Technical Report No. 197

IBP GRASSLAND/TUNDRA INTERNATIONAL MODELLING-SYNTHESIS WORKSHOP: SUMMARY OF OUTPUT WORKBOOK

Natural Resource Ecology Laboratory (NREL)
Colorado State University
Fort Collins, Colorado
14 to 26 August 1972

F. E. Wielgolaski
Associate Professor
Director of Norwegian IBP Tundra Studies
University of Oslo, Norway

GRASSLAND BIOME
U.S. International Biological Program

December 1972

TABLE OF CONTENTS

ABSTRACT

by

George S. Innis
Natural Resource Ecology Laboratory
Colorado State University
Fort Collins, Colorado

From 14 to 26 August 1972 the Grassland and Tundra Biomes of the International Biological Program hosted a workshop attended by some 75 participants from 19 counties. Prior to the workshop, data collected by the IBP research sites in these countries were sent to the Natural Resource Ecology Laboratory of Colorado State University and processed into machine readable form. A workbook summarizing these materials was presented to each participant early in the workshop.

During the intensive two-week meeting, these data, additional data brought by participants, and numerous ideas about biological systems and data synthesis were reviewed, analyzed, and tried. This learning experience and exchange of ideas were the principal benefits of the workshop. This report is a summary of the activities of the workshop. A more detailed output workbook containing the detailed, if preliminary, results of the workshop is the major source document. Because of its great size and preliminary nature, the output workbook has been distributed only to workshop participants.

IBP GRASSLAND/TUNDRA INTERNATIONAL MODELLING-SYNTHESIS WORKSHOP

Natural Resource Ecology Laboratory (NREL)
Colorado State University
Fort Collins, Colorado
14 to 26 August 1972

SUMMARY OF OUTPUT WORKBOOK*

by

F. E. Wielgolaski†

INTRODUCTION

This workshop was organized and conducted to facilitate the exchange of information on the synthesis of IBP Grassland and Tundra data. Many research programs had entered or were entering a synthesis phase of their activities. Different programs had taken different approaches to synthesis and, therefore, had developed different strengths which, in the workshop format, could be exchanged and tested. As a consequence, the benefits derived by the participants was more important than the synthesis and modelling results reported here.

As preparation for the workshop, requests were sent early in 1972 to people in the participating countries responsible for IBP Grassland or Tundra project data. The data received were filed in a computer data bank An input workbook§ containing tables and graphs which summarized the data from each site was distributed to the participants early in the workshop. This workbook was often updated and provided a basis for the synthesis and modelling activities.

---

* International Biological Program PT Section, Grassland and Tundra International Working Groups Report on the Modelling and Synthesis Workshop, NREL, August 1972. 498 p.

† Associate Professor, Director of Norwegian IBP Tundra Studies, University of Oslo, Norway.

§ IBP, PT, Grassland and Tundra - Modelling and Synthesis Workshop, NREL, August 1972. Approximately 500 p.

The goals of the workshop, after discussion on the first day, were defined as:

1. The workshop should be an educational experience for all participants in various forms of synthesis and modelling and presentation of results about IBP Grassland/Tundra studies throughout the world.

2. Preliminary tabular and graphic synthesis and comparison should be made of research results from throughout the world. These syntheses would include statistical interpretation and investigation of the data.

3. Total system and subsystem models of dynamic processes within the system should be developed.

To work for these goals the participants of the workshop were organized in smaller groups of 2 to 10 people. Each work group had the following categories of persons: (i) a chairman, (ii) a recorder, (iii) at least one analyst, and (iv) the remaining members to be acquainted with the subject matter area involved with the work group effort (see Table 1). It was tried during the whole workshop to have a close cooperation between the groups, especially through daily meetings between the chairmen and analysts but also in 1-hour daily report meetings with all group members.

The following groups were working on synthesis and modelling of international data:

- Group I. International synthesis IBP volumes discussion group
- Group II. Intercomparability of biomass data
- Group III. Dynamics of abiotic determinants of growing seasonal biomass
- Group IV. Grassland/Tundra system simulation model (subdivided into five groups as seen in Table 1)
- Group V. Photosynthesis process model
- Group VI. Environment modification model

GROUP II. INTERCOMPARABILITY OF BIOMASS DATA

It was found that data summaries from each site could be presented in a form of static model as shown in Fig. 1. The boxes represent minimum, maximum, and mean seasonal standing crop (whether live or dead) in g/m^2, and the flows represent annual fluxes in $g/m^2/year$. The apparent net annual primary productivity for aboveground parts was calculated by the following methods:

1. Summation of positive increases in the total aboveground standing crop. The latter is the sum of aboveground live biomass, standing dead, and litter.

Table 1. Membership of working groups (see Appendix I for full names and addresses).

Group	Chairman	Recorder	Analyst(s) and Programmer(s)	Participants
II	Coupland	French	Singh	Hildyard Johnson Misra Numata Petrusewicz Ricou
III	Van Wyk	Jones	Haydock Steinhorst	Jonsson Morris
IV*a* General				Gustafson Innis
IV*b* Abiotic	Smith	Ripley	Sauer Shipley	
IV*c* Producer	Wielgolaski	Pandeya	Godron Noy-Meir Robinson	Ares Dodd Ketner Luti Runge
IV*d* Consumer	Hutchinson	Lamprey	Anway Keith	Breymeyer Dyer Ellis Lamotte Stenseth
IV*e* Decomposer	Heal	Rosswall	Hunt Peltz	Coleman
IV*f* Nutrient cycling	Moore	Till	Randell Rodell Peltz	
V	Brittain	Connor	Penning de Vries Whitfield Baker	Eckardt Moser Ruetz
VI	Marshall	Marshall		Parton

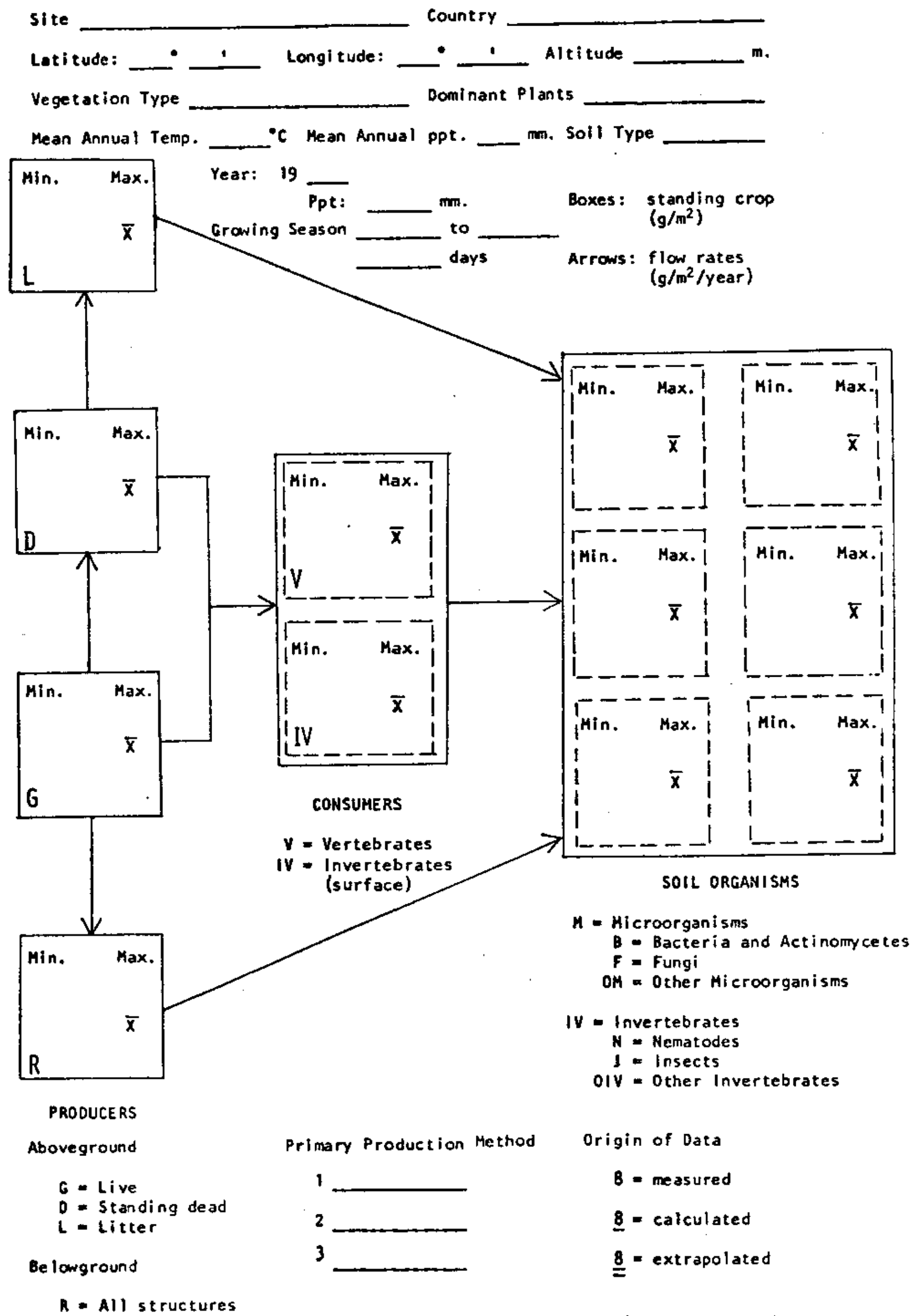

Fig. 1. Form to be used to assemble plant biomass data required to calculate productivity and to provide a basis for graphical representation of seasonal changes.

2. Summation of peak live weights of individual species with subtraction of eventual live weight values before the growing season starts.

3. Summation of positive increases in the aboveground live biomass plus summation of positive increases in the standing dead for only those periods when the increase in the standing dead matter could not be accounted for by a decrease in the live biomass. Similarly, belowground productivity was calculated by summing positive changes occurring from repeated sampling during the year.

From the data available, 49 static models (from 31 sites in 12 countries) were completed during the workshop as far as data allowed.

If more detailed information is needed the forms in Fig. 2 to 4 are proposed to be used. Fig. 2 shows a form for collection of information on the seasonal changes in plant biomass. It includes woody parts (but still no division into live and dead roots which may be of interest when measured or calculated), and permits some interpretation of data. The form in Fig. 3 gives some subdivisions of animals to groups, and the one in Fig. 4 makes it possible to include some more abiotic measurements. Another method for presentation of seasonal relative changes in aboveground plant biomass (live and dead) is shown in Fig. 5. The working group did also prepare a list of availability of various types of data from the sites, as well as a list of people responsible for each type of data in the different countries. A brief, standardized method of classifying Grassland/Tundra sites was found desirable. In the IBP-CT handbook a classification method was found that was applied to the sites for which data were available (Table 2).

The range of plant measurements and computations of Grassland/Tundra sites were, as expected, great. In Table 3 is given some of the ranges that were found from the available data.

In graphs the maximum aboveground live biomass as well as aboveground net primary production showed an inverse curvilinear trend with increasing latitude (Fig. 6 and 7, respectively). The maximum aboveground live biomass showed an inverted parabolic relationship with mean annual precipitation (Fig. 8) and a positive curvilinear relationship with mean annual temperature (Fig. 9). The belowground/aboveground live biomass ratio exhibited a positive curvilinear trend with latitude (Fig. 10) (and thus a similar negative trend with temperature) while there was a weak inverse relation between this ratio and the mean annual precipitation (Fig. 11). Even if there are variations in the sample methods used at different sites, these relationships found are possibly indicating trends in the plant data compared to the environment.

