

## PROJECT SUMMARY

The shortgrass steppe (SGS) occupies the middle of the productivity gradient along which the LTER grassland sites lie. It is unique among North American grasslands for its long evolutionary history of intense selection by both drought and herbivory, leading to an ecosystem that is very well adapted to withstand grazing by domestic livestock. The distinctive features of the SGS are both its vegetation and the concentration of biological activity and organic matter belowground. The vegetation of the SGS is characterized by lowgrowing plants that are either tolerant or resistant to grazing and drought. The large concentration of biological activity belowground reflects the distribution of plant production (Milchunas and Lauenroth 1992) and the enhanced rates of energy flow through heterotrophs belowground (Lauenroth and Milchunas 1992). It is also explained in part by the fact that most biologically active elements in grasslands are protected from natural disturbances by being stored in soil organic matter (SOM).

The SGS LTER project has been in operation since 1982, and currently supports 46 longterm experiments, numerous shortterm experiments, and has a large emphasis in integrative simulation analysis. SGS LTER work is divided into 5 major areas: populations and processes, biogeochemical dynamics, paleoecology and paleopedology, water and energy dynamics, and disturbances.

### **Populations and Processes:**

Work in this area is organized by the idea that two kinds of populations are most important in the longterm dynamics and sustainability of the SGS. The first are dominant species, such as the shortgrass blue grama ([Bouteloua gracilis](#)), which overwhelmingly dominates the SGS. The second kind of important population is those that have a large effect on the ecosystem because of their unique traits; these are keystone species and we propose that prairie dogs (*Cynomys ludovicianus*) and prickly pear cactus ([Opuntia polyacantha](#)) are keystone species in the SGS. SGSLTER past and continuing work has focused a great deal on population dynamics of blue grama and the factors that influence its role in the system. In addition, population dynamics of other species across the trophic structures are also studied. New work is proposed for the next 6 years to focus on two aspects: 1.) the biology of prairie dogs and prickly pear cactus as keystone species, and 2.) population genetics of blue grama as they influence its resistance to grazing.

### **Biogeochemical Dynamics:**

Our research in this area focuses on elucidating the key abiotic and biotic

variables that control biogeochemical dynamics. Continuing longterm experiments are designed to assess how precipitation, temperature, topography, and soil texture interact to control spatial and temporal patterns of primary productivity, nutrient cycling, and trace gas loss. Proposed new work will address the importance of atmospheric inputs to ecosystem processes.

**Paleoecology and Paleopedology:** Over evolutionary time scales, climatic variation has been the major force influencing the structure and function of SGS ecosystems. Our work in this area involves sampling the extensive paleosols across the SGS site, and evaluating their longterm vegetative and physiographic history by analyzing the stable C isotope signatures of soil organic matter, phytoliths, and CaCO<sub>3</sub>. These studies provide information on the distribution of C<sub>3</sub> and C<sub>4</sub> plants during the Holocene soilforming intervals.

**Water and Energy Dynamics:**

The SGSLTER project identifies this area as important because water availability is the key variable driving SGS ecosystem structure and function. Measurements of precipitation, temperature, microclimate, and soil water are part of the longterm program. A weighing lysimeter measures daily evapotranspiration. We propose to initiate a new study to quantify the potential impact of current land use on the SGS by coupling a mesoscale atmospheric model with an ecosystem dynamics model.

**Disturbance:**

Two key hypotheses organize SGS LTER work in the area of disturbance. The first is that smallscale disturbances are the most important source of mortality for the dominant plant, blue grama, and as such, these disturbances represent a major influence on the sustainability of the shortgrass steppe. The second is that the distribution of biotic components with a large bias towards the belowground portion of the system leads to a high degree of resistance of the ecosystem to aboveground disturbances such as grazing or fire, but a high vulnerability to disturbances such as cultivation that disturb the soil system. In addition, the evolutionary adaptations of organisms in the SGS provide additional resistance to grazing. Continuing SGSLTER experiments evaluate the long and shortterm effects of smallscale disturbances, grazing, and recovery from cultivation on plant communities, primary productivity, nutrient cycling, and belowground foodweb dynamics.

In addition, investigators involved in the SGSLTER program continue to be involved in many synthesis activities. The SGSLTER project will produce a synthesis book this coming year. One of the areas that has made the SGSLTER unique is our emphasis on integrating our knowledge about SGS ecosystems

into simulation models. Our models are some of the most widely used worldwide. We plan to continue to use them to encapsulate and test our knowledge about SGS ecosystems.

## **SECTION 1: RESULTS FROM PRIOR SUPPORT**

We produced 117 papers in refereed journals, 22 book chapters, 21 dissertations and theses, and 81 abstracts from national and international meetings. We supported a large number of graduate (36) and undergraduate (160) students and post doctoral fellows (5). Scientists at our site are involved in a number of LTER network activities, through comparative modeling studies, international collaborations, and development of new crosssite experiments. This section is organized by a modified version of the LTER core areas. Because of space constraints, comprehensive and [more detailed results from our experiments and monitoring](#) can be found on our World Wide Web data page.

### **Populations and Processes:**

This work includes short and longterm population dynamics, foodweb structure, as well as competition, ecophysiological, demographic and phenological, and genetic structure studies (see also Sections [2A](#), [2B](#), and [2E](#)). *Bouteloua gracilis* (blue grama) is the most drought and grazing tolerant grass species and it is also the dominant plant species of the shortgrass steppe (SGS) (Milchunas et al. 1990, Lauenroth and Milchunas 1992). Similar to many other dominant perennial grasses in North American grasslands, blue grama recruits infrequently (Lauenroth et al. 1994) and has a long life span (Coffin and Lauenroth 1989, Lauenroth et al. 1996). Key processes for recruitment are seed production (Coffin and Lauenroth 1992)([Fig. 1.1](#)), dispersal (Section [2A](#)), establishment (Lauenroth et al. 1994, Section [2A](#)), and competition from established individuals (Aguilera and Lauenroth 1993, 1995, Section [2A](#)). Loss of this species results in more diverse but unstable systems ([Fig. 1.2](#)). Competition between blue grama and subdominant *Buchloe dactyloides* (buffalo grass) can be very intense under conditions of both low and high water and N availability (Aguilar 1995). Disturbance favors buffalo grass and drought favors blue grama (Aguilar et al. submitted, Aguiar 1995). Defoliation studies, assessing variables such as tiller and leaf dynamics, indicate that competition and defoliation act additively in interactions between blue grama and *Agropyron smithii* (western wheatgrass)(Gill 1992, Atsedu 1995). However, photosynthesis and stomatal conductance of western wheatgrass indicate

positive responses to defoliation, which may explain its persistence even though it is a highly preferred species by a number of herbivores (Fahnestock and Detling, in prep). Ecophysiological and demographic responses of plants are often related to landscape topography and/or previous history (Milchunas et al. 1992, Gill 1992).

Our research on consumer populations ranges from swift foxes to nematodes. Fiftyfour of 68 captured swift foxes, a Category II species, have been radio-collared and ear tagged. Comparison with data from the late 1970's suggests a population increase over the past 20 years and that the Central Plains Experimental Range (CPER) has a higher density of foxes than the surrounding area (Fitzgerald, in prep). Coyote predation is the most important source of fox mortality.

Diets of great horned owls are composed mostly of lagomorphs, although most individual prey items taken are rodents ([Fig. 1.3](#), Zimmerman et. al., submitted). Thirteenlined ground squirrels and other rodents (Fig 1.4) are most abundant in shrublands in association with high orthopteran density (Higgins and Stapp 1995). The spatial distributions of shrubs and orthopterans concomitantly increase along a soil texture gradient from grassland (sandy loam) to shrubland (loamy sand) (Stapp 1995a, Stapp 1995b, Stapp 1994, Stapp et al. 1994, Stapp and Van Horne 1995). The shrubby, sandy lowlands in SGS appear very important to landscapelevel biodiversity, even though the area of this habitat is small. Preliminary work on landscapelevel plant diversity suggests a conceptually similar relationship; most of the diversity is concentrated in habitat types that make up a small proportion of the total landscape (Hazlett, unpublished).

Nematodes at the CPER occur within 6 orders, 23 families and 40 genera and fall into five trophic groups(i.e. bacterial feeders, fungivores, omnivores, predators, and plant parasites). Populations are approximately twice as large in soil under individuals of blue grama than in the interspaces between individuals and appear to be unaffected by grazing.

Our work on patterns in detrital food webs supports the "dynamics hypothesis" that food chain length is a function of the limitations that increased length places on the likelihood of the system recovering from a minor disturbance (Moore et al. 1993a, b, Moore and De Ruiter 1993, Moore et al. accepted, De Ruiter et al. submitted). A second important result is that the feasibility of food chains (ability to maintain positive population densities at steady state) is a function of productivity and detritus inputs. Higher levels of productivity

sustain longer food chains. The conclusion of this work is that the energetic organization of communities forms the basis of ecosystem stability.

## **Biogeochemical Dynamics :**

Our research in this area ([Section 2B](#)) encompasses spatial patterns of processes in native grassland, responses to manipulations and landuse, and fluxes of trace gases.

In addition to longterm monitoring of net primary production ([Table 1.1](#), [Fig. 1.5](#)), we have been very active in issues concerning patterns and controls on primary production, as well as in assessing method-ological problems, developing new techniques, and spanning spatial scale issues (Boindini et al. 1991, Milchunas and Lauenroth 1992, Lauenroth and Sala 1992, Todd et al. 1993, McNaughton et al. in press). Early modeling and analytical work showed that traditional means of estimating NPP could lead to serious errors (Singh et al. 1984, Lauenroth et al. 1986, Sala et al. 1988). A longterm <sup>14</sup>C experiment substantiated these findings, and provided realistic estimates of NPP and an alternative to errorprone methods (Milchunas and Lauenroth 1992).

Spatial patterns of aboveground net primary production (ANPP) at the CPER are controlled by location on catenas at a toposequence scale, and soil texture at the larger landscape scale (Liang et al. 1988). Soil texture is also an important control on plant functional types with different rooting distributions (Milchunas et al. 1992, Lee and Lauenroth 1994). Analyses of temporal patterns of ANPP showed a positive relationship with precipitation, but that ANPP was more variable than precipitation (Lauenroth and Sala 1992). An important result from comparing these data to a regional data set was that spatial and temporal relationships between ANPP and precipitation are not interchangeable ([Fig. 1.6](#)). Grazing has negative but small effects on ANPP and variability in cool-season precipitation has a large effect on ANPP (Milchunas et al. 1994).

The SGS is characterized by patchy plant cover and associated spatial heterogeneity of soil resources (Hook et al. 1991). Heterogeneity in soil organic matter (SOM) at this scale is as strong as that induced by topography, and is tightly associated with root biomass (Hook et al. 1994, Kelly et al. in press). Enrichment of C and N under plants is associated with perennial bunchgrasses (Vinton and Burke 1995), and develops at a rate that corresponds with plant community successional dynamics (Burke et al. 1995). Death in individual bunchgrasses results in rapid depletion (3 years) of the enriched zone with

respect to mineralizable N and labile SOM pools, but heterogeneity of total C and N persists for decades ([Fig. 1.8](#), Kelly and Burke, submitted).

Additional factors in smallscale nutrient distributions involves the influence of aboveground structures on erosion processes, and on the quality of inputs by different plant species. There is substantial accumulation of wind and water-transported material under blue grama and plains pricklypear (*Opuntia polyacantha*). Grazing increases the movement from interspaces to underplants, and these effects are greatest in summit and midslope topographic positions (Burke et al. unpubl.). Plant species differ in quantity and quality of biomass, but differences in nutrient cycling under their canopies are slight (Vinton 1994). Soils under bunchgrasses had more microbial biomass and activity than under a rhizomatous grass, and soils under annuals had the highest mineralization rates. Comparing the importance of plant cover pattern to that of plant species effects across a gradient from the CPER to Konza, we found that plant cover pattern is most important in SGS, and plant species differences are most important in causing spatial pattern in tallgrass prairie (Vinton 1995).

SOM and nutrient availability are also strongly influenced by both soil texture and topographic position ([Fig. 1.7](#), Hook and Burke in prep). In two longterm <sup>15</sup>N studies (Delgado et al. 1995 and Hook et al. in prep), we have found that toeslope areas tend to retain up to 90% of <sup>15</sup>N added 10years ago, while summits and midslopes retain half or less. Grazed pastures retain less <sup>15</sup>N than ungrazed pastures.

Our trace gas flux studies (Mosier et al. 1991, 1993, 1994a,b, 1995, Bronson and Mosier 1994, Parton et al. 1994, Scholes et al. 1994) are confirming that aerobic SGS soils are important sinks for atmospheric CH<sub>4</sub>, and that gaseous N losses may be important to longterm N balance and productivity. Calculations using IPCC global warming potential indicate that the SGS has a net global warming capacity of 1100 (sink for greenhouse gases), and N gas loss rates are similar to atmospheric inputs. Fertilization has a large effect on N<sub>2</sub>O emissions and CH<sub>4</sub> uptake ([Fig. 1.9](#)).

## Paleoecology/Paleopedology:

In our investigation of paleosol geochemistry at the CPER, we proposed a Holocene paleoclimatic scenario (Kelly et al, 1993). A number of factors indicated that the early Holocene was cooler than either the midHolocene or current soil forming intervals, and that temperature has not increased from the midHolocene to the present (Blecker et al., in press). The <sup>13</sup>C/<sup>12</sup>C ratios of

paleosol SOM, phytoliths and CaCO<sub>3</sub> established the dominance of C<sub>3</sub> vegetation in the soil forming interval spanning 10,000-8,000 y.b.p., and the dominance of C<sub>4</sub> vegetation in both the 5,000-3,000 y.b.p. and contemporary soil forming intervals (Kelly et al, 1993). Organic C and phytolith data suggest that both the early and mid-Holocene climatic conditions were more favorable for plant productivity than the present climate ( [Fig. 1.10](#) , Kelly et al. submitted). This suggests cooler, moister conditions than presently occur. Pedon development in both the early and mid-Holocene paleosols suggests wetter soil moisture regimes than in the present (Blecker, 1993).

