the Diet Selection Model

The diet selection model developed in the workshop is simple in structure, with two state variables and a single net flow. The state variables are the amount of food in an unspecified number of food classes (702) and the amount of food in each class eaten by the consumer (703) (the sum of which is the composition of the diet). State 702 is designated to contain only those foods which are utilized at least occasionally by the consumers in question. Otherwise, this state variable would contain all potential nutrient and energy sources, and the model would have to operate over evolutionary time in order to narrow down this set of potential foods to a set of foods best fit for the consumption of a particular consumer. The flow (702-703) signifies the rate of consumption of each food class (R_i, ..., n) as grams of food class i consumed per day. Secondary control variables act to modify these flow rates through their effects on preference,

food density, and consumer selectivity--the three primary controls of the diet selection process. The interaction of these controls determines the flow rate of each food class as shown in Fig. 6.1.

The amount of food eaten by an animal per unit of time gives the rate of food intake. Intake requirements may have a direct effect on the kinds of food selected, as hypothesized by Jarman (unpublished) in that small animals with lesser requirements can afford to be more selective than larger animals. Likewise, young animals may be more selective than older ones for similar reasons.

In the diet selection model, daily intake determines how much total food will be removed from all food classes combined. It is a basic function of the size and metabolic rate of the consumer, but may also be influenced and modified by several control variables.

Food intake (daily) = f(body size, metabolic rate, environmental conditions, food quality, food density, reproductive and physiological state of the consumer)

In the model, daily intake is measured in grams per gram body weight.

6.4.2 Primary Controls of the Diet Selection Process

Much of the variation in diets of consumers can be accounted for by variations in the values of four major components of diet selection: Intake, preference, selectivity, and food density. Ivlev (1961) uses the terms "electivity, predilection, and accessibility," the latter two of which are synonymous with the terms of preference and food density as used here. In order to develop a general model for diet selection, it is necessary to

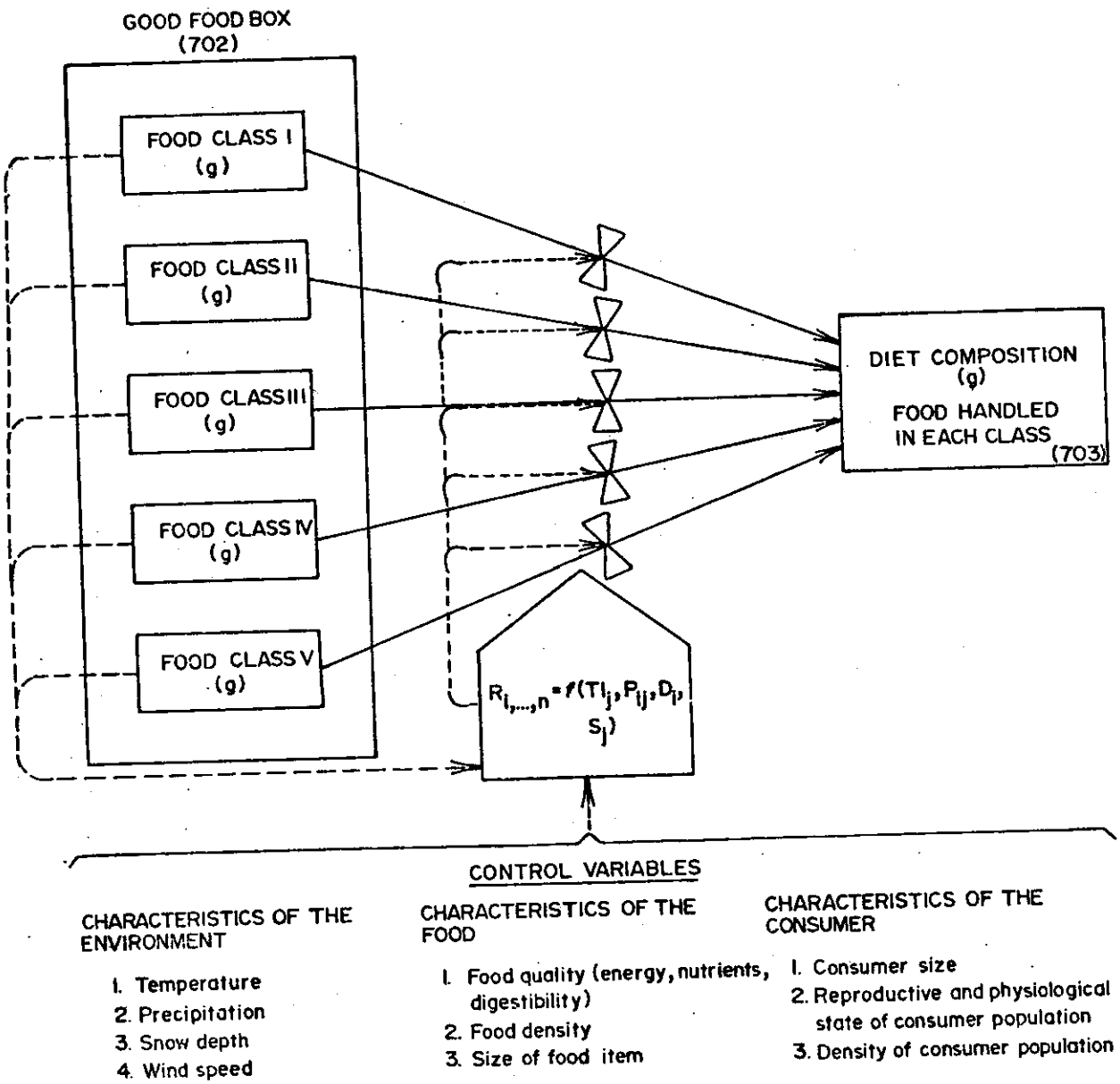

Fig. 6.1. Structure and operation of the diet selection model (see section 6.4.4 for term designations).

include food intake, although this is often considered constant where a specific consumer is involved. Ivlev recognizes that the "electivity" of consumers varies with satiation. Here the selectivity component is introduced to deal with this and similar phenomena.

6.4.2.1 Preference. The preference or predilection of a consumer for a particular class of food is a measure of how well the consumer "likes" the food relative to other kinds of food and independent of considerations of availability. It is similar to the concept of palatability. Preference is extremely difficult to measure, but preference indices can be constructed based on the selection of one kind of food over another when all are more or less equally available. Although there is an evolutionary basis for food preference (i.e., those sizes, shapes, and distribution of foods which can be profitably exploited), preference may be modified by changes in the requirements of the animals, as in pregnancy, or changes in the composition of food, as in maturing plants.

Preference = f(food quality, food size, reproductive and physiological state of the consumer)

For this model, preference is quantified as a relative preference index based on information about past consumption.

6.4.2.2 Food Density. Food density is a measure of the abundance of the various food classes and, as used here, is synonymous with Ivlev's (1961) "accessibility" or availability. In many natural situations food density may be the primary determinant of the composition of the diet; in other words, many animals must eat what is available to them regardless of preference.

Density is measured directly as grams per meter squared of food, but is converted to a relative density index so that abundances of different

foods are comparable. It is modified by the consumers' removal rate and thus must be updated continuously in this model. The density of food available to consumers may be somewhat different than actual density because of physical barriers such as snow, thorns, etc.

Food density = f(g/m^2 of food, snow depth, or other physical factors)

6.4.2.3 Selectivity. Selectivity is included as a major model component to account for the empirical observation that consumers will sometimes take foods in strict proportion to food densities in the environment (i.e., non-selective feeding), but at other times they will consume foods on a preference basis (selective feeding). Ivlev (1961) summarized his experiments on food selection in fish as follows: "While the animal is hungry it eats up [sic] all, or practically all, [of] the food objects it finds. As it becomes satiated, especially in the case where taste is the animal's guiding sense, it becomes more discriminating, and finally, when the degree of satiation reaches an almost maximum value, it only eats the items it likes best."

Another example is provided by Royama (1970) who noted that the foods gathered for nestlings by adult Great Tits included a wide variety of food types, although the bulk of the food at any one time included only a few types. His hypothesis suggests that Great Tits continuously monitor a variety of food sources even while drawing the majority from a particular source; thus the birds are generally aware of the abundance of a wide variety of foods and can direct their foraging efforts in accordance with abundance.

In this model, selectivity takes values ranging from 0 (no food selection, food taken strictly in proportion to abundance) to 1 (complete selection, food taken in proportion to its preference value).

Selectivity = f[physiological state of the consumer (hunger level), consumer size, food density, consumer density]

6.4.3 Secondary Controls on Diet Selection

The three primary controls interact to determine the amount and composition of foods consumed on a daily basis. The values of these components and thus the diets of consumers are modified by a number of characterisitics of the foods, of the environment, and of the consumers represented here as a set of secondary control variables regulating the rate of flow materials from food categories to consumers.

6.4.3.1 Characteristics of the food. Three major characteristics of food were included as control variables in this model. Initially several others were considered which are influential under certain circumstances. However, for operational simplicity it was necessary to limit the number of control variables considered. Those selected were: (i) food quality (including energy content, nutrient content, edibility, and digestibility), (ii) food density (or quantity), and (iii) food size (particularly important to various carnivores and insectivores which must subdue their food before eating it).

All of these are readily quantifiable. In the model they are treated as independent variables affecting the values of the flow or primary controls. The functional form of these relationships remains to be worked out; however, several hypotheses about these relationships can be posed. Concerning total intake, it is likely that:

1. Intake increases with increasing food quality.
2. Intake increases with increasing food density over a limited range of density.

3. Intake is not a strong function of food size.

For preference, it is likely that:

1. The preference value of a food is a direct function of food quality.
2. Preference is unaffected by food density.
3. Preference is a strong function of food size among certain kinds of consumers, particularly carnivores.

Concerning consumer selectivity, it seems probable that:

1. The expression of selectivity is limited by the variety and density of foods.

6.4.3.2 Characteristics of the environment. The preliminary remarks concerning the number of possible influential food characteristics and the reasons for limiting these also applies to the environmental and consumer characteristics. It was decided that the major environmental control variables which would be included in the model are temperature, precipitation, snow depth, and wind speed. Following the format used in the previous section, a number of hypotheses concerning the action of these secondary control variables on the primary controls can be posed. Concerning total intake, it is likely that:

1. Total intake is a function of all four of the environmental control variables in that extreme values will influence the activities of consumers and thus their foraging abilities.

Preference is not likely to be materially altered by environmental conditions. Concerning food density it is probable that:

1. Density of foods may be *functionally* altered by heavy snows or precipitation.

Selectivity may be altered:

1. By environmental effects on food density.
2. By environmental effects on animal activity.

6.4.3.3 Characteristics of the consumer. The consumer characteristics most likely to control the rate of flow of various foods are the reproductive and physiological state of the consumer, the density of the consumer population, and the size of the individual consumer. Concerning total food intake, it is probable that:

1. Total intake is a direct function of consumer size.
2. Intake rates are strongly modified by changes in the physiological or reproductive state of the consumer.

For preference, it seems likely that:

1. The preference for particular kinds of foods may vary with the physiological or reproductive state of the consumer.

Food density will certainly be modified:

1. By the density of consumers.
2. By the size of the individual consumers.

Selectivity is likely to be influenced:

1. By the size of the consumer.
2. By the reproductive and physiological state of the consumer.

In summary, the general structure of the model involves 2 states, 1 flow, 11 secondary controls, and 3 primary controls. The rate of flow of materials from one state to the other is determined by the food intake rate and the values and interactions of the three primary controls (i) consumer food preference, (ii) food density, and (iii) consumer selectivity. The values of these are regulated by the series of secondary control variables. The

number of major controls hypothesized to impinge on each major component is five for food intake, three for consumer food preference, four for food density, and four for consumer selectivity.

The hypotheses concerning the nature of the effects of these controls on the components are largely untested; thus one of the major areas of uncertainty in the model is the form of the various control relationships. The other major area of uncertainty involves the manner in which the controls interact to regulate food flow rates.

6.4.4 Operation of the Diet Selection Model

Assuming that the values of the flow are determined by the various control variables, we can then speculate on how these components interact to determine the flow rates of the various food classes. It should be reemphasized that state 702 includes only those foods potentially acceptable to the consumers in question.

In this conception of the diet selection process, the *total food intake* of a particular consumer is designated TI_j; *food density* of a particular food class is designated D_i; *preference* of a particular consumer for a particular food is designated P_{ij}; and the *selectivity* of a particular consumer is S_j, where i is the i^{th} food class and j is the j^{th} consumer.

At the outset, *food density* (D_i) and consumer food *preference* (P_{ij}) are given values relative to all other consumed food classes such that

$$\Sigma P_{ij} = 1.0 \text{ and } \Sigma D_i = 1.0.$$

Thus D_i becomes RD_i (relative density of food class i), and P_{ij} becomes RP_{ij} (relative preference of consumer j for food class i).

Next, all foods appearing in state 702 are ranked relative to each other in terms of their relative density and the animals' relative preference. So, $RP_{ij} \cdot RD_i = RRa_{ij}$ (the relative rank of food class i for consumer j). The RRa_{ij}'s are next scaled so that:

$$\Sigma RRa_{ij} = 1.0$$

Total food intake could be entered at this point and a simple calculation ($TI_j \cdot RRa_{ij}$) would then give the grams of food consumed in each food class. However, it is first necessary to consider *selectivity*. *Selectivity* ranges in value from 0 to 1. It reaches 0 when no food selection is exerted, i.e., foods are taken strictly in proportion to their relative densities. It reaches 1 when foods are taken in strict proportion to their relative preference. Then:

$S_j \cdot TI_j$ = the amount (in g/day) of food consumed on a preference basis

and

$1 - S_j \cdot TI_j$ = the amount of food (in g/day) consumed on an availability (food density) basis

Thus, the final form of the general diet selection model is:

$$R_{j(i, \ldots, n)}\begin{pmatrix}\text{Grams of food class i}\\ \text{consumed per day}\\ \text{by consumer j}\end{pmatrix} = (S_j)(TI_j)(RRa_i) + (1 - S_j)(TI_j)(RD_i)$$

and

$$\sum\begin{pmatrix}\text{Grams of food classes i, ..., n}\\ \text{consumed per day}\\ \text{(composition of the diet)}\end{pmatrix} = (S_j)(TI_j)(RRa_1 + RRa_2, \ldots, RRa_n) + (1 - S_j)(TI_j)(RD_1 + RD_2, \ldots, RD_n)$$

The diet selection process regulates the rate of flow of food to consumer (702-703), and hence forms the trophic link between plants and animals and between prey and predators. In order for the proposed diet selection model to function, certain input information must be available. This includes the density of the food classes appearing in state 702, the nutrient and energetic composition of these foods, their digestibiltiy and edibility, and in some cases, the size of food items. Output from this model specifies the total amount of food consumed per day in each food class (703).

6.5 CONCLUSIONS AND RECOMMENDATIONS

There are two major areas of uncertainty in the diet selection model:

1. There are reasonable doubts about the three primary controls. Are they conceptually sound, and if so, is this conception of the interaction adequate?
2. In many instances, it is not known exactly how these primary controls are affected by the secondary control variables.

Thus while this model seems to include most of the elements necessary to account for differences in diet, the actual mechanisms remain uncertain.

To obtain a clearer perception of the diet selection process then, it is necessary to (i) develop a more firm understanding of the concepts of selectivity and preference, (ii) determine the nature of the interactions of food density, food intake rates, consumer preference, and consumer selectivity, and (iii) determine how variations in these components affect diets. Additionally, it is necessary to determine the form of the functional relationships between the secondary control variables and the three primary controls.

The flow and primary controls might best be studied in a field context using large herbivores. Food density could be sampled and food intake rates determined using techniques now employed in the Grassland Biome studies. Selectivity and preference are conceptually the most difficult components and will require more attention. Therefore, they should have the highest priority for diet selection studies. The control relationships might best be studied in the laboratory or in a combination field-laboratory study (using birds or small rodents) by applying different levels of each secondary control variable and monitoring the effects upon each primary control. Again, selectivity and preference are the more difficult concepts with which to deal and emphasis should be placed on functional relationships between them. However, an understanding of the nature of these intercontrol relationships will be incomplete until we have a better understanding of each of the primary controls themselves; hence the greatest need is for a firmer conception of selectivity and preference.

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CHAPTER 7. CONSUMER SUBSYSTEM: ENERGETICS MODEL

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7.1 ABSTRACT

An energetics model, part of the consumer subsystem, has been described in this report of the Process Studies Workshop held early in 1972. There are 14 state variables with 16 flows described. Within the basic model, 11 state variables with 12 flows or processes and 3 state variables associated with specialized food handling functions are also discussed.

Each of the major flows is discussed and defined, and where pertinent data have been found in literature reports, selected portions or reworked values are given in this report. Much of the energetics model is centered around the controls affecting the process of eating and two processes dealing with metabolic rates, standard metabolism, and maintenance metabolism. It was discovered that many of the controls are redundant in the model, i.e., the controls operate on many different processes in the same manner. For this reason, we suggest that critical thought be given to evaluating the necessity of many of the state variables and the associated flows and, in subsequent reviews, to simplify the model accordingly. A detailed and complex matrix of consumer types and transfers of state for these several types is presented. The committee felt that many of the consumer types and states were realistic for grassland consumers in that these biological states actually exist. However, it is generally agreed that the listing is far too long and creates a great deal of unneeded complexity for an information-gathering or functioning model. Thus more thought must be given to an aggregation scheme that will decrease the complex nature of consumer types, but yet retain a relatively high degree of resolution for the consumer model as a whole. Some attention has been given to a basic mode of dealing with all consumers by emphasizing rates of respiration of the animal in its environment.

7.2 INTRODUCTION

The energetics model of the consumer subsystem deals with various ways an animal can treat its food after the food has been obtained through processes described in the diet selection model.

In a mechanistic sense, the process of eating can be regarded as the most important single event and one that can be concentrated upon intensively. Several facets of a species' niche characterization are integrated implicitly into this one process. It is assumed a priori that physiognomy of the animal, microhabitat, and behavioral responses to the physical and biotic environment are all coadjusted, so that a given animal has no constraints to which it cannot adapt during a particular block of time. Once this rather undefined homeostatic state is achieved, a series of controls can be imposed to observe how the animal responds under differing conditions.

Foods are ingested by a given animal, and whatever nutritive or non-nutritive materials that exist in the food are dealt with according to that animal's specific methods. Thus there are many known and potential feedback systems that tend to increase or decrease the rate of intake and correspondingly affect the status of the animal in time. For instance, if insufficient essential food materials are lacking with a given volume of food intake, it is obvious that an animal which has evolved successfully in the grassland ecosystem must have developed the proper feedback capabilities in terms of new and/or different physiological or behavioral strategies in order to cope with the stress of insufficient nutrition. The antithesis of this successful strategy is the inability to cope with the stress, and the obvious result is the death of the animal. If the stress is encountered by sufficient members of the population, and if in a sufficiently large proportion of the cases

death results, we can easily imagine how segments of a population or perhaps the entire population can be affected to the point where the population completely drops out of the particular part of the ecosystem, or perhaps the entire ecosystem. However, the individuals of a species that feed successfully will react within the community to remain a viable part of the ecosystem.

Thus, following in this report are some strategies that the workshop group, as a whole, deemed important in gathering information on animal energetics. Literature on grassland inhabitants is immense and diverse. For the most part, however, many of the workshop participants were disappointed and frustrated at the way in which much of the literature is reported. For various reasons only a small fraction of the known papers concerning large herbivores, other mammals, birds, and insects were applicable to our data gathering exercise. For instance, a vast amount of the literature deals with biological events in time and often does not clearly relate cause and effect relationships. For our efforts, time is not necessarily a driving factor or a control function. Events all occur in time, obviously, but as a function of some definite series of control events. A definite lesson can be provided to many biologists in their approach to experimental design if there is a concerted effort to bring meaning into their work through a modeling approach!

One major exception can be stated to the almost basic axiom that time is not a driving or control variable. This involves the recently elucidated study of free running rhythms. A vast literature has opened up in circadian rhythms, especially for birds and some small rodents and, more recently, approximate annual cycles (circennial rhythms) have been recognized. For the most part, these studies provide an interesting academic base for our

consideration; but, at the moment, we feel that the degree of resolution such studies provide is much more than we can handle. Even so, some note is given to specific instances later in this review where some potential for major revisions of present approaches might be fruitful through investigation of rhythms. Thus for the present, this vast and fast growing literature has been somewhat ignored; however, the pathway is left open when additional materials are needed to augment other sources in the literature or experiments that develop and evolve from the report of this workshop.

Processes or flows and their controls as we perceived them for animal energetics are presented flow by flow followed by a general presentation of the model. This is followed by an analysis of the relationship of this subsystem model to the rest of the models discussed during the workshop and, finally, recommendations are discussed.

7.3 REVIEW

7.3.1 Consumer Type in the Grasslands and Change of State

In order to trace major shifts in energetics demands, it is almost necessary to handle the consumers in the grasslands by differentiating highly specified functional groups, or in some instances, differentiating to the species level. Obviously there are extreme difficulties in being able to keep track of the large number of consumers or even of consumer types. Furthermore, to catalog each consumer and its energetic peculiarities means an endless amount of field and laboratory work to collect adequate data sets so that as much bias as possible is eliminated in a functioning consumer subsystem model. We were not able to make the necessary discriminations during our workshop discussions to recommend definite courses of action.

However, to a certain degree, we were able to condense the list of consumers considered in the grassland ecosystem modeling effort. This listing is shown in Table 7.1.

For many reasons it is desirable to consider the change of state of an animal when tracing its energetic needs through its life history. The changes common to all consumers are those of maturation from an embryonic or fetal state to a newborn or newly hatched state into that of a mature animal, and ultimately to senescence and death. There are obvious differences in energetic needs encountered along this pathway and maturation processes displayed among different groups of animals. It is for these two differences that handling the model becomes so complex.

Thus we went through the mental exercise of listing all the states we thought were applicable to the consumers listed in Table 7.1 and constructed a change-of-state matrix (Table 7.2). Our initial matrix was reworked by Oscar Paris and Martha Wagner and is presented more or less intact from that effort.

7.3.2 Rationale and Development of the Model

Within the final version of the model (Fig. 7.1) we, as a group, identified 14 state variable (SV) compartments necessary to identify flow of materials or to provide materials (such as excrement, SV 607 and SV 609) for other subsystems. Within the basic model there are 11 state variables that were finally agreed upon and kept throughout the workshop meetings. Between these 11 state variables, we identified 12 flows (= 12 processes in this instance). Three other state variables (SV 603, SV 604, and SV 605) were identified, but flow of material comes from outside the model

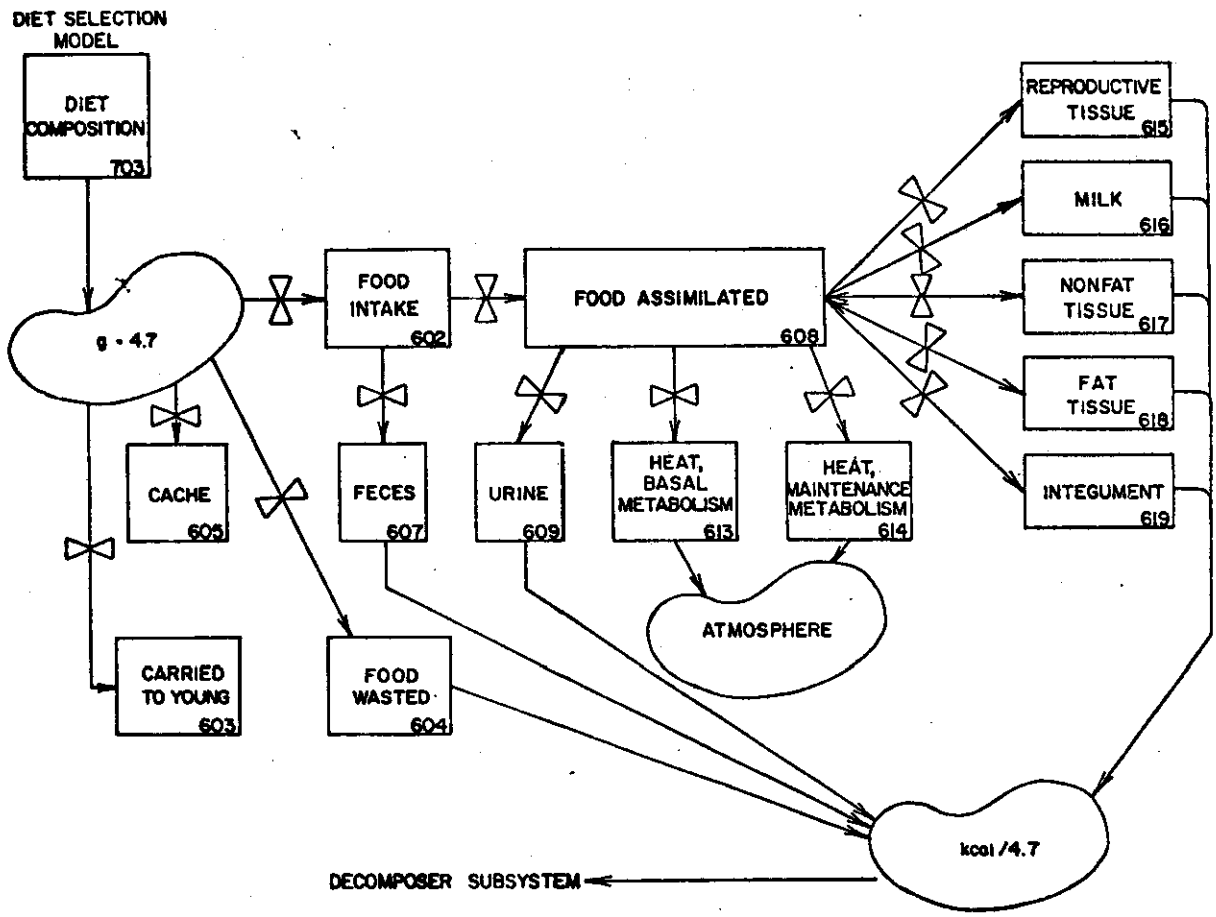
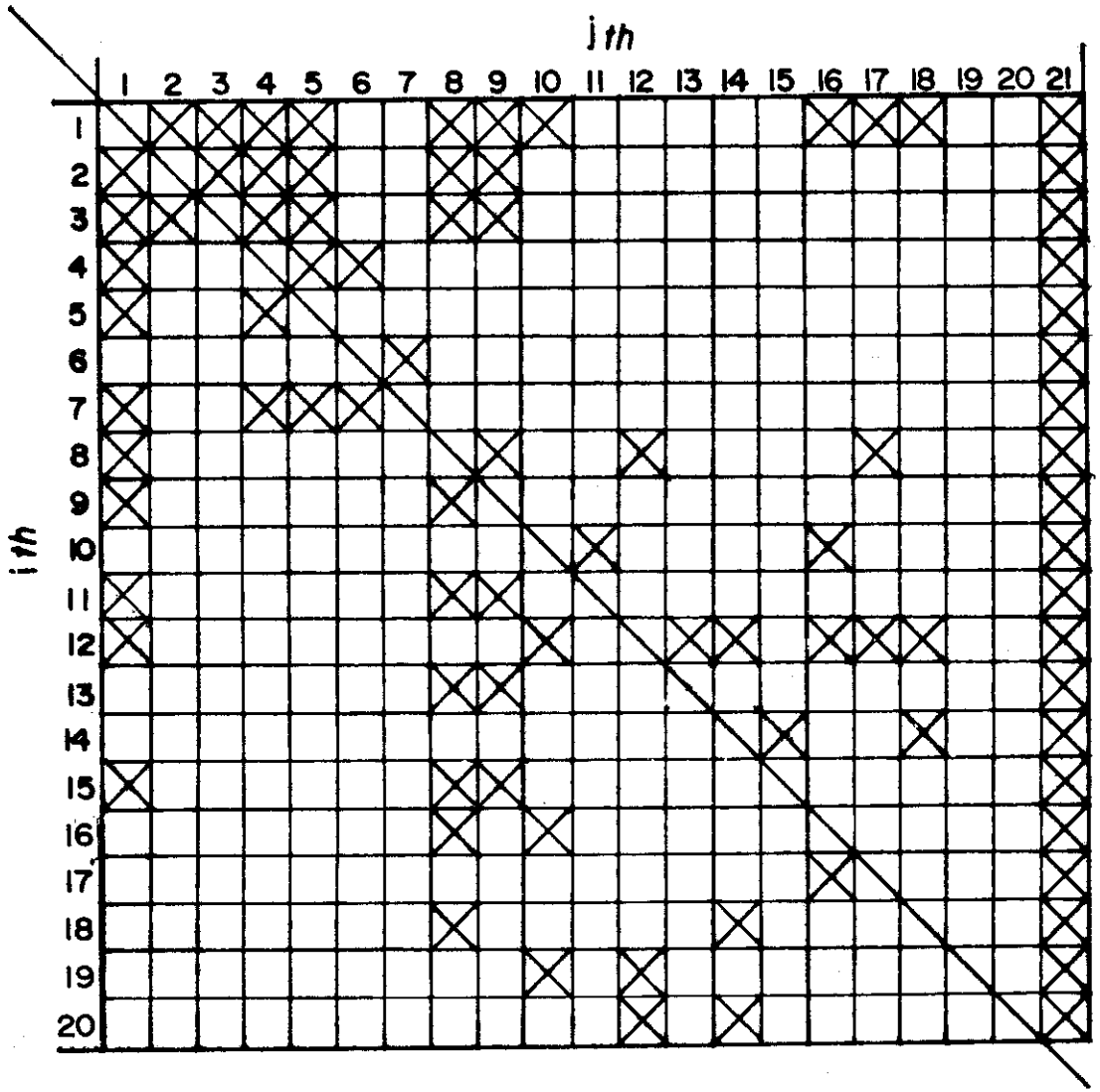


Fig. 7.1. Block diagram of consumer energetics model with state variables (SV in boxes) and processes (arrows) constructed by participants in the Grassland Biome Process Studies Workshop held in January, February, and March, 1972. Controls are not presented; see each process for control information.

Table 7.1. Types of consumers to be considered by U.S. IBP Grassland Biome process studies.

Species/Specialty Listing	Functional Grouping I	Functional Grouping II
Ruminants	Ruminants	Herbivores
	Other Herbivores	Poikilothermic
Shrews	Rodents	Normothermic
Lagomorphs	Lagomorphs	Normothermic/hibernators
Rodents	Insects	Carnivores
Pocket gophers	Birds	Poikilothermic
	Carnivores	Normothermic
Herbivorous insects	Mammals (non-shrew)	Normothermic/hibernators
Omnivorous insects	Shrew	Omnivores/Detrivores
Spiders	Bird	Poikilothermic
Carnivorous insects	Insects	Normothermic
Scavenging insects	Herps	Normothermic/hibernators
	Spiders	Domestic cow
Nematodes	Omnivores	
Mites	Insects	
Isopods	Birds	
Annelid worms	Mammals	
	Detrivores	
Carnivorous birds	Scavenging insects	
Omnivorous birds	Nematodes	
Herbivorous birds	Mites	
	Isopods	
Herps (turtles, snakes, lizards, frogs, toads, and salamanders)	Annelid worms	
Non-shrew carnivorous mammals		



1) Hibernating or Diapausing
2) Preproductive Feeding
3) Preproductive Nonfeeding
4) Male Sexually Active
5) Male Sexually Inactive
6) Male Incubating
7) Male Non-incubating
8) Female Sexually Active
9) Female Sexually Inactive
10) Female Lactating
11) Female Non-lactating
12) Female Gravid
13) Female Non-gravid
14) Female Incubating
15) Female Non-incubating
16) (Combination of 8 & 10) Female Sexually Active Lactating
17) (Combination of 8 & 12) Female Sexually Active Gravid
18) (Combination of 8 & 14) Female Sexually Active Incubating
19) (Combination of 10 & 12) Female Lactating Gravid
20) (Combination of 12 & 14) Female Gravid Incubating
21) Dead

Table 7.2. Matrix showing a possible transfer of state for many of grassland ecosystem consumers. A filled-in compartment denotes a possible change from an *ith* to a *jth* state with probable concomitant energetic changes.

