SECTION 1. Results from Prior Support

From 1996-2001, the Shortgrass Steppe (SGS) Long Term Ecological Research (LTER) Project produced approximately 190 papers in refereed journals, 60 book chapters, 29 dissertations/theses, and many abstracts from national and international meetings (**Table 1.1**). We supported 32 graduate students, 120 undergraduate students, 15 Research Experience for Undergraduate (REU) students, 23 Research Assistance for Minority High School Students (RAMHSS), and 2 post doctoral fellows. Scientists at our site are involved in LTER network activities through comparative modeling studies, international collaborations, and new cross-site experiments. Below, we highlight some of our results, prioritizing new areas of research this last round of funding. We organized the report using a modified version of LTER core areas (Section 2). Although we present results by core areas, activities are strongly linked across these areas.

Population Dynamics:

Our work in this area focuses on monitoring and experimenting to understand dynamics of species that are key to the structure and functioning of the SGS. Over this last funding cycle, we began a new emphasis on species that have increased in their importance (invasive species) and those that have been declining (e.g. prairie dogs); our summary here centers on those results.

<u>Invasive Plants</u>: A survey of invasive plant species in the western section of the SGS-LTER indicated that while invasive species occurred along roadsides, few were in the native steppe (Betz 2001). We measured soil seed content and manipulated water, nitrogen (N) and weed seeds on experimental plots. Invasive seeds declined exponentially from roadsides to 25 meters into the steppe, suggesting invasive species in the SGS are limited by seed dispersal (**Fig. 1.1**, see Section 2 for cited figures). Additions of water combined with N increased survivorship of the invasive annual grass *Bromus tectorum* by 3.6% compared to 0% in the control (Betz 2001). Thus, both seed and resource availability influence the success of invasive plants in the SGS.

<u>Prairie Dogs</u>: Over the past 100 years, one of the most observed changes in the SGS has been the reduction in prairie dogs and the consequence for biological diversity. Our studies have shown that the presence of prairie dogs benefits common species such as northern grasshopper mice, horned larks and lesser earless lizards, and rarer species such as Ord's kangaroo rats, mountain plovers and raptors. Prairie dogs negatively affect other species, such as thirteen-lined ground squirrels, lark buntings, northern many-lined skinks, and short-horned grasshoppers (Fig. 1.2). Additionally, the common practice on federal lands of recreational shooting of prairie dogs negatively impacts burrowing owls (Fig. 1.3). Our data indicate that prairie dog colonies are a key feature of SGS landscapes for maintaining species assemblages.

Prior studies on mixed-grass prairie have found that bison, elk, and pronghorn antelope preferentially graze on prairie dog towns (Whicker and Detling 1988). We investigated the use of towns by cattle in 12 pastures containing 15 black-tailed prairie dog towns. Towns occupied 3% of pastures, and cattle were present on them an average of 3.5% of the time, indicating cattle neither avoid nor prefer prairie dog towns on the SGS (Guenther and Detling 2001, Fig. 1.4).

Measurements of body temperatures of free-ranging adult black-tailed prairie dogs (*Cynomys ludovicianus*) during two consecutive winter seasons showed that they enter torpor when temperature drops dramatically during sudden cold spells (**Fig. 1.5**). Seasonal changes in diet and in lipid composition of white adipose tissue indicate that energy utilization patterns change during periods of environmental and physiological stress. Thus, black-tailed prairie dogs use a combined strategy for coping with unfavorable environmental conditions: they continue to forage throughout winter and practice facultative torpor when environmental conditions are unfavorable (Lehmer 2000).

<u>Other Small Mammals</u>: We continued surveys of small mammal populations to elucidate temporal and spatial dynamics. Deer mice (*Peromyscus maniculatus*) had higher densities in shrub than grassland areas and were highly variable over time (**Fig. 1.6**). Autumn densities of

northern grasshopper mice (*Onychomys leucogaster*), normally stable, were lower in 2000 than in any year since 1994. Drought conditions in late summer 2000 may have reduced availability of arthropod prey for both species. Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*) numbers in 2000 were similar to those in 1999. In contrast to earlier short-term studies (Higgens and Stapp 1996), squirrels were much more abundant in grassland than shrub areas in both 1999 and 2000, which highlights the necessity and utility of long-term studies. Spotlight surveys showed that black-tailed jackrabbits (*Lepus californicus*), were very abundant in summer 1996, and spring and summer 2000. In both years, high densities of rabbits followed years of unusually high spring rainfall, and consequently higher vegetation.

<u>Responses of Ecosystems to Grazing</u>: A great deal of our past SGS-LTER work has focused on ecosystem responses to cattle grazing. During 1996-2001, we continued our intensive field measurements, and produced several synthesis products. Milchunas et al. (1998) synthesized long-term data sets and showed that some organisms respond very positively to cattle grazing (e.g. the threatened mountain plover,—*Chavadrius montanus*, and the dominant grass, *Bouteloua gracilis*), and others respond negatively. Moore et al. (1996, and submitted) posited that grazing alters N and C cycling belowground by inducing a shift from the fungal to the bacterial pathway; annual monitoring has documented the beginning of this shift.

Biogeochemistry

Similarly to our population work, our biogeochemistry work focuses on pools and dynamics that are key to the structure and functioning of the SGS, and dynamics that may characterize responses to the important human-induced changes that are occurring and that we foresee.

<u>Belowground Primary Production</u>: Since its inception, the SGS-LTER has placed major emphasis on studying belowground dynamics because the majority of biomass is belowground. Our recent methods work has shown that the isotope-decay method of estimating belowground net primary production (BNPP) potentially overcomes assumptions and biases associated with traditional methods. Method development and estimates of BNPP were previously published using four years of data. A slow, distinctly different phase in isotope loss developed 5-10 years post-labeling (Fig. 1.7, Milchunas and Lauenroth 2001). BNPP estimates may be influenced by 1) ¹⁴C in soil embedded in growing roots, 2) a small proportion of roots that live a much longer time than the majority, and 3) methods of separating roots from soil organic matter (SOM).

<u>CO2</u> <u>Fertilization Study</u>: Several important new findings were revealed after 5 years of the Open Top Chamber CO2 project (jointly funded with the Agricultural Research Service, ARS, and several grants). Doubling ambient CO2 concentration led to enhanced production on the SGS, ranging from 20% in 1998 to 71% in 2000 (**Fig. 1.8**, Morgan et al. 2001), among the highest increases in grassland CO2 enrichment studies. Physiological measurements suggest that higher water use efficiency is one of the major causes. Highest growth enhancements occurred for *Stipa comata*, a C3 perennial grass of fair forage quality. Two high quality and drought resistant species, *B. gracilis* (C4) and *Pascopyurm smithii* (C3) exhibited no CO2 response, suggesting that increased CO2 may lead to lower drought resistance and lower forage quality. Large increases in BNPP occurred in response to CO2 enrichment, averaging 59% based on minirhizotrons and 43% based on root ingrowth cylinders. Trace gas flux data showed no detectable CO2 effect on ecosystem respiration, CH4 oxidation, or emissions of NO_x and N2O.

<u>Biogeochemical Consequences of Resource and Environmental Manipulation</u>: Resource alteration as a consequence of global change may have significant ecosystem consequences. We investigated the effects of altered water, N, daytime temperature, and their interactions on SGS biogeochemistry. Daytime temperature was increased with the construction of open top tents. Water and N availability were increased by doubling average precipitation, and adding twice the average estimated N mineralized. Data on CO₂, CH₄, N₂O, and NO flux (**Fig. 1.9**), N mineralization, decomposition, and total C and N were collected from 1996-1998. Our analysis

indicates that the alteration resource availability has immediate consequences on the biogeochemistry of SGS (Burke et al. in prep).

Biogeochemistry Along a Soil Chronosequence: One of our major foci has been extending our studies over longer time scales. We characterized soils in six alluvial terraces that span the last 600,000 years. Significant changes in chemical constituents occurred over geologic time scales. The accumulation of carbonate over time revealed a morphogenic sequence that positively associates soil development with age. Atmospheric deposition resulted in net accumulations of Ca, Fe, and Al, and losses of Si (Loadholt, 2001). Total P decreased over time, with the primary calcium-phosphate fraction declining slowly over time (Fig. 1.10) indicating a slow rate of primary mineral weathering. Occluded P increased from 7% to 10% of the total, organic P increased 23% over time (highest value at ~350,000 years old), and non-occluded P remained a very small percentage of the total P.

Land-Atmosphere Interactions

The most important abiotic variable influencing the SGS is water availability; much of our work focuses on ecosystem responses to and influences over this factor. In addition, as with the other core areas, we emphasize how ecosystem processes in SGS influence regional dynamics (e.g. trace gas emissions and sinks, radiative and water balance influencing climate), and feedback interactions with human impacts.

Trace Gas Exchange within the SGS: Our long-term, year round measurement of CH₄ and N₂O fluxes shows that 1) gas fluxes vary across the landscape, 2) N additions increase N₂O emissions and 3) the SGS is an important sink for CH₄ and a source of N₂O (Mosier et al. 1991; 1996; 1997). The data increased our understanding of temporal variation of CH₄ and N₂O flux, and of the importance of emissions of N gases (NH₃, NO_x, N₂O) from the soil as key regulators of the system (Martin et al. 1998; Mosier et al. 1998a; Mosier et al. synthesis volume). We used these data to develop simulation models (see Synthesis section below)

<u>Soil Water Dynamics and Vegetation Structure</u>: Our conceptual framework asserts that physiography has a large influence over SGS ecosystems. One of the key proximal regulators is soil texture as it influences soil water (H₂O), especially the depth of penetration and storage of H₂O. Field data on available soil H₂O by layer from sites with different soil textures were used to estimate parameters for a daily time step soil H₂O model. We simulated the 50-year average soil H₂O dynamics at each location. We found that: 1) coarse textured soils had a larger deep H₂O resource than fine soils, and were associated with a greater cover of shrubs; and 2) the additional H₂O in coarse soils resulted in higher plant productivity (NPP) (Wythers 1996).

Bare soil evaporation accounts for a large fraction of the total water loss from soil yet it is poorly understood. We evaluated effects of soil texture on water loss using mini-lysimeters (Wythers et al. 1999). Evaporation influenced soil water content to a 40 cm depth in all textures, in contrast to previous assumptions that bare soil evaporation only influenced the top 10-20 cm. The depth to which evaporation had its maximum influence varied among textures. Using these data, we found that previous parameter values for our soil water simulation model resulted in a 50% underestimate of bare soil evaporation over 10 days (Wythers et al. 1999).

<u>Feedback between the Atmosphere and Land Surface Processes</u>: Our recent work has focused on integrated modeling of atmosphere-biosphere interactions to extend our field measurements to larger realms. Investigation of the relationship between weather and vegetation growth with the RAMS-CENTURY coupled modeling system has shown that the simulated feedback between precipitation and aboveground vegetation results in wetter and cooler weather than would occur if this feedback were excluded (Lu et al. 2001). This suggests that land surface processes associated with vegetation changes may significantly impact regional weather patterns.

<u>Influence of Land-Use Change and Doubled CO₂:</u> We used the RAMS-GEMTM modeling system to investigate the effect of 1) changing the central Great Plains from current land-use to

an estimate of the natural landscape; 2) doubling CO₂ in the RAMS model; and 3) doubling CO₂ in the GEMTM component of the model. The control experiment (current landscape and CO₂) was compared against observed weather and vegetation growth data. Both the change to the natural landscape and the biological effect of doubled CO₂ produced a cooling over current conditions. This suggests that anthropogenic land-use change exerts a major effect on both short-and long-term weather in the SGS and that the effect of increased CO₂ on vegetation may have an important and rapid feedback to weather in the SGS (Eastman et al. 2001a, b).

Cross-Site Work:

Our site has a substantial involvement in both cross-site work and in synthesis activities (*entries in **Table 1.1**). These activities enrich our science at a local scale by providing important context, and allow us to extrapolate short and long-term site level studies to larger spatial extents and longer time scales. Below, we provide three examples of our ongoing cross-site work.

Isotopic analysis of carbon and water fluxes: We compared grassland, forest, and tundra systems with respect to the ^{18}O composition of soil water, soil CO_2 , and the flux of CO_2 from soil to the atmosphere. Field data combined with model runs indicated that soil water $\delta^{18}O$ values vary as a function of the isotopic composition of precipitation inputs and evaporative losses (Sulzman 2000). Values were significantly enriched in the grassland, as compared to forest and tundra. Incomplete isotopic equilibration between CO_2 and water was often observed under dry field conditions, suggesting that $\delta^{18}O$ values can be used as a marker to separate soil and vegetation components of ecosystem respiration from these systems.

Nitrogen mineralization across a Great Plains precipitation gradient: Our site has a long tradition of conducting comparisons across sites within the Great Plains, and in extrapolating results to regional scales (e.g. Sala et al. 1988, Parton et al. 1987, Burke et al. 1989, 1994, 1997). Recently, an SGS-LTER graduate student (McCulley) obtained a dissertation improvement award to study 5 sites spanning a precipitation gradient from the SGS to the Konza tallgrass LTER site. Growing season precipitation varied more than two-fold across the gradient and by >25% between years. Soil N pools and the N content of aboveground NPP (ANPP-N) increased from SGS to tallgrass prairie, and ANPP-N tracked interannual precipitation. However, estimated *in situ* net N mineralization rates did not increase across the gradient or reflect interannual differences (Fig.1.11). These data suggest that current methods of estimating *in situ* net N mineralization may not be effective for soils with large immobilization potentials.

<u>Understanding N Retention in Grasslands</u>: We examined the influence of soil organic carbon (SOC) and soil texture on N retention across 5 sites on a north-south gradient from Montana to Texas, including the SGS-LTER. We applied 2.5 and 50 g Nm⁻² of (¹⁵NH₄)₂SO₄ in 1996, and sampled plants and soils for two years. Soils were the major sink for added ¹⁵N. Low-N treatments retained a high proportion of N distributed in active and intermediate fractions of the soil-plant system. High-N plots retained 36 % of added N. SOC explained 55 and 43 % of the variance in N retention for low- and high-N treatments. Fine textured soils retained more N than coarse soils (Fig. 1.12, Barrett and Burke in press). We conclude that soils are the dominant sink for N and that stabilization is controlled in part by SOC and soil texture. We estimate the threshold for N retention in surface soils of semiarid grasslands to be less than 20 g N m⁻².

Belowground Food Web Structure, Dynamics and Stability: We addressed the roles of productivity in structuring ecosystems (Moore and de Ruiter 2000), the estimation of interaction strength using field data (de Ruiter et al. 1999), and the impacts of agriculture soil communities (Moore et al. 1996, Moore and de Ruiter 1997). Our studies suggested that the fungal pathway was less resilient to disturbance than the bacterial pathway. In addition, we found that interactions between prey and consumers changed with belowground trophic level: the negative effects of consumers on prey decreases with increased trophic position, with the inverse true for the positive effects of prey on consumers (de Ruiter et al. 1999, Moore and de Ruiter 2000).

<u>Information management (IM) and network leadership</u>: In addition to managing over 100 requests for data annually (Fig. 1.13 and 1.14) and over 120 data sets on-line, our site has a large investment in network level governance and particularly in leadership of IM efforts. Stafford chairs the LTER Network Information Managers Committee, and recently completed an NSF grant that focused on developing web-based software, integrating databases into seamless virtual databases, and providing value-added results and practical solutions to natural resource issues. Burke served on the LTER Network Executive Committee from 1997-2000.

Synthesis

We continue to be involved in many synthesis activities through review papers, modeling, and our synthesis book, Ecology of the Shortgrass Steppe: Perspectives from Long-Term Research. At this time, all but two chapters are out for review and we anticipate sending the document to the publisher in 2-4 months. As examples, we recently published a new model of SGS trace gas fluxes (Del Grosso et al. 2000a, b), reviewed the Great Plains N (Burke et al. in revision), analyzed the role of grazing in influencing regional climate (Eastman et al. 2001a, b), developed a model that integrates grazing and belowground process (Moore et al. in revision), reviewed the role of prairie dogs in the Great Plains (Stapp 1998), and evaluated the relationship between BNPP and environmental variables (Jackson et al. 2000, Gill et al. in press).