Site and Vegetative Type: ____________________

Please fill in the following table for all sampling data available.

Reporting year: 19 ____ Dry weights (including ash)

☐ oven dry

☐ air dry

Aboveground Plant Parts						Belowground Plant Parts		
Date	Green (live)	Woody * Stems	Standing Dead	Litter		Date	All Parts	

* If greater than 5% of live.

Please indicate:

1. Height of clipping:
2. Litter in collected includes ☐ coarse ☐ coarse and fine
3. Depth of sampling belowground ________ cm and proportion of total belowground parts included in above weights ________ %.

History of stresses imposed:

Year of last grazing ________ (Date d/m/y) Light ☐ Moderate ☐ Heavy ☐

Year of last mowing ________ If immediate preceding and sampling date give: Height of mowing ____ cm

Litter removed ☐

Litter not removed ☐

Year of last tilling (plowing) ____________

Year of last burning ____________

Utilization history ________________________

Sampling areas: ☐ permanent exclosures

☐ yearly or seasonal exclosures

☐ temporary exclosures

Duration__________ weeks

Comments ________________________

Fig. 2. Form to be used to assemble plant biomass data required to calculate productivity and to provide a basis for graphical representation of seasonal changes.

CONSUMERS AND DECOMPOSERS

Reporting Year: 19 ___

	$\bar{X}$	Min	Max	No. of Sample Periods	Units*
Macroorganisms					
Vertebrates					
Large Mammals					
Small Mammals					
Birds					
Other					
Invertebrates					
Aboveground					
Total					
Belowground					
Nematodes					
Enchytraeids					
Others					
Total					
Microorganisms					
Bacteria + Actinomycetes					
Fungi					
Others					
Total					

* If not ovendry weight (including ash) per meter square, indicate unit of measurement and area.

Fig. 3. Form to be used for assembling data concerning standing crops of consumers and decomposers.

SOIL CHARACTERISTICS

Topography: ___

Parent material: ___

Depth (cm): ___

Color: ___ Organic matter (%): ___

Texture: ___ pH: ___

Drainage: free ☐ impeded ☐

Soil classification: ___

Classification system: ___

Soil Temperature: Minimum ___ Maximum ___ Depth ___

Water holding capacity: ___ cm or ___ %

CLIMATE

	Long Term	Year of Study
Temperature (°C, Stevenson Screen)		
Mean annual		
Mean in coldest month		
Mean in warmest month		
Precipitation (mm)		
Mean annual		
Growing season		
Length of growing season		

OTHER INFORMATION

Please attach:

a. A list of specialists participating in the study.

b. A list of reports and research papers resulting from the study.

Fig. 4. Form to be used to summarize edaphic-climatic characteristics of site.

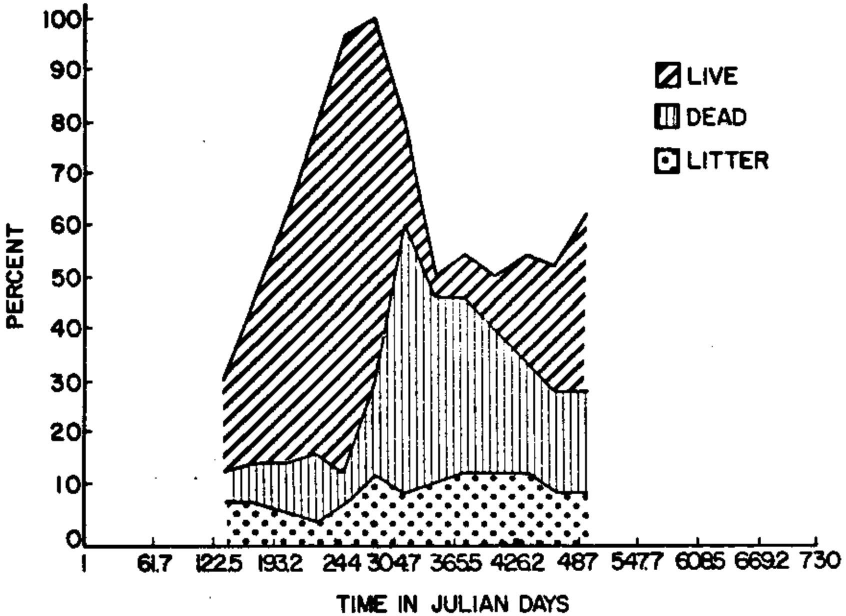

Fig. 5. Form developed for presenting seasonal changes in aboveground biomass. Seasonal maximum of aboveground biomass is 100%.

Table 2. Classification of sites by applying data from the workshop input workbook in the suggested scheme.

SITE	Tropical	Subtropical	Temperate	Subarctic	Dry	Humid	Tall	Short	Closed	Open	With Trees	With Shrubs	With Herbs
UK01			x			x		x	x			x	x
SAF01		x			x			x		x	x		
UK02			x			x		x	x			x	x
JAP01			x			x	x		x			x	
JAP02			x			x		x	x				
JAP03			x			x	x		x			x	
JAP05			x										
JAP06			x			x	x		x			x	
USA11			x		x			x		x			
USA09			x			x	x		x				
IND01	x				x			x	x		x		
CAN01			x		x			x	x				
IND02	x				x			x	x		x		
IND03	x				x			x	x		x		
JAP04			x			x	x		x			x	
IVC01	x					x	x		x		x		
FRA01			x			x		x	x				
CZK01			x			x	x		x				
CZK02			x			x	x		x				
CZK03			x			x	x		x				
NET01			x		x			x	x				x
NET02			x			x		x	x				x
NOR01				x		x		x		x		x	x
NOR02				x		x		x	x			x	x
NOR03				x		x		x	x			x	x
NOR04				x		x	x		x		x	x	x

Table 3. Range of parameter values found from available data.

Parameter	Unit	Range
Maximum aboveground live biomass	g/m^2	97.00-1974
Maximum standing dead	g/m^2	13.00-1268
Maximum litter	g/m^2	107.00-1504
Maximum belowground biomass	g/m^2	139.00-3871
Belowground/aboveground live biomass ratio		0.34-0031
Aboveground net primary production	g/m^2/year	126.30-3396
Belowground net primary production	g/m^2/year	18.20-1465
Percent of total net primary production reflected aboveground	%	10.40-0095.1

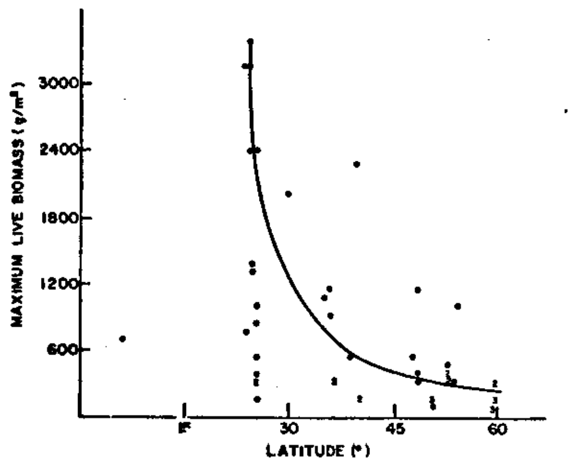

Fig. 6. Relationship between maximum live biomass and latitude.

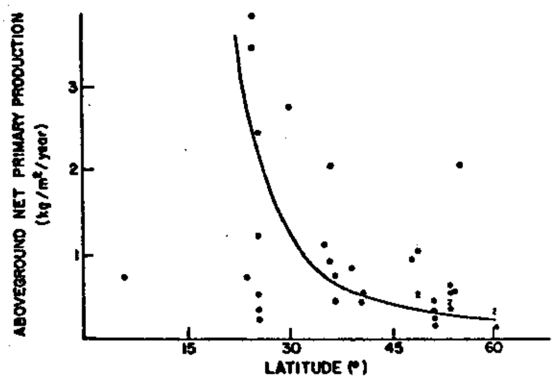

Fig. 7. Relationship between latitude and aboveground net primary production (kg/m^2/year).

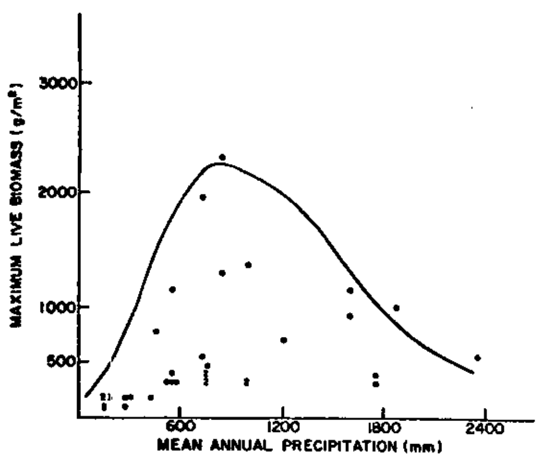

Fig. 8. Relationship between maximum live biomass and precipitation.

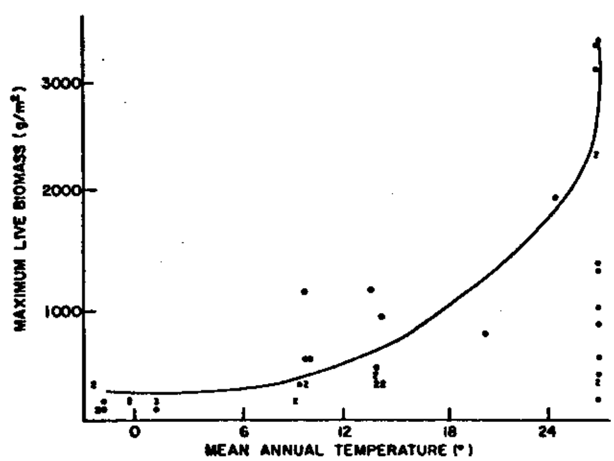

Fig. 9. Relationship between mean annual temperature (°C) and maximum live biomass (g/m^2).

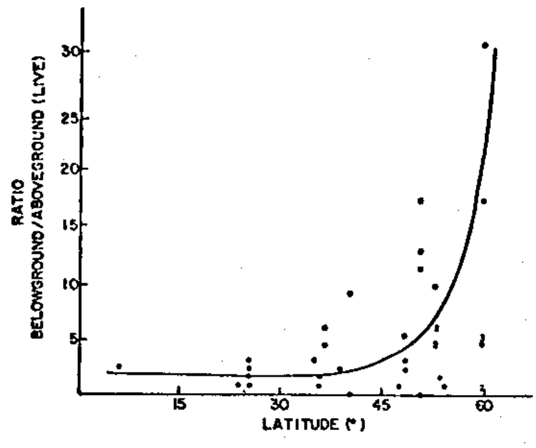

Fig. 10. Relationship between latitude and belowground/aboveground live biomass ratio.

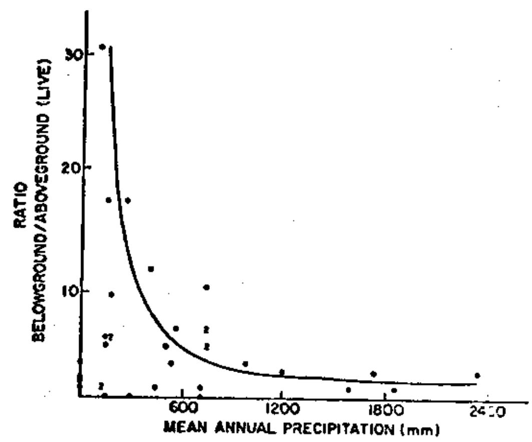

Fig. 11. Relationship between mean annual precipitation (mm) and belowground/aboveground live biomass ratio.

