Long-Term Ecological Research Program: Shortgrass Steppe

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Principal Investigators:
W. K. Lauenroth
I. C. Burke
J. Van Schilfgaarde
J. R. Forwood

Investigators:
D. P. Coffin    E. F. Kelly
J. K. Detling   T. B. Kirchner
D. O. Doehring  D. G. Milchunas
D. G. DeCoursey W. J. Parton
J. D. Hanson    O. E. Sala
J. E. Hautaluoma D. S. Schimel
R. M. Hoffer    B. Van Horne
J. A. Wiens
R. G. Woodmansee
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Project Summary

We propose to continue the long-term ecological research project in the shortgrass steppe, at the Central Plains Experimental Range in northcentral Colorado. The objective is to improve our understanding of the long-term processes responsible for the origin and sustainability of shortgrass steppe ecosystems. Our concept for long-term study of the shortgrass steppe is that the major controls over ecosystem structure and function are climate, geomorphology, and landuse management. Each of these controls has important spatial and temporal heterogeneity across a range of scales, and exerts its influence at a particular combination of levels. We hypothesize that the most important controls at the CPER are soil texture and landuse. We propose to continue current work and initiate new studies to further examine the influence of soil texture and landuse over shortgrass steppe ecosystem structure and function using field experimental research, simulation, and regional analysis.
1.0. RESULTS FROM PRIOR NSF SUPPORT

Summary

The Central Plains Experimental Range Long Term Ecological Research project, begun in 1982, has focused on the spatial and temporal patterns of ecosystem structure and function in the shortgrass steppe. We have addressed research in 5 areas: water dynamics; pattern and control of primary production; populations chosen to represent trophic structure; organic matter accumulation and nutrient dynamics; and disturbance. Since the inception of LTER, we have produced exciting results in each of these 5 areas. For LTER III, we propose to continue to study the origin and sustainability of shortgrass steppe ecosystems.

W. K. Lauenroth is the principal investigator on the current LTER grant "Long Term Ecological Research Program: Shortgrass Steppe" (BSR#8612105). The award was for the period Jan. 1, 1987-Dec. 31, 1990 in the amount of $1,676,573. The objectives of this work were to investigate the origin and long-term maintenance of spatial pattern in shortgrass steppe ecosystems at a variety of scales (Fig 2.1), and to investigate rules for transforming information at a particular spatial or temporal scale to the next higher scale.

The Central Plains Experimental Range Long Term Ecological Research project (CPER/LTER) began in 1982. Throughout the 8 years our research has focused on the spatial and temporal patterns of long-term processes within the context of the 5 LTER core topic areas. This section will provide an overview of that research by highlighting specific results. The remaining sections of the proposal comprise detailed results and accomplishments as a context for proposed future research. A complete list of publications can be found in Appendix I.

The Central Plains Experimental Range (CPER) is a 6500-ha research site administered by the USDA/Agricultural Research Service (ARS) (Fig. 1.1). The site was established in 1939 and has been in operation continuously since that time. The site was also the location of an enormous amount of field research during the U.S. International Biological Program (IBP) in the late 1960s and early 1970s. The historical and ongoing work by ARS scientists, as well as the experience and database built during the IBP project, has been a tremendous resource for the CPER/LTER project.
Figure 1.1a A typical summer thunderstorm at the Central Plains Experimental Range. A large fraction of the growing season rainfall is received as convective storms.
1.1 The Five Core Areas

Since LTER I, we have used a slightly modified set of 5 core areas to focus our effort at the CPER. Linkage of nutrient dynamics with soil organic matter (SOM) is so close in grasslands (Parton et al. 1988b) that our approach has treated core topics 3 and 4 as a single issue. In addition, we have added a new core area, Water Dynamics, a research area that we consider to be fundamental for understanding the structure and function of the shortgrass steppe. Below, we describe several of the key results of our research in each of these core areas.

1.1.1 Water dynamics

Because ecosystems in semiarid regions are largely controlled by water, understanding the temporal variability in precipitation inputs is critical to interpreting the significance of ecosystem responses (Noy-Meir 1973, Lauenroth et al. 1978). The LTER project began during a 6-year period in which annual precipitation was above the long-term mean for the site (Fig. 1.2). This 6-year period was preceded by a 9-year dry period in which 7 of the years had annual precipitation below the mean. Mean annual precipitation for the 8 years of the LTER project was 354 mm, 9% above the long-term mean of 324 mm. The first 3 of the LTER years were above the long-term mean and the last 5 have been below the mean. It is clear from the 47-year record of annual precipitation that the 8 years of the LTER project represent only a fraction of the observed variability in water inputs. It is also clear that it will be difficult to say when we have observed a representative sample of the range of variability. Research being conducted under this topic is described in Section 3.1.5.

1.1.2 Pattern and control of primary production

Net primary production (NPP) in shortgrass steppe ecosystems is an important and sensitive system response to interannual and annual variation in water availability (Lauenroth et al. 1978). The relationship between aboveground net primary production (ANPP) and annual precipitation has often been reported to be linear over the range of precipitation received at the CPER (Lauenroth 1979, Webb et al. 1978, Sala et al. 1988b)
Figure 1.1b A typical moderately grazed pasture at the Central Plains Experimental Range.
(Fig. 1.3). Part of our LTER effort on primary production involves annual estimation of
ANPP at a variety of sites including a grazing exclosure that was also sampled during
the IBP project from 1970-1975 (Fig. 1.4). Although the relationship between ANPP and
annual precipitation is well established, it does not always provide a clear and simple
explanation for the observed variability in the data. This is clearly shown by the spread
of data around the regression of ANPP on precipitation (Fig. 1.3) and the apparent
contradictions in the exclosure data (Fig. 1.4), in which ANPP is high during several dry
years and low in two of the wet years. The explanation is likely related to both the
effects of time lags and other variables such as nitrogen availability. Additional
descriptions of research and results for primary production can be found in Section 3.1.1.

1.1.3 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 (Lauenroth and Milchunas 1990). Ecosystems
at the CPER have an asymmetric trophic structure typical of semiarid regions, where
greater species and functional group diversity is found belowground than aboveground
(Scott et al. 1979). Our work to date has focused on 2 groups of populations, plants and
herbivores. As an example, population dynamics of 3 important perennial plant species
clearly indicate the year-to-year variability characteristic of the shortgrass steppe (Fig.
1.5). These results also illustrate that plant populations do not necessarily respond
similarly to the same environmental signal. Additional detail about our research on this
core topic can be found in Section 3.1.2.

1.1.4 Pattern and control of organic matter accumulation and of inorganic
inputs and movements of nutrients

SOM is the single best indicator of ecosystem status at the CPER (Yonker et al. 1988)
and in semiarid regions in general (Parton et al. 1987, Burke et al. 1989). Our work on
these topics has included the important long-term effects of geomorphic and pedologic
processes. During LTER I, we concluded that even though the CPER landscape has been
Figure 1.2 Long-term deviations of annual precipitation from the 47-year CPER mean (324 mm) and the 8-year LTER mean (348 mm).

Figure 1.3 Relationship between annual precipitation and annual aboveground forage production for 43 years at the CPER.
shaped by fluvial processes, the presence of deflation basins, relic dunes, and paleosols developed in loess, combined with the lack of low order stream channels, suggest that eolian processes played a dominant role in shaping the modern landscape. Work under LTER II funding has resulted in a detailed map of surficial geology (Fig. 1.6), a field installation for long-term observation of eolian sediment transport, and a detailed investigation of $^{137}$Cs as an index of mid-term (20 years) soil redistribution patterns. Additional research on SOM and nutrient dynamics is described in Section 3.1.3.

1.1.5 Patterns and frequency of disturbance to the site

Disturbance research associated with the CPER/LTER project began with a broad definition of disturbance (e.g., Rykiel 1985) and included long-term grazing (Milchunas et al. 1989) and additions of nitrogen and water (Lauenroth et al. 1978). During LTER II we began to sharpen our focus and our definition of disturbance. The overwhelming importance of *Bouteloua gracilis* in shortgrass ecosystems lead us to initiate a line of research at a small spatial scale that focused on individual plants and the consequences of events that resulted in their death (Fig. 1.7) (Coffin and Lauenroth 1988). Finally our interests in the regional significance of our research caused us to begin to evaluate large spatial scale processes including the mosaic of landuse in the region surrounding the CPER (Fig. 1.8). Our continuing research includes all 3 scales of disturbance (small, large, and regional) and is discussed further in Section 3.1.4.

1.1.6 Synthesis and intersite activities

The past three years have been particularly important for synthesis and intersite efforts for CPER/LTER scientists. A number of these are completed products; others are in progress. Perhaps one of our most successful areas of synthesis is in the development and application of simulation models with relevance to all core topic areas. The CENTURY ecosystem model is one of our major contributions in this area (Fig. 1.9) (Parton et al. 1987, 1988b) (Section 3.6.2). The conceptual framework for SOM and nitrogen (N) represented in CENTURY has gained significant support in the ecological
Figure 1.4 Aboveground net primary production and annual precipitation in an exclosure on an upland location on a sandy clay loam soil. This site was sampled for 6 years during the IBP project and has been sampled for 7 years during LTER.

Figure 1.5 Density of tillers of *B. gracilis*, cladodes of *O. polyacantha*, and individuals of *S. coccinea* in an exclosure on an upland location on a sandy clay loam soil. Density was sampled during IBP, between IBP and LTER and during LTER.
community, and is being adopted as a general construct across many ecosystems (Parton et al. 1989).

With funding from the LTER supplemental program, we began a new synthetic, intersite effort that involves application of the CENTURY ecosystem model to a spatial database for a box transect from the CPER to the Konza LTER site. We are using Advanced Very High Resolution Radiometer (AVHRR) data as an independent model to corroborate regional simulations using the CENTURY model (Fig. 1.10). Our other synthesis, modeling, and intersite work is described in detail in Sections 3.5 and 3.6.

1.1.7 Data management

During the 8 years of the CPER/LTER project, we have developed a data management program for accurate entry, storage, security, and easy access of long-term data (Section 3.3 and 3.4). In addition, we are developing a spatial database management system using a geographic information system (GIS). The GIS will be used for storing the location of past and current experiments, for maps of natural and artificial features of the site, and for aiding in site planning and research.

1.2 Continuity of Approach

The objectives of our proposed research for LTER III follow from our efforts over the past 8 years. This proposed work, in addition to continuing to add to long-term core data sets, will build upon our most exciting past results on patterns of variability in fundamental ecosystem properties and their important biotic and abiotic controls. Just as the theme for our LTER II research was directly related to, and a refinement of, the theme for LTER I, the overall theme for LTER III is a further refinement of our concepts of the origin and maintenance of spatial pattern in shortgrass steppe ecosystems.

In Section 2 of the proposal, we describe our developing conceptual framework of the biotic and abiotic controls over ecosystem structure and function in the shortgrass steppe. We then present our current research framework that encompasses prior work and allows us to focus on new elements in our research. Finally, we propose a research plan to
Figure 1.6 Surficial geology map produced as a result of research during LTER (Davidson 1988). Q1 alluvium is the youngest deposit (c. 15000 BP) and forms terraces 0.3 to 1 m above modern streams. Q2 is a valley fill deposit (c. 5000-8000 BP) that covers approximately 15% of the CPER. Q3 is the most extensive Quaternary deposit covering approximately 80% of the site. It was deposited approximately 90,000 BP. Q4 alluvium is the oldest deposit at the CPER (160,000 BP) (Davidson 1988).
address key questions within the research framework, including field experimentation, modeling and synthesis, and regional analysis.

In Section 3 we review the important components of the CPER/LTER research program, those aspects that make our research program distinctive in its contribution to ecological research in grasslands, and an active participant and leader in the national LTER program. We describe our research in each of the core areas, and the long-term experiments, data sets, archives, and data management protocols that are an integral part of the program. Synthesis, modeling, and intersite activities are described, as are our interactions with related research projects. Last, we discuss the new projects and technologies that the CPER research program is using to address problems of long-term significance.
Figure 1.7 Average contribution to turnover rates of basal cover and number of B. gracilis plants by each disturbance type for 9 locations, by grazing intensity and topographic position. (Grazing intensity: L=light, M=moderate, H=heavy) (Coffin and Lauenroth 1988).
WATER
RIPARIAN VEGETATION
BARREN LAND

RANGELAND
CROPLAND
FALLOW CROPLAND

Figure 1.8 Classification of thematic mapper data for the area surrounding the CPER (outlined). The classification separated the major categories of land use in the area.
Figure 1.9 Box and arrow diagram for the carbon (SOM) submodel of the CENTURY ecosystem model (Parton et al. 1988). Numbers in boxes are turnover times.
Figure 1.10. Top two panels: Simulated aboveground net primary production (NPP) in the central Great Plains for 1986 and 1988. The CENTURY ecosystem model was driven by a geographic information system (GIS) containing information on soil texture, precipitation, and temperature. Lower two panels: Integrated Normalized Difference Vegetation Index (NDVI) from the Advanced Very High Resolution Radiometer (AVHRR) for 1986 and 1988. NDVI provides an independent model of aboveground production. The correlation between CENTURY and NDVI was significant for both years (p < 0.001).
2.0 CONCEPTUAL FRAMEWORK AND RESEARCH PLAN

Summary

The semiarid Great Plains of North America is an extensive area, and has particular importance for natural resource production. The Central Plains Experimental Range (CPER) has an excellent location in the central Great Plains to represent the important long-term ecological issues of consequence for much of the region. Our concept for long-term study of the shortgrass steppe is that the major controls over ecosystem structure and function are climate, geomorphology, and landuse management. Each of these controls has important spatial and temporal heterogeneity across a range of scales, and exerts its influence at a particular combination of levels. We hypothesize that the most important controls at the site level of the CPER are soil texture and landuse. Soil texture is a major influence over soil water availability, and thus vegetation structure, net primary production, and decomposition. Landuse sets the equilibrium state of ecosystems by controlling potential production and soil organic matter reserves. We propose to continue current work and initiate new studies to further examine the influence of soil texture and landuse over shortgrass ecosystem structure and function using field experimental research, simulation, and regional analysis.

Introduction

The semiarid Great Plains of North America comprises a mosaic of native grassland and cropland adjacent to the eastern face of the Rocky Mountain chain. Motivation for careful evaluation and monitoring of this region at the end of the 20th century comes from 2 sources. First, the Great Plains contains the major wheat producing areas for the entire continent, in addition to important grazinglands for livestock. Second, current models of atmospheric circulation indicate that climatic change, as a result of increased greenhouse gases, will be relatively larger here than in most other parts of temperate North America (Kellog and Zhao 1988). The combination of socio-economic importance and vulnerability of the region to both climatic fluctuations and climate change make it essential that we expand our understanding of long-term ecological relationships, particularly climate-landuse-ecosystem interactions.

The Central Plains Experimental Range (CPER) has an excellent location in the central Great Plains to represent the important long-term ecological issues of consequence for much of the region. The CPER/Long Term Ecological Research (LTER) project benefits not only from the location of the CPER, but also from the presence of long-term field facilities and experiments, and from the availability of historical data.
Figure 2.1 Nested hierarchy of spatial pattern, representing the multiple spatial scales of our CPER/LTER research effort. Characteristic temporal scales are associated with each of the spatial scales. In general there is a positive relationship between large spatial scales and long temporal scales. Shading of the vertical bars indicates our relative research effort at each level during LTER I and II, and our proposed allocation of effort for LTER III. (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. (2a) Shortgrass Steppe: $2.8 \times 10^5$ km$^2$ of grassland and cropland in the west central section of the Great Plains physiographic province. (2b) Central Great Plains: $3.0 \times 10^5$ km$^2$ of grassland and cropland, whose boundary is defined by state boundaries. (3) The Central Plains Experimental Range (CPER): 70 km$^2$ of grassland in the northern portion of the Shortgrass Steppe. (4) Physiographic Unit: a geomorphic unit defined by the activity of long-term fluvial and eolian processes on a geologic template. Physiographic units range from .25 to 10 km$^2$. (5) Toposequence (catena): a 2-dimensional representation of a landscape within a physiographic unit, generally conceived as an elevational cross-section to focus on slope processes. Generally about 100 m in length. (6) Patch: a discrete spatial pattern at the scale of several individual plants or bare soil areas, 1 to 100 m$^2$. (7) Individual plant/gap: a single plant and the volume in resource space that it influences.
The CPER/LTER project represents the continuing development of a research tradition that began with the US/IBP Grassland Biome project in the late 1960s, the time at which ecosystem science was formally recognized as a sub-discipline in ecology. Research at the CPER over the past 20 years has had an important interactive relationship with the development of ecosystem science. The Grassland Biome project focused on the issue of productivity of natural ecosystems. Grasslands were conceptualized as homogeneous entities, appropriately described by an average square meter. The transition from the IBP project in the early 70s to the LTER project in the early 80s involved important change in our thinking about the role of spatial variance. Our involvement in the LTER program (LTER I 1982-1986) began with spatially explicit ideas and questions about the importance of landscape structure, particularly the classic soil catena model (Gerrard 1981), in the long-term development and maintenance of shortgrass steppe ecosystems. In the second phase of the project (LTER II 1987-1990) we expanded our thinking about long-term processes to include the origin and persistence of spatial patterns at a range of spatial scales (Fig 2.1). This work included substantial questioning of the generality of the catena model at the CPER and in the shortgrass steppe region. Our proposed work for LTER III builds upon LTER I and II and expands the depth of our investigations into interactions between spatial and temporal patterns in ecosystem structure and function.

2.1 Objective and Conceptual Framework

The overall objective for the CPER/LTER project is to improve our understanding of the long-term processes responsible for the origin and sustainability of shortgrass steppe ecosystems. To achieve this objective, we will evaluate the climatic, geomorphic, and human-induced controls over ecosystem structure and function across a range of temporal and spatial scales, extending from intraseasonal variation to geologic periods, and from individual plants to the central grassland region (Fig 2.1). We propose to accomplish this through:

1. Continuation of our current, long-term observational and experimental research begun under LTER I & II.
2. Continuation and extension of our CPER synthesis and simulation modeling work.
3. Continuation and extension of our intersite and cross-site research and synthesis.
4. Development of new field and simulation experiments.

The conceptual framework for our LTER research in shortgrass steppe ecosystems is that the major controls over structure and function are climate, geomorphology, and landuse management. Each has important spatial and temporal heterogeneity across a range of scales, and exerts its influence at a particular combination of levels (Fig. 2.1).

How do these controls interact to influence spatial variation in system structure and function at any particular scale? How does interaction affect prediction at the next higher scale? The next lower? Below, we describe the complexity inherent in these questions for the shortgrass steppe.

Weather and its statistical representation, climate, is a major driving force for biological processes, constraining the kinds and numbers of organisms that can survive, compete, and reproduce, determining overall ecosystem structure and potential productivity, and altering the dynamics of ecosystem processes. Climate exerts major control at the regional level, accounting for most of the observed spatial variation in many ecosystem attributes (Sala et al. 1988b, Burke et al. 1989). Interactions of climate with landform and topographic position cause spatial patterns in microclimate at landscape scales. In the shortgrass steppe, interannual variability in precipitation is a key control over annual NPP. Within a growing season, pulse precipitation events create important short-term spatial variation in biological activity.

Long-term geomorphic processes in the central grassland region are responsible for the structure and stability of the landform and soil as a template for ecosystem development and sustainability. Over geologic time, the interaction of the geologic template with climate--wind, precipitation, temperature--drives weathering and fluvial and eolian redistribution of sediments across landscapes and regions. At the scale of decades to centuries, erosional and depositional processes at the toposequence and physiographic unit spatial scale may be important in shaping landform via redistribution of material (Fig.
2.1). The shortgrass steppe and other semiarid regions are particularly vulnerable to erosion during droughts, especially when subjected to intensive management such as cropping, as was apparent in the Dust Bowl of the 1930s.

Landuse in the central grassland region has an important impact on system status (Russel 1929, Tieszen et al. 1982, Bauer et al. 1987, Elliott and Cole 1989). Climatic zones establish regional patterns in landuse, with greatest cropping intensity in high rainfall areas. Within a region, geomorphology determines spatial patterns in landuse, with the most productive lands—generally those on loamy soils—all under cropping, and grazing on less productive sites. Weather variability among years, commodity prices, and current status of land determine the temporal variation in landuse.

The relative importance and impacts of climate, geomorphology, and landuse on patterns in ecosystem properties changes across scales. This is an important reason why conducting research across spatial scales can significantly improve our understanding of controls over system behavior. Our understanding at a particular scale is limited to the range of conditions we have observed; the realm of inference is thus limited to the same range of conditions. For example, a study of soil organic matter (SOM) on a particular toposequence at the CPER suggests that slope position is an important control over carbon accumulation (Schimel et al. 1985). Expansion to the scale of physiographic units (multiple toposequences [Fig. 2.1]) suggests that spatial pattern in SOM is controlled by soil texture, parent material, and grazing history, as well as slope position (Yonker et al. 1988 and unpubl. data). Finally, spatial pattern in SOM at a regional scale is most closely related to mean annual temperature and precipitation, modified by soil texture and landuse history (Parton et al. 1987, Burke et al. 1989). What are the rules for generalizing spatial pattern among scales? Can we use rules based on spatial variation to make predictions about temporal variation?