The SGS-LTER project has been involved in simulation analysis as a key part of our activities since 1982. Models have been particularly useful for helping us test our understanding, design experiments and extrapolate to long temporal and large spatial scales. SGS-LTER contributed to developing the Century Global model (Schimel et al. 1997) and the daily Century model, Daycent (Parton et al. 1998). The SGS-LTER extensive trace gas data were used to develop Daycent trace gas flux submodels. SGS-LTER was substantially involved in developing the Tragnet (Ojima et al. 2000) global data set for trace gas fluxes (CO₂, N₂O, CH₄, NO_X).

SGS scientists were also involved in a set of model comparison activities. As part of the LIDET cross site decomposition experiment, Century was compared to 3 other models (Moorhead et al. 1999) and the LIDET litter decay data, and was used to compare decomposition of different types of litter from all 28 LIDET sites (Gholz et al. 2000). We contributed to developing global NPP data sets (Scurlock et al. 1999) and compared Century Global model results with those from other major global ecosystem models (Cramer et al. 1999). We participated in the GCTE elevated CO₂ and temperature model comparison (Mooney et al. 1999), a soil water model comparison (Shao and Henderson-Sellers 1996, Parton et al. 1996), and the VEMAP climate change model comparison activity (Pan et al. 1998, Schimel et al. 2000). These model comparison activities have increased our understanding of how ecosystems function and how models may be better formulated to represent these dynamics.

Education:

The SGS-LTER has played a leadership role in education at all levels. We developed an education component that includes traditional research experiences for undergraduates, K-12 outreach in the forms of high school student mentoring, curriculum development, teacher professional development, and Schoolyard Ecology, and a strong emphasis on serving first generation and low income (FGLI) students, in addition to informal education activities with museums and centers, and most recently, education research. The effort was facilitated by SGS-LTER in collaboration with the Math and Science Teaching Center at the University of Northern Colorado, resulting in over \$3,000,000 in external funding to support FGLI HS students, undergraduates, graduate students, faculty and K-12 teachers through NSF and DOE programs (Section 5). The work has resulted in support for up to 14 graduate students, 2 post-doctoral fellows, and up to 10 K-12 teachers through 2003; the development of schoolyard ecology plots throughout NE Colorado; and two publications (Moore et al. 2000a, b, Rham et al. submitted).

SECTION 2. CONCEPTUAL FRAMEWORK AND RESEARCH PLAN

INTRODUCTION

Over the last two decades, our research has centered on understanding the processes that account for the origin, structure and function of the shortgrass steppe (SGS). The key questions that continue to organize and guide our research are:

- 1. What factors regulate SGS ecological structure and function over space and time?
- 2. How do the factors that regulate ecological structure and function, and the coupling of biotic and abiotic components, vary spatially and temporally within the SGS?
- 3. What are the biotic and abiotic thresholds that determine the vulnerability of the SGS to changes in the factors influencing ecological structure and function?

Since the last funding cycle our long-term monitoring, short- and long-term experimentation, and modeling efforts have provided new insight toward addressing these key questions. Our ongoing interdisciplinary studies, and the development of new analytical techniques and modeling efforts, promise substantial advances in our ability to expand our understanding of SGS structure and functioning. In the following section, we present a synthesis of our conceptual framework, focal hypotheses, continuing long-term studies, and future plans for short- and long-term research.

CONCEPTUAL FRAMEWORK

We use our conceptual framework (**Fig. 2.1**) to express the relationships between the various components of the SGS ecosystem. The conceptual framework serves to guide us in generating hypotheses, evaluating the importance of both long- and short-term experiments, and examining the contribution of proposed experiments in light of the entire scope of the project.

Our conceptual framework asserts that climate, natural disturbance, physiography, human use, and biotic interactions are the major determinants of the ecological structure and function of the shortgrass steppe. We understand that our recognized determinants of SGS structure and function operate at a variety of spatial and temporal scales. At the spatial and temporal scales of most studies, the basic determinants of ecosystem dynamics are perturbations caused by short-term climatic fluctuation, changes in land use, landscape variability imposed by physiography, and natural disturbance caused by various animal species. Over centennial to millennial time scales, the determinants of ecosystem dynamics are climate change, atmospheric deposition and the slow release of nutrients from parent materials.

Next to each of the 5 factors in the conceptual framework, we present an icon to symbolize it. When we describe our proposed work we will use the icons to demonstrate how the work is connected to our conceptual framework.

Climate



The annual amount and seasonal distribution of precipitation is a major determinant of the ecological structure and function of the SGS. Mean annual precipitation across the LTER site ranges from 320 mm on the western edge to 420 mm in the northeast. Most of the precipitation occurs as rain between May and

September, with a distinct dry period from December through February (Lauenroth and Burke 1995). However, interannual variation in precipitation is high (Lauenroth and Sala 1992).

Biotic response to interannual and seasonal variations in precipitation is large, and there are important interactions between ecosystem structure and function in these responses. Plant responses depend on photosynthetic pathway and plant type (Lauenroth and Sala 1992). Perennial C₄ bunchgrasses maintain their presence and cover in all years, while C₃ 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 NPP (Lauenroth and Sala 1992), net N mineralization (Hook and Burke 2000), and trace gas flux (Mosier et al. 1991) are also very responsive to interannual and seasonal variation in precipitation.

Mean annual temperature ranges from 8.6 to 9.3°C. A summary of long-term data suggests that daily minimum temperatures in the spring are negatively correlated to aboveground NPP (ANPP) of *Bouteloua gracilis*, the dominant plant (Alward et al. 1999). These results strongly indicate that the SGS ecosystem may be sensitive to increases in daily minimum temperatures comparable to those being observed globally. There are significant feedbacks from SGS ecosystems to atmospheric processes, including reflected radiation, H₂O vapor (Pielke et al. 1997), and trace gases (Mosier et al. 1991).

Natural Disturbance

Natural disturbances are responsible for some of the spatial variability observed in SGS ecosystems. Most disturbances are small (0.1 m² to several hectares), and there is an inverse relationship between size and frequency (Coffin and Lauenroth 1989b). The most frequent disturbances are 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. Although fire is a major component in tallgrass and mixed grass ecosystems, its role in the SGS is poorly understood. Because of the low fuel loads, pre-settlement fires probably provided small disturbances. Our experimental work on fire in the SGS suggests that there is no significant reduction of any functional group of plants, nor effects on tissue nitrogen (N) content such as those observed in other ecosystems (Milchunas, personal communication). Both drought and large herbivore grazing are excluded from our list of natural disturbances due to the long evolutionary history of these selection pressures in the SGS.

Physiography

Physiographic features, namely, landscapes and elements of landscapes (eg. topographic positions) within the SGS vary at a spatial scale of 0.1-100 kilometers and have very slow temporal dynamics (centennial to millennial timescales). The distribution and properties of landscapes provide the template for many of our field investigations and are key to scaling exercises. 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 (Blecker et al. 1997) resulting in systematic variations in soil properties such as H₂O holding capacity and inorganic nutrient content among soils ranging in age from 5,000 to 600,000 YBP (Loadholt 2001). Thus, many aspects of physiography are important in influencing the SGS; landscape position, soil age, soil depth, and surface texture appear to have important implications for evaluating many biotic interactions such as ANPP (Singh et al. 1998), N availability (Burke et al. 1999, Hook and Burke 2000) and prairie dog activity (Stapp 1998).

Human Use



Human use has been and continues to be a major determinant in the structure and function of SGS ecosystems. The role of humans has broadened and represents land uses as diverse as livestock grazing, dryland and irrigated row-crop agriculture, and urbanization. While land use formerly varied at relatively large spatial extents (from field scale to several km²), it is now evident that land use and its spatial

distribution has resulted in a fragmentation of the SGS, with privately owned lands rapidly being subdivided from formerly large ranch/farm operations to smaller "horse properties" for commuters to the cities. For the remaining native SGS, cattle grazing continues to be the dominant land use. Our LTER site has the oldest, largest, and most numerous livestock grazing exclosures in the entire shortgrass region. Our past LTER research indicates that SGS ecosystems are relatively resistant to negative effects from livestock grazing (Milchunas et al. 1988, 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 *B. gracilis* (Milchunas et al. 1989). Furthermore, heavy grazing appears to reduce the vulnerability of the plant community to invasion by exotics (Milchunas et al. 1992). Soil organic matter (SOM) pools and turnover are only slightly influenced by grazing, because aboveground forage represents a minor portion of the organic matter (Burke et al. 1997).

Sixty percent of the SGS is currently being cultivated (Lauenroth et al. 1994) and up to 30% more was cultivated within the past 100 years. Conversion to cropland drastically alters biological diversity, reduces SOM (Haas et al. 1957, Burke et al. 1989, and many others), and alters the temporal and spatial distribution of plant biomass. Because of the importance of cropland regionally and within the boundaries of our LTER site, and the long recovery period following abandonment, we focus some of our work on the influence of cultivation. Our hypothesis is that cultivation management represents a key threshold in ecological responses, due to the focus of the disturbance on the belowground components, which contains the major concentrations of carbon and nutrient stores and biological activity.

The effects of human disturbances on biotic interactions are addressed to some degree in every research area (Fig 2.1). We have not evaluated the impacts of urbanization of the SGS to date, but other associated projects suggest that biological diversity, hydrology, biogeochemistry, and land-atmosphere interactions are strongly altered. This is a topic that we will explore under separate funding.

Biotic Interactions



Beyond the obvious role of organisms as elements of the structure and function of SGS ecosystems, interactions among and between organisms and climate, natural disturbance, physiography, and human use are the critical determinants of both the current state and the future vulnerability of SGS ecosystems. Our past work indicates that there are important interactions between ecosystem structure and function

(Lauenroth and Sala 1992). Biotic interactions provide the mechanisms whereby ecosystem structure and function are affected by and, in turn, feed back to other determinants (climate, disturbance, physiography and human use). Our studies of biotic interactions focus on accounting for patterns of biological diversity, assessing the role of species and communities in governing ecosystem function, determining the responses of community patterns to abiotic factors (climate, disturbance, physiography and human use), and assessing vulnerability to future species extinctions and invasions.

Summation

Our conceptual model (Fig. 2.1) suggests that the current state and vulnerability of SGS ecosystems (structure and function) requires understanding of climate, natural disturbance, physiography, human use, and biotic interactions and their interactions with the ecosystem. Our past, present and future research is focused on this topic. The purpose of the conceptual framework is to truly integrate our understanding of the processes that account for the origin, structure and function of shortgrass ecosystems.

Our conceptual framework implicitly embodies the original five core areas of the NSF-LTER program which were originally used as organizing foci for the first set of LTER projects (Callahan 1984). These original core areas were: 1) Patterns and controls on primary production, 2) Spatial and temporal patterns of populations, 3) Patterns and controls of organic matter accumulation, 4) Patterns of inorganic inputs and transport, and 5) Patterns and frequency of disturbances. Although the core areas provide foci for our research and ecosystem monitoring, we have found that our historical areas of scientific expertise and our current research interests are best summarized under the umbrella of three research areas: *Population Dynamics* (core areas 2 and 3), *Land-Atmosphere Interactions* (core areas 3 and 4), and *Biogeochemical Dynamics* (core areas 1, 3 and 4). We consider disturbances (core area 5) as a major determinant of our ecosystem that is embodied in each of our three research areas.

SHORTGRASS STEPPE LTER SITE

Our SGS-LTER site encompasses a large portion of the Colorado Piedmont Section of the western Great Plains (Fig. 2.2). The extent is defined as the boundaries of the Central Plains Experimental Range (CPER), which is managed by the Agricultural Research Service (ARS), and the Pawnee National Grasslands (PNG), which is managed by the U. S. Forest Service. Expansion into the PNG has allowed us to explore the biotic interactions of the SGS ecosystem across a range of climatic, geologic, topographic and land use conditions. The CPER has a single ownership and landuse (livestock grazing). The PNG is characterized by a mosaic of ownership and land use. Ownership includes federal, state or private and land use consists of livestock grazing or row-crops. In addition, there are NGO conservation groups that exert influence over the area, particularly on federal lands. This varied land use and diversity associated with land users and land managers substantiates the importance of our long-term ecological research program to the area. We have advanced our use of remotely sensed data to encapsulate the wide array of landscapes, land uses and their potential influence on biotic interactions. We have developed new partnerships with the USDA-NRCS, USFWS, the Nature Conservancy, and a wide range of national, state, and local land managers, owners and environmental groups (See our Outreach and Management sections for a description of some of these interactions).

CONTINUING AND PROPOSED RESEARCH

We have divided our continuing and proposed work into three key areas (Fig. 2.1): Population Dynamics (divided into plant dynamics/ecosystem interactions and faunal dynamics/ecosystem interactions), Biogeochemical Dynamics, and Land-Atmosphere Interactions, as described above. Within each area, we describe our long-term and short-term experiments, and simulation modeling, which is integral to synthesizing and advancing our understanding. Our research is tightly integrated, such that any organization we chose would include multiple connections among the different sections. We use tables to summarize our experiments and related data sets (Tables 1.2, 1.3 and 1.4). Published experiments are cited in the text below and described in less detail than new experiments. In cases where we felt the reader might want more detail on experimental design or sampling, and we are constrained by space, we reference our web page (http://sgs.cnr.colostate.edu/), using the notation WEB. On the home page, there is a link to Proposal 2002, and then to Methods. If you are reading this document electronically, you may click on these links for connection to the appropriate web site.

1. Population Dynamics:

1.a. Plant Dynamics and Ecosystem Interactions

1. a. i. Monitoring

Grasses, shrubs, forbs, and succulents are the major components of the vegetation structure of the SGS. Because of its overwhelming importance to cover and biomass, our past plant population work has focused heavily on the grass *B. gracilis* (blue grama). Associated with our long-term study of blue grama population dynamics, we also collect data on other species in the same permanent quadrats.

We are proposing to initiate long-term studies of population dynamics of *Opuntia* polyacantha (prickly-pear cactus). Although this species comprises a relatively small proportion of biomass or NPP, its growth form and the consequent protection afforded to other species may have a large effect on ecosystem dynamics under cattle grazing (Bayless 1996)

have a large effect on ecosystem dynamics under cattle grazing (Bayless 1996).

Ecosystems in the SGS have, to date, been little affected by invasive plants (Kotanen et al. 1998, Hazlett 1998). Given the rate at which plant material is being introduced to new habitats (Mooney and Hobbs 2000), there is a strong likelihood that plants that are pre-adapted to SGS will eventually arrive. We are proposing to start long-term sampling specifically to detect the introduction of potential invasive plant species as part of our research.

Below, we describe our long-term experiments, simulation modeling, and proposed new work. Our work is organized under six hypotheses (P1 - P6).

Population dynamics of blue grama: LT 1 and LT49, WEB

This study focuses on the spatial and temporal variability in recruitment, growth and mortality. We currently sample annual seed production as well as examining the relationship between environmental variability and recruitment, growth, and mortality on permanent plots that are mapped annually. Our blue grama population dynamics work is guided by the following hypothesis:

(P1): The long-term sustainability of SGS ecosystems is dependent upon the sustainability of populations of B. gracilis, because it is the most grazing and drought tolerant plant species in the ecosystem. It is the key species for management for both conservation and livestock production.

Recruitment of blue grama is an infrequent event controlled by the availability of viable seed, temperature, soil H₂O, 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 seed production is strongly influenced by soil texture, grazing, and neighboring plants; and that seed storage is limited and variable in time (Coffin and Lauenroth 1989a, 1992, Aguilera and Lauenroth 1993b, 1995, Hook et al. 1994). Simulation using an individual plant-based model (Coffin and Lauenroth 1990) has suggested an important role for seed dispersal in the recovery of blue grama from disturbances (Coffin and Lauenroth 1989a,b). Recent research (Fraleigh 1999) has indicated important roles of wind and cattle on seed dispersal.

Population dynamics of plains prickly-pear: LT49 and NEW LT.

The common view of prickly-pear is that it increases as a result of grazing, although research in SGS and mixed prairie has failed to support this idea (Houston 1963, Hyder et al. 1975, Dougherty 1986). Past analyses have shown important responses of prickly-pear to interannual variabiability in precipitation (Fig. 2.3, Dougherty 1986) and irrigation (Fig. 2.4, Dougherty et al. 1996). Recent work has suggested a critical role for prickly-pear in maintaining plant species richness (Fig. 2.5) and soil C and N (Fig. 2.6) under cattle grazing (Bayless 1996, Burke et al. 1999).