## Water and Energy Dynamics:

Water is the key driving variable for the dynamics of SGS ecosystems. Because of this, many of the interesting results of our work with soil water are best presented in the context of the response variables it controls (see other sections of this report).

Soil water monitoring data emphasize the interannual and seasonal variability in soil water as well as the critical role that soil texture plays in mediating storage and losses ([Fig. 1.11](#), Singh et al. in prep). Soil water availability is critical in controlling recruitment of blue grama (and probably other species) by influencing seed production, germination and establishment (Lauenroth et al. 1994, Section [2A](#)). Soil water availability is closely related to ANPP (Singh et al. in prep). Relationships between ANPP and precipitation (see [Biogeochemical Processes](#) above) assume that precipitation is a good surrogate for soil water. At large temporal (growing season or larger) and spatial scales (km<sup>2</sup> or larger) this is a good assumption.

Water losses (evaporation and transpiration) are largely controlled by water availability. Energy to evaporate water is almost always far in excess of the supply as indicated by the annual or seasonal ratio of precipitation to potential evapotranspiration (Parton et al. 1981). Sala et al (1992) found that the probability of a ratio of precipitation to potential evapotranspiration >1 was only 0.1 at the daily scale and decreased exponentially to 0.01 at the monthly scale. Quantifying bare soil evaporation and understanding how it is affected by soil texture are critical issues in understanding water loss. Results from an experiment with minilysimeters confirm a 2-stage water loss pattern with a short period of high water loss followed by a long period in which losses decrease exponentially (Wythers et al. in prep). By contrast, the minilysimeter results contradict the idea that the depth to which evaporation can remove water from

a soil decreases as coarseness of soil texture increases. We found the greatest depth of loss for a coarse sand.

Many of our questions about structure and function of SGS ecosystems require an understanding of longterm patterns of soil water dynamics. We used a simulation model to generate 30 years of soil water data for the CPER to provide this longterm view (Sala et al. 1992). Several key results were identified by this work. First, the general temporal pattern in soil water at the daily scale is not identical to the pattern in precipitation because of an interacting pattern of atmospheric demand. The peak in average soil water precedes the peak in average precipitation by almost a month. Second, the layer that most frequently had available water was very shallow (415 cm) ( Fig. 1.12 ). Layers above this were drier because of bare soil evaporation and layers below because most precipitation events are too small to move water that deep in the soil. Third, on average water penetrated to 100 cm (Fig. 1.12 ). In wet years, it reached 135 cm but in dry years it only reached 45 cm. These data provide important information for understanding vegetation structure in the SGS.

## Disturbances:

Our work in this area is extensive. We divide this section into natural and humaninduced disturbances (see Conceptual Framework Section 2 for distinctions). Currently landcover in the SGS is 60% cropland and 40% native grassland grazed by cattle (Burke et al. 1993).

**Natural disturbances:** The majority of natural disturbances are small (<100 m<sup>2</sup>) and there is an inverse relationship between size and frequency (Coffin and Lauenroth 1989). The most frequent disturbances (cattle fecal pats, harvester ant nest sites, root feeding invertebrates, and burrows from small animals) produce patches that range in size from 540 cm diameter ( Fig. 1.13 , Hook et al. 1994) and are important in shaping plant community structure and diversity across the landscape (Coffin and Lauenroth 1990). An important focus of our natural disturbance work has been the effect of disturbances on individuals of blue grama and its subsequent recolonization of disturbed patches. Previous studies had reported that blue grama can not recover after disturbance. In a study designed to look at the effects of patch size and neighbors on blue grama seedling growth and survival, we found that in openings <30 cm diameter, established neighbors could preempt resources and inhibit seedling establishment (Aguilera and Lauenroth 1993). Openings >30 cm were large enough to result in seedling establishment. Hook et al. (1994) reached a similar

conclusion about the size of a regeneration gap based upon how the root systems of neighbors explored patches created by disturbances ( Fig. 1.14 ). Simulation analyses and assessments of recovery on abandoned fields (see below) confirm that blue grama does reestablish following a disturbance although in some situations the rate may be quite slow ( Fig. 1.15 , Coffin and Lauenroth 1990, Coffin et al. 1996, Lauenroth et al. 1994). Recovery rates are dependent upon the characteristics of the disturbance, and in particular size and soil texture (Coffin and Lauenroth 1994, Coffin et al. 1993).

Root feeding by white grubs (June Beetle larvae) can cause mortality of blue grama over areas ranging from 0.1 to 100s of m<sup>2</sup>. A longterm experiment to follow recovery on grazed and ungrazed areas affected by white grubs (Coffin et al. submitted, [Table 1.1](#), Section [2E](#)) has produced the following results: 1. successional dynamics of plant functional types on patches affected by white grubs were similar to other disturbances; 2. strong relationships between survival of blue grama on the affected patches and cover on ungrazed areas indicate the importance of initial conditions; 3. the importance of grazing increased over time and the importance of initial conditions decreased.

#### **Humaninduced disturbances:**

We are continuing our research on the recovery of plants and soils on abandoned agricultural fields along precipitation and temperature gradients in Pawnee National Grasslands and soil texture gradients at the CPER (Burke et al. 1995, Coffin et al. 1996). We found a large variability in recovery of the vegetation that could not be explained by climatic factors. Recovery may be related to soil texture, since the ability of blue grama to recover through seedling establishment is affected by silt content of the soil (Lauenroth et al. 1994). Net N mineralization and other indicators of active SOM were lowest on cultivated fields, but were not significantly different between abandoned and native fields. Recovery of SOM in abandoned fields appears to involve accumulation of C and N under perennial plants. Higher N mineralization and turnover in cultivated fields may make them more susceptible to N losses (Ihori et al. 1995a), and recovery of N cycling in abandoned fields appears to involve a return to slower N turnover and tighter N cycling similar to native SGS. Although variation in native soil C and N correlated with climate and soil texture (Ihori et al. 1995b), soil losses due to cultivation were not explained by these variables. Rates of recovery were small compared with loss rates due to cultivation( [Fig 1.16](#) ).

We are also assessing recovery on nutrientenrichment treatments (Lauenroth et al. 1978). Invasions by exotic species and the development of characteristics of highly disturbed plant communities did not occur until several years after

treatments were terminated ( [Fig. 1.17](#) , Milchunas and Lauenroth 1995). The tendency of existing plant populations to continue to occupy a site when conditions become unfavorable, can create timelags in response that represent important challenges for environmental monitoring. The existence of timelags means that an ecosystem can pass through a threshold to an alternate state before it is detectable in species composition. These results have important implications for such things as global climate change and sulfur and nitrogen oxide pollution which also have the potential to act as enrichment stressors.

The SGS has a long evolutionary history of grazing by large herbivores. The importance of this force in shaping currentday structure and function of this system, and the importance of cattle grazing on both public and private land, have been reasons for the emphasis in research at this site in plantanimal interactions and longterm effects of grazing. Research in this area spans all five major areas. Although differences among plant communities on different grazing treatments have been found to be relatively minor (Milchunas et al. 1989), longterm ungrazed SGS plant communities are more similar to disturbed than were longterm grazed communities (Milchunas et al. 1990). Ungrazed compared to heavily grazed communities were found to be more susceptible to invasion by "weed" species ( [Fig. 1.18](#), Milchunas et al. 1992). Currentyear defoliation does have important effects on individual plants and on nutrient uptake by plants (Milchunas et al. 1995, Varnamkhasti et al. 1995). Increased forage quality in response to defoliation suggests a positive feedback between plants and grazers.

Although plant population changes with grazing are minor, other populations display a wide range of responses to grazing ( [Fig. 1.19](#) , Milchunas et al. in prep.). Groups such as aboveground arthropods, birds, and lagomorphs show large changes in abundance, dominance, or diversity in response to grazing, whereas groups such as microarthropods and nematodes show very little change. Endemic birds associated with SGS prefer to nest in heavily rather than lightly grazed treatments. Changes in biodiversity do not relate to changes in other structural or functional characteristics of the ecosystem.

Little or no effects of grazing on root and crown biomass have been observed (Milchunas and Lauenroth 1989). On average, ANPP declines slightly with grazing ( [Fig. 1.20](#) , Milchunas et al. 1994), but differences between treatments can shift depending upon levels of water resource and currentyear defoliation (Varnamkhasti et al. 1995). Soil nitrogen and carbon pools are not affected at moderate intensities of grazing (Burke et al. submitted), but have lower values than ungrazed treatments in heavily grazed lowlands (Milchunas and Lauenroth 1993).

In a grazing experiment initiated in 1991, we are examining longterm grazed and protected and newly ungrazed and protected SGS at 6 sites at the CPER ( [Section 2E](#) , [Table 1.1](#)). Key results to date focus on C and N dynamics. Total soil C and N pools were unaffected by moderate grazing or enclosure following both 2 and 53 years of treatment ( [Fig. 1.21](#) , Burke et al. submitted). Pools representing recent belowground litter inputs and substrate available for decomposition (particulate SOM and microbial biomass) were also unaffected by grazing treatments. However, mineralizable C and N, representing the most active pools of SOM, were significantly higher under longterm enclosure than longterm grazing, but only in bare soil areas between plants. Small decreases in mineralization may reflect slight erosion due to reduced canopy and litter cover, but the overall small effects of grazing may be due to increased plant basal cover that ameliorates thermal effects of reduced litter.

## **Synthesis:**

We have produced many synthesis products ( [Table 1.5](#)) over the past 5 years. Chief among our accomplishments is our simulation models, which we have linked to represent the interactions of plant communities, ecosystem dynamics (nutrient cycling and trace gas flux), and soil water. We describe our current activities in detail in [Section 2F](#).

## **SECTION 2: CONCEPTUAL FRAMEWORK AND RESEARCH PLAN**

In this Section we describe our conceptual framework, long- and short-term experiments, and how they fit into our conceptual framework. We have utilized tables and figures to summarize this information. [Table 1.1](#) summarizes our long-term experiments, including their design and sampling frequency. Published experiments are described in less detail, with references listed. We use figures and tables to highlight progress from past and ongoing research; numbered figures are cited in the text, un-numbered figures provide important additional information. Finally, our [complete progress report](#) from the past 6 years of LTER funding is on our World Wide Web page.

## **I. INTRODUCTION**

Our research focus over the past 14 years has been to understand the processes that account for the origin and maintenance of structure and function in shortgrass steppe (SGS) ecosystems ( [Fig2.1](#) ). The key questions that continue to organize and guide our research are:

1. How are the distribution and abundance of biotic components of the SGS maintained through time and over space?
2. To what factors are the distribution and abundance of biotic components vulnerable?
3. How do changes brought about by these factors influence biological interactions and ecosystem structure and function?

We have made significant progress toward answering these questions through research efforts that include long- and short-term experiments, monitoring, survey, simulation analyses, and spatial analyses. In the following section, we present a synthesis of our conceptual framework, our focal hypotheses, and research progress and plans.

## A. Conceptual Framework

Our conceptual framework asserts that one must consider the interplay of several forces, which occur at a variety of spatial and temporal scales, in order to understand the structure and function of SGS ecosystems. There are five components that we have identified as particularly important in shaping the SGS: climate, natural disturbance, physiography, human use, and biotic interactions ([Fig. 2.2](#)). Below, we provide an overview of the SGS in order to frame the unique interactions of these components, and then elaborate on each in turn.

### 1. Overview

The SGS occupies the middle of the productivity gradient along which the LTER grassland sites lie. It is unique among North American grasslands for its long evolutionary history of intense selection by both drought and herbivory, leading to an ecosystem that is very well adapted to withstand grazing by domestic livestock (Mack and Thompson 1982).

The distinctive features of the SGS are both its vegetation and the concentration of biological activity and organic matter belowground. The vegetation of the SGS is characterized by low- growing plants that are either tolerant or resistant to grazing and drought. The most common plants are two species of C<sub>4</sub> grasses, a cactus, and several species of dwarf-shrubs, all of which have a large fraction of their biomass belowground. The vegetation is strongly dominated by *Bouteloua gracilis* (blue grama), the grass species with the greatest tolerance to grazing and drought (Weaver and Albertson 1944). This species contributes 60-

80% of the plant cover, biomass, and net primary productivity of shortgrass ecosystems. The large concentration of biological activity belowground reflects the distribution of plant production (Milchunas and Lauenroth 1992) and the enhanced rates of energy flow through heterotrophs belowground (Lauenroth and Milchunas 1992). It is also explained in part by the fact that most biologically active elements in grasslands are protected from natural disturbances by being stored in soil organic matter (SOM).

This distribution of biotic components, with a large bias towards the belowground portion of the system, leads to important predictions about the response of SGS ecosystems to disturbances: those events that largely affect aboveground plant biomass, such as fire or grazing, are not likely to cause changes in total organic matter, or large alterations in the biotic community ( [Fig. 2.5](#) ). Recovery from such disturbances may occur in as few as 2-3 years due to the tolerance of the biota and the high rate of turnover of aboveground plant biomass. In other types of grasslands, there may be shifts in plant species composition in response to grazing or drought, leading to alterations in biota, and ecosystem structure and function. However, the evolutionary adaptations of organisms in the SGS provide additional resistance to grazing.

## **2. Conceptual Framework:** *Five important components*

Climate atmospheric processes including radiation inputs determine the water and energy balance of the system. Precipitation is the key driving variable for the temporal variability of biota in SGS ecosystems (Lauenroth and Sala 1992). Interannual variation in precipitation is high, but despite this, the seasonal pattern is quite reliable, with a peak in May and June and a dry period in December, January, and February (Lauenroth and Burke 1995). Spatially, atmospheric inputs are variable on the scale of kilometers.

