Long-Term Ecological Research Program: Shortgrass Steppe

PROPOSAL SUBMITTED TO
NATIONAL SCIENCE FOUNDATION
ECOSYSTEMS STUDIES PROGRAM
April 10, 1986

Principal Investigator: W. K. Lauenroth
Co-Principal Investigators: R. G. Woodmansee
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APPENDIX IV

NATIONAL SCIENCE FOUNDATION

PROJECT SUMMARY

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RECTORATE/DIVISION	PROGRAM OR SECTION	PROPOSAL NO.	F.Y.

ME OF INSTITUTION (INCLUDE BRANCH/CAMPUS AND SCHOOL OR DIVISION)

COLORADO STATE UNIVERSITY

DRESS (INCLUDE DEPARTMENT)

NATURAL RESOURCE ECOLOGY LABORATORY

RINCIPAL INVESTIGATOR(S)

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TITLE OF PROJECT

Long-Term Ecological Research Program: Shortgrass Steppe

TECHNICAL ABSTRACT (LIMIT TO 22 PICA OR 18 ELITE TYPEWRITTEN LINES)

We propose to continue the long-term ecological research project in the Shortgrass Steppe, at the Central Plains Experimental Range in northcentral Colorado. The theme of this work revolves around the ideas of the origin and maintenance of spatial pattern in shortgrass ecosystems and the rules for transforming information about a particular temporal or spatial scale to information about the next higher scale in a hierarchy. The research we are proposing is organized by a nested hierarchy of spatial scales ranging from a single plant up to the Central Grassland region of the United States. The five LTER Core Topics provide a secondary organizing structure for the proposed work. Experiments are proposed for a range of spatial scales over each of the Core Topics. Our overall objective for this work is to begin unraveling some of the apparent complexities surrounding the issues of spatial and temporal heterogeneity and relationships among various scales of each. Even partial confirmation or rejection of these ideas will provide essential information to help move ecosystem ecology in the direction of principles for relating ecological processes and structures to spatial and temporal heterogeneity.

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TABLE OF CONTENTS

I. INTRODUCTION

Meaningful analyses and explanations of spatial heterogeneity, its temporal counterpart and the relationships among the various scales of each, are prime deficiencies currently impeding the progress of ecosystem ecology. What is the origin of the spatial patterns in landforms, soils, and vegetation that exist in the Shortgrass Steppe? How are those patterns maintained? Which processes are primarily pattern generators? Which processes are primarily pattern neutralizers? What are the roles of punctual versus gradual processes in the origin and maintenance of patterns? How are the answers at one time or space scale related to the answers for a different scale? The spatial and temporal scaling issues inherent in these questions will guide the Central Plains Experimental Range (CPER)/LTER program for the next four years.

LTER I was organized around the theme of the interplay among geomorphological, pedological, and biological processes in shaping the structure and dynamics of Shortgrass Steppe landscapes. Current work was woven into a foundation provided by the 5 Core Topics from the LTER Request for Proposals. We expanded these 5 topics under LTER I to include: (1) Interrelations among geomorphology, landscapes, soils, and vegetation structure; (2) Weather and atmospheric deposition; (3) Erosion and sedimentation; (4) Soil water dynamics; (5) Primary production and plant nutrient dynamics; (6) Elemental cycling and organic matter; (7) Secondary production and population dynamics of selected consumers; and (8) Specific disturbances.

Results from the first four years have, in the balance, raised more questions about spatial and temporal pattern than they answered. Our original <u>catena model</u>[1] was based upon classic soil science concepts and proved to be too simple. While we found textbook examples of catenas at several locations, soils and vegetation at other

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[1]Webster's definition of catena is a connected series of related things. In our usage the related things are soil types and associated vegetation.

locations refused to fit the model. Our ideas about the fluvial origin of landforms at the CPER have also proven difficult to substantiate with data. Finally, the relative uniformity of A horizons from location to location is a puzzle. The resolution of these instances of lack of fit with current models was a major breakthrough for our concepts about semiarid regions. Research proposed under LTER II is planned to reconcile these differences over a range of spatial scales.

An important feature of the vegetation at the CPER and throughout the shortgrass region is the conspicuous pattern at small (0.1 m^2) to medium (several m^2) scales. Analyses of this pattern during LTER I could not link it to soils. If spatial variability in soils is not the explanation for these patterns, what is? Current patch dynamics theory (Watt 1947, Shugart 1985) suggests the idea of gap phase replacement and small-scale events, which result in the killing of individuals of <u>Bouteloua</u> <u>gracilis</u> (blue grama), as a likely source of this pattern. Does the killing of an individual of <u>B</u>. <u>gracilis</u> initiate a sequence of events belowground in a shortgrass plant community, that is analogous to the events that occur aboveground in forests? Is the pattern that is so obvious in shortgrass plant communites the result of gap dynamics? We propose to test this idea under LTER II and evaluate the range of spatial scales over which gap phase replacement is an important pattern-generating process.

This proposal is organized around nested hierarchies. The long-term nature of the project defines a nested hierarchy of time (viz., decades within centuries, years within decades, months within years, etc.). Because we are dealing with a range of time scales, we are compelled to consider a range of spatial scales. These too, have been conceptualized as a nested hierarchy (Fig. III.1). Finally, we have organized our ideas and hypotheses around the Core Topics for LTER. Within each of the Core Topics the organization is according to spatial scale. The conceptual development for the temporal and spatial scales is contained in Section III.

The research we are proposing to continue from LTER I and to initiate in LTER II is focused on the issues of scaling, spatial heterogeneity and the significance of long-term processes in the origin and maintenance of ecological systems at the CPER and throughout the shortgrass region. We believe that resolving these issues is central to developing a paradigm for long-term ecological research.

II. PROGRESS DURING LTER I

Geomorphology, Landscapes and Soils

The CPER covers 6500 hectares and has about 100 meters of relief. The topography is gently rolling and exhibits numerous stream terraces that are located adjacent to three major drainages. These terraces are capped with alluvium typical of the Quaternary deposits found in the Colorado Piedmont. Published geologic maps of the area show extensive deposits of alluvium but no eolian or windblown deposits. However, LTER I geomorphic-pedologic studies have shown that the landscape bears the imprint of both fluvial and eolian processes. The presence of deflation basins, relic dunes and multiple paleosols developed in loess deposits indicate past eolian activity. If one considers that fluvial processes produce channels (i.e., irregularities) in the landscape and eolian processes tend to smooth or bevel the terrain, then these geomorphic agents may be viewed as competing to produce different types of landscapes. Therefore, the striking deficiency of low order streams suggests that eolian processes have played an important, if not dominant, role in shaping the modern landscape.

The spatial distribution of soils at the CPER is a complex mosaic of soil types that is extremely variable. Extensive sampling over the entire site resulted in a map for soil parent materials (Fig. II.1)[2] and a map of significant landscape units that we termed physiographic units (Fig. II.2). Each physiographic unit is a unique

[2]The figures for the progress report are in Appendix 1.

combination of elevation, drainage density, relief ratio, and parent material. Physiographic units provided a classification for catenas. Because the classic concepts of soil catenas do not apply to many of the soils, it follows that gravity is not the sole agent that transports pedologic materials. Carbon-14 dates of paleosols developed on eolian materials have yielded dates ranging from approximately 4000 to 7000 years B.P. These dates include the Altithermal, a period of eolian activity in the western U.S. Similar episodes also occurred across the western U.S. about 1 A.D. and again in more modern times extending up to the 1930's.

Some of the more important questions raised by our work include the following. What is the relative importance of fluvial and eolian processes? Currently? During the recent past? Have there been clearly defined episodes dominated by fluvial and eolian activity? If so, when did they occur? How long did they persist? Does their occurrence correspond to similar activity in other parts of western North America. What has been their impact on the biota?

Plot studies to measure fluvial and eolian erosion have been initiated. Hydrologists from the Agricultural Research Service (ARS) in cooperation with the CPER/LTER project are establishing highly instrumented plots that will yield measurements of fluvial erosion rates. Eolian sediment samplers have been deployed adjacent to these plots and elsewhere at CPER to provide companion measurements.

ARS scientists from Durant, Oklahoma have developed a technique for estimating erosion rates based on measurements of ^{137}Cesium in the soil. ^{137}Cesium was produced from nuclear testing and has circulated through the atmosphere since the 1940's. A transect across the U.S. was used to establish a relationship between ^{137}Cs and mean annual precipitation. Samples taken from the CPER do not fit this relationship and contain about three times more ^{137}Cs than predicted. The radioisotope was found to a depth of 12 cm at the CPER. Apparently, ^{137}Cs accumulation at the site is not strictly controlled by precipitation as elsewhere.

Vegetation Structure Along Catenas

This study was designed to answer the question: (1) Do spatial, intracommunity patterns of abundance and diversity of plant species correspond to catena and landscape patterns in soils?

The simplest answer to this question is no; which represents our most significant finding about vegetation patterns. Shortgrass plant communities at the CPER do not exhibit the clear soil/community patterns plant ecologists expect. One explanation for this finding may reside in the fact that A horizons at the CPER may be changing so fast that vegetation cannot come to the kind of steady state we expect. One alternative the relative uniformity of A horizon depth and texture from location to location may provide for relatively uniform vegetation from location to location. This is an idea that will be pursued during LTER II.

Atmospheric Deposition and Meteorology

We are continuing our association with the National Atmospheric Deposition Program, as well as maintaining our monitoring stations for meteorological variables.

Soil Water Dynamics

Neutron probe access tubes have been installed at six slope positions on three representative catenas. One of these catenas is also one of the locations where we are estimating aboveground primary production. In addition, we are continuing to sample soil water at several locations that have been sampled since 1969. One of these sites is our large weighing lysimeter, which allows us to monitor inputs and evapotranspiration of water very accurately.

Soil water differences among catenas are greatest at the toeslope position, with greater soil water retention in fine-textured than in coarse-textured soils (Fig. II.3). Changes in soil water content before and after large rain events indicate a fairly uniform degree of soil wetting across all catena positions (Fig. II.4a). Differences in soil moisture content before and after snow storms indicate major differences in soil water content with catena position (Fig. II.4b). The steepest slopes of a catena were not wetted by snow melt. This suggests that snow removal by wind and snowmelt runoff over frozen ground prevents recharge of soil water content on steep, windward sections of catenas. Snow depth measurements have been taken to further examine this phenomenon.

Regarding soil water we need to answer the following questions on a long-term basis: (1) Which soil layer is most often wet? What is its frequency distribution? Answers to these questions will provide information on the location of the most active zone for soil processes and will allow us to understand the relative success of plant life forms with different rooting patterns. (2) What is the maximum depth to which water most frequently penetrates? This will tell us how frequent deep-percolation events occur and therefore if leaching is an important pathway for nutrient losses. (3) What is the relative contribution to total water loss of the different pathways (transpiration, bare soil evaporation, deep percolation, etc.). How do the relative magnitudes of these pathways change from dry to wet years? This information will allow us to assess how well the system tracks the temporal variability in resource availability. We also need to know how different land uses and management techniques improve or impair the ability of the system to track variability in resource availability. (4) What is the difference in precipitation pattern between dry and wet years? We need to know the nature of the variability in precipitation. Are small events more variable than large events? During dry years, is spring precipitation more affected than yearly precipitation?

To answer these questions we have developed a simulation model which represents the movement of water in 11 soil layers and the major water losses. It uses as inputs daily values of temperature, precipitation, and soil and vegetation characteristics. Long records of these data are available for several sites in the Shortgrass Steppe. We plan to continue pursuing these questions in LTER I and into LTER II.

Primary Production

Our research under the core topic of primary production is unique and broad in that we are addressing the production question over a range of spatial and temporal scales as well as attempting to solve the very important belowground production problem.

Aboveground

We are measuring aboveground primary production at two locations. One is a level upland that has a data record extending back to 1970. At the landscape level, we are monitoring NPP on a catena at summit, backslope, and toeslope topographic positions (Fig. II.5).

Long-Term Forage Production

Measurements of forage production for a variety of pastures has been made in 45 out of the past 46 years by ARS personnel (Fig. II.6). We have begun to pull that information together in an effort to understand the relationship among variability in production, climatic variability and location.

Primary Production of the Central Grassland Region of the United States

The objectives of this ongoing work are to describe the spatial pattern of primary production for the Central Grassland Region of the United States and to identify the major controls at regional and site scales (Fig. II.7). We are using a Soil Conservation Service (SCS) data set for primary production, soil and climate characteristics for 9498 sites throughout the region. At the regional scale annual precipitation accounts for 90% of the variance in production. At the site scale, the model of production includes annual precipitation as well as soil water-holding capacity and it predicts that when precipitation is less than 370 mm/y sandy soils with low water-holding capacity will be more productive than clayey soils with high water-holding capacity. The effect of water-holding capacity will be the opposite when precipitation is greater than 370 mm/y.

The Belowground Problem

The CPER/LTER has been working on ways to improve estimation of primary productivity. We attacked the problem on two fronts: (1) the development of new techniques to estimate root production that will avoid the harvest techniques (Milchunas et al. 1985), and (2) the improvement of calculations of productivity from time series of biomass data. Singh et al. (1984) and Lauenroth et al. (1986) demonstrated that the most commonly used techniques can produce an overestimation in net root production of up to 700%.

This problem is not restricted to root production. It also occurs when estimating aboveground primary production. Objectives of the next step of the conceptual analysis will be to (1) show analytically that random error in the estimations of biomass will always result in an overestimation of net primary production; (2) demonstrate that the larger the number of time intervals considered, the higher the overestimation error; (3) estimate the magnitude of the overestimation error and use it to correct the estimation of production, and (4) to develop confidence intervals for the corrected estimates of production.