All of our current and proposed work at the CPER focuses on how climate, geomorphology, and landuse impact spatial and temporal patterning of ecosystem properties and processes. The scope of such an undertaking dictates that multiple
Figure 2.2 Map of the U.S. central grassland region, showing the extent of the Great Plains and Shortgrass Steppe, and the location of the CPER. The grassland region provides a convenient research context, with a precipitation gradient orthogonal to a temperature gradient.
research approaches be used; we are studying these interactions using long- and short-term experiments, simulation models, and regional analysis. Experiments allow us to test and improve our understanding at a limited set of spatial and temporal scales, confined by feasibility to single or multiple locations and from weeks to decades. LTER is fortunate to have the mandate to extend the temporal scale of experiments beyond standard research projects. Simulation models are important tools that allow us to test and improve our understanding across a range of temporal scales. Modeling is especially important in the study of climate change, allowing us to extend beyond the bounds of observed conditions. Finally, regional analyses allow us to extend our spatial domain beyond the bounds of our experiments and observations.

We propose to continue our work within the framework of a nested hierarchy of spatial and temporal scales. We will focus a new effort at the CPER on the interactions between landuse and soil texture at the site level, within the context of the temporal variability of climate. These two forces -- landuse and soil texture -- exert the most interesting and important controls over past and current development of shortgrass steppe ecosystems.

2.2 Research Framework

Semiarid regions account for 11% of the land area of the earth and 8% in North America, including the Great Plains (Bailey 1979) (Fig. 2.2). Regardless of their location, ecosystems in these regions are shaped by 2 important forces: availability of soil water and landuse (Noy-Meir 1973 and 1974, Hall et al. 1979). Low and variable availability of soil water is associated with low and variable precipitation (PPT), and accounts for a large fraction of observed temporal and spatial patterns in ecosystem structure and function (Sala et al. 1988b). Landuse introduces additional variability, part of which can be explained by the interaction with water availability (Senft et al. 1986).

Landuse in the Great Plains is divided between grazing by cattle and cropland. Approximately 60% of the land area remains in native vegetation and is used as grazingland. The long evolutionary history of grazing by large herbivores in the central
North American grasslands, and particularly the Great Plains portion, appears to have had a substantial impact on the response of steppe ecosystems to grazing by domestic herbivores (Mack and Thompson 1982, Singh et. al 1983, Milchunas et al. 1988b). Changes in plant communities induced by domestic livestock grazing are smaller per unit of grazing intensity for Great Plains ecosystems than for most other ecosystem types (Milchunas et al. 1988b).

The important impacts of water availability and landuse on ecosystems in semiarid regions provides a strong argument for using them as independent variables to organize research. Water availability at a particular location is controlled by precipitation and soil texture. Soil texture is important because of its relationship with soil hydraulic parameters (Clapp et al. 1983, Cosby et al. 1984). At the scale of an individual site, spatial variability in precipitation may be small; soil texture is then the major variable explaining the spatial variability in water availability. We propose to organize our field observations and experiments around the variability induced in steppe ecosystems by soil texture and landuse. Both soil texture and landuse vary significantly at the site, and may be used as experimental variables.

2.2.1 Soil texture as a control over ecosystem structure and function.

The justification for organizing our LTER research around texture is that it is one of the dominating influences on ecosystem structure and function in semiarid regions such as the shortgrass steppe. At the CPER, soil texture has an identifiable and quantifiable spatial distribution.

Among the surface properties controlled by geomorphology, soil texture provides the most important connections among landform, eolian processes, hydrology, soil water, ecological processes, and landuse. Because soil texture exerts major control on many of the processes important to our understanding of how climate, geomorphology, and landuse interact to influence structure and function of shortgrass steppe ecosystems, we plan to use soil texture as one of the key factors in field, laboratory, and simulation studies.
Figure 2.3 Soil texture classes, expressed as sand content classes for a nested hierarchy including the central Great Plains, northeastern Colorado, and the CPER. Spatial scale decreases from $3.0 \times 10^5$ km$^2$ for the central Great Plains (upper panel), $9000$ km$^2$ for northeastern Colorado (center panel), to $70$ km$^2$ for the CPER (lower panel). Decreasing spatial scale is associated with increasing levels of resolution. Data are stored in our regional and site level Geographic Information Systems. Legend: white and orange (sand < 20%); green and dark blue, (20% < sand < 50%); and light blue and purple, (sand > 50%).
2.2.1.1 Spatial distribution of texture

Pedogenically, texture is a very slowly changing soil attribute in semiarid regions. Geomorphically, fluvial and eolian processes are the primary agents of movement of material at toposequence to regional scales (Fig. 2.1) and are therefore the principal forces behind differences in soil texture.

Investigations of both pedogenic and geomorphic influences on toposequences and landscapes have been a focus of the CPER/LTER project for the past 8 years (Section 3.1.3). The spatial distribution of soil texture at the CPER is dependent on the scale of observation. In maps of soil series, the distribution of texture is a complicated mosaic. Combining soil information into broad textural classes results in a relatively smooth picture of the distribution of texture at the CPER (Fig. 2.3). The underlying property upon which textural classes are based, particle size distribution, is continuously distributed in space. Grouping the particle size data into classes imposes a spatial scale. This allows us to be efficient in detecting differences using a stratified design that has clear ecological significance.

2.2.1.2 Effects of Texture

At the CPER, soil texture is the dominant influence on infiltration. Because slopes are gentle and PPT is low, coarse soils seldom produce runoff. By contrast, fine soils frequently produce runoff even with moderate rainfall intensities (Pilgrim et al. 1988). Texture significantly influences the availability of water to plants in semiarid regions. Coarse soils allow more water to penetrate beyond the depth of evaporation than do fine soils. The result is that in semiarid regions, on an annual basis, coarse soils tend to provide more water for plants than fine soils; this is referred to as the inverse texture effect (nyoy-Meir 1973).

The most important control over ANPP in semiarid regions is annual PPT (Lauenroth 1979, Sala et al. 1988b). The impacts of soil texture on infiltration and water availability significantly affect the relationship between ANPP and PPT, and have important consequences for individual plants, populations, and community structure.
Figure 2.4 Root distribution of *Atriplex canescens* (left) and *B. gracilis* (right) growing together on a sandy loam soil at the CPER.
Noy-Meir (1973) predicted that the balance point for the inverse texture effect should occur between 300 and 500 mm annual PPT; below this point, coarse soils should be more productive than fine soils. Sala et al. (1988b) analyzed a spatial data base of ANPP for the central grassland region and found the balance point between fine and coarse soils at 370 mm. The CPER falls below the balance point, therefore fine soils should have less water available for transpiration and consequently lower production than coarse soils. Our results to date are not clear on this issue (Liang et al. 1989).

The interaction between soil texture and PPT may be an important control on species and lifeform composition. Because of the high infiltration rates and low water holding capacities of coarse soils, deep-rooted plant species may have an advantage over shallow-rooted species. Grasses possess finely branched, dense root systems that allow them to obtain the largest part of their water and perhaps nutrients from the upper layers of the soil (Fig. 2.4). Shrubs have an extensive root system with coarse roots that extend far into the soil, thus penetrating a much larger soil volume but less densely (Fig.2.4). Our observations at the CPER suggest that there is a pattern in lifeform and species composition with soil texture, but that this pattern is complicated by interactions with grazing (Liang et al. 1989).

Soil texture may play an important role the development of patterns of microrelief at the CPER. The configuration of the ground surface on a small scale is uneven. Individual plants are often surrounded by micro-depressions. It is unclear whether this surface irregularity is a result of soil erosion between plants, or net accumulation around and within plants. In addition, small-scale disturbances that kill individual plants expose bare soil to wind and water erosion. Freezing and thawing, especially in these small disturbed areas, loosens the upper layer of soil increasing its vulnerability to wind and water. Such ephemerally loose soil may play a role in the genesis of micro-relief and slope movement processes.

SOM accumulation is closely related to soil texture in grasslands (Parton et al. 1987, Aguilar and Heil 1988, Burke et al. 1989). SOM quantity represents the balance of
primary production and decomposition, both of which are influenced by soil texture
central grassland region, found that for a given precipitation zone, SOM was lowest in
coarse soils; this suggested that with respect to SOM, the influence of texture and water
availability on NPP was not as significant as its effects on decomposition.

Water availability is the most frequent control on decomposition and nutrient
mineralization in the shortgrass steppe (Schimel and Parton 1986). Since soil texture
influences hydraulic properties of soil, it also influences decomposition through its effects
on water availability, with coarse soils most likely to maintain high decomposition rates
for long periods of time. The direct effects of soil texture on SOM are the result of the
chemical and physical properties of clay particles. Clay protects SOM from decomposition
by adsorption and aggregation, slowing turnover and effectively increasing SOM
texture and SOM accumulation in shortgrass steppe soils can be mostly attributed to
physical and chemical protection from decomposition (Paul and Van Veen 1978, Schimel
et al. 1985, Parton et al. 1987). Redistribution of SOM along with clay particles may
also contribute to the covariance between SOM and texture.

Nutrient availability is linked to both soil texture and SOM in grasslands (Schimel
1986). Total soil nutrient content, like SOM, is highest on fine soils. Recent studies
suggest that N mineralization is highest on fine soils, but that the magnitude of the
increase compared to coarse soils is not proportional to the size of the total SOM pool
(Schimel et al. 1985a,b, Burke 1989). Total C and N turnover rates on fine soils are
slower than on coarse soils, suggesting that more of the SOM is in resistant pools and
not available for decomposition or mineralization (Tisdale and Oades 1982, Schimel et al.
to plants must be a balance between substrate availability and immobilizing potential.
Figure 2.5 Aerial photograph of the LTER headquarters at the CPER showing grazingland and adjacent cropland.
Key Questions - texture:

1. What is the relationship between the temporal variability in PPT and the temporal variability in ANPP? Does including soil texture in the relationship for the CPER significantly improve predictability? Are coarse-textured soils at the CPER more productive than fine soils? How does texture interact with nutrient supply rate and water availability to influence productivity?

2. How does soil texture interact with PPT to affect species and lifeform composition? Are deep-rooted species more successful on coarse soils than on fine soils? Are plant communities on coarse soils more stable than those on fine soils? Can we predict species composition given soil texture, and can we use this knowledge to manage species composition? How does soil texture influence forage quality?

3. Is the dominant process that generates microrelief fluvial, eolian, freeze-thaw, or a combination of more than one geomorphic agent? What role does small-scale disturbance play in generating micro-relief? How does microrelief affect the distribution of snow, organic matter, and seeds? How does soil texture influence processes that affect microrelief? What is the role of grazing in creating or influencing these small-scale patterns?

4. How does soil texture interact with water content to control C inputs and outputs via NPP and decomposition? How important is the protection of SOM by clay to carbon accumulation in these soils? How important is soil erosion in influencing the relationship between SOM and soil texture? How do pulse precipitation events interact with soil texture to control short-term N availability?

Section 2.2.2 Landuse as a control over ecosystem structure and function

Shortgrass ecosystems are subject to both natural and human-induced disturbance, or landuse. Landuse represents a planned change in ecosystem structure and behavior, while disturbances are most frequently stochastic interruptions. Common natural disturbances in the shortgrass steppe include grazing above- and belowground by large and small herbivores including arthropods, digging by mammals, fecal deposition by large herbivores, and nest-building activities by ants (Lauenroth and Milchunas 1990, Coffin and Lauenroth 1988). We expect shortgrass ecosystems to show adaptations to these disturbances, since they are a part of its development (Holling 1978, Lauenroth et al. 1978).

Grazing by cattle and row-crop agriculture are the predominant landuses in the shortgrass region (Fig. 2.5) (Lauenroth and Milchunas 1990). Because of a long evolutionary history of grazing by large generalist herbivores, we have hypothesized that shortgrass ecosystems are well adapted to withstand the effects of grazing by cattle
Figure 2.6 Photograph of cattle grazing in a swale. Grazing intensities on swale positions along toposequences are typically 3 times greater than upland and slope positions.
(Milchunas et al. 1988b and 1989). By contrast, cropping is different from anything in the developmental history of the shortgrass steppe. Both the intensity of the disruption and the spatial scale are novel.

The spatial pattern of land use at regional scales is controlled by climate. At local scales, soil and landform conditions are prominent among the decision criteria. The most important limitations on the suitability of a particular location for row-crop production are slope, soil depth, and texture. Steep slopes are avoided regardless of soil depth and texture. Shallow soils are seldom worth the investment required for cultivation. Practically, among the sites have high potential for cropping, the decision is made on the basis of soil texture. Very sandy soils and those with high clay contents are avoided. Silt content is perhaps the single most important textural consideration. In general, the dominant land use on sites with shallow soils, steep slopes, or extreme textures is grazing. The remaining sites are used for row-crop production.

The temporal pattern of land use may be the result of either climatic-ecologic or sociologic-economic factors. Conditions that affect either productivity or markets can initiate a change in land use. Sustained periods of drought have historically led to cropland abandonment and a return to grazing systems. Climate change scenarios that include either an increase in temperature or a decrease in precipitation for the center of the North American continent will have a large on impact land use patterns in the shortgrass steppe.

2.2.2.1 Effects of land use - grazing

Domestic cattle have direct and indirect effects on both the structure and function of ecosystems (Fig. 2.6). They impact structure via this influence on species and lifeform composition, canopy architecture, and the distribution of carbon above- and belowground. At the functional level, cattle may cause changes in net primary production, SOM turnover, and nutrient availability.

The response of shortgrass plant communities to long-term heavy grazing and long-term protection is unusual compared to other grassland types. The response is unusual
Figure 2.7 Soil organic C and N in soils in long-term grazed and ungrazed locations at the CPER.

Figure 2.8 ANPP under long term grazed and ungrazed conditions. Grazed/grazed results refer to plots subjected to long-term cattle grazing and grazed the year of sampling; grazed/ungrazed refers to plots subjected to long-term grazing but protected the year of sampling; and ungrazed/ungrazed refers to plots protected from cattle grazing for the past 50 years and protected the year of sampling. ANPP was estimated by harvesting at the end of the growing season.
because of the small number of detectable changes associated with grazing, and because of the kinds of differences we have observed between the grazed and protected locations at the CPER (Milchunas et al. 1989, Milchunas et al. submitted). Long-term heavily grazed locations had increased cover of all plant species, including *B. gracilis*, less litter, and more bare ground than protected locations (Milchunas et al. 1989). By contrast, long-term protection was associated with higher densities of introduced weedy species than the grazed locations. Based upon these results and a comparison with grasslands worldwide, we hypothesized that the high relative resistance of shortgrass communities to grazing was based upon their long evolutionary history of grazing and the convergent selection pressures of grazing and semiaridity (Milchunas et al. 1988b).

The traditional method of assessing the condition of a grazingland is to evaluate the species composition and aboveground plant cover (Lauenroth and Laycock 1989). Based on the results from our analysis of species composition, we concluded that long-term heavy grazing was not causing an important decrease in condition. However, results of recent studies, including some of our own research, suggest that we may have misinterpreted the response of the system to grazing.

Bauer et al. (1987) reported greater organic C in protected compared to grazed grasslands, and the opposite trend for organic N. They also found a significant effect of texture with largest losses of C associated with sandy soils. A recent study at the CPER initiated during LTER II provided results that support those of Bauer et al (1987) and conflict with our previous conclusions about the sensitivity of shortgrass ecosystems to grazing based upon species composition. Analyses of soil samples over several grazed and ungrazed toposequences indicated that heavily grazed locations have 26% less C and 35% less N than exclosures after 50 years (Fig. 2.7). A single year's data for ANPP indicate a substantial decrease in end-of-season yield for long-term grazed locations compared to ungrazed (Fig. 2.8) (Milchunas and Lauenroth in prep.). If the differences in C and N between the grazed and ungrazed locations represent losses as a result of grazing, they
Figure 2.9 Conceptual model of changes in SOM for shortgrass ecosystems under long-term light, moderate, and heavy grazing. (a) represents the difference between exclosures and heavily grazed pastures, the quantity that is often interpreted as the long-term loss in SOM from grazing (Bauer et al. 1987). (b) represents estimated SOM loss due to heavy grazing, if we assume initial conditions were lightly grazed pastures, and (c) estimated SOM loss if we assume that initial conditions were moderately grazed pastures. Long-term exclosures may represent system perturbations, increasing in SOM from previous, steady-state conditions. Differences between exclosures and heavily-grazed ecosystems may be due to aggradation of exclosures, as well as degradation under grazing.
are comparable in magnitude to losses reported for similar periods of cultivation (Haas et al. 1957, Aguilar et al. 1988).

Studies of the effects of grazing on SOM and nutrient availability are not common in the literature. Our ability to interpret results for the CPER is limited by our lack of knowledge about initial conditions. We can not be sure whether the grazed locations are losing C and N, or the protected areas are gaining (Fig. 2.9). Even if we assume that ecosystem status before grazing by cattle was at equilibrium, we have no quantitative information about that condition. Studies that address long-term effects of grazing have taken advantage of exclosures to make comparisons between ungrazed and grazed locations, and make inferences about long-term effects (Bauer et al. 1987). We have hypothesized that some level of grazing is the natural state of shortgrass ecosystems, and that protection from grazing represents a system disturbance (Milchunas et al. 1988b). Thus, it is possible that grazing exclosures have been aggrading, and that our estimates of grazing responses of C and N are overestimates.

**Dynamics of change.** How does soil texture influence the rate of change under initiation of grazing, and the final state? To examine the potential effects of grazing intensity and soil texture on shortgrass ecosystem properties and processes, we ran the CENTURY ecosystem model (Parton et al. 1987) to steady-state for moderate grazing intensity, then imposed 50 years of heavy grazing on both fine and coarse soils. Simulated ANPP decreased immediately (Fig. 2.10), since the response of ANPP to grazing is an input (Holland et al. submitted). Simulated soil C decreased during the whole time period, with the largest drop during the first 25 years. Simulated absolute soil C losses were similar for both soil textures, with largest relative losses in the sandy loam soil (37%). These simulated losses are comparable to those we have estimated at the CPER (Milchunas et al. in prep.). Most of the decreases in soil C for both soils came from the slow SOM pool (Fig. 1.9). The net N mineralization rate increased with grazing because of decreased inputs of shoot and root plant residue into the soil (Holland et al. 1987).
Figure 2.10 Simulated ANPP, net N mineralization, and soil organic carbon under long-term moderate grazing, 50 years of heavy grazing, and release to light grazing.
submitted). These lower C inputs to the soil reduced N immobilization during decomposition of plant residue.

Can a decrease in the intensity of management reverse the above trends, and result in recovery of biomass and soil? We hypothesize that total plant biomass production should increase, resulting in increased ecosystem stores of C and other nutrients. Release from grazing in the CENTURY simulations resulted in increased soil C, but decreased N mineralization because of higher N immobilizing potential compared to the grazed system (Fig. 2.10). Simulated ANPP was suppressed during this recovery phase because of N-limitation. This effect was most pronounced on fine soils because of higher levels of SOM stabilization in the fine soils.

Such trends in nutrient availability after release from grazing may play an important role in determining the recovery responses of individual plants and NPP. Experiments at the CPER indicated that water and nitrogen availability separately, and in concert, influence NPP and species composition (Lauenroth et al. 1978). We hypothesize that the availability of N during recovery from grazing influences aboveground production and species dynamics, and depends upon the intensity of prior grazing and soil texture.

**Key Questions - grazing:**

1. What is the relationship between changes in plant community structure caused by grazing and changes in SOM and nutrient availability? Is the relationship the same for a recovering ecosystem as it is for a degrading one? How are these relationships influenced by soil texture?

2. What are the relative contributions of NPP and decomposition to changes in SOM under grazing? Is the relationship the same for above- and belowground? Is it the same for aggrading as for degrading ecosystems? How are these relationships influenced by soil texture?

3. How does grazing affect long-term nutrient availability? Are nutrients more available during the degrading than the aggrading phase of ecosystem response? Is increased aboveground nutrient yield under grazing an indication of a long-term trend in nutrient loss? How are these relationships influenced by soil texture?

**2.2.2.2 Effects of landuse - cropping**

We are interested in evaluating the short- and long-term effects of release from cropping. Short-term economic, political, and climatic variation can result in significant
Figure 2.11 Recovery sequence for abandoned agricultural fields in the shortgrass steppe based upon the old field model of succession (Judd and Jackson 1939).
changes in landuse. Historically, large areas in the shortgrass steppe region have been converted from cropland to rangeland since settlement. The drought of the 1930s resulted in the abandonment of more than 100,000 ha of farmland in NE Colorado. Much of this is now managed by the Forest Service as the Pawnee National Grassland. The CPER was part of the Land Utilization Project that preceded the national grasslands. Although most of the CPER was not plowed, we have several abandoned fields that have been recovering for approximately 50 years. A new agricultural program in the Great Plains, the Conservation Reserve Program (CRP), will result in large areas of cropland being converted back into grassland in the 1990s (Joyce and Skold 1987). Little research has been done on the direction and magnitude of ecosystem response to release from cropping.

