A Research Program for and the Process of Building and Testing Grassland Ecosystem Models

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Highlight: This paper reports on the organization and operation of the U.S. International Biological Program's Grassland Biome study. The study has involved in the past 8 years a large number of scientists from many disciplines working in an integrated and data-sharing mode. Field studies have been conducted on 11 western grassland sites to obtain data to drive and to validate mathematical simulation models and to provide cross-site comparative information. The models are based upon data from field studies, the literature, and rate process studies, often conducted in the laboratory. A multiple-flow, ecosystem level model called "ELM" which can be adapted to various sites by changing parameters is described. The types and sources of scientific outputs from the program are described.

Historical Aspects

The work on which we are reporting has been part of the International Biological Program (IBP) of which the United States component was organized through the National Academy of Sciences (U.S. National Committee, 1974). The part of the IBP of main interest to us here was originally called the Analysis of Ecosystems (AOE) study. There are also several other large integrated research programs in the US/IBP. The pertinent global objectives and the specific objectives of the US/IBP and the AOE study are:

1. to examine the biological basis of productivity in human welfare
2. to study organic matter production on a world-wide basis
3. to acquire information to develop and test ecological theory
4. to develop a theory of usefulness to man
5. to develop a theory of energy flow, nutrient cycling, trophic structure, spatial patterns, interspecies relations, and species diversity
6. to further examine the ecosystem processes by which the above observed characteristics are achieved and maintained.

Support for and Participants in the Grassland Biome Study

Our research has been supported primarily by the National Science Foundation with some inputs from the Atomic Energy Commission. We have also had cooperation from many state and federal experiment stations. The study has been an interdisciplinary, interinstitutional, integrated, basic ecosystem-oriented research program. Scientists from organizations in some 24 states have participated in the Grassland Biome field studies in 10 western states. We also have been cooperating with some 30 nations having IBP grassland projects. This paper is a general overview of progress and results, and we do not present detailed results of the work of the some 200 scientists (see Wright, 1971, and Hendricks, 1973) who have participated in the Grassland Biome study at various times in the last 6 years.

The general organizational structure during the main phases of the program divided the program into main experimental portions of (i) field validation studies, (ii) field and laboratory rate process studies, (iii) synthesis and integration efforts, and (iv) systems analysis and modelling (Fig. 1).

Grassland Biome Focus

Our original objectives included a series of broad questions which called for total-system research. No matter how narrow or detailed a single given subproject was, the relationship to the whole system was our dominant theme. A main mechanism for synthesizing our information into a whole was the use of mathematical models.

Our overall plans aimed at answering broad ecological questions. Analyses of these questions dictated early the need for detailed total system research. At the outset in 1968 it was clear that we would not be able to study all things about all
grasslands. Our major effort was to study intraseasonal rather than interseasonal dynamics of grasslands. We put priorities, in order of decreasing importance, on biomass (carbon), energy, nitrogen, phosphorus, sulfur, and eventually other elements that move through the system. Our design has one intensive site (Pawnee) and a network of comprehensive sites (see Fig. 2).

To obtain simultaneous data sets on a comparable basis, we established a number of grassland study sites (Fig. 2). In addition, field data were obtained from other sites in rate process studies. On all sites except Dickinson, Bison, and Hays, we have collected at least 3 years of data. Several scientists have been involved in data collection on each of these sites.

Table 1 places the sites into perspective by providing an overview of the grassland type, location, and coordinator.

A Systems View of Grasslands

We use a systems approach as a framework for integrating our knowledge about grasslands into dynamic simulation models of the ecosystem.

To characterize the systems we partitioned them into variables and constants. The variables were further divided into internal or external variables. The external or driving variables were variables "outside" the system which affect performance "inside" the system. Important external or driving variables included precipitation, solar energy input, wind, and temperature above the plant canopy, etc. Driving variables were considered "independent variables," that is independent of the central system under study.