The first phase of our experimental approach to the root production problem, an evaluation of a ^{14}C labeling technique, was completed in 1984 (Milchunas et al. 1986). This study (1) indicated that substantial errors in root production by ^{14}C dilution may occur due to seasonal patterns of carbon translocation to belowground organs and the transfer from labile to structural tissue (Fig. II.8); (2) determined that large quantities of carbon are lost by exudation; and (3) assessed sources of errors in harvest versus ^{14}C-dilution estimates of belowground net primary production (BNP).

Modifications of the ^{14}C-dilution method were made based on the above, and the second phase of this work was initiated in 1985. Our objectives are to assess both short-term dynamics (2 y) of carbon in aboveground/belowground, labile-structural, exudation, and respiration components as well as long-term (10-20 y) root production and turnover, surface litter and root decomposition, soil organic matter turnover, and carbon dynamics in soil microaggregates/macroaggregates.

Nutrient Dynamics

The nitrogen concentrations in grass, forb, and shrub species through the year and by catena position are being measured. These data, together with NPP, will be valuable in interpreting fluctuations in arthropod herbivore populations and spatial utilization of the landscape by all consumers. A significant time-by-species-by-catena position interaction was observed for preliminary analysis of 3 y of data.

Element Cycling and Soil Organic Matter

Internal Cycling

Water and nitrogen are the primary controls on primary and secondary production in semiarid regions. Cycling of nitrogen is complexly and intimately related to carbon and phosphorus and to fluctuation in soil water. Superimposed on nutrient interactions and abiotic drivers is the influence that soil and toposequence structure has on nutrient accumulation and cycling. The redistribution of organic matter, nutrients, and soil particles on a catena by wind and water can affect the availability as well as the turnover rates of nutrients at any specific location. The objectives of this portion of our work were (1) to examine the relationships between C, N, P, and soil texture across a toposequence and relate this to N availability and mineralization rates and (2) to determine the depth distributions of rates of N mineralization and nitrification in relation to various soil moisture regimes. The catena chosen for this work was one that fit the classic model.

Organic C, N, and P and total P mass increased downslope. Relative availability of N and P and N mineralization increased down the hillslope, whereas N mineralization expressed as a percent of total N was lowest at the footslope. Thus, N availability to the vegetation increased downslope, while turnover of N decreased. The reduction in the turnover of N may result from an increase in carbon input to the soil through increased primary production and through the formation of organo-mineral complexes. Highest rates of mineralization and nitrification occurred in the surface 2.5 cm such that 40 to 60% of the N mineralization in a 20-cm soil column occurred in the surface 2.5 cm (Fig. II.9). Measurements showed NO_3^- to be the dominant extractable ion (Fig. II.10), despite previous characterization of the Shortgrass Steppe as an NH_4^+-dominated system.

Mass Balance of N Inputs and Outputs

The volatilization of NH_3^0 from urea of large herbivores was thought to be a large N loss vector for the heavily grazed Shortgrass Steppe region. We assessed the NH_3^0 volatilization as influenced by soil water, temperature, and humidity in the laboratory, and season of year and catena location in the field. Results from these studies were used in conjunction with previous studies of cattle grazing behavior along catenas, stocking-harvest rates, N_2O flux, and atmospheric inputs from our NADP deposition samplers, to arrive at a mass-N balance.

Laboratory studies indicated that temperature, humidity, and soil water had different effects on urea hydrolysis, volatilization (Fig. II.11), and nitrification. Field studies, however, indicated that soil type, as represented by location on the catena, was more important than abiotic factors in determining volatilization losses from a pasture (Fig. II.12). All factors taken together suggest that the Shortgrass Steppe is aggrading, since total outputs including N_2O are less than equal to 0.19 g $N \cdot m^{-2} \cdot y^{-1}$ and wet deposition inputs equal 0.3 g $N \cdot m^{-2} \cdot y^{-1}$.

Secondary Production and Population Dynamics

Large Herbivores

With current land-use patterns in the shortgrass region, the most important component of aboveground secondary production is cattle. ARS personnel are monitoring cattle weights in a variety of experiments, one of which has been in progress for 46 years. We are assessing the effects of long-term grazing on plant communities along catenas that have been heavily grazed or not grazed since 1939, as well as developing a generalized model of the effects of grazing by large herbivores on grassland community structure.

Grazing patterns of large herbivores is a topic of immense interest among rangeland ecologists. We are approaching the topic by constructing a nested hierarchy of grazing patterns. Levels in the hierarchy were defined by the frequency with which animals make different kinds of decisions. Animals very frequently decide among plant species or plant parts, less frequently they decide among communities or landscape units. It can be predicted that animals will have maximum effect upon variables with frequencies similar to theirs. Most factors affecting grazing behavior and grazing pattern at finer scales are affected by animal activities and there is a feedback loop. At the upper levels of the hierarchy animals are not able to affect factors which modify the grazing pattern (i.e., landscape structure).

Arthropod Populations

Grasshoppers. Despite the fact that grasshoppers are one of the most important herbivores in semiarid regions, explanations of year to year fluctuations in the sizes of grasshopper populations are largely based upon conjecture. Grasshopper populations have been monitored at the CPER irregularly since 1969. In 1984 we initiated a monitoring program and research to test ideas about factors that regulate grasshopper populations.

Factors being monitored are parasitism, weather, and forage quality. Grasshopper populations are monitored weekly at 8 pastures throughout the summer months; average values are shown in Fig. II.13. Grasshopper collections (> 100/collection) also were made on three dates to detemine community composition and population age structure. Blue grama samples are collected weekly from each site for determination of nitrogen and tannin levels.

June Beetles. The larval form of June beetles, white grubs are an important disturbing force in the Shortgrass Steppe. White grubs feed on the roots of *B. gracilis* and in years of high density can cause wide spread grass mortality in patches ranging in size from 1 m^2 to 500 m^2. Populations of adults are being monitored with light traps (Fig. II.14).

Avian Populations

Avian populations are monitored using three types of surveys: (1) eight coverages of five spot-mapping plots of territorial birds, (2) one coverage of a 50-stop, 40 km long roadside survey in June, and (3) Christmas Bird Count (CBC) on 18 December. The results are compared with (1) 4 previous years (1972-74, 1978) of the spot mapping plots; (2) 11 previous years coverage of the roadside count (1968-1978); and (3) 19 previous years coverage of the CBC (1966-1984). In brief, breeding populations at the CPER are remarkably constant, whereas considerable variation occurred between years on the roadside survey and in the CBC circle.

Specific Disturbance

Disturbances to systems can be of a large or a small scale, endogenous or exogenous, impart stability or instability, and affect the successional status and heterogeneity of the landscape. Research concerning disturbances on the CPER/LTER site is being conducted in three areas: (1) small-scale disturbances created by western harvester ants, small-mammal burrows, cattle fecal pats etc.; (2) succession and stability on large-scale disturbances; and (3) the effect of grazing on plant community structure.

Small mammals and western harvester ants clear substantial areas of vegetation in their soil-moving and foraging activities. In this part of our research, we are examining types of small disturbances in relation to time of occurrence, soil type, and size. Studies of stored seeds in the soil and seed production are being conducted to estimate availability of seed to disturbed sites. Dynamics on the scale of the landscape will be examined by incorporating all disturbance types into a simulated blue grama-dominated landscape. A size distribution and frequency of occurrence will be used for each disturbance type.

In the second part of our disturbance research, we are concerned with large-scale exogenous disturbances and questions of a broad theoretical nature (see Core Topic 5, p. 33). Initial data analyses have been completed and will be updated for each new year of data. Many of the questions we wish to address will require at least 8-10 y of data.

We have a unique situation in having available plots from experiments that were begun under the IBP program. Two replicates (1 ha each) of a control, nitrogen, water, and water + nitrogen treatments that were initiated in 1970 have been sampled since 1982 (Lauenroth et al. 1978). We have access to the plots from a radiation experiment conducted from 1969 to 1978 (Frayley 1971). We are continuing sampling on the plots that has been conducted each year since 1969. An arthropod (white grubs) outbreak in 1981 provided plots on which the dominant species _B. gracilis_ was killed by root grazing. In each case, our interests are to observe how these plots return, if they do, to a community that is representative of the shortgrass communities at the CPER.

In the third part of our disturbance research, we are examining the impact of long-term grazing on plant community structure and diversity. We are working in areas that have been excluded from grazing or grazed at light, moderate, and heavy intensities since 1939. Sampling on these areas is compatible with that on the other disturbance plots, allowing us to construct a disturbance gradient and address such questions as (1) is the lack of grazing, rather than heavy grazing, a disturbance in a system that has evolved with heavy grazing?; (2) does the disturbance gradient form a continuum or discrete units?; (3) do the roles that species or functional groups play, in terms of stability of the system, change along the disturbance gradient?

For the grazing study our results indicate that (1) grazing intensities within a large pasture vary greatly between catena position; (2) as a result of 1, differences between grazed and ungrazed treatments differ with catena position; (3) species known to increase on disturbed sites show no relationship to grazing intensity; and (4) current theories predicting greater diversity at intermediate levels of disturbance and greater segregation of plant populations along environmental gradients with decreased grazing intensity may not be applicable to this system.

The inability of current disturbance or grazing models to accurately describe grazing impacts on the Shortgrass Steppe and the vast differences in vegetation changes with grazing that occur here versus those that occur in African grasslands, led us to a theoretical examination of the effects of large herbivores on grasslands. The emerging patterns of factors from this synthesis and an integration of the Huston (1979), Naveh and Whittaker (1979), and Connell (1978) hypotheses has led to development of a generalized model of the effects of grazing by large herbivores on grassland community structure.

<u>Data Management</u> (see Section VII)

<u>Synthesis</u>

We considered that the LTER project occupied a special position among the research projects conducted in the Range Science Department and Natural Resource Ecology Laboratory. Our LTER I proposal identified the LTER project as a catalyst for synthetic activities with the PIs taking a major responsibility for either accomplishing or instigating synthetic activities. We believe that we have been successful in following this model. Our synthetic activities can be divided into intra- and intersite components.

We proposed annual symposia on theory and applications in semiarid regions as an activity of LTER I. We were only partly successful in the endeavor. In 1984 we co-sponsored a symposium at the Ecological Society meetings that will result in a book in the Springer-Verlag Ecological Studies series. The symposium was titled, Theories of Secondary Succession and the Evaluation of Rangeland Condition. The book, which has been reviewed and accepted for publication by Springer, is in final draft form and will be submitted for publication by the end of April 1986. We also participated in an NSF-sponsored project to conduct a workshop in Buenos Aires, Argentina entitled, Disturbance in Temperate Grasslands: Its Role as a Major Ecological Factor. W. K. Lauenroth is the senior editor for the proceedings that will be published. It has been accepted by Springer-Verlag and should be complete before the end of 1986.

One of the projects from the IBP era that did not get completed was a shortgrass synthesis volume. We have begun putting together the work that has been completed at the CPER and other locations in the shortgrass region. A 120 page manuscript has been completed at this time. A subset of the material will be published as a chapter in a book edited by R. T. Coupland. The chapter is entitled The Shortgrass Steppe and the book is entitled Natural Grasslands and will be in Elsevier's Ecosystems of the World series. The large manuscript will be expanded into a book on the shortgrass region during LTER II.

Two additional synthesis efforts that will become part of the shortgrass book are under way, but will not be completed before the end of LTER I. The first is a 26-y simulation of soil water dynamics using the model of Parton (1978). This is proving to be an exceedingly interesting way to summarize and synthesize our field measurements of precipitation and soil water. We are also beginning an analysis of aboveground primary production for the shortgrass region and participating with another NSF-sponsored project (Cole, Heil and Coleman, BSR 8105281) to evaluate production for the entire Central Grassland region of the U.S. The analysis is based upon data collected by the Soil Conservation Service. Both efforts will result in manuscripts to be submitted to the refereed literature.

The final synthesis effort demonstrates the role of the LTER principal investigators as catalysts of such activities. We initiated a group and hosted the first several meetings at our headquarters at the CPER. The topic is controls on large ungulate grazing behavior. The group is now to the point of having a complete draft of a paper that is to go to BioScience later this spring.

Publications (See Appendix 2 for LTER I publications)

III. CONCEPTUAL DEVELOPMENT

Spatial and Temporal Patterns and Scale Issues in Semiarid Ecological Systems

Before LTER I, research in the Shortgrass Steppe focused on the m^2 or patch scale (Fig. III.1). Most process measurements were made over hourly, weekly, or monthly time periods and under an assumption of large-scale spatial homogeneity. Experiments were designed to average out spatial variability. The outcome of these efforts was a considerable increment in our understanding of processes, such as photosynthesis, plant growth, N-cycling, and how each was affected by temperature, water, etc. LTER I changed this approach by explicitly focusing on sources and significance of spatial and temporal variability at annual, decade and longer time scales. We proposed that shortgrass landscapes could be disaggregated into catenas which represented the major source of variation over both space and time.