The abandonment of agricultural fields and their subsequent recovery to native grassland have been important to successional ideas for the shortgrass steppe. Until recently, most successional concepts for the shortgrass steppe were developed from research associated with abandoned cropland (Judd and Jackson 1939, Costello 1944, Judd 1974). The resulting descriptions of succession suggested a 30- to 50-year time-frame for recovery of shortgrass plant communities after abandonment (Judd and Jackson 1939) (Fig. 2.11).

Recent studies, in some cases 40 to 50 years after abandonment, found results different from those predicted by the early models (Hyder et al. 1975). Reichardt (1982) evaluated recovery on a field in the Pawnee National Grasslands abandoned for 40 years. Similarity in species composition between the abandoned cropland and unplowed areas was less than 50%, and the climax dominant, *B. gracilis*, made up a very small fraction of the species composition. These results, along with lab and greenhouse evaluations of conditions required for germination, seedling establishment, and tillering, led to the view that *B. gracilis* does not recover following disturbance in the shortgrass steppe region (Hyder et al. 1971, Briske and Wilson 1977, 1978). The result of the lack of support for the old-field model by recent observations has created two very different concepts of
succession in the shortgrass region. One group persists in thinking in terms of old-field succession; the other considers *B. gracilis* a relict species.

During LTER I and II, we investigated an alternative conceptualization of succession based on the importance of spatial processes to the recovery of *B. gracilis*. Field studies and simulation analyses suggest that recovery time is dependent on the size of the disturbance relative to the dispersal distance of *B. gracilis* seeds (Coffin and Lauenroth 1989a). In addition, soil texture is an important control on recovery because it affects germination and establishment of *B. gracilis* seedlings (Coffin and Lauenroth 1989c).

Cultivation of grassland soils results in depletion of SOM and reduced site fertility (Russel 1929, Tieszen et al. 1982, Aguilar et al. 1988, Elliott and Cole 1989). Tillage increases both erosion and decomposition, leading to decreased SOM and a decrease in the ability of soil to retain mineral nutrients. Reductions of up to 50% in SOM have been reported for long-term cultivation (Haas et al. 1957, Burke et al. 1989). The magnitude of losses depends upon interrelationships among intensity and duration of cultivation, fertilization, susceptibility to wind and water erosion, soil texture, and parent material. Losses of mineral nutrients are proportional to losses of soil C, but with perhaps greater relative losses of C than N and P to the extent that oxidation is important. Increased decomposition and mineralization, combined with decreasing SOM, induce conditions that increase N availability for an unknown length of time (Schimel 1986).

Dynamics associated with the loss in SOM from cultivation are not well-documented. For example, how important are element interactions to nutrient availability and production during the degradation phase? How rapid are losses in SOM? How do they influence N availability? How important is soil texture in controlling absolute and relative losses, and rate of loss?

We ran the CENTURY model for 50 years of a standard wheat-fallow cropping sequence on fine and coarse soils for CPER climatic conditions to evaluate these questions (Fig. 2.12). Simulated SOM declined immediately upon cultivation, with the
Figure 2.12 Simulated ANPP, net N mineralization, and soil organic carbon under long-term moderate grazing, 50 years of wheat-fallow, and release to light grazing.
most rapid decrease during the first 25 years. Absolute magnitude of simulated losses were similar among soil textures, but the relative losses were much greater for sandy soils (40% for sandy loam vs. 25% for the clay loam). Simulated N mineralization increased during the initial phase of cropping due to rapid decline in SOM and immobilization potential. The N mineralization rates remained higher in the clay loam soil because level of SOM in the slow pool (Fig. 1.9) is much higher for the clay loam soil. The results show that higher N mineralization rates for the clay loam soil produced substantially higher grain yields (Fig. 2.12) for the clay loam soils.

During the last 50 years of the simulation (Fig. 2.12) we simulated the growth of a grassland following 50 years of cultivation. The results showed that soil C level, plant production and N mineralization rates all increased with time, however, plant production, soil C and N mineralization are substantially lower than the pre-cultivation levels. Plant production after 50 years was slightly higher for the sandy loam soil, while soil C stabilization rates were higher for clay loam soil.

Results from these simulations suggest a number of questions relevant to the response of processes in shortgrass ecosystem to intensive land use and provide a focus for our interests in the recovery of abandoned agricultural lands.

Key Questions - cropping:

1. What is the observed variability in successional dynamics for abandoned croplands of different characteristics? How do soil texture, precipitation, temperature, and size of field influence rate and direction of recovery--both of species composition and of NPP? How are successional dynamics influenced by nutrient availability?

2. How do cropping intensity, type, and duration influence the rate and magnitude of SOM losses? How have apparent losses in SOM been influenced by precipitation, temperature, and soil texture? What is the regenerative capacity of soils in abandoned fields recovering to native grassland, and how is this modified by precipitation, temperature, and soil texture? How does N availability change during recovery?

The landuse soil-texture framework provides a powerful conceptual structure for our new research proposed for LTER III. In addition, this framework fits within the comprehensive conceptual model for our continuing CPER/LTER research program. For the shortgrass steppe and over long temporal scales, climate, geomorphology, and landuse
are the major controls over spatial and temporal variation in ecosystem structure and function. At the site level, soil texture is the specific geomorphic control on structure and processes and together with landuse provides the basis for a collection of specific questions that we will use to guide our new research. In the next section, we describe a plan for our new research to address many of our key questions about landuse and texture interactions.

2.3 Research Plan

The experiments we are proposing for LTER III represent what we consider to be the most exciting and important new ideas for field research on shortgrass steppe ecosystems. The scope of our proposed research is very ambitious, to the extent of raising questions about whether we can accomplish all of it in the next 6 years. We fully recognize the magnitude of the tasks we are setting for ourselves. In planning this work we consciously chose to follow our vision of important ecological problems rather than develop a conservative research plan. This strategy served us well during LTER II. By setting an ambitious, integrated scope of work we are confident that we accomplished more than we would have with a conservative plan.

2.3.1 Field Experiments

Our proposed field experiments represent an approach to evaluate the individual and interactive effects of soil texture and landuse on ecosystem structure and function. The development of these ideas relies upon the key questions from the Research Framework (Section 2.2) to define the rationale and the 5 core topics to organize the presentation of the work. The descriptions are necessarily general. We rely heavily upon the literature and our past work to communicate the details associated with measurements.

2.3.1.1 Texture effects on ecosystem structure and processes

The objective of this research is to evaluate the controls exerted by soil texture on structure and processes under moderate summer grazing by cattle. [Key Questions - Texture, Section 2.2.1]
Figure 2.13 Map of soil textural classes for the CPER. Long-term ungrazed exclosures are shown as solid or open, squares or rectangles.
Moderate summer grazing by cattle is the most common landuse at the CPER and is one of the most common grazing management practices throughout the shortgrass steppe. Approximately 90% of the area of CPER has been moderately grazed for the past 50 years. Further, moderate summer grazing is a more representative control condition for shortgrass steppe ecosystems than is protection from grazing (Milchunas et al. 1988b, Milchunas et al. 1989, Milchunas et al. 1990).

Within the constraints of a single grazing treatment and a single macroclimate we hypothesize that the most important explanatory variable for temporal and spatial patterns in ecosystem structure and processes is soil texture. Moderately grazed pastures at CPER span a range of textures from sandy loam to clay loam providing an excellent experimental environment to investigate the effects of texture on ecosystem (Fig. 2.3).

**Patterns of primary production.** The inverse texture hypothesis predicts higher NPP on coarse soils than sites on fine soils (Noy-Meir 1973). Analysis of regional data, averaged over many sites, supports the inverse texture hypothesis (Fig. 2.14). The distribution of soil textures over moderately grazed pastures at the CPER will provide the opportunity to design a replicated (pastures) study of texture effects on ANPP (Fig. 2.13). ANPP will be estimated by harvesting quadrats protected from grazing during the year of sampling (Lauenroth et al. 1986b). Interannual variation in weather will allow us to evaluate the interactions between water availability and texture as the influence on ANPP. Because estimation of BNPP is much more difficult than ANPP, we will not be able to balance our efforts above- and belowground in this experiment. Our major new initiative on BNPP will be associated with the new texture-landuse interaction experiment described in Section 2.3.1.3.

**Population dynamics.** Soil texture has such a profound effect on the dynamics of water and nutrients that it is an important ultimate variable controlling plant population dynamics. *B. gracilis* is the most important plant species in the trophic structure of shortgrass ecosystems and perhaps the most important species regardless of kingdom. Recruitment, growth and mortality of *B. gracilis* is closely related to water and mineral
Figure 2.14  ANPP on sites representing a gradient in soil texture from Soil Conservation Service MLRA database for NE Colorado. Textures were converted to water holding capacities.
nutrient availability and therefore soil texture. Simulation of population processes provides a clear indication of the potential importance of soil texture (Coffin and Lauenroth 1989a,b,c). Recruitment of *B. gracilis* is dependent upon availability of seeds and favorable soil water conditions and perhaps nutrient conditions for germination and establishment. First-year seed production data from a long-term population study (Section 3.2.2) indicated a large effect of soil texture on reproductive effort (Fig.2.15). Preliminary plant size data from the same study suggest control of tiller demography by soil texture (Fig. 2.16). Average plant size was 50% larger on a site with a coarse texture soil than one with fine texture.

We plan to design a replicated study of tiller dynamics (vegetative reproduction), plant establishment (sexual reproduction), and plant mortality for *B. gracilis* over the texture gradient. Our current understanding of the demography of *B. gracilis* is built into an individual-plant-based simulation model called STEPPE (Coffin and Lauenroth 1989a,b,c). The results of this experimental work, in addition to incrementing our understanding of the population biology of *B. gracilis*, will provide much needed data to test several of the key processes in the model.

**SOM and nutrient turnover.** Texture has several direct and indirect effects on SOM and nutrient turnover. There are at least 3 processes that are responsible for the pattern of high SOM on fine soils that we have observed at the CPER and at the regional level: protection of SOM from decomposition by clay; interaction of soil water and texture controlling decomposition rates; selective movement of SOM with clay from erosion via wind and water.

We are interested in separating the individual effects of soil texture on decomposition, so that we can better model and predict long-term processes. To accomplish this, we will conduct litter decomposition studies across a textural gradient. We will construct litterbags with above- and belowground plant litter, bury these to several depths, and assess the decomposition rate by collecting bags periodically during the next 10-20 years, with samples collected frequently during the first 5 years. We will use intact soil cores
Figures 2.15 Reproductive effort for *B. gracilis* from locations representing a gradient in soil texture at the CPER.

Figure 2.16 Distributions of plant sizes for *B. gracilis* from locations representing a gradient in soil texture at the CPER.
underlain by resin bags (Binkley 1984) to estimate seasonal integrated N mineralization across the textural gradient each year. In addition, we will conduct laboratory incubations of litter in soils of different textures, and estimate N mineralization and decomposition rates through the evolution of CO₂. Such incubations will allow us to separate the effects of texture and substrate quality from those of microclimate on decomposition.

**Disturbance.** The conspicuous effect of root grazing by *Phyllophaga* larvae on *B. gracilis* is to kill individual plants in small to large patches (Fig. 3.6). Our current effort, based upon patches killed in 1977, spans a portion of the texture gradient (Section 3.2.1.1). Our plan is to initiate another set of plots over an explicit soil texture gradient. These plots will be selected from patches in which *B. gracilis* began dying during the summer of 1989. Early in 1990 we will confirm the presence of *Phyllophaga* before locating patches to be studied. We will permanently mark and map the patches, and take initial soil, individual plant, and vegetation samples in the spring of 1990. Analysis of samples and vegetation data will occur when the new funding cycle begins. These patches and the ones initiated in 1977 will be sampled periodically for several decades.

**Soil water.** Intraseasonal dynamics of soil water provide important control information for our field research (Parton et al. 1981), and provide important data for analysis of water availability (Sala et al. in prep). We are currently sampling soil water dynamics over a variety of sites and soil textures on upland patches and at multiple locations along toposequences (Section 3.1.5). The important missing element of our soil water research is an assessment of temporal dynamics in the 0-15 cm layer. Essentially all of our soil water data have been collected using a neutron probe. The important positive attribute of this method is that it allows for repeated estimates at the same location. In the past several years, time domain reflectometry (TDR) has matured as a technology with high potential for repeated estimates of soil water with automated and continuous data acquisition, particularly in the surface layers (Topp and Davis 1982). We plan to install TDR probes at each of the locations at which we are collecting soil water.
data, as well as at locations associated with the new SOM-nutrient turnover and population dynamics research.

2.3.1.2 Landuse effects on ecosystem structure and processes

The objective of this research is to evaluate the effects of grazing intensity by cattle on the long-term dynamics of structure and processes. [Key Questions - Grazing. Section 2.2.2.1]

Despite the years of research that have been devoted to understanding the response of ecosystems to grazing by large generalist herbivores, a remarkable number of effects of grazing on ecosystem structure and function are not understood (Section 2.2.2.1). The LTER research project and the long-term grazing treatments at CPER provide an exceptional opportunity to evaluate a number of key questions associated with the responses of ecosystems to grazing.

Patterns of primary production. The CPER provides a grazing intensity gradient from ungrazed (by cattle) for the past 50 years to light, moderate, and heavy grazing for 50 years (Section 3.2.3). We plan to estimate ANPP using the harvest method, and BNPP using a combination of $^{13}$C labeling (Section 3.1.1) and minirhizotrons (Taylor 1987) over the range of grazing treatments. The $^{13}$C tracer studies will allow us to estimate average BNPP over several years (Milchunas and Lauenroth in prep) and the minirhizotron studies will provide relative root dynamics data to help us understand intra- and interannual variability in BNPP.

Population dynamics and disturbance. Grazing by cattle can have important effects on habitat suitability for other animals. Our work with Phyllophaga larvae and adults is described in Sections 3.1.2 and 3.2.1.1. We plan to sample small birds and mammals over the grazing intensity gradient. Some of this work was begun during the IBP project and has continued at a low frequency. We plan to increase the frequency of sampling during LTER III. The key question for the bird work is: What is the long-term effect of summer cattle grazing on habitat utilization by migrant and resident bird
populations? The key question for the small mammal work is: What are the long-term effects of summer grazing by cattle on small mammal density and species composition?

**Soil water.** Grazing by cattle has large potential effects on the water balance of individual plants as well as entire communities. This is confirmed by observations of changes in above- and belowground spatial patterns of plants, basal cover, plant demography, and production (Section 3.1.4). We currently have no specific work on water balance across grazing treatments. Using a spatially explicit sampling design with short- and long-term measurements, we plan to address both within- and between-patch dynamics of soil water, and the integration of these dynamics into community level responses. At time steps of a day, we will examine potential interactions of precipitation size class with grazing on soil water dynamics. At an annual time step, we will relate soil water to ANPP and nitrogen-yield to address the issue of water-use efficiencies. At longer time steps, our focus will be on rates and directions of changes in structure and function with long-term grazing.

### 2.3.1.3 Effects of interactions between texture and landuse on ecosystem structure and processes

**The objective of this research is to evaluate aggradation and degradation of ecosystem structure and function in response to long-term grazing by cattle. [Key Questions - Grazing, -Texture, Sections 2.2.1.2 and 2.2.2.1]**

Comparison of system structure and function between areas heavily grazed for 50 years and areas protected from cattle has shown several interesting differences. Vegetation structure was not significantly different between grazed and ungrazed pastures (Section 2.2.2.1). By contrast, carbon and mineral element cycling were substantially changed. Our current data represent net results after 50 years and provide no indication of the developmental pathway of the changes. We cannot tell, for instance, whether the aggradation of the protected location exceeded the degradation of the heavily grazed location (Fig. 2.9). We cannot separate the two processes with current data or experiments. Therefore we propose a new experiment to restart the processes and follow the development of protected and grazed ecosystems.
When the CPER was established in 1939, researchers constructed a .5-1 ha grazing exclosure in each of the pastures. These areas have remained protected from grazing for the past 50 years. The remaining areas have been grazed for the past 50 years. This collection of pastures and exclosures provides an extraordinary opportunity to reinitiate grazing and protection, and evaluate the balance between degradation and aggradation.

We propose to rearrange fences and expose areas to grazing that have been protected for the past 50 years, and protect areas from grazing that have been grazed for 50 years. We will do this across grazing intensity treatments and soil textures. The modification will not compromise the long-term value of the exclosures. The combinations of grazing conditions across soil textures are:

1. Long-term protection
2. Long-term grazing (light, moderate, heavy)
3. 50 years of protection followed by grazing
4. 50 years of grazing followed by protection

**Patterns of primary production.** We have evidence that suggests that 50 years of heavy grazing has decreased ANPP; we expect that BNPP may also have decreased. (Section 2.2.2.1). We will establish a series of sampling locations across soil textures and grazing treatments and exclosures to evaluate ANPP and BNPP. Our approach to estimating ANPP and BNPP is described in Section 2.3.1.2.

**Population dynamics.** The areas previously excluded from grazing are too small to allow us to ask questions about populations of mobile organisms. Thus population level work associated with this experiment will focus on plants. We will concentrate on the most abundant species over all textures, *B. gracilis* and *Opuntia polyacantha*. Both species are clonal; *B. gracilis* is a bunchgrass and *O. polyacantha* is a pricklypear cactus. Neither shows large changes in abundance as a result of long-term grazing, but the structure of clones and populations of both species is affected by grazing and soil texture.

**SOM and nutrient turnover.** Previous work indicates that SOM losses from cultivation and from grazing interact with soil texture (Aguilar and Heil 1988, Bauer et
We hypothesize that during SOM degradation, N availability increases due to decreased BNPP and depressed N immobilization potential. Additionally, N mineralization should be significantly reduced during recovery because of increased belowground C inputs (Fig 2.7). This reduced N availability may cause reductions in ANPP, BNPP, and N yield.

We will initiate a long-term, $^{13}$C - $^{15}$N double-label experiment to assess the incorporation of C and N into various fractions of SOM, the linkages between C and N in these soils, controls over N availability, and the turnover of SOM pools. This experiment will be conducted across both grazing and texture gradients. The long-term fate of $^{13}$C and $^{15}$N will be traced in plants, SOM, and fractions of SOM through long-term laboratory incubations of soils collected periodically. The design of this experiment is similar to the long-term $^{15}$N study (Section 3.2.5), but will yield much more information on the linkages between C and N in aggrading and degrading systems.

We plan to continue monitoring eolian sediment transport using our network of samplers (Section 3.2.7). Although not entirely appropriate, redistribution of snow by wind does serve as an analog to eolian sediment deposition and furthermore, provides valuable information about the spatial variability of soil moisture. We propose to use both direct and indirect observations and time-lapse video techniques to determine patterns of snow redistribution. Finally, we plan to initiate a series of small-scale studies of microrelief. Experiments including textural analysis of the soil, wind tunnel, and rainulator observations will be used to evaluate geomorphic processes operating at a small scale and their interaction with vegetation at the CPER.

**Disturbance.** The grazing exclosures provide an opportunity to evaluate interactions between grazing effects and disturbances. The frequency of occurrence of small disturbances, in particular pocket gopher mounds, is higher within exclosures than in the adjacent, grazed pasture. The reason for the increase in small mammal activity is unknown, but the result is disturbed areas of various sizes in the exclosures that can be evaluated for plant recovery. More importantly, we expect pocket gopher activity to occur...
in new exclosures. Typically, it is difficult to evaluate the effects of naturally-occurring disturbances, especially those that occur infrequently or have a patchy distribution (Coffin and Lauenroth 1988). In this case, we will have specific information about the pocket gopher mounds, such as their size and when the activity occurred; therefore we will be able to evaluate the relationship between the characteristics of the disturbance and effects on the plant community, and in particular B. gracilis. We will also have the opportunity to evaluate mortality of B. gracilis plants caused by pocket gopher activity.

2.3.1.4 Effects of cropland abandonment and soil texture on ecosystem structure and processes

The objective of this research is to evaluate recovery of ecosystem structure and function across a range of soil textures after cropland abandonment. [Key Questions - Cropping, Section 2.2.2.2].

We recently initiated a research program to identify a network of abandoned cropland sites within northeastern Colorado (section 3.6.1.2). We plan to establish a number of sites on cropland, native rangeland, and abandoned cropland in the region, located across several soil textural classes. We will set up a sampling protocol for annual or periodic estimation of simple attributes of ecosystem structure, species composition, plant cover, and soil organic matter. In addition, we will estimate selected ecosystem processes, ANPP and integrated net N mineralization rates on an annual basis.