We plan to initiate a study of long-term population dynamics of prickly-pear using permanent plots located inside and outside cattle exclosures, associated with an existing long-term grazing study (LT32-41). Annually, a drawing of each clone will be updated with information about the numbers of live (new and surviving) and dead cladodes (joints). We will record which cladodes produced a flower and take a perpendicular digital image of each plot, which will be scanned and digitized into a GIS. This work will be guided by the following hypothesis:

P2: O. polyacantha is a key species for long-term conservation of SGS ecosystems because of the protection from grazing it affords to other plant species growing within the area influenced by its spines, and because of its ability to trap wind- and water-transported organic and inorganic material.

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 a) individual plants of C₃ and C₄ perennial grasses: Aristida longiseta, Sitanion hystrix, and Agropyron smithii; and 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. Plant size, basal area for grasses or canopy dimensions (height and two widths) for forbs and shrubs, will be estimated. Size and frequency of disturbances will be mapped as one source of mortality. This work is not hypothesis-driven, but rather an effort to understand key life history characteristics of these species for our plant community modeling efforts (Coffin and Lauenroth 1990).

Plant Phenology: LT2. WEB

The timing of major events in the life cycle of organisms provides important information. Plant phenology provides a plant-integrated assessment of environmental conditions. 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" approach3. Again, this work is not driven by a hypothesis, but rather by an objective to increase our understanding of the role of interannual variability in climate as it governs biotic responses.

Invasive Plant Species: NEW LT.

Two facts argue for the importance of instituting an effort to sample across habitats for the presence of potential invasive plants. The first is that we are in the midst of a major homogenization of the earth's biota (Vitousek et al. 1996) that has high potential for new plant introductions into the SGS. Even though the SGS has proven quite resistant to invasion (Kotanen et al. 1998, Hazlett 1998), the introduction of species that can successfully invade the SGS is inevitable. The second fact is that despite considerable effort, ecologists are still not able to predict which new plants will become invasive in any particular ecosystem type (Mooney and Hobbs 2000). We plan to survey to detect new plant introductions over the entire SGS LTER site using the primary habitat approach of Hazlett (1998, Fig. 2.7). When an invasion is identified, we will initiate a series of short-term and long-term studies to assess plant community and biogeochemical effects. Our past work showed that under increased N and H₂O, exotic species may establish, persist, and maintain high N availability (Milchunas and Lauenroth 1995, Vinton and Burke 1995).

Invasive Plant Species: NEW SYNTHÉSIS.

We plan to use our individual plant-based simulation model (STEPPE, Coffin and Lauenroth 1990) to explore the vulnerability of SGS communities to invasions by plants with a variety of combinations of potential characteristics in an effort to identify types with the highest probability of success. This simulation work will be combined with analyses using CLIMEX (Sutherst and Maywald 1985) to identify geographic locations globally with similar climates to the SGS. We will assume that plant introductions from areas with similar climate will pose a high risk of an invasion. The hypothesis that will guide our work on invasive species is:

P3: Invasions by plants represent one of the most damaging changes that can occur in an ecosystem because of the changes they cause in plant and animal communities and in biogeochemical cycling.

1. a ii. Effects of Natural Disturbances on Plant Communities

A strong conceptual emphasis of our continuing work focuses on the effects of natural and human-induced disturbance on SGS ecosystems. Most natural disturbances are small (<100 m²) while most human disturbances are large (>100 m²). We use experimental studies and simulation modeling to improve our understanding of disturbances and recovery on SGS ecosystems

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, and were largely ignored until we began studying them in 1984 (Coffin and Lauenroth 1988, 1989a,b). These small disturbances may have the largest potential effect on plant community structure and ecosystem dynamics. In ongoing studies, we evaluate the effects of western harvester ants, burrows from skunks and badgers, mounds from pocket gophers, and patches from larvae of June beetles, and continue our simulation analyses (Aguiar and Lauenroth 2001). The following hypothesis guides our work in this area:

P4: Small-scale disturbances are the most important source of mortality for B. gracilis. This occurs because 1) these natural disturbances have a high frequency, 2) B. gracilis represents a major proportion of the plant biomass and is tolerant to both grazing and drought, and 3) its removal leads to dramatic alterations in ecosystem structure and function. Thus small-scale disturbances have a major influence on the sustainability of the SGS.

Long-term sampling of recovery from small-scale disturbances: LT27. WEB

We will continue to examine the response of SGS ecosystems to small-scale disturbances by sampling plant cover and density at regular intervals on disturbed areas. This work, initiated in 1984, focuses on disturbances from 0.1 to <5 m², and uses gap dynamics concepts to explain the response of SGS plant communities to disturbance. We will also continue to measure soil heights in and out 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 from natural small-scale disturbances such as ant mounds. Data from these studies

have been critical in our plant community modeling work (Coffin and Lauenroth 1990).

Blue grama removal experiment: LT57. WEB

Both field (Milchunas et al. 1990) and simulation results have suggested large increases in plant species diversity following the deletion of blue grama. We initiated an experiment in 1997 to test this prediction and other impacts of removal of the dominant species. The experiment consists of two grazing treatments (grazed, ungrazed), two removal treatments (removal, control), and 6 replicates. Since we are still in the phase where the effects of the disturbance are greater than the recovery response, it is too early to reach conclusions about the effects of the treatments on diversity (Fig. 2.8).

Recovery from white grub disturbances: LT30. WEB

We will continue to sample plant dynamics at regular intervals on patches of vegetation killed by white grubs, the larvae of June beetles. The ARS initiated a field study of these patches in 1977 where 32 areas have been resampled six times. This study is currently part of the SGS-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. We reported the first 14 years of recovery in Coffin et al. (1998) (Fig. 2.9)

Interactions between pocket gophers and grazing: NEW LT.

We will initiate a new long-term study to assess the size and frequency of pocket gopher mounds, and particularly, the effects on plant community dynamics. Low densities of pocket gophers in the first 8-10 years of the LTER limited our ability to study this disturbance type. However, in the past several years, high densities of mounds have been observed. High densities were also reported in the 1970s (Grant and French 1980), suggesting that temporal variability in pocket gophers and effects on vegetation can only be evaluated with long-term sampling. In our new study, we will locate and map pocket gopher activity annually in three grazing intensity pastures (light, moderate, and heavy) as well as in 3-5 moderately grazed pastures on different soil textures. We will establish grids based upon maps from Grant et al. (1980) and will follow these areas through time.

Small mammal grazing effects on plant communities: NEW-LT.

Small mammals, including rodents and lagomorphs (but excluding prairie dogs in this study), have been thought to primarily influence community structure through their small-scale, scattered digging activities (Coffin and Lauenroth 1989b), because gross consumption is only about 3% of ANPP (Lauenroth and Milchunas 1992). However, observations suggest that in some years, shrubs and barrel cacti suffer mortality due to over winter herbivory, and that the high degree of dietary selectivity of small mammals may result in effects much greater than suggested by their dry matter intakes. Small mammals in the SGS increase with decreased grazing pressure by cattle (Grant et al. 1982, Milchunas et al. 1998), suggesting an interaction with large herbivores that potentially masks effects observed in large mammal exclosures that do not exclude small mammals. In 1996, an LTER cross-site study was initiated to assess the relative importance of large vs small herbivores across gradients of NPP and evolutionary history of grazing. Small and large mammal exclosures were constructed at a number of sites, including the SGS. A primary hypothesis posed in this and subsequent currently funded work was that large mammals would be relatively more important in productive subhumid environments than in less productive semiarid environments, whereas the opposite would occur for small mammals, because of differences in dietary selectivity and the capacity to exert control in productive systems. Sampling based on new funding in 2001 indicates that changes in plant diversity are beginning to occur in the small mammal exclosures that exceed changes in largemammal-only exclosures. Our proposed new LTER work will be directed towards examining the mechanisms behind these responses, and extending the current cross-site monitoring to better capture long-term fluctuations in NPP and small mammal population cycles. The hypothesis that will guide this work is:

<u>P5</u>: Because they are selective, small herbivorous mammals exert a greater influence on SGS plant community structure than large generalist herbivores that consume much greater amounts of dry matter.

1. a. iii. Effects of Human-Induced Disturbances on Plant Communities.

Our work on human disturbances encompasses the long-term effects of cattle grazing and successional dynamics following cultivation and nutrient enrichment stresses (the latter two are described under the Biogeochemistry and Land-Atmosphere sections). The following hypothesis guides our work in this area:

P6/B5/L2a: Disturbances that focus on aboveground components (fire, livestock grazing) are minor relative to those that focus on both above-and belowground compartments (cultivation, construction, mining, etc.) (Burke et al. 1997). This occurs because most of the organic matter and energy processing occurs belowground in the SGS, thus, disturbances that target belowground pools have a large impact on the system. These belowground disturbances generally result in complete removal of the plant community and large losses in nutrients

We have conducted many short- and long-term studies on effects of cattle grazing on various aspects of SGS ecosystems, from physiological responses of plants to population dynamics, plant and animal community structure, and rates of ecosystem processes (e.g. Milchunas and Lauenroth 1993, Milchunas et al. 1988, 1989, Coffin and Lauenroth 1989, 1990, Aguiar and Lauenroth 2001. We will continue our long-term studies and initiate one new study on the effects of grazing (see cross-site section at end of proposal).

Long-term evaluation of grazing effects on primary producers: LT31. WEB

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). The ARS sampled these treatments for ANPP and species composition through 1964, they were intensively sampled for plant and consumer groups during the International Biological Program (IBP, mid-1960's), and we have continued work in these treatments since 1984. Short-term studies encompass all treatments

Long- and short-term effects of grazing: an interdisciplinary study: LT32-41. WEB

As mentioned above, our previous work has shown that SGS plant communities do not appear to be negatively influenced by cattle grazing (Milchunas et al. 1989). However, it appeared that litter accumulation, small mammal disturbances and SOM were higher in exclosures than outside. We began an experiment in 1991 to address the short- and long-term effects of grazing and of exclosure on SGS ecosystems, and how these effects interact with soil texture. We will continue this experiment, which consists of treatments associated with 60-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. Our large-scale sampling program assesses plant communities (Fig. 2.10), individual plant survival, aboveground and belowground biomass and NPP, SOM dynamics, soil fauna, small-scale disturbances, aboveground foliar N content, and belowground food web structure.

1.b.Faunal Dynamics and Ecosystem Interactions

During the past funding cycle we focused our animal monitoring on small mammals because they are important as consumers of seeds, arthropods and other small vertebrates, and as prey for a wide range of predators. They alter the system through their burrowing and mound-building activities and by consuming key plant species. Thus dynamics of small mammals simultaneously reflect and affect both the structure and function of SGS ecosystems. We propose to continue our emphasis on the dynamics and ecological effects of small mammals, synthesizing and building upon our past research success. Broadly, these studies will fall into two areas: 1) a continuation of long-term studies tracking changes in small mammal populations, their resources, and predators; and 2) new research to examine linkages between black-tailed prairie dog (*Cynomys ludovicianus*) and associated small mammals, plants, underground invertebrates, and microbes. One purpose is to examine dynamics in the face of an introduced disease, sylvatic plague caused by the bacterium *Yersinia pestis*, which has indirect effects on flora and fauna of SGS because of extinction and re-settlement dynamics of prairie dog towns. Our work on faunal dynamics and ecosystem interactions is organized around 7 hypotheses (F1-F7).

b. i. Monitoring faunal populations

Long-term population monitoring: LT 4, 5, 6, 7, 8, 10, and 53, WEB

We plan to continue surveys of rodents, rabbits, and canids conducted since 1994. This entails live-trapping rodents on grassland and shrubland sites twice yearly, spotlight surveys of rabbits 4 times yearly through representative shortgrass habitats, counts of mammalian predator (coyote, swift fox) scats 4 times yearly, and changes in vegetation and abundance of arthropod prey. Finally, we sample bird populations using a Christmas bird count and breeding bird count in accordance with a continent-wide scheme. These data will be synthesized into models of both single-species and community dynamics to test a number of specific hypotheses which can be organized under one general hypothesis:

F1: Spatial distribution and temporal dynamics of predator populations mirror but lag behind trends in prey because they are driven by spatial and temporal variation in the availability and composition of plant cover and availability of arthropod prey.

In addition to providing important data for other research on the SGS site, these studies will allow comparisons of the patterns and dynamics of mammal populations across the SGS, Sevilleta and Jornada LTER sites.

1. b. ii. Effects of prairie dogs on SGS ecosystem structure and functioning.

We plan to extend and synthesize studies of the role of prairie dogs in determining both biodiversity and ecosystem function of the SGS. We began our prairie dog work with pilot studies over the past 6 year cycle, and now propose to increase our emphasis in this area. This is an important area for the SGS LTER because of the critical role of prairie dogs in the SGS, the opportunities it affords for conducting basic research in metapopulation ecology and the intense public interest in prairie dogs (Roach et al. 2001).

Prairie dogs were abundant on the SGS in the past (Koford 1958), but have been severely affected by poisoning, shooting, habitat destruction through cultivation, and, most significantly, by plague. Both poisoning and shooting have been curbed on the SGS-LTER since the designation, in 2000, of the prairie dog as a candidate for listing under the Endangered Species Act. Plague continues unabated and is the major cause of local extinctions of prairie dogs. *Yersinia pestis* was introduced into the western U.S. in 1900 and quickly spread eastward to the 100th meridian in the central US (Barnes 1993, Fitzgerald 1993, Lomolino and Smith 2001). It was first recorded in black-tailed prairie dogs in 1946 (Ecke and Johnson 1952), and causes close to 100% mortality in affected towns. Plague appears to be transmitted to prairie dogs by fleas, and apparently has reservoirs in other rodent species with moderate to high plague resistance (Barnes 1993; Fitzgerald 1993, Cully and Williams 2001). However, the possibility remains that plague maintains an enzootic cycle within the prairie dogs themselves.

Plague epizootics in prairie dogs are "explosive", occurring sporadically at 3-5 year intervals (Barnes 1993; Cully and Williams 2001). Our data, based on 20 years of surveys of prairie dog towns on the SGS-LTER, show fluctuations in prairie dog abundance in the face of plague (Roach et al. 2001). Several of the largest towns on the SGS-LTER (#'s 66 & 69) have experienced plague epizootics in the last two years (Fig. 2.11).

We propose to examine how the interactions between two species, a burrowing rodent and an introduced infectious disease, affect the functioning of the SGS. We will take advantage of both the large number of suitable prairie dog habitats on the SGS-LTER whose histories of occupancy are known (long-term USFS data), and the current patterns of extinction and recolonization. Prairie dog towns expand exponentially after post plague recolonization (e.g., see Cully and Williams 2001), and when towns are recolonized, prairie dogs tend to aggregate in the center area of the habitat that comprised the towns (Cincotta et al. 1987). The overall hypothesis governing this research is:

F2: Prairie dogs affect the SGS ecosystem by control of trophic structure, by the habitat provided by burrowing, and by selective grazing of plants.

(Note that our work on prairie dogs includes work on plant dynamics and biogeochemical dynamics, but is placed together in this section of the proposal under Faunal Dynamics.)

We will test this hypothesis through long-term sampling of 16 prairie dog towns, which will

begin with 8 occupied towns (5 of which were studied during the previous funding) and 8 unoccupied but suitable sites. Each site will have 2 replicated transects, emanating from the center of suitable habitat to surrounding area (Fig. 2.12), which we sample at 4 places: the active center, newly-recolonized areas at the edge of the town, unoccupied habitat further away from the center, and an area off the edge that never harbored prairie dogs. Unoccupied towns will have the same kinds of sampling areas but will include the center of the town that was most recently occupied, plots further away that were more recently colonized and then became extinct, unoccupied habitat farther away, and a plot off the edge of the prairie dog town. Although historical data suggest that new towns will be founded during the proposed funding cycle, if no new colonizations occur during the first three years, we will consider initiating 5 new prairie dog towns at that time by moving prairie dogs into suitable habitat on the SGS site.

We will sample transects on a yearly basis for soil microorganisms, plants, and small mammals. Blood and flea samples taken from captured rodents will be tested for plague at the CDC laboratories in Fort Collins. We will analyze the data for spatial and temporal patterns in aboveground and belowground communities (both abundance and overall biomass). We will examine 4 aspects of the ecology of prairie dogs and associated biota: dynamics of prairie dog towns between outbreaks of plague (epizootics), changes in allocation in belowground dynamics of nutrients and microorganisms, dynamics of plant diversity and biomass, and abundance of other small mammals.