Next we considered a series of internal or system state variables. These are the variables inside the system which change from time to time as a response to alterations in the driving variables or the condition of other internal variables. Examples include soil water levels, herbage biomass, and animal numbers. These are the dependent variables. In a flow diagram of the system the internal or system state variables are denoted as boxes. The boxes are connected with arrows, which represent the flows of matter or energy from part to part.
Fig. 2. Locations of US/IBP Grassland Biome study sites: ALE, shrub-steppe; Bison and Bridger, mountain grasslands; Cottonwood, Dickinson, and Hays, mixed prairie; Jornada, desert grassland; Osage, tallgrass prairie; Pawnee and Pantex, shortgrass prairie; and San Joaquin, annual grassland.

The items flowing in a flow diagram may be different things. They may be energy or matter; the matter may be water, carbon, nitrogen, numbers, dollars, etc.

The rate processes, i.e., the flows from one state variable to another, may be physically controlled or physiologically controlled. Examples of physical rate processes include infiltration and weathering. Examples of physiological rate processes include photosynthesis and metabolism. The rate processes causing input into a given state variable such as "live aboveground plant biomass," for example, would include photosynthesis and translocation up from the roots. The rate processes causing outputs from this compartment would include herbivory, weathering, trampling, translocation, and death. Each rate process can be affected by several variables. For example, photosynthesis is at various levels of resolution influenced by state variables such as leaf area, soil water, and others, and by driving variables such as solar radiation, temperature, and others.

In a mathematical description of a flow function for a given rate process, we need to use some constants or parameters. These are properties of the system that do not change during the time interval of simulation. One such constant might be the depth of the soil and the texture of the soil which we can measure in the field. Constants may also be applied to those processes whose mechanisms are unknown (e.g., nominal mortality rate) or whose level of resolution is more detailed than a system level model can reasonably encompass (e.g., a single activity factor for mammalian activity).

We also consider man to be a driving variable, or external force, in controlling certain flows to and from the system.

The system model is composed of a series of differential or difference equations which will show the change in the state variables as the functions of flows into and out of each compartment. In general, the equations in this system must each be a function directly or indirectly of the state variables, the driving variables, and time.

The Systems Process

Ecosystem simulation models are constructed largely from the results of process and literature studies and from accumulated experience. Experimental rate process studies provide data for the description of the physiological, physical, and ecological phenomena that account for transferring matter and energy within the ecosystem. These process studies may be conducted in the field or in the laboratory in a growth chamber, greenhouse, or metabolism apparatus. Such studies are designed to give the form of, and parameters values in, equations representing rate processes as the function of other variables.

Simultaneous measurements of the driving variables and state variables must be done in the field, as they cannot be obtained in the laboratory nor usually from the literature (see Table 1). The driving variable records are used as input to run or drive the models developed. The records of state variable response give us initial conditions needed to solve our difference or differential equation systems. State variable records also give results with which to compare model response.

Table 1. Sites, site characteristics, and coordinators for the US/IBP Grassland Biome study (Fig. 2).

<table>
<thead>
<tr>
<th>Grassland type</th>
<th>Site name</th>
<th>Land ownership</th>
<th>Coordinator</th>
<th>Site description reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shortgrass prairie</td>
<td>Pawnee</td>
<td>Federal, ARS</td>
<td>D. A. Jameson</td>
<td>Jameson 1969</td>
</tr>
<tr>
<td></td>
<td>Pantex</td>
<td>Federal, ERDA</td>
<td>J. L. Dodd</td>
<td></td>
</tr>
<tr>
<td>Mixed prairie</td>
<td>Cottonwood</td>
<td>State, South Dakota</td>
<td>E. W. Huddleston</td>
<td>Huddleston 1970</td>
</tr>
<tr>
<td></td>
<td>Dickinson</td>
<td>State, North Dakota</td>
<td>J. K. Lewis</td>
<td>Lewis 1970</td>
</tr>
<tr>
<td></td>
<td>Hays</td>
<td>State, Kansas</td>
<td>W. C. Whitman</td>
<td>Whitman 1970</td>
</tr>
<tr>
<td>Tallgrass prairie</td>
<td>Osage</td>
<td>Private</td>
<td>G. W. Tomanek</td>
<td>Tomanek 1970</td>
</tr>
<tr>
<td>Mountain grassland</td>
<td>Bridger</td>
<td>Federal, FS</td>
<td>P. G. Risser</td>
<td>Risser 1970</td>
</tr>
<tr>
<td></td>
<td>Rison¹</td>
<td>Federal, BSFW</td>
<td>D. D. Collins</td>
<td>Collins 1970</td>
</tr>
<tr>
<td>Shrub-steppe</td>
<td>ALE</td>
<td>Federal, ERDA</td>
<td>T. P. O'Farrell</td>
<td>Rickard and O'Farrell 1970</td>
</tr>
<tr>
<td>Annual grassland</td>
<td>San Joaquin</td>
<td>Federal, FS</td>
<td>W. H. Rickard</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>D. A. Duncan</td>
<td>Duncan 1975</td>
</tr>
</tbody>
</table>