[as a result of food handled (SV 703) defined by the diet selection model] and are dead-end as far as we are concerned. Thus, in total, there are 14 state variables and 6 flows to be dealt with (Table 7.3). Although in this initial report data are not necessarily presented for all, 27 controls are described and deemed important for all the above processes (Table 7.4). Many of the designated controls are imposed several times throughout the model, thus probably making certain parts of the model redundant. Even so, it was felt by the group that it was better to keep each of the controls and processes in the model for the time being, rather than to drop certain parts in favor of other portions and run the risk of missing certain items. Modifications, if necessary, can be made at a later time when following a first pass through the literature pertinent to the model.

7.3.3 Description of the Model

Food, after it has been gathered in SV 703 and mathematically converted to calories per meter squared (see Section 7.4.1), is taken in by the animal through the process of eating (703-602). Other food handling processes are carrying to young (703-603), wasting (703-604), and storing (703-605). These latter three are quite specific processes and are perhaps of little importance in terms of total energy flow. Thus, academically, they are important to other life history events of specific consumers such as small rodents that cut and store grass and other plants, grasshoppers or rodents that cut and waste plants, or predators that catch and carry food to young at nests or dens.

In the main energy flow pathway of the model after food is ingested, the process of digestion (602-608) delivers the metabolizable portion to SV 608

Table 7.3. Listing of processes for consumer energetics model.

Flow Designation	Section	Process
1. (703-602)	7.4.1	Food ingestion (eating)
2. (703-603)	7.4.2	Carrying food to young
3. (703-604)	7.4.3	Food wasting
4. (703-605)	7.4.4	Storing of food
5. (602-607)	7.4.5	Defecation
6. (602-608)	7.4.6	Digestion
7. (608-609)	7.4.7	Urination
8. (608-613)	7.4.8	Standard (or Basal) metabolism
9. (608-614)	7.4.9	Maintenance metabolism
10. (608-615)	7.4.10	Reproduction
11. (608-616)	7.4.11	Lactation
12. (608-617)	7.4.12	Growth of nonfat tissue
13. (608-618)	7.4.12	Growth of fat tissue
14. (608-619)	7.4.13	Growth of integument
15. (617-608)	7.4.14	Protein catabolism
16. (618-608)	7.4.15	Fat catabolism

Table 7.4. Tabulation of controls by workshop members thought to be operating on processes within the consumer energetics model. Note that not all are reported in this draft.

Control	Units	(703-602)	(703-603)	(703-604)	(703-605)	(602-607)	(602-608)	(608-609)	(608-613)	(608-614)	(608-615)	(608-616)	(608-617)	(608-618)	(608-619)	(617-608)	(618-608)
1. Food quality	% protein, nutrients	X				X	X										
2. Body size	$W^{0.75}$	X						X	X	X							
3. Temperature	°C	X			X			X	X	X							
4. Wind	mph	X							X	X							
5. Snow cover	cm	X															
6. Hunger level	Food intake rate[a/]	X															
7. Rain or water	cm/hr or cc	X						X	X	X							
8. Digestibility	g digested/g ingested	X															
9. Food availability	g/m^2	X		X	X								X	X		X	X
10. Density of species	Individuals or g/m^2	X			X				X	X							
11. Competitors	Individuals or g/m^2	X							X	X							
12. Predators	Individuals or g/m^2	X							X	X							
13. Disease or parasites		X				X	X		X	X							
14. Number of young or weight	Number or g/m^2		X							X		X					
15. Age of young	Days		X														
16. Phenophase	Time of year				X	X	X		X	X					X		
17. Food handled	g/m^2				X					X							
18. Rate of food ingestion	g/hr					X	X										
19. Animal age	Age in days	X				X	X		X	X	X	X	X	X	X	X	X
20. Rate of assimilation	kcal or mg/g food ingested					X	X					X	X	X	X	X	X
21. Lactation	g milk/(g female · day)	X							X	X	X		X	X		X	X
22. State of reproduction	g embryo or fetus/female								X	X	X	X	X	X		X	X
23. Fat feedback	g fat/g body wt													X			
24. Rate of digestion	g or cal/hr	X											X				X
25. Food capacity	g or cal/animal	X															
26. Aggregation	g/cm^2	X															
27. Blood metabolites	mg/cc	X															

[a/] Times t and t-1.

(food assimilated). The undigested portion is passed out of the organism through defecation (602-607) and is made available to the decomposer subsystem.

Assimilated food is metabolized by the body to produce metabolic by-products, heat, and various other products, including tissue and milk in mammals. Urine (SV 609) is disposed of and made available to the decomposer subsystem through the process of urination (608-609). The process of reproduction (608-615) gives gamete development and production of young; lactation (608-616) provides milk in mammals; growth and maintenance of nonfat tissue (608-617) provides muscle tissue, bone, and cartilage; synthesis of fat tissue (608-618) provides fat deposits that become energy stores for the organism; and growth of integument (608-619) provides skin, hair, feathers, and chitinous exoskeletons for invertebrates--all of which are major considerations for most consumers. Protein catabolism (617-608) is a physiologically known process in many animal groups that can provide a certain amount of energy to the individual, but is probably of little significance to the model. On the other hand, fat catabolism (618-608) is quite important since it is principally from fat stores that many animals derive their energy source during periods of fasting.

Two other processes deal with metabolism, standard metabolism (608-613) or perhaps basal metabolism, if this concept is preferred, and maintenance metabolism (608-614). These two processes, for the purposes of the energetics model, can be construed as being the most important within the model for maintaining a level of physiological activity for life history functions so that a given animal may, on the average, be successful during its life term. The measure of success in time is, of course, successful adaptation to the environment by providing a sequence of generations.

In order to make this model more meaningful, the basis for its operation must be discussed. Normally one would construct a collection of physiological processes producing what is ultimately observed as basal (or standard) or maintenance metabolism for the organism. Thus the sum total of all physiological processes would yield the heat produced by the organism which is what we define as total metabolic activity of that organism. But to attempt to model each of the processes and to sum up all the products to equal the total metabolic output becomes a Herculean task which can become easily bogged down. On the other hand, if we accept the fact that under a given set of circumstances over a long period of time, an animal or animal species that is well adapted to its environment will, a priori, demonstrate an empirical metabolic level necessary to carry out all the requisite life history functions. Thus it is this parameter that becomes an identifying characteristic of members of a species no matter what niche or other ecological categorization is pertinent for defining that animal's association in the ecosystem. Once we have a basic description of the metabolic relationship to basic parameters, such as size, it is then possible to identify controls on the metabolic rate in differing sets of conditions and use these data in the modeling effort to act as controls or valves on the metabolic rate which, in turn, regulates flow elsewhere in the model. We predict, as noted in the first part of this introduction, that the main effect or the most sensitive area will be exhibited in the process of food intake or eating (703-602).

7.4 PROCESS AND CONTROL DESCRIPTIONS

7.4.1 (703-602) Food Intake (Eating)

This flow of material from the diet composition box (SV 703) presented in the diet selection model (Chapter 6) is one of the most basic considerations of the energetics model. For literature-reported controls, we expressed eating rates (Fig. 7.2) as follows:

Food intake = f(body weight, digestibility of gross energy, nutrient content of food, lactation, food availability, rate of digestion, food capacity, blood metabolites, temperature)

For other probable but largely unknown controls, we imagined:

Food intake = f(age, wind, body condition, snow cover, hunger level, rain, density of species, competitors, predators, disease or parasites)

Besides having the most controls described for any process within this model, it also has the most controls potentially attributable to a process within the model (Table 7.4).

Output of food materials obtained in the diet selection process is measured in g/(m^2 · day) and must be put into a sink-source complex (Forrester, 1961, p. 82) in order to interface with the energy quanta used in this model. There is a rather wide range of total energy values obtained from burning various types of foods, but generally the Zuntz-Schumberg table is accepted (Hawk, Oser, and Summerson, 1954). The caloric value for fats is 4.69; for carbohydrates 5.047; and for proteins 4.69, although Brody (1945) reported

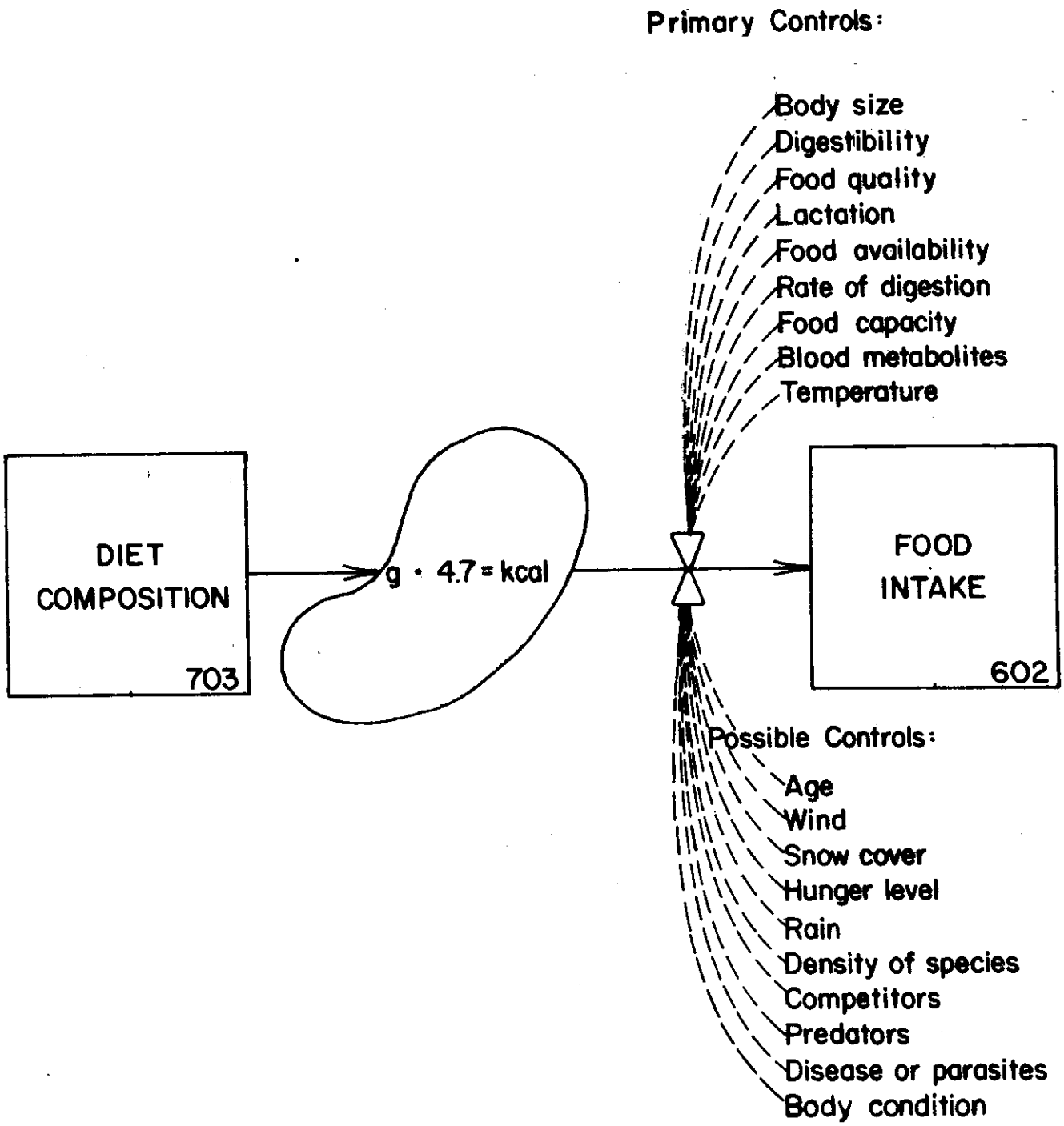


Fig. 7.2. Schematic of process (703-602) with its controls.

4.85. The conversion factor used by Brody (1945) for total digestible nutrients is 4.0 kcal/g dry wt of food material; but, as Brody noted, the exact value depends upon several variables such as species of consumer and type of food being consumed. Kleiber (1961) reported a different set of values for caloric equivalents (Table 7.3, p. 125) and argued logically for the value 4.7 kcal/liter (standard) O_2 consumed or 105 kcal/mole O_2. This latter value is the one we (participants in this section of the workshop) recommend.

7.4.1.1 Body size, weight in kilograms, or metabolic weight (= weight$^{0.75}$). For general animal food intake rates Kleiber (1961) stated that two consumers are on the same level when their intake of metabolizable food energy (= heat of combustion of food less heat of combustion of feces, urine, and methane) "is the same multiple or the same fraction of their standard metabolic rate. Since the standard metabolic rate is proportional to the metabolic body size, ... two (*or more*) animals may also be regarded as being on the same level of food intake when they consume the same amount of metabolizable food energy per kg$^{3/4}$ ..." (weight in kg$^{3/4}$ is Kleiber's unit of metabolic body size, italics mine). Kleiber (1961) also stated that not only is the total energy demand a function of the metabolic body size, but also requirements for protein and for most vitamins can be similarly expressed "because these dietary requirements are directly related to energy metabolism."

Additionally, Brody (1945) discussed physiological homeostasis at length and shows how maintenance metabolism is related to body weight first of all, and secondly, how energy requirements for work beyond maintenance is related to body size.

Arguments exist in the literature as to what equations should be used for various species or animal groups. I have listed some of the more accepted values in sections 7.4.8 and 7.4.9 dealing with processes (608-613) and (608-614).

For the most part, recent reviewers have dealt mainly with the mammals and birds in synthesizing common metabolic rates on a regression basis. A similar need is apparent for the invertebrates, but is beyond the scope of this initial report. However, certain specific information is available for insects and is shown in Fig. 7.3 and 7.4. The material reported here has been reworked from Parker (1930) and Smith (1959) by Robert E. Pfadt and myself.

Consumption rates are expressed in relation to body size (also an age classification) measured in grams. A family of curves is presented since the process is also temperature dependent. For six ages of the migratory grasshopper (*Melanoplus sanguinipes*) food intake rates (total wet weight) are estimated to be:

1. $Y = 0.693 + 0.033\ X$, $(R^2 = 0.965)$ at 22°C (7.1)
2. $Y = 1.862 + 0.045\ X$, $(R^2 = 0.914)$ at 27°C (7.2)
3. $Y = 5.214 + 0.143\ X$, $(R^2 = 0.824)$ at 32°C (7.3)
4. $Y = 1.273 + 0.170\ X$, $(R^2 = 0.996)$ at 37°C (7.4)
5. $Y = 3.224 + 0.157\ X$, $(R^2 = 0.948)$ for average of 32°C and 37°C data (7.5)

where Y = food intake rates

X = grasshopper weights

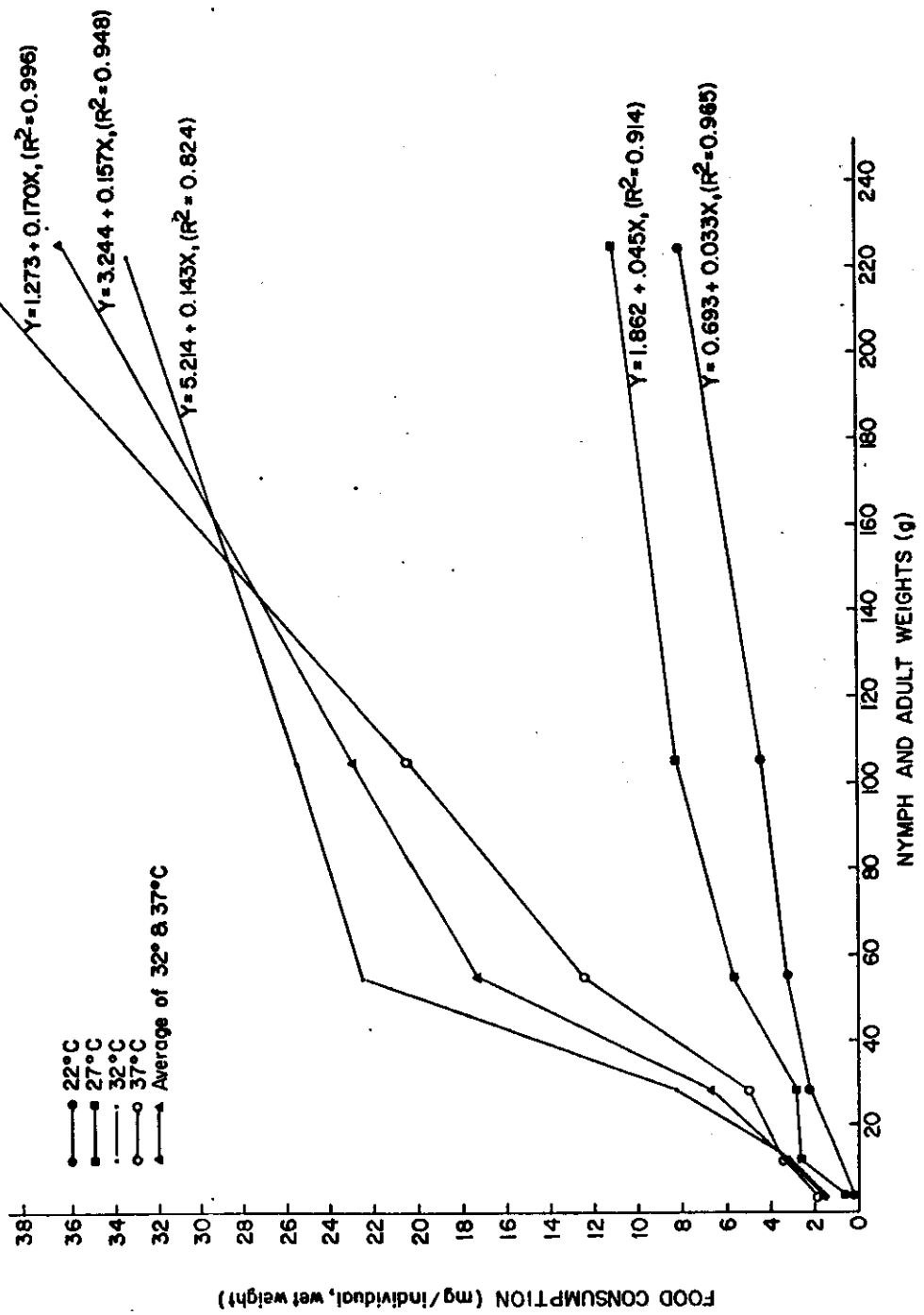


Fig. 7.3. Total wet weight food consumption rates for various weight/age classes of the grasshopper, *Melanoplus sanguinipes*, for a series of temperatures (Parker, 1930; Smith, 1959).

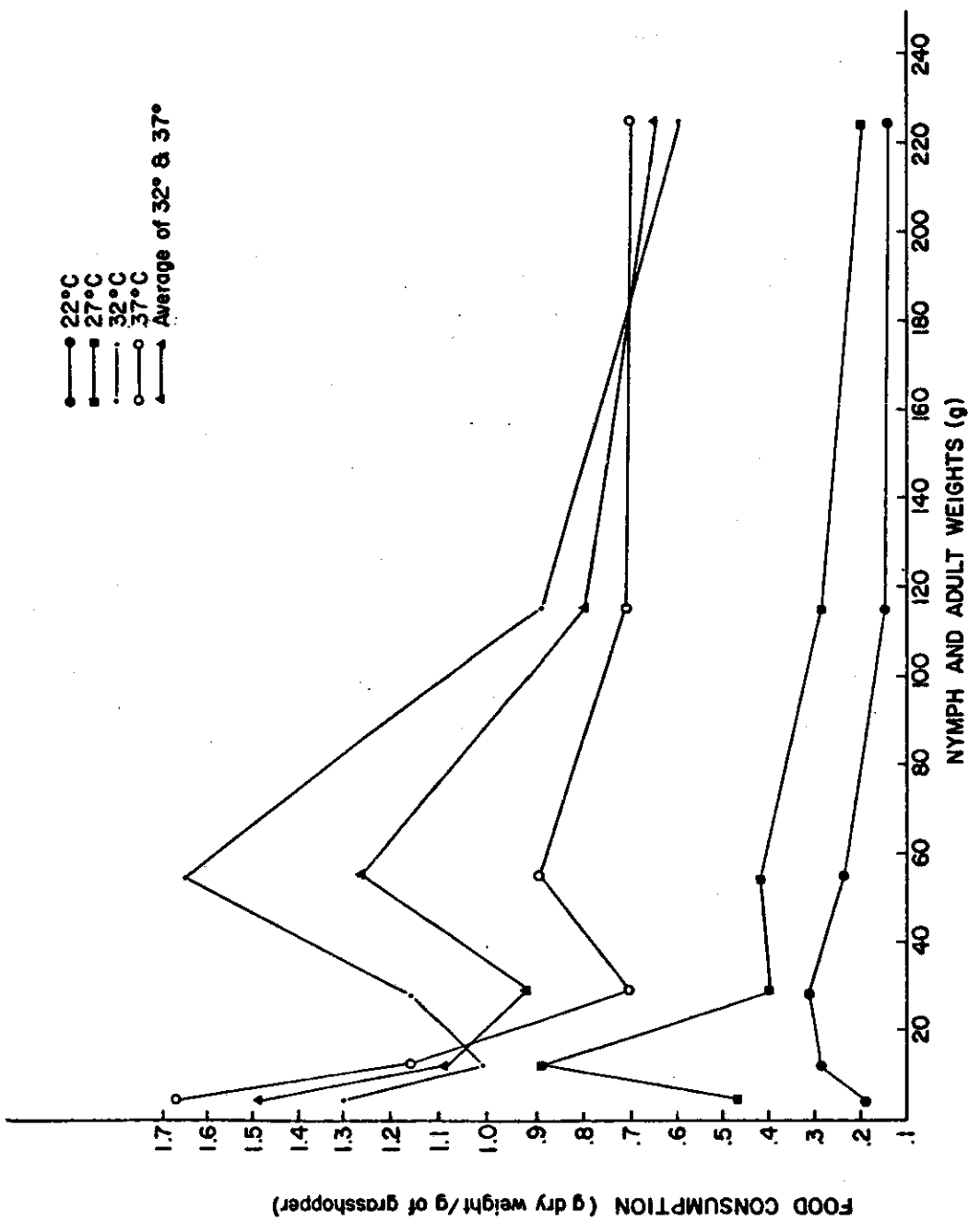


Fig. 7.4. Total dry weight food consumption rates for various weight/age classes of the grasshopper (*Melanoplus sanguinipes*) for a series of temperatures (Parker, 1930; Smith, 1959).

Aside from the metabolic data, there is other literature dealing specifically with food intake. Schoener (1968) summarized much of the avian literature and called attention to older reports giving weight-related intake rates (notably Nice, 1938). However, Schoener's report (p. 127) suffers from an erroneous presentation of avian daily food consumption levels as a function of weight; he gives a slope value of 1.09 ± 0.11, whereas a recomputation of the values from the original data gives a relationship of

$$\log_{10} Y = \log_{10} 0.526 + 0.626 \log_{10} X, \ (R^2 = 0.958) \qquad (7.6)$$

The data are presented in Fig. 7.5. The original data were presented in terms of food intake per day measured as a function of percent of total body weight. This percent relationship has also been calculated from Nice's (1938) data and is

$$\log_{10} Y = \log_{10} 52.112 - 0.373 \log_{10} X, \ (R^2 = 0.889) \qquad (7.7)$$

The important feature of the above relationships for birds is that the values have been taken from individual species representing six orders and nine families, ranging from large predatory falconiforms to small seed-eating passerine birds. Nice (1938) originally noted that the size-dependent features were very likely related to heat loss expressed as a function of the relative amount of surface compared to weight.

Nothing is known about the status of the animals from this report, but it must be assumed that they were in constrained conditions so the data most likely represent a maintenance type of existence with few or no normal movement patterns. Even so, it is significant that such a good relationship

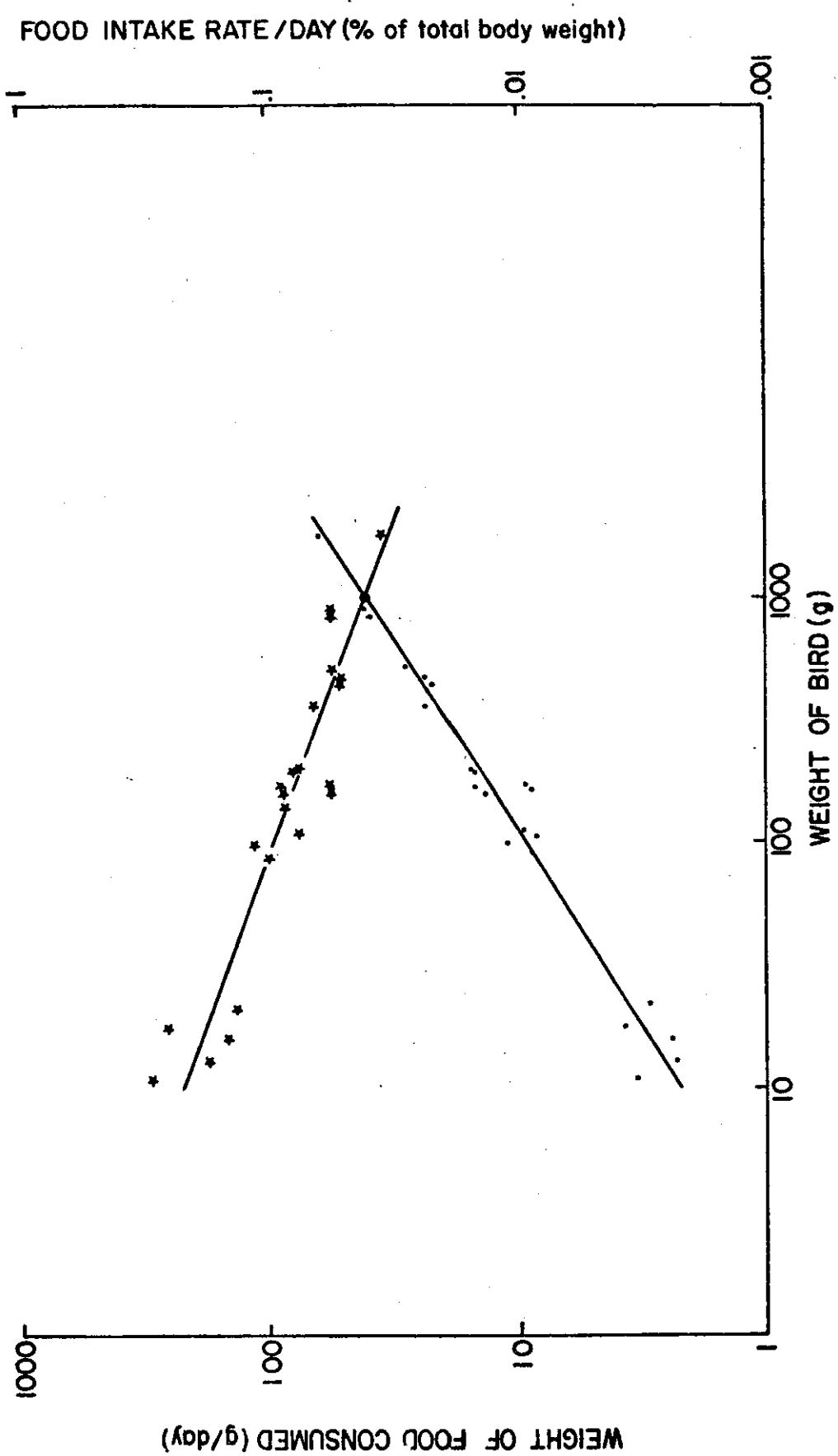


Fig. 7.5. Relationship of total food intake (·) and percent of total body weight per day (*) to weight of bird (Nice, 1938).

exists for these birds, and the data provide a good basis for treating diverse avian consumers with common sets of regression curves and for defining intake rates over a 24-hr period as a function of weight. For a first approximation, this avenue can give, at worst, low resolution values for food intake. As more information is collected, a finer degree of resolution can be obtained that represents meaningful food intake needs of birds over a given period of time throughout the year.

Total intake rate has been correlated with body size and concurrent maturation for the European hare (*Lepus europaeus*) (Pilarska, 1969). The intake rate, measured in kcal/(animal • day), is also clearly a double logarithmic function (Fig. 7.6) with

$$\log_{10} Y = \log_{10} 0.7071 + 0.857 \log_{10} X, \ (R^2 = 0.988) \qquad (7.8)$$

as the definitive expression for the data.

These data serve as a basis for many other consumers in the general relationship of the curve to the weight of the animal. The slope need not be the same for all consumers since there are likely species-specific features about the growth rate and requirements for the animals presented thus far that are not shared by other types of vertebrates for which there is no data accumulated to this point.

Unpublished data from A. Johanningsmeier indicates that vole (*Microtus* sp.) intake rates range from 0.67 to 1.43 kcal/(g • day) on grass diets. Golley (1960) reported that the consumption rate is 0.53 to 1.55 kcal/(g • day). For jackrabbits (*Lepus californicus*) the intake rate is 0.21 kcal/(g • day) on alfalfa and 0.22 kcal/(g • day) on native forage which includes green material (A. Johanningsmeier, unpublished data).

Dry weight consumption values measured in grams dry weight per gram of grasshopper presents a slightly different picture although the data are still clearly temperature dependent. In general, the largest intake rate per unit weight exists during the early nymphal stages in high temperatures and gradually levels off during later instar and adult periods. It can also be inferred that there will be a threshold effect for the warmer temperatures. There is no indication what the threshold will be, but perhaps the data for 32°C and 37°C noted for the grasshopper can be grouped together. This means that for the initial material, equation (7.5) above replaces (7.3) and (7.4).

These data should be accepted with some caution since they are the results of other synthesis work, not carefully designed experiments to show size-related cause and effect. New experiments are needed to confirm these estimates. In general, no feeding of a similar nature is known for other insects at this time. Thus all that can be done at the moment is to utilize the general shape of these curves for treating other insect data and to speculate that size-specific intercepts can be inferred on the basis of weight. However, there is some indication that the 37°C data should be used with caution because of an increased mortality rate observable in Parker's (1930) original data.

A considerable amount of literature also exists for metabolic rates for birds and how size affects total metabolism. More is stated about these data in the section dealing with metabolic rates; but as previously noted, there is some concern here where total intake rate can be made quite dependent upon metabolic rate, which in turn has been shown to be size dependent.