Recommendations

1. Data collected in different years from the same site and in the same year from different sites should be so identified by the contributor.

2. The units of measurement should be specified in every instance, even when in the standard units requested.

3. Where calculated (converted) values are given, the conversion factor should be presented.

4. Height of clipping and depth to which belowground biomass values apply should be given. Where depth of sampling belowground is not to the maximum depth of biotic activity, the proportion in the sample data (of the total) should be noted.

5. Sampling methods (such as the means of collecting litter) should be noted where these have a bearing on the measurements made.

6. A uniform site classification system, emphasizing nature of the plant cover, should be applied.

7. The need should be stressed to check all submissions carefully and to make them as complete as information will allow (while encouraging brevity). On the other hand, where only partial data are available, they should be submitted, but with a complete site description.

8. The need is apparent for both vertical and horizontal (where applicable) data collectors to interchange data received by them and for contributors to send duplicate sets in these instances.

GROUP III. DYNAMICS OF ABIOTIC DETERMINANTS OF GROWING SEASON AND BIOMASS

The variables studied included latitude, altitude, radiation, air temperature, precipitation, and soil water content. Data for soil water balance were obtained for 10° of latitude × 10° of longitude areas over the earth's land surface (except for the Czechoslovak and Netherlands sites where actual data were available). The participants of the workshop were asked to estimate the average date on which growth begins and ends at each site.

Three basic techniques were applied to data from 12 sites documented in sufficient detail.

1. A windrose method in which circular plots of the monthly data for any variable were compared for area and shape across sites (the one o'clock position corresponding to January or July in the northern and southern hemisphere, respectively). Similar diagrams were constructed for the proportional changes across month for each value (Fig. 12).

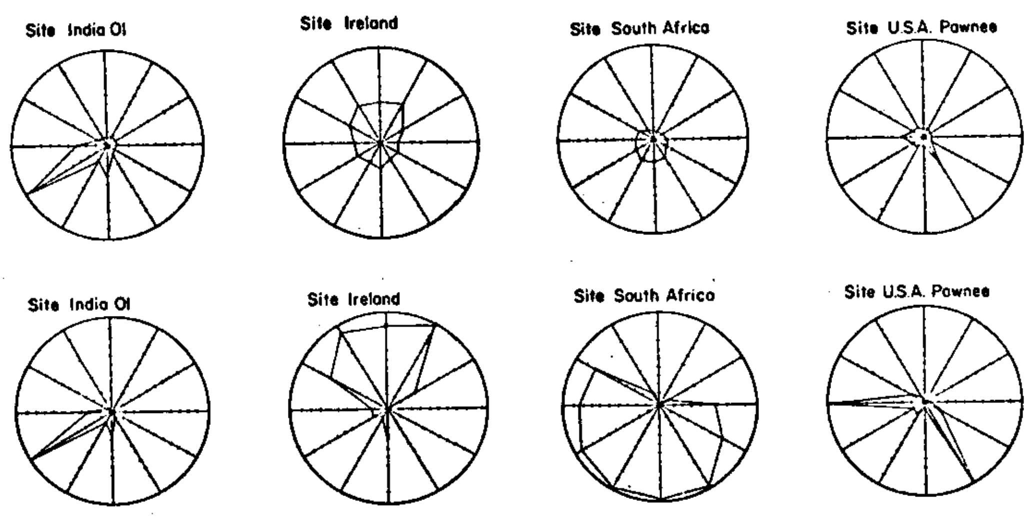

Fig. 12. Windrose diagram for precipitation. Upper row: Precipitation in millimeters; scale: one division = 50 mm; range: 50 to 450 mm. Lower row: Percent of range; scale: one division = 10%.

2. A template method designed to compare the estimated growing season with the season predicted by reference to the precipitation values and threshold values for air temperature and soil water balance. The following threshold values were used:

Air temperature:	Arctic lichens, 1°C Temperate annuals and perennials, 3°C Tropical annuals and perennials, 5 to 10°C
Soil water balance: (normalized values)	Sandy to silty soils, 0.05 Silty-clay soils, 0.15 Clay and sandy-clay soils, 0.25

Precipitation was only considered in assessing predicted growing season when no threshold of air temperature or soil water balance were apparent. The predicted growing season was mostly found to be somewhat longer than the estimated season. The probable abiotic determinants of beginning and ending of growing season at the 12 sites are shown in Table 4.

3. Statistical analyses is the third method. The techniques used were multivariate discriminant analysis, principal component and cluster analyses, canonical analysis, and, adding biomass of primary producer data, a regression analysis of growing season dynamics.

The objective of the discriminant analysis was to take the externally defined growing season and discover if precipitation, temperature, soil water, latitude and altitude were sufficient to classify months at any site in the study as in or out of the growing season. Even with these crude data, the results were mostly gratifying (weakest results for India and Ivory Coast). To increase discrimination capability, one might use weekly data from a wider range of sites and consider variable changes such as using lagged precipitation and soil water as a variable. Day length could also contain significant information to be included in the analyses.

For most of the eight cluster analyses carried out, choice of clustering algorithm and similarity measure made a large difference to the clusters formed, suggesting that the data were possibly inadequate and the results spurious. Euclidean distances based on mean monthly temperatures seemed, however, useful in these analyses as a measure of similarity between sites.

Also in the principal component analyses, temperature gave more ecologically meaningful results to characterize the particular sites than precipitation and soil water balance. The data were mostly of such short term that annual variation could have played quite an important part. The temperature ordination provides a separation into warm and cool sites on the first axis (see Fig. 13). The second component ranked the sites from those with a small annual variation in temperature (like the Ivory Coast near the equator and Ireland with an oceanic climate) to those with a large annual range (like Czechoslovakia and the United States sites with continental climates).

Table 4. Probable abiotic determinants of beginning and ending of growing season at 12 sites. P = precipitation, S = soil water, T = air temperature.

Site	Factor Apparently Limiting Onset of Growing Season	Factor Apparently Limiting End of Growing Season	Remarks
CZECHOSLOVAKIA Lanzhot	T	P	Soil water balance below threshold for most of growing season.
INDIA Kurukshetra(01)	S	P	Temperature above threshold for whole year.
Vindhyan(02)	S	S	Temperature above threshold for whole year.
BHU(03)	P	P	Temperature above threshold for whole year.
Rajkot(04)	P	P	Temperature above threshold for whole year.
IRELAND Glenamoy(01)	T	T	Soil water never limiting.
IVORY COAST(01)	(?)	(?)	No real indications. Burning believed responsible for onset.
NETHERLANDS *Puccinellietum maritimae*	T	S	Temperature and precipitation remain adequate beyond end of growing season.
NORWAY(01)	T	T	Not marked. Soil water balance may affect end of growing season.
SOUTH AFRICA Welgevonden(01)	S	P	Temperature above threshold for whole year.
UNITED KINGDOM Moor House(02)	T	T	
UNITED STATES Pawnee(11)			

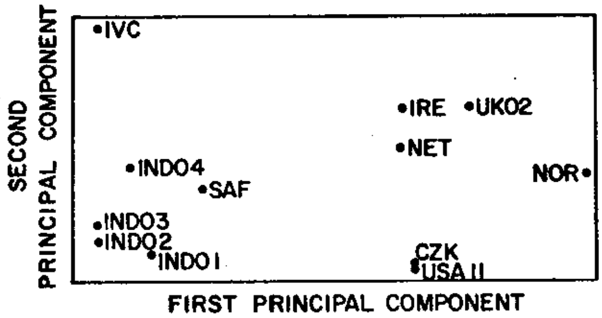

Fig. 13. First and second principal components based on the Euclidean distance matrix between sites.

The distribution of the 12 months in two-dimensional canonical space showed along the first canonical variate a separation of summer months from the winter months. Taken together, the first and second variates indicated the close similarity between the months of December, January, and February and also between the months July, August, and September.

The comparison of biomass on a *normalized* scale was accomplished by fitting quadratic curves through each site's growing season *live and dead* biomass data. Fig. 14 shows the curve for the South African site (R = 0.96, n = 8). Curves from many of the other sites look the same. Most different is the shape of the curves at the Norwegian birch forest site and the site at Czechoslovakia.

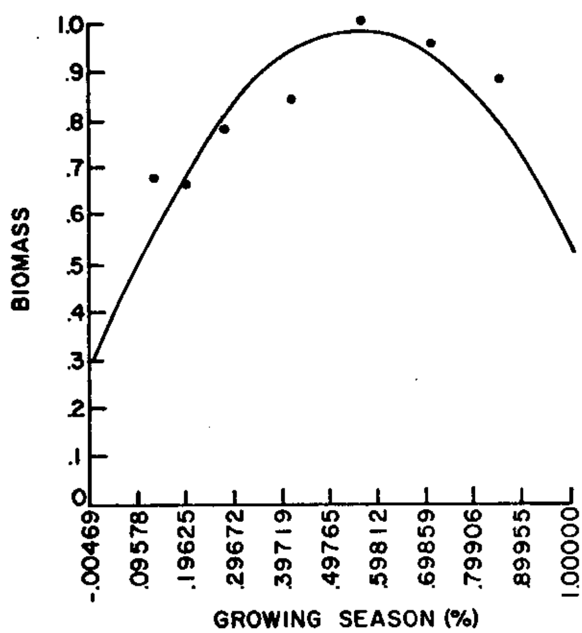

Fig. 14. South Africa LIVE + DEAD biomass data.

GROUP IV. GRASSLAND/TUNDRA SYSTEM SIMULATION MODEL

The objective of the group was to develop a dynamic low resolution point model of Grassland/Tundra systems generally, mostly as a learning experience during the workshop for the group participants. The group was divided into five subgroups to develop submodels on abiotic factors, producers, consumers, decomposers, and nutrients, respectively. These submodels were to be linked together to a total system model.

Abiotic Submodel

There are two distinct roles of an abiotic submodel: (i) simulating soil water hydrology and (ii) generating driving variables. The availability was determined (x) of sufficient site data to generate driving variables and (xx) of "information" from other submodels needed to "control" abiotic flow processes.

Fig. 15 shows the flow diagram for the soil water model. Precipitation (number of rain days in four storm classes 0.1 to 5 mm, 5 to 10 mm, 10 to 25 mm, and > 25 mm) is filling each storage element in succession to field capacity in the soil dependent on bulk density, while evaporation, transpiration, and drainage depletes the water held in the storage elements. The water holding capacity of the vegetation layer is a function of surface area, which is a function of the biomass. When the air temperature is below 0°C, precipitation occurs as snow. If water content exceeds a nonfrozen soil depth, it is runoff from the litter layer. Snowmelt is a function of air temperature and wind speed. The potential evapotranspiration is calculated for each time step, based on net radiation, and a running account of the water that can be evaporated during one time step is then set equal to this potential evaporation. Water stored in the canopy is first evaporated, then water in litter and soil transpiration is said to be a function of root density in the Ith layer, live aboveground biomass, the potential evapotranspiration, and millimeters soil water above the millimeters of water at wilting percentage.

Fig. 16 shows the generators for day length, radiation, temperature, and wind. Given the latitude of the site and date, extraterrestrial radiation at the earth's outer atmosphere is generated. These values are attenuated according to site-specific linear regression parameters to generate mean surface radiation. The different daily temperatures in air and litter layer are generated from annual mean temperature and annual temperature range using a sine wave function, modified by actual surface radiation. (Ratio: simulated insolation to mean insolation is used, so air temperature is lower on cloudy days.) To generate soil temperature, parameter values for thermal diffusivity and specification of soil depth are needed in addition to annual mean air temperature. There is said to be no seasonal change in the wind speed.