¹Transitional between northwest bunchgrass and mountain grassland.
Models utilizing the data in this way predict the dynamics of the system's state variables. Models can be validated by comparing model output with the measurements made in the field. This comparison leads, in subsequent years, to both model modification and redesign of field and laboratory studies. We will give later some examples of output from our simulation models. We also note here that we use optimization models in our studies, but their description is beyond the scope of this paper (see, for example, Swartzman and Van Dyne, 1972, 1975).

Treatments and Testing Hypotheses

Conducting an intensive survey of an ecosystem even in great detail gains only a limited amount of information about interrelations of structure, function, and utilization. Hypotheses about interrelations of structure, function, and utilization can be developed from intensive surveys, and inclusion of experimental stress treatments allows testing of such hypotheses. In each major field study we included a minimum set of treatments or stresses on the system, and within each treatment we measured a selected set of abiotic, producer, consumer, and decomposer variables and a certain number of processes (Swift and Bokhari, 1972; Swift and French, 1972).

We selected for inclusion in our design what we considered would be the most important stresses in grasslands which we could accomplish within our expected financial and time framework. At each major field study site, we investigated replicated areas where there had been very limited or no grazing by large herbivores for many years (excellent or good condition ranges) vs intensive or heavy grazing by large herbivores (fair or poor condition ranges). Other stress treatments were included on certain sites, especially Pawnee. These included nitrogen fertilization, irrigation, herbicides, insecticides, and other levels of grazing intensity. Our models were developed to predict general responses to these kinds of stresses.

We have two replicates of each of the two treatments on any given site. Thus, data from that site may be analyzed independent of data from other sites. We also make comparisons of all treatments of all sites and all types. Having sites in each of seven types of grasslands provides us the opportunity to make statistically designed comparison of phenomena. We are further interested in fully interrelating or correlating these data with information in the literature.

Some Outputs from the Program

We cannot detail here many of the outputs from the program, but our sequential information flows generally as follows:

![Flow diagram of an ecosystem level model for grasslands; controls on flows are omitted for clarity. The third dimension, or layers, in portions of the diagram represents different species or groups of plants and animals or layers in the soil profile (See further description in the text.)](image)
Ecosystem Level Model: ELM

We have developed more than 50 models of grassland systems and major subsystems. But our substantial effort has been toward a multiple-flow, ecosystem-level model which can be adapted to various sites primarily by changing parameter values. An overall diagram of our main ecosystem level model shows some of the complexity of the system (Fig. 3). The model, for all its complexity, is still very much simplified. The model was built to address the effect on net or gross primary productivity of influences such as type of herbivory, soil water, temperature, and added nitrogen and phosphorus.

ELM is considered a total system model as the abiotic, producer, consumer, decomposer, and nutrient components are all represented: (i) The abiotic submodel simulates the abiotic variables by a water flow submodel and a heat flow submodel which are stratified through the air, vegetation canopy and the soil layers is important feedback mechanism. The allocation of rainfall and the evaporation of water are the important processes considered. Daily rainfall, relative humidity, cloud cover, wind speed, and maximum and minimum air temperatures are used as driving variables.