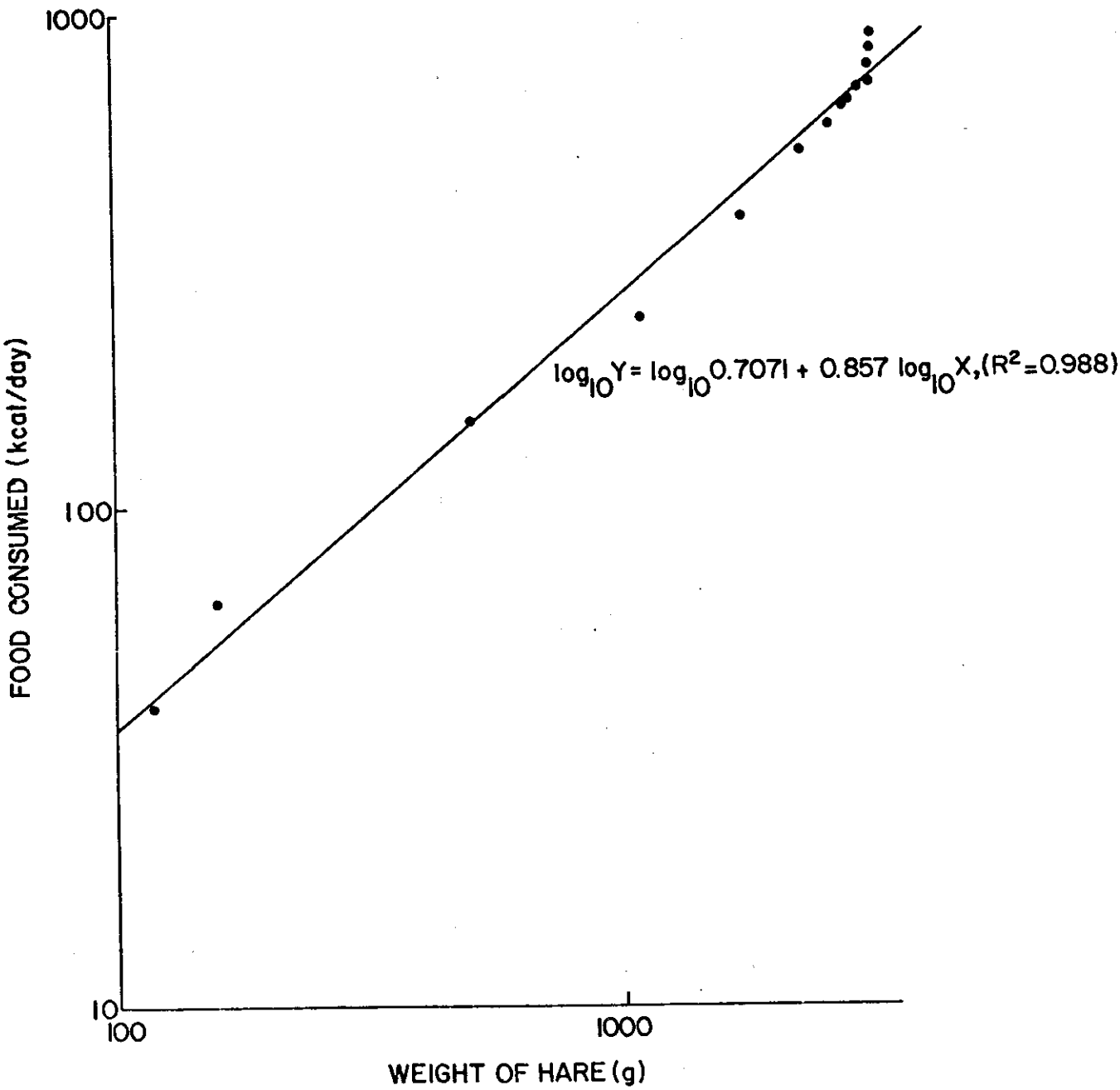


Fig. 7.6. Relationship of total food intake to total body weight of the European hare (Pilarska, 1969).

Drozdz (1968) reported intake rates in total weight (wet weight assumed), total caloric value, and the total caloric amount assimilated for four species of small rodents in Polish grasslands and forests (Table 7.5). The data were collected under laboratory conditions at 20°C. In his summary, Drozdz (1968) specified intake rates for assimilated food as being 0.432 kcal/(g · day) for *Clethrionomys glareolus* (average weight was 22.8 g), 0.462 kcal/(g · day) for *Microtus arvalis* (average weight was 22.2 g), 0.561 kcal/(g · day) for *Apodemus agrarius* (average weight was 21.5 g), and 0.387 kcal/(g · day) for *Apodemus flavicollis* (average weight was 26.9 g).

Johnson and Groepper (1970) reported intake rates for nine species of small rodents; the data are presented in Table 7.6 and Fig. 7.7. Even though there are some differences in the diets of the rodents, there is a clear relationship in the rate of the caloric intake per unit weight to size ($\log_{10} Y = \log_{10} 1292.72 - 0.3022 \log_{10} X$) among these nine rodents.

Food intake rates change during the growth and development of young of one species in a manner similar to differences noted among different size animals from different species. Royama (1966) presented data for young of the Great Tit (*Parus major*) that show a general increase with increasing weight.

The general shape of the curve is sigmoid, indicating a logistic relationship between the amount of food ingested with increasing weight which is a direct function of increasing age of the nestling (Fig. 7.8). The logistic relationship is not reported in Royama's paper, nor are the data for the figure tabulated (Royama, 1966, Fig. 7, redrawn here as Fig. 7.8). Consequently, I have extracted approximate data from his figure, and these are

Table 7.5. Daily consumption rates and assimilation of foods by common voles, bank voles, and mice (means for 10 to 15 animals ± standard deviations) (from Drozdz, 1968).

Species	Diet	Average Body Weight (g)	Consumption (g)	Consumption (kcal)	Assimilation (kcal)
Microtus arvalis	Oats	22.6 ± 2.2	4.24 ± 0.73	16.20 ± 2.81	14.52 ± 2.01
	Green wheat	21.8 ± 2.1	25.00 ± 1.41	15.01 ± 0.85	9.80 ± 0.75
Clethrionomys glareolus	Beechmast	22.7 ± 2.6	1.92 ± 0.25	13.25 ± 1.73	11.79 ± 1.73
	Mixed	23.1 ± 2.1	2.26 ± 0.30	25.18 ± 2.05	12.90 ± 2.03
	Oats	22.9 ± 2.0	3.40 ± 0.48	13.01 ± 1.85	11.20 ± 1.87
	Greens	22.4 ± 3.6	18.26 ± 2.90	12.75 ± 2.07	9.23 ± 1.88
Apodemus agrarius	Oats	22.3 ± 1.6	3.46 ± 0.53	13.24 ± 2.06	11.78 ± 1.12
	Compound	20.6 ± 2.2	3.00 ± 0.25	16.92 ± 1.45	15.04 ± 0.81
Apodemus flavicollis	Hazelnuts	27.9 ± 4.1	2.12 ± 0.33	16.28 ± 2.56	14.84 ± 1.91
	Acorns	24.1 ± 3.2	3.50 ± 0.55	12.78 ± 1.95	10.07 ± 1.55
	Mixed	28.8 ± 5.5	2.06 ± 0.31	14.66 ± 2.92	12.93 ± 2.01

Table 7.6. Intake rates in cal/(g • day) for nine species of small rodents (from Johnson and Groepper, 1970).

Species	Sample Size	Diet	Mean Weight (g)	Energy Intake Maintenance (cal/g/day)
Deer mouse	6	Rat chow	20.1	485 ± 25
Meadow vole	5	Rat chow	28.6	658 ± 54
Red-backed vole	5	Rat chow	20.5	734 ± 23
Meadow jumping mouse	8	Rat chow	16.1	778 ± 46
Feral house mouse	5	Rat chow	16.2	668 ± 19
Ord's kangaroo rat	5	Rolled oats	63.0	268 ± 13
	4	Pearled barley	56.4	294 ± 6
Olive-backed pocket mouse	6	Rolled oats	10.9	583 ± 44
	2	Pearled barley	12.2	336
Richardson ground squirrel	3	Rat chow	303.1	244 ± 43
Thirteen-lined ground squirrel	5	Rat chow	132.4	315 ± 14

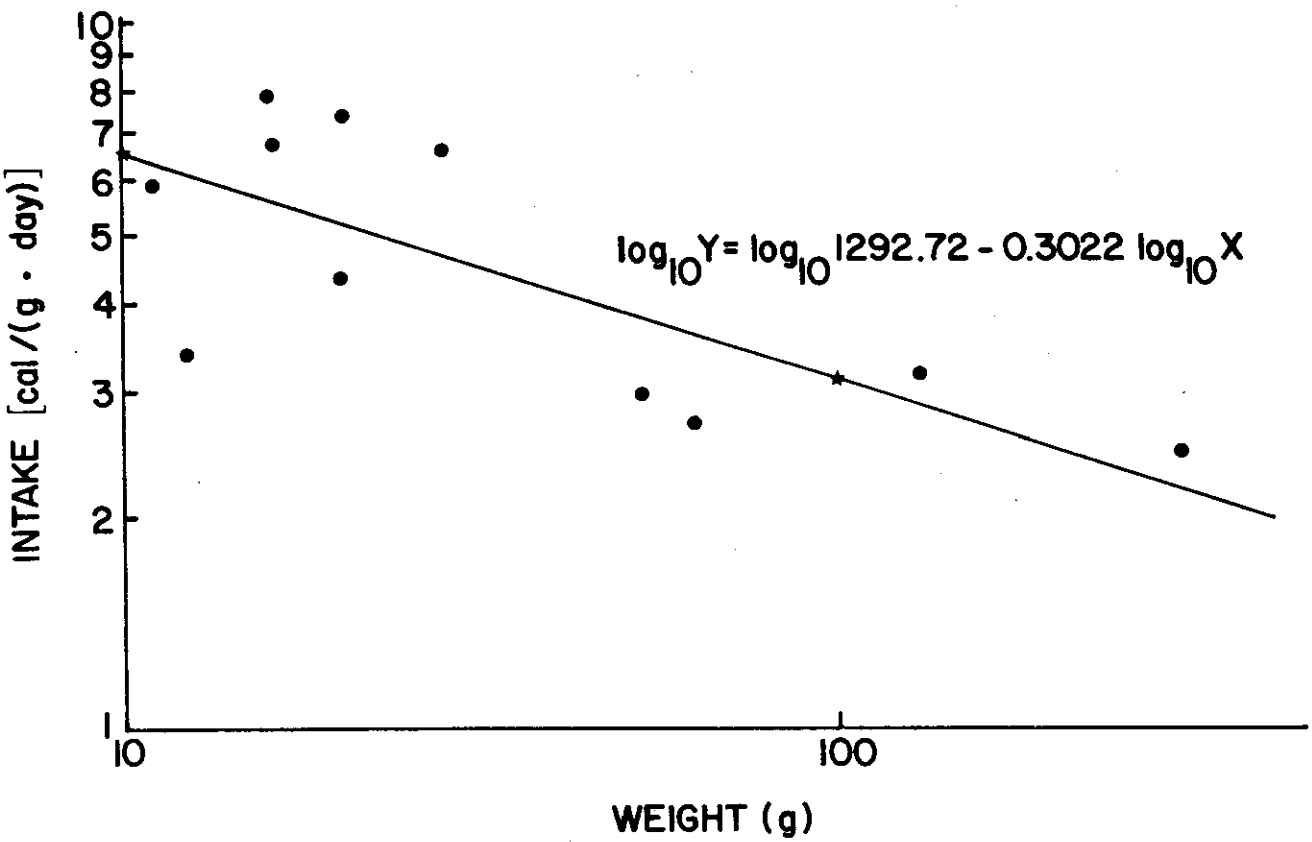


Fig. 7.7. Relationship of intake rates to weight for nine species of small rodents (Johnson and Groepper, 1970).

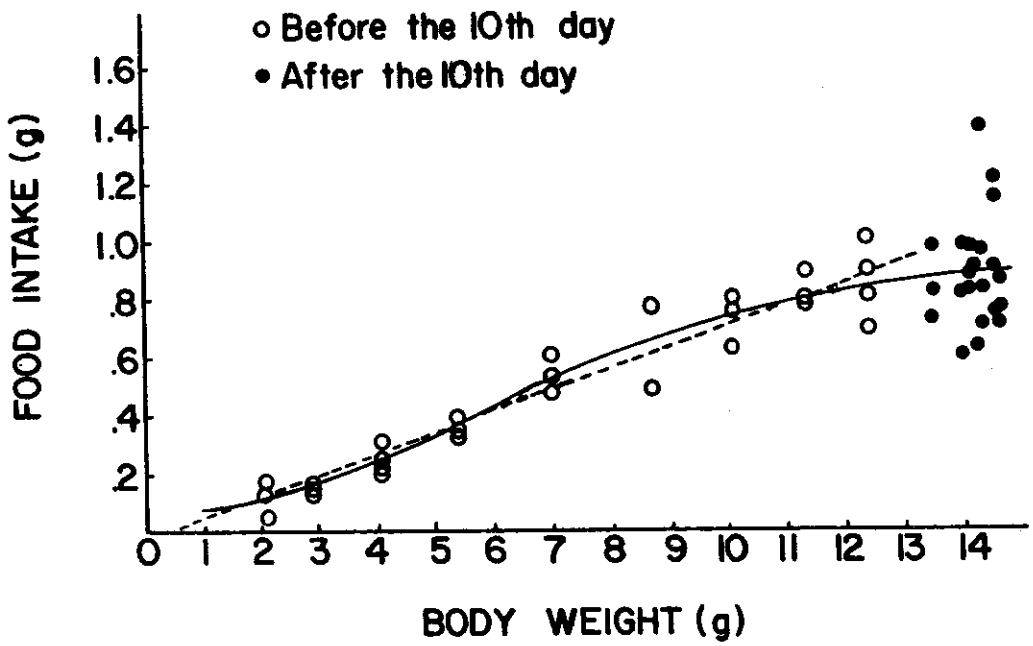


Fig. 7.8. The relationship between the average food intake (dry weight in g) and the average body weight (fresh weight in g) of individual nestling Great Tits (*Parus major*) (from Royama, 1966).

presented in Table 7.7. I also have computed the intake rates in grams of dry weight food per unit weight nestling and compared these with the total weight of the nestling. By expressing the data in this way, it appears that the relationship is parabolic in form (Fig. 7.9). A linear regression [$Y = 0.60 + 0.0004\ X$, ($R^2 = 0.019$)] does not give a good fit; thus there is probably some, as yet undefined, relation between the food intake rate expressed in grams per unit weight compared to the size of the bird for Royama's data (and perhaps other data similar to that reported by Royama) during growth and maturation of small animals. A similar supposition was discussed in terms of undefined physiological stress to nestling Red-winged Blackbirds by Ronald, Foster, and Dyer (1968).

In contrast to the above picture of food intake per unit weight as the animal grows, Royama (1966) presented data which show the effect of brood size on the rate of intake per individual (Fig. 7.10). I have not been able to compute the relationship, but would estimate that here too, as reported for mice (Prychodko, 1958), the fit is exponential in form. Again the hypothesis is that, up to a certain point, several animals in close proximity tend to share and redistribute radiated energy, thus decreasing the metabolic rate per individual and ultimately the food requirements. The addition of individuals in this manner tends to function similarly to addition of cells to a clone. Thus the brood becomes a "superorganism" rather than a collection of individuals huddling together.

7.4.1.2 Density of species. Aggregation, i.e., grouping of two or more individuals, has been shown to affect total intake rates for the MA_f/SP strain of laboratory mice (*Mus musculus*) (Hart, 1971; Prychodko, 1958). Data were

Table 7.7. Great Tit nestling development and food intake levels.

Weight of Young (g)	Weight of Food (g)	Weight of Food/ g of Young
2.1	0.05	0.024
2.1	0.13	0.061
2.1	0.17	0.082
2.9	0.11	0.039
2.9	0.14	0.048
2.9	0.17	0.057
4.1	0.20	0.050
4.1	0.23	0.056
4.1	0.25	0.062
4.1	0.31	0.075
5.4	0.35	0.065
5.4	0.33	0.061
5.4	0.38	0.071
7.0	0.47	0.067
7.0	0.52	0.075
7.0	0.60	0.085
8.7	0.48	0.056
8.7	0.76	0.087
10.1	0.62	0.062
10.1	0.75	0.074
10.1	0.79	0.078
11.3	0.76	0.068
11.3	0.79	0.070
11.3	0.88	0.078
12.4	0.69	0.055
12.4	0.80	0.065
12.4	0.89	0.071
12.4	0.99	0.080
13.6	0.73	0.053
13.6	0.81	0.060
13.6	0.97	0.071
14.0	0.60	0.043
14.0	0.81	0.058
14.0	0.98	0.070

Table 7.7. Continued.

Weight of Young (g)	Weight of Food (g)	Weight of Food/ g of Young
14.1	0.83	0.059
14.1	0.87	0.061
14.1	0.97	0.069
14.1	0.90	0.064
14.3	0.64	0.045
14.3	0.95	0.067
14.3	1.37	0.096
14.5	0.74	0.051
14.5	0.90	0.062
14.5	1.13	0.078
14.5	1.20	0.083
14.7	0.71	0.048
14.7	0.75	0.051
14.7	0.85	0.058

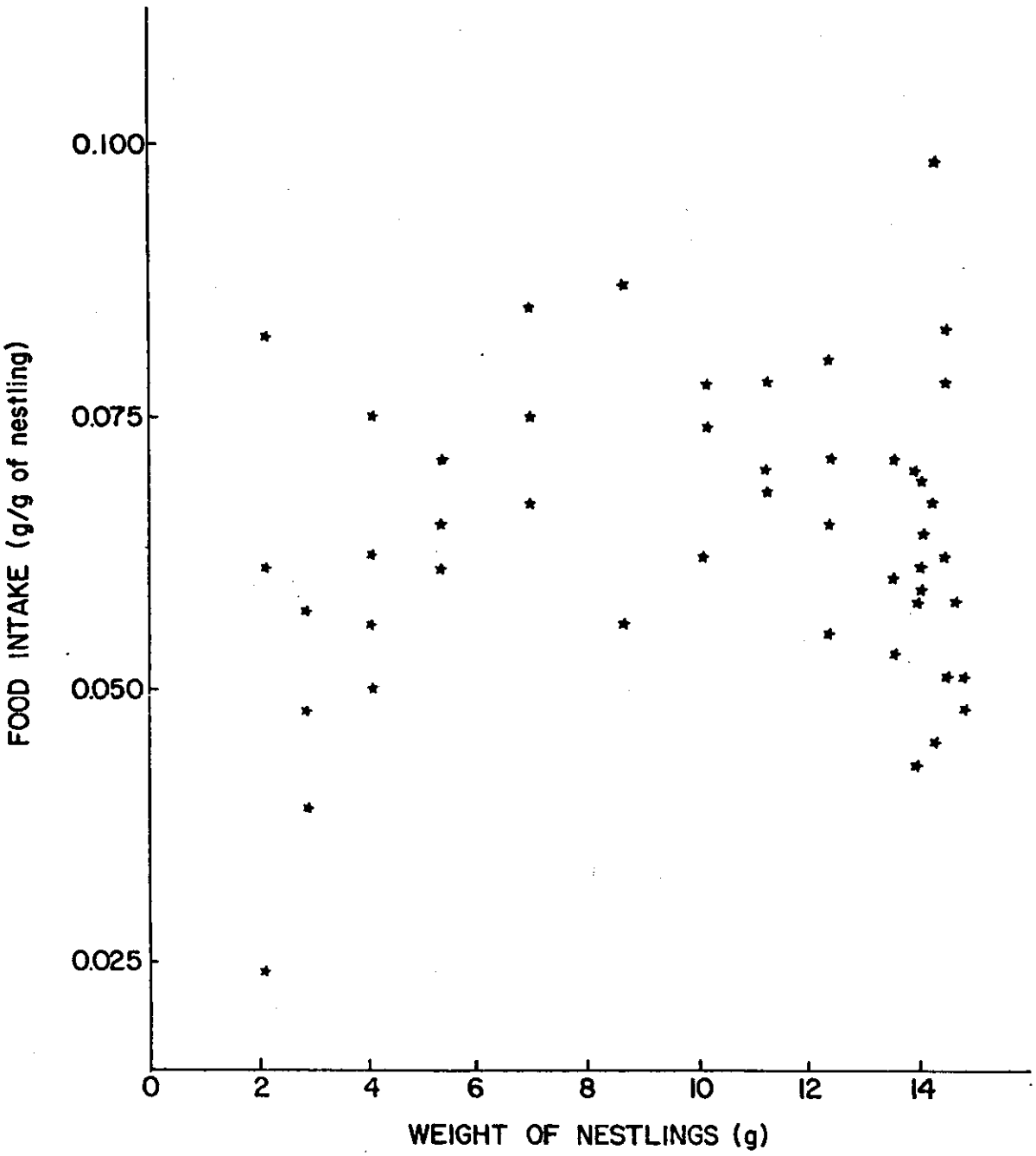


Fig. 7.9. Relationship of food intake to nestling Great Tit weights (Royama, 1966).

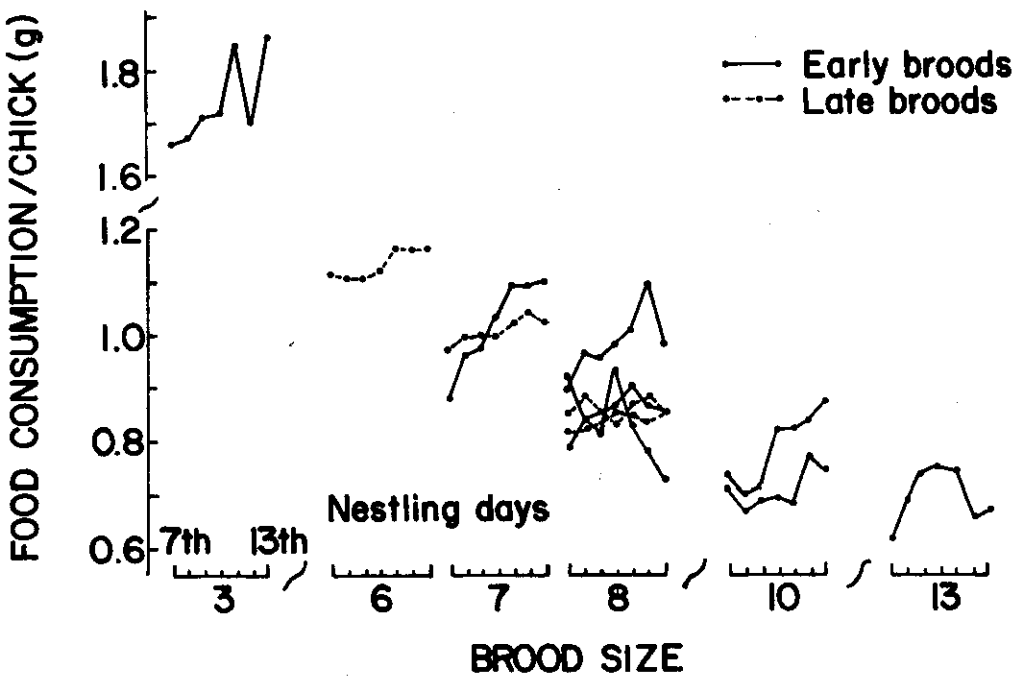


Fig. 7.10. The inverse relationship between the food consumption (dry weight in g) per nestling Great Tit (*Parus major*) per day and the brood size. A period between only the 7th and the 13th nestling days is considered (from Royama, 1966).

reported to show how food consumption was affected by temperature levels for single animals, for groups of two, and for groups of five (Fig. 7.11). Basically the data show much the same response as standard metabolism demonstrates in response to changing temperature when animals are tested below the thermoneutral zone or point. Clearly, it can be seen that there is a pronounced group response; the food intakes for groups of two and five are significantly lower than the food intake rates for individuals held alone in cages. The relationship can be seen much more clearly when the data are rearranged in the form shown in Fig. 7.12. Even though the original data are not available for statistical testing, one can see the remarkably constant relationship between mean food consumption per gram body weight and mean food consumption per mouse when compared with the number of mice in three test conditions. The data are summarized below. For mean food consumption measured in grams per gram body weight:

1. At 25°C: $\log_{10} Y = \log_{10} 0.166 - 0.101 \log_{10} X$, $(R^2 = 0.997)$. (7.9)
2. At 4°C: $\log_{10} Y = \log_{10} 0.314 - 0.219 \log_{10} X$, $(R^2 = 1.0)$. (7.10)
3. At -3°C: $\log_{10} Y = \log_{10} 0.350 - 0.208 \log_{10} X$, $(R^2 = 1.0)$. (7.11)

For mean food consumption per mouse:

1. At 25°C: $\log_{10} Y = \log_{10} 4.15 - 0.64 \log_{10} X$, $(R^2 = 0.806)$. (7.12)
2. At 4°C: $\log_{10} Y = \log_{10} 7.819 - 0.266 \log_{10} X$, $(R^2 = 0.96)$. (7.13)
3. At -3°C: $\log_{10} Y = \log_{10} 8.862 - 0.273 \log_{10} X$, $(R^2 = 1.00)$. (7.14)

where

$\log_{10} X$ = log of number of animals in each experimental group

$\log_{10} Y$ = log of mean food consumption for each measurement condition

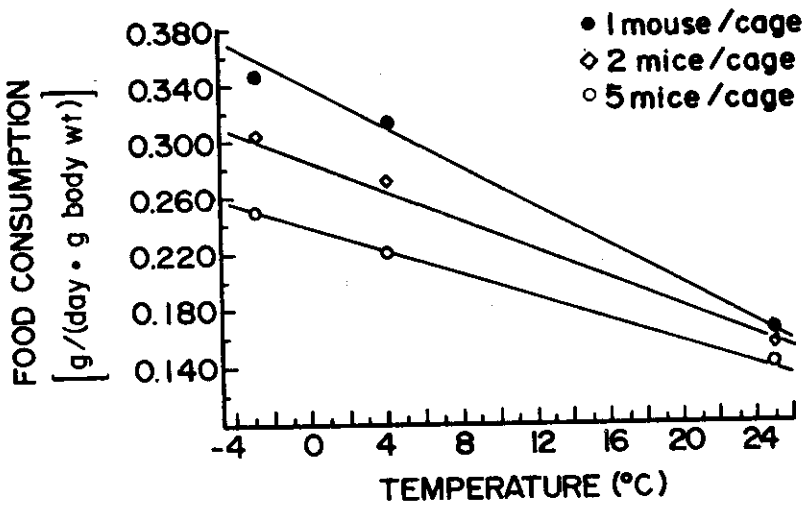


Fig. 7.11. Effect of huddling on food consumption in MA_f/SP male mice.

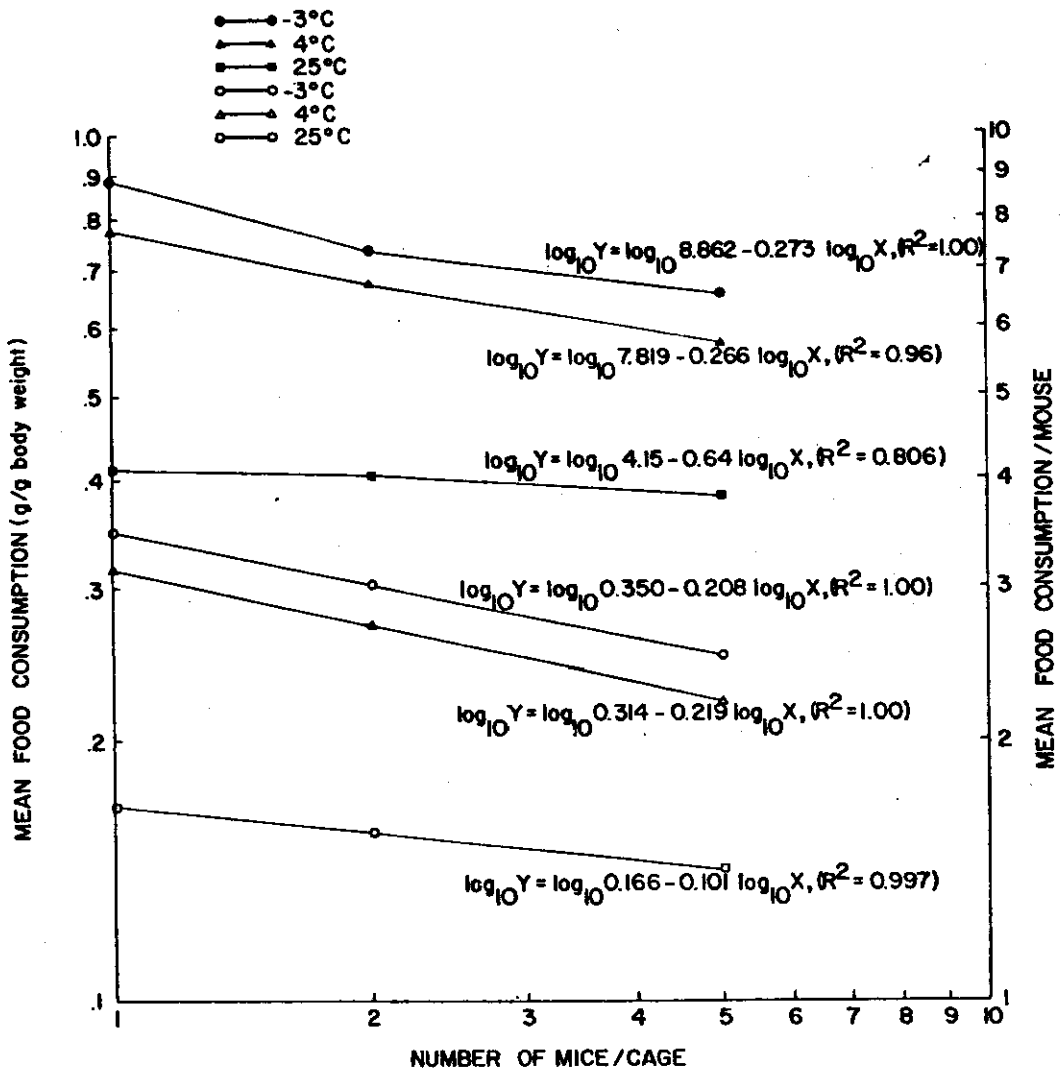


Fig. 7 12. Food consumption rates for laboratory white mice held singly and in groups and tested at several temperature ranges. The top three lines correspond to the right-hand vertical axis, and the bottom three lines correspond to the left-hand vertical axis (see Fig. 7.11 for symbols). (Data reworked from Prychodko, 1958.)

Some slight difference does exist between the two sets of data. Prychodko (1958) stated that statistical comparison among groups for the data measuring mean food consumption in grams per gram body weight was significant for all combinations ($P < 0.001$); however, for comparisons of mean food consumption per mouse, differences were found between his groups (II) and (III) ($P < 0.01$) and between groups (I) and (III) ($P < 0.001$) but not between groups (I) and (II) ($P > 0.3$). Some evidence of these differences can be seen by comparing the R^2 values for the above relationships. The R^2 values for mean food consumption measured in grams per gram body weight were all very high, whereas for the mean food consumption values per mouse at 25°C, they showed considerably more variability ($R^2 = 0.806$). However, for the most part either expression, whether food consumption measured in grams per gram body weight or grams per individual, will serve well in predicting variations and control over total food intake rate for small rodents, and may serve as a basis for exercising control over intake rates in other consumers as well. This potential is real as long as there is an aggregation behavioral complex observed during any or all parts of a given consumer's life history.

Anis (*Crotophaga ani* and *C. sulcirostris*) have been shown by Smith (1971) and Rand (1953) to double their rate of food intake when foraging in the presence of other animals, whether other anis or ungulates, when compared to rate of food intake when foraging alone. In these behavioral studies, rate of food intake was measured as number of captures per unit time during normal feeding in pastures with short grass. When several individuals are present, the rate of disturbing grasshoppers and other insects is higher and results in more captures in a given time (Fig. 7.13).