Prairie dog dynamics: LT 61, LT 62, ST 35 WEB and NEW LT.

Past prairie dog monitoring on the SGS site provides a long-term data set describing suitable habitat, whether the site was occupied at that time, and the area of the town. Detailed short-term studies of persistence and functioning of the prairie dog towns, including their demography and population genetics, are the subject of a separate proposal submitted to NSF by co-PI Antolin. That work includes analysis of the long-term town size and occupancy database that we have collected since 1982, and molecular genetic analyses that extend the work of Roach et al. (2001). The focus of our LTER work is to provide long-term monitoring data that are valuable on their own, and will support efforts to understand the population dynamics of prairie dogs. We will continue annual surveys of prairie dog towns by recording GPS coordinates of the outside boundaries of occupied towns to estimate size and location during a 4 week period in July of every year. Active burrows will be counted by sighting prairie dogs, fresh scat and digging, to estimate prairie dog densities. Visual counts of prairie dogs correlate well with actual prairie dog population size when the active area of the town is known (Biggins et al. 1993). The hypothesis to be tested by these data is:

F3: In times between plague epizootics, prairie dog towns will expand exponentially in size and number of prairie dogs, because of their capability for rapid population growth and migration. The current plague induced dynamics of extinction and recolonization represent an alternative but stable population structure for prairie dogs.

Changes in Belowground Allocation and Food Web Stability: NEW LT. WEB

Colonization and grazing by prairie dogs reduces the amount and quality of plant material entering the soil. At other sites, grazing has been shown to increase labile carbon (C) available to plant roots, increase N-mineralization and decomposition rates, and induce shifts from the fungal to the bacterial pathway (Ingham et al. 1985). (Fig. 2.13)

F4: The bacterial pathway is more active than the fungal pathway on occupied prairie dog towns compared to both unoccupied sites and adjacent unsuitable steppe habitat because prairie dog activity (e.g., burrowing and grazing) alters soil structure much like agricultural tillage, releasing occluded SOM and decreasing the amount of recalcitrant plant materials entering the SOM pool.

As a consequence of these soil changes, the system may shift to one that favors weedy plant species with accelerated root turnover (reduced plant and SOM C:N ratios). Such shifts may respond quickly to extinction-colonization episodes. The alternative pathways also favor different belowground food webs (Fig. 2.14), and the altered feeding rates and changes in the pattern of interactions within soil communities are expected to have lower stability (Fig. 2.15. Fig. 2.16).

F5: N retention is more likely to be lower in sites colonized by prairie dogs than in non-colonized adjacent SGS because prairie dog activity changes soil structure, plant community

structure and plant quality (lower C:N), inducing a shift in the soil community from stable to unstable trophic structures.

A prediction from the hypothesis is that sites not disturbed by prairie dogs will possess soil food webs that are dynamically more stable than occupied sites, and that after plague epizootics remove prairie dogs, towns will converge in community structure to undisturbed adjacent SGS. The stability and resilience of soil food webs constructed above will be assessed using techniques developed by Moore *et al.* (1993) and de Ruiter *et al.* (1995) and are described in more detail on our web page (WEB). We will estimate belowground community biomass and C:N for different functional groups, including: bacteria, fungi, protozoa, nematodes, and arthropods. We will use standard culturing, phospholipid fatty acid analysis, and enumeration methods.

Effects of prairie dogs on plant dynamics: LT 60, ST 36 WEB and NEW LT.

Prairie dogs have direct effects on plant communities, and indirect effects on other grazers and ground nesting birds in mixed grass prairie (Whicker and Detling 1988). Work on cattle grazing on the SGS-LTER has shown that long-term, heavily grazed plant communities have lower diversity and lower numbers of exotic species than ungrazed communities (Milchunas et al. 1989, 1990). In contrast, prairie dog colonies can have higher diversity and numbers of exotic species (up to 6 times higher) than off town locations (Bonham and Lerwick 1976, Milchunas et al. 1992). It is likely that prairie dogs create islands of habitat for less common native opportunistic plant species, as well as centers for exotic invasions. We will use our individual plant based simulation model to evaluate the long-term effects of prairie dogs and their plague induced dynamics on plant community structure.

We will address the hypothesis that grazing and burrowing by prairie dogs favors plant communities with a high diversity of native plant species and exotic invaders compared to nearby off town sites. This will entail making measurements in the plots along transects that differ in

their most recent history of occupancy or colonization by prairie dogs.

F6: Plant biomass: aboveground plant biomass will be lower on active prairie dog towns than in native and unoccupied habitat because of removal by the prairie dogs. Plant species composition: we expect gradual shifts from a grass dominated system to one with increasing abundance of forbs, as prairie dog grazing resumes after recolonization; the shift occurs because forbs are better adapted to soil disturbances than the dominant perennial grasses.

Small mammals as reservoirs of plague near prairie dog towns: NEW LT.

Prairie dogs are probably incidental hosts for plague because mortality is nearly 100% and death occurs relatively quickly (Barnes 1993). In most areas, towns are isolated from one another by topographic barriers and unsuitable habitat, yet plague outbreaks occur. What accounts for these dynamics? The answer lies in discovering which parts of the suspected cycle of plague (Fig. 2.17) may transmit plague among prairie dog towns, or between prairie dogs and other rodents that may be plague reservoirs. All 4 rodent species most likely to interact with prairie dogs on the SGS, northern grasshopper mouse (Onychomys leucogaster), deer mouse (Peromyscus maniculatus), Ord's kangaroo rat (Dipodomys ordii), and thirteen lined ground squirrels (Spermophilus tridecemlineatus) have tested positive for plague (unpublished records, Centers for Disease Control, CDC, Plague Branch, CO). Grasshopper mice and kangaroo rats are more abundant on towns than on nearby grasslands, and all of these species share flea species among them, and with prairie dogs (Thomas 1988, Barnes 1993, Cully and Williams 2001). Models of human plague cases from the CDC (Parmenter et al. 1999, Enscore et al. in press) show that incidence of plague increases one year after high rainfall and decreases after years with high summer temperature. The rainfall effect is hypothesized to relate to population increases of rodents that act as reservoirs; the temperature effect is thought to arise because of decreased flea survival during hot summers. Similar patterns have been observed with hanta virus, and longterm records from Sevilleta LTER were important in answering key questions about this disease. By annually trapping and testing rodents and their fleas for plague with the design described above, we should be able to detect which rodents co-occur with prairie dogs, which harbor plague, which flea species are shared between rodent hosts, and which fleas test positive for plague. We will collect fleas from burrows in infected prairie dog towns to test those for plague as well. We will test all captured prairie dogs for plague antibodies (whether they are survivors of plague), to determine whether plague moves from other rodent reservoirs incidentally into prairie dogs to cause outbreaks, or whether prairie dogs maintain plague as an enzootic disease that occasionally flares up. We will be able to use molecular genetic markers to determine genotypes of plague isolated from different flea and host species (Klevytska et al. 2001), and to make genetic identifications of plague in both temporal and spatial contexts, suggesting that when plague appears in prairie dog towns, we will be able to identify the source. This plague surveillance work will be done in collaboration with the CDC. We will test the following hypothesis:

F7. Plague is locally maintained in populations of plague-resistant small rodents. Outbreaks in prairie dogs occur as a result of local changes in densities of both prairie dogs and associated rodents and environmental conditions that favor of plague transmission by fleas.

2. Biogeochemical Dynamics

Our work on biogeochemical processes represents an integral part of our conceptual framework. We conceive of biogeochemical processes as integrated functions of biotic components, those processes responsible for C and other nutrient fluxes in the ecosystem: NPP, decomposition, weathering, nutrient mineralization and availability, and trace gas flux. These processes are influenced by climate, biotic interactions, physiography, and natural and human-induced disturbances.

Our work in this area is organized around 5 major hypotheses. We address these hypotheses through continuing long-term measurements, short term experiments, new long-term experiments and simulation modeling. Below, we describe our work associated with these hypotheses.

B1: The key abiotic variables controlling biogeochemical processes (NPP and nutrient exchange dynamics) are H_2O availability and temperature, as they vary in time and space,

and soil texture as it varies across landscapes.

B2: The SGS ecosystem is dominated by belowground biomass, not because of higher belowground than aboveground productivity, but because the turnover rate of belowground material is slower than that of aboveground tissues. Root production is concentrated in upper soil layers in grass-dominated areas, and in lower layers in shrub-dominated areas, because of the difference in resource-exploitation of the two plant functional types. However, detrital C is higher than expected in deep soil layers because of slow decomposition rates at depth.

a. Monitoring

Long-term sampling of aboveground NPP: LT11, LT12, and LT13. WEB

We will continue to annually sample aboveground NPP (ANPP) and plant N concentration to evaluate the role of climate/weather, topography, and grazing. We sample 6 sites selected to represent topographic positions, soil texture, and grazing treatments (since 1983). In addition, we have data from the ARS on forage production (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 SGS structure and function, we also sample ANPP in each of 4 treatments at 5 sites (LT37).

Control over ecosystem processes by precipitation: NEW SYNTHESIS.

The most common interpretations of the dependence of ANPP on precipitation have had a strong agricultural bias in that wet, high production years have been interpreted as "good" years and dry, low production years as "bad" ones (Le Houerou and Hoste 1977, Smoliak 1986, Wisiol 1984). While this is certainly true in terms of forage production and weight gain by livestock, an ecosystem perspective leads to an alternative interpretation of wet and dry years and the following hypothesis:

B3: Fluctuations in precipitation can have both positive and negative effects on ecosystem structure and processes, because many organisms of the SGS are adapted for the dry years that bring low ANPP and plant cover. Maintaining biological diversity may thus depend on years of low plant cover and ANPP as well as years of higher ANPP.

As management of SGS incorporates objectives in addition to livestock production, information about the response of elements of SGS ecosystems to fluctuations in precipitation

will become of increasing importance. As an example, mountain plover is an important species of concern to conservationists. Plover require sites with low plant cover and biomass for successful nesting. During the 1990s, a series of wet, relatively high production years (Fig 2.24) has resulted in high plant cover and biomass and a precipitous decline in nest success by plovers (Mark Ball, US Forest Service biologist, personal communication). While this is only a single example, it is clear evidence that "good" years for livestock production can be "bad" years for other components of the ecosystem and may require novel management responses. We plan to test this hypothesis by assessing the relationships among our long-term data sets on precipitation, ANPP, and wildlife populations. Long-term population monitoring for most of the mammals and birds is already being done by the Forest Service, USGS, the Colorado Division of Wildlife, or NGOs such as the Colorado Audubon Society. We are currently, and will continue to, sample aboveground NPP and basal cover of plants at a variety of locations.

Warming, wetting, and N additions: LT14, WEB

A prediction of our conceptual framework is that there are 2-way interactions between the structure and function of SGS. Results from a long-term data set on ANPP suggested that ecosystem structure (plant community and soil pools) constrains ANPP (Lauenroth and Sala 1992). Production was greater in dry years and less in wet years than expected from data at other sites where mean annual precipitation corresponded to the wet and dry conditions. This led us to the question: How does the relationship between ecosystem structure and function change under altered climate and resource availability?

We initiated a long-term experiment in 1995 to ask how increased temperature, increased H₂O availability, and increased N availability influences the relationship between ecosystem structure and function. We began with funding from a Cross-Site LTER project, and a portion of the experiment is also being conducted in the Patagonian steppe in Argentina by our collaborator Osvaldo Sala. Since 1997, we have supported this experiment on the core LTER grant. In each of two blocks, we have implemented the 3 treatments and interactions (see WEB for details), and 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.

NPP and Nutrient Cycling Across Landscapes: Field Study NEW-LT.

Many of our long-term experiments have shown a strong correlation between landscape position and biogeochemical pools and processes (Schimel et al. 1985, Milchunas et al. 1989, Burke et al. 1999, Hook and Burke 2000). During the early LTER years, this work led to a hypothesis that focused on a 2-dimensional representation of the landscape as a catena (Ruhe and Walker 1968), which we proposed encompassed the major variability of the SGS. Since then, we have conducted detailed analyses of soils in a 3-dimensional, pedological context (Yonker et al. 1988, Loadholt 2001), which demonstrate that soil C varies in a more complex fashion across the landscape due to parent material, landscape age and soil development. Nonetheless, much of work continues to show strong catena patterns, which leaves us with the question of what is controlling these patterns, texture or topographic effects on H₂O availability? Most recently, Lauenroth et al. (submitted) reviewed the long term NPP data sets and found that if one separates texture from topography, ANPP is highest in swale positions, and is higher on coarse textured than fine-textured soils, supporting the inverse texture hypothesis (Noy-Meir 1973) (Fig. 2.18, 2.19). Similarly, Burke et al. (1999) and Hook and Burke (2000) found that soil C and N pools and N turnover dynamics have strong correlation with both landscape position and soil texture

The most likely causes of higher production in swales are 1) increased soil H₂O availability and 2) increased N availability. Irrigation and fertilization experiments (Dodd and Lauenroth 1979) show that fertilizer additions can increase aboveground NPP by 50% and that irrigation of the SGS can increase NPP up to 100%. Data suggest that N mineralization in swales is higher because of greater N retention in fine textured soils (Delgado et al. 1996) and deposition of SOM. The only explanation for higher H₂O availability in swales would be downslope movement, but to date, our long-term data do not indicate a higher H₂O availability in swales (Singh et al. 1998).

An alternate reason for the higher NPP on swales is that N losses are highest in summit, coarse-textured locations. Data from the SGS site on the impact of soil texture on soil gaseous N

loss show that NH_3 losses from animal urine patches (Schimel et al.1986) and NO_x soil losses are substantially higher on sandy soils (Martin et al. 1998). Preliminary model results using the Daycent plant-soil ecosystem model suggest that these higher gaseous N losses from sandy soils result in lower ANPP. Thus, the key challenge is disentangling the effects of soil texture and soil H_2O on biogeochemical cycling.

We propose to conduct a new experiment to separate the effects of soil texture and topography on NPP and nutrient turnover dynamics. Our key questions are: How do texture, topography, and landform influence H₂O dynamics and N input and outputs, and how important are lateral vs. vertical flows? We will establish a sampling design that includes two different approaches. First, we will examine 5 different topographic positions, each with varying soil textures due to different parent material (thus separating texture from topography). Second, we will examine three different, lithologically diverse toposequences. Within each toposequence, we will sample at least 3 different landscape positions. In each location, we will estimate *in situ* soil H₂O content (using TDR), NPP, trace gas flux (N₂O and NO), soil respiration, decomposition, and N mineralization. We will explore the potential use of cosmogenic Be-10 content of soils to evaluate differences in overland flow versus sub-lateral flow within each unit.

NPP and Nutrient Fluxes Across Landscapes: Simulation Analysis NEW-SYNTHESIS.

As a key part of the experiment described above, we need to test the extent to which we can explain the results using spatially independent processes. We will use the Century model to simulate biogeochemical dynamics of the ecosystem in the absence of lateral movements, allowing the current distribution of soil texture to serve as a proxy for both topography and landform. In the past, we have used a similar approach to test the importance of spatially explicit processes such as seed movement in determining plant community dynamics (Coffin and Lauenroth 1989a). Simulation analysis in this case demonstrated that one could not understand or predict plant community dynamics without including movement or spatially dependent processes on the landscape.

We plan to develop a model to simulate the spatial patterns in soil C and N dynamics, and ANPP and BNPP at a 50x50 m² resolution for the SGS site. Combining our existing data on the impact of soil texture on gaseous N losses, and soil, H₂O and nutrients on plant production, with data from the experiments described above will allow us to develop the spatial simulation. We propose to develop a spatially explicit version of the Century model for the SGS site that will include landscape level movement of H₂O, mineral soil, SOM, soil nutrients, and the impact of soil texture on gaseous N losses . Rosenbloom et al. (2001) recently developed a version of Century (CREEP) that included the movement of soil within the landscape, and another recent version (Century V. 5 http://www.nrel.colostate.edu/projects/century5/) accounts for soil and H₂O movement. The daily version of Century (Daycent, Parton et al. 2001) will be used to evaluate the impact of soil texture on gaseous N losses (NH₃, NO_x, N₂, N₂O). Components from CREEP, Century V. 5 and Daycent will be incorporated into the new SGS spatially explicit model. Spatially explicit databases already exist for the main driving variables needed for the new model, and include a high-resolution digital elevation map, soil texture maps and climatic data for the site.