Our research indicates that the biota have a large response to interannual and seasonal variations in precipitation (Lauenroth and Sala 1992). Perennial C<sub>4</sub> bunchgrasses maintain their presence and cover in all years, changing slowly with dry and wet periods. By contrast, C<sub>3</sub> grasses and annual forbs respond significantly to individual wet or dry years. Abundance and species composition of small mammals reflect precipitation- induced changes in vegetation structure (Grant et al. 1977) and resulting fluctuations in production of seeds and arthropods (Crawford 1991). Ecosystem functions such as net primary productivity (Lauenroth and Sala 1992), net N mineralization (Hook and Burke in prep), and trace gas flux (Mosier et al. 1991) are very responsive to interannual and seasonal variation in precipitation.

Temperature plays a lesser role in influencing SGS ecosystems because of its relatively small range of variability compared to precipitation. We have recently initiated a long-term experiment to evaluate the influence of increased temperatures predicted by climate change scenarios on ecosystem structure and function (see [Section 2.II.B](#)). There are significant feedbacks from SGS ecosystems to atmospheric processes, including reflected radiation, water vapor, and trace gases (see [Section 2.II.D](#)).

### *Natural Disturbance*

Natural disturbances are responsible for much of the spatial variability observed in SGS ecosystems. Most are small (0.1 m<sup>2</sup> to several hectares), and there is an inverse relationship between size and frequency (Coffin and Lauenroth 1988). The most frequent disturbances are fecal deposition by large herbivores (cattle), digging and burrowing by small mammals (pocket gophers, badgers, skunks, squirrels, and prairie dogs), outbreaks of root-feeding invertebrates (larvae of June beetles), and nest building by harvester ants. To a large extent, the ecological significance of a disturbance can be judged by its effects on the mortality of blue grama. This is because of the importance of blue grama to the structure and function of SGS ecosystems and because it has a slow rate of recolonization following a disturbance.

In distinguishing our 5 components, we exclude both drought and grazing from our list of natural disturbances due to the long evolutionary history of these selection pressures in the SGS. The climate of the SGS has fluctuated among subhumid, semiarid, and arid over the past 10,000 years (Table 2.1). At the time of settlement, the SGS was the home of native Americans and large numbers of bison, prairie dogs, elk, pronghorn, bighorn sheep, and deer. These herbivores had been present since the retreat of the Pleistocene glaciers, 10,000 years ago. Conceptually, we list herbivory except by cattle under biotic interactions, and cattle grazing under human use; drought is dealt with under atmospheric processes.

### *Physiography*

Physiographic features provide the parent material for soils and determine the rates of development and the mineralogical composition of the resulting soils. Temporal variability in physiography is very slow, operating on the scale of decades to centuries. Spatially, physiography is variable on the scale of 0.1-100 kilometers. Three aspects of physiography are most important in influencing ecosystem structure and function: landscape position, soil depth, and soil texture. In early years of the SGS LTER, we conceptualized the influence of physiography on ecosystems as a catenary landscape sequence, along which

soils became finer and deeper downslope (Schimel et al. 1985). Recently we have found that the geomorphic and pedologic history of the region has resulted in a complex array of physiographic units across landscapes (Yonker et al. 1988).

Soil texture and depth play an important role in controlling water availability, a key constraint for the biota of SGS ecosystems. In sandy soils, water moves to greater depths and surface evaporation is lower than in fine-textured soils, leading to lower bare-soil evaporation rates and different vegetation structure (Noy-Meir 1973, Lane 1995). Deep sandy soils often support large shrubs which, in turn, strongly influence the presence and abundance of small mammals (Stapp in prep). Soil texture also exerts control over decomposition and N mineralization ( Fig. 1.4). Areas of fine texture are characterized by higher SOM accumulation, due to the lower mass-specific decomposition rates, and leading to higher N mineralization (Hook and Burke in prep) and N<sub>2</sub>O flux (Mosier et al. submitted).

### *Human Use*

Human use has been and continues to be a major force influencing the structure and function of SGS ecosystems. Grazing by cattle is a major influence; virtually every hectare of native SGS is currently being grazed. Our LTER site has the oldest, largest, and most numerous livestock grazing exclosures in the entire shortgrass region. Our past LTER research indicates that shortgrass ecosystems are relatively resistant to negative effects of grazing (Milchunas et al. 1989). Long-term (50+ years) heavy grazing during the growing season has small effects on plant species composition and diversity and results in increased importance of blue grama( [Fig. 2.6](#))(Milchunas et al. 1989). Furthermore, heavy grazing appears to reduce the vulnerability of the plant community to invasion by exotics ([Fig. 1.18](#), Milchunas et al. 1992).

The SGS has been subjected to several periods of conversion to croplands and subsequent periods of cropland abandonment. Sixty percent of the SGS is currently being cultivated (Lauenroth et al. 1994) and up to 30% more was cultivated at some time in the past 100 years. As a result, a component of our studies deals with the recovery of abandoned croplands, although our research focuses on native steppe. Cropping drastically alters biological diversity (e.g. Holland and Coleman 1984), reduces SOM (Haas et al. 1957, Burke et al. 1989), and alters the temporal and spatial distribution of plant biomass. Our work on abandoned fields indicates that while vegetation, nematodes, active SOM, CH<sub>4</sub> consumption and N<sub>2</sub>O emissions may recover within 50 years, total SOM does not.

## *Biotic Interactions*

Beyond the obvious role of organisms as elements of the structure and function of shortgrass ecosystems, interactions among and between organisms and the other 4 forces (climate, natural disturbance, physiography, and human use) are the critical determinants of both the current state and the future vulnerability of SGS ecosystems. Biotic interactions provide the mechanisms whereby ecosystem structure and function are affected by and, in turn, affect climate, disturbance, physiography, and human use. Biotic interactions are the key focus of our LTER research ( [Fig. 2.3](#)).

In summary, our conceptual model ( [Fig. 2.2](#) ) suggests that the current state and vulnerability of SGS ecosystems (structure and function) requires understanding of five major components and their interactions with the ecosystem: climate, natural disturbance, physiography, human use, and biotic interactions. Our past, present and future research is focused on these components even though we have not organized this proposal explicitly around them.

## **B. Shortgrass Steppe Site Definition**

The SGS LTER project has been based at the Central Plains Experimental Range (CPER), a 6500-ha research site established by the USDA in 1937. The site was also a U.S. IBP site in the late 1960's and early 1970's. The work by USDA scientists and the IBP experience and database have been tremendous resources for the SGS LTER project (Table 1.4).

A recent analysis (Burke and Lauenroth 1993) suggested that the precipitation, temperature, vegetation, landuse, and soil characteristics of the CPER represent a small portion of the SGS. The areas not adequately represented include fine-textured soils and areas with mean annual precipitation >321 mm. To increase our realm of inference to better represent the SGS, and to increase the land area that we may use in our studies, we have increased the spatial extent of our LTER site to include both the CPER and the Pawnee National Grasslands (PNG) (Table 2.2). The PNG represents 78,100 ha of public lands administered by the U.S. Forest Service (USFS) adjacent to the CPER, and extending 90 km to the east. The PNG is discontinuously distributed across northeastern CO because these lands are the result of acquisitions of private land beginning in the Dust Bowl era. By expanding to our newly defined site, we increase our realm of inference to 23% of the SGS ( [Fig. 2.7](#) ; see also [Fig. 5.2](#)).

We have an agreement with the PNG based upon the Memorandum of Understanding between the USFS and NSF, and upon a letter of agreement that we have exchanged (Appendix 1). This new partnership has the potential to dramatically improve our ability to meet both our LTER mission and that of the USFS with respect to understanding and managing the SGS.

Increasing the spatial extent of our site during a period of decreased funding is an interesting problem. Our plan is to increase our work on the PNG slowly, beginning in Summer 1996, while maintaining all our long-term experiments at the CPER. We will begin to sample the status of the complete site remotely (i.e., TM and AVHRR for production, and NEXRAD for precipitation) with the beginning of the new funding cycle. We have already developed a detailed spatial database for the PNG as part of our larger regional analysis program.

## **II. CONTINUING AND PROPOSED RESEARCH**

We have divided our continuing and proposed work into five areas that represent the biology of the SGS (internal box in [Fig. 2.2](#)): Populations and Trophic Dynamics, Biogeochemical Dynamics, Paleoecology/Paleopedology, Water and Energy Dynamics, and Disturbances/Human Use. The list of our experiments and monitoring is very long and may at first seem very diverse. Our objective in initiating this work and in designing this proposal was to keep the research and the presentation focused either explicitly or implicitly on our conceptual framework and key questions. The new areas that we have prioritized for the next six years are: 1) the evaluation of keystone species, prairie dogs and cactus; 2) population genetics of blue grama 3) atmosphere-biosphere interactions; and 4) detrital food web dynamics. We refer to [Table 1.1](#) for ongoing long term experiments using the symbol LT#, and to new short-term and new long-term work using the symbols NEW-ST and NEW-LT, respectively. One of the areas that has made the SGS LTER unique is our emphasis on integrating our knowledge about SGS ecosystems into simulation models. This has had enormous benefits to us and ecological science in general. Our models are some of the most widely used worldwide. The models are an integral part of our research activity and we plan to continue to use them to encapsulate and test our knowledge about SGS ecosystems.

### **A. Populations and Trophic Dynamics**

This work is organized by the idea that two kinds of populations are most important in the long- term dynamics and sustainability of the SGS ( [Fig. 2.3](#) ). The first are those that because of their abundance have a large effect on the

ecosystem. The dominant plants and cattle are examples. The second are those that because of their effects on the ecosystem have a large effect on long-term dynamics. These are keystone species, and we propose that prairie dogs and plains prickly-pear are such species for the SGS. This organization implicitly creates a third category of those that are not very abundant and are not known to have large effects on ecosystems, which we examine at a lower level of priority. The status of such populations may change under altered biotic or abiotic conditions.

## **1. Plants**

Grasses, shrubs, forbs, and succulents are the major components of the vegetation structure of the SGS. One grass species, blue grama, contributes a huge fraction of the biomass and NPP. Because of its overwhelming importance, our past plant population work has focused heavily on blue grama. This work is closely related to our disturbance research ( [Section 2.II.E](#) ). Another grass species, *Buchloe dactyloides* (buffalo grass) can achieve co-dominant status on certain locations; we have recently begun to study its demography and interactions with blue grama. We are proposing to continue to study blue grama and buffalo grass as well as to initiate studies on the most important forb and shrub species. We are proposing to initiate long-term studies of population dynamics of *Opuntia polyacantha* (plains prickly-pear). This species makes up a relatively small proportion of biomass or NPP but because of its growth form and protection from grazing, it has the potential to have a large effect on ecosystem dynamics under cattle grazing.

### **Population dynamics of blue grama - LT1, NEW-ST, NEW-LT**

Our past work has focused on the spatial and temporal variability in recruitment and mortality of individual blue grama plants. We currently sample blue grama seed production each year ( [Fig.1.1](#) , [Table 1.1](#) ). We propose to continue this work as well as establish long-term permanent plots to investigate the relationship between environmental variability and recruitment, growth, and mortality. Our population dynamics work is guided by hypothesis 2.1 (Table 2.3). This hypothesis provides a direct connection between biotic vulnerability and ecosystem structure and function (Fig. 2.1, [2.2](#)).

Recruitment of blue grama is an infrequent event controlled by the availability of viable seed, temperature, soil water, and competition from established plants (Lauenroth et al. 1994, Aguilera and Lauenroth 1995). Requirements for germination and establishment are well known; we therefore focus our efforts on other processes. To date we have learned that (1) seed production is negatively related to soil clay content, and the shape of the relationship is

different for grazed and ungrazed locations (Coffin and Lauenroth 1992); (2) seed storage in the soil is very limited and variable in time and space (Coffin and Lauenroth 1989); and (3) the suitability of a site for germination and establishment depends strongly on proximity to an established individual of blue grama (Aguilera and Lauenroth 1993, 1995, Hook et al. 1994). We are also currently exploring the roles of wind and cattle on seed dispersal.

We have also conducted a simulation analysis using a soil water dynamics model (SOILWAT) to evaluate the frequency of climatic conditions suitable for the establishment of the blue grama seedlings. We found that the probability of establishment increases as soil silt content increases and that return times for establishment events range from <30 years (silty clay loam) to >5000 years (sand) (Lauenroth et al. 1994). These results lead us to design new experiments to test the hypothesis that seedling establishment of blue grama is related to soil texture, and in particular silt content. We will collect soils of different textures, place them in pots in a growth chamber, and water them with different amounts and frequencies of addition. Seeds collected from the CPER will be added to each pot. Germination and establishment will be determined for each soil texture and water treatment. At the end of the study, seedlings will be harvested for above- and belowground biomass as well as number and length of roots. We will also conduct a long-term field study adding blue grama seeds to a variety of microsite types (in tussocks and in openings of several sizes) at locations with different soil textures. Seeds will be added to each site each year and the number of surviving seedlings will be counted at regular intervals.

Little is known about mortality in long-lived clonal plants such as blue grama. Our field studies on the role of small disturbances suggested that mortality occurs only if the entire plant is affected by the disturbance ( [Fig. 2.8](#) ). To further investigate factors causing mortality of blue grama and the role of environmental variability on recruitment and growth, we will initiate a new study using permanent plots (0.5 m<sup>2</sup>) to evaluate individual and population dynamics through time. Five plots will be established on each of 2-4 soil textures in moderately grazed pastures and exclosures. Individual plants of all species will be mapped in each plot annually. Plots will be selected to include blue grama as well as other species. This study will also provide information about the demography of the co-dominant buffalo grass.

### **Performance of morphologically different genotypes of blue grama NEW-ST**

*B. gracilis* is characterized by high morphological variation. McGinnies et al. (1988), reporting on plant material from a garden in which 12 replicates of 60 clones of blue grama were established in 1982, provided evidence that at least

some of the variation is genetic. LTER now manages this garden and we plan to initiate studies to understand the mechanisms that maintain this high morphological variation. Genetic variation in plasticity of plant traits or fitness in response to a heterogeneous environment can be quantified as a "norm of reaction", defined as the array of phenotypes produced by a specific genotype in response to variation in the developmental environment. Genetic variation in phenotypic plasticity can be viewed as a genotype x environment interaction measured using standard family structured quantitative genetics approaches with sibships split into multiple environments. The hypothesis for this work (Hypothesis 2.2) is in Table 2.3.