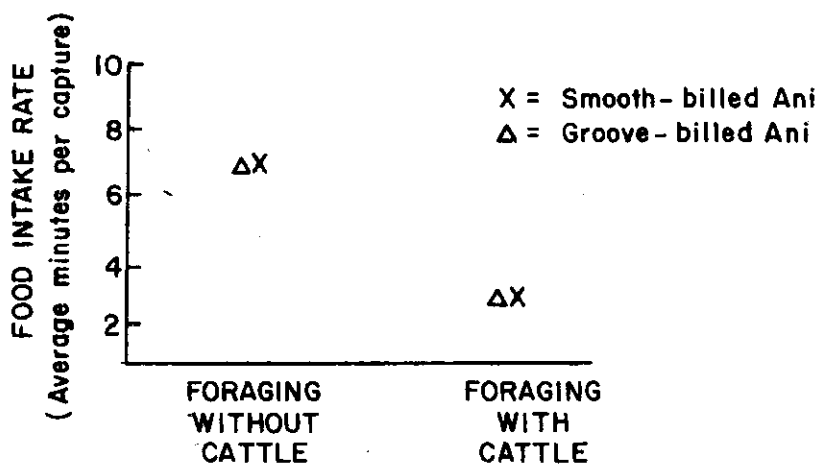


Fig. 7.13. Comparison of food intake rates when anis feed in presence of cattle vs. alone (data from Smith, 1971).

Energy requirement of the birds are assumed equal in social and in nonsocial situations, although this assumption must be accepted with caution. However, food intake rate increased in social situations from at least two causes: (i) increased accessibility of prey (from cattle disturbances) and (ii) external stimulation to greater effort in hunting.

7.4.1.3 Digestibility of gross energy. For cattle the intake rate is 1.5 $g/kg^{0.73}$ for each unit change in dry matter digestibility when digestibility ranges from 45 to 65% of dry matter (Conrad, Pratt, and Hibbs, 1964; Baumgardt, 1970; Corbett, 1969) (Fig. 7.14). At a digestibility of about 67% dry matter, neither total nor digestible intake is any longer a known function of dry matter digestibility. At this point, controls other than the physical capacity of the digestive tract operate to control intake. These factors are probably related to thermostatic or blood chemostatic mechanisms (Baumgardt, 1970).

Shenk, Elliott, and Thomas (1970) reported digestibility values for laboratory-held voles (*Microtus pennsylvanicus*). They used a triangular coordinate analysis (Fig. 7.15) to determine digestibility of various synthetic and laboratory diets and expressed digestibility in terms of percent fiber (FI), percent of readily available carbohydrate plus oil (CH + O), and percent casein (C). Their predicted response pattern was:

$$Y = -0.024 + 0.614(C) + 0.963(C)^2 + 0.948(CH + O) + 0.167(CH + O)^2, \quad (R^2 = 0.97,\ P < 0.0005) \tag{7.15}$$

With these digestibility values, total intake rate ranged from 2.20 g/day at (26C - 67(CH + O) - OFI) to 7.92 g/day at (9C - 22(CH + O) - 64FI).

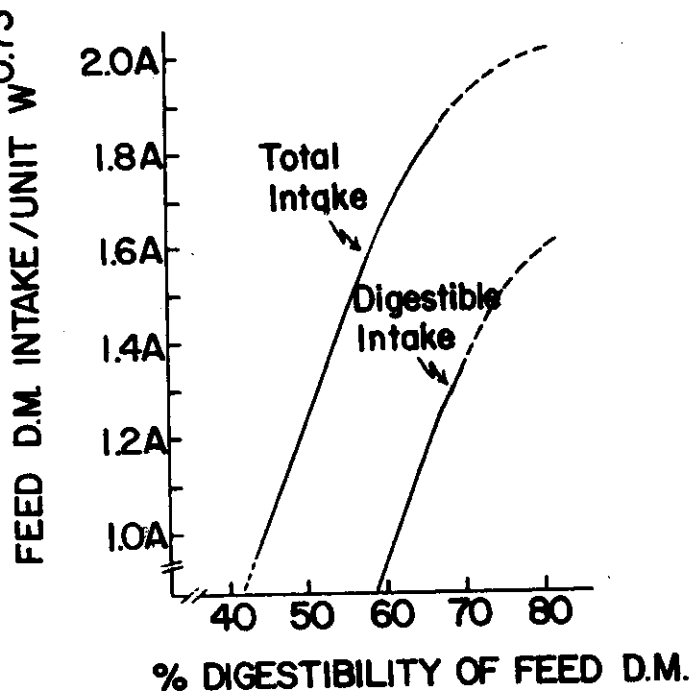


Fig. 7.14. Diagrammatic representation of relationships between feed digestibility and the intake and excretion of dry matter (D.M.) per unit of live weight ($W^{0.73}$) (from Corbett, 1969).

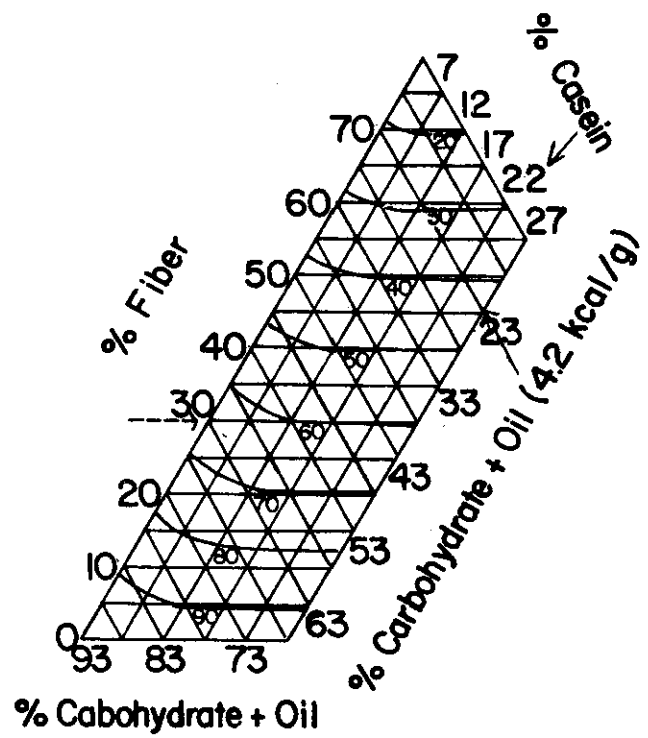


Fig. 7.15. Predicted apparent digestibility (Y) of voles for the studied portion of the triangular pattern, $R^2 = 0.97$ ($P < 0.0005$). The equation of response is $Y = -0.024 + 0.614(C) + 0.963(C)^2 + 0.948(CH + O) + 0.167(CH + O)^2$, where (C) = casein and (CH + O) = readily available carbohydrate plus oil in the diet (expressed as decimal fractions) (from Sbenk et al., 1970).

Average intake for all experiments was 4.43 g/day, the value that should represent the predictive equation for digestibility, although Shenk et al. (1970) do not explicitly state that this is the case.

7.4.1.4 Food quality. The effect of nitrogen content of the diet appears to be important to the intake of large ruminant herbivores. This effect is apparently a negative influence when the nitrogen content falls below a level of about 1% (Glover and Dougall, 1960; Corbett, 1969). The effects of the low nitrogen levels on forage intake appear to be related to the adequacy of the nitrogen for active microbial degradation of foodstuffs. Low nitrogen forages are usually reduced in intake by a factor of about 25 to 50% of that expected from the prediction based on the digestibility of the diet.

Shenk et al. (1970) reported intake rates as a function of percent fiber, percent carbohydrate plus oil, and percent casein in the diet of voles (*Microtus pennsylvanicus*) (Fig. 7.16). They reported two equations with the same degree of fit ($R^2 = 0.80$):

$$Y = 3.62 - 39.24(C) + 24.09(\sqrt{C}) - 5.66(CH + O) \cdot 0.0350/(CH + O) \quad (7.16)$$

$$Y = 7.81 + 12.24(C) - 56.83(C)^2 - 11.37(CH + O) \cdot 5.98(CH + O)^2 \quad (7.17)$$

Sibbald et al. (1957) showed that the amount of food consumed by rats was largely determined by the energy of the diet, although poultry have shown a feedback mechanism resulting in overconsumption of energy with diets low in protein in order to satisfy their protein demands (Donaldson, Combs, and Romoser, 1956). Shenk et al. (1970) supported the latter contention, showing increased intake at the 10 to 12% casein level when the fiber/carbohydrate ratio increased in the diet.

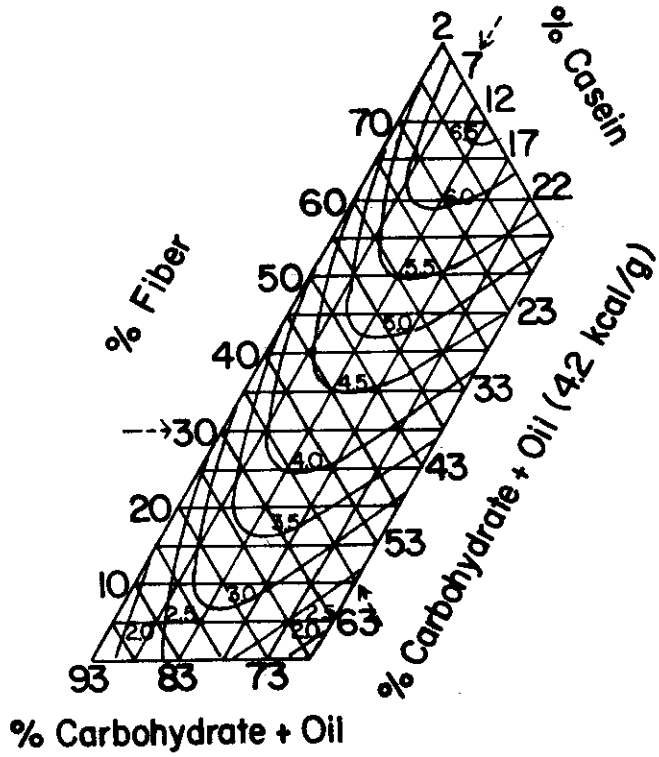


Fig. 7.16. Predicted intake per day (Y) of voles for the studied portion of the triangular pattern, $R^2 = 0.80$ ($P < 0.0005$). The equation of response is $Y = 3.62 - 39.24(C) + 24.09(\sqrt{C}) - 5.66(CH + O) + 0.0350/(CH + O)$, where C = casein and (CH + O) = readily available carbohydrate plus oil in the diet (expressed as decimal fractions). Another equation, $Y = 7.81 + 12.24(C) - 56.83(C)^2 - 11.37(CH + O) + 5.98(CH + O)^2$, also had $R^2 = 0.80$ (from Shenk et al., 1970).

Low total protein level (as determined from Kjeldahl analysis) did not show significant differences in total intake level in normal ranges experienced by Tree Sparrows (Martin, 1968). However, abnormally low levels (2% in diet) produced very low total intake rates compared to higher levels (4, 8, and 16%) (Fig. 7.17). Martin (1968) did not speculate as to the definitive cause of this relationship; however, many of his birds died and a moribund state probably produced this low intake reaction. It is obvious from these data that there was no tendency for the birds to compensate for the low protein content by an increase in intake rate.

7.4.1.5 Lactation. Most animals voluntarily consume more of a given diet during lactation. The increase in intake during lactation should be limited by the energy demands of the lactation and the maximum biological limit to intake as expressed above. For the purposes of this model, it is preferable to let lactation demands set the limits to intake. However, it can be noted here that lactating animals nursing young may increase intake about 1.5 times that observed in the non-lactating animal (Cuthbertson, 1969; National Research Council, 1970).

Little is known about the energy requirements of other mammals during lactation, but Johnson and Groepper (1970) reported the food intake for a lactating deer mouse was more than doubled. This ratio compares favorably with that noted above by Cuthbertson (1969).

For other vertebrates that secrete a milk-like substance for their young, daily caloric intake by pairs of Ring Doves (*Streptopelia risoria*) was shown to increase significantly when they were feeding young (Brisbin, 1969). When two young per nest were fed, the increase was approximately double that observed when only one young per nest was fed (Fig. 7.18).

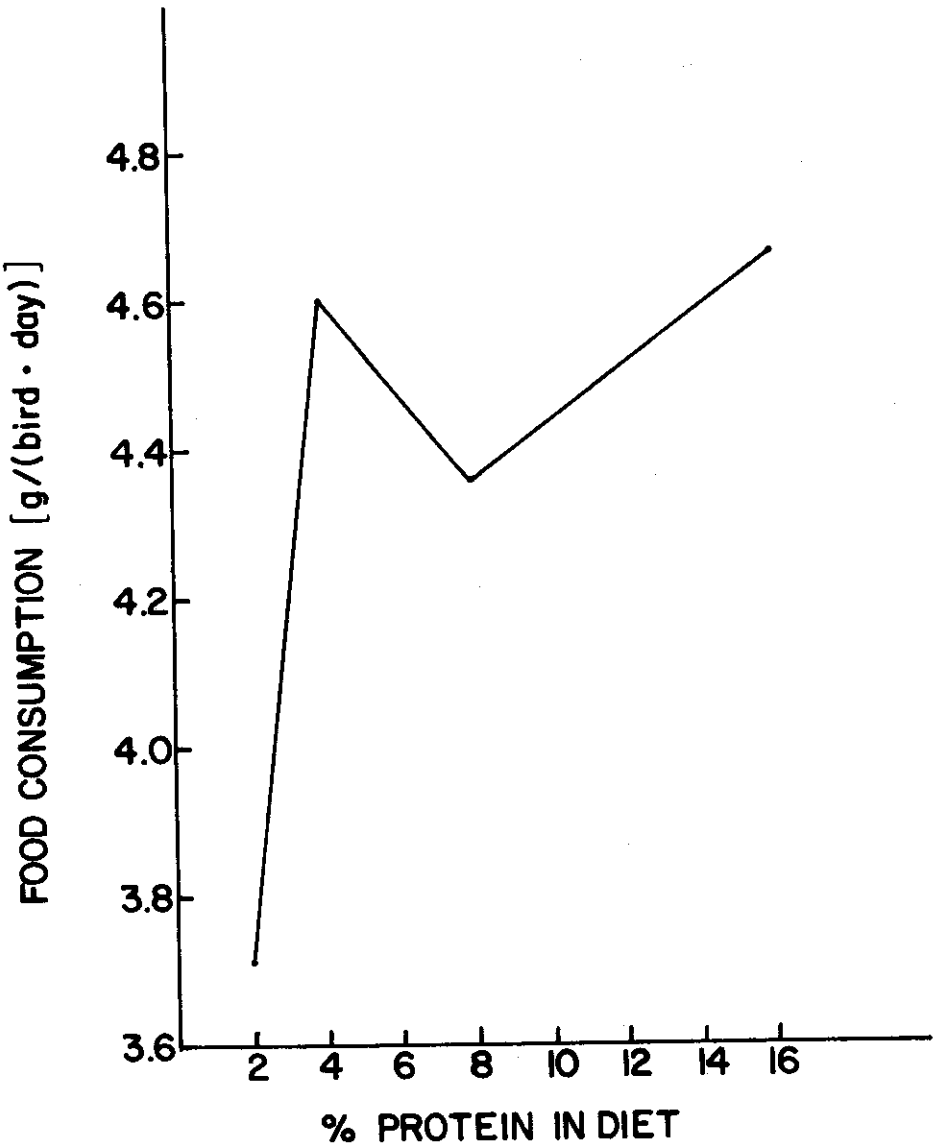


Fig. 7.17. Relationship of food consumption to amount of protein in diet for Tree Sparrows (Martin, 1968).

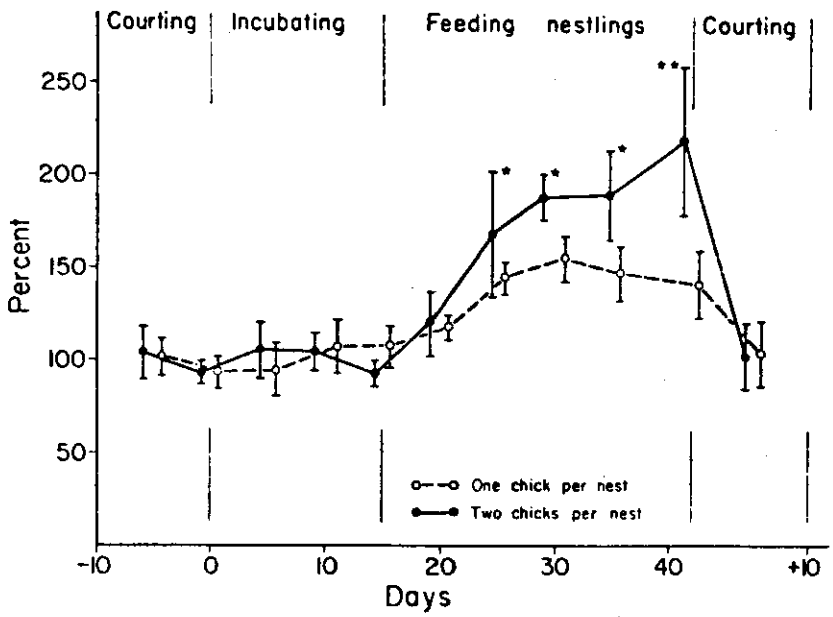


Fig. 7.18. Variation in mean total daily caloric intake of breeding pairs of Ring Doves. Caloric intake is expressed as percentage of mean daily caloric intake of the pair during the courting and incubating periods. Each point represents the mean of four pairs of birds and vertical bars represent 2 standard errors above and below the mean. Single stars indicate a significant ($P \leq 0.05$) difference and double stars indicate a highly significant ($P \leq 0.01$) difference between mean values for pairs feeding one young per nest and those feeding two young per nest (from Brisbin, 1969).

7.4.1.6 Food availability. Food availability is a difficult factor to describe in relation to intake; many factors obviously complicate any analysis. For instance, for herbivores, density/height ratio of plants is bound to affect the relationship, as well as availability as expressed in kilograms per hectare.

Willoughby (1959) reported that the live weight gain, and presumably the intake, by grazing lambs increased with an increasing herbage availability up to 1570 kg dry matter/ha. This value is certainly greater than that observed in many locations on the grasslands. Perhaps an approximation of this fact can be extrapolated from unpublished data belonging to Robert Bement, where he has shown that cattle can make a moderate gain when the availability of forage does not fall below 40 kg/ha. Fig. 7.19 shows the relationship between intake rate and the amount of food available from Bement's data. The expression should be related to both plant and animal density. This is taken into consideration in the expression as estimated in Fig. 7.19.

Food availability can be quite important to animals with low mobility and could easily become a limiting parameter to population growth and development simply on physical bases. Food types can be more plentiful in some areas than in others, and if these plentiful food supplies are relatively unavailable, starvation within the population can ensue or, more subtly, reduced fecundity can occur. Data from Smith (1959) gives an example on varying intake rates with varying food availability to the consumer (Fig. 7.20). For the grasshopper (*Melanoplus sanguinipes*) there is obviously a difference in total consumption rate per unit time for wheat and western wheatgrass for nearly all ages of nymphs. Just prior to maturation, the consumption rates are equivalent.

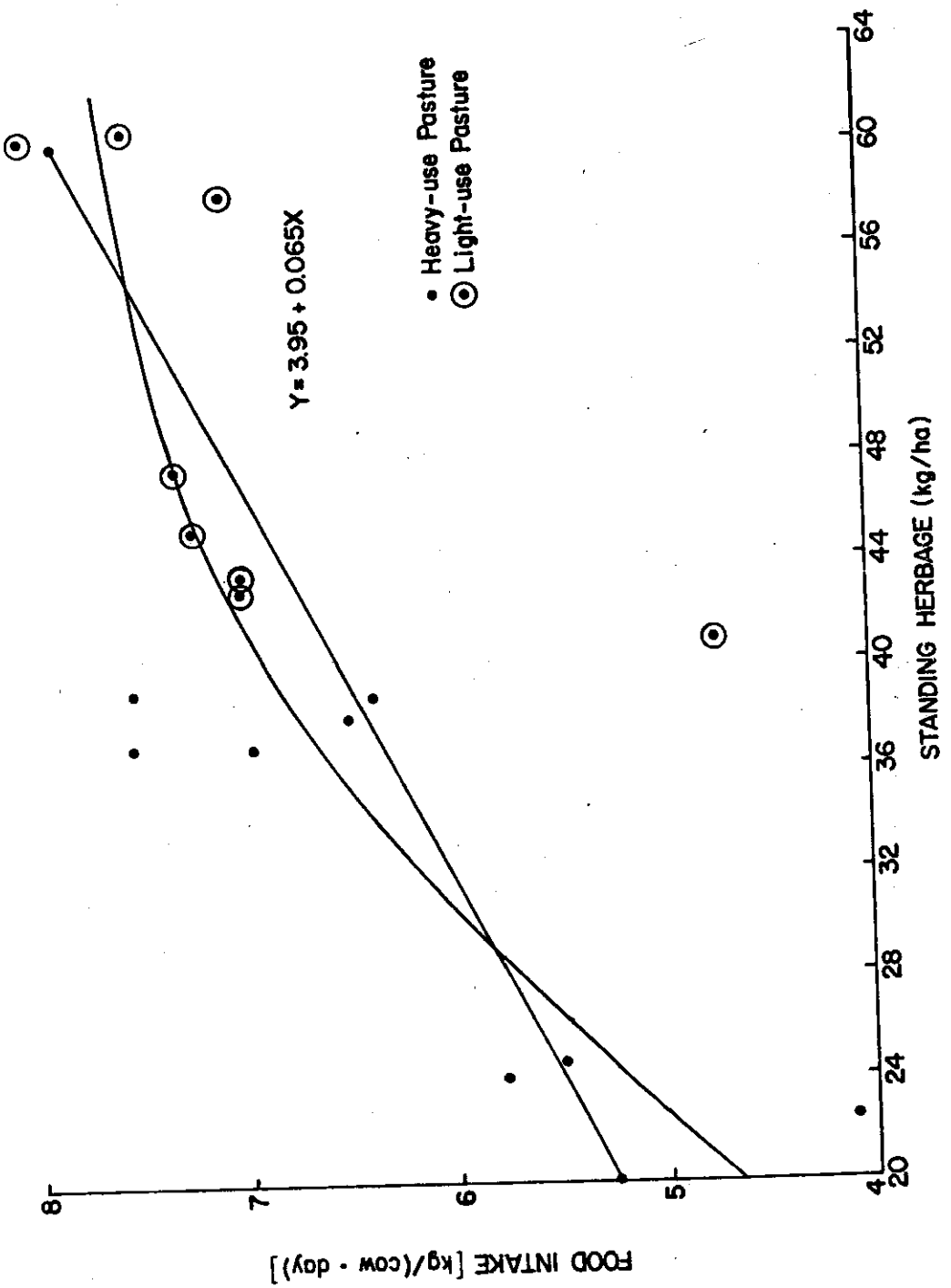


Fig. 7.19. Relationship of food intake to food availability for cattle on Pawnee National Grassland area (Robert Bement, unpublished data). Curvilinear estimate is fitted by eye.

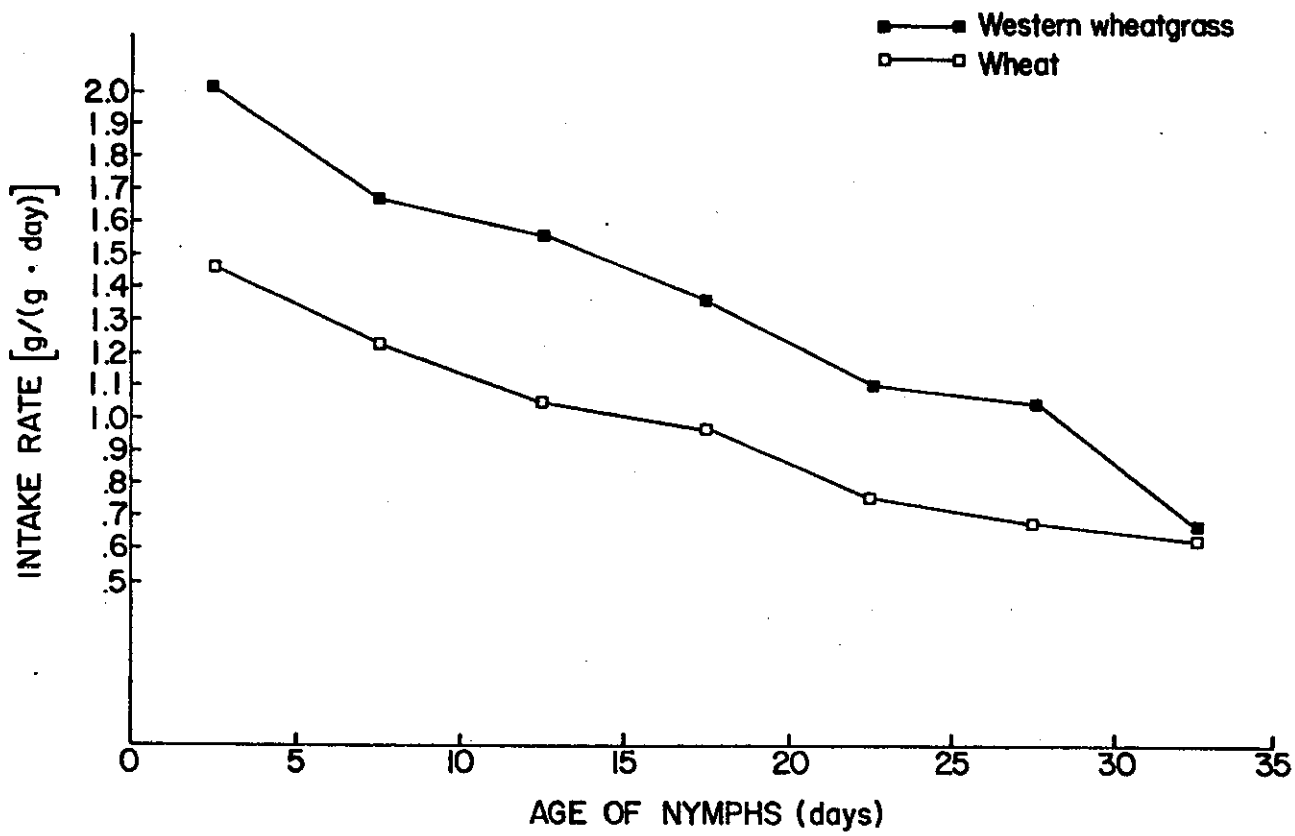


Fig. 7.20. Relationship of food intake to age for the migratory grasshopper (*Melanoplus sanguinipes*) when fed two different diet sources, wheat and western wheatgrass.

Temperatures affected the availability of mollusca used as food by the Redshank (*Tringa totanus*) (Goss-Custard, 1970). In the cold, the mollusca remained deeper in the mud where they were inaccessible; hence the rate of capture decreased. The birds had to expend more energy in prolonged hunting. In this case, the rate of food intake was limited by the behavioral characteristics of the prey, not the energy requirements of the birds. Probably similar effects occur on and contribute to the grasslands migration of the birds.

7.4.1.7 Rate of digestion. As the rate of digestion increases, the intake rate will tend to increase. This control is also related to digestibility; however, it is known that similar forages may have different rates of digestibility (Richard Rice, unpublished data). For the preliminary model, it is assumed that this rate of digestion and intake is related to nutrient content of the diet mentioned in Section 7.4.3.

7.4.1.8 Food capacity. Food capacity can be defined as approximately five times basal metabolic rate noted in Section 7.4.8.

7.4.1.9 Blood metabolites. Many blood metabolites apparently affect food intake. These factors are not well defined and operate only at the higher levels of digestibility (Baumgardt, 1970). These operants are reflected in the shape of the curve noted by Corbett (1969) (Fig. 7.14).

7.4.1.10 Temperature. Temperature per se has been reported as a major control of food intake rates. Again, it must be realized that the basic function or controlling principle is metabolic rate. However, since there are reports on the effect of temperature, it is useful to regard it as a single controlling variable.

Nice (1938) reviewed two reports on variations in intake rates for two Weaver Finches, the Red-billed Weaver (*Quelea quelea*) and the Masked Weaver (*Ploceus cucullatus*) (Fig. 7.21). Food intake rate in terms of percent of total weight is higher for the smaller species (Red-billed Weaver, 18 g) than for the other species (Masked Weaver, 40 g). There is plainly a curvilinear temperature effect; as temperature decreases the amount of food intake increases.

Temperatures have also been reported for some insect data. To show the effect of temperature upon rate of food intake, we have used Parker's (1930) data for grasshoppers.

Except for the intake rate of the third instar at 32°C, the curves in Fig. 7.22 show a consistent and reasonable trend. The intake rate increases as the temperature increases from 22°C to 32°C, then decreases slightly at a temperature of 37°C. The fact that the latter temperature is above the optimum for the species is indicated in Parker's (1930) study, wherein the death rate of early instars was very high at 37°C.

Temperature was also given as a direct cause for differences in food consumption rates for a strain of laboratory white mice (Prychodko, 1958) (Fig. 7.12). His entire study was dedicated to examining the effects of crowding and temperature on ecological associations of the mice, and he concluded that the two factors interact throughout a wide range of conditions. Thus it is important to consider the effects of temperature with the biomass or total numbers of individuals present in the colony as presented earlier in this report.

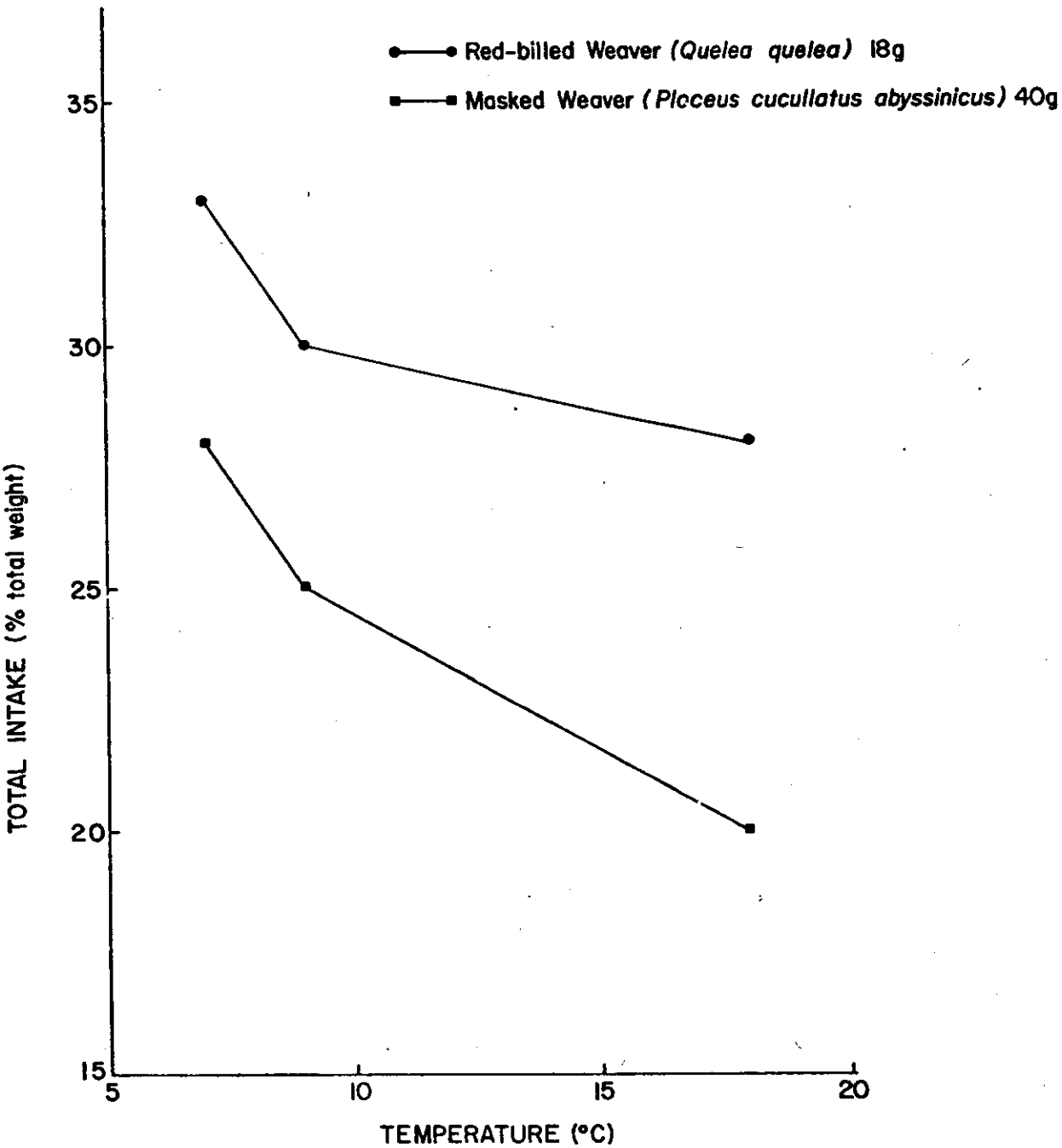


Fig. 7.21. Relationship of total food intake to temperature for two passerine birds (Nice, 1938).