Based upon the findings of LTER I, we have expanded our scope of interest in spatial pattern. We conceptualize this expanded scope as a nested hierarchy (Fig. III.1). The lower limit for this hierarchy is the individual plant and its soil

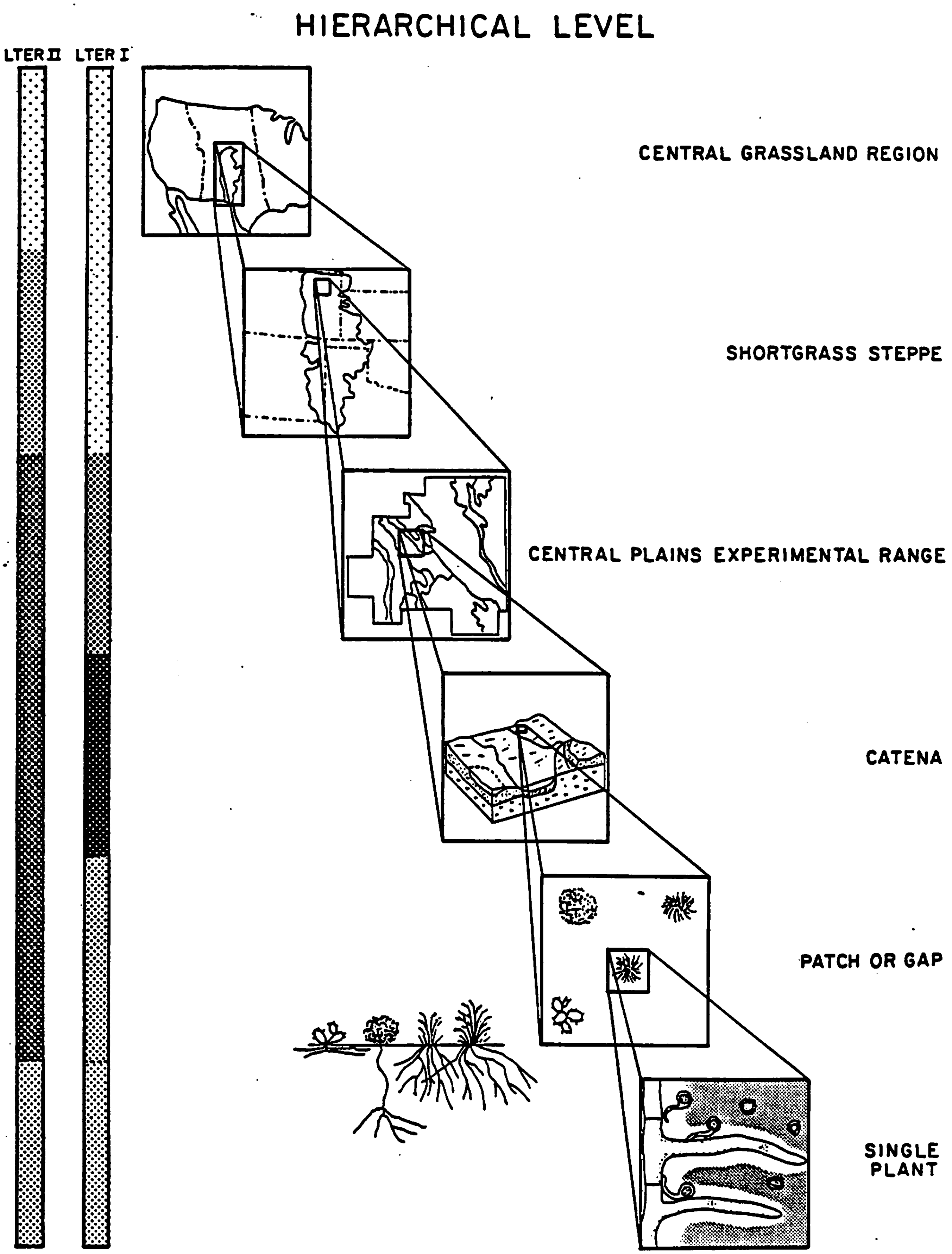
HIERARCHICAL LEVEL
LTER II
LTER I
CENTRAL GRASSLAND REGION
SHORTGRASS STEPPE
CENTRAL PLAINS EXPERIMENTAL RANGE
CATENA
PATCH OR GAP
SINGLE PLANT

Fig. III.1. Nested hierarchy of spatial pattern. (1) Central Grassland Region: 1.8 $\times 10^6$ km^2 of grassland and cropland derived from grassland in the Great Plains and Central Lowlands physiographic provinces of the United States. (2) The Shortgrass Steppe: 2.8×10^5 km^2 of grassland and cropland derived from grassland in the west central section of the Great Plains physiographic province. (3) The Central Plains Experimental Range: 70 km^2 of grassland in the northern portion of the Shortgrass Steppe. The CPER is composed of several physiographic units. (4) Catena: Physiographic units are made up of catenas with sites which range between 0.5 to 1 km^2. Different positions (summit, backslope, toeslope) along catenas are associated with the same soil and vegetation characteristics. (5) Patch or gap: Bare soil patches of approximately 0.1 m^2 are intermingled with patches of grass, shrub, herb, or succulents. (6) Single plant: Single plants are associated with microorganisms in the rhizosphere and non-rhizosphere environment. The shading of the vertical bars indicate how research effort was allocated over spatial scale during LTER I and our proposal for allocating effort during LTER II.

environment. Above the individual plant is the patch or gap scale. This is the area influenced by the occupancy or death of an individual B. gracilis clone. Above this is the catena scale which includes several soils over a hillslope and contains many patches. The next larger scale is the land-use-unit which in many cases fits our physiographic unit in that it represents a single parent material type. The Shortgrass Steppe is composed of many land-use-units, most of which are either areas of rangeland or cropland. The Shortgrass Steppe is one of several grassland types making up the Central Grassland region of the U.S.

Each spatial scale has characteristic behavior over time. At short time scales the dynamic behavior in this nested hierarchy will be associated with individual plants. As the time period is increased, patches and then catenas will show dynamic behavior (i.e., changes in soil properties). Further increases in time will involve increasingly larger spatial scales in the dynamic behavior. What will happen to the smallest scales at these longer time scales? Hierarchy theory predicts that their dynamics will appear to be noise and they will be best represented by their statistical moments (Allen and Starr 1982; O'Neill et al., in press).

The theme we are proposing for LTER II revolves around the origin and maintenance of spatial pattern and the rules for transforming information about a particular spatial or temporal scale to information about the next higher scale. This can be translated into two general questions: To what extent can long term ecological processes be explained by the aggregation of information about short term processes? How much of the spatial pattern at a selected scale can be accounted for by aggregation of the pattern which occurs at the scale immediately below it in the hierarchy.

The first question is one with which all LTER sites have been wrestling. Can long-term phenomena be represented by extrapolating the results from short-term experiments? We suspect that the answer to this will not be a simple yes or no. A more appropriate form of the question is: To what extent can the results from short-term experiments be used to predict long-term behavior of an ecological system?

The analogous question about spatial scale arises naturally as a result of the interdependencies of temporal and spatial scales in long-term ecological research. As an example of this kind of question, we are interested in knowing the relationship between patch scale successional processes and catena scale vegetation patterns. Primary production provides additional examples: What is the relationship between controls on net primary production at the catena scale and controls at the land use and Shortgrass Steppe scale? Is there a simple aggregation rule for calculating estimates of net primary production at the land use scale from estimates made at the catena scale? What fraction of the variability in net primary production can be explained by such aggregation? What are the sources of the errors in this approach? An additional complication that arises with spatial scales is associated with differences in the continuity of the scale variable between time and space. It is easy to accept time as a continuous variable. As one moves from short to long time scales one might reasonably expect continuous changes in associated ecological variables or processes. Such an expectation is not as clear for space. In many instances increases in spatial scale may be difficult to visualize as continuous.

These observations lead to contrasting ideas about the way information at a particular temporal or spatial scale may be extented to larger scales. In the case of temporal scale the relationships among scales can be visualized as in Fig. III.2. The explanatory power of a variable or a process increases or decreases continuously as scale changes. The spatial case, by contrast, is represented by groups of variables separated from other groups (Fig. III.3). Changes along the scale axis are conceptualized as discontinuous.

Understanding the extent to which spatial or temporal information can be extended over a range of scales will be of special importance in designing future investigations. If, for instance, we know that vegetation patterns at the

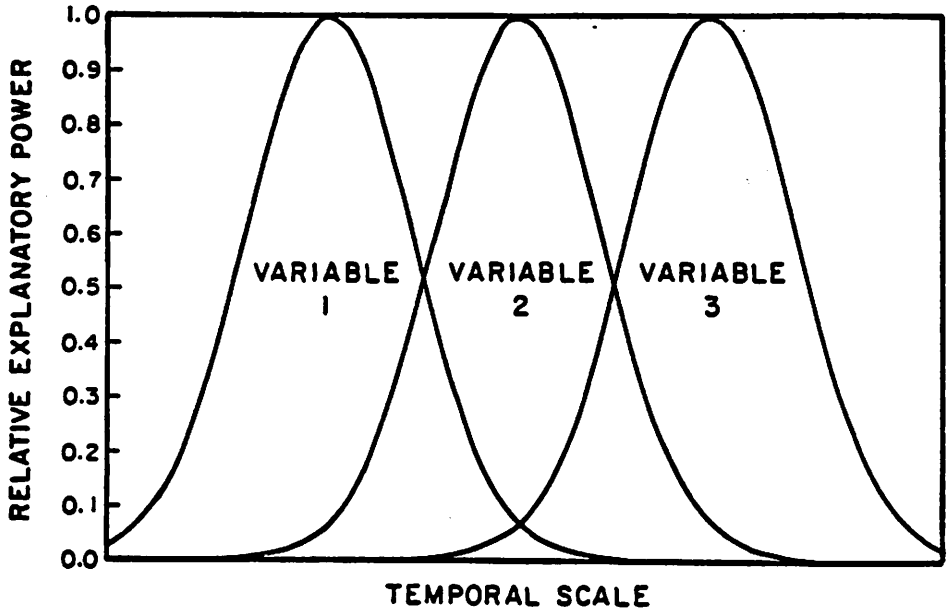

Fig. III.2. The relative explanatory power of each variable is maximum at a particular temporal scale and decreases as scale increases or decreases. Different variables form a continuum such that when the explanatory power of one variable decreases the explanatory power of the next increases.

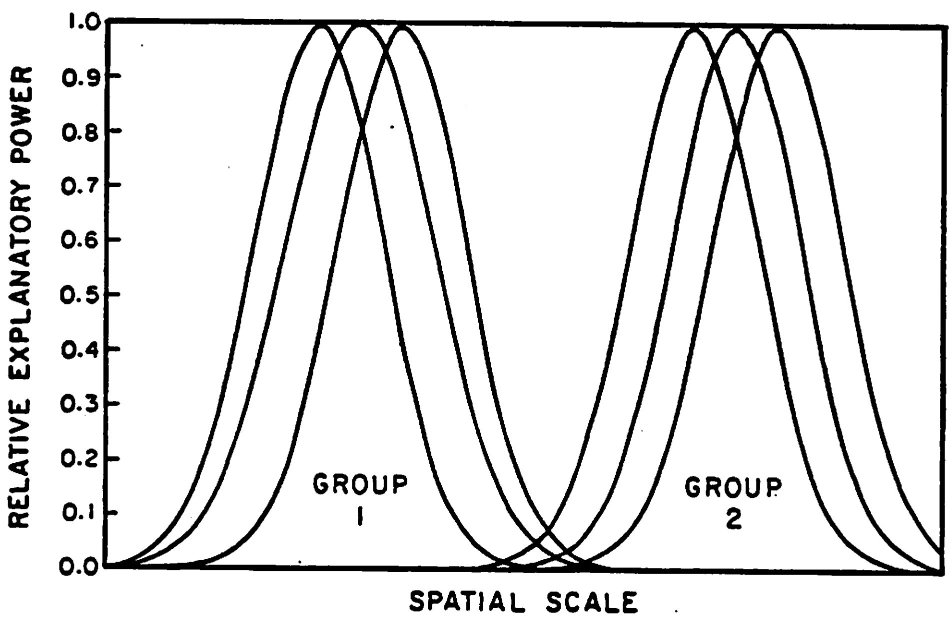

Fig. III.3. Variables are grouped according to the range of spatial scale at which their explanatory power is maximum. The explanatory power of one group of variables gives way abruptly to another group at specific points along the scale axis.

physiographic unit scale can be completely explained by gap phase replacement processes, future studies of vegetation patterns at this scale can ignore catena scale processes. Knowing the range of the explanatory power of variables and processes will allow us to simplify future studies that include a range of spatial or temporal scales.

Our plans for LTER II are to test these ideas in the context of the Core Topic research we are proposing. Our research work is organized along this nested hierarchy from the root-rhizosphere to the Grassland Region (Fig. III.1). The hierarchy is the structure that provides a thread and gives a meaning to the individual projects which make up LTER II. For some of the Core Topics, research will be done at most of the levels along the hierarchy. This is the case of the question associated with the pattern and frequency of disturbances, which will be addressed at five selected scales. Another group of Core Topics will be addressed at a few scales. These questions are related to the patterns and control of primary production, the patterns and control of organic matter accumulation, and patterns of inorganic inputs and movements of nutrients. Because of the nature of the processes associated with these questions, they will only be addressed from the catena scale upwards.

It should be clear that while our interests span this nested hierarchy, our efforts cannot be uniformly distributed over its entire range. The shading pattern in Fig. III.1 was included to convey this idea. In LTER I we focused intensively on the catena level. In LTER II we are proposing to shift our emphasis slightly higher in the hierarchy. The largest part of our work will be concentrated between the patch and land-use-unit scales. This work will be carried out at the CPER.

Even partial confirmation or rejection of these ideas about how one extends spatial or temporal information over a range of scales will provide essential information to help move ecosystem ecology in the direction of principles for relating ecological processes and structures to spatial and temporal heterogeneity.

IV. CORE TOPICS

Pattern and Control of Primary Production

We began LTER I with questions focused upon the relative importance of water and nitrogen as controls on long-term patterns of net primary production (NPP). We have expanded our thinking about NPP and are proposing ideas for LTER II that represent a step into the arena of large-space scales as well as long-time scales. In addition to asking questions about controls on productivity at the m^2 and catena levels, we are beginning to pose questions at the landscape, site and Shortgrass Steppe levels. As an example, Fig. IV.1 represents one way to evaluate aboveground primary production for the shortgrass region. Here we have applied a relationship developed from grassland data on a worldwide basis (Lauenroth 1979) to the Shortgrass Steppe. We plan to expand this investigation using data available from the SCS (a subset of the data used for the analysis of the Central Grassland Region; see Progress Report, p. 7) and using more sophisticated models than the regression from Lauenroth (1979). The theme of our interests is expressed by the following hypothesis.