Genotypes of blue grama that differ with respect to culm height, leaf length, culm number, and other key characters will be identified and collected in the fall from the LTER common garden. They will be cloned over winter in a greenhouse to produce the required number of plants. In the spring they will be transplanted into four cattle grazing treatments: grazed, protected, protected but clipped, and protected by prickly-pear. Measurements will be made on growth and fitness. If genotypes exhibiting alternative morphologies show changes in fitness rank across grazing environments, then a genotype x environment interaction model of the maintenance of genetic variation in blue grama will be supported.

### **Competitive interactions between blue grama and buffalo grass NEW-LT, NEW-ST**

We recently completed a study to evaluate intra- and inter-specific competitive interactions between blue grama and buffalo grass as a function of N and water treatments (Fig. 2.9). Results indicated that biomass accumulation and reproductive output are reduced under conditions of intra- and inter-specific competition for both species, but intensity and importance of competition were different for the two species (Aguiar et al. 1993). Simulation analyses indicated that differences in the response of the two grasses to disturbance and differences in recruitment may be more important than competition to explain observed patterns of relative abundance. We will initiate a new short-term experiment to evaluate the relative importance of disturbance and recruitment frequency on the relative abundance's of blue grama and buffalo grass. Our new long-term permanent plots will provide observation of this relationship, and allow us to determine if long-term trends are similar to short-term patterns.

### **Population dynamics of plains prickly-pear NEW-ST, NEW-LT**

The common view of prickly-pear is that it increases as a result of grazing. Research in the SGS and the mixed prairie has failed to support this idea (Houston 1963, Hyder et al. 1975, Dougherty 1986). Our past work on prickly-

pear has focused on long-term population dynamics using existing data ([Fig. 2.10](#)) (Dougherty 1986, and et al. in prep) and physiological responses to resource manipulation ([Fig. 2.11](#)) (Dougherty et al. 1996). Recent work has suggested a critical role for prickly-pear in maintaining plant species richness ([Figure 2.12](#)) and soil C and N ([Figure 2.13](#)) under heavy cattle grazing (Bayless in prep, Brannen 1995, and Madigan in prep). We plan to initiate short-term studies to test the importance of these results under the most common grazing intensity in the SGS (moderate) and in a long-term population dynamics study. This work will be guided by hypothesis 2.3 (Table 2.3)

We will initiate a study of long-term population dynamics of prickly-pear using 20 similar sized clones (> 30 cm dia.) in each of 3 moderately grazed pastures and exclosures. Annually, a drawing of each clone will be updated with information about the numbers of live (new and surviving) and dead cladodes (pads). We will also record which cladodes support a flower. This will be critical information for understanding the dynamics of clones as well as the role that prickly-pear plays in shortgrass ecosystems.

We will begin a short-term study to investigate the influence of prickly-pear on plant species richness, seed production and soil seed storage under moderate grazing and across several soil textures. We will sample 20 similar sized clones (> 30 cm dia.) in 3 moderately grazed pastures. Within each clone and in an adjacent space between clones, we will identify all plant species, harvest inflorescences, and take soil cores from which we will germinate stored seeds in a greenhouse.

### **Population dynamics of other species NEW-LT**

We will initiate a long-term study of population dynamics of other important plant species. Our objective for this work will be to assess the longevity and mortality of established individuals. We will map and measure individual plants of a) C<sub>3</sub> and C<sub>4</sub> perennial grasses: *Aristida longiseta*, *Sitanion hystrix*, and *Agropyron smithii*; b) perennial forbs and shrubs: *Sphaeralcea coccinea*, *Gutierrezia sarothrae*, *Atriplex canescens*, and *Chrysothamnus nauseosus*. Plants will be measured annually in 2-4 pastures of different soil textures at the CPER. Plant size (basal area for grasses or canopy dimensions (height and 2 widths) for forbs and shrubs) will be estimated. Size and frequency of disturbances will also be mapped and marked at these sites as one source of mortality.

### **Plant Phenology LT2**

The timing of major events in the life-cycle of organisms provides important information about the biological environment. Plant phenology provides a

plant-integrated assessment of environmental conditions, particularly temperature and precipitation. In 1996, we began a long-term project to assess 7 major phenological events for 31 species. These data are collected near our micromet station and employ an "average individual" approach ([Table 1.1](#)).

## **2. Animals**

### **Black-tailed prairie dogs (*Cynomys ludovicianus*) NEW-ST, NEW-LT**

Estimates of the presettlement numbers of black-tailed prairie dogs in North American grasslands range from hundreds of millions to billions, and it is thought that up to 170 other vertebrate species are dependent in whole or part on the activities of prairie dogs (Miller et al. 1994). Our proposed work on prairie dogs is one of the new thrusts of our project. We will focus on population dynamics, diet selection, effects of prairie dogs on plant species diversity, and their importance in the diets of mammalian and avian predators. We will be guided by hypothesis 2.4 (Table 2.3).

The importance of prairie dogs at a location depends on colony density, extent, and temporal persistence. Since 1981, the USFS has conducted annual assessments of colonies on the PNG. Numbers of active colonies have varied from 8 to 26; in 1994 13 colonies were active. Nine of these 13 were active in 1989. Global Positioning System locations have been obtained for 104 colony sites (active and inactive) and entered into our GIS database. Data and discussions with USFS personnel (Mark Bahl, per comm) indicate that it is common for colonies to go extinct after 5-10 years. Causes of extinction's are variously ascribed to control efforts and to plague. Control by ranchers is extensive in the western United States, and has greatly increased isolation and fragmentation (Miller et al. 1994). A proposal being submitted concurrently to the NSF program for post-doctoral research (Antolin and Bowser) would fund a genetic study of colony effective distance and relatedness. The proposed research would provide insights into the genetic implications of metapopulation dynamics in highly fragmented populations governed by founder effects.

We plan to identify 3 of the 9 active colonies and begin collecting long-term demographic data by live trapping. Black-tailed prairie dogs are moderately trappable, and by using large numbers of traps we will be able to capture nearly all individuals in the focal colonies (Hoogland 1995 for methods). Trapped animals will be marked with Passive Integrated Transponders and a temporary dye. Observations from a hunter's stand will allow us to identify and target-trap unmarked animals.

Fecal pellets from known animals will be used to assess early spring diets (influence on plant survival) and midsummer diets (influence on seedfall) to interpret plant community changes associated with the colonies. Samples will be analyzed at the Fort Collins Diet Composition and Analysis Laboratory. Dietary information will also be used to develop a proposal (Van Horne, Florant, Antolin) to study the role of dietary fatty acids in influencing hibernation patterns in prairie dogs.

Prairie dogs have been shown to have direct effects on plant communities, and indirect effects on other grazers and ground-nesting birds in mixed grass prairie (Whicker and Detling 1988). Although the effect of grazing by cattle has been assessed on the CPER, the role of small herbivores has received little attention, and may be very different. Long-term heavily grazed plant communities at the CPER have been found to have lower diversity and lower numbers of exotic 'weed' species than were ungrazed communities (Milchunas et al. 1989, 1990). In contrast, prairie dog colonies can have higher diversity and numbers of annual species than off-town locations (Bonham and Lerwick 1976). Areas near prairie dog burrows are heavily disturbed by digging, and soil disturbance can result in up to six times the number of 'weed' species compared to undisturbed areas ( [Fig. 1.18](#) ) (Milchunas et al. 1992). Prairie dogs may thus be important in creating islands of habitat for less common native opportunistic plant species, as well as potential centers for exotic invasions. Because prairie dogs and cattle appear to have opposite effects on plant diversity and/or invasion, grazing by both species in combination has unknown impacts on the SGS.

We will address the hypothesis that grazing by both large (cattle) and small (prairie dogs) herbivores will result in on-town plant communities with a high diversity of native plant species relative to off-town communities and low numbers of exotic invaders compared to plant communities grazed only by prairie dogs. This will entail protecting plots on prairie dog towns with cages with different mesh sizes; large mesh, open-sided cages allowing prairie dog access and excluding cattle, and small mesh cages that exclude both prairie dogs and cattle. The initial design would include 4 treatments: 1) off-town/cattle grazed, 2) on-town, grazed by both, 3) on-town, no cattle, and possibly 4) on-town, both excluded.

Prairie dogs are potential prey species for mammalian (coyotes, red or swift foxes, and badgers) and avian (Swainson's hawks, great-horned owls, prairie falcons) predators, representing a patchy, concentrated, and predictable (within-season) prey source. We plan to investigate the relative frequency of prairie dogs in diets of these predators. We expect that the relative frequency will be

high for predators near colonies, and will decline with distance to colonies. The scale of decline will vary with predator type.

To determine which predators utilize prairie dogs as a significant dietary source, we will review datasets on the food habits of local predators. We have identified an unpublished dataset that includes fecal and pellet material of mammalian and avian predators that was collected by a variety of investigators but as yet has not been analyzed. We will analyze these remains for the presence of prairie dog fur and/or bones using standard scat and pellet analysis techniques (Reynolds and Aebischer 1991, and Zimmerman et al. In press). The proportion of scats and pellets containing prairie dog remains will be used in conjunction with a Monte Carlo simulation to estimate the sample sizes necessary to detect, at a specified level of reliability, a real difference in each species' diet from scat and pellets collected at three different distances (<0.5 km, 0.5-1.0 km and > 1.0 km) from the prairie dog town (Reynolds and Aebisher 1991).

Two procedures will be used to collect the appropriate sample sizes of feces and pellets within these distance categories. During the growing season when feces and pellets are difficult to detect in the landscape, they will be collected at regular intervals from raptor nest sites and carnivore den sites. The distance from the closest prairie dog town will be used to categorize the remains. During the winter when fecal and pellet detectability is high, we will walk 2-3 km line transects that radiate from prairie dog towns with random orientations. All scat and pellets will be collected and identified to predator species based on scat and pellet morphometrics (Green and Flinders 1981, Danner and Dodd 1982) and comparisons with material collected at den and nest sites. Sampling intensity during both seasons will be based on the results of the power analyses and fecal and pellet densities. All scats and pellets will be analyzed for the presence of prairie dog remains. The effect of distance from a town on the proportion of prairie dogs in the diet of each predator species will be analyzed using logistic regression (Hosmer and Lemeshow 1989).

### **Population dynamics of other rodents and lagomorphs - LT3, LT4, LT5**

Fifteen rodent species have been captured or reported for the research site, but 3 species are most abundant ( [Fig. 2.14](#) ). In 1994, we began a long-term project to annually census populations of nocturnal rodents. Rodent densities are estimated in mid-spring (April/May) and late-summer (August/September) on three 3.14-ha trapping webs on upland prairie (dominated by blue grama) and three webs on shrubland/grassland (co-dominated by blue grama and four-wing saltbush (*Atriplex canescens*) [Table 1.1](#)). Distance sampling is used to estimate densities (Buckland et al. 1993). This modeling technique is useful for

census studies because it allows direct estimation of density (versus separate estimation of population size and sampling area), doesn't require unique individual marks, and because webs and transect are easy to establish and run. Our first year of results suggests that rodent diversity may be similar on uplands and shrubland / grassland sites, but that rodents are more abundant on shrub-dominated lowlands ( [Fig.2.17](#)).

In 1994, we began to annually census populations of nocturnal lagomorphs. We spotlight rabbits along a 32-km route of gravel roads and trails on one night in Jan, Apr, Jul, and Oct. Perpendicular distances from the vehicle to rabbits are recorded; these data are used to estimate density. Black-tailed jackrabbits (*Lepus californicus*) and desert cottontails (*Sylvilagus audubonii*) are the most abundant species ( [Fig. 2.15](#) ). White-tailed jackrabbits (*L. townsendii*) are relatively uncommon and occur primarily on upland prairie.

#### **Population censusing of canids - LT6**

In 1994 we began collecting scats in Jan, Apr, Jul, and Oct along the lagomorph survey route to census relative numbers of coyotes (*Canis latrans*) and swift foxes (*Vulpes velox*). All scats are removed from the survey route 10 d prior to sampling. During sampling, the route is driven slowly and the location, species and approximate age of all scats are recorded. These data provide an index of relative abundance ( [Fig. 2.16](#) ). Through funding on an ROA, we are also radio collaring swift foxes to characterize their movements.

#### **Population censusing of birds LT7, LT8**

We have censused populations of song birds along a 39.2 km roadside summer breeding bird transect since 1968. These data are part of the national survey that is coordinated by the National Biological Survey at Patuxent Wildlife Research Center, Laurel, MD. Lark Buntings (neotropical migrant) and Horned Larks (residents) have declined steadily over the 17 years. This result is consistent with a national trend for Lark Buntings.

#### **Population censusing of june beetles (*Phyllophaga* sp.) LT9**

June beetles represent an important population because of their effects on the system rather than as a result of their abundance. The larval stage of *Phyllophaga* feeds on roots of blue grama which in certain years results in widespread but patchy death of individuals (see disturbance section). Populations of adults were monitored from 1986-1990 using light traps. Because of their importance as sources of mortality of blue grama we plan to initiate long-term sampling in 1996.

### **Population censusing of arthropods LT10**

We began this work in 1994 and will continue for several more years to provide baseline density and diversity data. A reference collection is being compiled. Sampling will be repeated in the future on a 2-4 year cycle ( [Table 1.1](#)). Six 638 m<sup>2</sup> live pitfall trapping webs are located in six areas. Each web consists of 80 numbered traps, giving a total of 480 traps (80 traps x 6 webs). Each web is arranged in 8 rays radiating out from a central spot, with 10 traps per ray. The rays correspond to the cardinal compass directions. Trapping is conducted monthly from May through August (4 trapping sessions). Traps are checked daily for six consecutive days.