<u>b. Effects of Human Disturbances on Biogeochemical Dynamics</u>

Long-term studies of nutrient enrichment: LT 42 WEB and NEW LT.

Nutrient enrichment treatments established in 1971 have been sampled under LTER since 1982 (WEB); have shown interesting and unexpected time lags in plant community responses (Milchunas and Lauenroth 1995). The long-term enrichment treatments consisted of 2 blocks, each with 4 1-ha treatments of control, added H₂O, added N, and added H₂O plus N. Those treatments were halted in the late 1970's, but increased N availability and increased invasive plant species persist into the present (Vinton and Burke 1995, Milchunas and Lauenroth 1995). In 1997, we initiated 6 new treatments (on a new NSF grant) to evaluate our ability to reduce N availability and invasive species by adding various C sources to stimulate both microbial immobilization for short-term sinks, and humification, for long-term sinks of N: sugar, sawdust, lignin, sugar+sawdust, sugar+lignin, and control. We have begun to see responses for many of the treatments (Fig 2.20) and are now interested in their long-term persistence. We

propose to discontinue C supplements, and evaluate how each of the new treatments responds over decades. Our hypothesis is that N availability will increase again on the sugar only plots, but will remain low, with fewer invasive species, on the plots with recalcitrant C additions (sawdust and lignin) due to differences in turnover times of C source.

Long term ¹⁵N studies in the SGS: LT18 and LT19. WEB

In 1988, we initiated a long-term ¹⁵N study to evaluate the interaction of topographic position and grazing on N retention and distribution. We labeled plots on summits and toeslopes in each of three catenas, and in two grazing treatments, heavily grazed and exclosed areas. We plan to continue to sample these treatments on a decadal scale for an indefinite period of time; we sample for ¹⁵N in plant material and in mineralizable, slow (particulate SOM, Cambardella and Elliott 1992), and recalcitrant fractions of SOM. One important aspect of this research is that both C content and soil texture increase N retention at a regional scale (Figs. 1.12, 2.21, Barrett and Burke in press), but it is not clear that these same patterns hold at landscape scales, nor how grazing might interact with these controls. Our work in this area addresses the following hypotheses, as well as <u>Hypothesis P6/B5/L2a</u>, which states that aboveground disturbances have smaller effects than belowground ones.

B4: N retention in the SGS is governed by the processes that control C accumulation, because any process resulting in net C accumulation or storage has the potential for storing N as well. Thus, the pattern in C and N retention across the landscape is a complex result of topographic location and the resulting soil H_2O availability and soil texture, and land management practices as they influence NPP and decomposition.

As described in the *Plant Dynamics and Ecosystem Interactions* section, we have several long-term experiments to evaluate the effects of grazing on the SGS ecosystem. These experiments include assessment of nutrient turnover and retention (LT19, LT21, LT33, LT34, LT36). In addition to these, we have the following long-term experiments that utilize four different approaches: long-term field experimentation, short-term experiments, simulation analysis, and regional analysis. This work also crosses the sections of the proposal and is represented in each of them, e.g., the section on Land Atmosphere Interactions which describes our work to evaluate C balance of grazed grasslands and cultivated wheat systems.

Long-term recovery following cultivation and cropland abandonment: LT43-46. WEB

Approximately 25-30% of the CPER and the PNG was plowed and abandoned by 1937. In 1990, we sampled **vegetation** and **soil recovery** on 13 fields selected to represent the precipitation and temperature gradients across the PNG, including one field at the CPER (Coffin et al. 1996, Burke et al. 1995). In 1994, we began sampling old fields at the CPER. We sampled vegetation and soil on six fields in 1994 and will continue to sample a subset each year until all have been sampled. We will repeat sampling at ~15 year intervals.

Short- and long-term responses of the SGS to fire: LT 59 WEB and NEW LT.

Although a large amount of research has been conducted on the role of fire in tallgrass and mixed grass prairies (e.g. Knapp and Seastedt 1986, Hobbs et al. 1991), essentially no work exists to assess fire effects in SGS. Most investigators have assumed that the low standing biomass of the SGS created a system with a low probability of carrying fire, and thus a minimal historical role of fire. Nonetheless, there are years with aboveground biomass equivalent to the mixed grass prairie, and a high frequency of lightening storms.

Regardless of the historical role of fire in SGS, there are new questions regarding its utility in managing for the presence of the threatened mountain plover, which only nests in areas of low plant biomass. PNG recently initiated a burning program to address questions about using fire to increase plover habitat; we have collected data on some of these plots. Because the PNG strategy is for adaptive management, burning when and where conditions are suitable, it has been difficult to conduct the type of replicated and controlled long-term study that we would like. Both the CPER and the PNG are leased for grazing, and large-scale experiments such as burning are difficult due to lease considerations. We plan to work over the next 6 years to establish appropriate interactions to initiate a replicated and controlled experimental fire program, in cooperation with the USFS, ARS, and/or the Nature Conservancy.

One of the most important indicators of ecosystem change is alteration of element inputs. Although our site has long been a member of the National Atmospheric Deposition Program, and we have measured trace gas fluxes on many of our long-term plots, there are still several key areas of element balance that we do not understand. We recently synthesized more than 30 years of work on the N balance of the SGS (Burke et al. in revision), and found that we cannot close the N budget (Fig. 2.22). Our key gaps are in understanding total N inputs, volatile NH₃ losses from plants, NO₂ and NH₃ absorption by plants.

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 in providing baseline data on 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. 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). In addition, we will estimate NH₃ absorption and volatilization from plants, as well as constructing an NO₂ budget.

Our work in this experiment addresses the following hypothesis

B6: The atmosphere represents a major source of inorganic nutrients for the SGS. Previous budgets have underestimated atmospheric inputs because of a lack of tools to estimate the balance between weathering and atmospheric inputs of cations. NH₃ and NO₂ are significant atmospheric exchanges of N, also previously underestimated because of a lack of tools.

3. Land-Atmosphere Interactions

In this section of the proposal, we elaborate our work that addresses the interactions among climate, physiography, and biotic interactions. The processes with which we are primarily concerned in this section are H_2O , energy, and gaseous fluxes that represent important atmosphere-biosphere interactions. In some cases (C and N fluxes), the key processes overlap with work described under the biogeochemistry section of the proposal, but the focus here is on land-atmosphere interactions. Three major hypotheses guide the work in this section (L1–L3). The first of these is important for guiding a number of monitoring experiments focused on precipitation and soil H_2O .

 $L\bar{l}$. Soil H_2O is the key driving variable for SGS ecosystems, accounting for a large fraction of the variability in ecosystem structure and function, because of the very low H_2O availability in this semiarid system. Soil H_2O at any given time and place is controlled primarily by

precipitation, soil texture and atmospheric demand for H_2O .

In our conceptual model, precipitation is one of the key driving variables explaining the structure and function of SGS ecosystems. Within the period of record, we have had a year with annual precipitation more than two standard deviations below the mean (1964; 107 mm) and one year with almost three standard deviations greater than the mean (1967; 588 mm). In addition to interannual variability, there is substantial seasonal variability. Because H₂O is such an important driving variable, and because the supply is so variable, we invest considerable effort in understanding inputs, storage, and losses.

2. <u>a. Monitoring</u>

Microclimate: LT22 and LT23. WEB

We have had an automated microclimatic station since 1982 and manual data since the US-IBP Program (IBP) in 1970. Our automated system makes hourly measurements of precipitation, wind direction, wind speed at 3 heights, air temperature, surface temperature, dew point temperature, vapor pressure, total radiation, soil H₂O at 3 depths, heat flux, and soil temperature at 4 depths. We manually record air temperature, relative humidity, precipitation, open pan evaporation, and soil temperature at 7 depths.

Lysimeter: LT 24. WEB

During the IBP, a 3 m diameter weighing lysimeter was installed in the exclosure containing the microclimatic monitoring station, which is now linked to our microclimatic data logger for a continuous record of H₂O inputs and outputs. Comparison of daily

evapotranspiration for a wet and dry year shows important differences in season-long patterns of H₂O loss. We plan to continue collecting data from the lysimeter and to use it for more experimental work in the future.

Precipitation gauge network: LT 25. WEB

A frequent assumption of researchers in semiarid regions is that precipitation is spatially variable but that over a period of time such as a growing season, average amounts are similar for local areas (one to a few 100 km²). Because precipitation is such a critical variable for SGS, over the past 6 years we 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 suggest that amounts converge at monthly scales and that the variability among stations in daily rainfall can be explained by the size of the storm and the distance between the stations (Fig. 2.23) Currently our precipitation gauge network is limited to the CPER portion of the site. In the next phase of SGS-LTER, we plan to expand our network to include the western section of the PNG (approximately 15 additional recording gauges).

Soil water measurements: LT26. WEB

While we often use precipitation as a surrogate (**Fig. 2.24**), soil H₂O is the variable to which the majority of the biota responds. (Sala et al. 1992). In 1982, we established a series of 5 sites at which we have regularly measured soil H₂O using a neutron moisture gauge (Troxler Scientific Instruments) across catenas during the growing season. We are currently in the process of converting to measurements based upon Time Domain Reflectometry (TDR) and data loggers, due to problems with surface soil H₂O measurements and radiation safety considerations.

Soil water dynamics: NEW SYNTHESIS.

We plan to convert our existing neutron probe soil H₂O data that were collected at 2 week intervals during the growing season and monthly intervals for the remainder of the year into a daily soil H₂O data set using a soil H₂O model (Parton 1978, Sala et al. 1992) and nonlinear inversion (Doherty 2000, Wang et al. 2001). This is an inverse modeling approach in which we will select the optimal parameter values for the model that minimize an objective function that describes differences between observed and simulated soil H₂O values. This method is widely used by the physical science community (Enting et al. 1995, Doherty 2000, Wang et al. 2001) and much less so by ecologists. The model will be fit to each site-year data combination and a companion daily soil H₂O data set generated.

1. b. Disturbances and Land-Atmosphere Interactions

L2. Vulnerability of SGS structure and function to disturbance involves feedbacks between ecosystem and land-atmosphere dynamics, because vegetation influences energy partitioning as well as responding to available energy and water.

Fragmentation of the SGS from farming, domestic livestock grazing, and urbanization, in addition to environmental change, are important forces which have altered the character of the SGS, and which are likely to elicit even greater changes in the future. The ultimate outcomes of disturbances are likely to involve complex interactions of terrestrial and atmospheric responses. We offer the following discussion and hypotheses as a framework for considering short-term and long-term disturbances on the SGS through interactions between the landscape and atmosphere.

The two most widespread land-use practices on the SGS are domestic livestock grazing, and summer-fallow, winter wheat cropping. Despite years of grazing studies (e.g. Klipple and Costello 1960), there is little information on how these practices affect C balance. Defoliation can reduce plant assimilation by removing photosynthetic surface, but it can also enhance tillering and improve photosynthetic capacity of remaining leaves, thereby maintaining or even enhancing stand photosynthesis (Coughenour 1985; Morgan and Brown 1983; Painter and Detling 1981). Very few field photosynthesis studies have tested this response in actively grazed rangelands (McNaughton et al.1996; Richards 1993). LeCain et al. (in press) showed that while grazing can temporarily alter canopy CO₂ exchange, grazing-induced changes are relatively small in comparison to perturbations brought about by changes in soil H₂O (Fig. 2.25). No studies have yet been done to continuously monitor SGS pastures differing in grazing, nor to scale up leaf or chamber measurements to landscape scales or longer time scales. Our work here addresses

hypothesis P6/B5/L2a, that grazing has minimal effects on SGS ecosystem structure and function. We additionally hypothesize that:

<u>L2b heavy grazing (60% forage removal) may reduce C uptake by reducing plant cover and photosynthetic surface.</u>

Grazing effects on H₂O, energy, and CO₂: LT 55. WEB

We installed Bowen Ratio/Energy Balance systems in spring, 2000, to continuously monitor fluxes of CO₂ and H₂O in 3 adjacent pastures, one moderately grazed, the other exclosed from grazing (Fig. 2.25). This represents a new experiment that will be run 365 days a year, and will include periodic measurements of soil H₂O content, aboveground biomass by species, plant cover, and soil respiration. In addition to comparing CO₂ and H₂O fluxes in the grazing treatments, we will evaluate how plant development and the environment affect temporal variation in these fluxes. We will run these systems for at least 5 years.

Dryland cropping effects on H₂O, energy, and CO2 exchange: NEW LT.

Much of our previous research (Burke et al. 1995, Coffin et al. 1996, Ihori et al. 1995a a, b) has focused on the dynamics of abandoned wheat-fallow pastures within the SGS, but no work has yet been conducted on the landscape-scale effects of the interspersed wheat fallow cropping system. In work funded on an EPA grant, we initiated a study of CO₂ and H₂O fluxes on wheat fields using the Bowen Ratio methodology (Fig. 2.26). We propose to take over these measurements on the SGS LTER project, to better assess the long-term consequences of the interspersion of wheat fallow with grazing management in the SGS. We hypothesize that:

L2c: The incursion of winter wheat/fallow cropping systems into the SGS reduces annual C assimilation, and alters the dynamics of seasonal evaporation, transpiration and energy balance. This occurs because i) this cropping system significantly alters the albedo, ii) cultivation of soils increases decomposition and reduces transpiration, and iii) the plant functional type alters the distribution of NPP above and belowground from the SGS conditions.

Regional consequences of land use: a simulation study: NEW SYNTHESIS.

While we have conducted simulation modeling on regional consequences of cultivation management for C and N balance, we plan to extend this work by simulating atmospheric responses. Our 4th sub-hypothesis in this section states that

<u>L2d</u>: <u>Disturbances of domestic livestock grazing and winter wheat cropping systems at the field level affect the regional atmosphere and influence local weather patterns, through their influence on energy partitioning and balance.</u>

The rationale for this stems from an earlier study (Pielke et al. 1997) in which it was found that land use driven changes in the H₂O budget and seasonal patterns of the Bowen ratio can have an impact on mesoscale patterns of precipitation and other climatic variables (Section 1). In other work, Eastman et al. (2001 a, b) found that biogeochemical and biophysical effects of enhanced atmospheric CO₂ have an influence (in the model) on regional weather that is on the same order as land use change (Fig. 2.27). In contrast, the radiative effect of enhanced CO₂ over this time period has a minimal effect. These results further support the need to investigate the feedbacks between the atmosphere, soils and vegetation as fundamental components of the SGS climate system (Pielke 2001).

We will continue our scaling up exercises from measurements of individual landscape units and seasons of measurements (Bowen ratio towers describe above) to the SGS region (simulation analysis), and quantify the potential impact of the current landuse on mesoscale climatic patterns at the SGS site using the RAMS mesoscale model coupled to the CENTURY ecosystem model (Lu et al. 2001) and the GEMTM ecosystem model (Eastman et al. 2001a,b).

Changes in plant communities due to CO_2 enhancement: LT 20 WEB, NEW Synthesis.

Finally, as we describe in Section 1, results from a 5-year CO_2 enrichment open-top chamber (OTC) experiment showed a production increase due to enhanced growth of a C_3 grass of relatively low forage quality, *Stipa comata* (Morgan et al. in review; Fig. 2.28), with no response of *B gracilis*. We therefore hypothesize that

<u>L2e Rising atmospheric CO₂ concentrations will lessen the dominance of B gracilis in the SGS</u> in favor of less drought resistant, cool-season grasses thereby altering temporal and spatial

patterns of C assimilation, respiration, evaporation and transpiration. This will occur because of the already high water use efficiency of B. gracilis.

A plant physiological model (e.g., GRASS) will be adapted to evaluate different photosynthetic, H₂O relations and developmental responses of 3 major grasses (Stipa comata, Pascopyrum smithii and B. gracilis) to CO₂. We will also use a coupled RAMS/GEMTM model to explore what impact an altered species composition in the SGS in future CO₂-enriched environments may have in feedbacks with the weather.

3.c. Extending to Long Time Scales

Paleoclimate and Land-Atmosphere Interactions: NEW ST.

L3: Biogeochemical development and vegetation distribution in SGS has tracked temperature, precipitation and dust deposition because these factors have continuously controlled the structure and function of the SGS.