Hypothesis 1: The level of detail required to account for a constant fraction of the variability in NPP decreases from small to large spatial scale in the range of our nested hierarchy (Fig. III.1). Variables which change rapidly over space are most valuable for explaining the variability in NPP at the small scale. Candidate variables at this scale are such things as species composition and soil type. Variables which change slowly over space such as climate will be most valuable at the largest scale.

As a result of LTER I we are beginning to understand that parameters at the year-to-year time scale may well need to be treated as variables at long time scales. As an example, at the catena scale, NPP is closely tied to water availability and water availability is determined by the water-holding capacity of the soil. Models of NPP for a specific site typically contain parameters for the characteristics of the soil that influence water-holding capacity. What is the consequence of a rapid change (perhaps in one or two decades) in the characteristics of the A horizon on the NPP of a particular site?

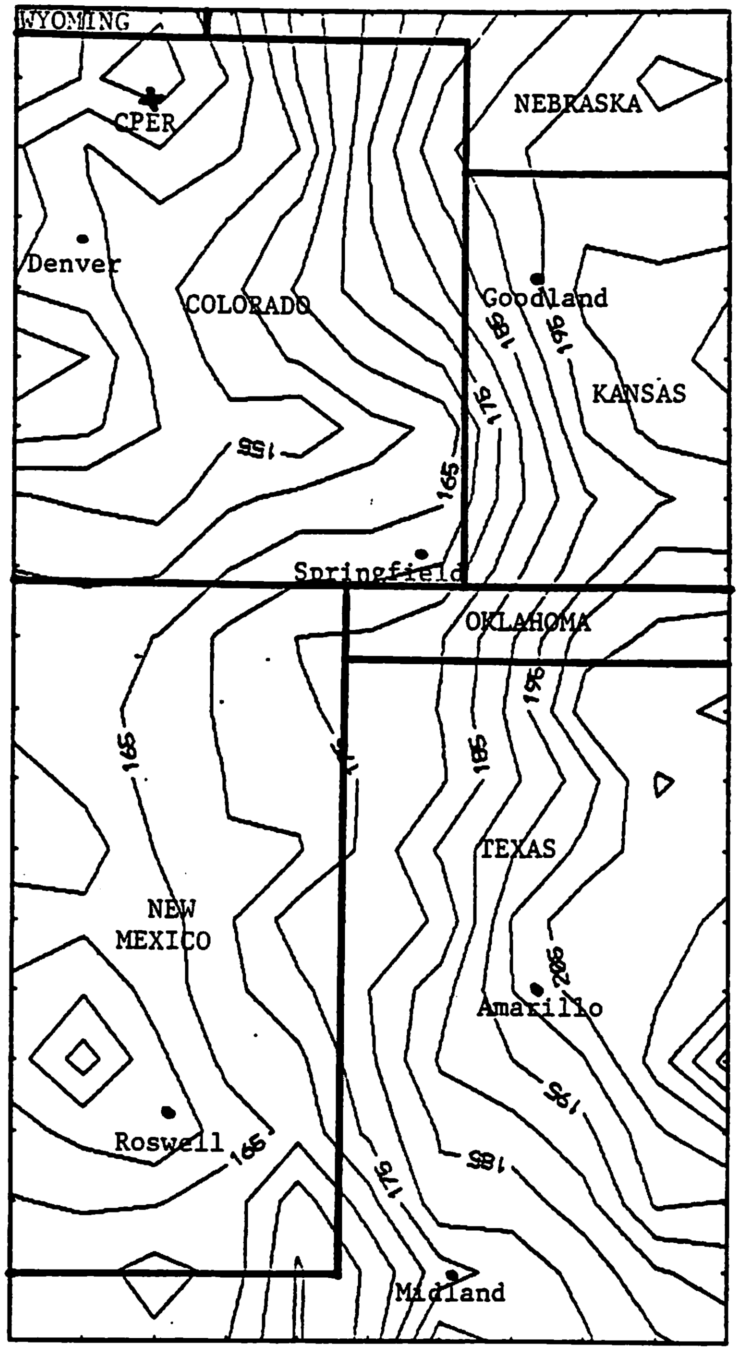

Fig. IV.1. Isolines of aboveground net primary production for the Shortgrass Steppe region.

Hypothesis 2: The relationship between changes in soil characteristics and NPP will be one of thresholds and breakpoints (May 1977). Incremental changes in properties such as A horizon thickness will cause incremental changes in NPP up to the points at which either life-form or species composition changes occur. At those points (there may be several), incremental changes in soil properties will cause very large changes in NPP.

At a scale larger than the catena, a land use unit such as the CPER, contains several different plant communities which are dominated by (1) warm-season grasses, (2) cool-season grasses, (3) shrubs with an understory of warm-season grasses, and (4) shrubs with an understory of cool-season grasses.

Hypothesis 3: The vegetation in semiarid regions, such as the Shortgrass Steppe, is made up of four life-forms of plants, grasses, shrubs, herbs, and succulents. The proportion of the four life-forms, which determines the structure of the vegetation at a specific location, is the result of the interaction between a set of life-form constraints and a set of environmental variables.

We make the following assumptions about life-form constraints: (1) Grasses possess finely branched, dense root system which allows them to obtain the largest part of their water from the upper layers of the soil. (2) Shrubs have an extensive root system with coarse roots which extend far into the soil, thus penetrating a much larger soil volume but less densely. Because grasses are so well suited to exploit the soil water in the upper layers, shrubs will obtain the largest portion of their water from the deeper layers (30-100 cm). We further assume that in semiarid regions, soil water is the most frequent limiting resource and therefore it is the most important environmental variable determining the structure of vegetation. Finally , if we make the assumption that the vegetation is not far from equilibrium and that there are not climatic differences among sites within the CPER, we can make the following deductions: (1) Differences in vegetation structure will be associated with differences in the soil water storage characteristics of the soils at each site. (2) A mix of life-forms of plants, approximately in equilibrium with the environment, will represent the maximum water use efficiency for that site. Similar efficiencies among sites will indicate that differences in soils, which resulted in differences in the availability and location of soil water, are being fully compensated by differences in plant strategies.

At scales of land use units or larger and time scales of growing season or longer, past research by ourselves and others (Noy-Meir 1973) points to precipitation as the control variable with the greatest explanatory power for NPP.

Precipitation in the Shortgrass Steppe besides being low is highly variable. An additional characteristic of the steppe is the large contribution of small events to total precipitation (Sala and Lauenroth 1982). Daily precipitation of less than 10 mm comprised 87% of the total events and 47% of precipitation at the CPER. Small events wet only the top layer of the soil where water is lost via evaporation, plant absorption and transpiration. Water received in large events penetrates deeper into the soil to a zone where evaporation is minimal. Based upon these observations, years with a high proportion of large rainfall events will have a higher water use efficiency than years with a low proportion of large events. However, most of the processes related with the nutrient cycles are located in the surface soil layers which are wetted by small rainfall events.

Hypothesis 4: Variability in the proportion of small, medium, and large precipitation events will account for a large proportion of the variability in annual NPP. Years with few large events will have low NPP. Years with many large rainfall events and few small events will have intermediate NPP. The largest values of NPP will be associated with years in which many small events, because of their effect on nutrient cycles, are combined with many large rainfall events.

This hypothesis provides an explanation for why the wettest years are not always the most productive. It is also consistent with results from a fertilizer and irrigation experiment that indicated once water was removed as a limiting factor for biomass production, nitrogen rapidly became limiting (Lauenroth et al. 1978).

Another variable that influences NPP through its influence on soil water availability is soil texture. Noy-Meir (1973) described an inverse texture effect for semiarid and arid regions. Above a critical amount of annual precipitation the most productive sites are those with relatively fine texture soils. Below the critical value the most productive soils are the relatively coarse textures. The explanation resides in the balance between bare soil evaporation and deep percolation of water below the root zone. In dry areas, bare soil evaporation accounts for a large proportion of total water loss from soils. Coarse textured soils store a larger fraction of their water below depths reached by evaporation and, therefore, are more productive in the driest locations. Additionally, runoff is lower on coarse texture soils than on fine texture soils. Under wet conditions, deep percolation is the major path of water loss and a large fraction of the water infiltrating into coarse textured soils is lost to deep percolation. By contrast, fine texture soils have a higher absolute water holding capacity and under dry conditions, a large fraction of their water is stored within the range of influence of evaporation and consequently losses are large. Under wet conditions their high water holding capacity prevents large losses via deep percolation.

We have tested this idea for the Central Grassland Region (see Progress Report p. 7). Results indicated the crossover point to occur at 370 mm annual precipitation. Noy-Meir (1973) suggested it should occur between 300-500 mm. We plan to test this idea for the Shortgrass Steppe using data from the SCS.

Spatial and Temporal Distribution of Populations Chosen to Represent Trophic Structure

The trophic structure of shortgrass ecosystems is dominated aboveground by grasses, cattle and macroarthropods such as grasshoppers and belowground by grasses, nematodes, fungi, bacteria, and protozoans. The asymmetry in the complexity of the trophic structure between the aboveground and belowground portions is typical of semiarid regions with greater complexity and biomass belowground. The evaluation of the significance of the populations comprising these groups, for the spatial and temporal heterogeneity of ecosystems, has proven to be a formidable task for ecology and no less so for us. In LTER II we plan to focus on two groups of populations, plants and consumers. In both cases we will rely heavily on models to evaluate their significance for the mission of LTER.

Throughout the shortgrass region, one plant species is far and away the most frequent dominant. Bouteloua gracilis is a C_4, warm season grass with a range from the Aspen Parklands of Canada well into Mexico. In the Shortgrass Steppe region it is the dominant species in terms of NPP and cover. At the CPER it is the dominant grass on sites ranging from uplands with thin soils to bottoms with very deep soils. A characteristic of plant communities at the CPER and throughout the region is a very strong spatial pattern at the scale of the individual clone of B. gracilis. The success of a plant population is directly related to its ability to control resource space. The critical resource space in the shortgrass region occurs belowground and the dimensions of the space are related to the availability of water and mineral nutrients, principally nitrogen. The success of B. gracilis is related to its ability to outcompete other populations for resource space.

Hypothesis 5: Because B. gracilis dominates shortgrass plant communities at the CPER so absolutely, the processes associated with recruitment and death of B. gracilis will have a profound effect on the population dynamics of the other species. The concept of gap phase dynamics proposed by Watt (1947) and used so successfully by forest ecologists (Shugart 1985), describes the small scale dynamics of shortgrass plant communities and will explain the small scale pattern that is so common throughout the site and the region.

The key step in the solution of this problem will be the definition of the size of the opening in the belowground space that will be required to initiate gap phase processes. We plan to utilize simulation models, very similar to those described by Shugart (1985), to evaluate the potential role of gap phase processes in plant community and landscape pattern.

There is little question that consumers influence the patterns of resource distribution and the subsequent spatial mosaic of plant community composition. An interesting question is: How would the Shortgrass Steppe appear in the long-term absence of macro-consumers? One possibility is no change. Weather, plant population processes and chance may suffice to maintain the spatial heterogeneity of the system. A second alternative is, without consumers the system would attain a homogeneous steady state similar to the present day Shortgrass Steppe. The spatial mosaic would be altered to one that is more finely textured and homogeneous than the present mosaic, but the system would remain intact. A final scenario is that without the influence of consumers the spatial mosaic would deteriorate. The resulting system would be much different, not only in spatial arrangement but in species composition, productivity, resilience, and stability. In this case, heterogeneity resulting from consumer activities is central to maintenance of ecosystem function.

Addressing questions about the roles of consumers, heterogeneity and the interaction between them, is a difficult problem that defies solution through traditional approaches. In fact, given the present state of knowledge, it is difficult to state the important questions, much less suggest specific experimental protocols. We plan to use simulation modeling to address such questions during LTER II.

Pattern and Control of Organic Matter Accumulation and of Inorganic Inputs and Movements of Nutrients

Soil organic matter (SOM) is a key constituent of terrestrial ecosystems. It is both a reserve of, and a source for, plant-available nutrients and, in most terrestrial ecosystems, it constitutes the largest pool of C, N, and P. By acting as a "big, slow" nutrient buffer, it plays an important role in ecosystem response to perturbation and reflects past productivity and perturbations (O'Neill and Reichle 1979). SOM through its interactions with mineral particles, exerts an influence over such soil physico-chemical properties as aggregation, cation exchange capacity, and erosion resistance. SOM content has long been recognized as a critical indicator of the potential productivity of natural and managed ecosystems; its loss is associated with instability and reduced productivity. Because of the large quantities of SOM in terrestrial ecosystems, small changes in SOM carbon can result in large changes in the global C cycle. Our interest in SOM has two main dimensions: First we are interested in the processes leading to the formation and breakdown of SOM and the catena level spatial variability in the processes; second, we are interested in the relationship between the geomorphic history of the CPER and current patterns of distribution of SOM.

A key concept to emerge from recent research on SOM is that of the active fraction. Janson (1958) suggested that only a portion of the total N in soils is active as a source of N for plants and microorganisms. Stanford and co-workers (1972, 1976) used the accumulation of NO_3^- in long-term incubations to estimate the active fraction, N_0, of N in soils, which has been widely used. Paul and co-workers extended the notion to soil C (Paul et al., 1964; Martel and Paul, 1974). Recently, Cole and Heil (1981) advanced a similar argument for P, suggesting that biologically active P is a small fraction of total organic P, and has a disproportionate effect on C and N cycles. The active fraction is often identified with the microbial biomass but must also include labile soil organic matter fractions (Paul and Juma 1981).

In grasslands, net N mineralization, an overall estimate of the active fraction of N (Schimel et al., submitted), and N turnover, expressed as the ratio between gross mineralization and total N, are highly correlated with soil texture. Net N mineralization tends to increase with increasing C inputs from primary producers (Pastor et al. 1984, Schimel et al. 1985, Vitousek 1982). Correlations between P availability and N mineralization and nitrification have been reported in several studies (Schimel et al. 1985, Pastor et al. 1984). These provide evidence that the size of the active organic matter fraction is related to P supply. No studies have yet been conducted in which N turnover is related to the results of a detailed analysis of P forms, but methods do exist for characterizing more and less labile P fractions (Tiessen et al. 1984).