The abiotic model gave acceptable performance for radiation, temperature in various layers, and precipitation used for Matador, Canada. So did the curve for snow accumulation and melt, while the behavior of water storage in various layers needs some more checking although the main pattern seems correct.

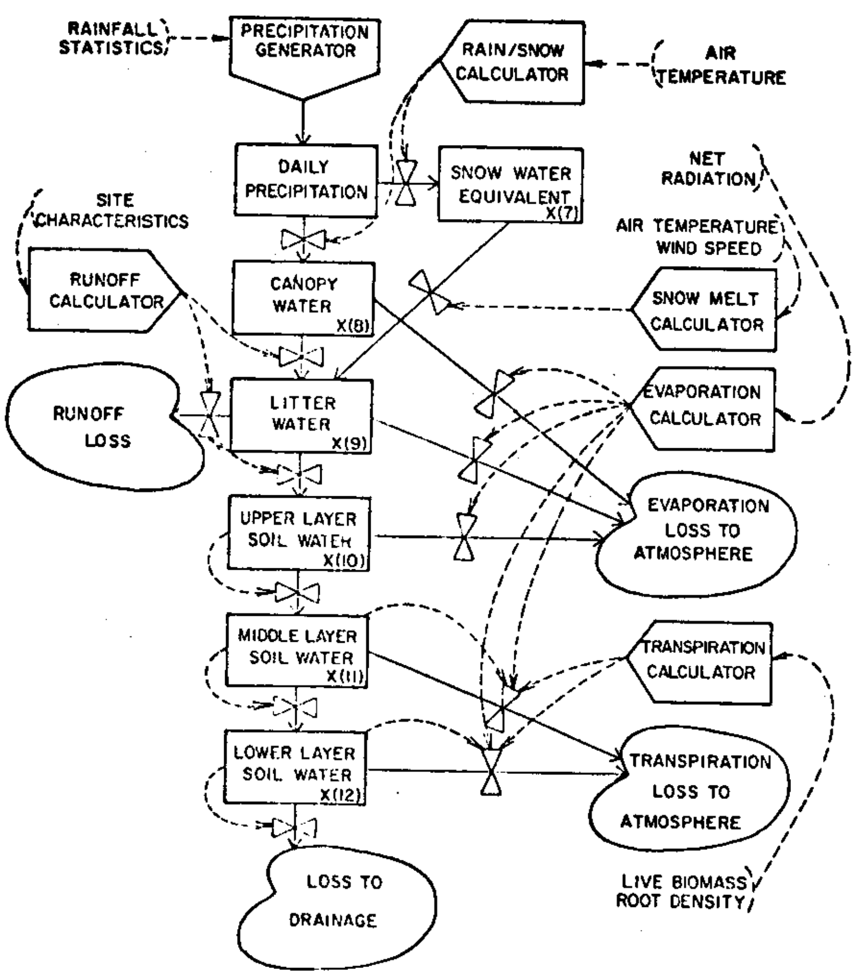

Fig. 15. Flow diagram for the soil water model.

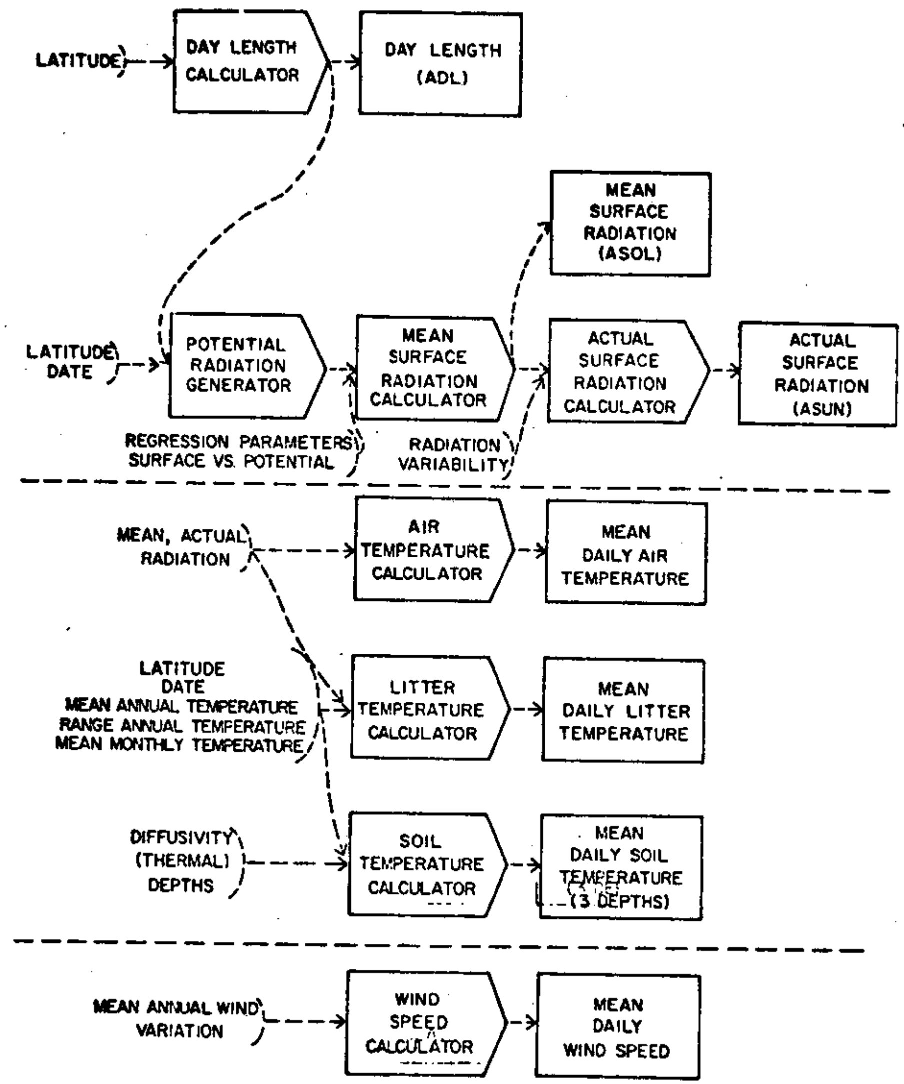

Fig. 16. Upper: Radiation and day length generator.
Middle: Temperature generators.
Lower: Wind speed generator.

Producer Submodel

The primary producer submodel consists of four main state variables (Fig. 17). All input into the system flows through live green biomass (calculated as g dry weight/m^2), resulting in an increase in this state variable and/or translocation to reserve (above and below ground) and to live roots. By definition, translocation is possible from reserves to live green biomass and/or to roots. The output flows from the system are dead material from all state variables and respiration from roots and reserves. Input to live green biomass is calculated as a *net* flow, and respiration from this state variable is thus only considered when photosynthesis is zero. Each of the four main state variables were subdivided into the state variables: woody plants, perennials, annuals, and cryptogams (belowground reserves of annuals and cryptogams said to be zero, as well as roots of cryptogams). Further subdivisions into herbaceous dicotyledons and monocotyledons and into nitrogen-fixing and non-nitrogen fixing plants were made when appropriate as a constant percentage for each site of actual state variables.

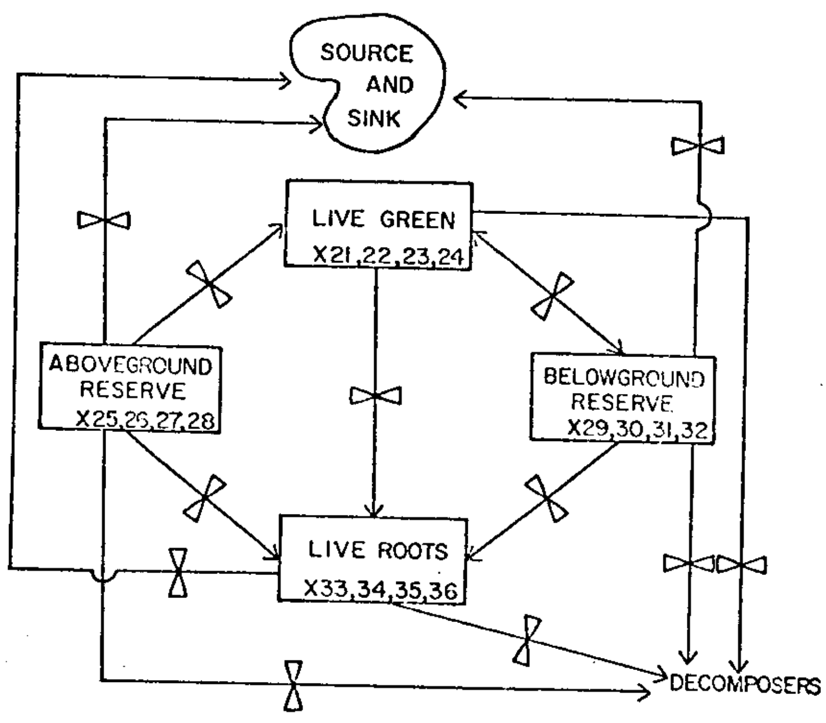

Fig. 17. Elementary diagram of the producer subsystem.

Net assimilation is said to be a function of air temperature, radiation, soil water, and the amount of green biomass. Net assimilation has a low and a high air temperature compensation point. Between these points the response of net assimilation to temperature is a piecewise linear function. A rectilinear saturation function is said to describe the relationship between radiation and net assimilation. Below the compensation points net assimilation may be negative. Response of net assimilation to soil water is a curvilinear saturation curve defined by the water content 0.5 between wilting point (where net assimilation is zero) and field capacity (where net assimilation is one). The soil water content is weighted by root proportion of each soil layer and dependent on the volumetric water content in the soil types at 0.3 atm and 15 atm. The response of net assimilation to live green biomass is a constant relative growth rate with increasing live green biomass, until the biomass gives a shading effect. From this point on, there is an inverse curvilinear relationship between the relative growth rate and increasing biomass (the absolute growth rate becomes constant).

It is assumed that at the beginning of the growing season there is a "reactivation flow" from reserves (above and/or below ground) to green shoots. This flow starts when both soil water and air temperature are above certain levels and stops when the green biomass exceeds a certain level. (The value of this translocation is negative.) When the green biomass is above a threshold value a slow translocation starts from live green to reserves which is said to be a constant proportion of the green biomass. At the end of the growing season as temperature and/or soil water and/or radiation decrease, there is an accelerated storage flow from shoots to reserve, which is proportional (up to a maximum) to the rate of deterioration in the environmental growing conditions and to the proportion of translocatable biomass in green shoots. Reserve to root translocation occurs during the reactivation stage at the beginning of the growing season and is proportional to the reactivation flow to the shoots at the same time. Shoot to root translocation occurs during the growing season when green biomass is above a certain minimum and growth conditions are not deteriorating. The rate is said to be a constant proportion of green biomass.

Both low and high temperatures and low and high amounts of soil water may influence the death rate of green material. Increasing aboveground live biomass will increase the shading effect and thus also the death rate. All these functions are said to be linear functions, except the increased death rate caused by soil water logging which is said to be a step function. Death of the reserves above and below ground (including woody parts of shrubs) takes place at a constant rate. Death of roots is dependent on the root biomass, the root/reserve ratio (step function if the ratio exceeds certain values), soil temperature, and soil water (the last ones according to the same sort of functions as death of green material).