We will utilize our extensive experience in the study of soil formation and paleosols to provide information on SGS biotic structure over the last 40,000 years. A paleosol is a soil formed in a landscape of the past that is subsequently altered as a result of climate change or burial. Recently, quantitative methods for extracting environmental information from soils have been developed (Kelly, et al 1998, Kelly et al 1991a; Kelly et al 1991b; Amundson et al 1989; Quade et al 1989; Cerling 1984). These methods use stable isotope geochemistry of C and oxygen, and permit reliable and high-resolution climatic information to be extracted from soils.

We have intensively studied the composition of ancient soils to determine climatic conditions that prevailed in the central Great Plains over the last 10,000 years. Recently, we identified sites that appear to pre-date our Holocene sequence of paleosols and will provide new pedological, mineralogical and isotopic records that date back approximately 30,000 to 40,000 YBP. We propose to use a new and more precise technique for documenting biotic. In our new approach, we will use C isotopic compositions of long-chain n-alkanes and lignin phenols from modern soil and paleosols to evaluate the organic C input from vascular plants. Both of these compound classes are used extensively to evaluate terrestrial inputs into both lacustrine and marine environments (Hedges and Parker 1976, Pagani et al. 2000a,b). We will use information derived from this study to provide validation for vegetation shifts predicted by our simulation modeling for changing atmospheric conditions over geologic timescales.

Paleoclimatic and vegetation modeling: NEW SYNTHESIS.

Vegetation distribution models were first developed to explain regional and global distributions of biome types based on relatively simple relationships between current distributions of natural vegetation and climate statistics (Holdridge 1976). The dynamic global vegetation models (DGVM) were developed to address issues of how plant communities may respond to environmental change through dynamic competition between functional groups (e.g., trees, shrubs and herbaceous species) and physiological groups (e.g., C₃ and C₄), allowing for transient responses to climate change. We plan to use a DGVM called Hybrid (Friend et al. 1997; Friend and White 2000), a model of vegetation and soil dynamics that can be applied at point to global scales. The model predicts vegetation type, productivity, leaf area, canopy height, and rooting depth, as well as how these change dynamically with transient changes in climate (i.e. air temperature, humidity, precipitation, and radiation), atmospheric CO₂, and N deposition. Soil C and N are also simulated, with N availability simulated as a control on vegetation type and productivity (Friend and White 2000).

4. Synthesis

The SGS-LTER project has a long history of synthesis activities that span synthesis of longterm data sets, cross-site experimentation, review articles, and simulation analysis (see Table XX which demonstrates our contribution to synthesis). Above, we have proposed 6 new synthesis projects that fit well within the core areas; some of these represent simulation analysis. We use models to help design and evaluate experiments, quantify relationships among individual components and the determinants of ecological structure and function. Our use of these simulation models provides integration and synthesis at many points along the research continuum and displays the true integrative nature of our project. Others represent proposed data synthesis activities. We also plan to complete our synthesis volume in the very near future.

In addition to those activities formally proposed above, we will continue to integrate knowledge in all of the possible ways. Each of our investigators has a large commitment to synthesis, as evident in our publications, and we anticipate a continued investment. The synthetic analyses of long-term data can occur both within and across research areas. The length and breadth of the SGS-LTER data base will allow us to test more general and integrative predictions that cross disciplines and research areas.

Below, we describe 2 additional experiments that we propose in the area of cross-site experiments. Cross- site research allows us to evaluate differences in fundamental processes across environmental gradients.

The importance of grasslands in terrestrial silica cycling: NEW CROSS-SITE.

A promising approach to studying modern and ancient silica cycling is the use of the germanium-silicon pair. Ge may be thought of as a "pseudo-isotope" of Si, given their similar chemical properties (Froelich and Andreae 1981). We hypothesize that the role of phytoliths in the Si cycle should be especially important in grasslands, given the high phytolith content of many grass species, and the low rates of mineral weathering associated with low annual rainfall. Ge/Si ratios may point strongly toward the importance of biological cycling of Si. We will collect plant and soil samples from a set of 13 grassland sites across a climatic gradient spanning the SGS, mixed grass and tallgrass, encompassing 3 watersheds, the Platte, Missouri and Mississippi Rivers. We have access to long term NPP and climatic data at 8 of these sites (2 in the LTER network). We will characterize the phytolith content of dominant plant species, and surface and subsurface horizons to assess the range in Ge/Si ratios for each pedologic system. Soil and river waters will also be analyzed to make direct comparisons of the 3 grassland systems.

Effects of different-sized grazers on N cycling: NEW CROSS-SITE.

Large herbivorous mammals can have profound effects on the sustainability and productivity of grasslands through their effects on nutrient cycling. Herbivores can strongly influence the N by returning large amounts of N to soil through waste products and favoring more nutrient-rich plant litter. Alternatively, they can alter N cycling by modifying plant species composition, litter quality, and thus N turnover. These effects vary dramatically across sites. In the proposed study, we plan to test how effects of mammalian herbivores on N cycling vary across a temperate grassland productivity gradient. We will sample within an existing cross-site study for the effects of different-sized herbivores on grassland biodiversity and ecosystem function. Established in 1996, this study consists of replicate 30 x 30 m exclosures (with an unfenced control) of only large (> 10 kg) or both large and small to intermediate (1-100 kg) herbivores within each of 8 sites. These sites include 3 LTER sites (Cedar Creek, Konza, and SGS), 3 sites in Utah and 1 site in the Netherlands and encompass an order of magnitude range of NPP. We propose to measure N mineralization, N and C pool sizes in plant material and soil, plant community composition and diversity. These measurements should provide valuable insights into the influence of different herbivore species on N cycling in grasslands.

5. SUMMARY

The research proposed here will expand our understanding of SGS ecosystem structure and function, by continuing a substantial suite of long-term experiments and initiating new long-term monitoting, long- and short-term experiments, and simulation analyses. Our work will focus on the key biotic responses and feedbacks as influenced by humans, natural disturbances, physiography, and climate. Our work includes: 1) new studies of invasive species, the prairie dog and its biology, and cactus; 2) new studies of control by landscapes over biogeochemical cycling, new studies of the N balance of SGS ecosystems, and 3) new studies of carbon balance over landscape to regional scales, and the interactions between landuse and regional climate. We are also expanding experiments associated with our past work in paleoecology and pedology, plant community dynamics, and biogeochemistry. We plan to continue our 60 long-term experiments, and to initiate 14 new long-term experiments and 10 new short-term, synthesis and cross site experiments over the next six years.

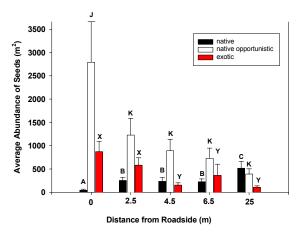
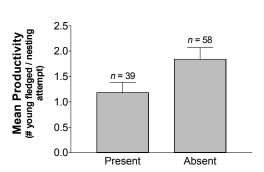


Figure 1.1. Average abundance of native, native opportunistic, and exotic seeds as a function of distance from roadsides in the shortgrass steppe. These data are based on a seedbank survey of 14 randomly chosen roadside locations within the Central Plains Experiment Range in 1999. Bars with the same letter are not significantly different at P=0.05 (Betz 2000).

Figure 1.2. Density of short-horned grasshoppers on and off prairie dog colonies on the Central Plains Experimental Range in 1997.



Recreational Shooting Status

Figure 1.3. Mean productivity of burrowing owls (*Athene cunicularia*) on prairie dog colonies with and without the presence of recreational shooting on the Central Plains Experimental Range (Woodard 2001).

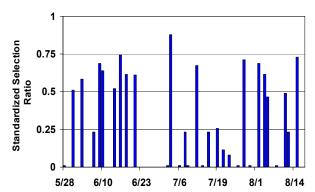


Figure 1.4 Standardized resource selection ratios (B_i) for cattle occurring on prairie dog towns from driving survey data (n=31) for all pastures from May 28 to August 15, 1999. Values above 0.5 represent selection for prairie dog towns, values below 0.5 represent avoidance of prairie dog towns, and 0.5 represents random use of prairie dog towns (Guenther and Detling 2001).

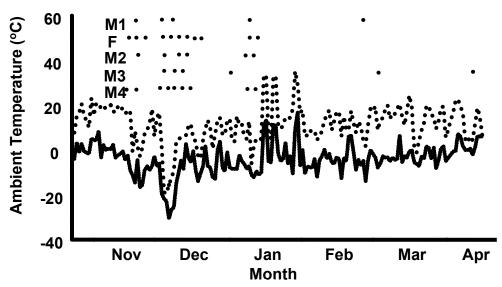


Figure 1.5. Relationship between ambient temperature (T_a) and torpor in black-tailed prairie dogs monitored at the Central Plains Experimental Range. Horizontal bars represent periods in which animals were torpid. Dashed lines represent daily maximum T_a . Dotted lines indicate daily minimum T_a . M1= male subject #1, M2= male subject #2, M3= male subject #3, F1= female subject. Prairie dogs entered torpor in response to sudden reductions in T_a , but not all reductions in T_a resulted in animals entering torpor. Both major (dark bars) and minor torpor bouts (light bars) occur simultaneously at separate colonies, indicating that the stimuli for entering torpor generalize over this spatial scale (Lehmer 2000).

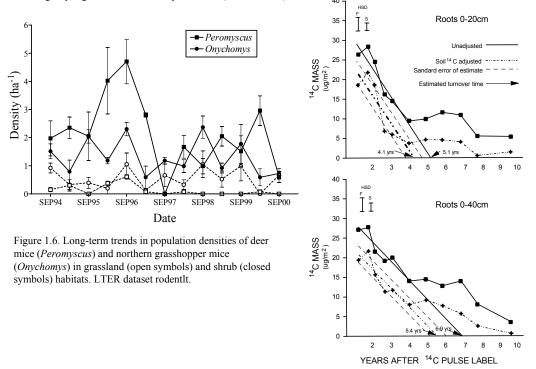


Figure 1.7 14 C mass loss (μ g1 14 C/m²) over 10 years Post-pulse labeling for root data unadjusted and adjusted for soil 14 C embedded in root tissue (ash), with their associated turnover regressions and turnover times. The standard error of the estimate is for the soil 14 C adjusted regression with r^2 =0.90 for (A) 0-20 cm roots and r^2 =0.89 for (B)0-40 cm roots. HSD are PP=0.05 confidence intervals for the first-phase(F) and second phase (S) dynamic portions of the unadjusted data. First phase dynamics do not include 1^{st} -year data prior tothe stabilization of labile 14 C (Milchunas and Lauenroth 2001)

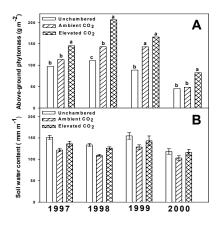


Figure 1.8. The effect of manipulations in ambient and elevated CO_2 on above-ground phytomass (A) and soil water content (B) conducted in an open-top chamber experiment on the shortgrass steppe LTER from 1997 to 2000. Bars with the same letter are not significantly different at P=0.05. Error bars are one standard error of the mean (Morgan et al. 2001).

CH, Uptake (g C ha-1 day-1) CO2 Efflux (Kg C ha' day-1) 120 12 10 100 80 60 (C) 1.2 N₂O Efflux (g N ha'day¹) 0.0 670 0.0 700 0.0 700 0.0 800 0 30 NO Efflux (ug N m² hr-1) 25 20 15 10 WN W WN Treatment Treatment

Figure 1.9. Trace gas flux response to increased water (W), nitrogen (N), temperature (T), water and nitrogen (WN), and water and temperature (WT), compared to controls (C). Data collected from 1996-1998, experiment conducted on the Shortgrass Steppe LTER research site. Bars with the same letter are not significantly different at P=0.05. Error bars are one standard error of the mean. (Burke et al. in prep).

Changes in P fractions with time

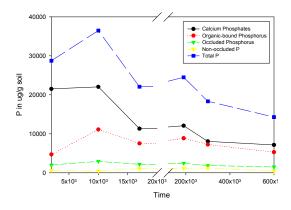


Figure 1.10. Changes in P fractions over geologic time.

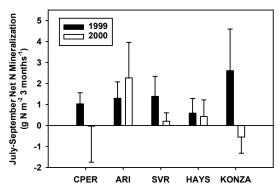


Figure 1.11. Net nitrogen mineralization for five grassland sites along an east-west precipitation gradient in the Great Plains of the U.S. CPER=Central Plains Experimental Range, Colorado, ARI=Arikaree River, Colorado,HAYS=Ft. Hays State University, Kansas, and KONZA=Konza Prairie LTER, Kansas.

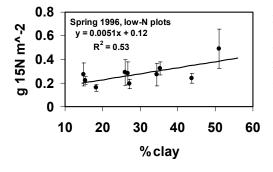


Figure 1.12. Retention of 15N as a function of soil clay content along a north-south environmental gradient in the Great Plains of the U.S. (Barrett and Burke in press).

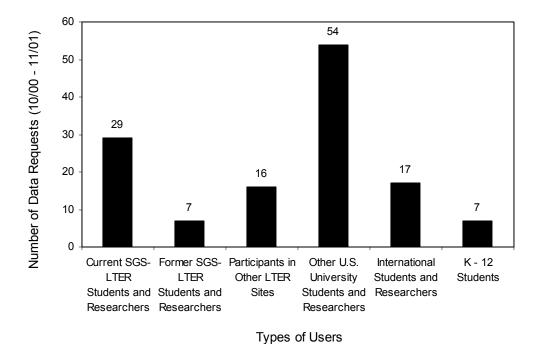


Figure 1.13. Number of requests for SGS-LTER data by user group

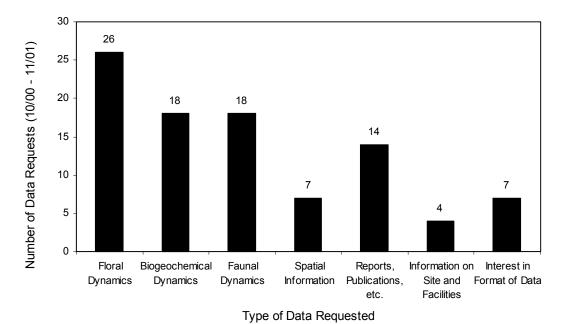


Figure 1.14. Number of requests for SGS-LTER data by data type

Determinants of SGS Structure and Function:

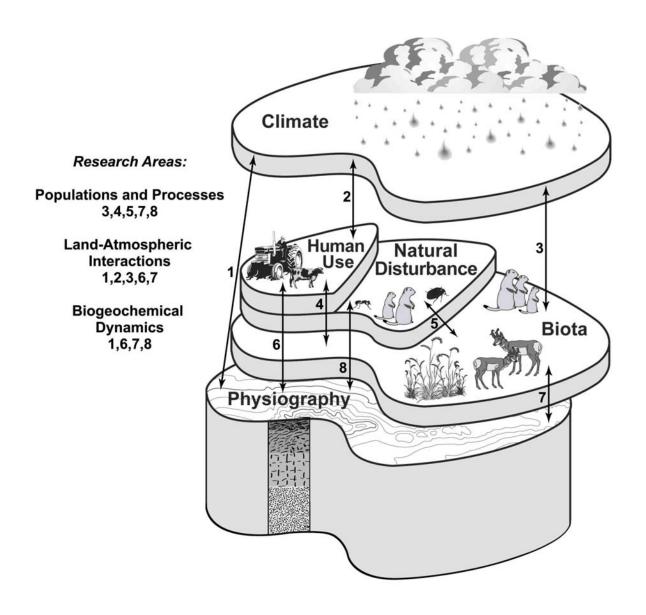


Figure 2.1. Conceptual framework

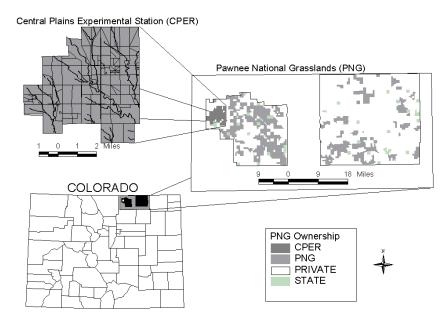


Figure 2.2. Map of the Central Plains Experimental Range and the Pawnee National Grasslands

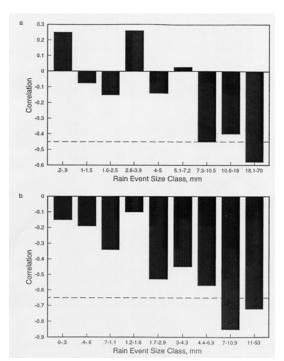


Figure 2.3. Correlations between annual change in *O. polyacantha* and frequency of rainfall in different size classes in two locations, the CPER (a) and Miles City, Montana (b). (Dougherty, unpublished data)

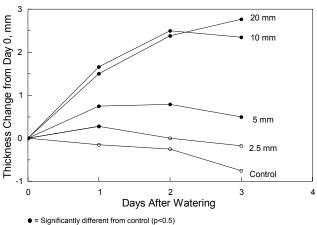


Figure 2.4. Response of *O. polyacantha* cladode thickness to watering. Significant differences from control group thickness are indicated. (Dougherty et al. 1996).