Our current simulation model for SOM incorporates grazing, organic matter input, texture, and C:P ratios as controls over the distribution of soil carbon into pools of various turnover times. The model has been evaluated at several sites and is currently being tested on a large number of additional sites. Our current conception of SOM fractionation, based on both experimental and modeling results, is shown in Fig. IV.2. The model shows hypothesized controls on SOM dynamics. Recalcitrant plant material (i.e., lignin) is placed in a separate compartment, since it apparently is not a source of carbon for microorganisms (Zeikus 1981). Recalcitrant plant material may, however, have to be degraded in order for microorganisms to obtain closely associated C and N compounds. Recent results indicate that grazing, by affecting C input, N balance, and N immobilization may also have a significant impact on SOM levels and turnover.

The objectives of this work are to investigate the interactions of C, N, and P in the soil plant system over a spatial range of individual patches to catenas. These interactions must take place within the active SOM fractions, although, over time, these interactions will ramify through the spectrum of fractions. We will incorporate knowledge of these interactions into existing and new models of element dynamics.

Hypothesis 6: The amount and proportion of SOM found in the active fraction are controlled by (a) soil texture (b) carbon input rate, and (c) amount of biologically active P.

Hypothesis 7: The amount of active C and N will be correlated with the amount of P in the labile fraction because the C:P ratio of the active fraction is narrower (~20-80) than C:P ratio of the whole soil (40-250).
Corollary: Inorganic P additions should rapidly affect newly formed microbial and labile SOM C:P ratios, since high P availability generally results in low C:P ratios in microorganisms.

Hypothesis 8: Grazing increases the amount of active N by direct return of N in animal excreta and by reducing N immobilization in root and shoot detritus.

Our approach will combine modeling with experimental studies on locations along catenas with contrasting textures, carbon input rates, and litter chemistry. We will use new and existing, C and N isotope-labelled plots to measure fluxes through various soil and plant pools. The new plots will be designed to outlast the current study, so that they will be useful as long-term resources for the study of the more-recalcitrant fractions. We will use three sites on each of two catenas with different soil textures as well as paired grazed and ungrazed sites along a catena.

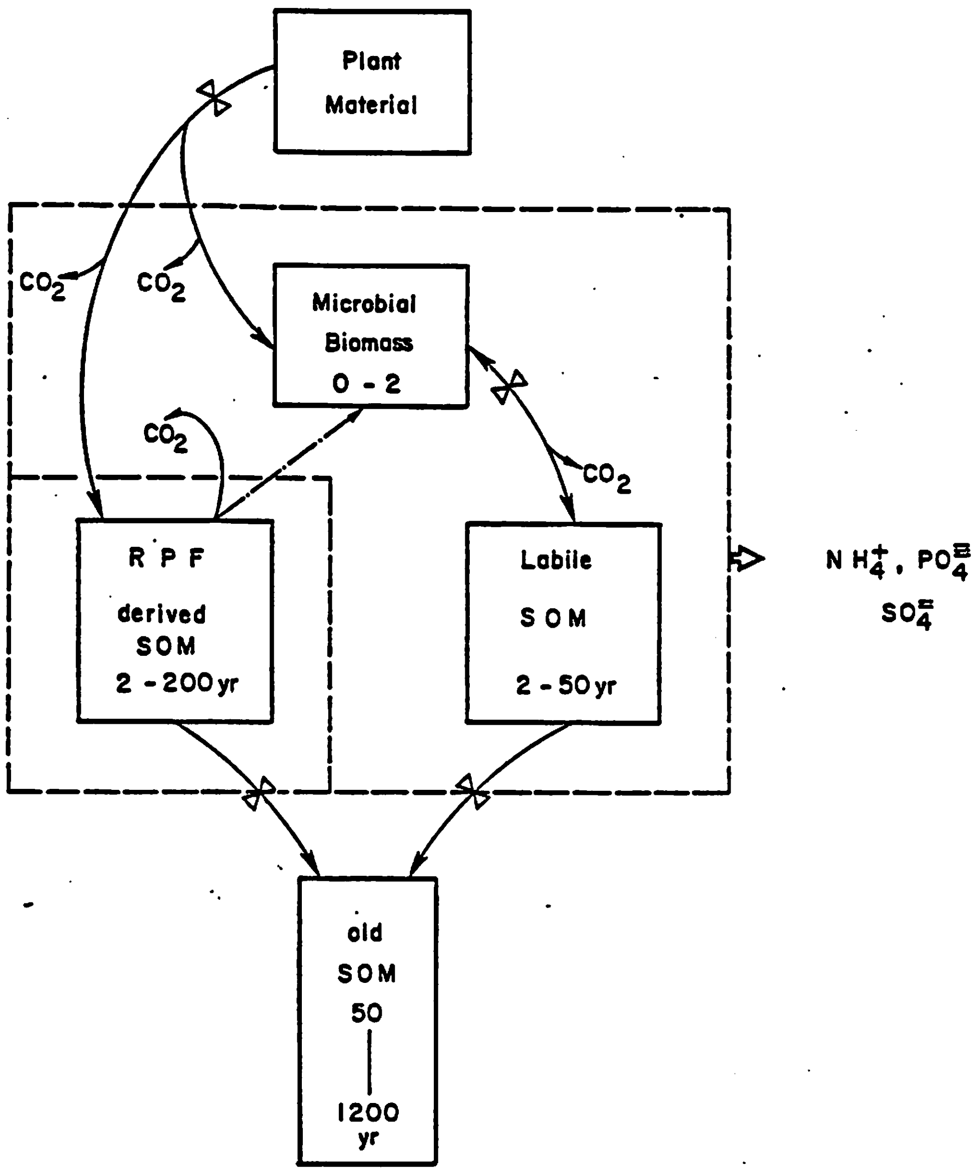

Fig. IV.2. This conceptual model shows plant C, N, P and S flowing into either a recalcitrant fraction (RPF) or into the microbial biomass. Nutrients then cycle between the biomass and labile SOM, with nutrients being extracted from the RPF as needed. We hypothesize that old or stabilized SOM is derived chiefly from labile SOM. Its rate of formation driven by labile SOM dynamics, rather than by RPF inputs.

The geomorphic history of the CPER has exerted a considerable influence on the biogeochemistry of the site via several processes. The first is through the control of soil properties that affect contemporary (1-100 y) rates of nutrient turnover. These properties include texture, phosphorus content and depth to lime (Schimel et al., 1985). These properties all affect SOM, nutrient content, and turnover rate primarily in surface soils and interact with the labile soil organic matter fractions (Parton et al., 1983). The second class of processes whereby geomorphology influences biogeochemistry result from the long-term (500- to 10,000-y) geomorphic history of the site. Processes include the burial of soils during periods of intense erosion and the slow but constant reworking of the surface layers of the soil. The site has apparently experienced periods of 1 to 100 y during which erosion rates were above background interspersed with periods of gradual erosion. Episodic erosion resulted in large amounts of organic matter being stored in paleosols at various depths below the current surface, which are removed from the influence of current conditions. The alternation of periods of gradual erosion, which tend to reduce spatial heterogeneity, and episodic erosion, which intensifies heterogeneity, requires that the influence of geomorphic processes on biogeochemistry be studied at several scales of time and space. Steady processes which tend to homogenize spatial pattern can be studied at plot-sized scales, using traditional rate measurements. Episodic processes, which intensify heterogeneity, occur infrequently, tend to be large in spatial scale and therefore must be studied at landscape scale using the techniques of paleoecology.

Hypothesis 9: Geomorphologic processes influence organic matter accumulation by: (1) controlling soil properties that influence SOM dynamics (i.e., texture, lime, etc.); and (2) burial and removal of soil horizons containing SOM. Part 1. of this hypothesis will be tested by the catena studies described under the active fraction studies.

Patterns and Frequency of Disturbance to the Site

Our approach to disturbances in LTER II will include a range of spatial scales. At the lower limit we are interested in the impact of cattle fecal pats on individual clones of B. gracilis, and at the upper scale we are interested in the impact of land use changes on the large scale spatial mosaic of the Shortgrass Steppe.

The Shortgrass Steppe shares a pattern of disturbance with most other ecological systems in which the size of the disturbance is inversely related to its frequency of occurrence. Hierarchy theory suggests that as one considers increasingly longer periods of time, one should expect dynamics at increasingly larger spatial scales. Because of the time scale of LTER, we can expect to observe disturbance events that span the size range from individual patches to those that influence the entire Shortgrass Steppe.

What is the significance of disturbance events in the size range of 0.01 m^2 to approximately 2.0 m^2 on the dynamics of shortgrass landscapes? What fraction of the current variability in landscapes is accounted for by landscape scale events such as fire, drought, arthropod outbreaks, etc.? In the first question, landscapes are conceptualized as the aggregate of a large number of small units each undergoing its own development. In the second question, landscapes are conceptualized as whole units and explanations must be sought in terms of events that have influenced the entire landscape. Our approach to disturbances will address both of these questions and pose additional questions about how disturbance at a particular scale can explain pattern at scales above it in the hierarchy.

Our research on small scale disturbances will be closely tied to the research on gap phase dynamics of shortgrass plant communites which was described under Core Topic 2 and therefore will not be repeated here.

Our middle scale disturbance experiments are aimed at evaluating the recovery behavior of several of different disturbance types. Connell and Sousa (1983) concluded that the idea of population or community stability based upon the existence of equilibrium states has seldom if ever been tested because of the difficulties associated with defining an equilibrium, estimating the strength of the disturbing force, and estimating the rate or degree of recovery in natural communities. Part of the problem is that studies are not carried out long enough and there are not adequate controls. Several experiments established during the IBP (see the Research Plan p. 49 for descriptions) provide ideal sites for posing and testing hypotheses about disturbance, succession, stability, and their interrelationships.

We define an equilibrium, for our disturbance experiments, relative to the control. This is a dynamic equilibrium because year-to-year weather induces fluctuations in the state of the control plots. Similarity of the disturbed system to the control provides an estimate of the distance it has been deflected from equilibrium by the disturbance, since short-term fluctuations and long-term directional movement of the control has been accounted for. The magnitude of fluctuations in the state of the disturbed plot as a result of weather fluctuations is an estimate of its stability relative to the control. The recovery trajectory of the disturbed plot is a line fit to the annual coefficients of similarity between the disturbed plot and the control. If this trajectory is approaching 1 (i.e., perfectly similar to the control) the conclusion is that the disturbed plot is returning to equilibrium. The slope of the trajectory will provide an estimate of the rate of recovery. We are interested in testing the following hypothesis for our disturbance experiments:

<u>Hypothesis 10</u>: Following a disturbance, the stability and the rate of recovery of the disturbed system will be function of the distance deflected from equilibrium by the disturbance. This function will be nonlinear because the distance deflected and the impact of the disturbance on stability, will increase faster than the intensity of the disturbance.

The following are testable deductions from this hypothesis: Two disturbed systems that have different similarity coefficients with their corresponding controls, will differ in their fluctuations in response to weather. The system with the smallest similarity coefficient will fluctuate the most; Two disturbed systems that have different similarity coefficients with their corresponding controls, will have different trajectories and different rates of recovery. The system with the smallest similarity coefficient will have the slowest rate of recovery.

At the scale of the Shortgrass Steppe and its internal distribution of land uses, we are interested in the effects of heterogeneity at the land-use scale on the ecological systems represented by these land uses.

Hypothesis 11: Native ecosystems track the environment more closely than alternative systems and therefore are more conservative. During wet years, alternative systems release larger quantities of water, mineral nutrients and greenhouse gasses and contribute larger quantities of sediments to river systems. During dry years, alternative systems lose larger quantities of particulate materials to the atmosphere than native systems. Alternative systems are more productive than native systems in wet years and less productive in dry years.

Hypothesis 12: Agricultural development of the shortgrass region has substantially increased regional species diversity. Many of these introduced species are as well adapted to the shortgrass conditions as the native species. Examples are the bird Sturnis vulgaris, the starling and the annual grass Bromus tectorum, downy brome. The spatial pattern of land use will have a large influence on the local success of introduced species. Patches of shortgrass steppe surrounded by agricultural development will be more likely invaded by introduced species than patches distant from this development.

Our interests in large scale disturbance are focused upon the size and shape of the shortgrass region. At the largest scale the shortgrass region is visualized as one of the units of the Central Grassland region. Here our questions are associated with the consequences of climatic change either nominal or humankind-induced on the status of the Shortgrass Steppe.

Hypothesis 13: The gradients that exist along the borders of the Shortgrass Steppe are different in each direction. The gradient to the west with the Rocky Mountains is very steep and not very susceptible to change as a result of climatic change. The gradient to the east is gradual and controlled primarily by the amount of annual precipitation. In the event of a change in climate this border will be very dynamic. The gradient to the north is only slightly steeper than the east. It is controlled by the seasonal distribution of precipitation and winter temperatures. Certain kinds of climatic changes will affect this border greatly, others only slightly. The gradient at the southern border is also controlled by the seasonal distribution of temperatures and precipitation. Here summer temperatures and summer precipitation are the major controls. This border will also be susceptible to certain kinds of climatic change.

Hypothesis 14: Certain kinds of climatic change will result in changes in the shape of the region, others will change its size and still others will change both. The kinds of climatic changes predicted to be associated with greenhouse gases will change both size and shape.

We believe that this work will have a very large payoff in the next several decades as the effects of changes in greenhouse gasses begin to affect changes in ecological systems in North America.

Water Dynamics

Because the availability of soil water is of such overriding importance to the structure and dynamics of ecological systems in semiarid regions we have elevated our work on the dynamics of water to a status equal to that of a Core Topic. Our interests in water are largely focused at the patch and catena scales.