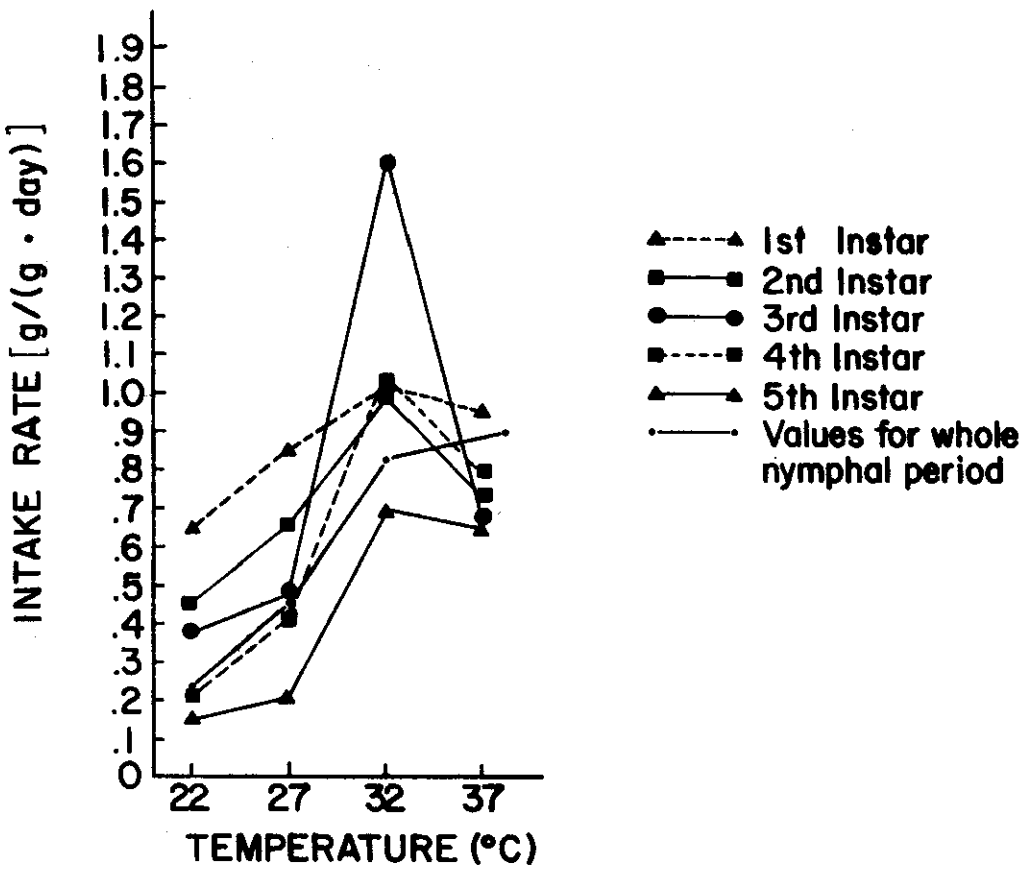


Fig. 7.22. Effect of temperature upon intake rate of food by nymphal instars of *Melanoplus sanguinipes* (Parker, 1930).

Myrcha (1968) reported the levels of food intake rate for the European hare. His data showed that for each degree drop, food intake rates increased 3.108 kcal/(kg · day) between the temperatures of 5° and -12°C (Fig. 7.23).

7.4.2 (703-603) Carrying Food to Young

This process is intended to define the amount of food collected by a parent animal and carried to its young prior to the time the young are independent and can forage for themselves.

During the workshop we expressed carrying food to young (Fig. 7.24) as:

Carrying food to young = f(number of young or weight, age of young)

To date, no adequate data have been reviewed for this report although Royama (1966), Orians (1966), and Orians and Horn (1969) should be examined critically to determine whether any of their material can be utilized in this process. For other materials, literature on predators (both mammalian and avian) ought to be more thoroughly checked. Literature on certain animals that regurgitate their food for young may also be pertinent for our considerations.

Consideration ought to be given to whether this process is altogether essential for a consumer energetic model. In some respects, the amount of energy being captured and disposed of by any parent can be accounted for by using the data in this process as a control on process (703-602) although such a reorientation may not account for many of the feeding strategies in grassland ecosystem consumers.

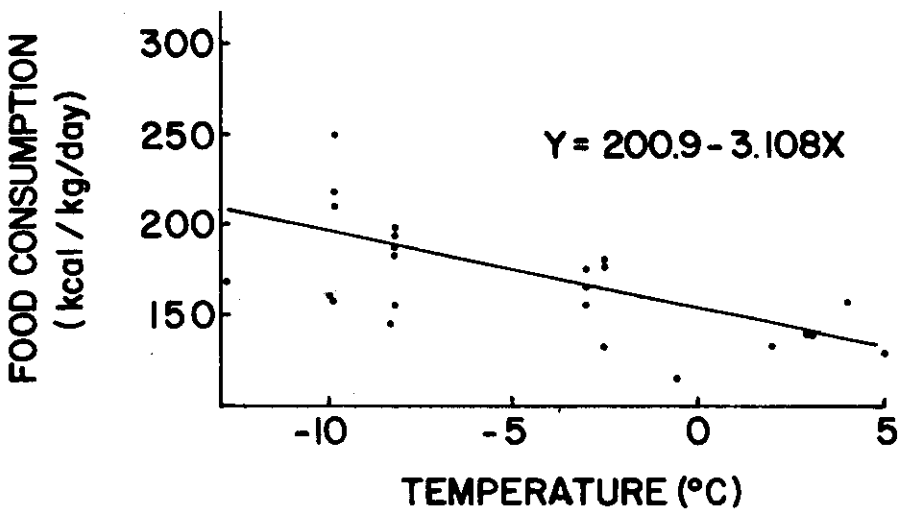


Fig. 7.23. Dependence of food consumption on environmental temperature (from Myrcha, 1968).

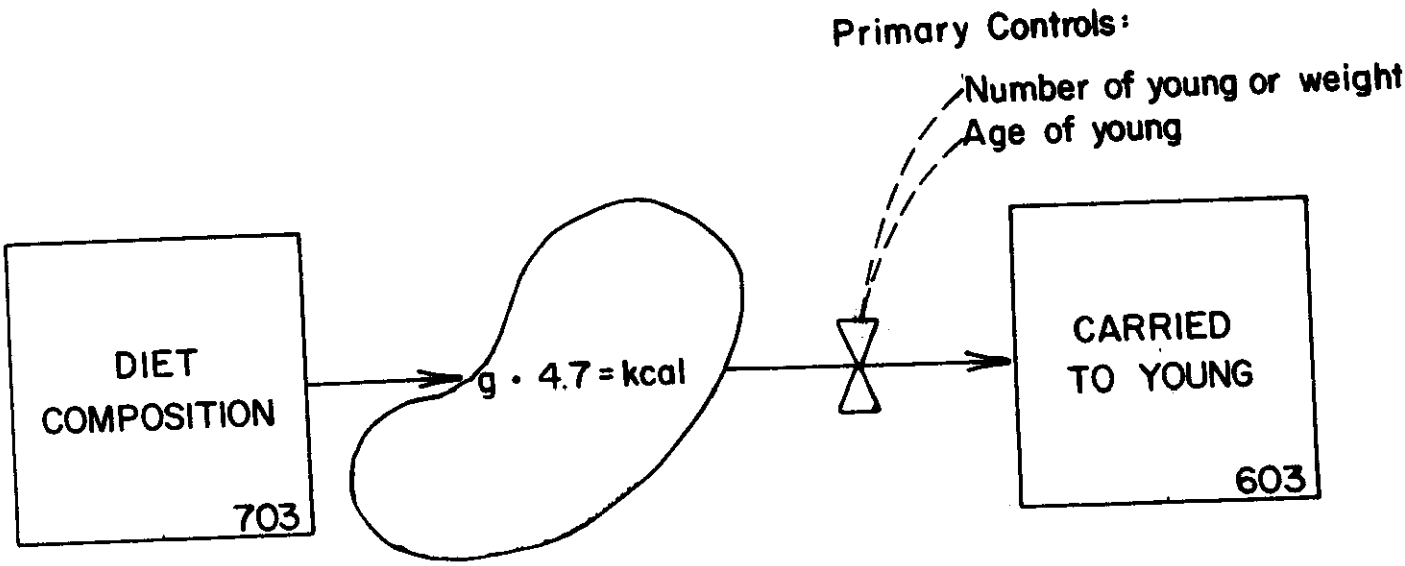


Fig. 7.24. Schematic of process (703-603) with its controls.

7.4.3 (703-604) Food Wasting

This process is intended to define the amount of food that an animal collects through the diet selection model and then does not ingest, thus making the material unavailable to the consumer energetic model. The material is delivered directly to the decomposer subsystem as noted in Fig. 7.1.

During the workshop we expressed food wasting (Fig. 7.25) as:

$$\text{Food wasting} = f(\text{food availability})$$

7.4.3.1 Food availability. One report relative to this process is known at present (Buckner, 1964). Buckner determined the amount of wastage and hoarding employed by four species of shrews when given varying levels of larch sawfly cocoons. His data are shown in Table 7.8 and Fig. 7.26. Clearly, as the amount of food available to the shrews increased, the rate of wasting steadily increased to a definite point, then leveled off. It is obvious from these data that the maximum degree of wastage is a constant proportion of food available.

Other potential sources for information should lie with certain insect data (notably for orthopterans and potentially for sucking insects where wounds in plants might continue to exude liquids), with rodent data (particularly for those that cut hay), and with predators that do not completely consume their prey during a meal or series of meals on large carcasses. To make this process more meaningful, further controls must be considered.

7.4.4 (703-605) Storing of Food

This process is intended to define the amount of food that an animal collects through diet selection processes and then puts into a cache or

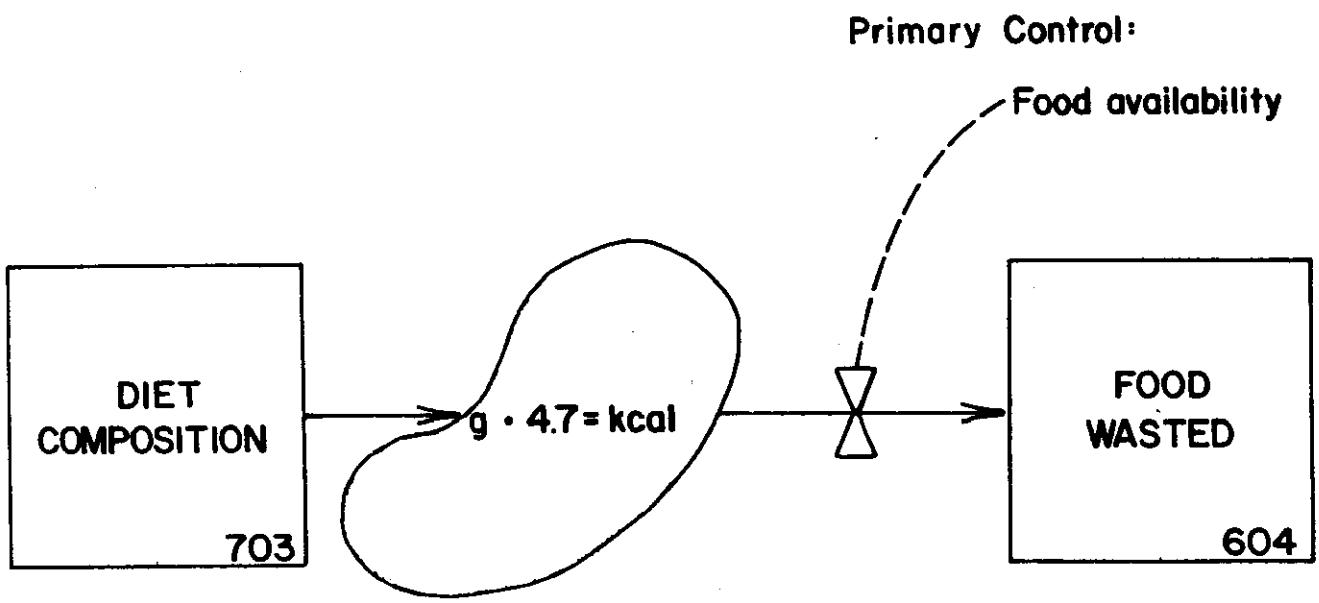


Fig. 7.25. Schematic of process (703-604) with its control.

Table 7.8. Relation between larch sawfly cocoon abundance and wastage in four species of shrews. Data show average number of cocoons wasted over a 24-hr period (after Buckner, 1964).

Species	No. Animals Tested at Each Density	No. Cocoons Available										
		200	400	600	800	1000	1200	1500	2000	4000	6000	8000
Sorex cinereus	10	14.3	98.1	193.4	209.6	252.6	368.5	421.2	591.4	586.5	573.2	592.9
Sorex arcticus	5	16.2	104.2	200.4	392.6	427.4	502.2	515.4	521.8	513.4	612.2	589.2
Microsorex hoyi	2	14.0	112.5	--	--	281.0	--	--	486.5	--	--	--
Blarina brevicauda	5	0.6	10.8	163.0	395.4	561.4	678.2	--	--	--	--	--

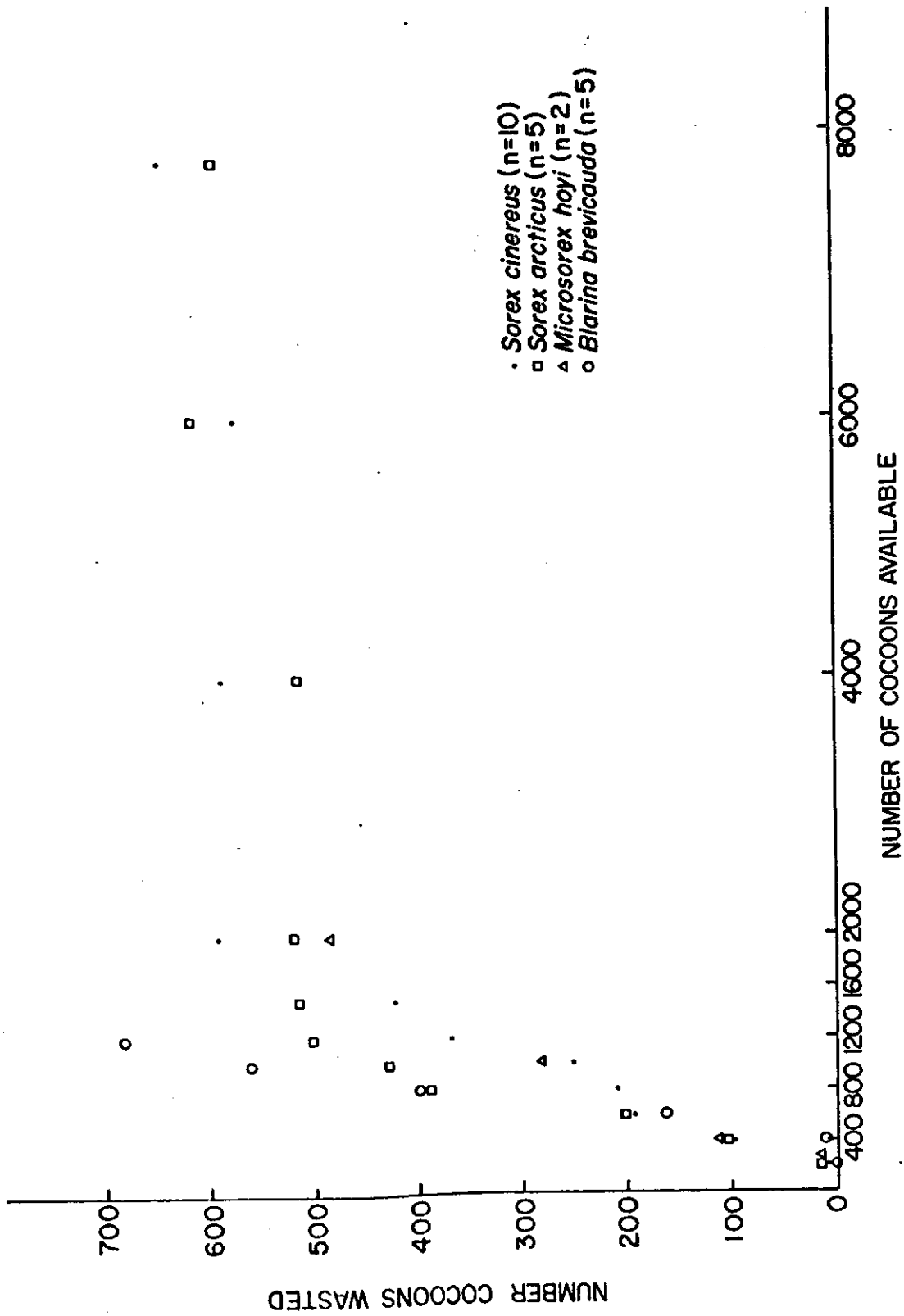


Fig. 7.26. Relation between larch sawfly cocoon abundance and wastage in four species of shrews per 24-hr period (Buckner, 1964).

storage area for later consumption. Then the mechanism of delivering the stored food into the consumer energetics model must be back through the diet selection model, for the animal is making some sort of choice in its preference to eat stored materials, or it is placed in a physical position of having only this food supply available to it during specific phenophases of its life history.

During the workshop we expressed storing of food (Fig. 7.27) as:

Storing of food = f(temperature, food availability, density of its own species, phenophase, food handled)

7.4.4.1 Food availability. Few reports are known for this process. Buckner (1964) reported the rate of hoarding of larch sawfly cocoons with increasing availability of this food supply (Table 7.9 and Fig. 7.28). The hoarding rate was clearly curvilinear.

Other materials should be available from literature reporting rates of hay cutting by small rodents, predators that store prey for short periods of time, and insects (mainly hymenopterans) that gather and store food.

7.4.5 (602-607) Defecation

Defecation, also noted for process (602-608), is directly related to intake rate and the degree of digestion and has the same controls listed as for process (602-608). Strictly speaking, this process is the reciprocal of the process of digestion, but does not have to be expressed indirectly because fecal output can be measured directly, whereas food digested and assimilated must be computed [see rationale in process (602-608), Section 7.4.6].

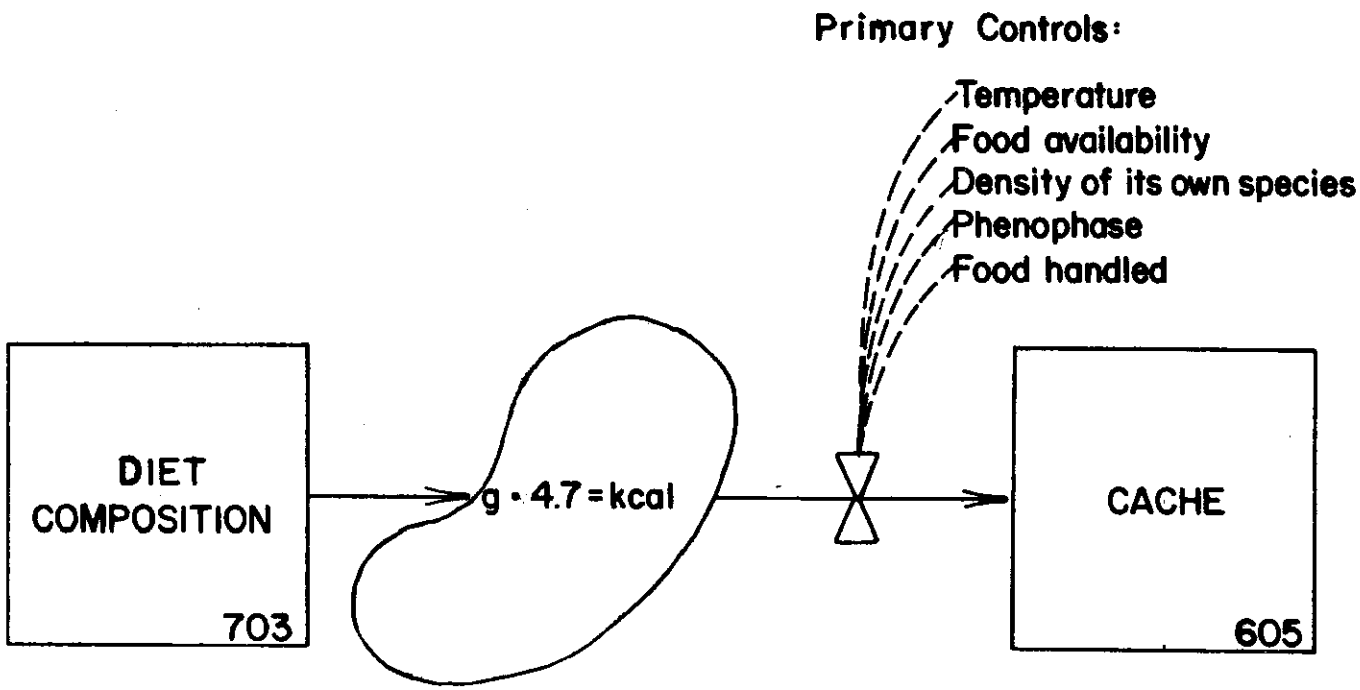


Fig. 7.27. Schematic of process (703-605) with its controls.

Table 7.9. Relation between larch sawfly cocoon abundance and hoarding in four species of shrews. Data show average number of cocoons hoarded over a 24-hr period (after Buckner, 1964).

Species	No. Animals Tested at Each Density	No. Cocoons Available										
		200	400	600	800	1000	1200	1500	2000	4000	6000	8000
Sorex cinereus	10	9.7	84.9	146.2	150.5	156.2	164.0	164.8	172.8	165.6	172.3	173.7
Sorex arcticus	5	0	75.2	134.2	172.0	195.6	209.2	215.6	219.4	217.2	223.4	217.4
Microsorex hoyi	2	5.5	62.0	--	--	120.5	--	--	180.0	--	--	--
Blarina brevicauda	5	0	0	63.8	189.8	214.0	262.8	--	--	--	--	--

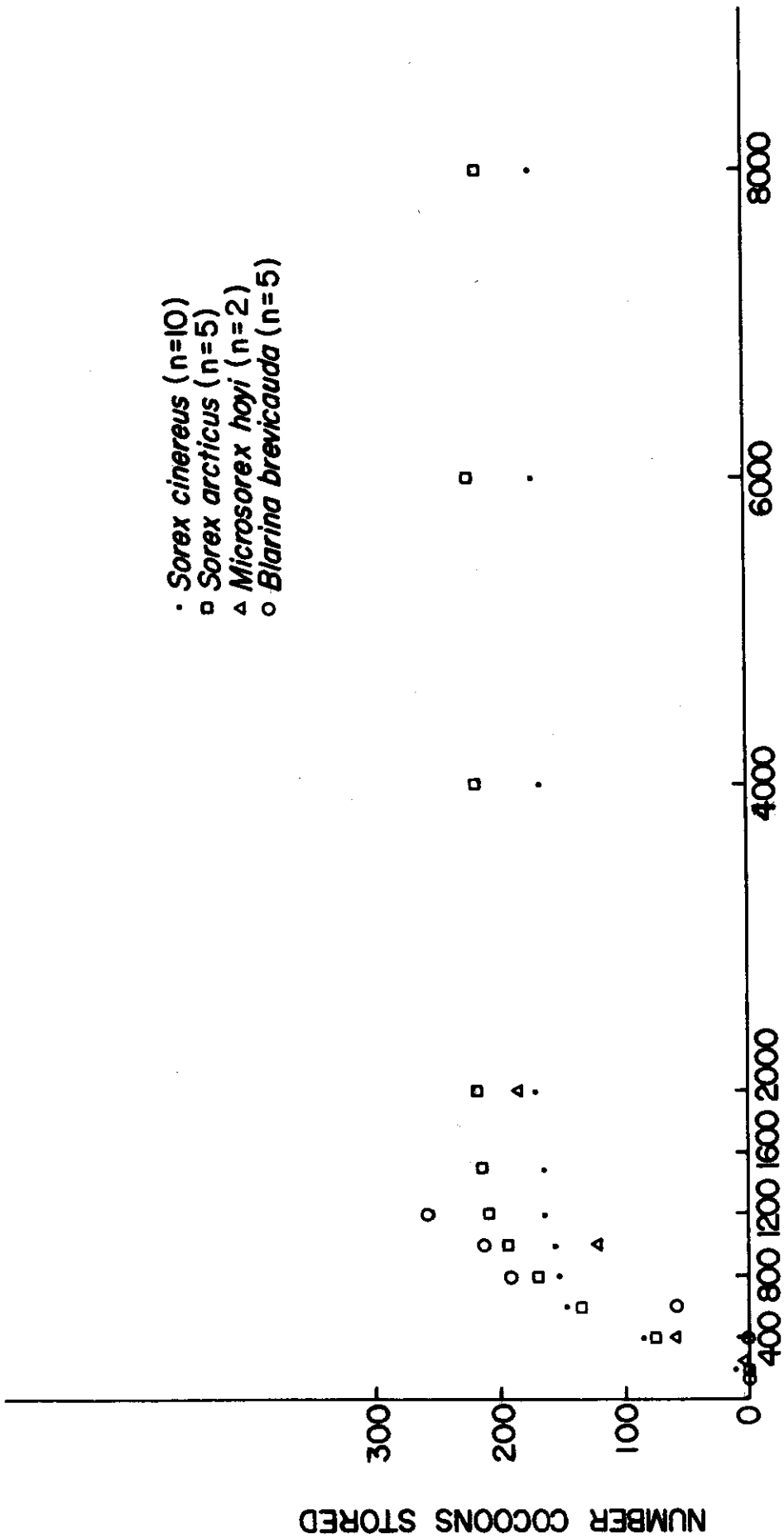


Fig. 7.28. Relation between larch sawfly cocoon abundance and storage rate in four species of shrews per 24-hr period (Buckner, 1964).

From the workshop discussions we expressed defecation (Fig. 7.29) as:

Defecation = 1/Digestion rate (defined in Section 7.4.6)

In additon to being an integral part of the consumer energetics model, it is necessary to compute defecation rates and the amount of material listed as feces in 607 in order to provide information for the decomposer subsystem. As noted in the Introduction to this subsystem, all the information should be handled in calories or caloric equivalents throughout the model. This is difficult to do at this particular time since much of the literature dealing with fecal output expresses the output in weight rather than energy. But strictly speaking, there should be a sink-source complex interfacing SV 607 and the decomposer subsystem whereby the caloric content of the fecal mass is divided by 4.7 to convert to weight per unit area.

7.4.6 (602-608) Digestion

During the workshop we considered digestion (Fig. 7.30) to be:

Digestion = f(plant maturity, nutrient content of food, i.e., nitrogen content, lignin, fiber, cellulose, and readily available carbohydrates)

The rate of digestion and assimilation of food is not measured directly; indirect methods are necessary. Kleiber (1961, p. 253) discussed the manner of expressing apparent digestibility given two parameters, (I) the amount of food consumed and (F) the amount of feces excreted in the same period of time. By definition $I - F$ is then the amount of food digested per unit time (day). Since there are other complicating features about such measurements, this equation becomes only that which is apparently digested

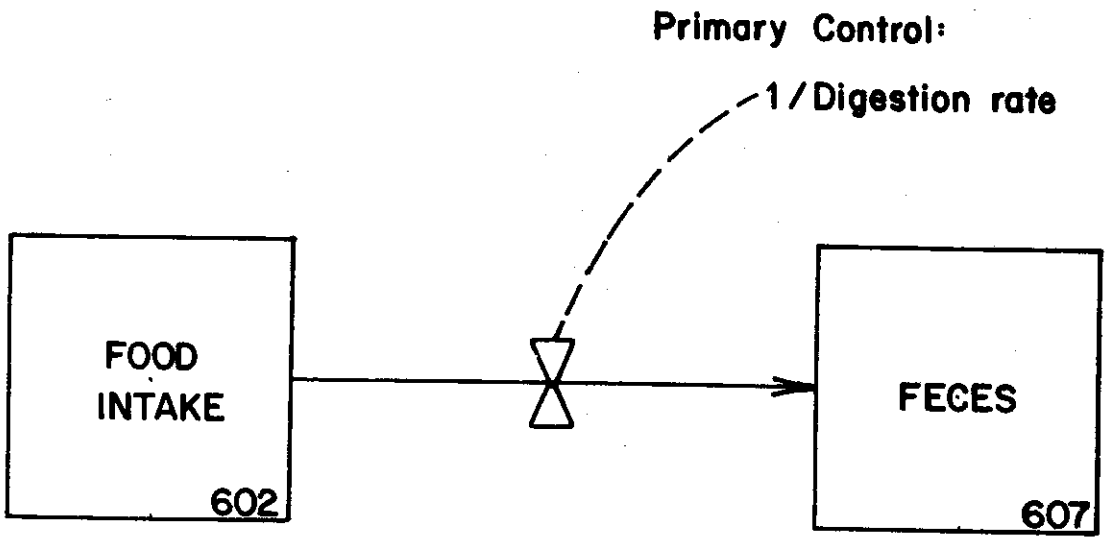


Fig. 7.29. Schematic of process (602-607) with its primary control.