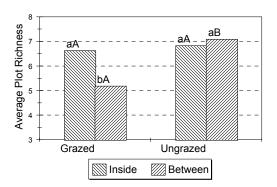


Figure 2.5. *O. polyacantha* is important for preserving species richness in grazed areas. Inside denotes inside cactus patches while between denotes between cactus Patches (Bayless 1996).

Opuntia polycantha 3.5 3 2.5 E D D Summit Midslope Toeslope

Figure 2.6. Height of soil mounds (indirect indication of organic matter accumulation) beneath patches of *O. polyacantha* by landscape position and grazing regime (Burke et al. 1999).

Table 1. A comparison of the number of plant species in six primary habitats and three duration categories for 406 native and 115 exotic plant species.

	Open steppe	Sandy soils	Breaks/ barrens	Cliffs/ ravines	Riparian	Roadsides/ disturbed soils	Total (%)
Native							
annuals	22	12	0	4	23	20	81 (20%)
biennials	5	1	1	4	10	2	23 (6%
perennials	80	19	28	50	112	13	299 (74%)
subtotal	107	32	29	58	145	35	406
Exotic							
annuals	0	2	0	0	26	41	68 (60%)
biennials	0	0	0	0	5	9	14 (12%)
perennials	0	0 2	0	0	20	12	32 (28%)
subtotal	0	2	0	0	51	62	115
Total	107	34	29	58	196	97	521
(percentages)	21%	6%	6%	11%	38%	18%	100%

Figure 2.7. (Kotanen et al. 1998)

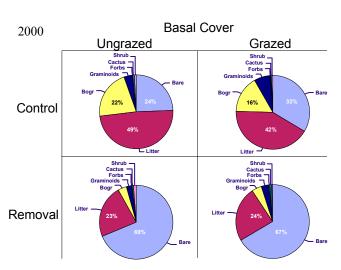


Figure 2.8. Effect of removing *B. gracilis* (Bogr) in grazed and ungrazed areas on the basal cover of plant functional types. LTER dataset LT57.

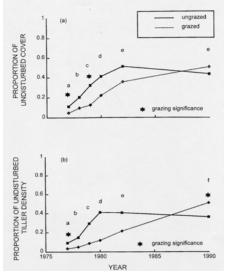
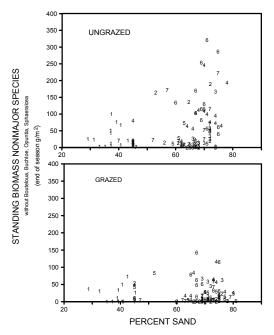


Figure 2.9. Recovery of *B. gracilis* on patches through time measured by (a) cover as a proportion of average undisturbed cover and (b) density of tillers as a proportion of average undisturbed tiller density (Coffin et al. 1998).



22.
28.
30.
29.
70.

70.

71.
71.
72.
66.
72.
73.
82.
74.

Primary Road
Primary Road
State
Prairie Dog Colony

Prairie Dog Colony

Figure 2.10. Plant diversity, as indexed by non-dominant species, increases with increasing sand content (quadrat scale) in long-term ungrazed treatment, but grazing smoothes this small-scale spatial heterogeneity in plant communities (Milchunas and Lauenroth, unpubl. data LTER dataset LT31).

Figure 2.11a Locations of prairie dog towns on the CPER and PNG. Polygons show the largest area of the towns during 20 years of monitoring between 1981-2001. Approximately 30% of the towns are occupied by prairie dogs,

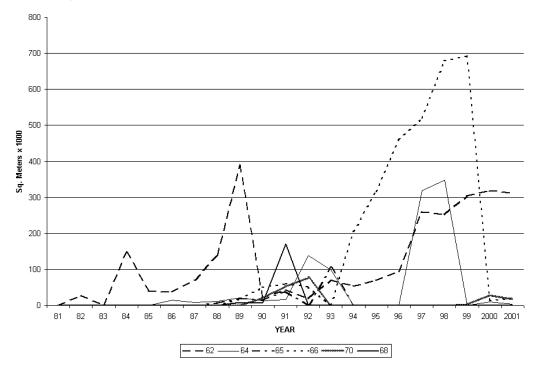


Figure 2.11b Prairie dog town areas (ha) of six prairie dog towns on the LTER and PNG between 1981 and 2001. Declines of prairie dog towns were either confirmed or presumed to be the caused by outbreaks of plague, although no other disease is known to have similar effects. Town 66 because inactive after a plague outbreak in 1999.

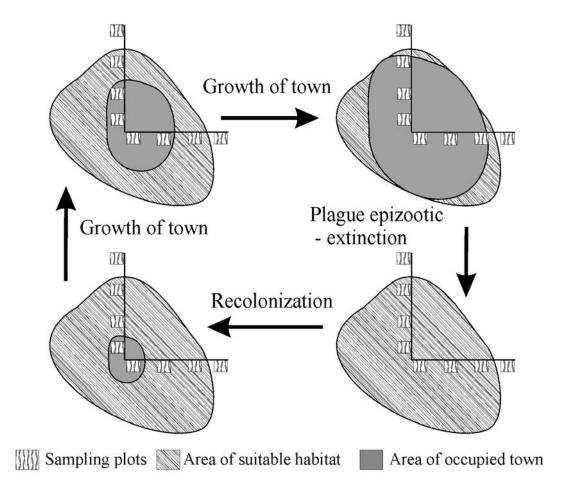


Figure 2.12 Sampling of prairie dog towns will capture the temporal dynamics of growth of prairie dog towns after recolonization, or the extinction of prairie dog towns because of plague epizootics. The hatched polygon describes the outermost extent of suitable prairie dog habitat, as determined by a combination of soil characteristics and slope (< 15%), embedded within habitat that historically has not been used by prairie dogs. The gray polygon in the center describes the extent of habitat occupied by prairie dogs, which will increase in the absence of plague, but would be dramatically reduced after an outbreak of plague. Sampling plots will be arranged along two transects. For invertebrates, plants, and soil microorganisms, sampling will occur at within each plot along each transect. Trapping of small mammals will be from two trapping grids on each transect, one at the center of the prairie dog habitat, another at the end of one of the two transects outside the suitable habitat on surrounding short grass steppe or shrub habitat.

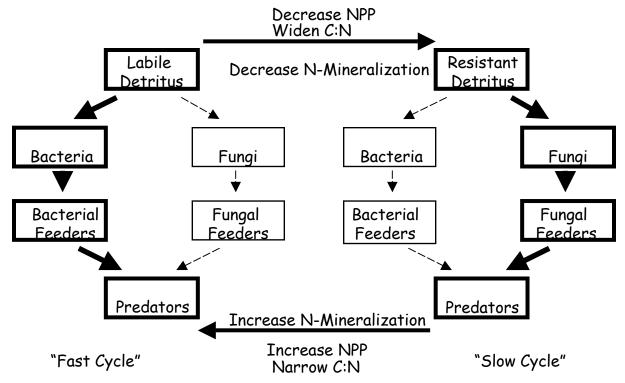
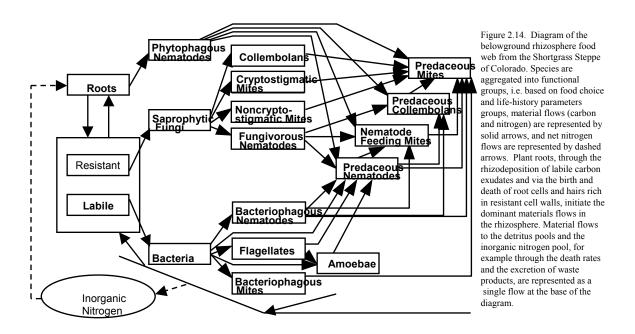


Figure 2.13. Simplified bacterial and fungal energy channels of a rhizosphere food web. The bacterial energy channel represents the 'fast cycle' due to the higher turnover rates of bacteria and their consumers relative to the fungi and their consumers. The fungal energy channel represents the 'slow cycle'. Changes in the C:N ratio of the detritus, NPP, or rates of N mineralization have been associated with shifts in the relative dominance of one channel to the other.



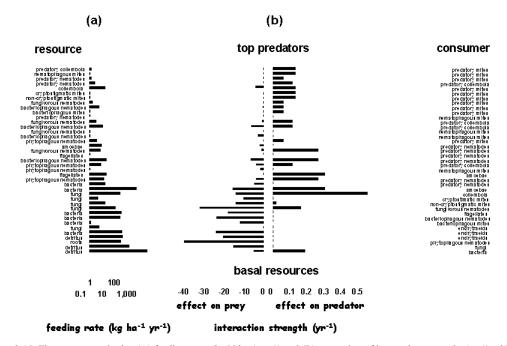
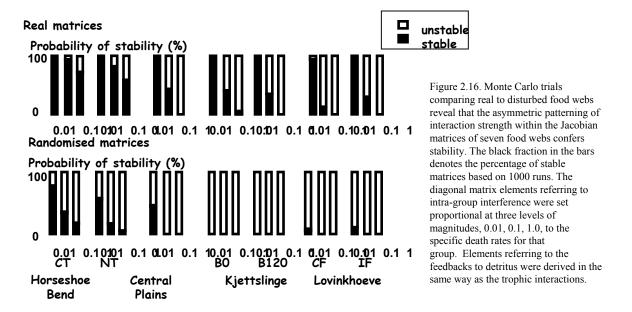


Figure 2.15. The asymmetry in the (A) feeding rates (kg N ha-1 yr-1) and (B) patterning of interaction strengths (yr-1) within the Jacobian matrix with increased trophic level (bottom to top) for the Lovinkhoeve experimental farm (conventional tillage) in the Netherlands. Similar patterns were observed for food webs from the Shortgrass Steppe in Colorado, and agricultural sites in The Netherlands, Sweden, and Georgia, USA. The bars correspond to the levels of feeding rates and interaction strengths for pair-wise trophic interactions in a food web arranged from resources (left) to consumers (right), starting with interactions at the base of the food web (basal resources) to the top of the food web (top predators).



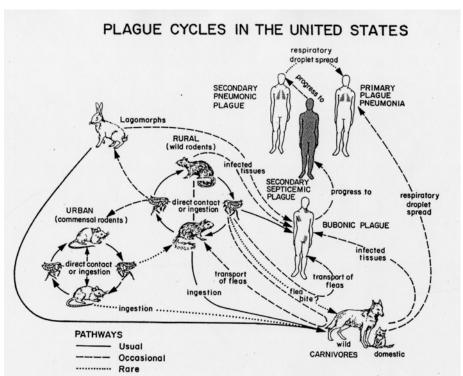


Figure 2.17. -- Hypothesized cycle for plague, courtesy of CDC. The rural (sylvatic) cycle may be entirely enzootic with species, or may involve alterations between reservoir rodent hosts and epizootic outbreaks in susceptible rodents like prairie dogs.

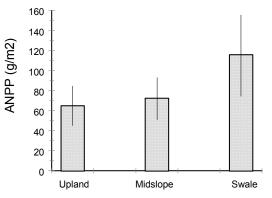


Figure 2.18. Effect of landscape position on annual aboveground Net primary productivity (ANPP) at the Shortgrass Steppe LTER research site.

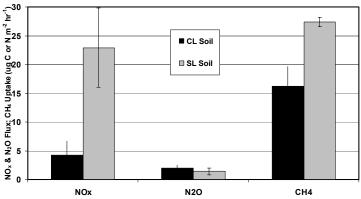


Figure 2.19. Trace gas flux as influence by soil texture

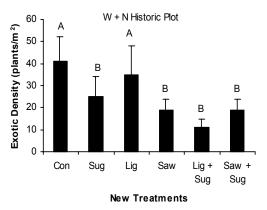


Figure 2.20. Effect of control, sugar, lignin, sawdust, lignin and sugar, and sawdust and sugar treatments on exotic weed density on a historic study site which received elevated water and nitrogen inputs from 1970-1975 (Lowe 2000).

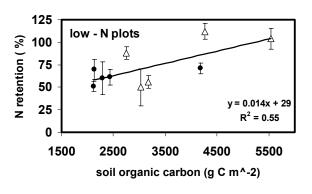


Figure 2.21. Effect of soil organic carbon content on nitrogen (N) retention (Barrett and Burke 2002).

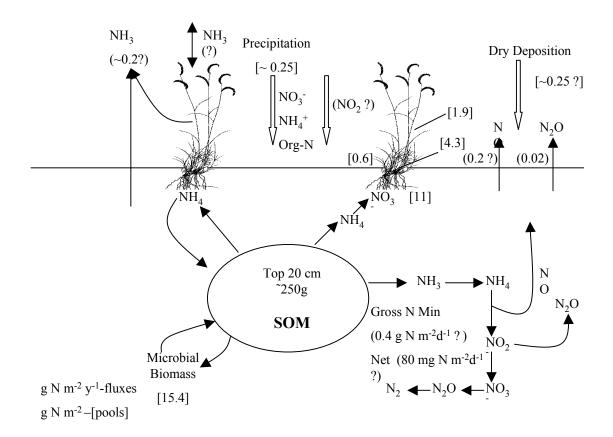


Figure 2.22. Grassland nitrogen budget.

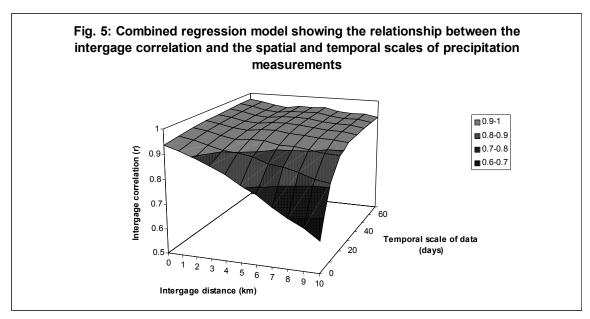


Figure 2.23

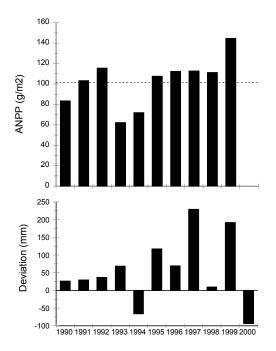


Figure 2.24. Relationship between annual net primary productivity (ANPP) and variation in precipitation at the Shortgrass Steppe LTER research site.

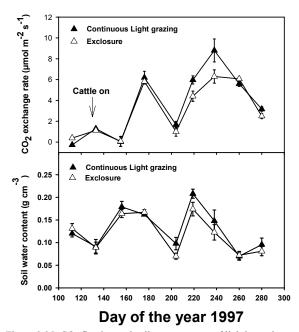


Figure 2.25. CO₂ fixation and soil water content of lightly- and nongrazed pastures of shortgrass steppe during 1997 growing season at the Central Plains Experimental Range in northeastern Colorado.

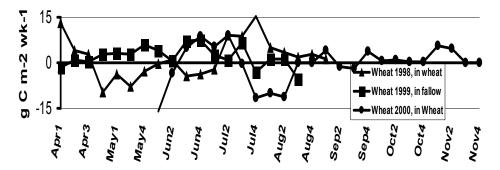
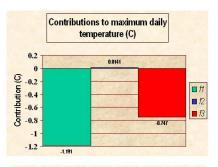
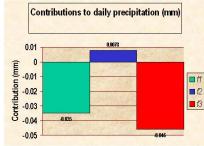


Figure 2.26. Carbon flux for cultivated and fallow wheat fields





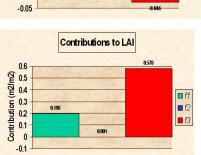
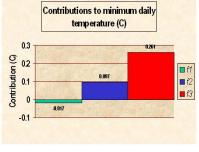


Figure 2.27. Model simulated 210 day growing season variations of average maximum and minimum temperature, daily average precipitation, and leaf area index for the central Great Plains in 1989 due to conversion back to the natural landscape (f1), due to the radiative effect of doubling carbon dioxide concentrations (f2), and due to the biological effect of doubling carbon dioxide concentrations (f3) (Eastman 2001)



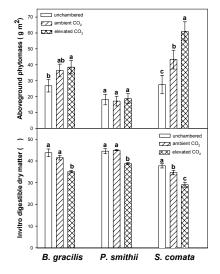


Figure 2.28. Aboveground productivity and in vitro dry matter digestibility of three shortgrass steppe forage grasses in ambient and elevated OTC plots and a non-chambered control.