At the individual patch scale, we observe bare soil areas intermingled with clumps of grasses, shrubs, herbs, or succulents. Bare soil patches are colonized by plants at the same time that patches are created as a result of the activity of insects, small mammals, or large ungulates (see Core Topic 2 for a discussion). Germination and establishment of *B. gracilis*, as determined by laboratory studies, is tightly controlled by a sequence of days of high water availability in the top soil layer. We will estimate, with aid of a model, the frequency with which these favorable conditions may occur at the scale of the CPER. Preliminary results indicate that this frequency is low, and probably not sufficient to account for the present dominance of *B. gracilis*.

Hypothesis 15: Microtopography, which results in short distance runoff, and the uneven horizontal distribution of roots and leaves generate a heterogeneous distribution of soil water within patches. The most favorable of these intra-patch microsites are the locations that are necessary to account for high frequency of germination and establishment that must occur in order for *B. gracilis* to maintain its dominance.

Our LTER I proposal suggested that the major link among units within catenas was water movement in the form of overland or subsurface flow. Our present data do not completely support this hypothesis, since we found a large amount of variability among catenas. We are still very much interested in questions associated with the frequency and amount of overland flow of water at the CPER. Our current ideas about overland flow lead to the following hypothesis.

Hypothesis 16: Exchange of water among units within a catena depends on the parent material of the soils. Soils developed in sandy alluvium tend to have very high infiltration rates and low probability of producing runoff. Soils developed in shale have lower infiltration rates and higher probabilities of runoff. Many of the catenas at the CPER have mixtures of both sandy alluvium and shale as parent materials. For those catenas runoff will occur on the soils developed in shale and infiltrate into the soils developed in alluvium.

A testable deduction from this hypothesis is that runoff is a frequent occurrence at the CPER but for most sites it occurs at a scale smaller than an entire catena. Confirmation of this deduction will explain why runoff has been very difficult to observe at the CPER and will aid our understanding of the movement of material along catenas.

V. RESEARCH APPROACH

The Role of Modeling

Investigation of ecological systems using the tools of systems analysis and simulation is an important strength of the CPER/LTER group. We consider modeling to be an important part of the approach to solving problems involving ecological systems. It should be clear that no single model is appropriate for all problems but an approach that includes the tools of systems analysis is often valuable.

Many questions associated with the study of long temporal and large spatial scales are appropriately addressed with simulation models. To a large extent, current models available in ecology are not well suited for these applications. The majority of our modeling objectives have been designed to address short term, detailed, process level questions (Innis 1978, Heasley et al. 1984, McGill et al. 1981). These models have tended to be large and complex and sacrificed representation of structure for realistic process representation. The combined attributes of size, complexity and emphasis on process representation has resulted in models ill-suited for long term simulations. When these models have been run for long times, they tend to be dynamically fragile, structurally unstable, and expensive. In summary, the majority of ecosystem models have been designed to address short-term process oriented questions, and have performed well at that task. However, these models have not performed well during long-term simulations.

A departure from this trend is a recent model developed by Parton et al. (1983) to simulate the long term (100- to 5000-y) dynamics of soil organic matter in grassland soils. This research represents a significant departure from past modeling experiences and is resulting in interesting information, not only about soil organic matter, but also about structuring long-term simulation models. Building on our past experience and recent successes, we can formulate several attributes for models used to address long-term questions. The most important of these attributes include: (1) Structural stability. This will allow modification of one portion of the model without unexpected anamolies being generated in another section. (2) Flexibility. This is required for convenient changes in and hypothesis testing about the organizational paradigms and conceptual representation of the modeled system. (3) Adaptability. Long-term models must accommodate new information as it becomes available. This attribute will allow expansion of the knowledge base on which the simulation is constructed. (4) Robustness. The new generation of simulation models should allow convenient, dynamic self-checking of system relationships as the simulation progresses. (5) Mutability. Since the questions we wish to address are long term, including successional and/ or evolutionary time scales, the model must be capable of adapting and changing <u>as the simulation progresses</u>. This dynamic adaptation to simulation-generated knowledge is the one attribute that will clearly separate the new generation of models capable of addressing long-term questions from the current models.

Development of simulation models with these five attributes will be facilitated through application of three principles. The first is hierarchical structure; the second is application of expert systems concepts in both the design and execution of simulations; and finally, simplification procedures that will result in conservative, parsimonious models which are rigorously related to the systems they represent.

An explicit hierarchical structure for the new models addresses the problems of structural stability and flexibility. Conceptualization of even very complex systems as a nested hierarchy should allow an unambigious statement of the information transfer structure, and the communication between model components (Simon 1973, Allen and Starr 1982). This will provide the basis for dynamic logic checking during model execution and also to maintain structural stability during model development.

Expert systems is a new technology that has potential for both the design and execution of simulation programs. Basic to the concept of expert systems is the separation of conceptual knowledge from procedural knowledge (Davis 1986). This separation will facilitate the rapid development of models which represent the best possible model give any specific objective and level of empirical knowledge. During execution of simulation models, this separation will allow dynamic modifications of the conceptual knowledge base controlling the simulation, and appropriate responses to this changing conceptual knowledge base by determining which body of procedural knowledge is applicable at a particular point during the simulation. Self-evaluation and dynamic modification of structure have remained illusive goals in traditional approaches to computer programming. These goals are compatible with the basic concepts of expert systems (Davis 1986, Waterman 1986, Negoita 1985).

The final principle of model structure is that of simplicity. The overall goal of parsimony and model simplification is generally accepted in ecosystem science (Innis and Rexstad 1983). Procedures for model simplification are of specific interest in development of "new generation" simulation models for several reasons. First, consolidation and simplification facilitates elucidation of a logically appropriate hierarchical structure for the system. Simplification, leading toward analytically tractable models, is also a desirable modeling goal. Levins (1966) argued that at most, two of three potential attributes (generality, precision, and realism) of ecological models can be achieved simultaneously. Representation of systems by rigorously related models of both high and low resolution may resolve Levins' dilemma. Simplification will also allow us to capitalize upon recent advances in numerical analysis (e.g., global stability analysis, Doedel 1981), and for the first time apply these powerful procedures to ecosystem level models. Finally, simplification has purely pragmatic value. Although the present rate of advances in computer technology are rapid and seemingly unrelenting, the dollar resources for simulation experiments <u>are</u> finite and limiting. Models which address questions of importance to long term research (such as succession, spatial patterns, and spatial dynamics) will be highly consumptive of computer resources. Simplification is, therefore, desirable, if not absolutely necessary, for such models.

The steps leading to the new generation ecosystem models are: (1) development of expert systems capable of designing specific subsystem models, (2) application of the expert design systems for development of targeted subsystem models, (3) systematic simplification of subsystem models, (4) development of an expert system controller for long-term simulation applications, and (5) interfacing subsystem models and long term simulation experiments utilizing the capabilities resulting from step 4. The CPER/LTER will cooperate with several other projects in the development of this new technology in ecological modeling.

The Role of Synthesis

Because of their unique time perspective, LTER projects can and should occupy a special position among research projects with respect to synthesis. This was true for the Range Science Department and Natural Resource Ecology Laboratory at CSU during

LTER I, and we plan to continue that concept into LTER II. Not only are LTER projects unique with respect to synthesis, but PIs of LTER projects have a special role to play in encouraging and supporting synthetic activities. One of the items that has often been missing from normal ecological research projects is time to address questions and hypotheses with spatial and/or temporal scales beyond the specific project. Consequently, system-level questions either do not get addressed or are addressed only superficially. LTER projects can play a critical role in facilitating such syntheses.

Our concept of synthesis spans a range from intrasite analyses over time, space or both to the development of global theories for systems ecology. While we believe that we can learn from synthetic efforts focused on the CPER, we are also very interested in intersite analyses of intraregional variables, processes, and concepts as well as intersite analyses that require that we consider systems different from the Shortgrass Steppe.

Specific Synthetic Activities

At the intrasite level we have two projects that were begun under LTER I that will continue into LTER II. The modeling of soil water for 26 y of CPER weather data will be completed in the first year of LTER II (see p. 15 of Progress Report). The second phase of that work, to be started in LTER II, will involve using a stochastic weather generator to evaluate soil water characteristics over century length periods. Here we will be asking questions about the frequency of conditions required for the germination and establishment of the dominant species at the CPER, _B_. _gracilis_. Analysis of forage production data, collected in 45 of the past 46 years, has been started under LTER I. The initial objective is to evaluate the controls on production at this scale. The second phase of this work will include the acquisition of other long-term data sets for other Great Plains grasslands to test the generality of our CPER results.

Our interests in intersite syntheses include both LTER and other sites. We are very interested in the relationship of the CPER to other sites in the Shortgrass Steppe and the relationship of the Shortgrass Steppe to other grassland types in the Central Grassland region. That interest is reflected by some of our LTER I work and by our LTER II plans. We plan to continue the analysis of regional production based upon the Soil Conservation Service data set (see Progress Report p. 7). As part of our interest in disturbances, we are planning to evaluate land use pattern and its development through time, as well as begin acquiring data, in the form of satellite imagery, that will provide a basis for judging changes in the size and shape of the Shortgrass Steppe over decade and longer time scales (see Core Topic 5, p. 36, for this material).

We are planning as a major activity during LTER II to finish a book on the Shortgrass Steppe (see Progress Report, p 15, for some background). Our experience with such projects suggests Springer-Verlag or Elsevier Scientific Publications Co. as the most likely publishers. The book will be dedicated to the memory of the founder of the Natural Resource Ecology Laboratory, Dr. George Van Dyne.

The CPER/LTER is involved with a NASA-funded project (NAS 5-28766) entitled Modeling energy flow and nutrient cycling in natural semiarid grasslands with the aid of thematic mapper data. The objective of the project is to evaluate grassland behavior for sites along a temperature and precipitation gradient utilizing the combined technologies of satellite imagery and simulation modeling. The CPER is one of the three primary sites in the gradient. An important immediate benefit of this project to the CPER/LTER will be a geographic information system.

We proposed annual symposia on theory and applications in semiarid regions as an activity of LTER I (see Progress Report, p. 15, for discussion). We plan to continue the spirit of that idea into LTER II. We now know that an annual time schedule is too ambitious. Our plan is to be opportunistic and take advantage of situations as they arise.

LTER Sites

We feel a special responsibility for intersite cooperation within the LTER network of 11 sites. We recognize two tiers of LTER sites for purposes of intersite cooperation. The first tier comprises those sites that are either biotically, abiotically, or in both ways similar to the CPER. This group includes Jornada, Niwot/Green Lakes, Konza, and Cedar Creek. Each of these sites can be viewed as a grassland, although each clearly is different from the CPER.

During LTER I, we began the ground work for cooperation in a ^{14}C labeling experiment among the CPER, Niwot, and Konza (Appendix 3). As may be expected in the use of radionuclides, we have run into substantial site-specific difficulties in carrying out the experiment. We plan to continue to develop the plan. The experiment was begun at the CPER in 1985 (see Progress Report p. 8 and Appendix 3 for discussion). If we are successful with Niwot and Konza, we will begin considering inclusion of Jornada and Cedar Creek and in the most optimistic view include a stand of *Spartina* at North Inlet.

Two CPER/LTER scientists (Parton and Schimel) have a NSF-funded project at Konza looking at the effects of fire on nutrient cycling. While fire is not as important at the CPER as it is at Konza, many of the nutrient cycling and simulation modeling approaches useful for the Konza project are those developed at the NREL and used by the CPER/LTER project.

Network Activities

The CPER/LTER project has been an active member of the LTER coordinating committee and has participated in all of the activities of the committee. During LTER I, CPER scientists participated in the workshops sponsored by the coordinating committee as participants and workshop leaders. We are very supportive of the idea of a coordinating committee as a way for the LTER program to have a value in excess of the sum of the science conducted at the individual sites.

VI. RESEARCH PLAN

Pattern and Control of Primary Production

Hypothesis 1 concerning the level of detail required to account for a constant fraction of the variability in NPP across scales will be addressed at the end of LTER II. At that time, we will have completed the analysis of pattern and control of NPP at different scales, from the catena level up to the Shortgrass Steppe.

In order to test Hypothesis 2 about pattern and controls of aboveground NPP at the catena scale, we plan to continue the sampling scheme initiated during LTER I (see Progress Report p. 7). Aboveground NPP will continue to be estimated along different catenas using the harvest method (Lauenroth et al. 1986). At this scale, we are also interested in the pattern and controls of belowground NPP. Our belowground production work using a ^{14}C labeling technique (Milchunas et al. 1985) will begin to pay off during LTER II. A description of our experiment and an associated intersite project is included as Appendix 3.

At the land use scale we will be testing deductions from Hypothesis 3 about the water-use-efficiency of different plant community types at the CPER. We will examine aboveground primary production using the harvest method (Lauenroth et al. 1986) on six sites. In the case of communities which include shrubs, the current growth will be identified and measured on selected shrubs. Production per shrub will be extrapolated to the community by taking into account height, diameter and density of the different species of shrubs (McKell et al. 1971). In order to estimate a water use efficiency we will construct water budgets for each site (Lauenroth and Sims 1976).

At a larger scale we will address Hypothesis 4. Here our questions relate to the control of production by precipitation and the relative importance of different size precipitation events. For this purpose we will use a long-term data set on aboveground NPP which is available for the CPER. Aboveground production has been estimated yearly from 1939 until the present. We will use multiple regression to construct models with different size rainfall events as the independent variables. The importance of the coefficients associated with each size class will provide the desired information.

At the level of the entire Shortgrass Steppe we will explore the relationship between climatic and soil characteristics and the pattern of production. A large data set on aboveground production and soil characteristics collected by Soil Conservation Service will be analyzed together with long-term climatic information using regression analysis. Maps of production generated with these data will be compared with maps based on different models (see Fig. IV.1).