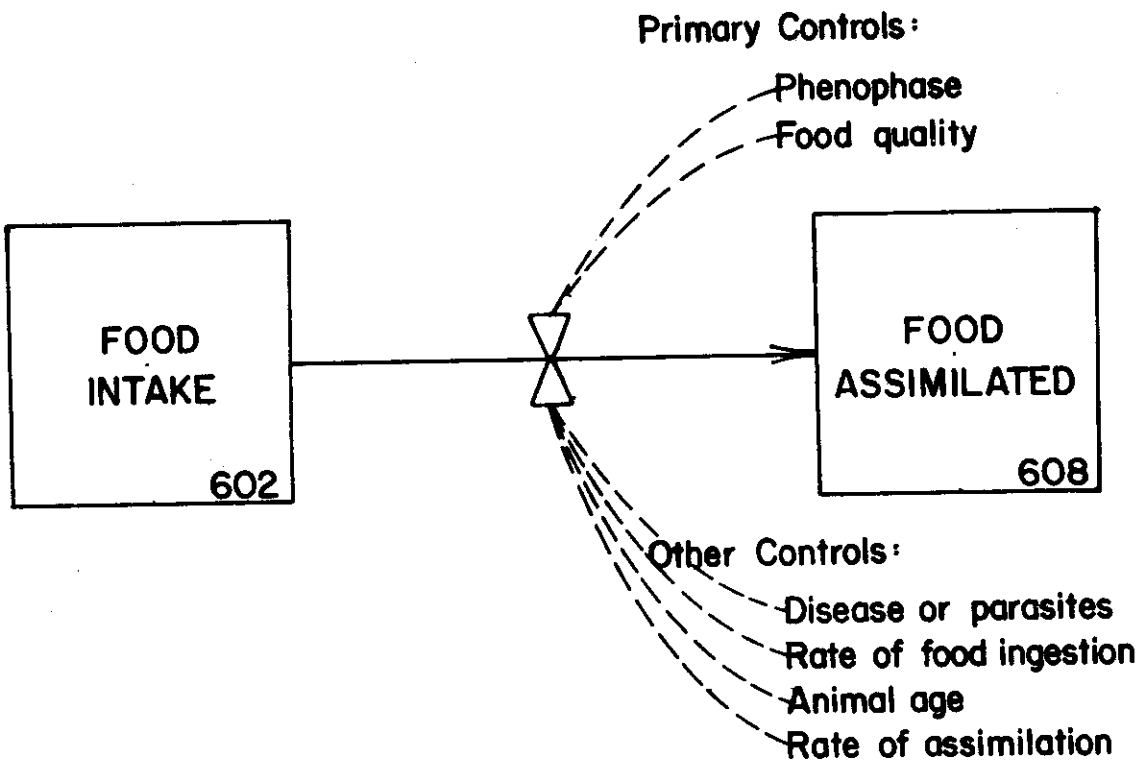


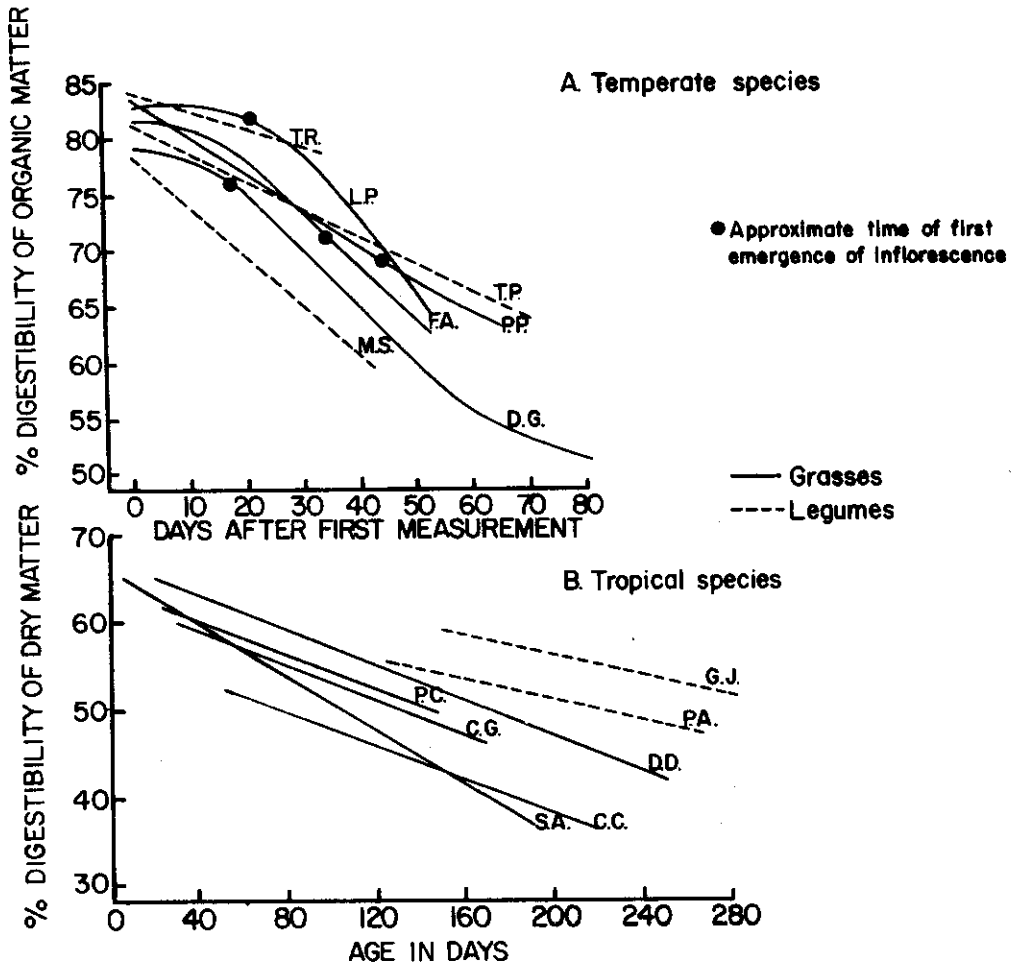
Fig. 7.30. Schematic of process (602-608) with its controls.

[$(I - F)/I$ or $1 - F/I$ is the *apparent digestibility* value or ratio]. Finally, the data are usually expressed in percentages; thus $(1 - F/I)100$ is that percentage of the food material ingested that is not excreted as feces which then equals *percent apparent digestibility*.

7.4.6.1 Phenophase (plant). The maturity of the plant is related to its phenology. It is possible to predict the digestibility of plants on the basis of maturity when these comparisons are made within species. However, there is a high degree of variation when this factor is used to compare various species of plants, as is a typical situation with the grazing herbivore. Corbett (1969) attempted to summarize some of these relationships and they are shown in Fig. 7.31 for several grass species and legumes. It is apparent that there is no exact relationship between digestibility and phenology, but the downward trend with maturity is clearly evident.

For this model we suggest using a linear relationship between the "average" phenology of available forage and digestibility of forages (much the same as presented for tropical species, Fig. 7.31). For large herbivores the range in digestibility should be from a high of about 75% to a low of 45% dry matter digestibility. This should be graphed linearly through the various phenological stages until better information is available.

Actually, on the Pawnee Site, animal diets do not approach the high levels of digestibility suggested by Corbett's (1969) data. This is because quite immature plants rarely constitute the majority of the diets for large herbivores. The ingested material contains some standing dead material so that seasonal digestibility may not go higher than 60 to 65% dry matter digestibility (Vavra, 1971).



Temperate species. Spring growths; dates of first measurements varied between species and between localities.

- L.P. *Lolium perenne* var. S23 (ryegrass)
- P.P. *Phleum pratense* var. S48 (timothy)
- F.A. *Festuca arundinacea* var. S170 (tall fescue)
- D.G. *Dactylis glomerata* var. S37 (cocksfoot or orchard grass)
- T.R. *Trifolium repens* var. S100 (white clover)
- T.P. *Trifolium pratense* var. Ultuna (red clover)
- M.S. *Medicago sativa* var. Dupuits (lucerne or alfalfa)

Tropical species

- S.A. *Sorghum almum*
- C.C. *Cenchrus ciliaris* var. Molopo (Buffel grass)
- C.G. *Chloris gayana* var. Callide (Rhodes grass)
- P.C. *Pennisetum clandestinum* (Kikuyu grass)
- D.D. *Digitaria decumbens* (Pangola grass)
- P.A. *Phaseolus atropurpureus* var. Siratro
- G.J. *Glycine javanica* var. Cooper

Fig. 7.31. Changes in the digestibility of temperate and tropical grasses and legumes with increasing age and maturity of the herbage (from Corbett, 1969).

7.4.6.2 Food quality. Nitrogen content should yield a graphed relationship which is the reciprocal of the material presented for maturity in Fig. 7.32. There is relatively more nitrogen available in younger plants than in older; therefore, one or the other presentation should be used but not both.

Crampton and Rutherford (1954) reported apparent digestibility of protein compared to the protein level in the diet of white laboratory rats (Fig. 7.32). The results are clearly curvilinear throughout the range reported. An increase of the protein in the diet from 5 to 20% caused digestibility to increase sharply from about 64% to approximately 84%, after which the rate of digestibility leveled off; an increase in the protein of the diet from 20 to 50% increased digestibility only an additional 10%. The curve (expected to fit $Y = a + bX + cX^2$ model) was not presented in the original paper, but results of a multiple regression using protein digestibility (Y) as the dependent variable, and grams of dry matter eaten (X_1), grams of protein consumed (X_2), grams of protein excreted in the feces (X_3), and grams of methocel consumed (X_4) as independent variables were reported. These variables accounted for 97% of all variability in the analysis, and 73% of this variability was directly accounted for by the quantity of protein consumed.

The material presented by Shenk et al. (1970) can also be used here. [See process (703-602), Section 7.4.1.3, to determine the effects of nutrient content on digestibility.]

The level of digestibility is generally quite high for rodents as reported by Drozdz (1968) in Table 7.10. Drozdz reported the percent material digested and the amount of feces (in percent) for four species of small European rodents fed eight different types of diets.

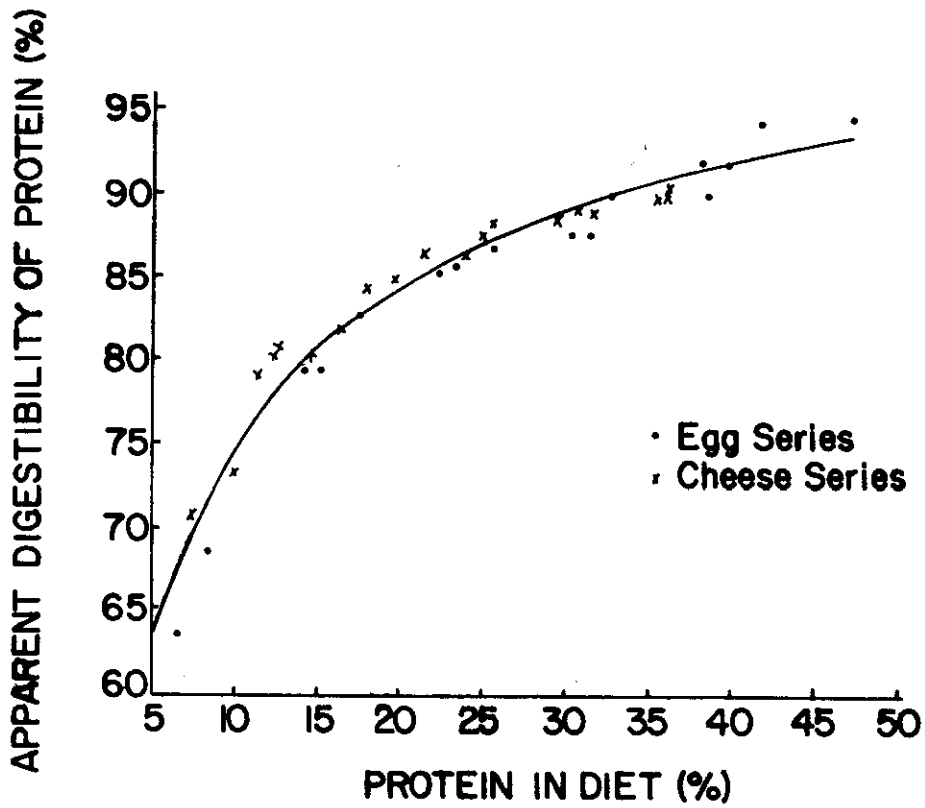


Fig. 7.32. Relation between the percentage of crude protein in the diet and its apparent digestibility (from Crampton and Rutherford, 1954).

Table 7.10. Digestibility and assimilation of natural foods of common voles, bank voles, and mice (in percent of energy intake) reported by Drozdz (1968) and Myrcha (1968) for the European hare (*Lepus europaeus*). Means ± standard deviations are given.

Species	Diet	Digested Energy	Feces
Microtus arvalis	Oats	92.32 ± 1.37	7.68 ± 1.51
	Green wheat	70.39 ± 1.55	29.61 ± 1.61
Clethrionomys glareolus	Beechmast	92.86 ± 1.29	7.14 ± 1.41
	Mixed	87.78 ± 1.38	12.22 ± 1.45
	Oats	89.11 ± 2.24	10.89 ± 2.25
	Greens	77.41 ± 3.48	22.59 ± 2.69
Apodemus agrarius	Oats	90.45 ± 1.15	9.55 ± 0.65
	Compound	89.62 ± 1.38	10.38 ± 1.74
Apodemus flavicollis	Hazelnuts	92.22 ± 0.95	7.78 ± 1.21
	Acorns	81.39 ± 1.58	18.61 ± 1.25
	Mixed	91.09 ± 0.53	8.91 ± 0.55
Lepus europaeus			
Male	Mixed[a/]	80.13 ± 3.1	19.87
Female	Mixed[a/]	79.92 ± 1.1	20.06

[a/] White carrot, red carrot, beetroot, and oats.

Golley (1960) also reported high digestibility ratios for voles (*Microtus*) when fed two diets, alfalfa (90%) and a standard diet consisting of lettuce, carrots, and oatmeal (82%). A detailed study made on *Microtus* by Keys and Van Soest (1970) showed that (i) dry matter digestibility decreased as cell wall content increased ($Y = 71.1 - 0.437X$ for legumes and $Y = 82.6 - 1.22X + 0.009X^2$ for grass-hay), (ii) cell walls and cellulose increased in digestibility as cell wall content increased ($Y = 8.7 + 0.62X$ for alfalfa and $Y = 1.11 + 0.541X$ for grass-hay), and (iii) hemicellulose digestibility followed a curvilinear pattern in that it decreased in digestibility as cell wall content increased (to about 28%); then digestibility of hemicellulose increased thereafter ($Y = 150.08 - 9.44X + 0.168X^2$ for alfalfa and $Y = 59.96 - 2.70X + 0.47X^2$ for grass-hay).

The European hare has a similarly high digestibility ratio (Myrcha, 1968) (Table 7.10). Thus, given relatively normal diets in both the wild and in laboratory conditions, small mammals apparently have the ability to digest a large proportion of the food they eat. The adaptive advantage of this strategy compared to eating a large amount of food, from which they can digest or assimilate smaller quantities, is clear. The combination of their small body size and their high metabolic rate relative to larger animals makes it imperative that they obtain the greatest amount of food value per unit effort possible.

The type of food component in these foods made considerable impact on the coefficient of digestibility (Table 7.11). The high level of digestibility (89% average) was, according to Drozdz (1968), mainly a function of the low fiber content. Because of a lower percentage of water in low fiber

Table 7.11. Coefficients of digestibility for individual food components expressed in percent of total intake (means for 10 to 15 animals) (after Drozdz, 1968).

Species	Kind of Diet	Dry Matter		Organic Matter		Crude Protein		Ether Extract		Crude Fibre		N-free Extract	
		% Digested	% of Diet	% Digested	% of Diet	% Digested	% of Diet	% Digested	% of Diet	% Digested	% of Diet	% Digested	% of Diet
Microtus arvalis	Oats	93.54	85.00	94.02	98.29	86.37	11.3	86.95	7.36	87.82	1.56	95.72	78.07
	Green wheat	73.94	12.40	74.49	96.89	63.20	18.75	87.01	3.03	74.69	27.50	77.36	46.29
Clethrionomys glareolus	Beechmast	88.17	95.01	90.15	95.01	87.47	30.50	94.11	49.63	81.79	7.25	84.66	7.63
	Mixed	80.98	94.96	82.85	97.25	71.61	17.12	96.87	51.58	81.26	14.84	44.93	13.71
	Oats	89.75	85.00	90.69	98.29	78.58	11.30	80.16	7.36	66.02	1.56	93.23	78.07
	Greens	74.01	13.80	75.82	92.15	82.29	14.06	70.47	3.15	77.20	33.12	92.40	42.42
Apodemus agrarius	Oats	91.70	85.00	92.13	98.29	74.51	11.30	83.55	7.36	89.74	1.56	95.86	78.07
	Compound	85.45	93.40	86.76	97.66	65.61	12.65	97.24	33.40	68.30	2.65	85.58	51.20
Apodemus flavicollis	Hazelnuts	88.95	94.65	89.53	97.62	79.57	14.49	97.03	67.14	76.66	2.10	67.96	23.89
	Acorns	82.31	85.79	82.82	97.49	70.73	5.74	91.24	6.85	65.26	4.52	84.18	80.36
	Mixed	85.55	95.24	86.65	96.96	81.18	15.41	95.35	63.70	73.16	7.39	47.16	8.46

diets, such diets have a higher caloric content than bulky foods, and thus animals eat smaller quantities. The low digestibility of bulky food is connected with three factors: (i) high fiber content (ranging from 25 to 33%), (ii) high rate of passage through the digestive tract, and (iii) a decrease in digestion rate because of the consumption of a greater amount of food to compensate for a lower quality.

Assimilation efficiencies (digestibility indices or ratios of other workers) were reported for nine species of small mammals of different age, sex, and physiological and nutrition classes by Johnson and Groepper (1970) (Tables 7.12 and 7.13). There plainly are differences among species and for different classes within each species, but no general relationship has been developed to date on these data. The total range was from 71 to 95% with most values in the 85 to 95% range, values which support those reported by Golley (1960), Keys and Van Soest (1970), and the European workers mentioned above.

7.4.7 (608-609) Urination

The many consumers of the grassland ecosystem employ several strategies of catabolic waste disposal from the body [see Prosser and Brown, 1961 (Table 22, p. 140 and 141, and Chapter 6)]. Even though much of the waste is nitrogen-based from protein catabolism, sufficient amounts of the excretory material is of carbon origin to be considered in this carbon-oriented model. Thus it is important to regard this process as an energy depleting source in the consumer subsystem as well as providing state variable information for the decomposer subsystem. Furthermore, energetic wastage in urine is expressed as heat of the fluids secreted plus the energetic value of the catabolic byproducts themselves.

Table 7.12. Metabolic statistics (mean ± SE) of captive rodents (after Johnson and Groepper, 1970).

Species	Sample Size	Diet	Mean Weight (g)	Assimilation Efficiency
Deer mouse	6	Rat chow	20.1	77.0 ± 2.1
(lactating)	1	Rat chow	22.0	77.1
(exercise wheel)	1	Rat chow	13.5	82.9
Meadow vole	5	Rat chow	28.6	81.1 ± 0.7
(exercise wheel)	1	Rat chow	24.7	78.9
Red-backed vole	5	Rat chow	20.5	78.9 ± 1.6
Meadow jumping mouse	8	Rat chow	16.1	71.5 ± 0.5
Feral house mouse	5	Rat chow	16.2	79.5 ± 1.5
Ord's kangaroo rat	5	Rolled oats	63.0	95.1 ± 0.4
	4	Pearled barley	56.4	97.7 ± 0.2
Olive-backed pocket mouse	6	Rolled oats	10.9	95.1 ± 0.3
	2	Pearled barley	12.2	95.3
(exercise wheel)	1	Rolled oats	11.4	95.0
Richardson ground squirrel	3	Rat chow	303.1	82.2 ± 0.2
Thirteen-lined ground squirrel	5	Rat chow	132.4	81.0 ± 1.3

Table 7.13. Assimilation efficiencies (mean ± SE) of North Plains rodent populations (from Johnson and Groepper, 1970).

Species	Site	Immature	Adult Female	Gravid or Lactating	Adult Male
Deer mouse	1	87.7 ± 2.4	87.4 ± 1.5	90.2 ± 1.7	90.0 ± 0.5
	2	88.1	86.1	87.9	91.4
	3	90.8	91.3	93.3	92.9
	4	92.2	82.2	92.8	91.5
(forest)	5	--	70.9	--	75.9
(grassland)	5	--	87.8	92.3	95.0
Means	-	89.7 ± 1.1	85.8 ± 1.7	91.3 ± 1.0	89.5 ± 2.8
Meadow vole	6-9	79.6	72.0	80.2 ± 1.9	76.3 ± 1.8
Red-backed vole	-	76.7	93.1	88.8	81.8
Meadow jumping mouse	-	91.0	94.8[a/]	90.6	94.8[a/]
Grasshopper mouse	-	--	85.7	--	87.0
Feral house mouse	-	--	94.8	94.9	91.0
Ord's kangaroo rat	3	--	91.1	94.4	93.1
Olive-backed pocket mouse	3	--	95.2	85.6	93.2
Richardson ground squirrel	10	--	79.9 ± 5.4	84.5	82.4 ± 3.8

[a/] Combined sample of both sexes.

From the workshop we expressed urination (Fig. 7.33) as:

$$\text{Urination} = f(\text{body size, temperature, water})$$

7.4.7.1 Weight of an animal. According to Brody (1945, p. 377), the amount of urine produced per day measured in quantities of nitrogen eliminated is

$$\text{mg N/day} = 201\ W^{0.72} \tag{7.18}$$

Brody (1945, p. 380) further stated that "the ratio of endogenous urinary or total nitrogen levels to basal energy metabolism tends to be the same in small and large animals, ... about 2 mg nitrogen per Cal."

Scattered literature reports on the amount of urinary nitrogen exist for birds and mammals, but little has been uncovered for other consumers such as the poikilotherms (including insects). To complete this section, a more thorough search of literature materials is imperative in order to build a pertinent review for grassland modeling.

7.4.7.2 Water. General reviews and texts discussing the effects of water on urinary nitrogens give little information on total quantity changes with changes of the amount of water available to the organism. Generally, the changes that come about have to do with shifts in the general type of nitrogen excretion. For a condensed review of this phenomenon, see Prosser and Brown (1961, Chapter 6). Little is presented that can be used for modeling purposes.

7.4.8 (608-613) Standard or Basal Metabolism

During the workshop we considered this process (Fig. 7.34 and 7.35) to be

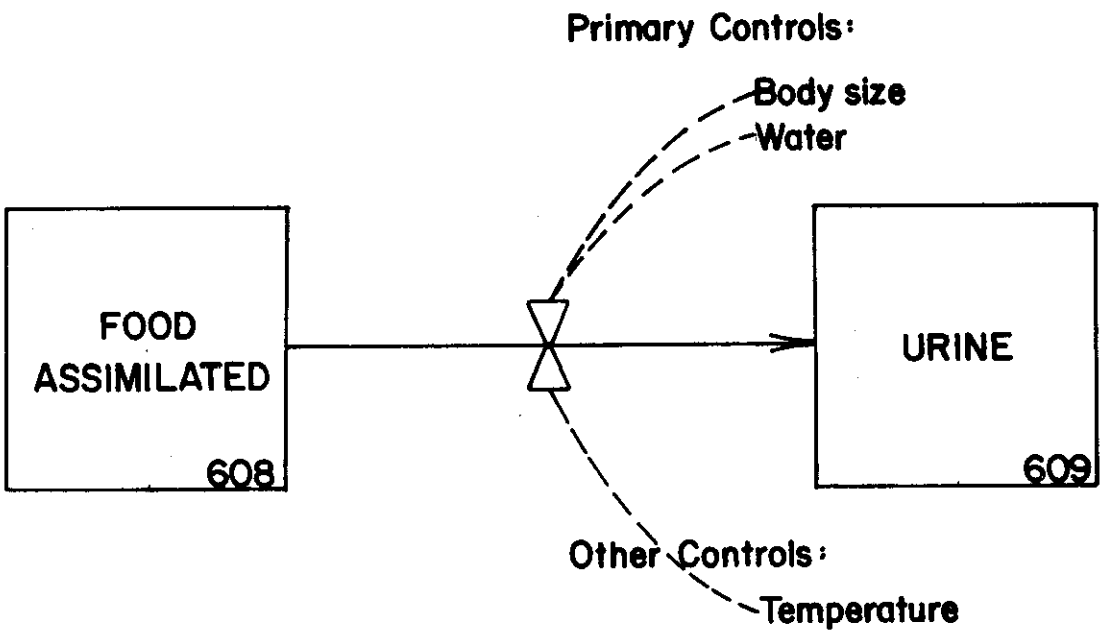


Fig. 7.33. Schematic of process (608-609) with its controls.

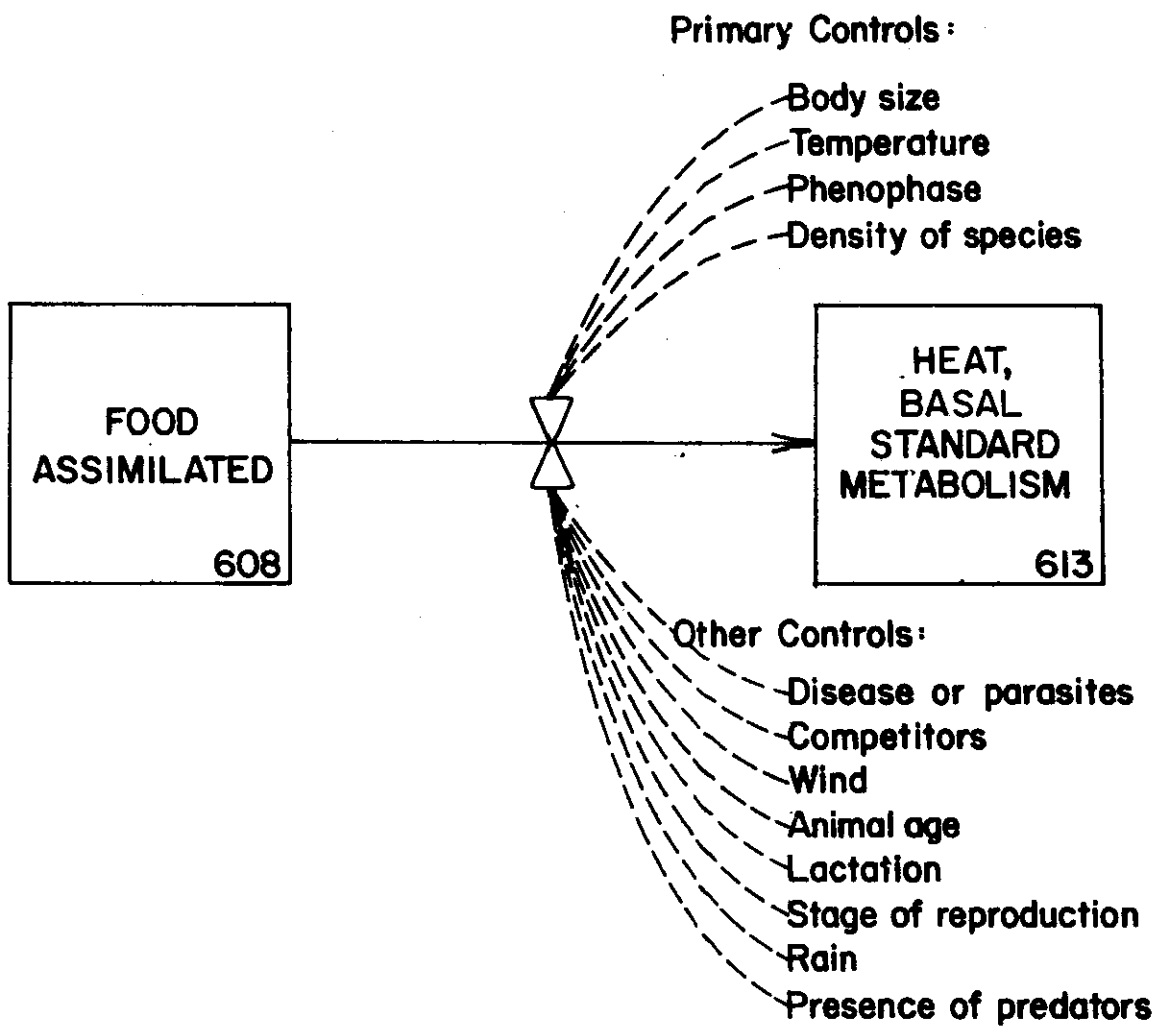


Fig. 7.34. Schematic of process (608-613) with its controls.

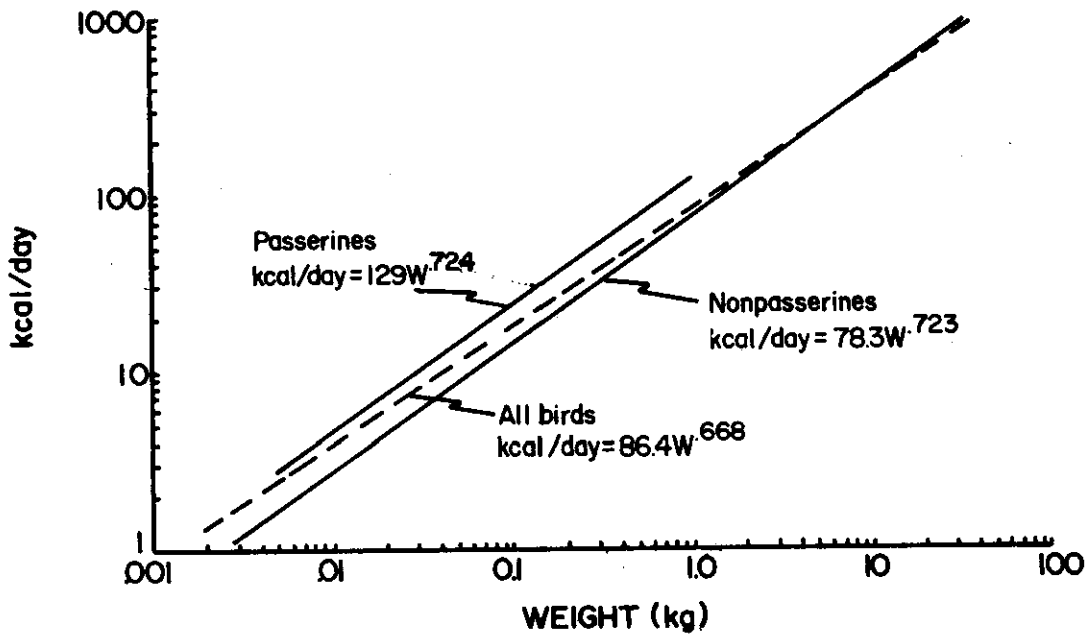


Fig. 7.35. A comparison of the regression lines for passerine birds, nonpasserine birds, and all birds (from Lasiewski and Dawson, 1967).

Standard metabolism = f(body size, temperature, density of species, wind, disease or parasites, phenophase, animal age, lactation, stage of reproduction, rain, competitors, presence of predators)

7.4.8.1 Body size. The classic work by Brody (1945) and follow-ups by Hemmingsen (1950) and Kleiber (1961) outline explicitly the physiological and thermodynamic relationships of metabolic activity of young and adult vertebrate homeothermic animals. However, there are at least three major updated versions of these two works that must be considered (King and Farner, 1961; Lasiewski and Dawson, 1967; Kendeigh, 1970).

Brody (1945) reviewed many early literature reports of metabolic relationships to body size and recomputed his own value for many mammals and birds. His recommended value for mammalian metabolism was Metabolism (or M) = $70.5\ W^{0.73}$, and for birds was $M = 89.0\ W^{0.64}$ (an average of several other reports).

Kleiber (1961) argued for a mammalian value of $M = 70.0\ W^{0.75}$, after giving an extensive historical review of previous reports and their pro and con arguments.