## **B. Biogeochemical Processes**

Our work on biogeochemical processes represents an integral part of our conceptual framework. We conceive of biogeochemical processes as the integrated function of biotic components, those processes responsible for carbon and nutrient fluxes in the ecosystem: primary productivity, decomposition, nutrient mineralization and availability, and trace gas flux. These processes are influenced by all of the 5 major forces in our system: climate, biotic interactions, physiography, and natural and human-induced disturbances. We address the influence of disturbances on biogeochemical processes under the Disturbances section. Our research on biogeochemical processes is guided by hypothesis 2.5 (Table 2.4).

### **Long-term sampling of aboveground net primary production LT11, LT12, LT13**

We plan to continue to annually sample aboveground net primary production (ANPP) on six sites selected to represent topographic positions, soil texture, and grazing treatments ([Table 1.1](#), [Fig. 1.5](#)). Four sites have been sampled since 1983, and two since 1991. Nitrogen concentrations and yields are determined for all long-term ANPP sites. In addition, we have data from the ARS on forage production, which is statistically related to ANPP (Lauenroth and Sala 1992), that date from 1938. As a result of an experiment started in 1992 to study the effects of grazing and protection from grazing on shortgrass ecosystem structure and function, we are also sampling ANPP in each of four treatments at five sites (LT37.).

### **Warming, wetting, and N additions LT14**

A prediction of our conceptual framework is that there are two-way interactions between the structure and function of SGS ecosystems. Results from a long-term data set on ANPP suggested that ecosystem structure constrained ANPP

(Lauenroth and Sala 1992). Production was greater in dry years and less in wet years than expected by comparison with sites with mean annual precipitation corresponding to the wet and dry conditions. How does the relationship between ecosystem structure and function change under altered climate and resource availability?

We initiated a long-term experiment this past summer (1995) that addresses questions about the effects of increased temperature, increased water availability, and increased N availability on the relationship between ecosystem structure and function. This study was begun with funding from an Cross-Site LTER project, and a portion of the experiment (temperature and water manipulations) is also being conducted in the Patagonian steppe in Argentina by our collaborator Osvaldo Sala. When the Cross-Site project is completed, we plan to support the continuation of the experiment from our LTER grant. In each of two blocks, we have implemented 4 treatments that each cover 1200 m<sup>2</sup>: irrigated, control, N fertilization, and N fertilization plus irrigation. In the control and irrigated treatments, we have installed 60 passive warming chambers, so that we can assess a total of 6 treatments (the prior 4 plus warmed, and warmed and irrigated). We are measuring the responses of vegetation structure (species composition and numbers of tillers), ANPP, and decomposition (leaf and root litterbags) to these treatments, which we plan to sample intensively for the next several years, and less intensively for 20 years or more.

### **Seasonal soil-atmosphere exchange of CH<sub>4</sub>, N<sub>2</sub>O and CO<sub>2</sub> LT15**

Since 1990, we have been sampling trace gas flux (CH<sub>4</sub>, N<sub>2</sub>O and CO<sub>2</sub>) at 10 locations weekly on the CPER throughout the year ([Table 1.1](#)). Most trace-gas budgets assume that trace-gas exchange between the soil and the atmosphere stops when soil is snow covered or soil temperatures drop to 0°C. Since soil temperatures are at this temperature or below for a large part of each year, we have chosen to continue measurements throughout the winter. Our results to date indicate that winter fluxes of NO, N<sub>2</sub>O, and CH<sub>4</sub> uptake make up 10-50% of the annual mean flux ([Fig. 1.9](#)).

### **Plant Production and Nutrient Cycling Across Soil Textural Gradients NEW-LT**

Several experiments were set up during the last 6 years to evaluate the impact of soil texture and nutrient cycling on plant production. The results from the comparison of sandy loam with sandy soil supported the inverse texture hypothesis (Noy Meir 1973) with higher aboveground production in the sandy soils. However, our comparison of plant production along catenas from sandy loam uplands to loamy swales showed that production was higher in the swale

sites ( [Fig. 1.5](#) ). The most likely causes of higher production in the swales are 1) increased soil water availability and 2) increased N availability. Data suggest that N mineralization in swales is higher because of greater N retention in fine textured soils (Delgado et al. 1995) and deposition of SOM. The only explanation for higher water availability in swales would be downslope movement, but our neutron probe soil water data are not resolved enough to detect this movement. We plan to seek additional funding to conduct an experiment to evaluate the relative importance of nutrient availability and water availability on the observed spatial patterns of plant production.

### **Long-term 14C plots, belowground production, and root biomass dynamics LT16, LT17, NEW-LT**

We plan to continue to evaluate belowground production using a radioisotope technique. Large plots (8 m<sup>2</sup>) were labeled with 14C to assess the implications of short- and long-term carbon dynamics on estimates of aboveground, crown, and root production using 14C dilution, 14C turnover, and traditional harvest methods ([Fig. 2.17](#)) (Milchunas and Lauenroth 1992). 14C turnover appears to provide reliable estimates of aboveground, crown, and root production, although they are an average over several years. In 1995 we collected our 11th annual samples from the 14C plots.

### **NEW:**

Equipment to sample minirhizotron tubes was obtained through a Colorado Agricultural Experiment Station equipment grant in 1995. We began this past growing season installing tubes adjacent to the 14C plots and the root-harvest plots, where we have 11 yrs of root biomass data collected through the growing season. Minirhizotron tubes will also be installed at our 6-site, 4- treatment grazing experiment, and in 2 shrub-dominated areas.

### **Short-term study on C distribution and decomposition throughout the soil profile NEW-ST**

A recent comparison of root biomass data ([Fig. 2.18](#))(Lee and Lauenroth 1994) and SOM data (Yonker et al. 1988) suggested that soil carbon profiles do not match those of root production or root biomass; the proportion of SOM at depth is significantly higher than one would expect from grass-dominated ecosystems. We will utilize the 14C plots to determine where the 14C is going in terms of labile and recalcitrant soil C pools. Results will allow us to infer the rate of SOM stabilization throughout the soil profile. In addition, we will conduct a litterbag study to evaluate decomposition rates with depth. We will incubate root litterbags at 7 depths in 10 replicate profiles, to be collected at intervals of 4 mo., 1, 2, 3, 5, 10, and 20 years. This work will be guided by hypothesis 2.6 (Table 2.4).

### **Long term 15N studies in the SGS LT18, LT19**

In 1988, we initiated a long-term <sup>15</sup>N study to evaluate the interaction of topographic position and grazing on N retention and distribution ( [Fig. 2.19](#) ). We labeled 3 1-m<sup>2</sup> plots on summits and toeslopes in each of 3 catenas, and in two grazing treatments, heavily grazed and protected. We plan to continue to sample these treatments on a decadal scale for an indefinite period of time. We sample each plot to determine <sup>15</sup>N retained in plant material (leaves, crowns, and roots), and in mineralizable, slow (particulate SOM, Cambardella and Elliott 1992), and recalcitrant fractions of SOM. This study will be important to assess the interactions of abiotic variables and management in controlling N retention. Our work on N retention is guided by hypothesis 2.7 (Table 2.4).

### **The influence of plant functional type on N retention NEW-ST**

We are currently testing the influence of dominance by C<sub>3</sub> and C<sub>4</sub> plants on N retention. We have located two sites on the CPER that are co-dominated by C<sub>3</sub> and C<sub>4</sub> plants, and have initiated two experiments on these sites. Our hypothesis is that C<sub>3</sub> dominated plots will have highest losses of N in summer, when the rate of plant uptake is lowest, C<sub>4</sub> dominated plots will have highest rates of N losses during spring before plants are active, and co-dominated plots will sustain the lowest rates of N loss. We established 3 replicate plots of community type at each site, for each of 3 treatments: control, spring water addition, and summer water addition. Each plot has been augmented with 2 g<sup>15</sup>N m<sup>-2</sup>, and is being sampled at the end of the 1995 and 1996 growing seasons to assess N retention. Trace gas flux (N<sub>2</sub>O, NO, and CH<sub>4</sub>) is measured in each treatment on a weekly basis, from April through October ( [Fig. 2.20](#) ).

### **Study of enhanced CO<sub>2</sub> on SGS ecosystem structure and function LT20**

Atmospheric CO<sub>2</sub> concentrations have been rising over the past several decades at unprecedented rates, and are projected to continue rising (IPCC 1995). No field studies have addressed how elevated CO<sub>2</sub> might impact the SGS. A study such as this will be particularly interesting because the SGS is water-limited and C-enrichment may increase productivity, and because the SGS is very near the ecotone of dominance by C<sub>3</sub> and C<sub>4</sub> plant functional types which respond differently to enhanced CO<sub>2</sub>. Members of our PI's recently received funding to initiate a field and simulation experiment to examine the influence of enhanced CO<sub>2</sub>. We are coupling the use of open-top chambers for field CO<sub>2</sub> enrichment, soil N cycling and trace gas flux measurements with measurements on the physiological responses of two plant species, blue grama (C<sub>4</sub>) and western wheatgrass (*Agropyron smithii*, C<sub>3</sub>). We will incorporate new knowledge gained from the experiments into simulation models to extrapolate our results in time and space across the grasslands.

## **Interactions of plants, topography, and grazing on SOM and N availability** **LT21**

During the past 6 years, we put a great deal of energy into evaluating the influence of individual plants on C and N cycling. Hypothesis 2.9 has guided our work in this area (Table 2.4). We conducted numerous studies that indicate that the patchy distribution of individual plants results in high spatial heterogeneity of soil resources ( [Fig. 2.13](#) )(Hook et al. 1991, 1994, Burke et al. 1995, Vinton and Burke 1995, Vinton 1994), comparable or even higher than that at the landscape scale. Our results indicate that spatial heterogeneity is large, but is associated with SOM pools that change relatively rapidly, leading to both rapid development and decay of this small-scale patterning. We recently initiated a long-term study to evaluate the influence of individual plants on SOM and N availability. We are characterizing the interactions of plant species, topographic location, and grazing intensity on spatial heterogeneity of soil resources. We are sampling 3 landscape positions (summit, midslope, and toeslope), 3 micropositions (under blue grama, under prickly-pear, and between plants), and in two grazing treatments (heavily grazed and ungrazed), with 5 samples in each combination of treatments. In each location, we are measuring microtopography to estimate erosion/deposition, and sampling surface soil to assess the relative roles of organic and mineral deposition. We plan to sample at decadal intervals to assess the actual rates of accumulation and loss of material ( [Fig. 2.21](#) ).

The role of individual plants and community composition during succession  
([see Section E](#))

### Atmospheric inputs NEW-LT

One of the most important indicators of ecosystem changes is alteration of element inputs. Although our site has long been a member of the National Atmospheric Deposition Program, there are still several key areas of element balance that we do not understand. First, what is the relative contribution of weathering vs. atmospheric inputs? Second, what is total N deposition, including both wet and dry deposition? Our work on this topic will be guided by hypothesis 2.10 (Table 2.4)

The application of stable isotopes and mass balance models enable us to quantify the contribution of mineral weathering versus atmospheric inputs to biogeochemical cycles. These techniques, in addition to more traditional approaches such as soil micromorphology and total chemical and mineralogical analyses, will help us assess the critical nutrient thresholds in SGS ecosystems. A better understanding of the relationship between nutrient fluxes and ecosystem production will assist in the construction of predictive

models capable of evaluating soil nutrient response to perturbations. Strontium ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) isotope measurements will be combined with major and trace element analyses, and cation mass balance calculations to determine the quantity of weathering versus atmospheric input of cations. We will examine the distribution of stable Sr isotopes within soil profiles and among various biological components of the soil ecosystem (SOM, plant litter, standing biomass) to assess the degree of external inputs vs internal cycling of nutrients. This research will complement, and be conducted in concert with, on-going Sr studies in selected ecosystems of California and Hawaii.

Dry deposition is an important component of total atmospheric deposition (Lovett 1994). Current estimates of N deposition based upon precipitation underestimate the contribution of atmospheric N to the SGS. Reliable estimates of dry deposition will be useful in constructing more accurate N budgets and provide baseline data on the possible effects of increasing urban development on N deposition in the SGS. We plan to develop a dry N deposition program to provide baseline information and begin long-term sampling of atmospheric N inputs. The mass flux of N to the plant/soil surface will be estimated using a modified Bowen-ratio method with measured changes in temperature and nitric acid concentration with altitude (Huebert and Robert 1985).

## **C. Paleoecology and Paleopedology**

The evolutionary history of the SGS is preserved in Holocene paleosols, buried soils which were formed in ancient landscapes and retain an "imprint" of the climate and vegetation that prevailed during their formation. Sequences of paleosols in a variety of deposits around the world have been used as terrestrial proxy records of global climate change (Busacca 1989, Catt 1990). A fundamental aspect of our research is the evaluation of: 1) the range of variation, and 2) the rate of climatically induced ecosystem changes. This will require a re-thinking of previous soil- geomorphological research conducted at CPER and direct us to a more robust model of landscape- ecosystem evolution for the region. This work will be guided by hypothesis 2.11 (Table 2.5). Cooperators in this the research will include Dr. R. Madole, USGS, and Dr. A. Busacca, Washington State University.

### **Existing knowledge regarding the paleoenvironment NEW-ST**

A chronology of landscape stability has been proposed for the west-central portion of the Great Plains primarily through the use of dune stabilization studies and paleosol dating techniques (Muhs 1985, Forman and Maat 1990, Forman et al. 1992, Madole 1994, 1995). We have characterized approximately

40 paleosols at the CPER. Radiocarbon dates obtained for 7 paleosols corroborate existing chronologies and suggest distinct periods of stability and soil formation from approximately +10000-8000 YBP, 5000-3500 YBP and 1500 YBP to present, with intervening periods of instability (drought) resulting in dune formation and soil truncation or burial.