Spatial and Temporal Distribution of Populations Chosen to Represent Trophic Structure

The role of gap phase dynamics as a pattern generating process and an important successional process will be addressed in several ways. Field experiments on this topic have begun as part of our disturbance work (see Progress Report p. 12) and are planned to continue into LTER II. Seed production and seed bank size are being. estimated for two sites, one with fine texture soils and the other with coarse texture soils. Seed production is being estimated by protecting plants from herbivores and periodically harvesting ripe seeds. Seed bank is being estimated from soil core data. Cores are spread out in flats in the greenhouse, watered, and the seedlings identified and counted. Frequency of gap scale disturbances is being estimated from counts of cattle fecal pats, animal burrows, ant mounds, etc. Each are counted on a unit area basis in pastures chosen to represent coarse and fine texture soils. Colonization of gap size disturbances is being investigated in an experiment of disturbance size and disturbance date. Circular plots ranging from 0.5 to 1.5 m^2 were cleared of vegetation at three times of the year corresponding to times of highest probability of small scale disturbance on a fine texture soil and a coarse texture soil. Periodically counts of seedlings, their size and location are made for each plot. In addition to the field experiments, we are proposing to construct a simulation model during LTER II which will be in the same class of models as forest ecologists have used for their gap phase investigations (Shugart 1985). Several of the field studies were designed to provide information that will be required to estimate parameters for the model. One of the pivotal concepts in the theory of gap phase dynamics, and also a critical parameter in models, is the size of a gap (Shugart 1985). We defined the gap size for shortgrass plant communities in terms of the volume of soil occupied by the root system of a single clone of _B_. _gracilis_. We will estimate this parameter by labeling clones, with and without neighbors, with $^{14}CO_2$ and then evaluate their vertical and horizontal spread.

In order to address questions about the effect of macro consumers on the structure of the shortgrass ecological systems, we will utilize a modeling approach. One of the models we will use is the gap phase dynamics model described above. In this exercise, we will run the model under 4 hypothetical scenarios: (1) We will change the contribution to the seed bank of different groups of species. We will increase the proportion of those groups which we suppose are at present under represented because of the impact of grazing. We will reduce the contribution made by those species which we consider are very well suited to withstand grazing impact. (2) We will add a group of hypothetical species. These are species that are absent from current shortgrass plant communities because they were not able to withstand grazing. They will have traits of species not selected to avoid or resist grazing; such as an erect growth form and a high growth rate since they invest little in defenses and most of their energy and nutrients are routed to production. (3) We will delete a group of species that we assume to be present in current plant communities because they can withstand or avoid grazing. (4) We will change the disturbance regime. The new regime, will be characterized by a larger influence of non-consumer processes such as fire and wind and water erosion. Modeling results will be compared to information available on the effect of protection from grazing on the structure of vegetation at CPER. Species composition, leaf area, and basal cover have been monitored in areas under different grazing intensities and in exclosures set up in 1939 by ARS researchers (Klipple and Costello 1960).

Pattern and Control of Organic Matter Accumulation and Nutrient Movement

To test Hypotheses 6, 7, and 8, plots will be labeled with $^{14}CO_2$ and $^{15}NH_4^+$ at three catena positions in an ungrazed exclosure. $^{15}NH_4^+$ will also be added to adjacent grazed plots. At the summit where P availability is the lowest, two levels of P fertilizer will be added to plots labeled with ^{15}N and ^{14}C to test the effect of P on active C and N turnover. ^{15}N additions will be made to 20 cm diameter by 30 cm deep cores located randomly. Annual collections will be made from each treatment. The amount and activity (C and N) of roots, shoots, inorganic C and N, chloroform labile C and N, and organic C and N will be determined for each core (Schimel et al. 1985). Incubations will also be done and the rate of release of the ^{15}N and ^{14}C during incubation will be subject to kinetic analysis. By carrying out such incubations at years 1, 2, 3,....,n, we will be able to observe the incorporation of isotope into successively more resistant fractions. This will aid in the validation of our long-term SOM model (Parton et al., 1983).

Carbon dating will be carried out on soil samples from buried horizons and overlaying surface horizons. Three replicate samples will be dated in all cases. Samples will be screened initially to pass a 2 mm mesh. Remaining roots and other modern residue will be removed either by flotation in water or manually under a dissecting microscope to minimize contamination by modern material. Samples will then be ground to pass a 200 mesh screen. The samples will then be split. Half of each sample will be dated as a whole soil without further fractionation. This has proved to be especially interesting for buried soils. The other half of the sample will be treated with acid and base to remove all readily hydrolyzable material, leaving behind a residue of "humic" acid. This fraction is frequently found to be the oldest extractable fraction in soils and is especially useful when comparing modern soils and paleosols (Martel and Paul, 1974). All of the procedures used in preparing soils for carbon dating are currently in use in our laboratory. ^{14}C counting will be done at Geochron Laboratories, Cambridge, Massachusetts.

Patterns and Frequency of Disturbance to the Site

The small scale disturbance work was described under the gap phase replacement investigations for B. gracilis (see Research Plan p. 46). Tests of Hypothesis 10, at the next larger spatial scale, will utilize data from four different experiments in which the source of the disturbance (i.e., water and nitrogen additions, gamma radiation, arthropod outbreak, and cattle grazing) and the stage of recovery are different: (1) A set of water and nitrogen plots on which large additions of water and nitrogen were made, were initiated in 1970 and the experiment continued until 1976 (Lauenroth et al., 1978). Plant community structure was sampled throughout the experimental period and have been sampled by LTER I since 1982. (2) A radiation experiment utilizing very large doses, was begun in 1969 (Frayley, 1971). Irradiation by gamma photons was continued through 1978. Plant community structure data have been collected each year since 1968. (3) A number of areas throughout the CPER were affected by large populations of white grubs in 1981. One of the effects of the large populations was death of patches of B. gracilis ranging in size from 10^1 m^2 to 10^3 m^2. The structure of the vegetation on a number of these areas has been sampled by ARS personnel since 1981. (4) A grazing intensity study was initiated during the first year the CPER was established and has been continued for the past 46 years (Klipple and Costello 1960). Adjacent to the heavy stocking rate treatment is a strip of land, approximately 10 m wide and 1.6 km long, that has not been grazed for the past 46 years. In 1984, we began collecting information about plant community structure, on three catenas, at two topographic positions, on paired sites on each side of the fence shared by the grazed pasture and the protected strip.

For each of these experiments, the response variable, plant community structure is characterized by the species and life-form composition based upon basal cover, canopy cover and density. Data are collected using 0.5 m^2 quadrats and a 10-point frame.

Hypotheses 11 and 12 will be addressed using data collected from rangeland and adjacent cropland as well as by simulation modeling. Hypothesis 11 which addresses differences in the responses of native and alternative systems to environmental fluctuations will be tested by comparing the native steppe to a wheat field. We will install on the wheat field a sampling scheme similar to the one currently used to assess water balance and run off in 3 grassland catenas (see Research Plan p. 52). Water content will be assessed along catenas in both systems and losses via deep percolation, evaporation and transpiration will be calculated using a water balance technique (Lauenroth and Sims 1976). We will use a model of soil water dynamics to analyze the response of both systems to the range of conditions from very wet to very dry. Aboveground primary production will be estimated on the alternative system using the method utilized in Core Topic 1 (see Research Plan p. 45). We will compare the production pattern on the native steppe and on the wheat field. We will again rely upon simulation to evaluate conditions beyond the range of the field data. The hydrologic, erosion, and greenhouse gas portions of the hypothesis will be addressed by simulation modeling.

Hypotheses 13 and 14 will be addressed using satellite imagery from Landsat 1 for the period 1973-1985 and from Landsat 5 for 1986 onward. The multispectral scanner (mss) data from Landsat 1 will allow us to detect changes in units of 8 ha or larger. The thematic mapper (tm) data from Landsat 5 will allow us to detect changes of 2 ha or larger. We assume that the future will bring even more powerful sensors and data of higher resolution. We currently have the analytic capabilities within the College of Forestry and Natural Resources at CSU for handling satellite data.

Water Dynamics

In order to address Hypothesis 15, we will carry out two different studies. First, we will estimate the horizontal pattern of roots of *B. gracilis* on a soil-surface area basis. Contiguous cores will be extracted from 0.5 m^2 plots. Soil cores will be driven to a depth of 15 cm which will be sufficient to account for 70% of the root biomass. Maps of the space occupied belowground will be compared with maps of the space occupied aboveground to identify potential locations for seedling establishment.

The second study will include the refinement of a simple model of soil water dynamics. This model will use as inputs soil characteristics and daily values of precipitation and temperature to represent the water status of the top soil layer throughout a long period of time (50-100 y). With the aid of the model, we will estimate the frequency of occurrence of those conditions, determined in the laboratory, which lead to germination and establishment of *B. gracilis*. We will also estimate the frequency of favorable conditions needed in order for *B. gracilis* to maintain its dominance. Finally, we will calculate the magnitude of short-distance runoff needed to account for a replacement rate for *B. gracilis* that explains its continued presence as the dominant species at the CPER.

The Rangeland Hydrology Unit of the Agricultural Research Service is in the process of setting up a replicated runoff and water erosion experiment at the CPER in conjunction with the LTER project. The objectives for the experiment in addition to estimating runoff and water erosion includes providing data to test a simulation model that the hydrology group built for croplands and are in the process of adapting to rangelands (Knisel 1980). The experiment will utilize 6 plots of increasing length located on two catenas. Simulated (with a rainulator) as well as natural events will be evaluated. Variables to be measured include rainfall, runoff, sediment movement, soil water, plant biomass, air and soil temperature, radiation, and wind.

Simultaneously, we will continue measuring soil-water content along catenas of different soil parent material. Soil-water content is measured at 15 cm intervals, up to 90 cm of depth, using the neutron attenuation technique (Gardner and Kirkham 1952). Neutron probe access tubes have been located along three catenas based on a range of parent material from sandy alluvium to shale. Measurements have been made periodically during LTER I (see Progress Report p. 5) and will continue during LTER II. Using this configuration, water balances will be calculated for different positions along catenas using the technique of Lauenroth and Sims (1976). Finally, magnitude and frequency of runoff events will be calculated for different catenas and for different positions within catenas.

VII. DATA MANAGEMENT

During LTER I, we developed a data management system that centers upon a set of software tools to facilitate the transfer of data from sequential files (tape or disk) to a variety of data management and processing packages. The objective of this system is to minimize the amount of programmer time required to make use of the data.

Archiving

Data are currently stored in two modes: (1) computer accessible files on tape and disk, and (2) microfilm copies of the original data forms. The microfilm represents the most stable but least accessible form of the data. The computer files are most easily accessed for use of the data, but are less stable in that they need continued support for maintenance. We foresee a reduction in the effort required to maintain the archived computer data files once the technology for optical disks becomes stable and affordable.

The task of transferring original data forms to microfilm has been completed for the historical data sets. The 23 reels of microfilm are stored in the Range Science Department. The data contained within each reel are documented in a printed list and in a computer accessible file.

To date, all of the historical data files stored on the CSU Cyber have been transferred to the NREL Vax computer. A tape archiving system has been developed for the Vax to keep track of the data. During LTER II this system will be integrated into an interactive, user-friendly system for querying the data base, examining data description files, retrieving data, and extracting specified data from the files.

Managing Data

We are creating a database system for archiving data that focuses upon two concerns. The first goal is to store data in a historically accurate form. The second is to store data in an internally consistent format. In many cases these two goals can be met simultaneously.

Our data management system centers on a set of software tools that facilitates the transfer of data from sequential files (tape or disk) to a variety of data management and processing packages. We maintain the data as standard sequential ASCII files because we believe that this form will be most stable over the longest time span, and will require the least amount of maintenance in terms of insuring that the files will remain readable well into the future. In order to provide convenient access to the data, we are developing a set of programs (some are complete, others will be completed during LTER II) that will access the data files, extract requested information, and convert that data into a format that is compatible with other higher level data management utilities.

This system is based upon a set of data file descriptions that provide both human readable and machine readable documentation. These file descriptions are being created for the historical data sets at the present time. Abstracts produced earlier are being incorporated into the data descriptions. However, these abstracts are extremely terse, and are being edited to make them more readable. We are passing copies of the data description files down to a PC to be edited and completed by a secretary using a word processor program.

The machine readable portion of the data file descriptions includes one or more Fortran-style format statements which define the formats used to write the data files. Following the format descriptions is a table that assigns a variable name to each data field, defines its type (real, integer, alphameric, or logical), its location in the data records, and a description of the variable. This table is designed to allow the intermediate software tools to obtain the information required to read the data files. In some cases the intermediate programs will read a file description and then generate a specialized program. The specialized program will be able to read the data file, and process it. For example, we will have a utility which will produce programs that can read the data files and load the data directly into the data base program INGRES. We also foresee creating programs that will provide a similar interface to S and isp (two statistical packages on the Vax), to Lotus 1-2-3 (a spread sheet program for the PC), and other utilities.

The first intermediate program that we have written allows users to plot or print any numerical data from the data files. The user can specify the data to be used for the X- and Y-axes, specify scaling, choose logarithmic axes, label the plots, and have the plots drawn on a terminal or routed to a printer. One can also define new variables that are functions of the data variables, using Fortran-style statements that are interpreted at the time the plot is produced. The user can print such data in tabular form rather than plotting it. This program will soon be modified so that the data also can be summarized and analyzed using common statistics (mean, variance, minimum, maximum, skewness, kurtosis, goodness-of-fit to a normal or lognormal distributions, etc.). The program will also be modified to handle non-numeric data.

The information required to produce the standardized data summaries is included as a subset of the data description file. We have a program which reads the data file descriptions, extract this subset of information, and print the data summaries in the standardized format. The data summaries are typeset and printed automatically using a laser printer.