Initially, the portion of the model describing net assimilation was run separately, driven by simplified generators of the abiotic variables: sinusoidal functions of time for radiation and temperature and a piecewise linear function of time for soil water in each layer. The death functions were also simplified. This model was run relatively successfully for a period of 2 years on six sites with different climate and different plant types (lichen heath in Norway, heath shrub bogs in England, cool- and warm-season perennial grasslands in Canada and the U.S.A., winter annuals in Israel, and summer annuals in India). The complete primary producer model was run for winter annuals (Israel) and cool-season perennials (Canada), but has to be adjusted to be fully realistic.

Consumer Submodel

The principal aims of the subgroup were to build a very general model that would accommodate a wide range of consumer types representative of grasslands and tundra, and one that could be developed further to accommodate dynamic changes in the age-classes of the populations. The changes in population during one generation were controlled to follow an exponential survival curve. The metabolic requirements of the consumers were determined primarily from a multiple of basal metabolisms, and the consumer intake was set as a percentage of body weight which could be reduced as a function of dietary quality and food availability. Changes in the biomass (expressed as g live weight/m^2) of animal population are derived from the difference between digested (assimilated) dry matter intake and the daily requirement for digestible dry matter. The daily accumulated growth for the individual animal was obtained by multiplying the biomass by the reciprocal of the survival coefficient.

The following four consumer types were planned to be included in the model (see Fig. 18): (i) herbivores, (ii) carnivores, (iii) omnivores, and (iv) detrivores, but omnivores were omitted, and scavengers were to be included in carnivores. The more prominent representatives within 14 important animal groups in tundra, temperate, and tropical grasslands were marked, but because of lack of time only six "typical" animals within the biomes were used in the model running (mouse, cow/deer, grasshopper, wolf/fox, hawk/kestrel, and Oligochaetae) controlled by five factors (mean temperature, percentage of N and fibre, percentage of digestibility, food capacity, and weight of animal). The model was constructed mainly from the knowledge of the metabolism and feeding habitats of the cow. The maximum food intake per animal and day was estimated and modified for food quality and amount of food available. The dry matter digestibility (and thus the loss in feces) of the total aboveground available herbage was estimated from its nitrogen content using a rectilinear function. Other losses include methane, urine, and heat production. The model was running by the end of the workshop for cow and wolf, showing, e.g., a relatively realistic curve of biomass per unit area as a function of time. Many factors, on the other hand, have to be included before the whole consumer model is realistic, and it was found difficult to link the model with other submodels.

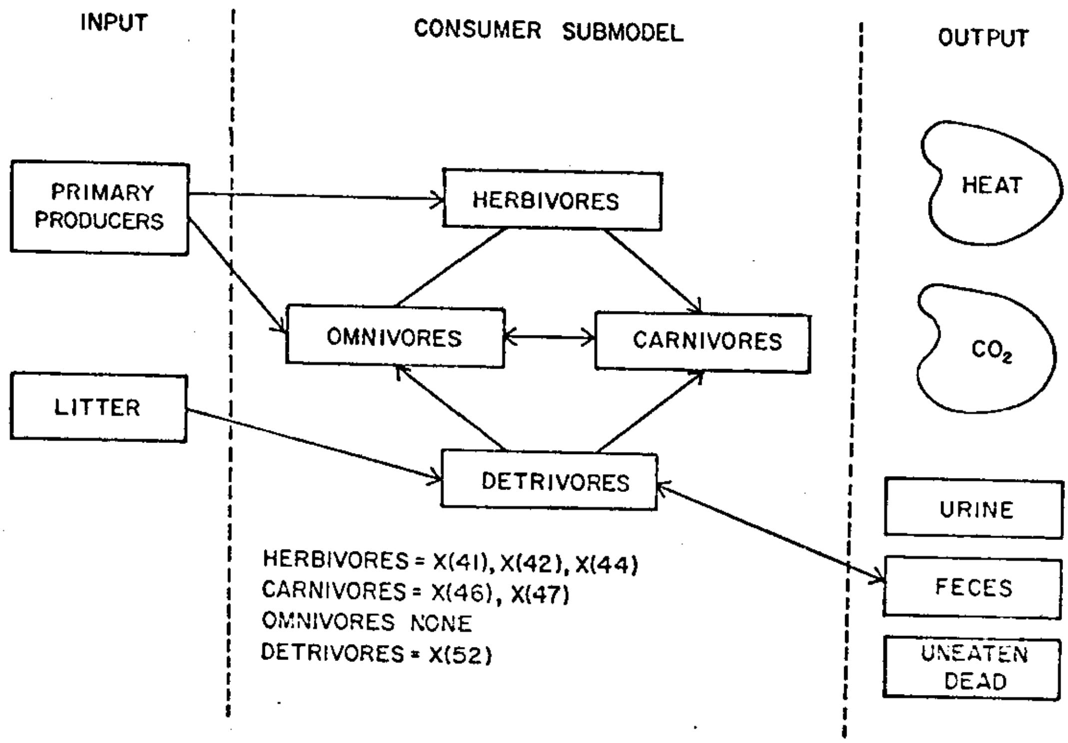

Fig. 18. Flow diagram of the actual running consumer submodel.

There is, however, relatively little information on the intake and utilization of energy in other consumer groups than the bovids. Some dietary and metabolic relationships are known for cows, some wild bovids, and cervids, and also for some small rodents. The question of food selection is, however, omitted in the present model.

Decomposition Submodel

Microbial processes of decomposition are examined in the model without incorporating microbial or faunal population components, because the process measurements, e.g., CO_2 output, are most readily measured and understood. Three models were developed: (i) a decomposition submodel to be coupled to the ecosystem model, (ii) a "Moor-House" model (as (i) but with abiotic variables and seasonal plant input included) derived from Moor-House data, and (iii) a litter bag model which is similar to (i) but is set up to examine the effect of age heterogeneity and thus in rates of decomposition in many of the state variables.

The decomposition submodel box-and-arrow diagram is shown in Fig. 19, and the state variables (expressed in g C/m^2) and transfers in Table 5.

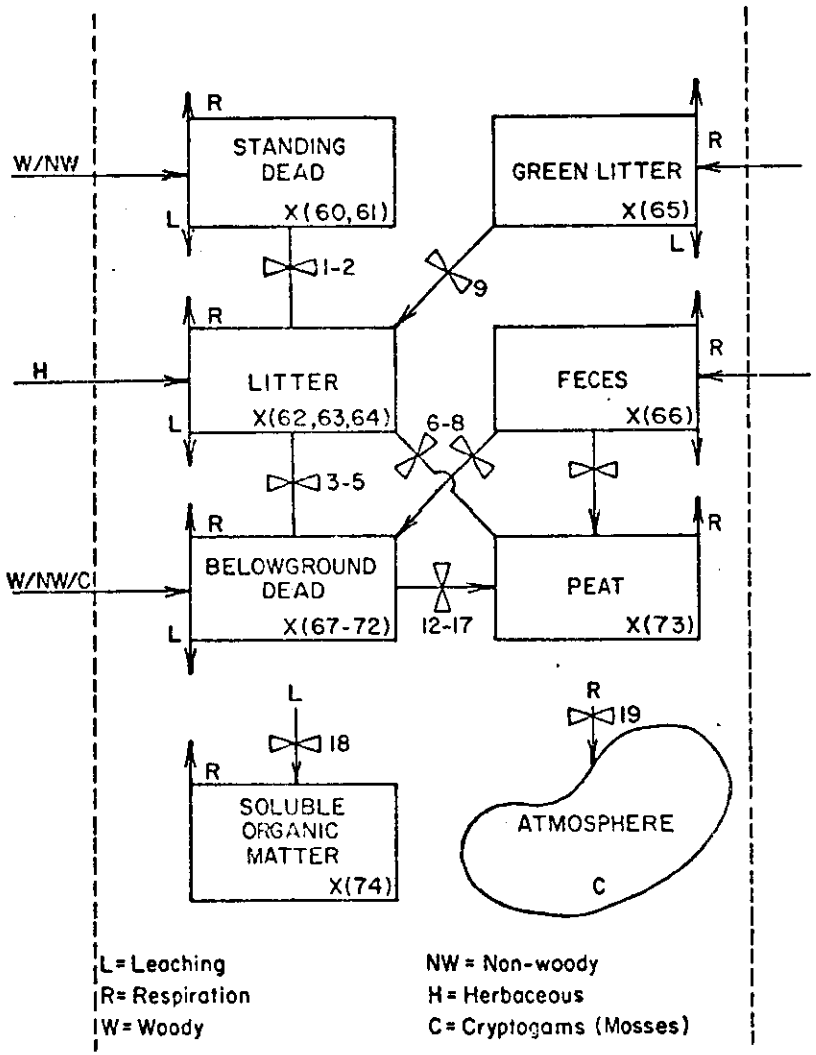

Fig. 19. Box-and-arrow diagram of the decomposition submodel.

Table 5. State variables (g C/m^2) and transfers in decomposition submodel.

State Variables

X(60) Standing dead leaves	X(68) Woody dead roots
X(61) Standing dead wood	X(69) Dead cryptogams (mainly mosses)
X(62) Litter--leaves	X(70) Belowground litter--leaves
X(63) Litter--wood	X(71) Belowground litter--wood
X(64) Herbaceous litter	X(72) Belowground herbaceous litter
X(65) Green litter	X(73) Peat
X(66) Feces	X(74) Soluble organic matter (leachate)
X(67) Non-woody dead roots	

Transfers

1. From X(60) to X(62)--standing dead leaves falling to the litter layer
2. From X(61) to X(63)--standing dead wood falling to litter layer
3. From X(62) to X(70)--leaves passing from aboveground litter to belowground dead
4. From X(63) to X(71)--litter wood passing from litter layer to belowground dead
5. From X(64) to X(72)--herbaceous litter passing to belowground herbaceous litter
6. From X(62) to X(73)--more than 50% decomposed leaves to peat
7. From X(63) to X(73)--more than 50% decomposed wood to peat
8. From X(64) to X(73)--more than 50% decomposed herbaceous litter to peat
9. From X(65) to X(62)--green litter to litter
10. From X(66) to X(70)--feces to belowground litter leaves
11. From X(66) to X(73)--more than 50% decomposed feces to peat
12. From X(67) to X(73)--more than 50% decomposed non-woody roots
13. From X(68) to X(73)--more than 50% decomposed woody roots
14. From X(69) to X(73)--more than 50% decomposed dead cryptogams
15. From X(70) to X(73)--more than 50% decomposed belowground leaves
16. From X(71) to X(73)--more than 50% decomposed belowground wood
17. From X(72) to X(73)--more than 50% decomposed belowground herbaceous litter

18-31. From X(60-72) to X(74)--leaching to soluble organic matter

32-45. From X(60-72) to sink atmospheric carbon--respiration

46. From X(73) to ______

47. From X(74) to ______

When graminoids and shrubs die, the leaves usually remain in the canopy as standing dead for varying lengths of time. The transfer to the litter compartment is a function of wind, rain, snow, and large mammals trampling. The functions are said to be rectilinear saturation functions and the effects of the factors additive. The transfer from standing dead wood to litter are said to be functions of the same factors except rain. Litter of various types and feces may be transferred to below ground by the action of, e.g., earthworms, ants, and termites. The total weight losses in decomposing material (calculated as functions of temperature and moisture) are in the submodel assumed to consist of losses to both CO_2 and peat (the proportion to peat as a constant for each compartment).