We have used the stable C isotope composition of paleosol SOM, phytoliths and CaCO<sub>3</sub> to estimate the relative proportions of C<sub>3</sub> and C<sub>4</sub> plants growing during soil forming intervals and made inferences to prevailing climate. We measured the quantity of SOM and phytoliths in paleosols and compared these data to contemporary soils to indicate relative climatic differences. Our results indicate that C<sub>3</sub> plants were dominant during the soil forming interval 10000-8000 YBP and that C<sub>4</sub> plants were dominant during both the 5000-3500 YBP and contemporary soil forming intervals (Kelly et al. 1993) ( [Fig. 1.10](#), Table 2.1). This suggests the early Holocene was cooler than mid Holocene or present. Organic C and phytolith mass is greater in early and mid Holocene paleosols than in contemporary soils, which suggests a wetter climate than present (Blecker et al. in press). Hypothesis 2.12 (Table 2.5) guides this work.

### **Evaluation of phytoliths from the mid Holocene soil forming intervals NEW-ST**

Although there is significant overlap in phytolith form among grass genera, three subfamilies can be reliably identified: Chloridoid, Festucoid and Panicoid (Twiss et al, 1969; Fredlund et al, 1985). The Chloridoid subfamily represents three tribes, Chlorideae, Erogrosteae and Sporoboleae. The Festucoid subfamily represents four tribes, Festuceae, Hordeae, Aveneae, and Agrostideae. The Panicoid subfamily represents three tribes, Andropogoneae, Paniceae and Maydeae. Each of these groups corresponds to a unique set of environmental (temperature and moisture) conditions.

Phytoliths will be extracted from the silt and fine sand sized fractions of <sup>14</sup>C dated paleosols. Phytoliths in both contemporary vegetation and soils will be characterized morphologically as reference samples. Existing phytolith classifications will also be used to identify grass taxa (Twiss et al, 1969; Brown, 1984). The stable C isotope composition of phytoliths and SOM from <sup>14</sup>C dated paleosols will be quantified to determine the relative importance of C<sub>3</sub> and C<sub>4</sub> plants present at the time the phytolith was deposited.

CPER paleosols appear to have been preserved as small "patches" (<100m<sup>2</sup> - 1 km<sup>2</sup>) rather than as extensive, continuous surfaces. It is unclear, given their contemporary landscape positions, what positions they occupied on the paleolandscape (Hypothesis 2.13, Table 2.5). A robust interpretation of the

Holocene paleoenvironment requires the determination of paleosol area and morphometry to determine if paleosols represent relic fluvial features with distinctive microclimates. A subset of representative paleosols from each of the soil forming intervals will be cored to determine their area and morphometry.

Madole (1994) stated that, under the present climate, eastern Colorado is near the threshold of widespread mobilization of sediment by wind. We will estimate the area of paleosols for the PNG by correlating paleosol occurrence with stratigraphy and physiography. We will compare paleosol maps with existing data on location of sand sheets and other eolian features as well as soil survey information to assess the potential for paleosol exhumation (Hypothesis 2.14, Table 2.5).

We have used stable C isotope composition of SOM, phytoliths and  $\text{CaCO}_3$  to estimate the distribution of  $\text{C}_3$  and  $\text{C}_4$  plants during Holocene soil-forming intervals. This information, in turn, has been used to make inference to Holocene climate. Our regional interpretations of climate, to date, are based on data of limited geographic extent. We will date and characterize paleosols across the PNG to develop a more robust interpretation of regional climate change. Further, we will utilize published stratigraphic and archaeological data pertaining to this area to refine our interpretations (Hypothesis 2.15, Table 2.5).

## **D. Water and Energy Exchange**

In our conceptual model, precipitation is one of the key driving variables explaining the structure and function of SGS ecosystems. Precipitation at the CPER is low (321 mm/yr; n=52) and variable (CV=32%) (

In our conceptual model, precipitation is one of the key driving variables explaining the structure and function of SGS ecosystems. Precipitation at the CPER is low (321 mm/yr; n=52) and variable (CV=32%) ( [Fig. 2.22](#) ). Within the period of record, we have had a year with annual precipitation more than 2 standard deviations below the mean (1964;107 mm) and one almost 3 standard deviations greater than the mean (1967;588 mm). In addition to interannual variability, there is substantial seasonal variability. Winter is the dry season and at this time most precipitation is received as snow. Late spring and early summer is the wet season with May and June averaging nearly 60 mm/mo ( [Fig. 2.23](#) ). Because water is such an important driving variable, and because the supply is so variable, we invest considerable effort in understanding inputs, storage, and losses. Hypothesis 2.16 guides work in this area (Table 2.6).

### **Meteorological monitoring and water balance LT22, LT23**

Microclimate: We have an automated microclimatic station that has been functional since 1982. It is at a site on which microclimatic monitoring was begun in 1970 under the US-IBP program. In addition to the automated system, we make manual observations that also link to a data set begun in 1970. Our automated system makes hourly measurements of precipitation, wind direction, wind speed at 3 heights (1, 2, and 4 m), air temperature, surface temperature (infrared), dew point temperature, vapor pressure, total radiation, soil water at 3 depths (fiberglass blocks; 5, 10, and 20 cm) soil heat flux, and soil temperature at 4 depths (2.5, 5, 10, 20 cm). Manually we record air temperature, relative humidity, precipitation, open pan evaporation, and soil temperature at 7 depths (1" 2.25" 4" 8" 20" 40" 72"). Observations are made once daily in the morning. We plan to continue both automated and observations.

### **Lysimeter:LT24**

During the IBP program, a large (3 m diameter) weighing lysimeter was installed in the enclosure containing the microclimatic monitoring station. In 1986, we connected the lysimeter to our microclimatic data logger and now have a continuous record of inputs and outputs of water. Comparison of daily evapotranspiration for a wet and dry year shows important differences in the season long pattern of water loss, the maximum daily losses, and the total amount lost ( [Fig. 2.24](#)). We plan to continue collecting data from the lysimeter and we hope to use it for more experimental work in the future. For instance, in 1995 the vegetation on the lysimeter was manipulated using herbicides as part of an experiment to estimate bare-soil evaporation. Since resodding the lysimeter is a relatively simple matter, such uses do not have permanent negative effects on its long-term value. We plan to continue to promote such uses.

### **Precipitation gauge network LT25**

A frequent assumption of researchers in semiarid regions is that precipitation is spatially variable, but that over some time period (a growing season is commonly assumed), average amounts are similar for local areas (one to a few 100 km<sup>2</sup>). Because precipitation is such a critical variable for SGS, over the past 6 years we have established a network of 11 gauges at the CPER to estimate the spatial variability of rainfall and the time period over which local areas converge in rainfall amounts. Initial analyses of these data suggest that amounts converge at the monthly scale and the the variability among stations in rainfall received on a daily basis can be explained by the size of the storm and the distance between the stations ( [Fig. 2.25](#)).

### **Soil water measurements LT26**

While we often use precipitation as a surrogate, soil water is the variable to which the majority of the biota responds. Understanding both long and short-term patterns of soil water availability is a critical component of our understanding of biotic responses (Sala et al. 1992)(Fig. 1.12, [2.26](#) ). In 1982, we established a series of 5 sites at which we have regularly measured soil water using a neutron moisture gauge. Three of the sites consist of a sequence of measurement points along a catena from a summit to a swale and 2 were upland sites on which soil water measurements have been made since 1970. From 1982 to 1990 soil water was measured biweekly during the growing season (May- September) and monthly for the remainder of the year. Data from 1986 (dry year) to 1990 (wet year) illustrate nicely some of the range of variability ( [Fig. 1.11](#)). While our long-term measurements have been and continue to use neutron probes, many of our ongoing studies utilize time domain reflectometry.

### **Oxygen isotope analysis: NEW-ST**

We will utilize the stable isotope characterization of oxygen ( $^{18}\text{O}/^{16}\text{O}$ ) in meteoric, soil and plant water to determine the mechanisms involved in the loss of water from soils, as well as feedbacks to the atmosphere. We will look at the total water budget along with the interfaces and feedbacks between biological and nonbiological water cycles in the SGS and agricultural ecosystems (Kelly et al, 1992; Hsieh et al, 1995). This approach will allow us to investigate changes in water storage and losses over landscapes and provide important information about water balance and transport in semiarid areas.

### **Atmosphere-biosphere Interactions NEW-ST**

Changes in the landuse at and around the LTER site have had large impacts on the soil-plant microclimate. Moderate to heavy grazing reduces live plant biomass and results in increased soil temperatures and a decrease in the Bowen ratio (ratio latent to sensible heat flux). Wheat-fallow cropping modifies the microclimate by increasing transpiration rates in the spring of the wheat year compared to native steppe and reducing transpiration rates and increasing soil temperatures during the fallow year. Use of minimum and no tillage cropping are increasing the efficiency of storing soil water during the fallow year with a resultant increase in transpiration rates during the wheat year and reducing evaporation and transpiration rates during the fallow part of the cycle. Pielke et al. (in press) found that landuse driven changes in the water budget and seasonal patterns of Bowen ratio can have an impact on mesoscale patterns of precipitation and other climatic variables ( [Fig.2.27](#) ). In two simulation experiments, a landscape representing current landuse was compared to a

uniform native steppe. The initial and lateral boundary conditions for the Regional Atmospheric Modeling System (RAMS, Pielke et al., 1992) were identical for the two landscapes. The differences in simulations were due solely to differences in average Bowen ratio and albedo over the region plus the spatial discontinuities of these values in the native steppe simulation. In the current landscape case, a deep thunderstorm developed (observed in the field on the date of this simulation), while only shallow cumulus clouds were simulated for the uniform landscape. The implication of these simulations is that the SGS site is directly influenced by precipitation changes associated with landuse changes in its vicinity. It is very difficult to measure and validate that the landuse driven changes in the microclimate have had any impact on the mesoscale climatic patterns because most of the current landuse patterns have been stable for over 60 years and could have resulted in a change in the climate of eastern Colorado (Hypothesis 2.17, Table 2.6).

We propose to quantify the potential impact of the current landuse on the mesoscale climatic patterns at the CPER site using the RAMS mesoscale model. RAMS will be combined with the CENTURY ecosystem model (Parton et al. 1987) and current landuse patterns. CENTURY will simulate landuse impacts on the seasonal patterns in plant growth and RAMS will simulate changes in water loss patterns and microclimate and evaluate the impact of these changes on mesoscale climate patterns. RAMS will use a nested grid centered on the research site. The horizontal grid spacing will be 10 km, but we will also be able to window down to site-specific locations using the specification of land cover and turbulence similarity theory. The larger domain will include most of the contiguous United States so that we can represent synoptic weather features as they propagate into the region and influence weather at the site. The major focus of the research will be to evaluate the impact of current landuse patterns on the mesoscale climatic patterns, however we will look at the potential impact of changing the cultivation practice and the grazing levels in the region.

## **E. Natural and Human-Induced Disturbances**

A great deal of our past and present work focuses on the effects of disturbance on SGS ecosystems. We have a strong conceptual emphasis on disturbance (see [Fig. 2.28](#), Table 2.7 for hypotheses). This work is closely related with our work in all other areas; we provide cross- references where necessary. We place our disturbance work into two broad categories, naturally- occurring and human-induced disturbances. There is an important difference between natural and human disturbances in their spatial scale. Most natural disturbances are

small (<100 m<sup>2</sup>) while most human disturbances are large (>100 m<sup>2</sup>). We are using experimental studies and simulation modeling to improve our understanding of the effects of disturbances on shortgrass systems.

### **A. Naturally-occurring disturbances**

Most studies of recovery in SGS systems have focused on large-scale disturbances, and in particular the cultivation and abandonment of agricultural fields. Small, patch-producing disturbances are also important, but were largely ignored until we began studying them in 1984. These small disturbances may have the largest potential effect on plant community structure and ecosystem dynamics. In our ongoing studies, we are evaluating effects of cattle fecal pats, nest sites of western harvester ants, burrows from skunks and badgers, and patches from larvae of June beetles. In our new studies, we will include pocket gopher mounds and prairie dog colonies. Hypothesis 2.18 (Table 2.7) guides our work in this area.

#### **Long-term sampling of recovery from small-scale disturbances LT27, LT28, NEW-LT**

We will continue to sample the response of SGS ecosystems to small-scale disturbances by sampling plant cover and density at regular intervals on disturbed areas ([Table 1.1](#)). This work, initiated in 1984, focuses on disturbances from 0.1 to <5 m<sup>2</sup>, and uses gap dynamics concepts to explain the response of SGS plant communities to disturbance. We will also continue to measure soil heights inside and outside of these disturbed areas at regular intervals to determine the time required for small-scale soil heterogeneity to recover. In addition, we follow the recovery of vegetation to natural small-scale disturbances such as ant mounds.

#### **Blue grama deletion experiment LT29, NEW-LT**

As a result of simulation results that showed large increases in plant species diversity following the deletion of blue grama, we initiated an experiment in 1994 to test this prediction. All blue grama plants in 2x2m areas were either killed by herbicide (Roundup) (aboveground structure intact) or by removing aboveground material with a shovel. Five plots of each treatment are grazed and five have exclosures. We will follow these plots through time. We will also expand this study by beginning the same treatments on at least 2 other soil textures in both the eastern and western sections of the PNG, to capitalize on the precipitation gradient.

#### **Recovery from white grub disturbances LT30**

We will continue to sample at regular intervals the response of plants on

patches of vegetation killed by white grubs, the larvae of June beetles. A field study of these patches was initiated in 1977 by the ARS. These 32 areas have been resampled six times (1978, '79, '80, '82, '90, '95), and this study is currently part of the LTER. For some pastures, paired areas were found inside and outside cattle exclosures; therefore we have been able to analyze effects of grazing on recovery.