Producer Submodel

Carbon and phenological dynamics of the primary producers are simulated for up to 10 species or groups concurrently. The producers can be changed as a model is adapted for various types of grasslands, but the example described in detail (Anway et al., 1972) and simplified descriptions are given by Innis (1972, 1975). A preliminary mammal submodel was reported by Anway (1973) and the producer submodel by Sauer (1973). The model is being adapted for various types of grasslands, but the example graphs of model output that follow all are for shortgrass prairie on the Pawnee Site. This version of the model is described in detail in papers submitted for publication.

Abiotic Submodel

A part of the abiotic submodel which simulates flow of water through the vegetation canopy and the soil layers is structured to include the important feedback mechanism between the biotic and abiotic state variables. The allocation of rainfall and the evaporation of water are the important processes considered. Daily rainfall, relative humidity, cloud cover, wind speed, and maximum and minimum air temperatures are used as driving variables.

Producer Submodel

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1 Manu scripts submitted to Ecological Monographs for consideration for joint publication:

- Anway, J. C. A canonical mammalian model. 82 ms. p.
- Innis, G. S. Rationale and procedures for building a simulation model for grasslands. 18 ms. p.
- Parton, W. J. Abiotic section of the ELM grassland system model. 51 ms. p.
- Rodell, C. F. A grasshopper model for a grassland ecosystem. 73 ms. p.
- Sauer, R. H. A simulation model for grassland primary producer phenology and biomass dynamics. 61 ms. p.
- Wondymansee, R. G. Critique and analysis of the grassland ecosystem model ELM 73. 52 ms. p.
phenophases is regulated by maximum air temperature, insolation, soil water potential, and soil temperature. The biomass of the model species may be distributed or proportioned through several phenophases simultaneously.

An example of the dynamics of warm-season grass and cool-season grass live aboveground vegetation is shown (Fig. 4). Differences in climatic conditions between years cause the differences in the standing crop dynamics. The cool-season grasses grow earlier in the year and reach their peak standing crop (live + dead) at an earlier date than do the warm-season grasses. The cool-season grasses show relatively more response to favorable growing conditions in the fall of each year.

An example of the dynamics of the litter compartments is shown (Fig. 5) and compared to the 95% confidence limits based on field sampling for the same treatment. Note that biomass of litter greatly exceeds combined biomass of standing live herbage of grasses (compare Figs. 4 and 5) and that there is a high plot-to-plot variability in the litter as denoted by the large confidence intervals on field measurements.

Consumer Submodels

The mammalian submodel considers relationships and functions which are common to all mammalian consumer types. Submodels for mammals, insects, nematodes, and birds have been developed, but as of this writing only mammals and insects are incorporated in ELM. The assumption is mammal consumers affect grasslands primarily through food intake and animal products. The principal control on these processes is metabolism or energy balance, which is influenced in turn by air temperature, animal weight, wastes, activity, reproductive state, population density, animal phenology, hunger, potential intake amount, food availability or accessibility, preference, and digestibility of foods.

Figure 6 shows an example of a prediction of a consumer variable. Cattle weight (not weight gain) expressed in kilograms of carbon per head is shown for a heavy grazing treatment on a shortgrass prairie in 1970.

The objectives of the grasshopper submodel are to consider what effect grasshoppers have on the functioning of the total system and to use the model as a means for estimating the energy flow via grasshoppers through the ecosystem. Daily air temperature and moisture conditions are important factors and have a direct influence on the flows involving forage intake, litter production, and life cycle phenomena (hatching, development, sexual maturation, egg laying, and mortality). The close agreement of model prediction and field data for grasshopper biomass dynamics over time is shown in Figure 7.

Food selection in the various consumer submodels is a function of several factors. The food categories utilized are determined by the characteristics of the consumer being modelled. The quantity chosen from any of 1 to 15 food
categories is influenced by amount of food available, food maturity, consumers' physiological status, and climatic conditions.

Table 2 gives an example of prediction of food intake composition. Data are given there for model and field sampling. There is reasonable agreement between predicted percentage composition and actual composition of the diet in most instances.

Decomposer Submodel

The decomposer submodel is designed to simulate at various soil depths the dynamics of belowground litter, dead roots, and decomposer biomass, which have varying proportions of a rapidly and a slowly decomposing component. Decomposition rates are influenced by temperature, water tension, and the concentration of the inorganic nitrogen. The decomposer biomass states are "active" and "inactive." During periods of activity, substrate is assimilated and the respiration rate is high. Decomposers are susceptible to death by freezing, drying, and starvation.