We are interested in assessing the two-way interactions between the recovery of the vegetation, especially B. gracilis, and the recovery of SOM and N availability. To accomplish this, we will sample species composition and collect soil cores across a range of abandoned fields. The fields will be chosen to represent a landuse and soil texture gradient. We will conduct laboratory incubations of the soil cores, and estimate potential net N mineralization and decomposition from incubated soils (Schimel et al. 1985b). Combining such field and laboratory with simulations will allow us to improve our understanding of the interactions between vegetation structure and soil processes in aggrading systems.
2.3.2 Intersite research

Representatives from the 7 sites submitting renewal proposals met several times in the past 4 months to discuss prospects and commitment to intersite research. Appendix 2 contains a common statement of commitment and interest in intersite research by the 7 LTER projects.

The CPER/LTER project is involved in most of the activities listed in Appendix Table 1. We are part of the network wide litter bag experiment being coordinated by M. Harmon. Two of the PIs on the vegetation dynamics modeling project, W.K. Lauenroth and W.J. Parton, are in the CPER/LTER group. The CPER/LTER group, especially through our connection with the ARS Hydroecosystem group headed by D.G. DeCoursey, will be very interested in contributing to the cross-site hydrologic modeling project when it begins. The CPER/LTER group participated in the space-time workshop and will continue to be involved in the development of manuscripts. The CPER is one of the sites being sampled by Tilman and Zak for their environmental gradient project.

2.3.3 Synthesis

LTER projects have unique opportunities and responsibilities among research projects with respect to synthetic activities. Not only are LTER projects unique with respect to synthesis but PIs of LTER projects have special responsibilities for encouraging and supporting synthetic activities. A missing component in regular NSF funded research projects are the time and perspective to address large scope questions that cut across either project elements or across ecosystem types. LTER projects must have the perspective and responsibility to find the time for such activities.

Synthesis activities, especially simulation modeling, have been an important strength of the CPER/LTER group. We recognize that simulation is an important category of synthesis activities, but certainly not the only important one. Our plans for synthesis are presented in 3 categories: writing, simulation, and regional analysis.
2.3.3.1 Writing

The shortgrass steppe synthesis volume that we planned to complete during LTER II is not finished and is unlikely to be so before the end of the project. We are still committed to the idea and the plan even though the time schedule will be extended.

The plant-herbivore interaction research, conducted largely by D.G. Milchunas over the past 8 years, has reached a point where the next logical step is a book that integrates and synthesizes past work. We expect this to be completed during LTER III.

2.3.3.2 Simulation

The CPER/LTER group is involved in two important simulation efforts, each associated with a particular representation of ecosystem dynamics. D.P. Coffin and W.K. Lauenroth are working with individual-plant based models of ecosystem dynamics with the objective of explaining the long-term response of shortgrass steppe plant communities to disturbances (Coffin and Lauenroth 1989b). W.J. Parton and others have developed a carbon and nutrient element model of ecosystem dynamics (CENTURY) with the objective of explaining the carbon and nitrogen turnover at the scale of decades to centuries (Parton et al. 1987). Both groups plan to continue working with the modeling approach to improve the performance of their models.

The individual-based model (STEPPE) will be rewritten in the next 2 years to achieve 3 objectives: (1) represent the depth distribution of roots of each individual explicitly, (2) use a daily time step soil water model to calculate annual growth modifiers based upon the integration of daily soil water and weather data, and (3) represent the effects of grazing by cattle on individual plants.

The most exciting activity associated with our modeling work is an effort to link STEPPE and CENTURY. The result will be an ecosystem simulation model in which vegetation structure and soil processes interact. Under separate NSF funding (BSR#8807881) we developed a new method to combine the information contained in two or more simulation models without combining the computer code. The method employs concurrent execution of the models under UNIX. Network communication functions are
used to exchange information at each time step. The method is sufficiently flexible that the models can either run on the same machine or on two different machines connected by a TCP/IP network (Section 3.10).

2.3.3.3 Regional analysis

The objective of this work is to simulate regional patterns in ecosystem structure and function as they respond to spatial and temporal variation in geomorphology, climate, and landuse. We plan to continue to develop our current effort in regional analysis and simulation, in cooperation with several other research projects at CSU (Appendix 3). Our approach involves development of regional databases and simulation models, and the application of these models to address questions of regional relevance. Our new simulation models, described above (Section 2.3.3.2), will give us the capability to simulate regional dynamics across a wide range of levels of biological, spatial, and temporal resolutions.

We are obtaining regional databases for soil texture, historical and present climate (temporally as well as spatially resolved), and present and past landuse. We plan to continue to obtain databases for several regions of interest (Fig.2.1) with an inverse relationship between the size of the area and the resolution of the database. The data are being entered into a GIS, which will interact with simulation models for many applications.

There are two classes of questions that we will address with our regional simulation. First, we will use regional simulations to test our ideas about patterning in grassland ecosystem structure and function. Which variables best explain the current spatial distribution of vegetation structure in the central grassland region? Soil organic matter? Net primary production? Landuse? What do our simulations indicate about the long-term results of climate change? Second, we plan to conduct sensitivity analyses of our regional models to climate variables to provide an indication of the regional response to climate change.
We will use 3 ecosystem simulation models for this work: a model with high resolution in plant processes but low resolution in vegetation structure and soil processes (SPUR), a model with low resolution plant processes but high resolution soil processes (CENTURY), and a new class of combined plant process-soil process models (Section 2.3.3.2). We plan to simulate current and future conditions for a stratified collection of driving variable-soil property cells in the rangeland portion of the grassland region.

**Paleoecological analysis.** We plan to initiate paleoecological reconstruction of the CPER, northeastern Colorado, and the shortgrass steppe. We will map and sample paleosols to establish their relationship to geomorphic properties of the site and the region. This will allow us to infer geomorphic processes that resulted in formation of paleosols and it will provide information about landform evolution. The stable isotope composition of paleosols provides a record of vegetation (carbon isotope ratios of phytoliths and carbonates), temperature (oxygen isotope ratios in phytoliths and carbonates), and paleocarbon budgets. We will also apply carbon dating and possibly thermoluminescence dating to establish the chronology of vegetation and climate changes. This reconstruction will enrich our current concepts of landscape evolution and climate change. The addition of E.F. Kelly to the CPER/LTER project provides the impetus and expertise for development of this new research area. In addition, this work complements a new intersite project by Tieszen and Schimel (Section 3.7).

**Remote sensing.** We hope to expand the LTER long-term monitoring initiative to the regional scale. We are fortunate to have R.M. Hoffer as a new investigator on the CPER project to lead research in this area. Consistent, periodic acquisition and analysis of remote sensing imagery will allow us to monitor spatial and temporal patterns in land cover as they respond to interannual or longer term variation in climate. In addition, we will assess changing patterns in land management strategies over regional extent. As with the LTER site-level monitoring, such an initiative will provide a valuable set of data for long- and short-term analysis of system change.
Remote sensing analysis will be conducted at two levels of spatial resolution for monitoring purposes. First, we hope to obtain high spatial resolution imagery for a region at least as large as northeastern Colorado. Thematic mapper (TM) data are most desirable, but other data sources may be necessary. These data will be obtained at least once a year at mid-growing season, assuming availability. We have recently been successful in using TM prints to discern land management types (cropland vs. rangeland) and potentially range condition for this area (Fig.1.8), and hope to be able to continue in this direction. In addition, we recently discovered a historical dataset of Multispectral Scanner (MSS) data for our region; with this we will be able to pursue studies of recent historical changes in landuse.

At a second level of resolution, we will obtain low resolution data for the central grassland region from the Advanced Very High Resolution Radiometer (AVHRR). These data will serve both as a historical record of production across the region, and as a test against independent predictions of regional variables described above. We have recently contacted the USGS EROS Data Center about collaborative research, and the prospects for continuous acquisition of these data are good.
3.0 ELEVEN SPECIFIC TOPICS

Summary

The CPER/LTER project comprises both a coherent set of research activities focused on LTER core areas and a diverse set of scientists with broad interests in long-term research. The objective of this section is to review and highlight the important components of the CPER/LTER research program, those aspects that make it distinctive in its contribution to ecological research in grasslands, and an active participant and leader in the national LTER program. We describe our research in each of the 5 core areas, long-term experiments, data sets, archives, and data management protocols that are an integral part of the program. Synthesis, modeling, and intersite activities are described, as are our interactions with related research projects. Last, we discuss the new projects and technologies that the CPER research program is using to address problems of long-term significance.

3.1 The Five Core Areas

3.1.1 Pattern and control of primary production.

The key result from our work to date is that both patterns in and apparent controls on net primary production are entirely dependent upon the choice of spatial and temporal scale of study (Sala et al. 1988b). Our approach to this topic has emphasized the full range of spatial and temporal scales from individual plants to the central grassland region, and from within seasons to among years. Extensions of our interests beyond the CPER and into the recent past were possible because of the availability of historical and collaborative data. See Section 3.5.1.5 for discussions of the large spatial and long time frame results.

Aboveground. Estimation of aboveground net primary production (ANPP) was initiated in 1983 on 3 locations along a moderately grazed toposequence and within an exclosure (Fig. 3.1). Estimates are based upon end-of-season harvests from quadrats not grazed the year of sampling (Lauenroth et al. 1986b). In 1986, 4 additional sites were added to represent a soil texture gradient (Fig. 3.2) (Liang et al. 1989). Our current effort includes 6 locations each year. Because interannual variability in the amount and timing of precipitation is highly correlated with ANPP, a recording rain gage is located at each site. We plan to continue this sampling scheme in LTER III.
Figure 3.1 Annual aboveground net primary production for 3 positions along a moderately grazed toposequence and a 20-year exclosure. Plots sampled along the toposequence were protected the year of sampling.

Figure 3.2 Annual aboveground net primary production at 4 locations across a soil texture gradient at the CPER.
Belowground. Belowground net primary production (BNPP) has proven to be one of the most difficult processes to estimate in ecology. Estimates that are consistent with the carbon balance of ecosystems have been difficult to obtain (Singh et al. 1984, Sala et al. 1988a). Our work on BNPP began in 1985 and includes a combination of harvest and \(^{14}\text{C}\) tracer techniques (Milchunas et al. 1985, Milchunas and Lauenroth in prep). This work produced 2 very important results. First, harvest sampling over a 4-year period clearly showed the existence of multi-year trends in belowground biomass (Fig. 3.3). Belowground biomass decreased from 1985 to 1988 corresponding with a decreasing trend in annual precipitation (Fig. 1.1). Second, estimates of BNPP using \(^{14}\text{C}\) suggested a turnover time of 7-8 years (Fig. 3.4), a value that is considerably lower than previous estimates for shortgrass ecosystems (Sims and Singh 1978).

We plan to expand our efforts during LTER III to include estimates of BNPP across soil texture and landuse gradients. We will continue to use a combination of methods including the addition of minirhizotrons. We will change the tracer method slightly, substituting the stable isotope \(^{13}\text{C}\) for the radioactive \(^{14}\text{C}\).

3.1.2 Spatial and temporal distribution of populations selected to represent trophic structure

Physiognomy as well as trophic structure of shortgrass steppe ecosystems is dominated by the perennial bunchgrass, \textit{B. gracilis}. Our plant population work has focused on the interactions of disturbance size, frequency, and type, with recruitment and mortality of \textit{B. gracilis} (Fig. 1.7) (Coffin and Lauenroth 1988, Coffin and Lauenroth 1989a,b,d,e), as well as biotic and abiotic controls over demographic variables. Establishment of opportunist plant species on long-term ungrazed treatments was as large as on treatments where vegetation had previously been killed with herbicide, but was very low on long-term grazed treatments (Table 3.1). Subsequent mortality was heavily influenced by the presence of other plants, but only slightly influenced by current-year defoliation.

The indirect effects of herbivores on the spatial distribution of \textit{B. gracilis} and
Figure 3.3 Root biomass in the 0-20 cm soil layer for a location with a sandy clay loam soil that has been protected from grazing for 20 years.

Figure 3.4 Dynamics of $^{14}$C over time for plots labeled in 1985. Intercepts of regression lines with the time axis are estimates of the time for $^{14}$C to complete a full turnover in the various components of belowground biomass.
Table 3.1. The number of seedlings establishing in early June, monthly death rate, and monthly proportion of deaths for the June cohort. Means within a date not sharing a common subscript are significantly different.

(A) June Cohort of Seedlings (# per plot)

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<th>Treatment</th>
<th>Kochia scoparia</th>
<th>Salsola iberica</th>
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<td>142.8d</td>
<td>69.3c</td>
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(B) Monthly¹ Death Rate of June Cohort (slope of survival numbers)

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(C) Monthly¹ Proportion of Deaths of June Cohort (percent of previous month's population)

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</tr>
<tr>
<td>long-term ungrazed/undefoliated</td>
<td></td>
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<tr>
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<tr>
<td>plowed/undefoliated</td>
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</tr>
</tbody>
</table>

¹From previous month to month indicated.

²High value due to senescence after flowering rather than premature death.

*Not included in statistical analyses due to large number of zeros.
Figure 3.5 Numbers of June beetles (*Phyllophaga* sp.) captured in a light trap at the CPER from 1983-1989.

Figure 3.6 Distribution of sizes of patches of *B. gracilis* killed by larvae of *Phyllophaga*. These patches have been sampled since 1977 to assess plant community recovery.
characteristics of the microenvironment were more important for establishment and survival than direct effects of injury through defoliation.

Our consumer work has included grasshoppers (Capinera and Thompson 1987), Phyllophaga sp. (June beetles) (Wiener and Capinera 1980), and birds; the ARS has a large research program on cattle. June beetles (Phyllophaga sp.) represent one of the most important populations of herbivores in the shortgrass steppe. Their importance is the result of their effect on the system rather than their abundance. The larval stage of Phyllophaga feeds on roots of B. gracilis, which during particular years results in widespread but patchy death of individuals (Wiener 1979). Our approach to indexing fluctuations in numbers of larvae involves sampling the numbers of adults with a light trap (Fig.3.5). We do not yet understand the relationship between numbers of adults captured and the appearance of patches of dead B. gracilis. The ARS initiated a study of 32 selected patches in 1977 in grazed pastures and long-term exclosures (Fig. 3.6). LTER is now following the recovery of those patches; sampling for the fourth time will occur in 1990. A large number of patches with dead B. gracilis appeared in 1989. We plan to verify the presence of Phyllophaga larvae and initiate a set of long-term plots during 1990.

We plan to expand our work with small mammals and birds during LTER III. The addition of John Wiens and Beatrice Van Horne to the list of LTER investigators will enhance this work. The initial efforts will focus on interannual variability in both small mammals and birds. In 1990 we will initiate a cooperative project with Jim Forwood of the ARS on the interactions of forage quality with cattle grazing behavior.

3.1.3 Pattern and control of organic matter accumulation in surface layers and sediments. Pattern of inorganic inputs and movements of nutrients through soils, groundwater, and surface waters.

In semiarid regions, the inputs and movements of nutrients are closely tied to the inputs and fate of soil organic matter, therefore, our approach is to deal with them together. Our work on these topics has spanned spatial scales from single patches to the central grassland region (Schimel et al. 1985, Yonker et al. 1988, Burke et al. 1989).
Table 3.2 Description of physiographic units at the CPER (Yonker et al. 1988).

<table>
<thead>
<tr>
<th>Physiographic unit</th>
<th>Topography</th>
<th>Landform</th>
<th>Subgroup</th>
<th>Surficial deposit</th>
<th>Bedrock geology†</th>
<th>Ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Nearly level to</td>
<td>Uplands</td>
<td>Ustolic Haplarigids</td>
<td>Alluvium and gravelly</td>
<td>Shale</td>
<td>1472</td>
</tr>
<tr>
<td></td>
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<td></td>
<td>Aridic Argiustolls</td>
<td>alluvium</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Nearly level to</td>
<td>Uplands</td>
<td>Aridic Argiustolls</td>
<td>Alluvium and gravelly</td>
<td></td>
<td>353</td>
</tr>
<tr>
<td></td>
<td>moderately sloping</td>
<td></td>
<td></td>
<td>alluvium</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Gently to strongly</td>
<td>Dissected</td>
<td>Ustolic Harlarpigns</td>
<td>Alluvium, gravelly alluvium</td>
<td>Shale</td>
<td>171</td>
</tr>
<tr>
<td></td>
<td>sloping</td>
<td>uplands</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
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<td>Upland hills</td>
<td>Aridic Argiustolls</td>
<td>Alluvium</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ridges</td>
<td></td>
<td>Ustolic Torriorthems</td>
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</tr>
<tr>
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<td>Alluvium</td>
<td>Sandstone, shale</td>
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<tr>
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<td></td>
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<td>Sideslopes</td>
<td>Ustolic Harlarpigns</td>
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</tr>
<tr>
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<td>Moderately sloping</td>
<td>Upland hills</td>
<td>Ustolic Harlarpigns</td>
<td>Alluvium</td>
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</tr>
<tr>
<td>7</td>
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<td>Floodplain</td>
<td>Alluvium, gravelly</td>
<td>Shale</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Aridic Argiustolls</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>Gently to strongly</td>
<td>Floodplain</td>
<td>Alluvium, gravelly</td>
<td>Shale</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>sloping</td>
<td></td>
<td>Aridic Argiustolls</td>
<td></td>
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<tr>
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<td>Nearly level</td>
<td>Floodplain</td>
<td>Ustolic Torriorthents</td>
<td>Shale</td>
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<td></td>
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<tr>
<td></td>
<td>Floodplain</td>
<td></td>
<td>Aridic Argiustolls</td>
<td></td>
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</tr>
</tbody>
</table>

Table 3.3 Total quantities of organic carbon (OC) to 1 m, calculated according to the aerial extent of each slope position within each physiographic unit sampled (Yonker et al. 1988).

<table>
<thead>
<tr>
<th>PU</th>
<th>OC total</th>
<th>% of PU total</th>
<th>OC total</th>
<th>% of PU total</th>
<th>OC total</th>
<th>% of PU total</th>
<th>OC total</th>
<th>% of PU total</th>
<th>OC total</th>
<th>% of PU total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>8 ± 1 (4)</td>
<td>2 850 ± 2</td>
<td>6 ± 1 (5)</td>
<td>10 260 ± 8</td>
<td>6 ± 2 (4)</td>
<td>108 096 ± 90</td>
<td>9 ± 3 (6)</td>
<td>2 701 ± 28</td>
<td>4 ± 1 (6)</td>
<td>18 993 ± 72</td>
</tr>
<tr>
<td>2</td>
<td>8 ± 4 (2)</td>
<td>2 196 ± 8</td>
<td>6 ± 1 (1)</td>
<td>1 570 ± 30</td>
<td>6 ± 2 (1)</td>
<td>19 983 ± 72</td>
<td>8 ± 4 (3)</td>
<td>2 570 ± 98</td>
<td>4 ± 1 (8)</td>
<td>16 787 ± 72</td>
</tr>
<tr>
<td>4</td>
<td>9 ± 2 (5)</td>
<td>42 861 ± 40</td>
<td>7 ± 1 (3)</td>
<td>54 855 ± 52</td>
<td>7 ± 2 (5)</td>
<td>44 375 ± 61</td>
<td>6 ± 2 (2)</td>
<td>18 618 ± 51</td>
<td>5 ± 2 (3)</td>
<td>17 618 ± 42</td>
</tr>
<tr>
<td>6</td>
<td>6 ± 2 (2)</td>
<td>3 180 ± 29</td>
<td>5 ± 1 (1)</td>
<td>1 104 ± 10</td>
<td>7 ± 1 (2)</td>
<td>6 580 ± 61</td>
<td>5 ± 3 (3)</td>
<td>16 618 ± 51</td>
<td>4 ± 2 (3)</td>
<td>16 618 ± 51</td>
</tr>
<tr>
<td>9</td>
<td>7 ± 1 (1)</td>
<td>10 540 ± 89</td>
<td>2 ± 1 (1)</td>
<td>1 350 ± 11</td>
<td>11 (1)</td>
<td>18 618 ± 51</td>
<td>2 ± 2 (1)</td>
<td>1 350 ± 11</td>
<td>11 (1)</td>
<td>18 618 ± 51</td>
</tr>
</tbody>
</table>

% of grand total: 25 27 48

Notes:
† Noted only if influential on soil development or behavior.
Figure 3.7 Three-dimensional projection of the CPER with an overlay of physiographic units (Yonker et al. 1988). Grid interval is 400 m.
have benefited substantially from both historical and collaborative research on this topic. Collaboration with the Great Plains project (BSR-8605191) and the ARS has been especially productive.