### **Interactions between pocket gophers and grazing NEW-LT**

We will initiate a new long-term study to assess the size and frequency of occurrence of pocket gophers. Low densities of pocket gophers in the first 8-10 years of the LTER suggested that this form of disturbance may not be important in the dynamics of shortgrass systems. However, in the past 1-3 years, high densities of mounds have been observed in some pastures at the CPER. High densities of mounds were also reported in the 1970s (Grant and French 1980) which suggests that temporal variability in pocket gophers and their effects on vegetation can only be evaluated with long-term sampling. In our new study, we will locate and map pocket gopher activity in the three grazing intensity pastures (light, moderate, and heavy) as well as in 3-5 additional moderately grazed pastures on different soil textures. These pastures will be sampled and mapped annually for pocket gopher activity. We will also establish grids based upon maps from Grant et al. (1980) and will follow these areas through time.

### **Effects of Prairie dogs on SGS ecosystems (NEW - [see section IIA](#))**

## **B. Human-Induced Disturbances**

Our work on human disturbances encompasses the long-term effects of grazing and successional dynamics following cultivation and nutrient enrichment stresses. Hypothesis 2.19 guides our work in this area (Table 2.7).

### **1. Effects of grazing by cattle**

We have conducted many short- and long-term studies on effects of grazing by cattle on various aspects of SGS ecosystems, from physiological responses of plants to population dynamics, plant and animal community structure, and rates of ecosystem processes. We will continue our long-term studies and initiate several new studies on effects of grazing.

### **Long-term evaluation of grazing effects on primary producers LT31**

We have been studying the long-term effects of grazing on plots established by the ARS in 1939 that represent ungrazed, lightly, moderately, and heavily

grazed treatments (0, 20, 40, and 60% removal of annual forage production) ([Table 1.1](#)). The ARS sampled these treatments for ANPP and species composition through 1964, they were intensively sampled for plant and consumer groups during IBP, and we have continued work in these treatments since 1984. Short-term studies encompass all treatments. Long-term sampling focuses on ungrazed and heavily grazed treatments, because they represent the extreme conditions. We will continue to sample these treatments, as well as to conduct short-term experiments that provide a basis for our synthesis efforts.

### **Long- and short-term effects of grazing: an interdisciplinary study LT32-LT41**

We found in previous work that plant communities in SGS do not appear to be negatively influenced by grazing (above section) ([Fig. 2.6](#)). However, it appeared that litter accumulation (Milchunas et al. 1989, Table 2.8), small mammal disturbances and SOM ([Fig. 1.21](#)) were higher in exclosures than outside. An experiment was initiated in 1991 to address the questions: what are the short- and long-term effects of grazing and of exclosure on ecosystem structure and function, and how do these effects interact with soil texture? We will sample this experiment which consists of treatments associated with 50-year-old exclosures in 6 locations across a soil textural gradient: long-term grazed, currently grazed; long-term grazed, recently protected; long-term protected, currently protected; and long-term protected, currently grazed. The very large-scale sampling program assesses plant communities ([Fig. 2.29](#)), individual plant survival, aboveground and belowground biomass and net primary production, SOM dynamics ([Fig. 1.20](#)), soil fauna ([Fig. 2.32](#)), small-scale disturbances, aboveground foliar nutrient concentrations, and soil erosion. This sampling will continue at regular intervals (see [Table 1.1](#) for intervals for each variable).

### **Relationships among grazing, microclimate, and exotic species NEW-ST**

Using our exclosure experiment, we will continue to study the relationship between grazing and invasion by exotic species. In our initial work, we found that exotic species are more abundant in ungrazed compared to grazed treatments (Table 2.8). A subsequent experiment separated indirect, long-term effects of grazing from direct, short-term effects ([Fig. 1.18](#), Milchunas et al. 1992). Microenvironmental conditions for germination in ungrazed communities were more important in establishing populations of exotics than levels of competition from existing plants. Because of the microenvironmental differences between grazing treatments, we will conduct a new study to assess the small-scale, short- time scale soil water dynamics and soil temperature

effects of grazing, and the implications of reductions in litter versus compaction on the soil surface microenvironment.

## **2. Effects of Nutrient Stress**

### **Long-term studies of nutrient enrichment LT42**

Nutrient enrichment treatments established in 1971 have been sampled under LTER since 1982. Identical sampling procedures to those used for the grazing treatments has allowed comparisons among a range of disturbance intensities ([Fig. 1.2](#), Milchunas et al. 1990). Results from this study have demonstrated some interesting and unexpected time-lags in response of the plant community ([Fig. 1.17](#), Milchunas and Lauenroth 1995).

## **3. Effects of cultivation and subsequent abandonment**

This work comprises four different approaches: long-term field experimentation, short-term experiments, simulation analysis, and regional analysis. Here, we focus only on our long-term experiments. Simulation and regional analysis are described under Synthesis.

### **Long-term recovery following cultivation and cropland abandonment LT43-46**

Approximately 25-30% of the CPER and the PNG were plowed and abandoned by 1937. In 1990, we sampled vegetation ([Fig. 2.30](#)) and soil recovery ([Fig. 2.31](#)) on 13 fields selected to represent the precipitation and temperature gradients across the PNG, including one field at the CPER ([Table 1.1](#), Coffin et al. 1996, Burke et al. 1995). In 1994, we began sampling old fields at the CPER. We sampled vegetation and soils on 6 fields in 1994 and will continue to sample a subset each year until all have been sampled. We will repeat sampling at decade intervals.

### **Management effects on soil-atmosphere exchange of CH<sub>4</sub>, N<sub>2</sub>O and CO<sub>2</sub> LT15**

Since the fluxes of CH<sub>4</sub> and N<sub>2</sub>O from the earth's surface to the atmosphere are primarily controlled by biogeochemical processes, changes in N cycling in soils due to management have contributed to the increases in atmospheric N<sub>2</sub>O and CH<sub>4</sub> observed during the past century and will help dictate future changes. The influence of management (grazing and crops) on N<sub>2</sub>O emissions and CH<sub>4</sub> consumption in soils are not well known. We initiated a long-term flux measurement program ([Table 1.1](#)) to assess the soil-atmosphere exchange of trace gases in a variety of systems ranging from native grassland to irrigated cropland. The fluxes of CH<sub>4</sub> and N<sub>2</sub>O are measured using chambers adapted to

the particular system being studied. Flux measurements are made daily to bimonthly and year-round, depending upon the time of year and management situation.

#### **4. Comparison of grazing and plowing effects**

##### **Influences of above- and belowground disturbances on the detrital food web LT35 and NEW-LT**

Hypothesis 2.19 (Table 2.7) suggests that the belowground food web should be more sensitive to belowground than to aboveground disturbances. We are interested in testing this hypothesis, and in evaluating the successional dynamics of the detrital pathway in response to both kinds of disturbances. We are currently sampling belowground community structure on the grazing/exclosure experiment (LT35), and plan to initiate a new belowground disturbance experiment by plowing native SGS. We will sample using the same methods used on the grazing experiment, sampling the changes in the soil community prior to and following the disturbance and comparing these soil communities to control plots. Paired plots of newly plowed and native SGS will be established. The plot sizes will be 25 m<sup>2</sup>, a size that should ensure desirable recovery rates (decadal levels), and will be replicated 5 times. Belowground community structure (microbial and invertebrate densities and functional diversity; following Moore et al. 1988) will be estimated ( [Fig. 2.32](#)). Sampling will be intense prior to and the year following disturbance (2-3 week intervals) in order to capture the changes in structure. During years 2-4, sampling will be reduced to quarterly intervals. We will then develop a functional food web, (DeRuiter et al. 1995) for soils within each site and treatment, and estimate interaction strength as the elements of the community matrix,  $A$ , using the field data. We will determine the stability of communities for each ecosystem through Monte Carlo simulation using the field/laboratory generated estimates (mean interaction strength and variance) of interaction strength, and use these results to determine if currently observed patterns in interaction strength form the basis of ecosystem stability.

#### **F. Synthesis**

We have 4 main areas of synthesis: simulation, regional analyses, synthesis/review papers, and cross-site analyses. All of these activities are supported by LTER to some degree, but in addition most are also supported by other grants (Table 7.1).

##### **1. Simulation Analyses:**

The SGS-LTER project has been involved in simulation analysis as a key part of our synthesis activities since 1982. The development of simulation models is a continuing process in which we incorporate our knowledge into models, test them against data, and modify the models. Our models have been particularly useful for helping us design experiments and for extrapolating our understanding to long temporal and large spatial scales.

Two models have been developed under LTER funding that continue to provide opportunities for integrating our work. STEPPE (Coffin and Lauenroth 1990) is an individual-based plant community dynamics model that is a key synthesis tool for our ideas about mechanisms that have led to the persistence of a single dominant plant, blue grama in SGS ( [Fig. 2.33](#) ). Our iterations between field experimentation and analysis with STEPPE have led to considerable progress in our understanding of SGS responses to disturbances, the importance of spatially explicit processes such as seed dispersal, and responses to directional climate change (Coffin and Lauenroth 1989, 1990, 1993, in press). The second model, CENTURY (Parton et al. 1987), represents C and N dynamics in grasslands ( [Fig. 2.34](#) ). We and others have used CENTURY to evaluate potential responses of grassland ecosystems to management (e.g. Parton and Rasmussen 1994), and to assess potential responses of grasslands to climatic change (Parton et al. 1994). Because of the importance of water availability, we have recently linked both models to a soilwater model (SOILWAT) (Lauenroth et al. 1993).

Our conceptual framework and current areas of interest have led to new developments in which we are linking SOILWAT, STEPPE, and CENTURY to simulate interactions among climate, plant community dynamics, and biogeochemistry. Our key questions are: 1. what are the ecosystem-scale consequences of altering plant community structure and biodiversity for grasslands? 2. what disturbances may lead to removal of blue grama and what are the ecosystem consequences? 3. are there transient responses to climatic change that occur when we explicitly consider community- biogeochemistry interactions that do not occur when we consider biogeochemical and plant community dynamics alone?

We are currently developing process-based trace gas flux models. Because trace gas flux is so temporally and spatially variable, it is necessary to develop simulation models that describe fluxes from a wide variety of soils and climates. Such models are needed to assess site-scale and regional fluxes and to assess the impact of perturbations on these gas fluxes. Using the information collected during the past four years, we have developed a set of first generation, process-based models which describe the oxidation of CH<sub>4</sub> and production of

N<sub>2</sub>O in the soil (Parton et al. submitted). Further refinement of these models and linkage to CENTURY is planned. Once that phase is accomplished, the models will be linked with a GIS database to develop site-wide and regional flux models.

## **2. Regional Analysis:**

Our initial regional analysis work was funded by LTER (Burke et al. 1990, 1991), but since 1990, we have obtained separate funding for this work from NSF and other agencies. We have developed an extensive spatial database for the central grasslands region of the U.S., and conducted numerous analyses (see [Table 1.5](#)), which we do not report here because they are not a focal LTER activity at this time.

## **3. Synthesis and Review Papers:**

We have produced a number of synthesis/review papers during the past funding cycle ( [Table 1.5](#)). We plan to continue our efforts in this area through contributed and invited papers. Our current focus is producing a book that organizes the current state of knowledge about the SGS. We have signed an agreement with Springer-Verlag, with a tentative release date of early 1997. We are well along the way in the production of this book, with first drafts of many chapters completed.

## **4. Cross-Site Field Analysis:**

During the past 6 years, we have been involved in numerous cross-site analyses that compare grassland ecosystem dynamics among LTER and other long-term ecological research sites ( [Table 1.5](#)). Investigators from our project have successfully received funding for 4 Cross-Site LTER projects in the past 2 years.

## **G. Summary**

We plan to continue our 46 long-term experiments, and to initiate 12 new short-term experiments and 12 new long-term experiments over the next 6 years. There are numerous interesting and important new things to study on the SGS, but for this proposed round of funding, we are prioritizing aspects that will fill critical gaps in our knowledge. This work includes: 1) new studies of keystone species in our ecosystem, the prairie dog and its biology, and plains prickly-pear; 2) new studies of population genetics of blue grama; 3) new studies of atmosphere-biosphere interactions, and 4) new studies of detrital food web

dynamics. We are also initiating follow-up experiments to our past work in paleoecology and pedology, plant community dynamics, and biogeochemistry. In addition to these specific experiments, we are planning to conduct simulation analyses and other synthesis activities that draw upon our long-term databases and those of other sites within the network.

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#### **SECTION 4: PROJECT MANAGEMENT**

During this recent funding round, the structure of the SGS LTER project has changed in several ways. The most significant changes involve a broadening of the scientific participation and leadership of the project.

Our project structure during LTERI (1982-86) and LTERII (1986-90) consisted of 2 CSU PI's and 1 PI representing USDA-ARS, and a very large (~20) group of co-investigators with various levels of project participation. Since the SGS-LTER began, we have prioritized gradual change in leadership to ensure both stability and influx of new ideas. For LTERIII (1990-6), we began with essentially the same structure, with WKL as lead PI, ICB Co-PI, and 2 ARS PI's, and the plan to switch responsibilities between WKL and ICB after 3 years.

During the last 5 years, however, several fundamental things have changed. The number of scientists who are significant participants in our project, the number of collaborators, and the visibility and national connections of LTER have all grown enormously, leading to a huge leap in administrative responsibility associated with LTER. In 1993, we initiated an Executive Committee of 9 persons that meets once biweekly to make all of the major scientific and administrative decisions, including budget decisions, for the project. The Executive Committee consists of the CSU and ARS Co-PI's of this proposal and the data manager. This structure has worked extremely well, and has increased the investment of individuals in the project, as well as ensuring long-term stability, with a large number of persons that are knowledgeable about the project and capable of being leaders. ICB and WKL handle day-to-day administration of the project. In 1993, we initiated a Project Manager position to handle the administrative details of the project and free time for scientific activity for ICB and WKL. However, the recent budget reductions have not made it possible for us to hire a fulltime project manager, thus, we are supporting WKL and ICB each for 2 months for project management.

We remain committed to the idea of gradual changes in leadership, and feel that this new structure will allow us to make a transition that preserves continuity in the future. Thus far, we have not identified a Co-PI to take on the new leadership role, but we hope that this will evolve naturally over the course of this funding cycle.