The effect of rainfall on leaching is said to increase linearly to a maximum at 15 mm/day. Different coefficients give maximum amounts leached from the different types of decomposing material. Respiration rates are controlled by temperature and moisture. A $Q_{10} = 2$ relationship has been used for temperatures up to 35°C. At higher temperatures the respiration and thus decomposition is said to decrease linearly to zero at 40°C. The effect of moisture on respiration differs in above and below ground. For all aboveground dead material including litter and feces the effect is a rectilinear saturation curve for increasing water (from 0.5 to 22 g H_2O per g litter C). The effect of soil water is said to vary with the normalized soil water content derived from the water contents at 0.3 and 15 atm (maximum respiration at normalized water content of 0.8 to 0.9). Respiration of all types of material is also a function of litter "quality" said to be expressed as percentage N of dry matter and of pH (soil or litter). The maximum decomposition rate under optimal conditions was said to be 8% per day (at pH $\geq$ 7 and %N $\geq$ 3 and optimal water and temperature conditions).

The decomposition submodel did run with many state variables responding in close to the anticipated fashion. It was felt that the most useful validation points will be CO_2 outputs from components or horizons and dry weight losses observed in litter bag studies. The necessity for more explicit radiation data was strongly emphasized. A decay rate probably declines with ageing of the substrate. Chemical and physical criteria cannot yet be used to define/predict decay rate, and there is the apparent anomaly that the N concentration increases with age and decreasing decay rate, while in the fresh substrate it is positively related to decay rate. The change in decay rate with age and initial quality can be incorporated into a generalized model by arranging different rates (DMAX) to a series of compartments. Inputs from other compartments as assigned according to their quality, i.e., higher quality material is entered into the compartment with the higher DMAX value. DMAX is defined as a function of initial chemical and physical state (Fig. 20).

An attempt should be made to develop a model appropriate for periods of years rather than days and to examine the development of the soil system, its chemical and physical properties, and its interaction with the vegetation.

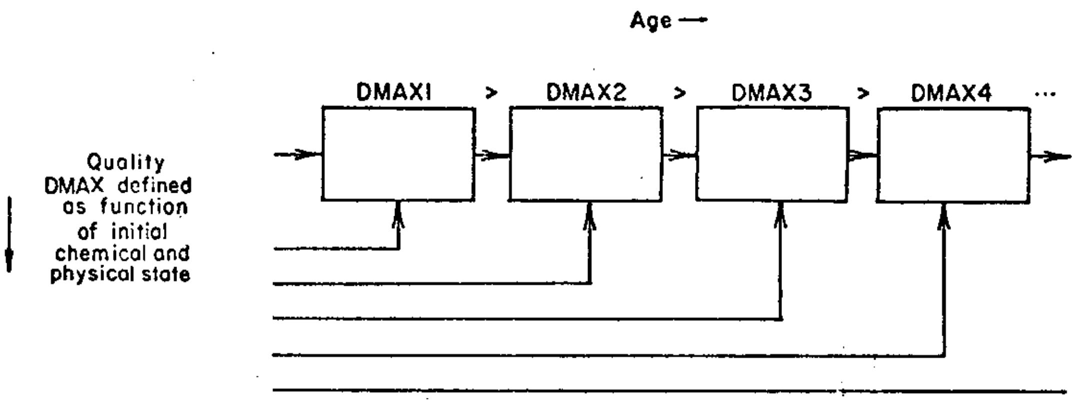

Fig. 20. Possible method for combining effects of age and quality.

Nutrient Submodel

Nitrogen was the only nutrient that time permitted to be linked to the total model. The flows in the phosphorus and calcium submodels were, however, very similar to the nitrogen submodel. The flow diagram for nitrogen is shown in Fig. 21. The source/sink is to represent sources as atmospheric nitrogen, nitrogen salts in rain, and sinks such as loss through wind erosion or runoff. "Available" soil nitrogen includes both NH_4^+ and NO_3^- from the soil top two layers. The nutrient flows are derived from three sources and given in g nutrients/m^2/day.

1. Independent external driving processes such as fertilizer applications and supplementary feeding.

2. Derived by simple modification of other flows generated in different submodels (multiplying the appropriate material flow by the corresponding nutrient concentration).

3. Generated by mechanistic consideration of processes, sealed by empirical values.

Absorption of nitrogen by the roots from the available pool is designed to maintain a designed nitrogen to root biomass ratio given the proper conditions of root respiration and nitrogen availability. Possibilities of nitrogen fixation (from sink to belowground live) were modelled both as a result of fixation by symbionts and lichens. The fixation by lichens was said to be dependent on the ratio: amount of N in the lichens/lichen biomass, modified by soil temperature (exponentially increasing from 0 to 1 between 5 to 25°C) and soil water (linearly increasing from 0 to 1 at normalized soil water 0.2 to 0.4 in the top layer modified if dew). The fixation by legumes was dependent on the biomass, soil type, soil water in the middle layer, and effect of translocation. Soil water is totally inhibitory when normalized values are below 0.2 or above 1. Flow of nitrogen from belowground live plant material to dead is proportional to flows in the death of these parts, modified by the proportion of nitrogen in the belowground live categories. Mycorrhizal action (modified by soil water conditions) may move nitrogen from dead to live parts and modify the flow from live to dead belowground parts.

The nitrogen model did run during the workshop; but, as output from other submodels were absent till the last day, no useful output of the nutrient model was obtained.

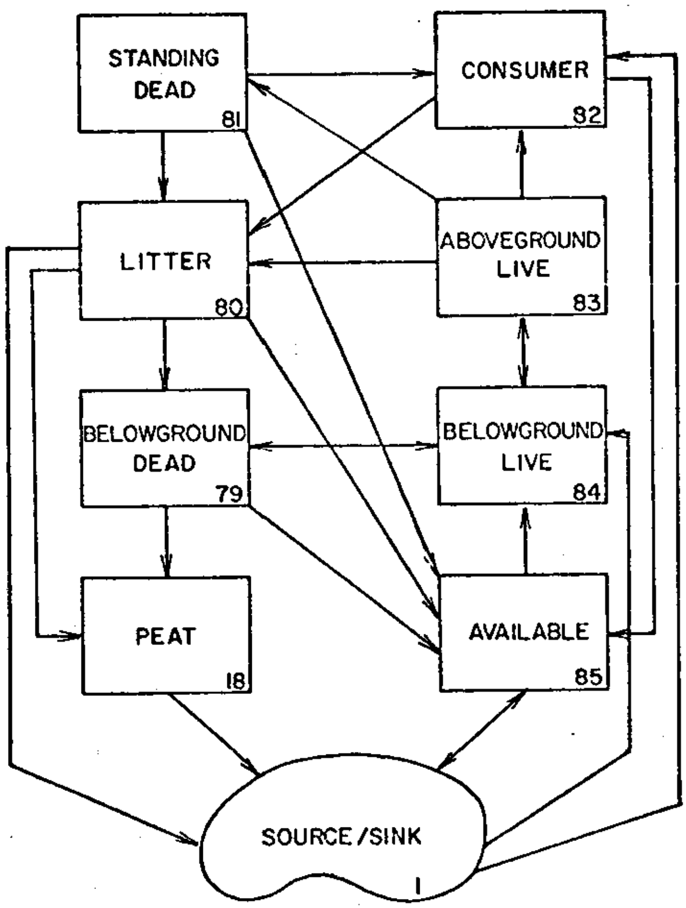

Fig. 21. Flow diagram for nitrogen.

Overall Model

The submodels discussed above were combined into a single total system model, and data from the Matador Site (Canada) were used for driving variables, initial conditions, and (qualitative) validation. It was felt that the data for the model were not, in general, readily available. Additional data are needed. The abiotic group suggested that weather records from appropriate nearby national weather stations be obtained. For plausible driving variable generation, it is very important that solar radiation, rainfall, and soil physical properties be available for all sites (also for the non-growing season) in addition to temperature. Lists of abiotic factors pertinent to any other submodel should be generated by those working with these submodels. Working with the submodels and the overall model determines which data are needed and the accuracy of the data. The consumer group stated that their model must be developed to be more dynamic to be realistic. Predation and disease as mortality factors are functions of age. Migration into and out of the system in response to food and water availability could be useful. The nutrient subgroup felt that they should have been part of the other biotic subgroups to be more effective. If another 2 to 5 days work had been possible on the linkage of the submodels it was felt that it would have been of great benefit to the total model.

GROUP V. PHOTOSYNTHESIS PROCESS MODEL

The model consists of two parts, a photosynthesis simulator and a water relations modifier, which are linked directly through stomatal behavior (see Fig. 22) but also indirectly by the control that changes in plant biomass mediated by photosynthetic activity placed upon the amount of water that can be held within the plant system. Fig. 23 summarizes the main steps in the logic of the program.

Photosynthetic products feed into the carbohydrate reserve pool and from here are apportioned to above- and belowground biomass. Respiratory losses are involved in the utilization of the carbohydrate pool and in maintenance of above- and belowground biomass (related to temperature and the amount of biomass). Gross photosynthetic rate of a canopy is simulated by use of hourly calculation of sun angle as a function of latitude and time (separate rates for completely clear and completely overcast conditions). Maximum photosynthetic rate is modified by temperature and by plant water status (multiplicative) via its effect on leaf diffusive resistance. Photorespiration, if present, modifies the leaf photosynthesis light response and is considered not to be a separate sink for photosynthate.

The water content of the plant community (g/m^2) is updated 10 times per hour by subtracting the outflow (transpiration) and adding the inflow (root uptake) of water. Transpiration is dependent on saturation vapor density at temperature T, LAI, and leaf and air resistances. Root water uptake is dependent on the difference in soil and plant water potentials, root biomass, and root and soil resistances. Leaf resistance is related

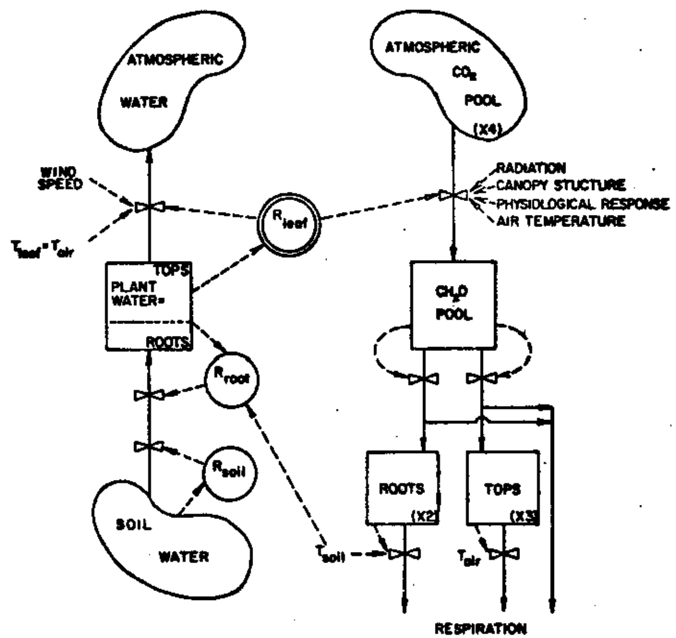

Fig. 22. Water and photosynthesis box-and-arrow diagram.