Subsequent to these reports, Lasiewski and Dawson (1967) reviewed a larger set of avian data and argued for new set values [replacing the Brody proctor values and the King and Farner (1961) values (Fig. 7.35 and 7.36)]. For the most part, the values reported below are presently accepted for birds, and to a major degree the values generally accepted for mammals.

$$\text{Passerines:} \quad M = 129.0\ W^{0.724} \tag{7.19}$$

$$\text{Nonpasserines:} \quad M = 78.3\ W^{0.723} \tag{7.20}$$

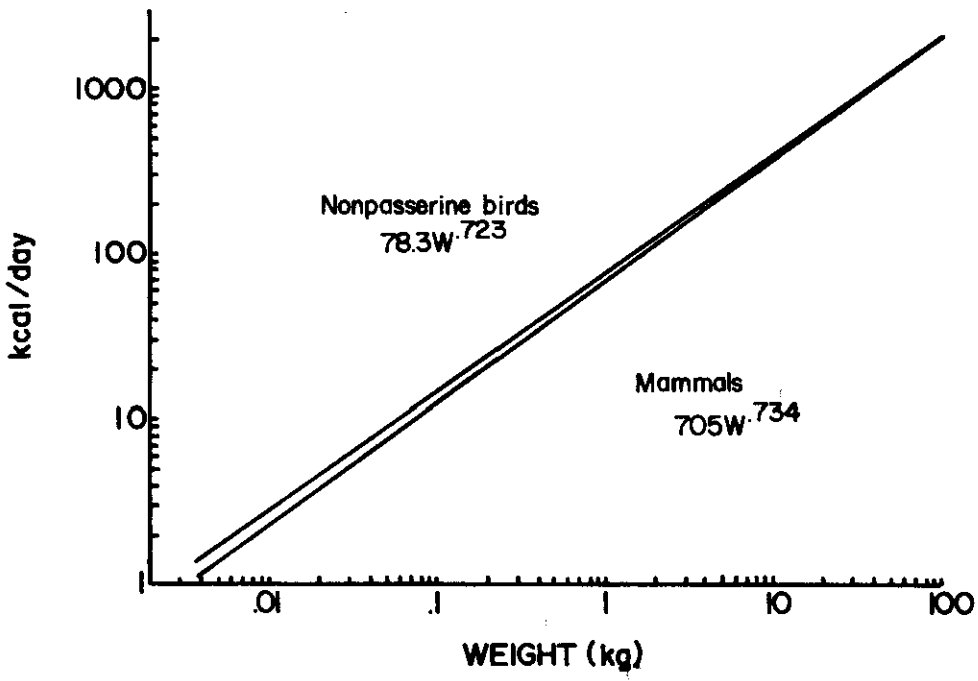


Fig. 7.36. A comparison of the regression lines for nonpasserine birds and for mammals (from Lasiewski and Dawson, 1967).

All birds: $M = 86.4\ W^{0.668}$ (7.21)

Mammals: $M = 70.5\ W^{0.734}$ (7.22)

One major criticism of the above values has been offered by Zar (1968*a*, 1969). He contended that the method of computing the value by log-log methods rather than by iterative methods using a power function gave a poorer fit to the same data on which Lasiewski and Dawson (1967) reported.

The values listed below are those that Zar (1968*a*) preferred:

Passerines: $M = 76.7\ W^{0.741} \pm 39.4$ (7.23)

Nonpasserines: $M = 113.0\ W^{0.632} \pm 7.87$ (7.24)

All birds: $M = 77.9\ W^{0.737} \pm 31.5$ (7.25)

Several rebuttals passed back and forth between Lasiewski and Dawson and Zar without a clear settlement of the total picture to this point. There is considerable value in staying with Lasiewski and Dawson's (1967) data because Zar (1968*b*) recomputed Lasiewski and Dawson's material and gave statistical relationships for the among and between family and ordinal groups. Those data are presented in Table 7.14. For anyone with an interest in the detailed statistical differences as Zar (1968*b*) reported them, I refer them to his paper.

7.4.8.2 Phenophase or rhythms. The above discussion relates to standard metabolism values, i.e., those that are measured in an arbitrarily defined resting condition in the zone of thermoneutrality. Within the past few years, data have been accumulated that criticize the above approach as being too inclusive for representation of vertebrate metabolism (more specifically, for birds) (Lewies and Dyer, 1969; Aschoff and Pohl, 1970*a*,*b*). The controversy has to do with measurements of animals without regard to circadian fluctuations.

Table 7.14. Empirical statistics for the standard metabolism (kcal/bird · day) vs. body weight (kg) regressions (from Zar, 1968*b*).

Group	Number of Data Points	a	log a	b	SE of M	SE of log M
Apodiformes	9	114.0	2.06	0.769	0.201	0.0558
Strigiformes	7	66.4	1.82	0.692	11.100	0.0989
Columbiformes	10	92.1	1.96	0.858	2.680	0.0491
Galliformes	13	72.6	1.86	0.698	15.300	0.0904
Falconiformes	5	65.3	1.82	0.648	45.300	0.1080
Anseriformes	9	95.8	1.98	0.634	23.400	0.0524
Ciconiiformes	7	86.9	1.94	0.737	22.000	0.0464
Passeriformes	48	129.0	2.11	0.724	8.710	0.0806
Corvidae	8	126.0	2.10	0.709	23.300	0.1470
Ploceidae	17	164.0	2.21	0.794	1.400	0.0808
Fringillidae	19	125.0	2.10	0.714	1.020	0.0473
All nonpasserines	72	78.5	1.90	0.723	42.800	0.1110
All species	120	86.3	1.94	0.668	52.800	0.1330

It is clear that circadian fluctuations exist as free running endogenous rhythms (Aschoff and Pohl, 1970*a*,*b*) for a large series of animals and that day/night differences exist for a large number of animals (including birds) over a large weight range (Fig. 7.37). Thus with this information now being acquired, it is very likely that data obtained from short-term experiments, using standard metabolic values such as those reported by Lasiewski and Dawson (1967), do not necessarily represent mean values of the day/night differences reported by Aschoff and Pohl (1970*a*,*b*). One study (Lewies and Dyer, 1969) reported a statistical analysis of these day/night differences throughout a wide temperature range for one species, and it is obvious from this work that the picture is very complicated and inadequately developed to this point.

7.4.8.3 Temperature. See Section 7.4.9.2.

7.4.8.4 Density of species. See Section 7.4.1.2.

7.4.9 (608-614) Maintenance Metabolism

In the workshop we defined maintenance metabolism (Fig. 7.38) as:

Maintenance metabolism = *f*(body size, temperature, wind, disease or parasites, weight or number of young, phenophase, food handled, animal age, lactation, stage of reproduction, density of species, rain, competitors, predators)

Most studies have dealt with the standard metabolic values as indicators of variations in thermoregulation, and there is a complex approach of defining maintenance metabolic requirements that is yet to be considered. Maintenance

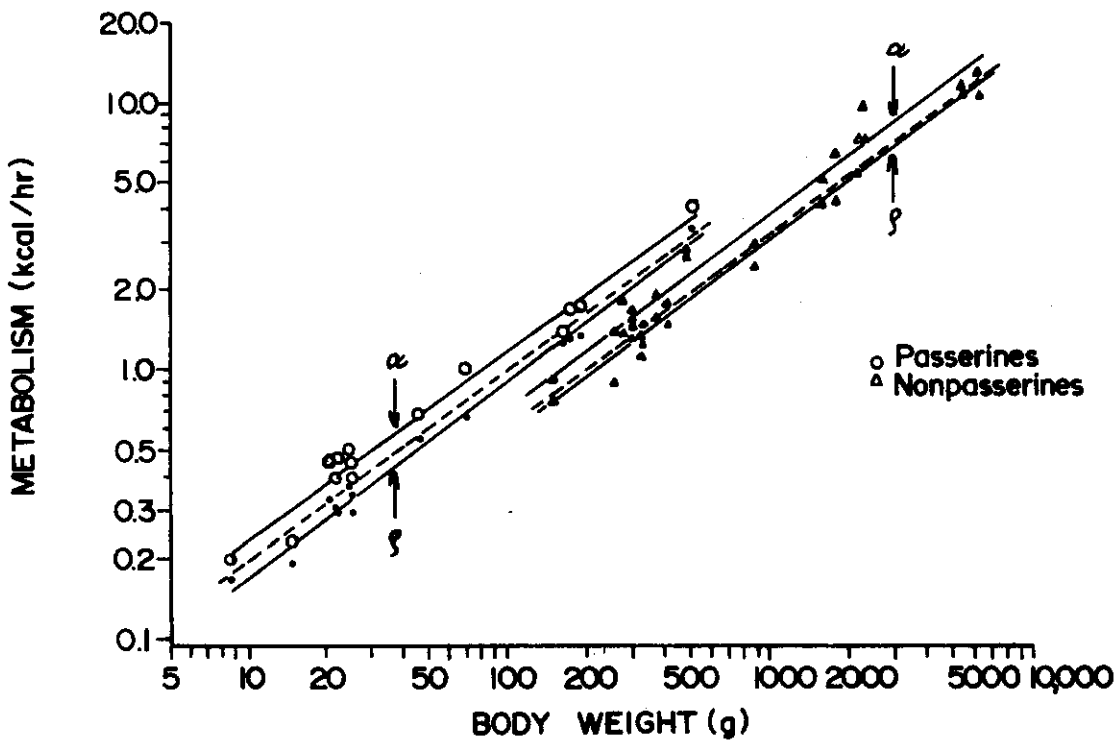


Fig. 7.37. Standard metabolic rate as a function of body size in passerine and nonpasserine birds. Open symbols are measurements during activity time (α). Solid symbols are measurements during rest time (ϕ). All data are from birds at rest and in darkness. Thin dashed lines are according to Lasiewski and Dawson (1967) (from Aschoff and Pohl, 1970*a*).

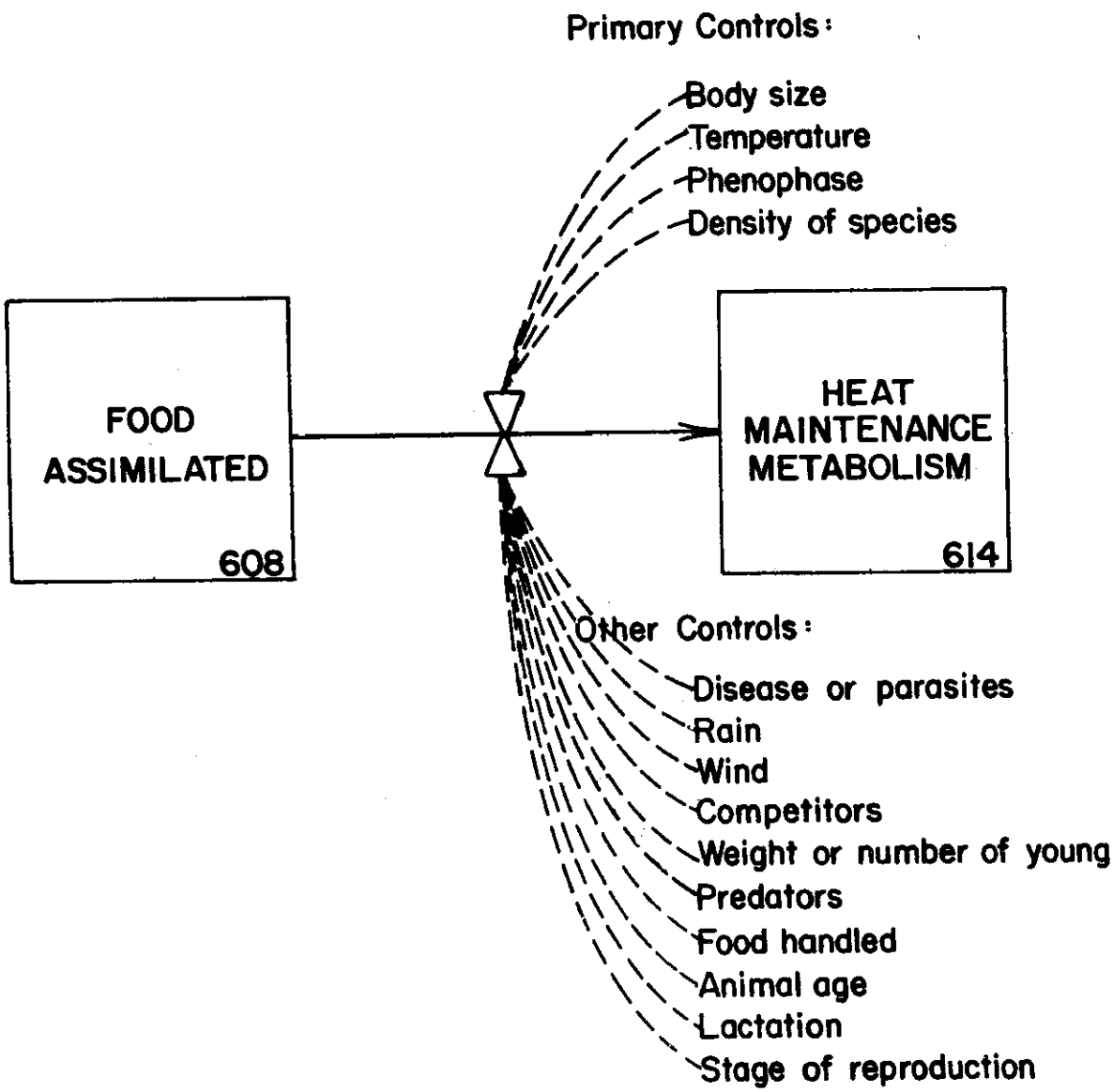


Fig. 7.38. Schematic of process (608-614) with its controls.

energy data automatically integrate all energetic requirements into their values, since the studies are taken over longer periods of time and have built features of energy expenditures into their design during various types of work requirements. In this sense, there may be several degrees of what can be construed as maintenance metabolism, as reported in the literature, ranging from energy requirements in caged conditions (employed during an experiment) to actual total maintenance energy requirements necessary to maintain successful life history events over relatively long periods of time (energy requirements in the natural environment).

7.4.9.1 Body size. Kendeigh (1970) reported initial values for maintenance energy requirements based on weight for several passerine and nonpasserine birds and compared these to the Lasiewski and Dawson (1967) standard metabolism reports (Fig. 7.39). Kendeigh's (1970) values are listed below:

$$\text{Passerines, } 30°C: \quad M = 1.5720\ W^{0.6210} \tag{7.26}$$

$$\text{Nonpasserines, } 30°C: \quad M = 0.5404\ W^{0.7545} \tag{7.27}$$

$$\text{All birds, } 0°C: \quad M = 4.3372\ W^{0.5300} \tag{7.28}$$

7.4.9.2 Temperature. One important set of data missing from the above consideration of metabolic relationships to weight is that of response through a series of temperatures. The report by Lewies and Dyer (1969) gives a statistical basis for predicting that all energetic requirements will follow specific patterns of daily rhythm and temperature controls. The curves presented by Kendeigh (1970) then could be estimated for a series of temperatures, ranging from the thermoneutral zone for passerines and nonpasserines to lower temperature levels experienced by animals in their environment.

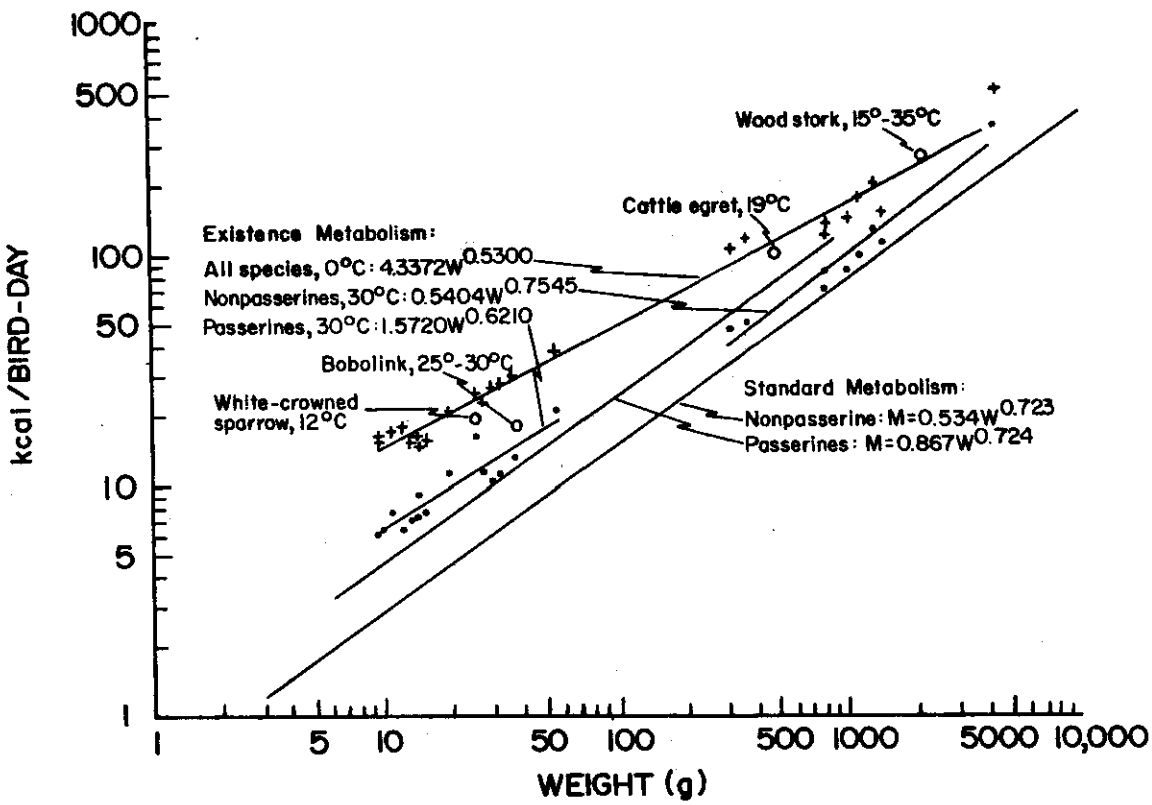


Fig. 7.39. Relation of existence metabolism and standard metabolism to weight in birds. The regression lines for existence metabolism are drawn from the logarithmic form of the allometric equations shown in the figure. The regression lines for standard metabolism are from Lasiewski and Dawson (1967) with the allometric equations expressed for weight in grams instead of kilograms. The solid circles and crosses are calculated from the equations given in Table 1 [see Kendeigh (1970)]; the open circles are additional data for other species at particular temperatures as follows: Cattle Egret, *Bubulcus ibis* (Siegfried, 1969); Wood Stork, *Mycteria americana* (Kahl, 1964); White-crowned Sparrow, *Zonotrichia leucophrys gambelii* (King, 1961); and Bobolink, *Dolichonyx oryzivorus* (Gifford and Odum, 1965). Figure from Kendeigh (1970).

7.4.9.3 Density of species. See Section 7.4.1.2.

7.4.9.4 General ecosystem energy relationships. On an ecosystem basis, at least two papers deal with animal maintenance metabolism throughout the year, in contrast to total net production in the ecosystem (Engelmann, 1966; McNeill and Lawton, 1970) (Fig. 7.40 and 7.41). Two distinct consumer groups have been identified on a gross level by the authors, and homeotherms and poikilotherms have been subdivided by McNeill and Lawton (1970) into short-lived and long-lived forms (Fig. 7.41; see also Engelmann's presentation, Fig. 7.40). The basic function definition is animal maintenance metabolism compared to net production or annual productivity in the ecosystem. As can be seen in Fig. 7.40 and 7.41, there is the familiar log-log relationship. This relationship, in its general form, is the same as described for individual animals in laboratory-held conditions. Thus, in this representation of utilization within the ecosystem, there becomes a common denominator for dealing with energetics and ecosystem relationships for many diverse consumers.

The total ecosystem requirements become, according to Engelmann (1966):

$$\text{Homeotherms:} \quad \log M = 2.59 + 1.75 \log P \tag{7.29}$$

$$\text{Poikilotherms:} \quad \log M = 62 + 0.86 \log P \tag{7.30}$$

where

log M = logarithm of maintenance metabolism

log P = logarithm of net productivity

and according to McNeill and Lawton (1970) becomes:

$$\text{Homeotherms:} \quad \log R = 1.7418 + 0.9812 \log P \tag{7.31}$$

$$\text{All poikilotherms:} \quad \log R = 0.3757 + 1.0733 \log P \tag{7.32}$$

$$\text{Short-lived poikilotherms:} \quad \log R = 0.1352 + 1.1740 \log P \tag{7.33}$$

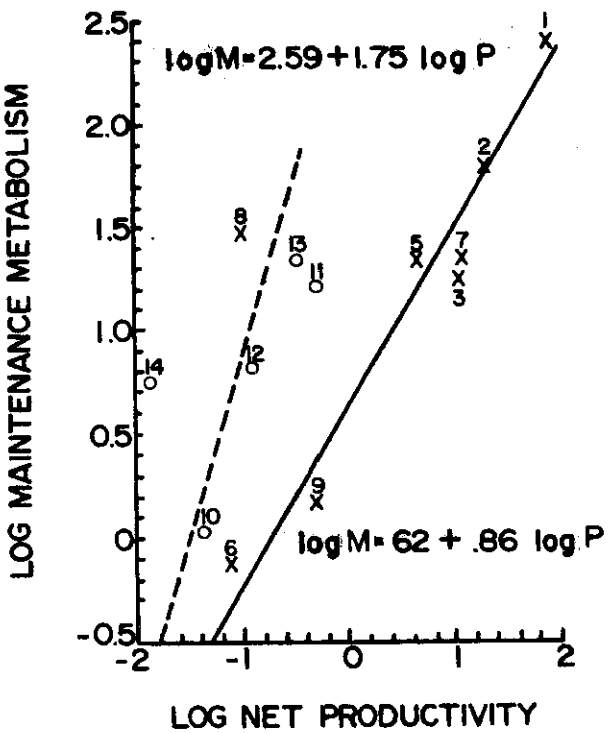


Fig. 7.40. The relationship between maintenance metabolism and net productivity. The points represented by "x's" are poikilotherms and the "o's" are homeotherms. The solid line represents the poikilotherm regression while the dotted line represents homeotherm regression. The numbers associated with each point correspond to the identification numbers in the left-hand column in Table 8 [see Engelmann (1966)].

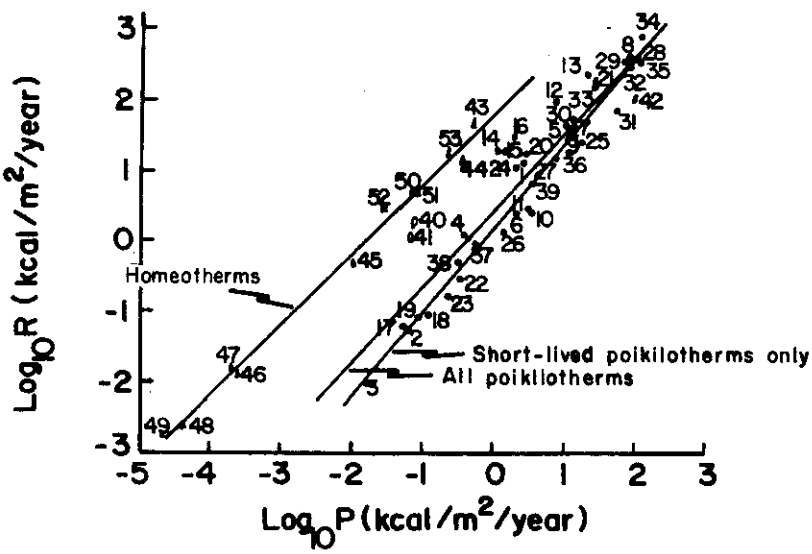


Fig. 7.41. The relationship between annual production (P) and annual respiration (R) (kcal/m^2/year) in animal populations. The numbers associated with each point correspond to the numbers in the first column of Table 1 [see McNeill and Lawton (1970)]. Δ = Homeotherms; o = long-lived poikilotherms; • = short-lived poikilotherms.

where

log R = logarithm of respiration measured in kcal/(m^2 · year)

log P = logarithm of productivity measured in kcal/(m^2 · year)

McNeill and Lawton argued that productivity is an independent function for comparing dependent animals by which a dependent animal respiration function can be compared within the ecosystem. This approach produces the above values. Alternatively, they also presented a case for the fact that productivity cannot exist in the absence of respiration, and thus the coordinates can logically be reversed. When the relationships are computed in this manner they become:

Homeotherms:	log P = -1.7761 + 1.0137 log R	(7.34)
All poikilotherms:	log P = -0.2367 + 0.8233 log R	(7.35)
Short-lived poikilotherms:	log P = -0.0948 + 0.8262 log R	(7.36)

where log P and log R equal the parameters as identified above.

7.4.10 (608-615) Reproduction

During the workshop we defined reproduction (Fig. 7.42) as:

Reproduction = f(animal age, lactation, stage of reproduction)

For large herbivores the nutrient requirements for pregnancy are usually not large (Fig. 7.43). The last trimester of pregnancy is the period when the growth of the fetus demands considerable energy. This is about 20% of maintenance, or a cost of pregnancy throughout the gestation period of approximately 7% above maintenance (Blaxter, 1962).

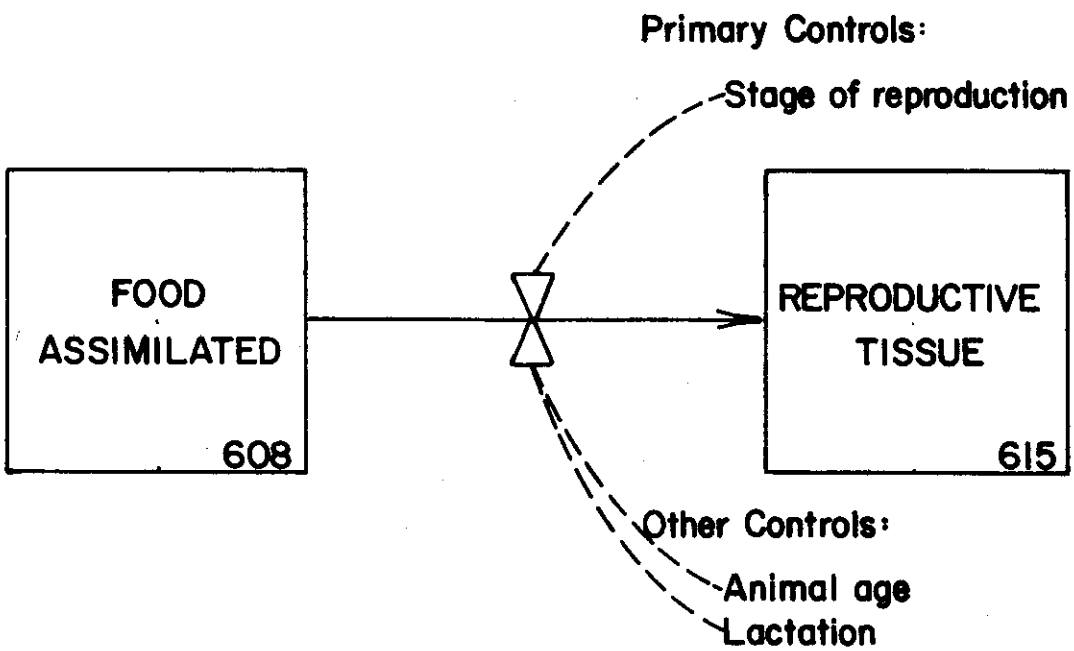


Fig. 7.42. Schematic of process (608-615) with its controls.

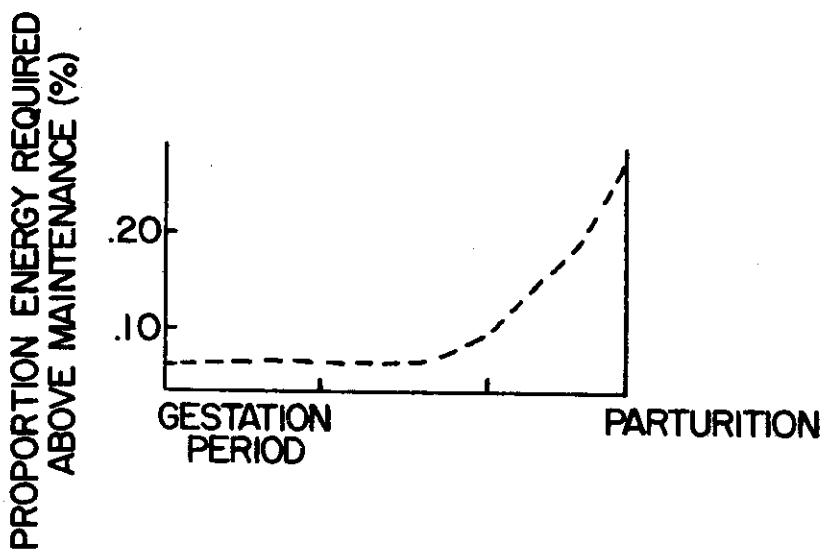


Fig. 7.43 Estimated increase in energy needed above maintenance metabolism for large herbivores during pregnancy.

For the Willow Ptarmigan (*Lagopus lagopus*) food intake requirements of laying females were higher (171.7 kcal/(bird • day) than for nonlaying, molting summer females (101.5 ± 17.7 kcal/(bird • day) (West, 1968). The excretory energy for the laying birds averaged 45.71 kcal/(bird • day); this left a total of 125.99 kcal/(bird • day) of metabolized energy for other activities while laying an average of 0.587 eggs/(bird • day) over 44 days. The average dry weight of a whole egg was 7.023 ± 0.409 g of which 18.19 ± 1.58% was ash. The caloric value of the eggs was 6.592 ± 0.11 kcal/g ash free dry weight, and thus the total caloric value averaged 37.875 ± 2.210 kcal/dry egg. At a laying rate of 0.587 eggs/day, the amount of metabolized energy used in the eggs was 22.23 kcal/(bird • day), which leaves a balance of 103.76 kcal/(bird • day) for the energy involved in the conversions of producing the egg and of other maintenance activities. This figure is almost identical to the metabolized energy of the nonlaying, molting females. The daily intake requirement for producing eggs is apparently equivalent to that for molting, as the intake requirement for nonmolting, nonlaying summer females is calculated as 98 kcal/(bird • day) (West, 1968).

7.4.11 (608-616) Lactation

During the workshop we defined lactation (Fig. 7.44) as:

Lactation = f(weight or number of young, animal age, rate of assimilation, stage of reproduction)

For large herbivores, lactation requirement is approximately 18.2 kcal/kcal milk produced. Since lactation has been measured in very few animal

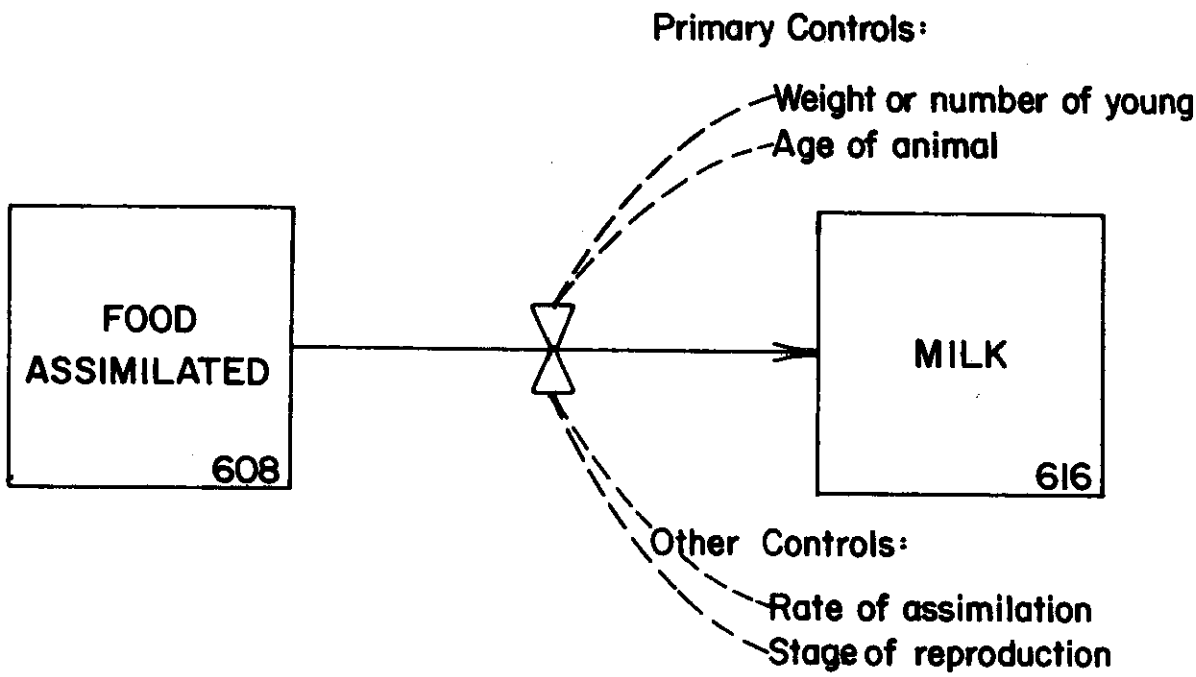


Fig. 7.44. Schematic of process (608-616) with its controls.

species, this value is difficult to relate to animal daily requirements. Most animals that graze produce milk for nursing young only. The amount produced is related to the number, age, and weight of offspring. Young herbivores rarely depend upon milk for their total energy requirement for more than 4 to 8 weeks of life. Therefore, the proportion of nutrients arising from milk for young declines with age. In domestic livestock, milk production rises to a peak and maintains itself for the nursing period which, in most herbivores, is restricted to the growing season of herbage. In domestic cattle and sheep nursing young, the lactation period results in an increase in the energy requirement of about one times the maintenance requirement (National Research Council, 1970, 1971). Also, see the report by Johnson and Groepper (1970) and Section 7.4.1.4 for energy costs in lactating rodents.