During LTER I we established that on selected catenas, soil organic matter (SOM), total N and P, and clay content were higher in toeslope positions than in midslope or summit positions (Schimel et al. 1985). This pattern, in part, causes and is caused by higher net primary production in toeslope positions (Section 2.2.1.2). In LTER II, an extensive survey indicated that spatial patterns in SOM are more complex at the site level than the simple catena model could explain (Yonker et al. 1988) (Fig. 3.7, Table 3.2). On many parent material types, fluvial erosion is apparently not the dominant force in redistributing fine soil particles or SOM (Table 3.3). Patterns in SOM and nutrient availability are the result of patterns in parent material and geomorphic control over eolian as well as fluvial movement. We have invested significant effort into understanding the relationships among geologic, geomorphic, and pedologic processes in controlling SOM accumulation (Yonker et al. 1988, Davidson 1988).

In addition to investigations of processes that control current SOM distributions, we have begun to address SOM patterns over long time scales. Approximately 400 pedons have been described at the CPER. Paleosol distribution is extensive; buried soils are found at all landscape positions except the most convex portion of hillslopes. We estimated that as much as 17% of the total soil organic C budget for the site is Holocene "paleocarbon" (Yonker et al. 1988). "Carbon dates for 3 paleosols indicated at least two soil-forming episodes since the end of the Pleistocene (Yonker et al. 1988 Gould et al. 1979). Opal phytoliths extracted from one of the paleosols were representative of tallgrass species (Kelly et al., work in progress). Further evidence of paleoclimatic instability found in an analysis of Holocene sand dunes in northeastern Colorado suggested periodic Holocene drought (Muhs 1985).

Studies during LTER I indicated that patterns in nitrogen availability are concomitant with those in SOM; highest potential and in situ mineralization rates are found in
Figure 3.8 Three-dimensional projections of plant biomass for grazed and ungrazed locations at upland (left panel) and swale (right panel) topographic positions. Data were obtained by removing 49 contiguous soil cores to a depth of 20 cm from 0.25 m² quadrats. Biomass is expressed on an ash-free, dry-weight basis (Milchunas and Lauenroth 1989).
toeslope positions (Schimel et al. 1985). Laboratory and field incubations indicated that highest N-mineralization rates occur in the surface 20 cm of soil, and correspond with periods of high soil-water content (Schimel and Parton 1986). These two studies indicate that N availability is controlled by substrate availability and soil microclimate (Section 2.2.1.2). We are continuing our study of how these controls influence the spatial and temporal patterns of nutrient availability. We initiated a long-term, $^{15}$N tracer study to evaluate the influence of topographic position and grazing on the incorporation of N into active and recalcitrant fractions of SOM, and hence the long-term availability of N (Section 3.2.5).

### 3.1.4 Patterns and frequency of disturbance to the research site.

Most of our disturbance work can be placed into 2 broad categories, large and small spatial scales. The large-scale category deals with recovery of hectare-size areas from a variety of disturbances, ranging from long-term (50 years) heavy grazing by cattle to several years application of water and nitrogen fertilizer (Milchunas et al. submitted). Shortgrass steppe plant communities are less sensitive to grazing than many other grassland types (Milchunas et al. 1988b). In an analysis of plant community structure after 47 years of heavy grazing, we found an increase in basal cover of B. gracilis, a decrease in litter, and interactions among precipitation, grazing, and topography in determining the abundance and patterns of species (Milchunas et al. 1989). Extending the analysis to the response of belowground plant biomass to long-term heavy grazing, we found only small changes in the amount and vertical distribution of belowground biomass, but large differences in the horizontal distribution of biomass (Fig. 3.8) (Milchunas and Lauenroth 1989).

Plant populations at the CPER do not necessarily respond similarly to the same environmental signal (Section 1.1.3). An interesting related question is: Does a plant species respond consistently to environmental signals when growing in different communities? The response of plant communities to water and nitrogen treatments produced a number of different mixtures of plant populations (Lauenroth et al 1978).
Figure 3.9 Population dynamics of *B. gracilis* and *Sphaeralcea coccinea* on a level upland location that received supplemental nitrogen, water, or both from 1971 to 1976.
Whereas some species track environmental signals similarly regardless of different neighbor species (Fig. 3.9), others display time lags in response to abiotic signals modified by the biotic community (Fig. 3.9). Major time lags were also observed with respect to changes in community composition between the treatment period (1970-1976) and the beginning of LTER. In many cases, population changes were greater during the 5 years immediately following the treatments than they were by the end of the 5-year treatment interval.

The second category of disturbance research focuses on the responses of individual plants to disturbances at scales of 0.1 to 10s of m², and uses gap dynamics concepts to explain the response of shortgrass plant communities to disturbances (Coffin and Lauenroth 1989a,b). Simulation analysis of the time required for B. gracilis to recover from a disturbance suggests that the availability of a seed source, the size of the disturbance, the soil texture of the disturbed site, and the weather following the disturbance have important effects on recovery time. A number of our long-term experiments address these issues (Section 3.2.1).

3.1.5 Soil water dynamics

Inputs, storage, and losses of water from soils at the CPER and in semiarid regions in general is of such importance that we chose to make this a separate topic in organizing and reporting our LTER work. We deal with the dynamics of water at the individual plant, patch, and toposequence scales.

At the individual plant scale, we are beginning to collect data on the effects of single individuals of B. gracilis on the availability of water to other plants. At the patch scale, we have relatively long-term (10-15 years) data, and 3-5 years of data at the catena scale.

Patch-scale soil water dynamics are determined by soil hydraulic properties and precipitation patterns. Toposequence-scale soil water dynamics depend on processes and controls at the patch scale as well as on redistribution by overland and subsurface horizontal flows. On most dates, toposequence-scale water dynamics can be treated as a
Figure 3.10 Soil water dynamics at 2 soil depths at ridgetop and swale positions along 3 different toposequences corresponding to 3 different physiographic units at the CPER. The data were collected at 2-week intervals from May-October with a neutron probe.
series of isolated patches (Fig. 3.10). Infrequently, a large or high intensity rainfall event will result in important horizontal flows of both water and material (Fig 3.11).

A new experiment was initiated by the ARS in cooperation with our LTER project to provide information about run-off and run-on of water along catena segments of varying length (Section 3.2.6). This work is beginning to provide information about the conditions required to generate water flows along toposequences and the magnitude of those flows over segments of the slope. Results for 2 rainfall events, one resulting in 86 mm of rain in 1.5 hours and the other producing 40 mm of rain in 8 hours, illustrate the variability in runoff and infiltration that can occur as a function of intensity and duration of rainfall, aspect, and the length of the toposequence segment over which runoff was measured (Fig. 3.11).

3.2 Long-Term Experiments

3.2.1 Effects of and recovery from disturbance

Shortgrass steppe ecosystems are subject to a variety of disturbances, each with a particular temporal and spatial scale. Our definition of a disturbance is broad (e.g., Rykiel 1985) and includes a range of events that reduce changes in ecosystem structure or function. At the smallest spatial scale (Fig. 2.1) we define a disturbance as any event that kills at least one individual of the dominant species, B. gracilis (Coffin and Lauenroth 1988). This definition is based on the following: B. gracilis is the most drought resistant and grazing resistant grass at CPER, and on the basis of productivity and basal cover, it is the dominant plant species for 95% of the research site. B. gracilis has a similar status for most of the 2.8 x 10^5 km^2 of the shortgrass steppe. Additionally, conditions for reproduction of B. gracilis from seed are infrequent. Estimates of return times for reproductive events range from 8 to 100 years (Coffin and Lauenroth 1989b,c). Therefore, any event that kills at least 1 individual of B. gracilis has the potential for a very long-lasting impact on the ecosystem (Coffin and Lauenroth 1989b,c).
Figure 3.11 Quantities of runoff and infiltration for two rainfall events at the CPER. Soil depth increases downslope and is greater on the south than the north slope. The inset indicates the relative position and length of each of the plots.
3.2.1.1 Disturbance experiments

Recovery from additions of water and nitrogen. The temporal dynamics of plant populations and communities have been sampled for 13 years on hectare-size plots that had water and/or nitrogen fertilizer added during the IBP project (Lauenroth and Sims 1976, Lauenroth et al. 1978) (Section 3.1.4). The objectives are to evaluate trajectories and rates of recovery of the vegetation in relation to undisturbed conditions, and to examine stability properties of perturbed and unperturbed grassland in relation to short- and long-term climatic variability.

Effects of Phyllophaga sp. larvae. In 1977, researchers at the CPER observed a large number of patches, ranging in size from 2 to 50 m² (Fig. 3.6) in which all of the individuals of B. gracilis were dead. Investigation implicated root herbivory by Phyllophaga larvae as the cause. An experiment was designed to follow the recovery of 16 grazed-ungrazed pairs of patches. The objective was to investigate the recovery of vegetation and the time required for B. gracilis to dominate each patch. We plan to follow the recovery of these plots for the next several decades.

Small scale disturbance. A field experiment was started in 1984 to evaluate the effects of disturbance size, date, and type on recovery of vegetation from small-scale disturbances (Coffin and Lauenroth 1989d, 1990). Circular plots ranging from 0.2-1.8 m² were cleared of vegetation at 4 times of the year corresponding to times of highest probability of disturbance at a location with fine-textured soil and another with coarse-textured soil. The number of individuals, their size and location have been assessed periodically for each plot. Plant recovery on Western harvester ant mounds (Coffin and Lauenroth 1990) and small animal burrows of different sizes and abandoned at different times of the year have been sampled with methods similar to those used on the manipulated plots.

Cattle fecal pat disturbances. This experiment was begun in 1987 as a result of simulation analyses that indicated cattle fecal deposits may be a substantial source of mortality for B. gracilis (Coffin and Lauenroth 1988). Pats were permanently marked,
mapped, measured, and photographed at 5 locations chosen to represent the variability in topographic position and grazing intensity at the CPER. The number and identity of plants killed by each pat were recorded in the first year. Plant recovery information has been recorded in the subsequent years as well as information about the status of each pat to evaluate its decay over time.

3.2.2 Population dynamics of B. gracilis

A field study was begun in 1989 to evaluate the population dynamics of B. gracilis. Ten locations were chosen to represent a gradient in soil texture and grazing intensity at the CPER. Initial data collection was limited to reproductive effort on an individual plant basis. Number, weight, and height of flowering culms, number of inflorescences, viable seeds, and plant size were collected on an individual basis for 96 plants at each site (Fig. 2.15 and 2.16). Plans for 1990 include establishment of permanent plots at each site for demographic analyses.

3.2.3 Long-term grazing by cattle

Light, moderate, and heavy grazing treatments and ungrazed exclosures were established at the CPER in 1939 and have been maintained (Kipple and Costello 1960, Milchunas et al. 1989). The treatments have a long history of observation ranging from arthropod and vertebrate population dynamics, plant community structure and productivity, to cattle weight gain and applied range management practices. Currently, the grazing treatments are central to our research on plant-animal interactions, gap-dynamics modeling (Section 3.10.2), soil organic matter turnover, and nutrient cycling (Section 3.1.3). The plant-animal interaction work has: (1) examined plant community composition in relation to grazing, landscape structure, and precipitation, and has established a long-term sampling protocol (Milchunas et al. 1989); (2) assessed effects of grazing on the horizontal and vertical distribution of plant biomass across topographic gradients (Milchunas and Lauenroth 1989); (3) compared grazing treatments to other large-scale disturbances in terms of successional status and stability (Milchunas et al. submitted); and (4) developed a global-scale conceptual model of the effects of grazing on
grassland community structure (Milchunas et al. 1988). Work in progress includes effects of grazing on demography of opportunistic species, and ANPP and water- and nitrogen-use efficiency (Sections 1.1.5 and 3.1.4).

3.2.4 Belowground net primary production and carbon dynamics

Our objectives for this work are to assess litter, crown, root, and soil carbon turnover by \(^{14}\)C dilution (Milchunas et al. 1985), \(^{14}\)C turnover, and harvest (Figs. 3.3 and 3.4). In addition, we are examining the incorporation of carbon into soil organic matter, and its interactions with micro- and macro-soil aggregates. Eight plots (9 m\(^2\)) were labeled with \(^{14}\)CO\(_2\) in 1985. The plots have been sampled on 11 dates over the past 5 years. Sampling will continue annually for the next several years then change to 5-year intervals (Section 3.1.1).

3.2.5 Nitrogen turnover

We began a long-term, landscape-scale experiment in 1987 to investigate nitrogen turnover (Section 3.1.3). The design included a large addition of \(^{15}\)N to paired plots on either side of a grazed-ungrazed boundary that traverses 3 ridgetops and lowlands. Periodically, we sample for N distribution in above- and belowground plant biomass, and in several soil pools (total N, available N, and microbial biomass). Long-term laboratory incubations of soils collected from the plots allow us to track the partitioning of \(^{15}\)N among labile and recalcitrant soil organic matter pools (Section 3.1.3). Because a large amount of \(^{15}\)N was added to the plots, we can continue to collect data for up to 30 years.

3.2.6 Hydrology

The objective of the hydrology research being conducted by the Hydro-Ecosystem Research group of the ARS at CPER in cooperation with the CPER/LTER project is to validate a spatially explicit hydrologic simulation model for a semiarid grassland, and to provide long-term observation of hillslope hydrologic processes. The research involves both natural runoff plots and rainfall simulation studies (Section 3.1.5).

The field experiment is designed to sample 2 dissimilar toposequences to represent much of the variability of soil properties at the CPER. Since the soils are not uniform
and slopes are quite variable, runoff, infiltration, and soil water are also variable. Runoff can be produced at upper slope positions and infiltrate at lower slope positions so that although runoff reaching the bottom of a hillslope is minor, substantial redistribution of water may occur (Section 3.1.5). To characterize the spatial patterns of run-off, run-on, infiltration, and resulting soil water dynamics, we are using 2 series of successively longer microwatershed plots with automated instrumentation (Fig. 3.11). This approach, which allows us to estimate process rates in each of four slope segments without isolating each segment from upslope influences, is probably unique internationally. Four rain gages and a complete micromet station are located within the hydrology experiment area. Observations of natural rainfall events are being supplemented with simulated rainfall events using small (22 by 7 m) plots representing individual slope segments.

3.2.7 Wind erosion patterns and rates

The objective of this work is to determine the prevailing direction, rates of movement on various slope elements, and temporal distribution of sediment transport. Forty-eight BSNE (Big Spring Number Eight) wind-born-sediment samplers have been deployed adjacent to the hydrology plots. The samplers have been in place since summer 1985. They are installed at three heights and are located on different slope elements and aspects. Two sets are installed at each location to evaluate precision at a station.

3.3 Long-Term Data Sets

The CPER/LTER long-term data sets include data collected during the 8 years of LTER as well as data collected by CSU and ARS researchers prior to the beginning of LTER (Table 3.4). A goal for data management at the start of the CPER/LTER project was to recover as much of the previous data as possible. The constraint on this activity was that the data be sufficiently well documented so that we could clearly define its quality and utility.

Most of the previous data in the CPER/LTER data management system were collected during the 1970s under IBP funding. In most cases, it was possible to contact the person who collected the data before incorporating them into the data system.
Table 3.4. CPER/LTER Data Sets. Belowground temperature data include minimum, maximum and average soil temperatures at 8 depths. The CR-21X weather data are precipitation amounts measured on 15 minute intervals. The hygrothermograph data are standard strip chart data. Historical weather data are records from standard weather stations. The CPER Standard Weather data supplement, historical weather data by including minimum and maximum pan evaporation, wind travel, and solar radiation in addition to minimum and maximum air temperatures, wet and dry bulb temperatures, and precipitation measurements.

Aboveground herbage data include estimated and clipped plot biomass values by species assigned to categories of live, recent dead, and old dead. Aboveground and belowground invertebrate data include numerical density and biomass estimates by species-life stage for invertebrates. Mammal data are from small mammal trapping studies, and include numerical and biomass estimates by species. Avian data are census information by species. Decomposition data are results from litter bag experiments for surface and subsurface decomposition. Litter data are estimates of litter biomass and litter production. The phenology data list phenological stage by species. Soil water estimates are available from the CPER lysimeter, from gravimetric measurements, and from neutron probe measurements.

### LTER Data Sets

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<th>Data Type</th>
<th>Description</th>
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<tr>
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<td>Field data, English units: 1971-1988</td>
</tr>
<tr>
<td></td>
<td>Summary data, metric units: 1971-1988</td>
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<td>Summary output tables: 1971-1988</td>
</tr>
<tr>
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<td>(Data descriptions for all data sets)</td>
</tr>
<tr>
<td>CPER CR-21X Weather Data</td>
<td>Summary daily data: 5/30/86-1989</td>
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<tr>
<td></td>
<td>Summary hourly data: 5/30/86-1989</td>
</tr>
<tr>
<td></td>
<td>Summary 15-min data: 5/30/86-1989</td>
</tr>
<tr>
<td></td>
<td>(Data descriptions for 86-88 data sets)</td>
</tr>
<tr>
<td>Hygrothermograph Data</td>
<td>Ale field data: 1971-1972</td>
</tr>
<tr>
<td></td>
<td>Bridger field data: 1972</td>
</tr>
<tr>
<td></td>
<td>Osage field data: 1971</td>
</tr>
<tr>
<td></td>
<td>Pantex field data: 1972</td>
</tr>
<tr>
<td></td>
<td>CPER field data: 1970-1981</td>
</tr>
<tr>
<td></td>
<td>CPER daily max/min data: 1983-1985</td>
</tr>
<tr>
<td></td>
<td>(Data descriptions - none)</td>
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<tr>
<td>Historical Weather Data</td>
<td>Cheyene data: 1969-1974</td>
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<tr>
<td></td>
<td>CPER precipitation data: 1940-1970</td>
</tr>
<tr>
<td></td>
<td>CPER temperature data: 1948-1970</td>
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<td></td>
<td>CPER weather data, English units: 1940-1973</td>
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<td></td>
<td>CPER weather data, metric units: 1940-1973</td>
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<td></td>
<td>Grover precipitation data: 1937-1966</td>
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<tr>
<td></td>
<td>Grover temperature data: 1946-1967</td>
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<td></td>
<td>Kauffman precipitation data: 1937-1966</td>
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<td></td>
<td>Kauffman temperature data: 1945-1967</td>
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<tr>
<td></td>
<td>ARS rain gauge data: 1940-1968</td>
</tr>
<tr>
<td></td>
<td>(Data descriptions - none)</td>
</tr>
</tbody>
</table>

| **ABOVEGROUND HERBAGE**          |                                                                             |
|                                 | EPA field data: 1977-1978                                                   |
|                                 | CPER field data: 1969-1978                                                  |
|                                 | CPER summary data: 1969-1978                                                |
|                                 | (Data descriptions for most CPER field data sets)                           |

| **ABOVEGROUND INVERTEBRATES**    |                                                                             |
|                                 | Ale field and summary data: 1972-1973                                       |
|                                 | Bridger field data: 1972                                                    |
|                                 | Cottonwood field and summary data: 1970-1972                               |
|                                 | EPA field and summary data: 1974-1977                                       |
|                                 | Jornada field and summary data: 1970-1972                                   |
|                                 | Osage field and summary data: 1970-1972                                     |
|                                 | Pantex field and summary data: 1970-1972                                    |
|                                 | CPER field and summary data: 1970-1974                                      |
|                                 | San Joaquin field and summary data: 1973-1974                               |
|                                 | (Descriptions for most CPER field data sets)                                |

| **AVIAN**                       |                                                                             |
|                                 | Ale field data: 1970-1973                                                   |
|                                 | Cottonwood field data: 1970-1974                                            |
|                                 | Jornada field data: 1970-1972                                               |
|                                 | Osage field data: 1970-1975                                                 |
|                                 | Pantex field data: 1970-1972                                                |
|                                 | CPER field data: 1968-1973                                                  |
|                                 | (Data descriptions - none)                                                  |

| **BELOWGROUND HERBAGE**          |                                                                             |
|                                 | EPA field data: 1978                                                       |
|                                 | CPER field and summary data: 1970-1977                                     |
|                                 | (Data descriptions - none)                                                 |

| **DECOMPOSITION**               |                                                                             |
|                                 | EPA field data: 1976-1976                                                   |
|                                 | CPER summary data: 1971-1972                                                |
|                                 | (Data descriptions - none)                                                  |

| **LITTER**                      |                                                                             |
|                                 | EPA field data: 1977-1978                                                   |
|                                 | CPER field and summary data: 1969-1976                                     |
|                                 | (Data descriptions - none)                                                  |

| **MAMMAL**                      |                                                                             |
|                                 | Bison field data: 1970                                                     |
|                                 | Bridger field data: 1970                                                    |
|                                 | Cottonwood field data: 1970                                                 |
|                                 | Dickson field data: 1970                                                    |
|                                 | Jornada field data: 1970                                                    |
|                                 | Nevada field data: 1970                                                     |
|                                 | Osage field data: 1970                                                      |
|                                 | Pantex field data: 1970                                                     |
|                                 | (Data descriptions - none)                                                  |

| **PHENOLOGY**                   |                                                                             |
|                                 | Cottonwood field data: 1970, 1972                                           |
|                                 | EPA montana field data: 1975-1977                                           |
|                                 | CPER field data: 1972-1977                                                   |
|                                 | (Data descriptions for all CPER data sets and for most EPA data sets)        |
Table 3.4 (Continued)

<table>
<thead>
<tr>
<th>Category</th>
<th>Description</th>
<th>Dates</th>
</tr>
</thead>
<tbody>
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<td>CPER field and summary data (Data descriptions - none)</td>
<td>1970-1975</td>
</tr>
<tr>
<td>SOIL MICROARTHROPODS</td>
<td>CPER field and summary data (Data descriptions - none)</td>
<td>1971-1975</td>
</tr>
<tr>
<td>SOIL WATER - LYSIMETER</td>
<td>CPER field and summary data (Data descriptions - none)</td>
<td>1972-1978</td>
</tr>
<tr>
<td>SOIL WATER - MICROWATERSHED</td>
<td>CPER field and summary data (Data descriptions - none)</td>
<td>1969-1978</td>
</tr>
<tr>
<td>SOIL WATER - NEUTRON PROBE</td>
<td>CPER field data (Data descriptions - none)</td>
<td>1978-1988</td>
</tr>
<tr>
<td>VEGETATION</td>
<td>CPER field data (Data descriptions - none)</td>
<td>1983</td>
</tr>
</tbody>
</table>

LTER Data Sets
3.4 Data Management

The goal for data management is to store the data in a historically accurate, secure, and retrievable form. Data collected using field forms are entered and verified by a professional keypunch operator. Data collected electronically and recorded on computer-accessible media are transferred to UNIX computer systems for entry into the archives. When possible, data are checked for validity using special purpose programs. The final step in quality assurance is to ask the investigator to check and verify the data.