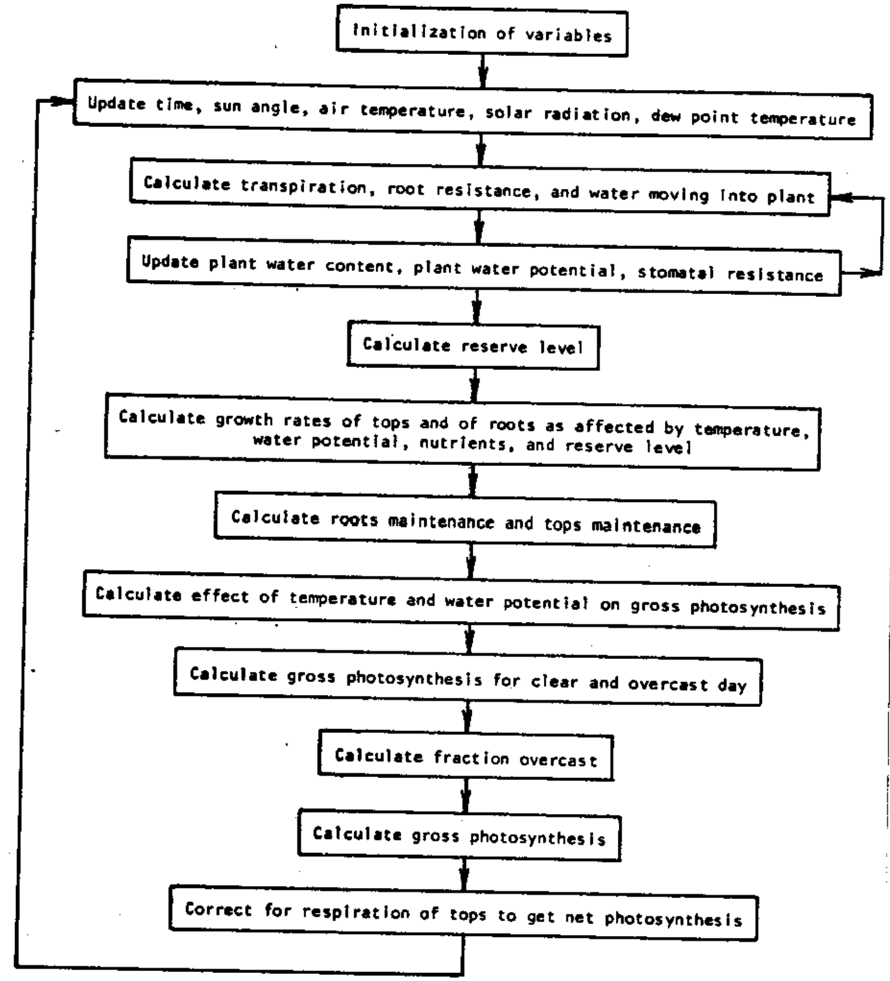

Fig. 23. Photosynthesis model word flow diagram.

to plant water potential and light intensity. Root resistance is a function of the soil temperature. The plant water potential is a function of the ratio: plant water content/plant biomass.

In the output, generalized leaf photosynthesis functions for C_3 and C_4 pathway types were considered satisfactory with contrasting light saturation levels and temperature optima. Difficulty was encountered, however, with the water relations parameters.

GROUP VI. ENVIRONMENT MODIFICATION MODEL

The structure of a model suitable for computer simulation from conceptual ideas on the effects of stock on microenvironments is shown in Fig. 24. The model is especially designed to look at the influence of different grazing intensities upon the long-term evolution of a grassland ecosystem. To model the system, three subsystems were considered necessary: (i) a producer subsystem flowing dry matter (Fig. 25), (ii) a hydrologic subsystem flowing water (Fig. 26), and (iii) a soil subsystem flowing soil material (Fig. 27). Simulations up to 25-year durations were envisioned to include the often long-lasting effects of many of the environmental modifiers shown in Table 6. The lower limit of time resolution of interest was taken to 1 day. The effects on environmental modification must be studied in conjunction with a total ecosystem model.

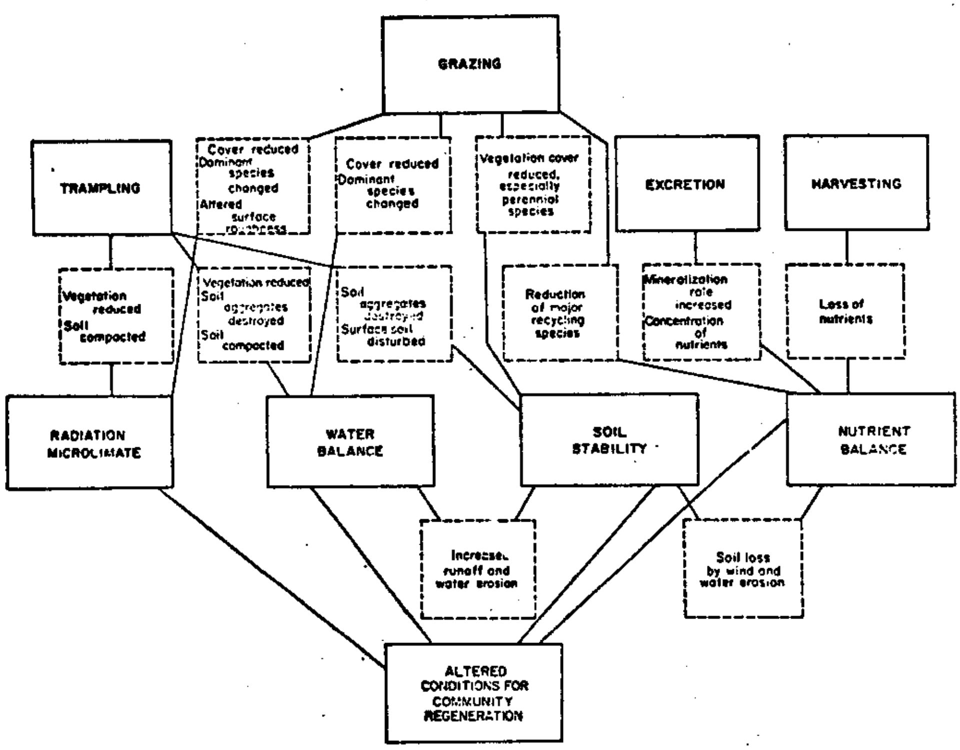

Fig. 24. Effects of stock on microenvironments showing four stock components (trampling, grazing, excretion, and stock harvesting) and four microenvironmental components (radiation microclimate, water balance, soil stability, and nutrient balance).

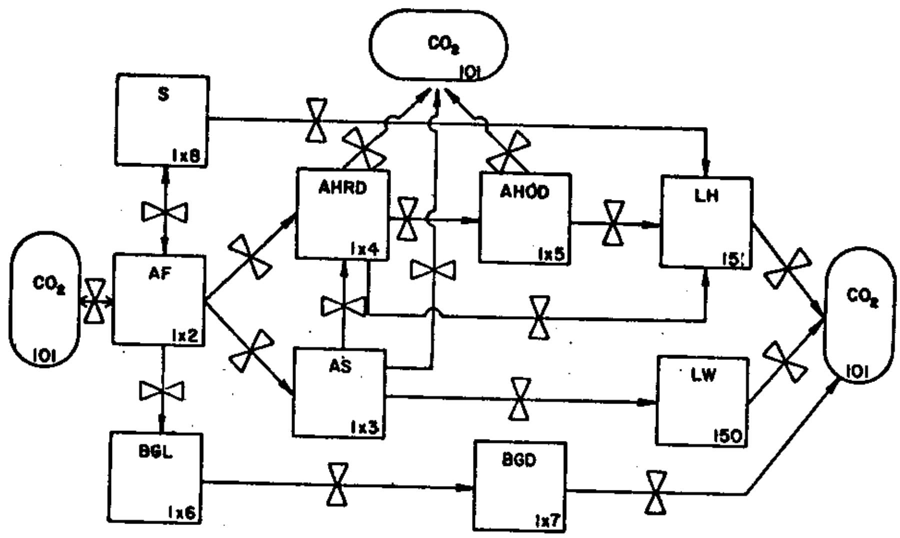

Fig. 25. Flow diagram of Subsystem I--Producers. Material flowing: g dry matter/m^2/day (conversion dry matter to carbon × 0.4). Interpretation of the three-figure numbering: first number (always 1) refers to the subsystem; the middle and last numbers refer to the state variable. Four producer groups are incorporated, and these are identified as follows:

Value of x	Group
0	Shrubs, warm-season
1	Herbaceous perennials, warm-season
2	Herbaceous perennials, cool-season
3	Herbaceous annuals, cool-season

The abbreviations are identified as follows:

State Variable	Abbreviation	Meaning
1x2	AF	Aboveground functional live
1x3	AS	Aboveground structural live
1x4	AHRD	Aboveground herbaceous recent (this season's dead)
1x5	AHOD	Aboveground herbaceous old dead
1x6	BGL	Belowground live
1x7	BGD	Belowground dead
1x8	S	Viable seed
150	LW	Woody litter
151	LH	Herbaceous litter
101	CO_2	Carbon source/sink

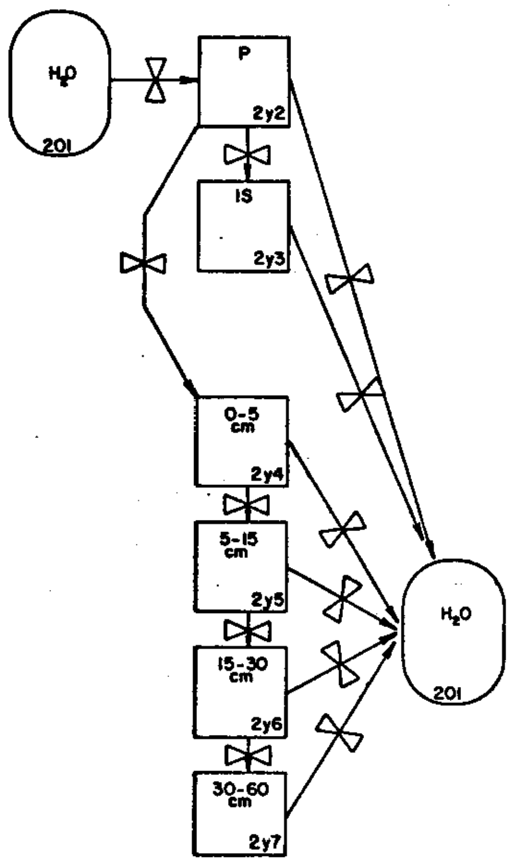

Fig. 26. Flow diagram of Subsystem II--Hydrology. Material flowing: cm $H_2O/m^2/day$. Interpretation of the three-figure numbering: same as in Fig. 25 except subsystem number is 2. Three micro-environmental components are incorporated and are identified as follows:

Value of y	Component
0	Shrub-covered ground
1	Herbaceous plant-covered ground
2	Bare ground

The abbreviations are identified as follows:

State Variable	Abbreviation	Meaning
2y2	P	Precipitation
2y3	IS	Interception store
2y4	0-5 cm	0 to 5 cm soil layer
2y5	5-15 cm	5 to 15 cm soil layer
2y6	15-30 cm	15 to 30 cm soil layer
2y7	30-60 cm	30 to 60 cm soil layer
201	H_2O	Water source/sink

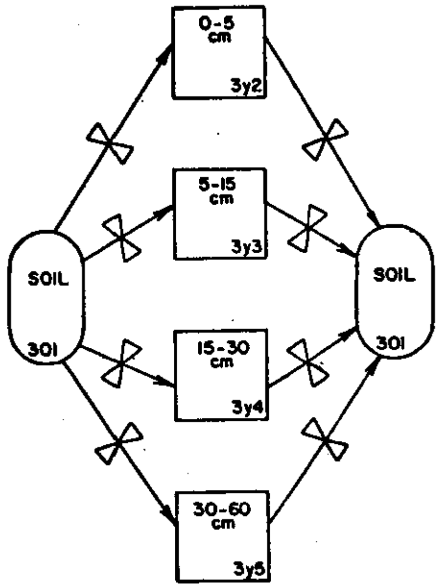

Fig. 27. Flow diagram of Subsystem III--Soil material. Material flowing: g soil/m^2/day. Interpretation of the three-figure numbering: same as in Fig. 25 except subsystem number is 3. The same three microenvironmental components are included here (denoted by y) as in Fig. 26. The abbreviations are identified as follows:

State Variable	Abbreviation	Meaning
3y2	0-5 cm	0 to 5 cm soil layer
3y3	5-15 cm	5 to 15 cm soil layer
3y4	15-30 cm	15 to 30 cm soil layer
3y5	30-60 cm	30 to 60 cm soil layer
301	Soil	Soil material source/sink

Table 6. Environmental modifiers--distribution of occurrence and information.