7.4.12 (608-617) Growth of Nonfat Tissue and (608-618) Growth of Fat Tissue

In the workshop we felt that both processes were governed by nearly the same controls even though two different types of material are produced along separate metabolic pathways. For growth of nonfat tissue see Fig. 7.45.

Growth of nonfat tissue = f(food availability, animal age, rate of assimilation, lactation, stage of reproduction)

For growth of fat tissue see Fig. 7.46.

Growth of fat tissue = f(food availability, animal age, rate of assimilation, lactation, stage of reproduction, fat catabolism)

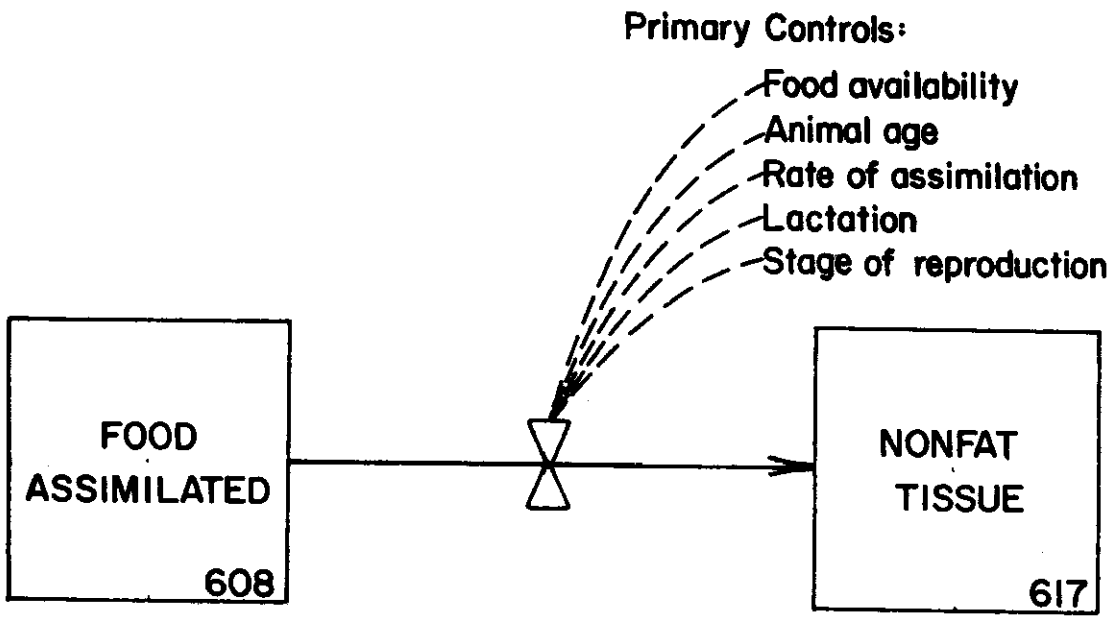


Fig. 7.45. Schematic of process (608-617) with its controls.

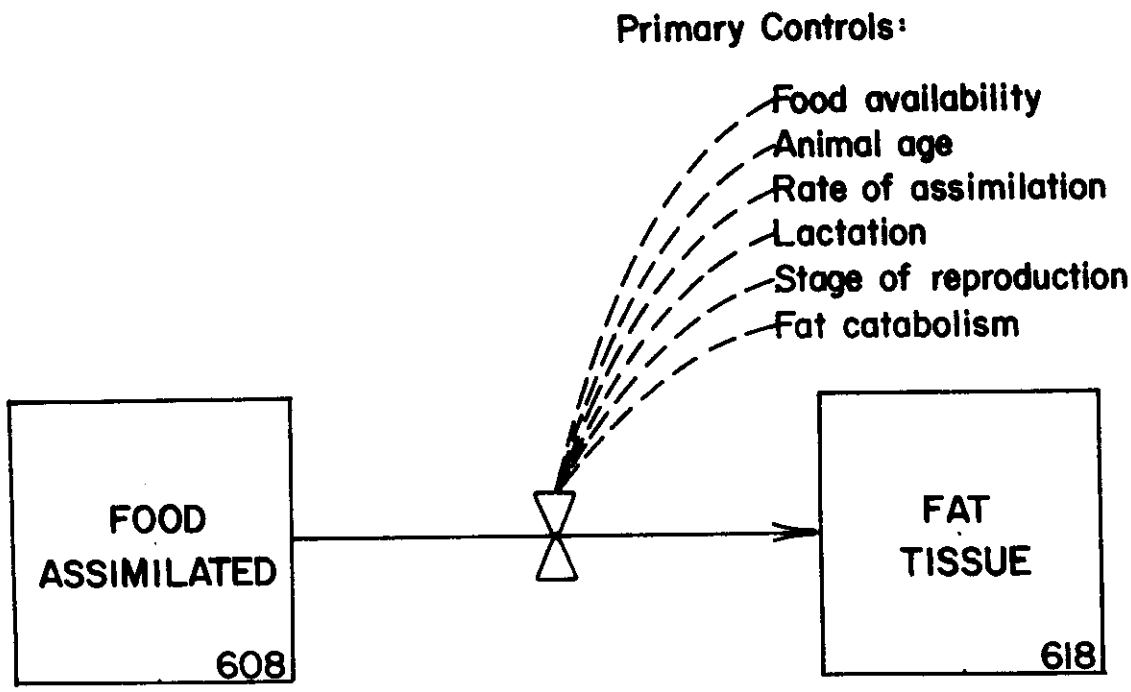


Fig. 7.46. Schematic of process (608-618) with its controls.

The efficiency of the use of metabolizable energy for growth and fattening (k_f) was described by Blaxter (1962) to be:

$$k_f = 0.81\ Q_m + 3.0$$

where Q_m is the proportion of gross energy which is metabolizable energy. If foodstuffs are assumed to contain 4.4 Mcal/kg dry matter (4.0 to 4.7 according to literature values), the relationship may be written as:

$$k_f = 18.4\ ME + 3.0$$

where ME is expressed as Mcal/kg dry matter of the feed (Greenhalph, 1969).

It is difficult to separate growth from fattening since both functions occur simultaneously in growing animals. The proportion of protein in body weight decreases as the animal approaches maturity. Weight changes in the mature animal can be considered to be fat unless there is a drastic weight loss, e.g., over 20% of live weight. The requirement for protein deposition is about 7.5 kcal/g protein tissue (Kielanowski, 1965).

Little information concerning the composition of growth is presently available. However, some early researchers have given some data (see review by Hedrick, 1968).

Most information indicates that weight has a greater effect upon the composition of the carcass than age. Muscle proportion tended to decrease with degree of fattening, but the proportion of carcass muscle in cattle was relatively constant at one-third of body weight (Hedrick, 1968). The proportion of water in the carcass declined as the amount of fat increased. Fig. 7.47 illustrates this relationship with cattle and was described by

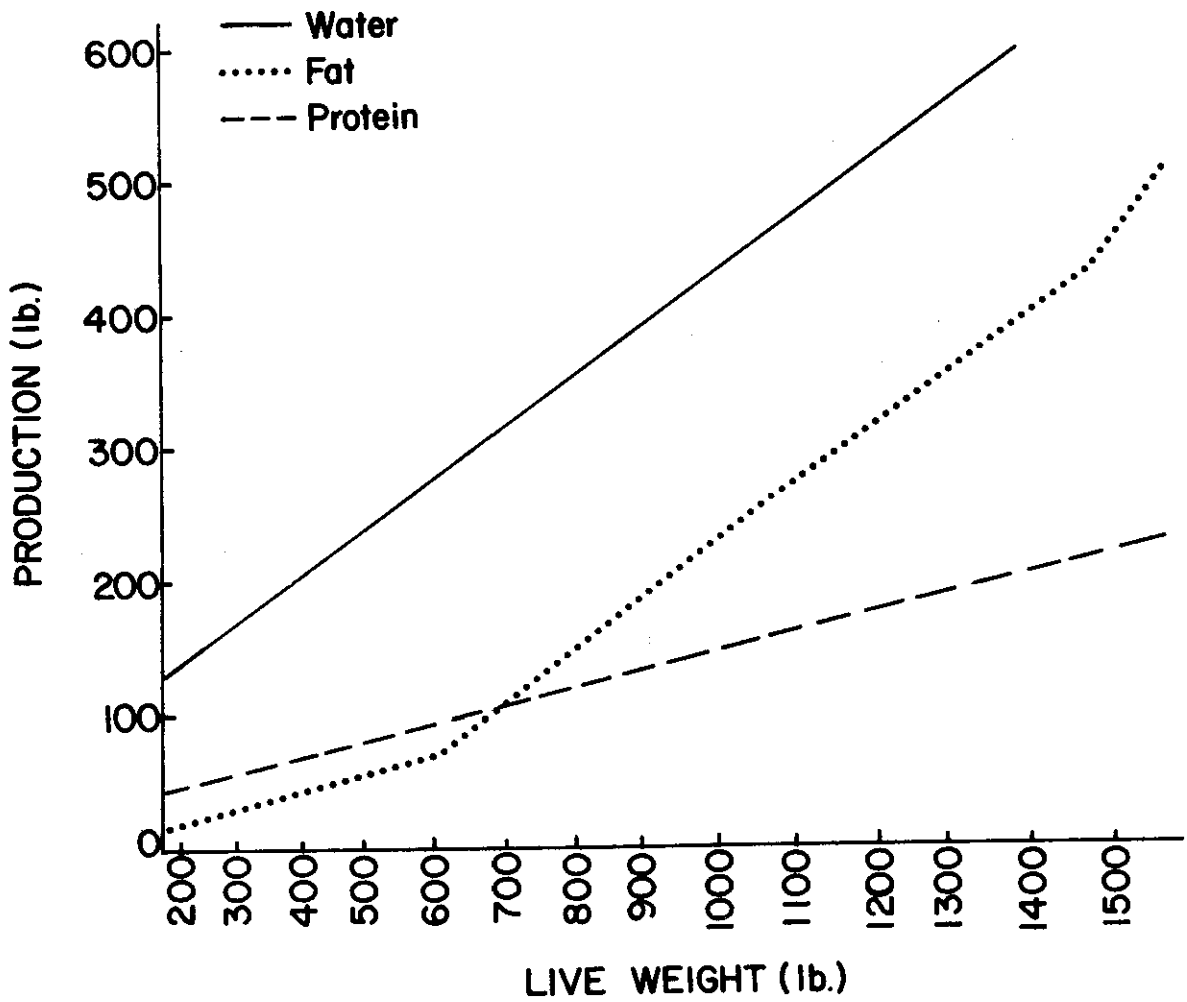


Fig. 7.47. Composition of growth in cattle. The rate of protein and fat synthesis is about equivalent until the animal reached one-half of its mature size. At this point, fat deposition accelerated while protein growth continued at the rather constant rate shown.

Haecker in 1920 (Hedrick, 1968). It can be seen that the growth of protein tissue was fairly constant up to mature size. The rate of fat deposition was similar to that of protein growth up to a weight equivalent of one-half mature size. At this point, the rate of fat deposition accelerated as the animal grew.

Cattle and sheep under good nutritional levels achieve fat levels of up to 40% of body weight. Wild herbivores rarely approach this level of fatness (Ledger, 1968). It appears that selection of domestic animals for rapid growth has increased the rate of fattening, while not changing the inherent rate of protein deposition. For this model we suggest that energy in excess of maintenance needs be allocated to protein growth to satisfy the rate expressed by Fig. 7.47. Then if any energy remains, fattening can occur.

With wild herbivores we must assume that protein and fat deposition will follow a similar relationship; however, wild herbivores are rarely able to fatten as rapidly because of the nature of their diets. For example, it is possible to reach fat levels approaching those in domestic livestock in American bison, but maximum growth rates of bison are usually not as great as those in cattle.

Accordingly, protein deposition can proceed in all herbivores at the rate shown for cattle, but fat deposition will not accelerate as rapidly in nondomestic herbivores, even under high nutrition.

Fattening should not occur until all other functions are supported. Then fattening can equal growth up to one-half mature size, providing that enough energy is available. In mature animals weight changes are assumed to be fat. Maximum rate of fat deposition in mature animals is estimated to be 0.004% of body weight.

If nutrients in excess of growth and fattening rates are available, the animal should reduce intake.

Fat deposition requires 11.8 kcal energy/g fat deposited.

7.4.13 (608-619) Growth of Integument

During the workshop we considered that growth of integument was of sufficient interest for some groups of animals (those that regularly molt pelages or plumages or shed their skins on seasonal bases, and those that molt on a schedule related to growth and development). We felt that the process of growth of integument (Fig. 7.48) was represented by:

Growth of integument = f(phenophase, animal age, rate of assimilation)

Few literature reports have been obtained specifically for this process to date.

The energy cost of molt in Brown-headed Cowbirds (*Molothrus ater*) resulted in a 13% increase in oxygen consumption at 35°C (Lustick, 1970). Below 20°C the increase in oxygen consumption was approximately 24%, with about half of this due to energy required for feather formation. In House Sparrows (*Passer domesticus*), the increase in metabolized energy with growing feathers, i.e., molt, amounted to 4 to 5 kcal/(bird • day) at maximum (Fig. 7.49). This was true at separate temperatures of 3°, 22°, and 32°C (Blackmore, 1969).

I feel that certain other papers dealing with molt in birds and mammals and growth rates of insects will perhaps provide some more basic information for this rate.

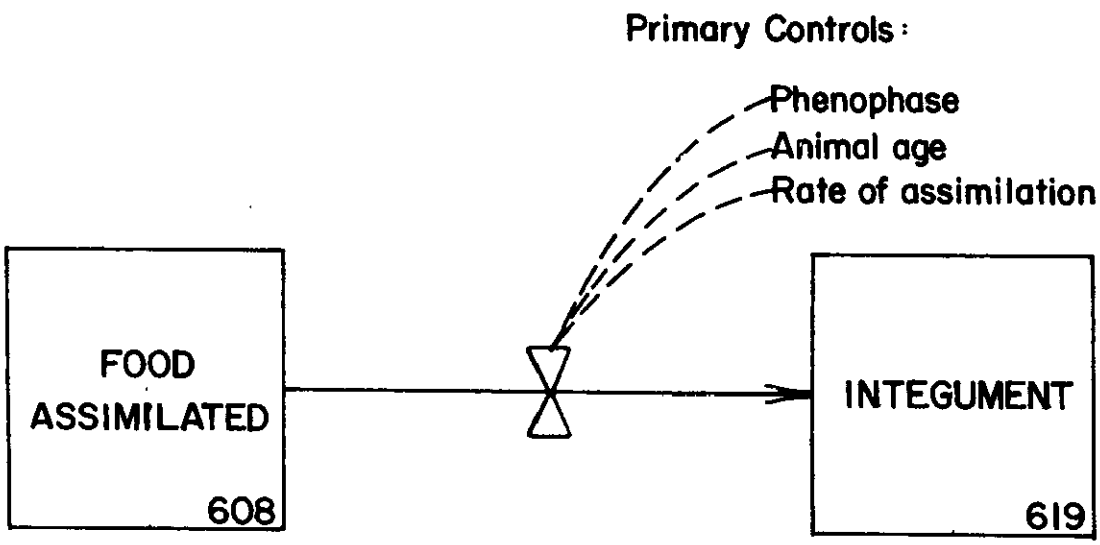


Fig. 7.48. Schematic of process (608-619) with its controls.

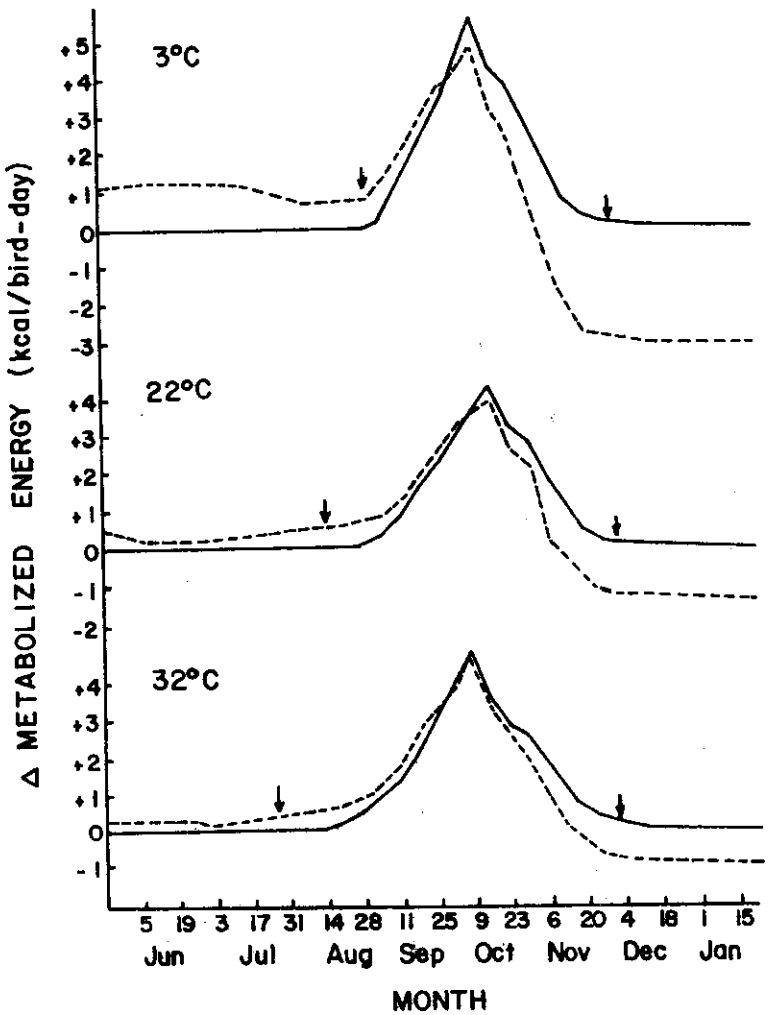


Fig. 7.49. The temporal relationship of the change in metabolized energy with growing feathers at 3°, 22°, and 32°C. Arrows indicate the beginning and end of molt. Solid lines represent relationships with the effects of time removed. Dashed lines represent relationships with the effects of time included (from Blackmore, 1969).

7.4.14 (617-608) Protein Catabolism

During the workshop we felt that protein catabolism (Fig. 7.50) is represented by:

Protein catabolism = f(food availability, animal age, rate of assimilation, lactation, stage of reproduction)

Some degree of transamination and deamination of protein reserves can occur in animals; however, for our consideration this process is more academic than practical. Thus I have paid little attention to this particular section and will let it suffice to note that we considered the process during the workshop.

7.4.15 (618-608) Fat Catabolism

During the workshop we estimated fat catabolism (Fig. 7.51) to be:

Fat catabolism = f(food availability, animal age, rate of assimilation, lactation, stage of reproduction)

Fat reserves are quite important for carrying many different animals through stressful periods when the animals do not eat, either from lack of available food or from specific behavioral or physiological adaptations peculiar to that species. For large herbivores, fat utilization occurs at about 70% efficiency and fat losses can occur to a level of 1.5 to 2.0% of the body weight. At this point, the animals reach a critical point and will usually die.

For small rodents, hibernation or estivation activities are periods when large demands are made on fat reserves. For a review of this literature see Fisher et al. (1967).

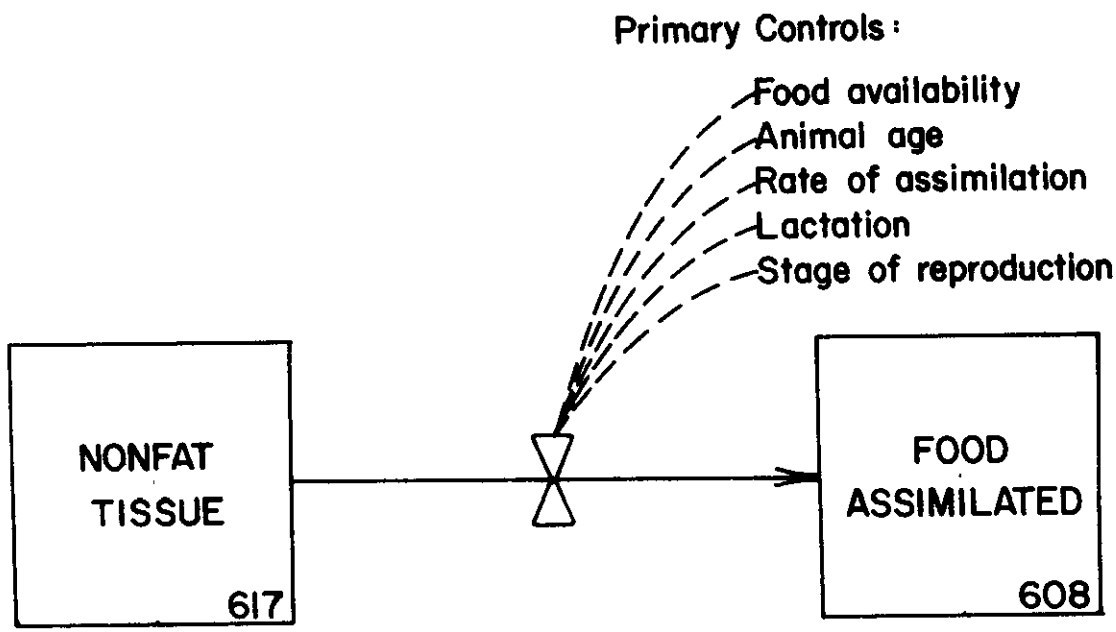


Fig. 7.50. Schematic of process (617-608) with its controls.

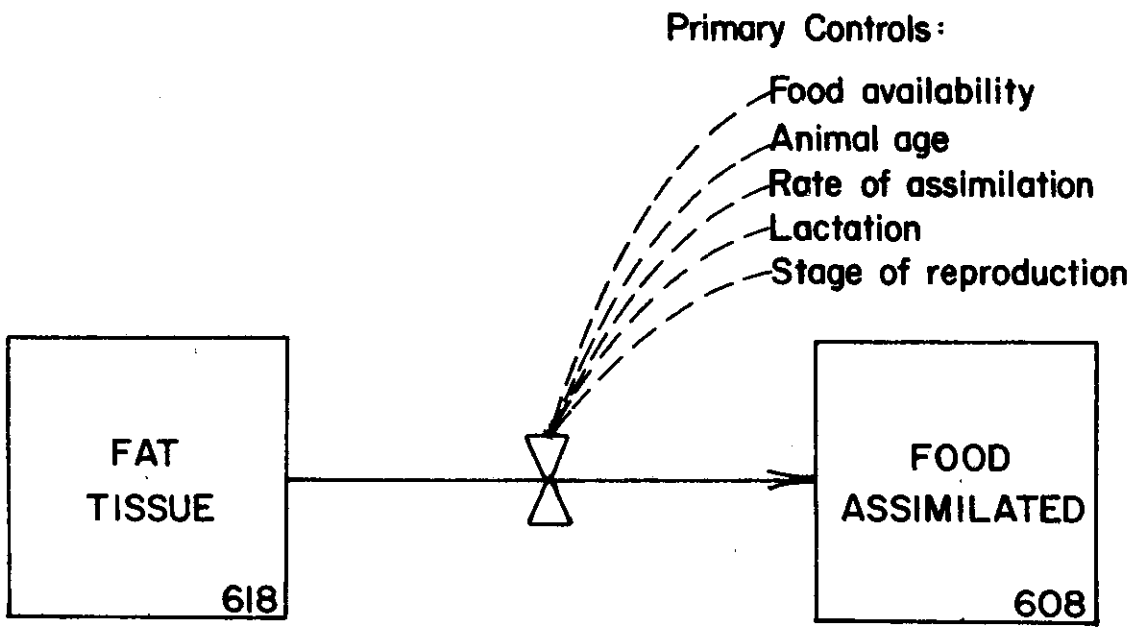


Fig. 7.51. Schematic of process (618-608) with its controls.

Birds also have peculiar physiological and ecological requirements for fat utilization, particularly during long fasting periods that occur at night and during heavy work of migration. For a comprehensive review see George and Berger (1966).

7.5 SUMMARY AND RECOMMENDATIONS

7.5.1 Discussion

An underlying feature for development of this model was a deliberate bias in favor of large herbivores, notably domestic cattle. There is a plethora of data structured in a way in which we could use them for the information-model building exercise, whereas most other animal groups have, at best, only partial sets of data to represent them. Thus, for the most part, it is not possible to force all consumers into all state variable boxes described nor will all consumers then contain the flows and controls for which we had decided to gather information. However, there are compromises made also in that not all of the material as presented in Fig. 7.1 and Tables 7.3 and 7.4 best fit large herbivore data or modeling attempts. Thus the following discussion is aimed at more directly satisfying large herbivore needs in information gathering and model construction.

The basic energetics of domestic ruminants, especially cattle and sheep, have been worked out experimentally and in great detail by Brody (1945), Blaxter (1962), Cuthbertson (1969), and Kleiber (1961). Research with wild ruminants has indicated that their energetics are similar to the well-studied domestic herbivores (Crawford, 1969; Wesley, Knox, and Nagy, 1970).

Also, the net efficiency of lactation for dairy and beef-type cattle has been shown to be similar. These animals represent the extremes of milk

production; and therefore, there is reason to believe that ruminants producing milk only for the nurture of the young as compared to ruminants which have been subjected to genetic selection and intensive management for high levels of milk production do so with equivalent net efficiency. This fact is probably due to the similarity of the basic biological and biochemical reactions involved in milk secretion in all mammals (Hohenboken et al., 1972).

Similarly, there is little reason to believe that the net efficiency for growth, fattening, and maintenance of ruminants differs. Therefore, the basic functions of living can be considered to occur with equivalent efficiency for the purposes of an energetics model for ecosystem modeling, at least for a certain number of consumers.

Differences among species of herbivores have been shown to occur in factors such as reaction to environmental exigencies including heat, moisture, wind, dietary habit, and behavior. These functions can be superimposed upon the basic energetics model to define the role of the various herbivores in the ecosystem.

Since the energetics of ingested food among the mammalian herbivore species should be similar, the proposed model for animal energetics can be used in an ecosystem model where the impact of the various herbivores can be simulated based upon energetics, food selection, behavior, and population dynamics.

The large herbivore energetics model can take many forms. However, the best approach appears to be one of working from the end products of energy metabolism which are maintenance, pregnancy, growth, and lactation. Amounts of energy consumed in excess of these requirements are assigned to fattening. There must be limits set upon the amount of excess food ingested so that

animals which reach the limit of fattening rate respond by reducing intake. These limits should rarely be reached because of the range of available energy values normally characteristic of the diets of grazing herbivores. Other limits necessary in the model must be set. The most important limitation to herbivore fattening is that of the limits on the amount of forage which the animal is capable of consuming.

It is proposed that this model take the form that sets limits to intake per day and to the maximum amount of fattening which can occur. These controls should aid in establishing the biological validity of the model.

Further, requirements for the various functions should operate on a priority basis and should reflect the opposite above, i.e., maximum intake and fattening allowed. The first priority for energy (or carbon) should be that of maintenance. When intake cannot support maintenance, the animal should deplete his fat stores and a certain amount of the nonfat body weight (negative growth) can be utilized to maintain life. There is a limit to this which would have to be set, a point at which animals in the population begin to die. These would be young and old first, followed by a proportion of the prime-aged group. In the case of the individual, it would be expected to die when a certain level of nonfat body tissue was depleted (negative growth).

Pregnancy maintenance probably has second priority; however, population pregnancy rates are normally affected by below-maintenance intake. Lactation probably has a lower priority and is generally decreased by low energy availability; it may cease. On a population basis, this should result in increased mortality of the young. Growth requirements are probably next in priority, especially in young animals. This would be followed by fattening which would occur only when requirements for the other functions have been met.

Assumptions which must be made before this model can be applied are:

1. The assimilation and utilization of nutrients by animals is similar. Differences among homeotherms are related to their differences in dietary habit and grazing behavior (Brody, 1945; Kleiber, 1961; Crawford, 1969).
2. Homeotherms have similar metabolic requirements and efficiencies of utilization of nutrients.

These assumptions are valid in the general case; however, it is clear that differences can occur within and among animal species in metabolic efficiencies (Brody, 1945; Kleiber, 1961; Hungate, 1966; Peden, 1971). This is the basis for survival of wild herbivores and for the improvement of domestic livestock through genetic selection.

For the purposes of the generalized consumer model at the level of resolution which we can hope to attain at this point, the above assumptions appear to be necessary. The reasons for this are twofold:

1. There is a paucity of information about inter- and intraspecies differences.
2. These differences are small in terms of the resolution possible in this version of a consumer model.

7.5.2 Recommendations

The basic recommendation that can be given at this time for the consumer energetics model is to provide for a more adequate survey of literature presentations that would fit this model. This is particularly true for the insects and the arthropods in general. Even though much of the literature reported to date did not deal with subject material in the way that we must

organize it for our modeling needs, it is felt that there is a great amount of information not yet utilized. The main difficulty to date has been an inability to search the literature systematically and thoroughly. For this effort, it is obvious that experts representing diverse facets of the many animal groups must be contacted in order to satisfactorily obtain the information. It is also obvious that it requires more work than a committee or workshop members can devote during a normal course of work responsibilities. Thus we recommend that attention be given to the possibility of contacting consultants for such information.

Another problem that must have critical attention given to it is that of the types of consumers and the change of states of the many different types. It is quite obvious that either for information gathering purposes during a process studies orientation such as presented here, or for a modeling exercise, it is not possible to regard all types as we have listed. There are far too many different organisms regarded to date as being potentially important in the grassland ecosystem; and furthermore, there is a great deal of potential detail in keeping track of any change of state that may or may not necessitate a concomitant change in energy requirements. A suggested mode of consolidating these large listings is to pay attention to rates of respiration in the environment over relatively long periods of time.

A third major recommendation is to seriously regard the shortening of this model. The amount of detail for most organisms as presented here very likely is not necessary, at least for a "first-pass." In this respect, there must be sensitive areas delineated from the model so that we can concentrate upon them. The best estimate at this particular time is to rework the model

so that we would concentrate on the amount of food intake or feeding rates as several functions of body size, and subsequent requirements in the model, and then to utilize what is known in the literature about standard and maintenance metabolism levels. It is unclear at this time exactly what sort of reorganization is necessary and how any reemphasis should be organized, but it is equally clear that we have not utilized fully this first approximation, i.e., that of concentrating on building a model based on food intake rates per se.

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