In addition to the Executive Committee, we support a number of other scientists on the project. The group of all LTER participants meets once every two weeks during the school year for either a seminar or to discuss project business.

During LTERIII, we recruited 5 new scientists to the project: Dr. Arvin Mosier, Dr. Bea Van Horne, Dr. Roger Pielke, Dr. John Moore, and Dr. Joy Bergelson. We actively recruited each because of our perceptions of project limitations, and those of reviewers. In each case, we initiated a discussion and began

funding at a small scale. This growth has been positive in many ways. However, one problem is that this planned growth was based on budget projections that were significantly more than we currently receive or are submitting for, so we are having to scale down our work in some other areas.

We have invested resources to attracting new scientists our site by implementing a summer graduate fellowship program. Each year, we fund a competition for 3 graduate students, 2 for CSU students, and 1 for a student from anywhere who is doing cross-site work. This has lead to new work on spiders, lizards, birds, and mammals, and represents one of our best investments. We have utilized the Supplement program through ROA awards to invite Dr. Jim Fitzgerald of the University of Northern Colorado to conduct research on swift foxes at our site, and Dr. Fitzgerald has become an important new member of our team. We have found that we receive numerous requests for letters of support from scientists who are submitting to conduct cross-site research here. For these scientists, we offer assistance in data entry and management, access to our field dormitories and laboratory, and in some cases, limited labor from our field crew.

Peer review has played crucial role in our recent changes in project structure. For instance, comments from our site-review led us to have a second, in depth external review of our data management system, which led to some very positive changes. We plan to divide our project into 6 subdivisions (Data management, Population and Processes, Biogeochemistry, Water and Energy Dynamics, Disturbances, and Paleoecology), and hold one detailed peer-review each year.

## **SECTION 5: DATA MANAGEMENT**

The primary goals of data management at SGS LTER are to provide secure, long-term data storage and make high quality data easily accessible to LTER scientists and the public in a timely fashion. We achieve these goals through three techniques: an organized and efficient data tracking system, secure data archiving procedures, and fully utilizing our SGS World Wide Web (WWW) site.

# **Database Management Policies and Procedures**

## **Data Tracking System**

The implementation of our data tracking system ([Fig. 5.1](#)) means that data management starts long before data are collected. Investigators must submit a request form to the data manager as part of the procedure to conduct research. The form contains specific information about the study that the data manager logs into the tracking system. After entering preliminary information about a project into the system, the data manager tracks the progress of the dataset from data collection through to availability on the SGS WWW site. The SGS data tracking system increases the efficiency of data entry into the system, improves project-wide awareness of the scope of research activities at any given point in time, and improves overall data quality by providing consistency among datasets through standardized data collection forms.

## **Data Delivery and Verification**

Contact with the investigator is maintained throughout the duration of the project and data are submitted to the data manager no later than three months following the end of the study. For experiments that use the LTER field crew, data are submitted directly to the data manager. The data manager then verifies each dataset with its data description to ensure that there are no inconsistencies between the actual data and the metadata. Immediately following verification, the data manager updates the database by storing each dataset as a separate table in the database and relating it to the metadata via a dataset ID code.

## **Data Archiving**

The data manager archives the data and metadata by storing them together in one ASCII text file per dataset. Using this format for data storage ensures readability over the long term. Datasets are stored redundantly via the following four methods to provide security against accidental data loss or destruction:

1. hard disk on a Sun workstation (daily)
2. system level back-ups on high-density 8-mm cartridges (daily)
3. SGS archives on high-density 8-mm cartridges (quarterly)
4. original data forms are copied to be microfilmed

## **Data Access**

The metadata to all datasets are made publicly accessible as soon as they are received from the investigator. Datasets are available to the public three years after the end date of the study or following the investigator's publication of study results (whichever comes first). Investigators are notified when data are scheduled to go public and may at this point submit a written request to extend the access restriction on their data. A committee reviews the request and determines whether the data may remain limited access and for how long.

## **SGS WWW Site**

Once a dataset is verified, the metadata will be automatically posted to our SGS WWW site. Our goal is to use the SGS web site as the primary mode of information dissemination for SGS scientists, the scientific community, and the public. *(The data access portion of our WWW site is currently being developed. We expect it to be operational by March 1, 1996. The rest of the site is fully functional now.)*

The design of our web site will enable scientists everywhere as well as the public to easily access our on-line data library (see Tables 1.2, 1.3, and 1.4 for lists of the datasets currently managed by SGS-LTER). We have developed a standardized list of keywords that forms the foundation for searching the SGS data library on our WWW site. A user may either travel through the hierarchy of research categories to locate datasets of interest or may utilize a keyword search. When viewing the data, the structure of our home page allows the user the following options: 1. data files containing the actual rows and columns of data; 2. the metadata text, describing the study and its datasets; 3. graphs of the data which are generated "on the fly" as the user queries the dataset; 4. graphic images associated with datasets such as experiment designs, maps, photos of the study site etc.

We have recently assembled a comprehensive species list that is available on our home site. The list includes every species found at the site and is broken down into 7 categories: plants, birds, mammals, arthropods, microarthropods, nematodes and herpetiles. For a more complete description of our data management policies and procedures, please see our data management policy posted on our Web site.

## **Data Management Software**

In the past, our data management system relied upon in-house software and programming that provided leading edge technology in the field. Given the

rapid improvement of commercial database systems software, we have re-evaluated the efficiency of in-house software development. We are currently in the process of migrating to a relational database system (ORACLE). As we write this, we are moving our data into ORACLE, and working to connect the ORACLE database directly to the WWW site using ORACLE html tools. This custom tailored system and its associated applications will allow us to meet the specific needs of SGS scientists.

We are very excited about the future of our data management system and our ability to maximize the utility of our relational database management system (RDBMS) to our scientists and the public. We envision a state-of-the-art RDBMS capable of providing high quality, long-term data storage and enhanced access to these data through a dynamic link to the SGS WWW site. Our web site will no longer store static data files, but will allow visitors to execute dynamic, on-the-fly data requests and analyses. By achieving a state of the art RDBMS, we will greatly contribute to the long-term success of SGS as an outstanding ecological research site well into the next century.

## **Data Management Personnel**

The Data Manager is a full time position that includes the following responsibilities:

1. working with scientists during experimental design and planning
2. managing the data tracking system
3. managing the database system
4. updating and maintaining the SGS WWW site
5. archiving datasets for long-term maintenance and storage
6. developing and maintaining user-friendly applications
7. assisting scientists with any data management/data access issues.

The GIS Data Manager is a half-time position that includes the following responsibilities:

1. GIS data acquisition and management
2. spatial analysis consultation
3. project analysis
4. map generation.

Undergraduate students are used as additional staffing resources.

# GIS Data Management and Research Support

Management of GIS spatial data and metadata supports four functions:

1. daily data management
2. research support
3. network access for local and remote users
4. long term data archive.

Table 1.3 lists the GIS data managed by the SGS LTER project.

## GIS Data Management

Daily GIS management accomplishes the collection of new data, extension of existing spatial data, and maintenance of metadata. Expansion of the SGS to include the Pawnee National Grasslands (PNG) allows us to acquire more ecologically complete landscape level data. Data new to the SGS study area include: (1) prairie dog town locations, (2) swift fox locations, (3) plant communities and associated range site descriptions, and (4) land use and Conservation Reserve Program (CRP) treatments.

We utilize an extended ARC/INFO data library structure for analysis and daily management of spatial data and metadata ( [Fig. 5.3](#)). These data are then made available across the WWW in several formats to accommodate the needs of investigators. Since many users simply wish to view the data, map views stored in a Map Atlas are accessible for viewing in raster format, and downloading in black-and-white or color postscript format for local printing of high-quality graphics.

A new method for access and retrieval of historical field study sites is now being adopted at SGS. This format stores each study location as a polygon in the Study Site library layer. This new format will allow scientists and data managers to more easily identify past and ongoing research based on plant or animal species, soil key words if appropriate, researcher names, dates of study, and of course geographic proximity. This structure will form a link between the GIS data library and the field data in the data management system.

GIS metadata at our site conform to the Content Standards for Geospatial Metadata. Approximately 75 percent of the metadata elements for this standard

are appropriate and used at our site, with approximately 20 percent of these being required elements. This information is currently stored in relational database tables and accessible for internal use and maintenance. Text output files are made available for outside and network users. For new and recent data layers, the required metadata elements are complete. Metadata for spatial data preceding the standard, although well-documented, may never have all of the required elements we currently collect.

## **Research Support**

GIS research analysis is conducted primarily using Arc/Info and IMAGINE software. These GIS analyses range from plant-level scanning and analysis of root characteristics, to plot-level identification of plant growth and mortality, to landscape-level and landscape-level assessments of nutrient run-off.

## **Network Access**

Prior to the advent of WWW Internet viewers, we supported machine and software independent views of our SGS Map Atlas through on-line map images. These map images could be viewed within the Colorado State University network using Unix-based non-GIS viewing tools, or transferred to remote locations via file transfer protocol for viewing. This served primarily as a mechanism to facilitate communication and visualization for research. These views are now supported and accessible through our WWW site.

## **Long-term Data Archive**

Purchased, SGS-automated, and project data are saved in duplicate on 8 mm tapes in the original format, with the second copy stored in a separate location from the first. Data automated or developed in-house are stored in Arc/Info export format and are reviewed yearly for compatibility maintenance. The final products of project data are stored and reviewed in a similar manner. Final products are also stored together with all associated work files on 8 mm tape in triplicate: two copies for our site and one copy for the researcher. These are identified with the name of the project, date of completion and the researchers' names.

## **References**

Federal Geographic Data Committee, 1994. Content standards for digital geospatial metadata (June 8). Federal Geographic Data Committee. Washington, D.C.

CPER Data Management Committee, 1994. Data Management for the CPER LTER Project (November 15).

Short Grass Steppe Long Term Ecological Research Site. Fort Collins, Colorado.

## **SECTION 6: OUTREACH**

Our primary efforts with our LTER activities have been focused on research at the CPER. As in previous funding cycles, during the past 5 years essentially all of our efforts have been devoted to producing new scientific information about SGS ecosystems. Our outreach activities have been limited to sponsoring an annual symposium, education (undergraduate, and graduate), and communication to the public through the media when opportunities arose. This is not to say that we do not recognize the value or the importance of outreach activities. We have been working over past several years to develop resources that will allow us to increase our interactions with a number of publics that have an interest in the SGS. To date we have not been successful, but we will continue to pursue the issue until we are successful. Therefore, to date, our plans exceed our accomplishments but we hope to correct that in the future.

### **The Central Plains Experimental Range Annual Symposium:**

In 1994, we began cooperating with the Agricultural Research Service to sponsor an annual symposium with the goal of reaching out to the research, management, and user communities that have an interest in the shortgrass steppe. The all-day symposium is characterized by a high degree of interaction, through poster presentations, short plenary sessions, focal discussion groups, and even games that focus on the shortgrass steppe. We have just completed the 3rd symposium, which was attended by 90 people, including scientists and managers from the ARS, managers and scientific staff from the U.S. Forest Service Pawnee National Grasslands, the rancher president of the Crow Valley Grazing Association, and representatives of the academic community (professors, graduate and undergraduate students, and technical support staff). We are finding that each year, the symposium grows in both numbers of attendees and in excitement level. Further, our relationship with the ARS, U.S.

Forest Service, and the livestock operators has improved markedly over the past 3 years, based upon a shared understanding of the ecology of the site and our priorities for new research. Our plan is to increase the scope of this symposium as we increase the size of our research site.

### **Education:**

During the past 5 years, we have increased our involvement in education, through increases in formal academic educational involvement at the site, and in numbers of fieldtrips led to the site. Each semester, we lead trips for at least one undergraduate and one graduate ecology class to the site to focus on the ecology and management of shortgrass steppe; these trips also feature visits to a local ranching operation. In the past 2 years, we have also begun to develop undergraduate research experiences through the REU program. We have leveraged support from several different grants to bring in 9 highly qualified undergraduates that include 5 CSU Honors students, 2 minority students, and 2 students from liberal arts institutions, working on projects on stable isotope studies, nematode populations, soil organic matter dynamics, plant ecophysiology, vegetation, soil respiration responses to warming treatments, mammal distributions, and prairie dog influences on raptors. One of these projects this past summer led to a result that we feel will be highly visible, that *Opuntia polyacantha* provides a refuge for plant species and significantly increases biological diversity in grazed grassland. We also supported two additional conservation biology undergraduate projects used for theses this past summer. These interactions have been very productive and exciting for the SGS group, and we plan to continue to encourage a great deal of undergraduate work at the site.

### **Field Trips:**

In the past several years, we have led numerous fieldtrips for interest groups to our research site. We have participated in the ARS Field Day, during which ranchers visit and learn about research at the site. We have led fieldtrips for the Sierra Club, for an educational group that works with Native Americans, and for the Soil Science Society of America.

### **Media Attention:**

We have been featured in regional and local newspapers several times since 1990. Both the New York Times and Washington Post covered our 1991 Nature article (Mosier et al. 1991) on the effects of management on trace gas flux in native steppe and croplands. The Fort Collins Coloradoan reported on

the SGS research program in 1990, and our synthesis that grazing is a long-term part of the disturbance regime of this system. In 1992, the Coloradoan highlighted our regional modeling result (from an LTER supplemental grant) that global warming will have small impacts on regional C budgets relative to long-term cultivation. A series of articles in the Denver Rocky Mountain News in winter 1995 featured our combined research and educational program as a highlight at Colorado State University. This fall, one of our class fieldtrips to the site was featured in the Coloradoan.

In addition, there is recent interest in featuring the SGS LTER in an article in Nature Conservancy magazine and in a video being developed by the Denver Museum of Natural History. Both approached us for information that would support their topic of "The Disappearing Shortgrass Steppe". We look forward to working with these organizations during the next several months to educate their staff as well as the general public that the shortgrass steppe is surprisingly resistant because of its ecological history, and is currently in relatively good shape.