Decomposer biomass is plotted in Figure 8 for four different depths. Note the lower biomass values at the deepest layer and the lesser seasonal fluctuations in biomass at that depth. Belowground, the decomposers feed on roots and other organic material depicted in the model as belowground litter.

It is not easy to measure microbial biomass directly in the field, but a main byproduct of microbial activity, CO₂, can be measured. Observed and predicted CO₂ evolution for the 1972 growing season are given in Figure 9. In most instances validation data for the model are provided by measuring standing crops of state variables in the field (e.g., see Fig. 5),
but it is also possible to measure for validation purposes a flux rate (e.g., see Fig. 9).

Nitrogen and Phosphorus Submodels

The nitrogen submodel incorporates eight major kinds of state variables of which five major belowground compartments are further divided into four subcompartments representing four depth layers. The depths represented by these subcompartments may be varied according to the characteristics of the site being considered. All nitrogen flows are described as a function of one or more of the following: time, soil temperature, soil water, daily growth, death or decomposition, and nitrogen or phosphorus content. Nitrogen concentrations for each biotic compartment are internally calculated, and can be used as control parameters by the respective biotic submodel. Example nitrogen model output is shown in Figure 10. Seasonal variability for amounts of nitrogen in shoots is greater than that in roots. Nitrogen in plants is more variable over time than in soil.

The phosphorus submodel incorporates 12 major state variables. The seven major belowground compartments are divided into three depth layers. The variables in the phosphorus submodel have dynamics similar to the equivalent variables in the nitrogen submodel.

Current Status—Grassland Ecosystem Models

The complexity and size of the ELM model may be illustrated in a number of ways. The flow diagram (Fig. 3) is a simplified picture of the approximately 180 state variables, 400 flows, and 500 parameters actually incorporated in the model. Simulations may be run from 1-day to 5-year time-spans, with a two-year simulation with a 2-day time step requiring approximately 7 minutes of machine time (compiling and running but not input-output time) on a CDC 6400. At the present time the model has about 20 man years of effort in its implementation and reporting. This does not include development of earlier models which provided a starting point.

The utility of ELM will be affected by completion of work in progress and in the future. Work in progress includes adaptations to several grassland sites; results of runs of these adaptations will be incorporated in the synthesis volumes of these grassland types. Contributions to the scientific literature will require considerable time for full evaluation. Considerable guidance to research has already been provided by these modelling efforts within the Grassland Biome study. The modelling process detected many areas of research needed for improving our comprehension of North American grasslands.

Retrospect and Prospect

Our experiments, based on hypotheses derived from ecological theory and resource management experience, result in data which are analyzed by either experimental design models or least squares prediction models. We have used various statistical models to derive parameters and equations to be used subsequently to structure either simulation models or optimization models. These equations may be either individual equations which are part of a total model, or they may be part of a single equation in the total model. Eventually we will need to combine simulation and optimization models into resource system management models. There is feedback to ecological theory and to resource management from the development and running of both systems simulation and optimization models. Large, interdisciplinary research programs, such as the Grassland Biome study, should result in the development of new, improved, or more quantitative ecological theory, and eventually better resource management. Early programmatic synthetic output already is being used in development of environmental impact statements. Overall, this long-term study has had three phases: "feasibility, respectability, and utility." We are convinced we have demonstrated the feasibility of doing this kind of research and producing a large amount of data. We are now in the process of demonstrating the respectability of the data and the models. We have yet to make full utilization of our results. The IBP terminated July 1974 as a formal program, but we hope to have through 1976 to finalize field and laboratory studies and to publish and reflect upon our results.

The final story of the IBP is not written, but in our opinion the overall results are positive. The US/IBP Grassland Biome study, and other national and international programs like it, have produced useful scientific information, perhaps almost
too much of it. There is now a major job in condensing it and making it available to the scientific and resource management community. It will take time and a group of unbiased individuals at the national or international levels knowledgeable about these programs to make the final judgments and interpretation of our results.

Literature Cited