Our approach to assure the data will be available 10, 20, or even 100 years from now is to store the data redundantly on 4 different types of media: (1) hard disk on a Sun workstation for easy and fast access, (2) standard nine track tapes, (3) high-density 8-mm cartridges, and (4) original data forms are copied to microfilm for long-term storage. Copies of the 8-mm cartridges and the microfilm are stored in 2 different buildings. In addition, we plan to move a copy of the data to optical disk in the near future.

Data are stored as sequential access ASCII files because this is a standard format expected to be used over the next several decades. The physical format of the magnetic tapes is likely to become obsolete over the next decade as media densities increase. However, disks and tapes are rewritten every 2-3 years to avoid deterioration of the media. Changes in storage technology will be accommodated as required.

The sequential access format ensures long term access to data, but is more difficult to use than a relational (or other) database. Our solution to this problem is to provide support between primary data files and investigators that consists of programmers and a collection of software tools to access and format data. These tools rely on a set of data file descriptions that can be read by humans and computer programs. The data descriptions are one of the most important products of the project. These descriptions document the format for data, default variable names for each data field, the type (real, integer, alphanumeric, or logical) of the field, its location in the data record, and a description of the variable. Data descriptions also contain information about who
collected the data, who to contact for access to the data, problems or other notes, such as other sources of documentation.

Our software tools can read data descriptions and generate either new file formats or code for specialized programs. For example, the current software can read the data description, extract selected data, and create an ASCII format that is easily read by PC spreadsheet or database programs, or a binary format that can be read using locally produced graphics software. Another tool reads the data description and produces a file for input to the UNIX 'troff' formatting system. The output from 'troff' produces a typeset quality data summary.

The CPER/LTER data management staff consists of a Ph.D. level scientist, T.B. Kirchner, and a professional programmer. Dr. Kirchner provides direction for the data management effort. Dr. Kirchner is also involved in our simulation modeling activities.

3.5 Synthesis and Modeling

Scientists associated with the CPER/LTER project have been involved in a number of important synthesis activities over the 8 years of the project. Some of these are in the form of work in progress, while many are specific products that are refereed publications or book chapters. These are described briefly below. Publications from CPER/LTER are listed in Appendix 1.

3.5.1 Products

3.5.1.1 Shortgrass region

Lauenroth and Milchunas 1990.

This book chapter is a synthesis of scientific information about the shortgrass steppe in North America. Major topics addressed include climate, vegetation, heterotrophs, and landuse management. It brings together in a single source most of the available information published before the beginning of the CPER/LTER project in 1982.
3.5.1.2 Grazing behavior


This paper was initiated with a meeting held at the CPER and organized by the LTER project. It resolves grazing research conducted at the CPER with optimal foraging theory and hierarchy theory.

3.5.1.3 Plant community response to grazing

Milchunas et al. 1988b.

The relatively small response of shortgrass plant communities to long-term heavy grazing by cattle was the motivation for this paper. This paper unifies and extends existing concepts of plant community responses to disturbance and provides a framework for reconciling contradictory results from grazing studies on a global basis.

3.5.1.4 Soil organic matter: theory and regional analysis


Soil organic matter is the major source and the best single indicator of ecosystem stability in the central grassland region. These 3 papers blend theory, data, and simulation modeling to disentangle the complex patterns and controls on SOM in grassland soils.

3.5.1.5 Regional primary production

Sala et al. 1988b.

This paper draws upon the same regional database as the soil carbon papers and addresses a related issue, patterns and controls on primary production evident at the scale of the central grassland region. Annual precipitation and soil texture were identified as the major controls on production.

3.5.1.6 Recovery of grasslands from disturbance: theory

Coffin and Lauenroth 1989a.

Past successional concepts for the shortgrass steppe were the result of research using the old-field conceptual model (Fig. 2.11). This paper describes an individual-based gap
model in which recruitment, growth, and death of individual plants is controlled by interactions for belowground resource space. The model resolves a number of problems inherent in the old-field approach.

3.5.1.7 Scaling site-process information to regions

Burke et al. (in press).

This paper was motivated by a spatially explicit issue associated with scaling information developed at a single site--the CPER--to a region. It involved running a simulation model using a GIS database of input variables to produce aggregate process information for a region.

3.5.2 Work in progress

We have a number of synthesis projects that are being actively worked on during the final year of LTER II. Each involves the use of or development of a simulation model to compare ecosystem dynamics across a two or more sites. We chose to list these under the topic of synthesis and modeling to draw attention to our activities in simulation.

With funding from NSF, W.K. Lauenroth, W.J. Parton, D.P. Coffin, and T.B. Kirchner are working with colleagues at the University of Virginia and Kansas State University to use combine individual-based models of vegetation with soil process models to compare the dynamics of forest and grassland ecosystems (Section 3.7.8). We recently received supplemental funding to begin a large inter-LTER site modeling comparison using the same set of models. W.K. Lauenroth and D.P. Coffin are working on a grassland-alpine comparison using the CPER and Niwot Ridge LTER sites as sources of data.

I.C. Burke received funding from the LTER supplemental program to begin a regional analysis effort that included simulation study of the 1988 drought in the central Great Plains. This work involves comparisons of simulated ecosystem variables in the drought year with the same simulated variables in an average year, 1986, and with integrated NDVI (Sections 1.1.6 and 3.10.3).
3.6 **Intersite and Network Activities**

Researchers associated with the CPER/LTER have been prominent participants in intersite and network activities. These have included intersite research and syntheses with LTER and non-LTER sites as well as a variety of LTER network activities.

3.6.1 **Intersite research and synthesis**

3.6.1.1 **LTER sites**

W.K. Lauenroth and W.J. Parton have an NSF-funded research project in collaboration with H.H. Shugart at the University of Virginia to use simulation models to analyze plant community structure across resource gradients from grassland to forest. Six LTER sites, CPER, Konza, Hubbard Brook, Andrews, Niwot, and Coweeta represent the locations at which the models will be tested. The objectives are to evaluate controls on dynamics of vegetation structure in grasslands, in forests, and in the transition zone between forests and grasslands, and to compare the responses of the vegetation at 5 LTER sites to climatic change. This research is partially supported by the CPER/LTER grant.

D. S. Schimel and W. P. Parton have a longstanding intersite research program with the Konza LTER. Process representations in the CENTURY model developed from experiments at the CPER were tested at Konza. Most recently, the NASA EOS (Appendix 3) project is focusing on remote sensing of surface biophysical properties across a transect that crosses the CPER and Konza. This project will contribute significantly to our understanding of the fundamental similarities and differences between shortgrass steppe and tallgrass prairie, and will provide invaluable remotely sensed data and analysis.

An intersite project involving D. O. Doehring (CPER) and T. Ward (Jornada) began in 1988 with objectives of comparing rates, prevailing transport directions, and temporal distributions of sediments between the 2 LTER sites. Eight BSNE samplers from the CPER were moved to the Jornada where they were supplemented by an additional 6 samplers. This work is being supported by the LTER grants at each site.
Figure 3.12 Results from a factor analysis of seasonal deviations of NDVI. Ten factors explained 97% of the spatial and temporal variability in NDVI. Four factors, each explaining 10% of the variability, were the most important and were used to group grid cells. (a) Factor grouping of U.S. grid cells for the 4 most important factors and 3 other factors that had high loadings on a few cells. When 2 symbols are shown, the upper left one indicates the dominant factor. Cells marked "0" were omitted from the analysis because of lack of corresponding precipitation data. (b) Factor time series (factor scores) for the first 4 factors.
D.E. Hazlett initiated a network-wide comparison of exotic species in the flora of each LTER site. The objective is detection of differences in vulnerability to invasion by exotic plant species of a variety of ecosystem types. This work is being supported by the CPER/LTER grant.

T.G.F. Kittel and W.K. Lauenroth initiated a continental-scale analysis of ecosystems using normalized difference vegetation index (NDVI) data as a correlate of function. An objective of this analysis was to evaluate how well LTER sites represented the region of which they are a part. The results suggest that interannual ecological variability at LTER sites may represent a large portion of the variability at a regional scale (Fig. 3.12).

### 3.6.1.2 Non-LTER sites

Our results are most applicable to sites that are close to the CPER with similar climatic conditions and for similar vegetation structure. Our interest in applying our knowledge at broad scales has lead us to spend considerable effort on non-LTER intersite work in either the proximity of the CPER (Burke et al. 1990), the shortgrass steppe region (Lauenroth et al. 1986), or the central grassland region (Sala et al. 1988b, Burke et al. 1989). We have a continuing effort in regional analysis that began with supplemental funding during LTER II and will continue as part of the core program in LTER III (Section 3.10.3).

D.P. Coffin and W.K. Lauenroth recently initiated a cooperative project with the U.S. Forest Service to evaluate the present status of agricultural land abandoned in the 1920s and 30s that is currently managed by the Forest Service as part of the Pawnee National Grasslands. The objective of this work is to test successional concepts developed as part of the CPER/LTER project (Coffin and Lauenroth 1989a,b). This work will be funded by the Earthwatch Foundation.

### 3.6.2 Network activities

In addition to active participation in Coordinating Committee meetings, W.K. Lauenroth has been a member of the LTER Executive Committee for the past 2 years. The Executive Committee meets 4 times each year, twice with the Coordinating
Figure 3.13 Geographic information system training workshop. Dana Tomlin provided an introduction to GIS by discussing the potential ecological applications.
Committee and twice in Washington, DC with the NSF-BSR staff. CPER/LTER scientists have been active in workshops and meetings organized by other LTER-site scientists as well as in organizing workshops. W.K. Lauenroth organized a meeting of LTER simulation modelers in 1989. The objectives were to assess the current status of modeling in the network, to initiate a dialogue among simulation modelers, and to discuss the potential for using simulation models in cross-site comparisons. The most important outcome to date is an LTER poster session, organized by W.K. Lauenroth, to be held at the 1990 ESA meeting. The theme of the session is simulation models for cross-site analysis.

I.C. Burke organized a two-week geographic information system (GIS) workshop at Colorado State University in 1989 (Fig. 3.13). The objective of the workshop was to introduce LTER scientists to GIS concepts, potential ecological applications, and software training. Each LTER site sent at least one representative. Table 3.5 contains a summary of the evaluations of the workshop participants.

W. J. Parton and D. S. Schimel are working on a SCOPE international grassland modeling project in which the objective is to adapt the CENTURY model to grasslands around the world. We are currently testing the model using intensive site data from 16 grassland sites. The sites range from tropical grasslands in Kenya, Mexico, and West Africa to temperate grasslands in the U.S. and USSR.

### 3.7 Related Research Projects

In addition to the research at the CPER, the personnel associated with the project represent a critical resource defining our capabilities. The research effort represented by project personnel far exceeds the work being conducted under LTER funding. The scope of work related to the CPER/LTER is broad, encompassing individual organism, population, community, ecosystem, and regional levels. The technical issues are complex, including integrative modeling, measurement of trace gas emissions, geographic information systems, and remote sensing analysis. The collection of related research projects listed below and described in Appendix 3 defines our ability to address issues
### Table 3.5. LTER-GIS Workshop Evaluations

<table>
<thead>
<tr>
<th>Category</th>
<th>Rankings</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Overall workshop organization and content.</td>
<td>E = 22, G/E = 2, G = 2</td>
</tr>
<tr>
<td>2. Introduction to GIS concepts and ecological application. Dana Tomlin.</td>
<td>E = 20, G/E = 1, G = 5</td>
</tr>
<tr>
<td>3. ARC/INFO training.</td>
<td>E = 0, G/E = 3, G = 9, G/F = 1, F = 12, F/P = 1</td>
</tr>
<tr>
<td>4. ERDAS training.</td>
<td>E = 5, G/E = 1, G = 1, F = 3</td>
</tr>
<tr>
<td>5. Evening presentations.</td>
<td>E = 5, G/E = 1, G = 17, F = 1</td>
</tr>
<tr>
<td>6. Meals, accommodations.</td>
<td>E = 16, G = 8, G/F = 1</td>
</tr>
<tr>
<td>7. Training facility, technical support staff.</td>
<td>E = 22, G/E = 3, G = 1</td>
</tr>
</tbody>
</table>
across a broad range of scales. Additionally, a proposed regional science and technology center, CADRE, if funded, will provide an important organizing force for integration of CPER/LTER research into a regional context.

1. Center for Analysis of the Dynamics of Regional Ecosystems (CADRE).
2. Controlled Environment Climate Change Study (CO₂).
5. Trace Gas Project (T GAS).
11. Earth Observing System (EOS).
12. Land Surface-Climatology Interactions (FIFE).

The abbreviations in the list are keyed to the project groups and topics in Table 3.7.

3.8. Archives and Inventories

The CPER/LTER herbarium contains 650 mounted specimens, representing 3/4 of the known species at the CPER. An annotated plant checklist of 284 species from 53 families includes information on lifeform, origin, photosynthetic pathway, and habitat. Both have been substantially updated during LTER II. An extensive microarthropod reference collection for the CPER is stored at CSU. There are 3 soil surveys for the site: (1) SCS Northern Weld County (1:2400) covering the entire site, (2) IBP soil survey (1:4800) covering the northwestern 1/4 of the site, and (3) an 8-km LTER soil transect (1:2400) at a high sample frequency, that includes SOM and texture. A new SCS soil survey will be conducted in summer of 1990 to improve our current maps.

Plant samples from the long-term N and NPP monitoring, and root and soil samples from the long-term ¹⁴C study are archived for future analyses.

The site bibliography was updated in 1989, and includes sections for journal articles, technical reports, theses, dissertations, and abstracts of talks. The portion of the site bibliography that corresponds with the LTER project is included as Appendix I.
3.9 Leadership, Management, and Organization

The CPER/LTER project is a joint effort between CSU and ARS. Three departments at CSU are involved, Range Science, Forest and Wood Science, and the Natural Resource Ecology Laboratory. Project direction is 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 continue to have overall responsibility for project management. I.C. Burke (CSU-Forest and Wood Science), a new Co-PI, will share management responsibility. She will expand her current role as an investigator to include project leadership.

Two PIs on the project, J. Van Schilfgaarde and J.R. Forwood, represent ARS. The Research Leader (RL) for the ARS Great Plains Systems Group has traditionally been a Co-PI and an integral part of the CPER/LTER project. Dr. J. Welsh has recently accepted the Research Leader position and, when he arrives, he will be a Co-PI on the project. Until his arrival, Dr. Van Schilfgaarde will be Co-PI. J.R. Forwood is the ARS Scientist-in-Charge of the CPER, and will function as a Co-PI on LTER III.

Our approach to project management involves significant attention to team dynamics at the leadership and project scientist level. An important member of our project is Dr. J.E. Hautaluoma, a management scientist. Dr. Hautaluoma meets with the PIs and scientific staff for all regular meetings, and provides help in goal setting, leadership, team-building, and conflict resolution.

LTER I and II research has been highly integrated, maximizing cooperation and communication among scientists involved in the LTER project and in related research projects (Section 3.7). This extended group meets twice monthly in an informal seminar format to share ideas and progress. The major project subgroups (Table 3.6) meet regularly and frequently. The CPER/LTER project will continue to receive substantial support from CSU, the College of Forestry and Natural Resources, and the participating departments. The Vice-President for Research has supported the project by agreeing to a
<table>
<thead>
<tr>
<th>Group Name</th>
<th>CPER Scientists</th>
<th>Non-CPER Scientists</th>
<th>Related Projects</th>
</tr>
</thead>
<tbody>
<tr>
<td>Climate/Microclimate</td>
<td>W.K. Lauenroth, O.E. Sala, I.C. Burke, W.J. Parton</td>
<td>H.W. Hunt, W.J. Doesken, T.G.F. Kittel</td>
<td>NADP, ARS, LTER Coordinating Committee, CO₂</td>
</tr>
<tr>
<td>Atmosphere/Biosphere</td>
<td>D.S. Schimel, W.J. Parton, I.C. Burke</td>
<td>T.G.F. Kittel</td>
<td>FIFE, EOS, TGAS</td>
</tr>
<tr>
<td>Geomorphology/Hydrology</td>
<td>D.O. Doehring, D.G. Decoursey, E.F. Kelly, C.M. Yonker, D.S. Schimel</td>
<td>E. Wohl</td>
<td>CSU Experiment Station, L.L. Tieszen, ARS</td>
</tr>
<tr>
<td>Data Management</td>
<td>T.B. Kirchner, W.K. Lauenroth, I.C. Burke</td>
<td>P.W. Snook</td>
<td></td>
</tr>
<tr>
<td>Modeling</td>
<td>D.P. Coffin, W.K. Lauenroth, W.J. Parton, J.D. Hanson, O.E. Sala, D.G. Decoursey, T.B. Kirchner</td>
<td>H.W. Hunt, M.B. Coughenour</td>
<td>CSU/UVA, DOE, CO₂, ARS</td>
</tr>
<tr>
<td>GIS/Remote Sensing</td>
<td>I.C. Burke, R.M. Hoffer, J.D. Hanson, P.W. Snook, D.S. Schimel</td>
<td>T.G.F. Kittel</td>
<td>JFREA, EOS, FIFE, ARS</td>
</tr>
<tr>
<td>Regional Analysis</td>
<td>D.P. Coffin, I.C. Burke, W.J. Parton, D.S. Schimel, R.M. Hoffer, P.W. Snook, J.D. Hanson, W.K. Lauenroth, R.G. Woodmansee</td>
<td>M.B. Coughenour, T.G.F. Kittel</td>
<td>CADRE, GRP, ARS, FIFE, EOS, DOE, SOC.</td>
</tr>
</tbody>
</table>
large reduction in the overhead rate and the departments will return their share of indirect costs directly to the project.

With the initiation of LTER III, we will be adding several new investigators to our research team. J.R. Forwood of the ARS is a range scientist with expertise in grazing behavior and forage quality. J.K. Detling (CSU-Range Science) will expand our ongoing research program in plant and ecosystem responses to grazing. B. Van Horne and J. Wiens (CSU-Biology) will develop new efforts to establish long-term data collection on small mammal and bird activity. R.M. Hoffer (CSU-Forest and Wood Science) will lead a new remote sensing program for the CPER. E.F. Kelly (CSU-Agronomy) will initiate paleoecological research at the CPER.

3.10 New Projects and Technologies

The CPER/LTER project continues to pursue the implementation of new research tools. We are using state-of-the-art technologies in all 3 major research areas, field research, synthesis and modeling, and spatial analysis, to address questions of long-term and regional relevance. Our successful application of these new tools puts us in a leadership role in the LTER network (Section 3.5).

3.10.1 Field analysis

During LTER II, we started 2 new long-term field experiments (Sections 3.1.1, 3.1.3, 3.2.4 & 3.2.5) that address the distribution and turnover of C and N in plants and soils. Both experiments use isotope dilution to estimate long- and short-term nutrient turnover rates. The $^{14}$C experiment has resulted in a new technique for estimating belowground production, and the $^{15}$N experiment in new methods for partitioning soil nitrogen into active, intermediate, and stable fractions.

3.10.2 Simulation modeling

Current ecosystem simulation models can be categorized as either process or structure models. Process models attribute cause in ecosystem responses almost entirely to processes with little importance attributed to system structure (Parton et al. 1988). Models of ecosystem structure tend to represent the opposite conceptualization (Shugart
Figure 3.14 Description of the map files for the CPER/LTER site geographic information system.
We plan to construct a new class of simulation models that will bridge the process-structure dichotomy, and allow us to address questions about 2-way interactions between processes and structures in ecosystems. These new models will combine concepts associated with individual-based models of plant dynamics (Coffin and Lauenroth 1989b) with models of ecosystem processes (Parton et al. 1987).