Country	Site	Vegetation	Herbivore Increase	Herbivore Decrease	Vehicular Traffic	Tourists	Increased Precipitation (experimental)	Windbreaks (addition)	Fire	Oil Spillage	Eutrophication (experimental)	Drainage	Flooding	Short Season	Extreme Dry Year	Extreme Wet Year	Exceptional Late Frost	Exceptional High Wind	Research Workers
Argentina	Sierras de Cordoba (non-IBP)	Bunch grassland	X						X			X							
Canada	Devon Island	Meadow			X					X				X					X
		Beach ridge			X														
		Rocky outcrops	No known modifiers																
Canada	Matador	Grassland	X						X										
England	Moor House	Shrubs	X						X							X			
France	Pin-au-Haras	Meadow	X												X				
Germany	Solling	Montane meadow	No known modifiers																
Holland	Terschelling	Salt marsh	X	X	X	X											X		
Holland	General	Grasslands											X						
India	Rajkot	Summer annual grasslands	X						X			X			X	X		X	
Ireland	Glenamoy		X	X				X	X		X	X							X
Japan	Hakkoda		X			X													
Kenya	Serengeti	Savanna	X		X	X			X						X				
Norway	Hardangervidda	Lichen heath	X		X	X		X											
South Africa	Welgevonden	Savanna	X						X						X	X			
Sweden	Abisko	Bog			X														
U.S.A.	Pawnee	Short grassland	X		X		X				X				X	X			
U.S.A.	Osage	Tall grassland	X	X															

No results were obtained from the model during the workshop. Most of the model, however, was checked out in the testing procedure.

CONCLUSIONS

1. From the point of view of education there can be no doubt concerning the success of the workshop in terms of the individual, not only for those who were previously uninitiated in synthesis modelling and more practically oriented but also for those who could be categorized in the opposite camp. Singular success was also rated in communal education while the international aspects in this context cannot be overemphasized.

2. In terms of the opinion of some participants, one concrete achievement of the workshop output included the formulation of a unique, complex ecosystem model which is considered capable of functioning with input from any environment.

3. The activities of this workshop have highlighted the many gaps which presently exist in the data on fundamental measurements of the environment. These data are essential for the validation of the theoretical models for synthesis which have been already developed or will be developed in the future.

4. In regards to attempts to compare data across ecosystems, it was considered fundamental to plan new experiments well in advance. Such a comparison would necessitate (i) standardization of the observations from a set of treatments across sites with at least some "comparable" ecological characteristics, e.g., aspect, slope, stress applied, etc., and (ii) precise study of the vegetation in terms of structure in space and time. It was accepted that a small workshop might be organized for the purpose of planning future environmental studies, with a practically oriented bias, for synthesis analysis.

ACKNOWLEDGMENT

The participants in the workshop wish to express their thanks to all members of the staff of NREL for all their work carried out before, during, and after the workshop. One important reason for the success of the workshop was the effectiveness of the staff of the data processing section of NREL, including the programmers. All participants appreciated very much the support from the secretarial and publications staff who worked long days, when necessary, to complete everything at the right time.

APPENDIX I

INTERNATIONAL GRASSLANDS AND TUNDRA WORKSHOP

List of Participants

14-26 August 1972

Natural Resource Ecology Laboratory (NREL)
Colorado State University
Fort Collins, CO 80521
USA

Dr. Jerry C. Anway
Animal Range and Wildlife Sciences
New Mexico State University
Las Cruces, New Mexico 88001

Mr. Jorge O. Ares
Faculty of Agronomy and
Veterinary Medicine
University of Buenos Aires
Argentina
(NREL until September 1973)

Mr. Van Baker - NREL

Dr. Alicja Breymeyer
Head, Department of Grassland
Ecosystems
Institute of Ecology, PAS
Dziekanow k. Warszawy
Poland

Dr. Edward G. Brittain
Botany Department
Australian National University
P.O. Box 4
Canberra 2600 Australia

Dr. David C. Coleman - NREL

Dr. D. J. Connor
School of Agriculture
La Trobe University
Bundoora 3083
Victoria, Australia
(NREL until February 1973)

Dr. Robert T. Coupland
Matador Project
University of Saskatchewan
Saskatoon, Saskatchewan
Canada

Dr. Jerry L. Dodd - NREL

Dr. Mel I. Dyer - NREL

Dr. F. E. Eckardt
Section d'Eco-Physiologie
BP 5051
34033 Montpellier
Cedex, France

Mr. James R. Ehlinger
Department of Botany
San Diego State University
San Diego, California 92115

Mr. James E. Ellis - NREL

Dr. Norman R. French - NREL

Ms. Sue Fullerton - NREL

Dr. James H. Gibson - NREL

Dr. Michel P. Godron
CNRS
CERE Louis Emberger
BP 5051
Montpellier 34, France

Mr. Jon D. Gustafson - NREL

Mr. K. P. Haydock
Cunningham Laboratory
Mill Road, St. Lucia 4067
Queensland, Australia
(NREL until December 31, 1972)

Dr. Oliver W. Heal
The Nature Conservancy
Merlewood Research Station
Grange-over-Sands
Lancashire, England

Dr. Peter Hildyard
Agricultural Counsellor (Scientific)
Embassy of South Africa
3051 Massachusetts Avenue
Washington, D.C. 20008

Dr. Henry W. Hunt
Entomology Department
Texas Tech University
Lubbock, Texas 79049

Dr. Keith J. Hutchinson
CSIRO Pastoral Research Laboratory
Armidale, NSW 2350 Australia

Ms. Elizabeth Wright Ingraham
Wright-Ingraham Institute
1228 Terrace Road
Colorado Springs, Colorado 80904

Dr. George S. Innis - NREL

Dr. Donald A. Jameson
Range Science Department
Colorado State University
Fort Collins, Colorado 80521

Ing. Donald Johnson
Centro de Investigaciones Pecuarias
del Estado de Sonora
Gral. Yocupicio y Blvd. Kino
Hermosillo, Sonora, Mexico

Dr. John G. W. Jones
Senior Research Fellow
Department of Agriculture
University of Reading
Earley Gate, Reading
RG6 2AT
United Kingdom

Dr. Sten Jonsson
Department of Entomology
University of Uppsala
Box 561
S-75122 Uppsala
Sweden

Ms. Vicki Keith - NREL

Dr. Pieter Ketner
C/O Frankrijkstraat 49
Eindhoven
Netherlands

Dr. Maxime Lamotte
Professeur à l'Université de Paris
Labo. de Zoologie
École Normale Superiéure
46 rue d'Ulm
Paris 5 France

Dr. Hugh F. Lamprey
Director, Serengeti Research Institute
Serengeti National Park
P.O. Box 3134
Arusha, Tanzania

Dr. Ricardo Luti
Catedra de Geobotanica
Facultad de Ciencias ex. fis.
y Naturales
Avda. Velez Sarsfield 299
Cordoba, Argentina

Dr. John K. Marshall - NREL

Dr. Ramdeo Misra
Department of Botany
Banaras Hindu University
Varanasi - 5
India

Rev. Dr. John J. Moore
Department of Botany
University College
Belfield
Dublin, 4, Ireland

Dr. Jeff W. Morris
Botanical Research Institute
P.O. Box 994
Pretoria
South Africa

Dr. Walter Moser
Alpine Forschungsstelle Obergurgl
Universitaetsstrasse 4
A-6020 Innsbruck, Austria

Dr. Imanuel Noy-Meir
Department of Botany
Hebrew University
Jerusalem, Israel

Dr. Makoto Numata
Laboratory of Ecology
Faculty of Science
Chiba University
Yayoi-cho, Chiba
Japan

Professor S. C. Pandeya
Head, Department of Biosciences
Saurashtra University
Post Bag 9
Rajkot (Gujarat) India

Dr. William J. Parton
Botany Department
University of Oklahoma
Norman, Oklahoma 73069

Mr. Jerry Peltz - NREL

Dr. F. W. T. Penning de Vries
Department of Theoretical
Production Ecology
Landouwhogeschool
De Dreyen 3
Wageningen, Netherlands

Professor K. Petrusewicz
Institute of Ecology, PAS
Dziekanow k. Warszawy
Poland

Dr. Robert L. Randell
Room 310, Biology
University of Saskatchewan
Saskatoon, Saskatchewan
Canada

Dr. Germaine Ricou
Maitre de recherches INRA
16 rue Dufay
76100 Rouen, France

Dr. Earle A. Ripley
Meteorologist and Micrometeorologist
Matador Project
University of Saskatchewan
Saskatoon, Saskatchewan
Canada

Mr. Bob Robinson - NREL

Dr. Charles F. Rodell
Animal Science Department
South Dakota State University
Brookings, South Dakota 57006

Dr. Thomas Rosswall
Department of Microbiology
Agricultural College
S-750 07 Uppsala 7
Sweden

Dr. Wolfhard Ruetz
C/O School of Forestry
Oregon State University
Corvallis, Oregon 97331

Dr. Michael Runge
Geobotanisches Institute 34
Goettingen, Untere
Karspuele 2, West Germany

Dr. Ronald A. Sauer
Ecology Section
Battelle Northwest Laboratory
Richland, Washington 99352

Mr. Richard Shipley - NREL

Dr. Jai S. Singh
Department of Botany
Kurukshetra University
Kurukshetra (Haryana)
India
(NREL until June 1973)

Dr. Freeman M. Smith - NREL

Dr. R. Kirk Steinhorst - NREL

Dr. Nils Stenseth
Zoological Laboratory
University of Oslo
Blindern, Oslo 3 Norway

Mr. David M. Swift - NREL

Mr. Arthur R. Till
Senior Research Scientist
CSIRO
Pastoral Research Laboratory
Private Mail Bag
Armidale
NSW 2350 Australia

Dr. George M. Van Dyne - NREL
Grassland Research Institute
Hurley, Maidenhead
Berkshire, SL6 5LR
England
(until September 1, 1973)

Dr. Jacobus Van Wyk
Department of Botany
Potchefstroom University
Transvaal
Republic of South Africa

Dr. Patrick J. Webber
Institute of Arctic and
Alpine Research
University of Colorado
Boulder, Colorado 80302

Dr. Douglas W. A. Whitfield
Devon Island Project
Room 71 Commerce
University of Saskatchewan
Saskatoon, Saskatchewan
Canada S7NOWO

Dr. Frans-Emil Wielgolaski
Botanical Laboratory
University of Oslo
Blindern, Oslo 3
Norway
(NREL until December 15, 1972)