New Tasks

We are in the beginning stages of two new initiatives relative to data management. The first of these concerns the maintenance of the data currently in the database. The tapes on which the data are stored need to be checked periodically to insure that they remain readable. We are designing a plan to schedule such checks on a regular basis, and developing a set of procedures to use should a tape become damanged. We are also investigating alternative storage media, such as optical disks, which should have much longer lifetimes than any magnetic media.

We are also developing a plan to insure that newly collected data are properly archived. This plan will include complete descriptions of the flow of data from the field through keypunching, processing, summarizing, microfilming, and entry into the LTER database. The plan will include a means of logging all data as it flows through the system. We are developing procedures to insure that the data are collected in a form that will minimize the amount of transcription required to produce machine readable files. In particular, we will be replacing any out-of-date data forms currently in use, and developing tools for producing standardized data forms and new data description files as required.

VIII. ORGANIZATION AND MANAGEMENT

Project Organization and Management

The CPER/LTER project is a joint effort between CSU and USDA-ARS. Two CSU units are involved, the Range Science Department and the Natural Resource Ecology Laboratory, and one ARS unit, the Great Plains Systems Research unit. Project direction will be set by the PIs, who meet weekly during the academic year and monthly during the summer. W. K. Lauenroth is the project and site director and will have overall responsibility for project management. The PIs are advised by a Local Advisory Committee of senior scientists from the regional scientific community, and an External Advisory Committee (Table 1) of scientists chosen from the national community.

Table 1. LTER External and Local Advisory committees.

External Advisory Committee

Dr. R. O'Neill	Oak Ridge National Laboratory, Oak Ridge, Tenn.
Dr. E. Paul	Michigan State University, Lansing, Mich.
Dr. P. Risser	Illinois Natural History Survey, Champaign, Ill.
Dr. F. Swanson	USDA-FS Forestry Sciences Laboratory and Oregon State University, Corvallis, Ore.

Local Advisory Committee

Dr. C. V. Cole
USDA/ARS and Colorado State University

Dr. D. G. DeCoursey
USDA/ARS, Fort Collins, Colo.

Dr. J. K. Detling
Colorado State University

Dr. J. L. Dodd
University of Wyoming

Dr. E. T. Elliott
Colorado State University

Dr. H. Goetz
Colorado State University

Dr. R. D. Heil
Colorado State University

Dr. H. W. Hunt
Colorado State University

Dr. D. Klein
Colorado State University

Dr. W. A. Laycock
University of Wyoming

Dr. W. J. Parton
Colorado State University

Dr. G.A. Peterson
Colorado State University

Dr. L. R. Rittenhouse
Colorado State University

Dr. D. S. Schimel
Colorado State University

Dr. G. E. Schuman
USDA/ARS, Cheyenne, Wyo.

Dr. M. Shoop
USDA/ARS, Fort Collins, Colo.

Dr. N. Stanton
University of Wyoming

Dr. M. J. Trlica
Colorado State University

Dr. W. Willis
USDA/ARS, Fort Collins, Colo.

Dr. B. A. Wunder
Colorado State University

Guidance for decisions about the several components of the LTER project is provided by working groups. The groups are (1) Vegetation and Primary Production; (2) Nutrient Cycling and Soil Organic Matter; (3) Consumer Populations; (4) Modeling. Our approach to LTER I research has been highly integrated, maximizing cooperation with related projects. As appropriate for specific tasks, our management approach has included a large amount of central control. We have resisted the independent component model for the project in favor of a model in which all participants take part in addressing the global project objectives as well as those specific objectives that fit their disciplinary training. We are satisfied that this model is working well for us and plan to continue it into LTER II. During LTER I we were successful in attracting cooperators from a large number of departments on campus as well as from state and federal agencies. Faculty from Entomology, Microbiology, Agronomy, Range Science, Earth Resources, Fisheries & Wildlife Biology, Zoology, Psychology, Botany, and Radiation Biology have all participated in LTER I. We expect to be able to continue to enlist their support during LTER II.

Site Management

The Central Plains Experimental Range is under the administration of the Great Plains Systems unit of the ARS. A memorandum of agreement between CSU and ARS is the basis for the use of the CPER and LTER program. Decisions about LTER use of the site are made by the PIs in consultation with a Site-Use committee. This committee is chaired by the ARS Scientist-in-charge of the CPER, Dr. M. Shoop, and includes W. K. Lauenroth and the LTER site manager, Dr. D. Hazlett. This committee has as its major responsibility to ensure that experiments do conflict.

IX. FACILITIES AND EQUIPMENT

CPER Facilities

The LTER project has good facilities at the Central Plains Experimental Range. The project headquarters consists of a 215-m^2 office/laboratory building, a 135-m^2

storage and work building, and a six-unit dormitory building. Each of the dormitory units consists of two rooms, sharing a bath. The office building has a 53-m^2 meeting room, with a large blackboard, a workroom with a PC, two offices, a kitchen/dining room, and two large laboratories. The laboratories are used mostly for sample preparation. Materials are transported to campus (60 km) for most analyses.

A large animal-handling facility is located approximately 1 km from the headquarters. It consists of four pens (10 × 15 m), a working chute and scale, and an adjustable loading ramp. The facilities adjoin a 22-ha holding pasture.

A 4-ha exclosure, constructed in 1968, contains the main micrometeorological station, a National Atmospheric Deposition Program station, and a 3-m-diameter weighing lysimeter, which has been used for evapotranspiration research.

The site manager lives in a 120-m^2 home located on the site. The home is fully furnished and is the year-round residence for the manager.

Campus Facilities

The campus headquarters for the LTER project is in the Range Science Department. Facilities here consist of an office for Lauenroth, an office for a one-third time secretary, two research associate/postdoctoral offices, a workroom with PCs and a terminal to the CSU mainframe and NREL VAX computers, and offices for four graduate students. A suite of offices and a soil-preparation laboratory is located adjacent to the Range Science Department. The project files are kept in the Range Science Department, including a library of CPER and Shortgrass Steppe publications. A complete set of IBP Grassland Biome Technical Reports, as well as a library of computer printouts from IBP data analyses are available.

The LTER facilities in the Natural Research Ecology Laboratory consist of offices for Woodmansee (NREL Director) and Lauenroth, laboratory space, and access to the computing facilities of the lab, which consist of a VAX 11/730 computer, a Sun System workstation, and terminals linked to the CSU mainframe computers.

X. LITERATURE CITED

Allen, T. F. H., and T. B. Starr. 1982. Hierarchical structure: Perspectives for ecological Complexity. University of Chicago Press, Chicago. 310 pp.

Cole, C. V., and R. D. Heil. 1981. Phosphorus effects on terrestrial nitrogen cycling. Ecol. Bull. (Stockholm) 33:363-374.

Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. Science 199:1302-1310.

Connell, J. H., and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. Am. Nat. 121:789-824.

Davis, R. 1986. Knowledge based systems. Science 231:957-963.

Doedel, E. 1981. AUTO: A program for the automatic bifurcation analysis of autonomous systems. Congr. Num. 30:265-284.

Frayley, L., Jr. 1971. Response of shortgrass plains vegetation to chronic and seasonally administered gamma radiation. Ph.D. Thesis. Colorado State University, Fort Collins. 170 pp.

Gardner, W., and D. Kirkham. 1952. Determination of soil moisture by neutron scattering. Soil Sci. 73:391-401.

Heasley, J. E., W. K. Lauenroth, and T. P. Yorks. 1984. Simulation of SO_2 impacts. Pages 161-184 in The Effects of SO_2 on a Grassland (W. K. Lauenroth and E. M. Preston, eds.). Springer-Verlag, New York. 207 pp.

Huston, M. 1979. A general hypothesis of species diversity. Am. Nat. 113:81-101.

Innis, G. S. 1978. Grassland Simulation Model. Springer-Verlag, New York. 298 pp.

Innis, G. S., and E. Rexstad. 1983. Simulation modeling simplification techniques. Simulation July:7-15.

Jansson, S. L. 1958. Tracer studies on nitrogen transformations in soil with special attention to mineralization-immobilization relationships. Annu. Rev. Agric. Coll. Swed. 24:101-361.

Klipple, G. E., and D. F. Costello. 1960. Vegetation and cattle responses to different intensities of grazing on shortgrass ranges on the Central Great Plains. USDA Tech. Bull. No. 1216.

Knisel, W. G. (ed.) 1980. A field scale model for chemicals, runoff, and erosion from agricultural management systems. USDA Conservation Research Report No. 26, 640 pp.

Lauenroth, W. K., and P. L. Sims. 1976. Evapotranspiration from a shortgrass prairie subjected to water and nitrogen treatments. Water Resources Research 12:437-442.

Lauenroth, W. K., J. L. Dodd, and P. L. Sims. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. Oecologia (Berl.) 36:211-222.

Lauenroth, W. K. 1979. Grassland primary production: North American grasslands in perspective. Pages 3-24 in Perspectives in Grassland Ecology (N. French, ed.). Springer-Verlag, New York. 204 pp.

Lauenroth, W. K., H. W. Hunt, D. M. Swift, and J. S. Singh. 1986. Estimating aboveground net primary production in grasslands: A simulation approach. Ecol. Model. (in press).

Levins, R. 1966. Strategy of model building in population biology. Am. Sci. 54:421-431.

Martel, Y. A., and E. A. Paul. 1974. The use of radiocarbon dating of organic matter in the study of soil genesis. Soil Sci. Soc. Am. Proc. 38:501-506.

May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269:471-477.

McGill, W. B., and C. V. Cole. 1981. Comparative aspects of organic C, N, S, and P cycling through organic matter during pedogenesis. Geoderma 26:267-286.

McKell, C. M., J. P. Blaisdell, and J. R. Gordon. 1972. Wildland Shrubs: Their biology and utilization. USDA Forest Service General Tech. Rep. INT-1.

Milchunas, D. G., W. K. Lauenroth, J. S. Singh, C. V. Cole, and H. W. Hunt. 1985. Root turnover and production by ^{14}C dilution: Implications of carbon partitioning in plants. Plant and Soil 88:353-365.

Naveh, Z., and R. H. Whittaker. 1980. Structural and floristic diversity of shrublands and woodlands in northern Israel and other Mediterranean areas. Vegetatio 41:171-190.

Negoita, C. V. 1985. Expert Systems and Fuzzy Systems. Benjamine & Cummings Publ. Co., Menlo Park, Calif. 190 pp.

Noy-Meir, I. 1973. Desert ecosystems: Environment and producers. Annu. Rev. Ecol. Syst. 4:25-51.

O'Neill, R. V., and D. E. Reichle. 1979. Dimensions of ecosystem theory, p. 11-26. In R. H. Waring (ed.) Forests: Fresh Perspectives from Ecosystem Analysis. Oregon State Univ. Press.

O'Neill, R. V., D. De Angelis, J. Waide, and T. F. H. Allen. A Hierarchical Concept of the Ecosystem. Princeton University Press, Princeton, New Jersey (in press).

Parton, W. J. 1978. Abiotic section of ELM. Pages 31-53 in Grassland Simulation Model (G. S. Innis, ed.). Springer-Verlag, New York. 298 pp.

Parton, W. J., D. W. Anderson, C. V. Cole, and J. W. B. Stewart. 1983. Simulation of soil organic matter formation and mineralization in semiarid agroecosystems. In Nutrient Cycling in Agricultural Ecosystems (R. R. Lowrance, R. L. Todd, L. E. Asmussen, and R. E. Leonard, eds). College of Agriculture Experiment Station, Spec. Publ. No. 23. University of Georgia, Athens.

Pastor, J., J. D. Aber, C. A. McDaugherty, and J. M. Melillo. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. Ecology 65:256-268.

Paul, E. A., C. A. Campbell, D. A. Rennie, and K. S. M. McCallum. 1964. Investigation of the dynamics of soil humus utilizing carbon dating techniques. Trans. 8 Int. Congr. Soil Sci. 3:201-208.

Paul, E. A., and N. G. Juma. 1981. Mineralization and immobilization of soil nitrogen by microorganisms. Ecol. Bull. 33:179-195.

Sala, O. E., and W. K. Lauenroth. 1982. Small rainfall events: An ecological role in semiarid regions. Oecologia (Berl.) 53:301-304.

Schimel, D. S., M. A. Stillwell, and R. G. Woodmansee. 1985. Biogeochemistry of C, N, and P in a soil catena of the shortgrass steppe. Ecology 66:276-282.

Shugart, H. H. 1985. A Theory of Forest Dynamics: The Ecological Implication of Forest Succession Models. Springer-Verlag, New York. 298 pp.

Simon, H. A. 1973. The organization of complex systems. Pages 3-27 in Hierarchy Theory (H. H. Pattee, ed.). George Braziller, New York. 156 pp.

Singh, J. S., W. K. Lauenroth, H. W. Hunt, and D. M. Swift. 1984. Bias and random errors in estimates of net root production: A simulation approach. Ecology 65:1760-1764.

Stanford, G., and S. J. Smith. 1972. Nitrogen mineralization potentials of soils. Soil Sci. Soc. Am. J. 36:465-472.

Stanford, G., and S. J. Smith. 1976. Estimating potentially mineralizable soil nitrogen from a chemical index of soil nitrogen availability. Soil Sci. 122:71-76.

Tiessen, H., J. W. B. Stewart, and C. V. Cole. 1984. Pathways of phosphorus transformation in soils of different pedogenesis. Soil Sci. Soc. Am. J. 48:853-858.

Vitousek, P. M. 1982. Nutrient cycling and nutrient use efficiency. Am. Nat. 119:553-572.

Waterman, D. A. 1986. A Guide to Expert Systems. Addison-Wesley Publ. co., Reading, Mass. 419 pp.

Watt, A. S. 1947. Pattern and process in the plant community. J. Ecol. 35:1-22.

Zeikus, J. G. 1981. Lignin metabolism and the carbon cycle. Polymer biosynthesis, biodegradation, and environmental recalcitrance. Adv. Microb. Ecol. 5:211-243.