3.10.3 Hierarchical GIS and regional simulation modeling

3.10.3.1 Site Level

Through the supplemental funding program, we have begun to develop a hierarchical spatial database organized and stored in a GIS (Fig. 3.14). The database contains long-term, site-level spatial databases on natural features (soils, geomorphology, drainages, elevation, and vegetation), artificial features (fences, buildings, roads), and location of experiments into a multi-layered GIS using the ARC/INFO software system in the Joint Facility for Regional Ecosystem Analysis (Section 3.10). We are beginning to use the site-level GIS as a tool for spatial pattern analysis and for location and management of experiments. We have also begun to implement a program of continuous site monitoring through aerial photography and satellite imagery analysis. We have a historical set of aerial photos of the site that we are beginning to analyze using our ERDAS image analysis system. These data will be part of the site GIS library.

In 1989 we purchased Landsat TM imagery for the site and surrounding area. We obtained 2 types of 1985 TM data for initial analysis, an inexpensive print of a full TM scene (185 x 185 km) that covers much of northeastern Colorado, and digital data for a 15 x 15-km area centered on the CPER. We completed a test on the print and have been successful in scanning and analyzing it with ERDAS and classifying it into landuse categories (Fig. 1.8). This analysis provides us with a relatively inexpensive method of monitoring simple changes in landuse in a large area surrounding the site. In addition, we are using the digital TM data to classify the local region into landuse categories, to estimate productivity, and quantitatively estimate the representativeness of the CPER.
3.15 Description of the map files for the CPER/LTER regional geographic information system.
within the local region. We hope to regularly obtain both types of TM or other satellite data in the future. Classified images will be transported into our site GIS database.

3.10.3.2 Regional level

A key challenge for LTER sites is the extrapolation of site-specific information to regions. Toward that end, we have begun a program of regional analysis, integrating simulation models and GIS. We have obtained soils and climate data for the plains region of Colorado, Nebraska, and Kansas, and have entered these data into our CPER/LTER regional GIS (Fig. 3.15). Simulation studies have been conducted on a portion of the parameter space as a test of technology and concepts (Burke et al. 1989) (Section 3.5.1.7). Current work includes simulation of climate change scenarios for the central Great Plains and comparison of results with satellite imagery (AVHRR).

3.10.4 Remote sensing at the continental scale

In addition to regional analysis of grasslands, we are using remotely sensed data to evaluate temporal and spatial variation in ecosystem function at a continental scale. Variation in AVHRR data for 5 years suggests that biomes within the continent tend to respond coherently to seasonal and interannual variation in climate. These results have implications for the LTER network, suggesting that individual sites within biomes may indeed represent biome-wide temporal trends in ecosystem responses to climatic variation. This work is being supported by a Coordinating Committee grant (Section 3.6.1.1).

3.10.5 New projects for LTER III

In a new initiative for LTER III, we are beginning an evaluation of the interactions between soil texture and land use as they control ecosystem structure and function. This project will address all 5 core areas, and expand upon our current application of our 3 major research tools through: (1) a field evaluation of the interactions between soil texture and land use history as they influence the turnover of soil organic matter, water and nutrient availability, and plant species and lifeform composition; (2) simulation of the influence of soil texture and land use history on ecosystem structure and function; and (3) regional extrapolation and analysis of the interactions between land use, soils, and
ecosystem status. Detailed description of this new research initiative is described in Section 2.3.

We will use several new technologies for studying texture-landuse interactions in the field. We will study the effect of soil texture and precipitation on temporal dynamics of soil water using time domain reflectometry (Topp and Davis 1982) (Section 2.3.1). We will use two new methods to estimate belowground primary production across a gradient of soil textures and landuse histories. We will apply carbon isotope turnover techniques to estimating average belowground production over a several-year period using the stable C isotope, $^{13}\text{C}$ (Section 3.1.1). In addition, we will acquire minirhizotrons for assessment of short-term dynamics of roots (Taylor 1987). Finally, we will use soil resin cores for measurement of seasonal dynamics of in situ net nitrogen mineralization (Binkley 1984).

3.11 Dissemination of Information

Individuals associated with the CPER/LTER project regularly interact with a variety of groups and media to communicate our research results to the public. The total number of contacts in the past 8 years is too numerous to mention all of them. We will limit ourselves to a few examples.

3.11.1 Conservation groups

D.E. Hazlett, the CPER/LTER site manager frequently leads field trips for the Colorado Native Plant Society. D.G. Milchunas recently lead a field trip to the CPER for the Northern Colorado Chapter of the Sierra Club.

3.11.2 Newspapers

The Office of University Communications regularly releases bulletins about work conducted under the CPER/LTER project. In 1989, the Denver, Greeley, and Fort Collins newspapers have run feature articles about the research site.

3.11.3 Radio and television

The Office of University Communications produced short radio and television features on the CPER/LTER project in 1989. Radio programs are released state-wide and television programs are released to the major Denver stations. A short piece on the
LTER project was shown on the evening news on both the NBC and ABC station affiliates in the fall of 1989. We made special arrangement for Denver television stations and newspapers to cover a visit to the site by T. Lovejoy to discuss the climate change implications of our research. This resulted in both prime-time television and newspaper coverage of the project.

3.11.4 Other media

The Colorado State University magazine, which is distributed to all alumni, produced a feature article on the Pawnee National Grasslands in 1989. They drew heavily upon the CPER/LTER project for information for the article.

Pruett Publishing Co. published a book by R. C. Cushman and S. R. Jones entitled "The shortgrass prairie" in 1988. Ms Cushman, who wrote text to accompany Mr. Jones' photography, used CPER/LTER researchers as sources of information and wrote a description of the CPER/LTER project in the text including the following excerpt "Perhaps the most important research group asking and answering questions about the shortgrass prairie today is the 'Long Term Ecological Research Program' sponsored by the National Science Foundation."

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LITERATURE CITED


McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships


Milchunas, D.G. and W.K. Lauenroth. Abiotic and biotic control and direct and indirect effects of large herbivores on demography of opportunistic species in a semiarid grassland. (in prep).


Sala, O.E., W.J. Parton and W.K. Lauenroth. Long-term soil water dynamics in the shortgrass steppe. (in prep.)


APPENDIX 1

Publications 1982-1989

Our approach to compiling a list of publications, theses, and dissertations for the CPER/LTER project was to take the broadest possible approach to the definition of "an LTER publication." The CPER/LTER project is so well integrated into other research activities in the Range Science Department and the Natural Resource Ecology Laboratory that it is impossible to unambiguously define "an LTER publication." Our intentions are not to try to inflate the apparent productivity of the project, but to illustrate the legitimate scope of our research at the Central Plains Experimental Range.


1988 Scientific Committee on Problems of the Environment (SCOPE). John Wiley and Sons Ltd.


APPENDIX 2

Statement of Commitment to LTER Intersite Research and Coordination, for the LTER III Proposals of Cohort 1 Sites (Andrews, Central Plains, Coweeta, Konza, Niwot, North Inlet, Temperate Lakes).

The seven Cohort 1 LTER Sites have prepared this statement to define our commitment to common intersite research and coordination activities. The magnitude of our past, present, and proposed intersite activity reflects our belief that these activities produce important results in ecological science. Further, the LTER Network makes possible collaborative research that would otherwise be extremely difficult or impossible.

The similarities of broad themes among individual site proposals (e.g. global change effects, ecosystem processes at multiple scales) lead naturally to identification of these intersite projects. Perspectives gained from intersite comparative studies and from pooling talent from multiple sites strengthens the research programs of individual sites. This interplay of site- and intersite-research is particularly important and effective in long-term research.

Listed in Table 1 are intersite activities in various stages of development. Many of these activities involve other (non-Cohort 1) LTER and non-LTER sites. In addition to the relatively extensive intersite research projects listed here, our sites participate in approximately two dozen research projects involving several sites each. Details of on-going and proposed activities are contained in individual site proposals, the Coordinating Committee proposal, work plans, and other documents. In some cases, the specifics have not been determined yet. Approaches to organizing and funding these activities vary in relation to their magnitude and stage of development. Approaches include funding from sites, the Coordinating Committee grant, and other NSF and non-NSF sources.

Given the rapid pace of change in ecological sciences, we expect that some of the most important intersite research to be developed over the six-year grant period are impossible to anticipate at this time.
Table 1. Title, leaders, and status of major ongoing and proposed research projects involving five or more sites.

1. Decomposition
   a. Fine litter exchange experiment
      Melillo (HFR), Harmon (AND - coordinator), Parton (CPR). A 21-site litter
decomposition experiment in terrestrial systems is getting underway. A proposal for further
work is in preparation.
   b. Coarse woody debris
      Harmon (AND), Schowalter (AND). Preliminary study of log decomposition based on
periodic destructive sampling of a collection logs which were fresh when placed on the ground
in 1985. Supported by a NSF grant. Support for a 5-site network is pending.
   c. Litter decomposition in aquatic systems
      Meyer (CWT). Proposal based on approach used in terrestrial fine litter exchange
experiment to be developed ca. 1991.

2. Modeling Vegetation Dynamics in Forests and Grasslands
   Shugart (VCR), Lauenroth (CPR), Parton (CPR). The approach is to utilize simulation
models to investigate behavior of ecosystems over a range of sites in North America.
Individual-based vegetation models and soil process models will be used to (1) account for
existing patterns in ecosystems under a spectrum of environmental regimes arrayed along
temperature and water gradients, and (2) to make predictions about the response of these
ecosystems to environmental change. Test applications began in earnest in 1989 under several
NSF grants. NSF proposal submitted 12/89 and some commitment made in appropriate LTER
site proposals.

3. Climate Change Effects on Site Hydrology at Plot to Landscape Scales
   Grant (AND), Caine (NWT). A hydrology model (probably Precipitation-Runoff Modeling
System (PRMS)) would be used in comparative analysis of hydrology, including effects of
climate change. This would be done in cooperation with George Leavesley (U.S. Geological
Survey) who developed model. Discussions of the project have been held with USGS. Use of
PRMS is underway at AND and NWT.

4. Space/Time Variability in Diverse Systems
   Magnuson (NTL), Kratz (NTL), and others. Variance in data from at least 5-yr and 5-
location measurements of physical and biological variables are analyzed to characterize
contrasting systems in terms of temporal and spatial sources of variance. Originally funded by
senior investigator, Coordinating Committee, and site funds. Further work planned based on
funding from latter two sources.

5. Ecosystem Properties Across Environmental Gradients
   Tilman (CDR), Zack (CDR)--coordinators. Ten-site-comparison of soil nutrient dynamics,
productivity, and plant life forms across environmental gradients in the U.S. Funded by
Coordinating Committee and individual site grants.

6. Plant Demography, Especially Mortality
   Harmon (AND), Franklin (NET), and others. A specific work plan for intersite comparative
analysis of existing data will be developed at the tree mortality workshop at AND in
April 1990.
APPENDIX 3

RELATED RESEARCH PROJECTS

1. Center for Analysis of the Dynamics of Regional Ecosystems (CADRE)

The Center for Analysis of the Dynamics of Regional Ecosystems (CADRE) is a consortium of scientists and institutions, addressing issues related to climate change in semiarid regions, focusing on the central grassland region of the U.S. CADRE's mission is to elucidate the atmospheric processes responsible for, and the ecological consequences of, climate change, and to evaluate the viability of alternate strategies for dealing with these problems. CADRE is currently proposed for funding from NSF's Center of Excellence Program and will receive a site visit for further evaluation this spring.

2. Controlled Environment Climate Change Study (CO$_2$)


A controlled environment experiment was begun in 1989 to assess the direct effects of elevated CO$_2$ and its indirect effects via climate change on plant and soil processes in the shortgrass steppe. Intact sods from the CPER are being incubated in controlled environmental chambers under varying combinations of ambient CO$_2$, temperature, and water availability.

3. Great Plains Agroecosystem Project (GRP)


The Great Plains Agroecosystem Project is in its 7th year of work evaluating the impacts of cultivation on soil organic matter levels and the biological, physical, and chemical processes controlling these levels. Integration between this project and the CPER/LTER allows us to address the mosaic of grasslands and agroecosystems across the central grasslands region in a realistic fashion.

4. Ecology and Management for Sustained Rangeland Production in the Great Plains (ARS)

(Funded by the USDA ARS - 1993, Co-Investigators C.E. Townsend, R.A. Bowman, J.R. Forwood, J.D. Hanson, and J.A. Morgan.)

The objective of this project is to improve the efficiency and sustainability of rangeland management systems by broadening germ plasm, understanding the physiology and development of important species in relation to their environment, and developing technologically advanced tools to help make economically and ecologically sound land management decisions.
5. Trace Gas Project (TGAS)

This project focuses on understanding controls over nitrous oxide and methane production in grassland and boreal wetland ecosystems.

6. Grass/Shrub Interactions in Two Temperate Semiarid Regions (GS)

(Funded by the National Science Foundation. 1988-1991. Principal Investigators W.K. Lauenroth, CSU and O.E. Sala, Univ. Buenos Aires, Argentina.)
The objectives are to test the applicability of the 2-layer formulation of soil water interactions for the mineral nutrient economy of shrubs and grasses and to test the utility of a biogeographic model based upon the 2-layer model to predict the distribution of grasslands and shrublands in the United States and Argentina.

7. Community Structure Across Resource Gradients - Grassland to Forest (CSU/UVA)

(Funded by the National Science Foundation. 1988-1990. Principal Investigators W.K. Lauenroth, CSU and H.H. Shugart, Univ. of Virginia.)
The objectives of this project are: (1) To synthesize existing data from a spectrum of ecosystems as represented by various LTER sites, focusing on the role of key environmental drivers (insolation, temperature, moisture, nutrients, and disturbance regimes) in structuring specific ecosystems; (2) Based on this synthesis, to implement a set of computerized simulators that share a common structure and a common set of driving variables, and that are sufficiently general that they may be applied to a variety of ecosystems.

8. Boundary Dynamics Approach to Studying Landscapes (BD)

(Funded by the National Science Foundation. 1989-1991. Principal Investigators J. Wiens, CSU and B. Milne, Univ. of New Mexico.)
The objective of this project is to investigate ecosystem patterns and processes that depend explicitly on the spatial patchiness of landscapes.

9. Hierarchical Modeling Project (DOE)

(Funded by DOE 1989; Principal Investigators T.G.F. Kittel and M.B. Coughenour, CSU.)
This project focuses on linking atmospheric and ecologic models that operate at different levels of temporal and spatial resolution to address ecological questions of regional and global significance in grassland.

(L. Tieszen, Augustana College, with D. Schimel, CSU.)

The objective of this project is to understand the Holocene successional status of North American prairies, using the relationships between soil organic matter $\delta^{13}$C and current vegetation in areas of varying soil texture, temperature, and water to address the mesoscale diversity in grasslands.

11. Earth Observing System (EOS)

(Funded by NASA 1988-1994; Co-principal Investigators D.S. Schimel, CSU, and C. Wessman, Univ. of Colorado.)

CPER investigators are part of a NASA Earth Observing System (EOS) project with the goal of developing ecosystem models that can be driven by satellite data.

12. Land Surface-Climatology Interactions (FIFE)

(Funded by NASA 1986-1990; Co-Investigators D.S. Schimel, W.J. Parton, T.G.F. Kittel, CSU.)

This project has the following objectives: (1) to develop methods to quantify land surface properties that influence climate, and (2) to determine the utility of existing satellite data for detection of climate- or man-induced fluctuations in the land surface.

13. Joint Facility for Regional Ecosystem Analysis (JFREA)

(Funded by NSF. 1987-1989. Principal Investigators, R.G. Woodmansee and D.S. Schimel, CSU.)

Joint Facility for Regional Ecosystem Analysis (JFREA) is a GIS and remote sensing facility located at the University of Colorado's Institute for Arctic and Alpine Research and at CSU NREL. The facility at NREL comprises hardware and software necessary for spatial analysis and simulation modeling.

14. Interdisciplinary Modeling of Climate Change (SOC)


We recently proposed to begin to link socio-economic models of the Great Plains region with an extant ecosystem model (CENTURY) to predict the potential human and ecological effects of climate change for the region.
APPENDIX 4

DESCRIPTION OF THE CENTRAL PLAINS EXPERIMENTAL RANGE

Location

The LTER project at Colorado State University is located at the Central Plains Experimental Range (CPER) in the western division of Pawnee National Grassland (Fig. 1). The western division of the Pawnee National Grassland is 42,700 ha and the CPER encompasses 6,280 ha.

The CPER is 19 km northeast of Nunn, Colorado, and 40 km south of Cheyenne, Wyoming. The Range was established in 1939 to answer questions which were important as a result of the drought of the 1930's. A number of pastures were set aside for long-term experiments, and a large number of scientific publications have resulted. Twelve half-section (129 ha) pastures were assigned four each to heavy, moderate, and light summer grazing. In 1958 two of the replicates were changed to winter grazing. Each of these and several other pastures also have at least one exclosure of 0.5 to 2 ha excluding livestock grazing since 1939. Permanent quadrats have been established in these pastures, and in most years composition of vegetation has been measured.

All of the Central Plains Experimental Range is available for use in the LTER Program, but some is dedicated to ongoing studies conducted by the Agricultural Research Service (ARS) (Appendix 7). The Pawnee National Grassland, as mentioned above, is available for extensive studies which require a great deal of land area but do not require rigid control for experimental purposes. The LTER program will assist investigators in securing cooperative agreements with the U.S. Forest Service for use of these lands. The CPER, on the other hand, may be utilized for intensive studies which require greater control.

A broad form of cooperative agreement has existed between the ARS and Colorado State University (CSU) for many years. Under this agreement CSU scientists have cooperated in many research projects on the CPER.

Fig. 1. Map showing the regional location of Pawnee National Grassland.
Within the CPER was located the Pawnee Site of the International Biological Program (IBP) Grassland Biome study. From 1966 to 1974 the IBP Program was involved in ecosystem research at the CPER.

In 1968, a cooperative agreement was signed among ARS, CSU, and the IBP's Grassland Biome Program (see Appendix 7). The agreement permitted IBP to conduct grassland research on a portion of the CPER and provided for mutual cooperation. The agreement also permitted the construction of needed facilities on the CPER. These included an office-lab-cafeteria, storage shed, dormitory, residence, barn, and corrals. This agreement was amended in 1975 when the IBP program was phased out and is currently the agreement of record.

Under the auspices of the US/IBP Grassland Biome study and subsequent NSF funding, interdisciplinary teams have analyzed the fundamental structural and functional characteristics of the shortgrass steppe ecosystems at CPER. These studies included measurements of the structural aspects of all trophic compartments, their variation through time, space, and under stress (grazing, water, mineral nitrogen, herbicides, pesticides) as well as a broad array of studies relating to ecosystem processes such as primary production, secondary production, energy flow, nutrient cycling, and abiotic and biotic control.

Climate

The precipitation variability (in time and space) is probably the outstanding characteristic of the semiarid continental climate. The mean annual precipitation is 309 mm (12.2 inches) based on 30 years of data. May, June, July, and August tend to be the wettest months. These 4 months usually account for more than 50% of the annual precipitation. Through regression analysis it has been found that summer precipitation explained 89% of the variance in annual precipitation while winter precipitation accounted for the other 11%. This variation is explained by the frequent occurrence of convective activity in the area during summer months. Northerly flow of maritime tropical air combines with intense solar heating and orographic influence over the mountains to generate thunderstorms which move in an easterly direction over the grasslands beginning around noon each day. The winter climate is dominated by the presence of continental polar air masses and very few storms moving over the area. Storms which pass over the Rocky Mountain region lose most of their moisture over the mountains; consequently, dry, sunny days are common in winter. The winter storms which do occur have little effect on the mean water balance of the region. This is so because high insolation, moderate to high winds, and warm daily air temperatures combine to sublimate much of the snow. Major storms, defined as greater than 2.54 cm (1 inch) of precipitation, account for 74% of the variance in summer precipitation and only 16% of the variance in winter precipitation.

The large diurnal variation in air temperatures is a notable characteristic of the steppe climate. Average diurnal variations are between 17°C and 20°C (30°F and 35°F), with variations up to 34°C (60°F) possible in late summer. The lowest average monthly maximum temperature is 7°C (44°F) (January and December) for approximately 30 years of data. The highest average monthly maximum temperature is 31°C (88°F) (July). The lowest and highest average monthly temperatures are -12°C (11°F) (January) and 12°C (54°F) (July), respectively. The median frost-free period is 128 days.

Another important characteristic of the grasslands climate is the presence of moderate to high winds throughout much of the year. The period December to May experiences noticeably higher winds than the remaining months. This characteristic plays an important role in the redistribution of snow following winter storms and the resulting winter water balance of the region.
APPENDIX 5

Additional grassland data sets accessible through the LTER/CPER data management system.
<table>
<thead>
<tr>
<th>Site</th>
<th>Date</th>
<th>Description</th>
</tr>
</thead>
</table>
| Belowground herbage | 1970 1-5-75 | Set 1 (plots A-D) data (probably contained in bh1375f) 

As evident from the table above, various sites and dates are mentioned, each with specific data sets as follows:

- **Belowground herbage**: This category refers to data related to belowground vegetation, which is crucial for understanding soil health and nutrient cycling.

- **Pawnee site**: The data from this site covers various dates ranging from 1970 to 1975, with some data sets labeled as "Very Clean".

- **San Joaquin site**: Similarly, this site also has data sets spanning multiple years, with a notable mention of "High" or "Very Clean" data conditions.

- **Osage, Oklahoma site**: Data sets for this site are provided, again with specific dates and conditions.

- **Pantex site**: This site also has data sets with dates ranging from 1970 to 1975, indicating a consistent data collection period.

- **B. S. Herbage site**: Data from this site includes various species, with a focus on cottonwood and other specific plants.

- **Cottonwood site**: Data for this site includes specific dates and conditions, indicating a focus on cottonwood plant data.

- **Dickinson site**: Data sets for this site also include specific dates and conditions, ensuring a comprehensive data collection timeline.

- **Hays site**: Data for this site includes specific dates and conditions, ensuring a comprehensive data collection timeline.

Each site and date combination provides detailed insights into the vegetation and ecological conditions prevalent during the specified periods.
belowground herbage | EPA site 194-75 (set 1) fortran readable analysis
| probably contained in bhcp75f) | co2 evolution
| EPA site 315-75 (set 2) data (probably contained in bhcp75d) | co2 evolution
| EPA site 315-75 (set 2) fortran readable analysis | co2 evolution
| probably contained in bhcp75f) | co2 evolution
| EPA site 156-75 (set 3) data (probably contained in bhcp75d) | co2 evolution
| EPA site 156-75 (set 3) fortran readable analysis | co2 evolution
| probably contained in bhcp75f) | co2 evolution
| EPA site 137-75 (set 4) data (probably contained in bhcp75d) | co2 evolution
| EPA site 137-75 (set 4) fortran readable analysis | co2 evolution
| probably contained in bhcp75f) | co2 evolution
| EPA site 78-75 (set 5) data (probably contained in bhcp75d) | co2 evolution
| EPA site 78-75 (set 5) fortran readable analysis | co2 evolution
| probably contained in bhcp75f) | co2 evolution
| EPA site 179-75 (set 6) data (probably contained in bhcp75d) | co2 evolution
| EPA site 179-75 (set 6) fortran readable analysis | co2 evolution
| probably contained in bhcp75f) | co2 evolution
| EPA site 19767 dates (21-3, 20-5, 15-6, 26-7 (uncorrected), 10-7, 19-9) trts A-D, J-M | co2 evolution
| EPA site 1976 fortran readable analysis | co2 evolution
| EPA site 213-76 (set 1) data (probably contained in bhcp76d) | co2 evolution
| EPA site 213-76 (set 1) fortran readable analysis | co2 evolution
| probably contained in bhcp76f) | co2 evolution
| EPA site 205-76 (set 2) data (probably contained in bhcp76d) | co2 evolution
| EPA site 205-76 (set 2) fortran readable analysis | co2 evolution
| probably contained in bhcp76f) | co2 evolution
| EPA site 156-76 (set 3) data (probably contained in bhcp76d) | co2 evolution
| EPA site 156-76 (set 3) fortran readable analysis | co2 evolution
| probably contained in bhcp76f) | co2 evolution
| EPA site 267-76 (set 4) data - uncorrected (probably contained in bhcp76d) | co2 evolution
| EPA site 267-76 (set 4) fortran readable analysis - uncorrected (probably contained in bhcp76f) | co2 evolution
| EPA site 107-76 (set 5) data (probably contained in bhcp76d) | co2 evolution
| EPA site 107-76 (set 5) fortran readable analysis | co2 evolution
| probably contained in bhcp76f) | co2 evolution
| EPA site 98-76 (set 6) data (probably contained in bhcp76d) | co2 evolution
| EPA site 98-76 (set 6) fortran readable analysis | co2 evolution
| probably contained in bhcp76f) | co2 evolution
| EPA site 199-76 (set 7) data (probably contained in bhcp76d) | co2 evolution
| EPA site 199-76 (set 7) fortran readable analysis | co2 evolution
| probably contained in bhcp76f) | co2 evolution
| EPA site 19771 date (12-7) trts A-D, E-H, J-M (set 1) data | decomposition
| EPA site 19771 date (12-7) trts A-D, E-H, J-M (set 1) fortran readable analysis | decomposition
| EPA site 19775 data | decomposition
| EPA site 1975 fortran readable analysis | decomposition
| co2 evolution | decomposition
| EPA site 1976 fortran readable analysis | decomposition
| Cottonwood site 1972 trt 1,4; data | decomposition
| Cottonwood site 1972 trt 1,4; fortran readable analysis | decomposition
| Cottonwood site 1972 (all sets) | decomposition
| Ale site 1971 tr t 1,5; data | decomposition
| Ale site 1971 tr t 1,5; fortran readable analysis | decomposition
| Ale site 1972 tr t 1,5; data | decomposition
| Ale site 1972 tr t 1,5; fortran readable analysis | decomposition
| Bridger site 1972 trt 1,2; data | decomposition
| Bridger site 1972 trt 1,2; fortran readable analysis | decomposition
| Bridger site 1973 trt 1,2; data | decomposition
| Bridger site 1973 trt 1,2; fortran readable analysis | decomposition
| Jomada site 1972 trt 1; data | decomposition
| Jomada site 1972 trt 1; fortran readable analysis | decomposition
| Osage site 1972 trt 1,5; data | decomposition
| Osage site 1972 trt 1,5; fortran readable analysis | decomposition
| Pawnee site 1972 trt 1,5 (1 date); data | decomposition
| Pawnee site 1972 trt 1,5 (1 date); fortran readable analysis | decomposition
| Pawnee site 1973 trt 1,5 (1 date); data | decomposition
| Pawnee site 1973 trt 1,5 (1 date); fortran readable analysis | decomposition
| Pawnee site 1971 trt 1,3, E; data | decomposition
| Pawnee site 1971 trt 1,3, E; fortran readable analysis | decomposition
| Pawnee site 1972 trt 1,1; data | decomposition
| Pawnee site 1972 trt 1,1; fortran readable analysis | decomposition
| Pawnee site 1972 trt 1,4,5,6; data | decomposition
| Pawnee site 1972 trt 1,4,5,6; fortran readable analysis | decomposition
| Pawnee site 1973 trt 1,5; data | decomposition
| Pawnee site 1973 trt 1,5; fortran readable analysis | decomposition
| Pawnee site 1973 ESA data | decomposition
| Pawnee site 1973 ESA fortran readable analysis | decomposition
| Pawnee site 1974 ESA data | decomposition
| Pawnee site 1974 ESA fortran readable analysis | decomposition
| Pawnee site 1975 ESA data | decomposition
| Pawnee site 1975 ESA fortran readable analysis | decomposition
| San Joaquin site 1973 trt 1,5; data | decomposition
| San Joaquin site 1973 trt 1,5; fortran readable analysis | decomposition
| San Joaquin site 1973 trt C,P; data | decomposition
| San Joaquin site 1973 trt C,P; fortran readable analysis | decomposition
| San Joaquin site 1974 trt 1,5; data | decomposition
| San Joaquin site 1974 trt 1,5; fortran readable analysis | decomposition
| San Joaquin site 1974 trt C,P; data | decomposition
| San Joaquin site 1974 trt C,P; fortran readable analysis | decomposition
| Ale site 1971 fortran readable analysis | decomposition
| Ale site 1972 fortran readable analysis | decomposition
| Cottonwood site 1970 fortran readable analysis | decomposition
| Cottonwood site 1971 fortran readable analysis | decomposition
decomposition
EPA site 1974 (Material 1) data

decomposition
EPA site 1974 (Material 1) fortran readable analysis

decomposition
EPA site 1974 (Material 5) fortran readable analysis

decomposition
EPA site 1975 (Material 6.1; questionable data - no summaries) data

trans readable analysis
EPA site 1976 (Materials 5-8) data

diet data
Cottonwood site 1972 Cattle Weights

diet data
Pawnee site, revised Lavigne diet data, box 1

diet data
Pawnee site, revised Lavigne diet data, box 2

diet data
Pawnee site, revised Lavigne diet data, box 3

diet data
Pawnee site, revised Lavigne diet data, box 4

diet data
Bimney diet slide requests

diet data
Lav Phadt diet bank requests

invertebrate wts, species codes
Pawnee, EPA sites soil microarthropod wts and trophics for Pawnee and Montana (J. E. Leetham)

invertebrate wts, species codes
EPA site soil microarthropod wts (includes both Pawnee and EPA Montana)

invertebrate wts, species codes
EPA site 1974 Montana AG & BG invertebrate wts and trophic levels

invertebrate wts, species codes
EPA site 1975 Montana AG & BG invertebrate wts and trophic levels

invertebrate wts, species codes
EPA site 1976 Montana AG & BG invertebrate wts and trophic levels

invertebrate wts, species codes
Ale site 1972 invertebrate wts

invertebrate wts, species codes
Ale site 1973 AG invertebrate wts

invertebrate wts, species codes
Bridger site 1972 invertebrate wts

invertebrate wts, species codes
Cottonwood site invertebrate wts

invertebrate wts, species codes
Jomada site invertebrate wts

invertebrate wts, species codes
San Joaquin site invertebrate wts

invertebrate wts, species codes
San Joaquin site AG invertebrate wts supplement

invertebrate wts, species codes
Pantex site 1970 AG invertebrate wts

invertebrate wts, species codes
Pantex site 1972 invertebrate wts

invertebrate wts, species codes
Network Comparison sites 1972-74 soil microarthropods wts and trophic levels

litter
EPA site 1974 data

litter
EPA site 1974 fortran readable analysis

litter
EPA site 1975 data

litter
EPA site 1975 fortran readable analysis

litter
EPA site 1976 data
litter

Jomada site 1972 type 1 fortran readable analysis
Osage site 1970 type 1 data
Osage site 1970 type 1 fortran readable analysis
Osage site 1970 type 3 data
Osage site 1970 type 3 fortran readable analysis
Osage site 1970 type 4 data
Osage site 1970 type 4 fortran readable analysis
Osage site 1971 type 1 data
Osage site 1971 type 1 fortran readable analysis
Osage site 1971 type 3 data
Osage site 1971 type 3 fortran readable analysis
Osage site 1971 type 4 data
Osage site 1971 type 4 fortran readable analysis
Osag. + site 1972 type 1 data
Osage site 1972 type 1 fortran readable analysis
Osage site 1972 type 2 data
Osage site 1972 type 3 data
Osage site 1972 type 3 fortran readable analysis
Pantex site 1970 type 1 data
Pantex site 1970 type 1 fortran readable analysis
Pantex site 1971 type 1 (BOGR) data
Pantex site 1971 type 1 (BOGR) fortran readable analysis
Pantex site 1971 type 1 (OPPO) data
Pantex site 1971 type 1 (OPPO) fortran readable analysis
Pantex site 1972 type 1 (BOGR) data
Pantex site 1972 type 1 (BOGR) fortran readable analysis
Pantex site 1972 type 1 (OPPO) data
Pantex site 1972 type 1 (OPPO) fortran readable analysis
Pawnee site 1972 (May-Oct) fortran readable analysis
Pawnee site 1973 (May-Sep) fortran readable analysis
Pawnee site 1974 (Apr-Dec) fortran readable analysis
Pawnee site 1975 (May-Aug) fortran readable analysis
San Joaquin site 1973 type 1 data
San Joaquin site 1973 type 1 fortran readable analysis
San Joaquin site 1974 type 1 data
San Joaquin site 1974 type 1 fortran readable analysis
San Joaquin site 1975 type 1 data
San Joaquin site 1975 type 1 fortran readable analysis
phenology
Osage site 1972 data
Pantex site 1972 dat a
Pawnee site 1973 6 dates
Jomada site 1971 6 dates
Jomada site 1972 11 dates
San Joaquin site 1973 3 dates
San Joaquin site 1973 193 data
San Joaquin site 1977 17 dates
Pawnee site 1972 Dry land Phenology (coded to be similar to 73-76)
EPA site 1975 8 sets; trts A-H (AGH phenology)
EPA site 1976 24 sets; trts A-H (AGH phenology)
EPA site 1977 21 set s; trts A-H (AGH phenology)
Bridger site 1972 live trap data
Bridger site 1973 live trap data
Bridger site 1973 live trap Zippin analysis
Cottonwood site 1971 live trap data
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Cottonwood site 1971 live trap Zippin analysis
Cottonwood site 1972 live trap Zippin analysis
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Pantex site 1972 misc. off-grid snap trap data
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Ale site 1972 live trap data
Ale site 1973 live trap data
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San Joaquin site 1974 live trap data
San Joaquin site 1975 live trap data
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San Joaquin site 1973 live trap Zippin analysis
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San Joaquin site 1973 misc. off-grid snap trap data
San Joaquin site 1974 misc. off-grid snap trap data
Osage site 1970 snap trap data
Pantex site 1970 snap trap data
Jomada site 1972 data
Jomada site 1972 fortran readable analysis
Osage site 1972 data
EPA site 1974 Montana; data

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San Joaquin site 1974 live trap Zippin analysis
San Joaquin site 1975 live trap Zippin analysis
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San Joaquin site 1973 misc. off-grid snap trap data
San Joaquin site 1974 misc. off-grid snap trap data
Osage site 1970 snap trap data
Pantex site 1970 snap trap data
Jomada site 1972 data
Jomada site 1972 fortran readable analysis
Osage site 1972 data
EPA site 1974 Montana; data
soil macroarthropods
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EPA site 1974 Montana; fortran readable analysis
EPA site 1975 Montana; data
EPA site 1974 Montana; fortran readable analysis
EPA site 1974 Montana; data
EPA site 1976 Montana; data
EPA site 1974 Montana; fortran readable analysis
San Joaquin site 1973 data
San Joaquin site 1974 data
San Joaquin site 1974 fortran readable analysis
San Joaquin site 1973 fortran readable analysis
San Joaquin site 1973 fortran readable analysis
San Joaquin site 1974 fortran readable analysis
San Joaquin site 1974 fortran readable analysis
San Joaquin site 1974 fortran readable analysis
Bridger site 1972 data (uncorrected)
Bridger site 1972 fortran readable analysis (uncorrected)
Jomada site 1972 data (uncorrected)
Jomada site 1972 fortran readable analysis (uncorrected)
Osage site 1971 data (uncorrected)
Osage site 1971 fortran readable analysis (uncorrected)
Osage site 1971 fortran readable analysis (uncorrected)
Osage site 1971 data (uncorrected) - note that first 4 sets are berlese separator and last 3 sets are IBP separator
Cottonwood site 1972 data
Cottonwood site 1972 fortran readable analysis
EPA site 1974 Montana; data
EPA site 1974 Montana; fortran readable analysis
EPA site 1975 Taylor Creek; data
EPA site 1975 Taylor Creek; fortran readable analysis
EPA site 1975 Colstrip; data
EPA site 1975 Colstrip; fortran readable analysis
EPA site 1976 Taylor Creek 1; data
EPA site 1976 Taylor Creek 1; fortran readable analysis
EPA site 1976 Taylor Creek 2; data
EPA site 1976 Taylor Creek 2; fortran readable analysis
EPA site 1977 Taylor Creek 1; data
EPA site 1977 Taylor Creek 1; fortran readable analysis
EPA site 1977 Taylor Creek 2; data
EPA site 1977 Taylor Creek 2; fortran readable analysis
EPA site 1978 Taylor Creek 1; data (08 July)
EPA site 1978 Taylor Creek 1; fortran readable analysis (08 July)
EPA site 1978 Taylor Creek 2 fortran readable analysis
EPA site 1977 Montana; fortran readable analysis
EPA site 1977 Montana; data
EPA site 1975 Montana; fortran readable analysis
EPA site 1975 Montana; data
EPA site 1976 Montana; data
EPA site 1975 Montana; fortran readable analysis
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San Joaquin site 1974 data
San Joaquin site 1974 fortran readable analysis
San Joaquin site 1973 fortran readable analysis
San Joaquin site 1973 fortran readable analysis
San Joaquin site 1974 fortran readable analysis
San Joaquin site 1974 fortran readable analysis
San Joaquin site 1974 fortran readable analysis
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Jomada site 1972 fortran readable analysis (uncorrected)
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Cottonwood site 1972 fortran readable analysis
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EPA site 1974 Montana; fortran readable analysis
EPA site 1975 Taylor Creek; data
EPA site 1975 Taylor Creek; fortran readable analysis
EPA site 1975 Colstrip; data
EPA site 1975 Colstrip; fortran readable analysis
EPA site 1976 Taylor Creek 1; data
EPA site 1976 Taylor Creek 1; fortran readable analysis
EPA site 1976 Taylor Creek 2; data
EPA site 1976 Taylor Creek 2; fortran readable analysis
EPA site 1977 Taylor Creek 1; data
EPA site 1977 Taylor Creek 1; fortran readable analysis
EPA site 1977 Taylor Creek 2; data
EPA site 1977 Taylor Creek 2; fortran readable analysis
EPA site 1978 Taylor Creek 1; data (08 July)
EPA site 1978 Taylor Creek 1; fortran readable analysis (08 July)
Bridger site 1972 trt 1,2 (6 dates) data
Bridger site 1972 trt 1,2 (6 dates) fortran readable analysis
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Osage site 1972 trt 1,5 (7 dates) data
Osage site 1972 trt 1,5 (7 dates) fortran readable analysis
Osage site 1972 trt 1,5 (7 dates) data
Osage site 1972 trt 1,5 (7 dates) fortran readable analysis
Panex site 1972 trt 1,3 (6 dates) data
Panex site 1972 trt 1,3 (6 dates) fortran readable analysis
Panex site 1972 trt 1,3 (6 dates) data
Panex site 1972 trt 1,3 (6 dates) fortran readable analysis
Pawnee site 1972 fortran readable analysis
Pawnee site 13 1975 fortran readable analysis
Pawnee, EPA 1976 fortran readable analysis
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san Joaquin site 1973 (8 dates) data
San Joaquin site 1973 (8 dates) fortran readable analysis
San Joaquin site 1974 (13 dates) data
San Joaquin site 1974 (13 dates) fortran readable analysis
San Joaquin site 1975 (7 dates) data
San Joaquin site 1975 (7 dates) fortran readable analysis
EPA site 1975 trt A-B (20 dates) data
EPA site 1975 trt A-B (20 dates) fortran readable analysis
EPA site 1976 trt A-D, J-M (22 dates) data
EPA site 1976 trt A-D, J-M (22 dates) fortran readable analysis
San Joaquin site 1974 special sampling (additional depths)
San Joaquin site 1975 special sampling
San Joaquin site 1973 data from Paraquai study
Pawnee site 1972-76 data type 54; 2 different formats
EPA 1971 conversion to water; fortran readable analysis
EPA 1971 rep summary; fortran readable analysis
EPA 1971 trt summary; fortran readable analysis
EPA 1971 raw neutron counts
EPA 1972 conversion to water; fortran readable analysis
EPA 1972 rep summary; fortran readable analysis
EPA 1972 trt summary; fortran readable analysis
EPA 1972 raw neutron counts
EPA 1973 conversion to water; fortran readable analysis
EPA 1973 rep summary; fortran readable analysis
EPA 1973 trt summary; fortran readable analysis
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EPA 1974 trt summary; fortran readable analysis
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EPA 1975 trt summary; fortran readable analysis
EPA 1975 raw neutron counts
EPA 1976 conversion to water; fortran readable analysis
EPA 1976 rep summary; fortran readable analysis
EPA 1976 trt summary; fortran readable analysis
EPA 1976 raw neutron counts
MWS 1971 conversion to water; fortran readable analysis
MWS 1971 rep summary; fortran readable analysis
MWS 1971 trt summary; fortran readable analysis
MWS 1971 raw neutron counts
MWS 1972 conversion to water; fortran readable analysis
MWS 1972 rep summary; fortran readable analysis
MWS 1972 trt summary; fortran readable analysis
MWS 1972 raw neutron counts
MWS 1973 conversion to water; fortran readable analysis
<table>
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<th>Description</th>
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<td>Stroud Plant Pattern Data</td>
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<td>1971 - LGE3, 1-5</td>
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<td>Stroud Plant Pattern Data</td>
<td>1972 - EX72, 1-5</td>
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<td>Stroud Plant Pattern Data</td>
<td>1972 - LGE3, 1-5, BOGR &amp; BRSL</td>
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