SECTION 3: Project Management

Evolving Management Model:

Our priorities for managing the SGS-LTER project are to ensure that we support a broad range of interacting ecologists and stimulate new ideas and participation, all within the context of a high degree of stability and continuity for our long-term studies. Our project structure during LTER I (1982-86) and LTER II (1986-90) consisted of 2 lead CSU PI's, 1 lead PI representing USDA-ARS, and a very large (~15) group of co-investigators with various levels of participation. Since the SGS-LTER began, we have prioritized gradual change in leadership to ensure both stability and influx of new ideas.

For LTER III (1990-6), we began with essentially the same structure, with Lauenroth (WKL) as lead PI, Burke (ICB) Co-PI, and two ARS PI's, and the plan to switch responsibilities between WKL and ICB after three years. ICB took over the lead PI responsibilities (1993-96) and initiated the formation of an Executive Committee, which has persisted through LTER IV (1996-2002). The Executive Committee since that time has consisted of all local co-principal investigators (~10, including CSU, ARS, and the University of Northern Colorado scientists), a group that meets biweekly to make all of the major scientific and administrative decisions, including budget decisions, for the project. This structure has worked 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. In 1996, we also initiated a halftime Project Manager position to handle the administrative details and free time for scientific activity for ICB and WKL.

Midway through LTER IV (1999-02) Dr. Eugene Kelly (EFK) replaced WKL as the CSU Co-PI and Dr. Jack Morgan (JAM), representing USDA-ARS as a Co-PI, joined the project management team. EFK began the transition into the Lead PI role and will move into the lead PI role at the beginning of LTER V. Thus far, we have not identified a new Co-PI to replace ICB in

three years. We will address this issue during the first half of this funding cycle.

The planned turnover of the administrative role is possible because our management model depends on shared intellectual leadership and group decision-making. While the Executive Committee model has worked very well, our current assessment is that it results in too much time invested in management by the full scientific group; and while we wish to maintain a high level of participation of all scientists, we feel that this will be best accomplished if most of the full-group meetings are focused on our exciting science. We have therefore instituted a new management model that we think is an improvement on the Executive Committee model. In our new model, we have one Co-PI who represents each core research group: 1. Populations: Plant Dynamics and Ecosystem Interactions (Lauenroth, lead); 2. Populations: Faunal Dynamics and Ecosystem Interactions (Antolin, lead); 3. Biogeochemical Dynamics (Burke, lead); 4 Land-Atmosphere Interactions (Morgan, lead); 5. Information Science and Management (Stafford, lead). The membership of these groups is highly overlapping; many of our co-investigators belong to 2 of the groups and in one case 3. Note that WKL is not listed on the cover page due to lack of room, but he functions as a full Co-PI. Thus, we have a management structure that mirrors our reporting structure to NSF, and that ensures balance across our subdisciplines.

EFK will serve as the responsible PI representing CSU to NSF and as the Coordinating

EFK will serve as the responsible PI representing CSU to NSF and as the Coordinating Committee (CC) representative to the network. For day-to-day financial and other project decisions, EFK and ICB will share responsibility and coordinate activities with the Co-PI leaders of the research and information management areas. Interactions are at a daily level among PI's and the project manager and administrative assistant. The willingness of group leaders to handle requests within the scope of their research areas will allow much better connection between the science in that group and the management, while maintaining a connection to the entire project.

A key in this project management model is maximizing the involvement of all scientists in LTER activities. Kelly will serve as SGS's LTER CC member and, when CC meetings allow additional site representatives to attend, the group of Co-PI's will work to distribute our representation among our scientists. Minutes from these meetings are always distributed to the entire group. Workshop participation is encouraged and supported when possible.

We are very interested in improving our project and regularly involve scientists from other institutions and programs to assist us in this process. Peer review has played a crucial role in our recent changes in project structure and personnel. 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. In addition, we sought advice from many field biologists across the country as we have begun thinking about a new field station, through an organized workshop.

Recruiting of new scientists

Since 1990, we have been making major efforts to add depth in important areas that are crucial to understanding the SGS. Prior to LTER IV, we recruited four new individuals to strengthen the project in needed areas, Dr. Roger Pielke (mesoscale atmospheric sciences), Dr. Bea Van Horne (mammal ecology), Dr. Arvin Mosier (trace gas fluxes), and Dr. Joy Bergelson (plant population genetics). During LTER IV, we recruited 5 more new scientists to the project: Dr. Jack Morgan (plant ecophysiology and range ecology), Dr. Susan Stafford (information science and management), Dr. Michael Antolin (mammal ecology), Dr. Paul Stapp (mammal ecology), and Dr. Keith Paustain (agroecosystem ecology). In addition, we have recruited Dr. Myron Gutmann (University of Michigan) to represent our site in network efforts addressing socio-economic work. His work is supported by a related grant (NIH) with Parton and Burke. During this period we have also experienced some turnover. Dr. Debra Peters (formerly Coffin) moved from CSU to New Mexico and is now primarily associated with the Jornada and Sevilleta LTERs (though she maintains some long-term experiments at the SGS), Dr. Van Horne has recently accepted a position with the USFS in Washington DC, and Dr. Bergelson has completed her studies with the SGS.

Within CSU, there is a large community of scientists with interest in working at the SGS, and we employ several methods to increase our interactions with them and improve the possibilities of new collaborators at the site. First, we have a biweekly brown bag seminar, to which we invite all those on campus that we know are interested in grasslands. Second, we have invited several new investigators to advise a graduate student using summer scholarships for work at our site, and to advise REU students for work on the SGS (for instance, this was the basis of our first interactions with Antolin); we have several new faculty hires that we will target for this type of opportunity since they represent areas in which we have gaps (soil microbiology, evolutionary ecology).

Communication

Interactions among investigators are fostered, and scientific and programmatic information is disseminated in a variety of ways. All investigators (at CSU, UNC and at ARS) are on e-mail lists through which Dr. Sallie Sprague (project manager) distributes information and requests input. The entire group of all LTER participants (lead scientists, graduate students and staff) meets once every two weeks during the school year for either a "brown bag" seminar or to discuss project business. Faculty, post-doc, graduate and undergraduate students frequently present research results as oral presentations during the noon hour.

Finally, one of the benefits of the distributed management of the SGS-LTER is the broadly based research program that results when such a large group of scientists is actively involved in a common program. This "synergy" will continue to grow in LTER V as new initiatives are

encountered.

SECTION 4. Information Management (IM)

Data files at the SGS-LTER begin in the 1940s, with archived information from the CPER and International Biome Project. The SGS-LTER receives over 100 data requests (Fig. 1.13 and 1.14) yearly with users ranging from K-12 students and educators, land managers and policy makers, to international modelers and researchers. Over 120 datasets are available on-line (http://sgs.cnr.colostate.edu/Data/AcquisitionPlcy.htm). By the 1990s, the SGS-LTER network had expanded to over 20 separate UNIX drives, attached to many different physical computers and networked into a coherent yet cumbersome NFS (Network File System) model. PCs added to the complexity of data management by further decentralizing the location of data. In addition, there was no coherent rule for creating project directories with adequate metadata. This situation, although workable, begged for a more streamlined and efficient IM system. Therefore, a new storage technology, RAID (Redundant Array of Inexpensive Disks) was used to develop a centralized way to manage data, providing greater power to organize, manage, and publish our information. In the past one person managed our information. Now, we are using a team approach. This has kept SGS-LTER agile in terms of keeping up with new technology and informatics research.

The SGS-LTER Information Management team (Team) and researchers recognize that a successful long-term ecological research program needs a strong IM component (Stafford et al. 1986a,b). The Team supports our research and contributes to Network efforts in the ecoinformatics community (http://knb.ecoinformatics.org/informatics). Good IM practices are critical to allow our investigators to expand our temporal, spatial, synthesis, and modeling research (Michener et al. 1997).

Personnel: The Information Management Team: The Team is integrated throughout the process of initiation, implementation, and completion of SGS-LTER projects. A team of professionals with unique expertise in information technology, database and network administration, web development, metadata management, and IM leadership is able to work effectively through the process of scientific research. This team is tied closely to the leaders in IM, research, education, and outreach, both within LTER and beyond (**Fig. 4.1**). Co-P.I. Stafford chairs the LTER IM Committee.

Mechanisms for Researchers to Contribute Metadata to the Database: We have developed a strong web-based tool with the Agricultural Research Service (ARS). An on-line form allows researchers to automatically enter metadata in the SGS-LTER Access Relational Database Management System (RDBMS). End-users may query the database for project information dating back to 1940. We will continue to develop and refine these tools to participate in developing metadata content standards across the Network. (Fig. 4.2). (Please see http://sgs.cnr.colostate.edu/ars/).

Collecting, Verifying, Archiving and Publishing Data: Communication between researchers and the IM team begins with project initiation. The Team stays involved during data collection, verification, entry, QA/QC, archival, and publication (Brunt 2000) (Fig. 4.3). Currently, additional data are being directly downloaded to our database from data loggers in the field, thus shortening the time between data collection and entry. After digital data are assured for quality,

the information is transferred to the SGS-LTER RDBMS residing on the SGS-LTER server, where information becomes accessible to the public through our website (http://sgs.cnr.colostate.edu/Data/DataLibrary.htm).

Availability of Data and Data Access Policy and Procedures: The SGS-LTER data access policy is in compliance with the LTER-wide Information Management Policy (http://lternet.edu/data/netpolicy.html). Our data access policy is available online at http://sgs.cnr.colostate.edu/Data/AcquisitionPlcy.htm.

<u>Extensions for Restricted Access</u>: If a researcher wants to further restrict access, requests with justification must be made in writing to the Executive Committee. The Committee reviews the Investigator's request and determines whether the request will be granted and for how long the data set will remain restricted. Extensions are rarely requested or granted.

<u>Requests for SGS-LTER Data</u>: The Team tracks and logs requests for data, including information on who is requesting data and why. End or secondary users must use a recommended data citation, if they intend to publish the information. The Data Manager (DM) informs the PI of the request for information, which allows the PI to communicate directly with the interested party.

Participation in Network Information Systems (NIS): SGS-LTER participates in DTOC (Data Table of Contents), Personnel database, CLIMDB (All Site Climate Database), ANPP (All Site Annual Net Primary Production), and All Site Bibliography NIS modules that are maintained by the Network Office (http://lternet.edu/data/).

GIS Data management system, data distribution, and applications of spatial information: Spatial data are currently stored as ESRI shape files and coverages. A new data structure will be implemented using Spatial Database Engine (SDE) and Geodatabase. The benefits of these changes include a centralized management structure, versioning and transaction auditing, and the ability to define properties, behavior, and relationships. FDGC standard metadata will be incorporated in all GIS data sets.

Our GIS managers have a library of study site locations at the CPER and PNG: natural vegetation communities, watersheds, soils, human structures, disturbances such as prairie dog town areas, and different land uses. Over the past few years, we have created a digital historical spatial data set over several spatial scales. Some data sets include historical pasture information or herbicide applications that are related to ARS or PNG management of the land. Metadata for these data sets have been collected and standardized and are complete. Updates are made as spatial characteristics change over time.

Spatial data and information can be distributed in several hard media formats (CD, floppy, zip disk) and are provided by the DM upon request. Spatial data may be downloaded from a secure FTP site or via browser on an HTML site. Maps also are served on ArcIMS allowing users to view data for the CPER and PNG in the form of shape files, coverages and image formats. Maps served on ArcIMS may be viewed via internet browser or GIS tool, like ArcExplorer or ArcInfo. This capability now gives our users tremendous power in gaining an understanding of spatial information from our research sites.

Future Directions: Our goals for IM support long-term ecological research, modeling, and cross-site studies, as well as standardization and synthesis efforts across the Network. We must maintain an efficient and secure data flow into a centralized, safe, organized storage and data retrieval system. Our aim is to push the envelope of technology to better our science and allow science to challenge our technology. We are using new server technology to migrate existing files through a single point of entry and organize new files on a centralized database, within a newly designed directory hierarchy that serves as a gateway to publish data sets on the web. The centralized, hierarchal database will allow simplified access of data to the public and long-term, safe storage of data sets in a format conducive for use in the future and in synthesis research. Metadata will remain accurate and up-to-date, understandable, complete, and logically organized. Disaster recovery, system growth, and upgrades will be easier to manage than in the past.

We plan to migrate to a multi-user database from Access. Our Team has the expertise to facilitate this upgrade. Growth will also require the cooperation of Information Managers and PIs from ARS, SGS-LTER, and possibly PNG. The Team would like to continue to support our PIs by providing easy access to information, documenting and managing metadata, facilitating analyses of spatial and non-spatial data, publishing more data sets, and visualizing project information.

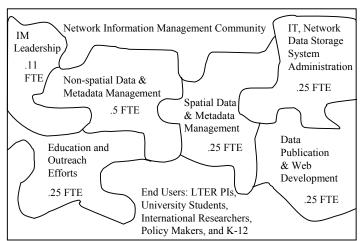
The "Decade of Synthesis and Standardization" of metadata continues to be a pressing issue at both the site and Network level (Stafford, personal communication and Baker et al. 2000). The Team also is excited about our active involvement with developing a "content standard" for metadata within the LTER community. This new tool, called Ecological Metadata Language (EML), will simplify data access (http://caplter.asu.edu/data/metadata/workshop012002.htm).

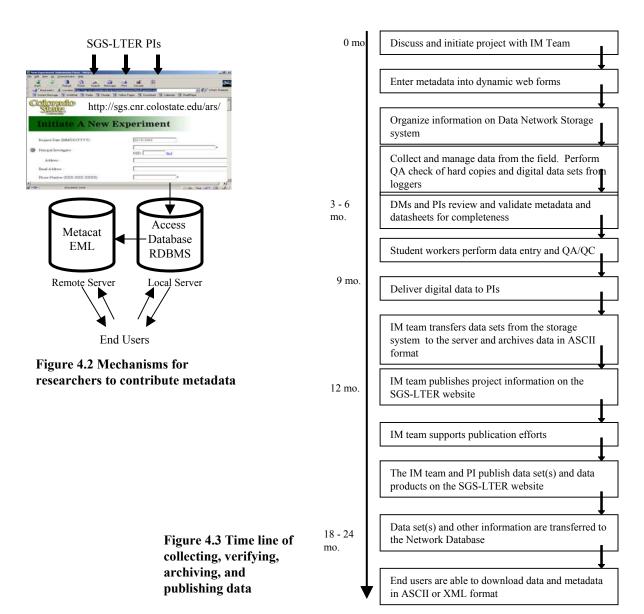
IM Leadership: SGS-LTER has identified areas in which we can become a leader in IM including managing models and their metadata, providing training and mentoring for other sites, and involving IM in our education and outreach programs. Managing metadata for models, controlling model versions, and documenting the range of validity, implicit assumptions, ecological context, and related long-term studies and data sets are challenging. The Team would like to develop efficient ways to store, document, access and publish this type of ecological modeling information. We will collaborate with other modeling-intensive LTER sites and share results with the LTER Network and greater scientific community.

Through the evolution of our team approach to IM, we have learned to balance the project's needs for cutting edge IT knowledge and development with efficient, more routine daily IM tasks, while maintaining a strong connection between the Team and the PIs. We would like to become a mentor to new LTER sites as they plan their IM activities and organization.

We see an opportunity to incorporate IM into Schoolyard LTER efforts and to impart a sense of the importance of IM to the next generation of scientists. We are able to work with existing education centers with ties to SGS-LTER, such as the UNC Math and Science Teaching Center and the Center for Learning and Teaching in the West. IM will be a part of distance learning programs, professional development programs for teachers, and will use the web as tool for data delivery.

Figure 4.1 Information Management Team: current and proposed personnel components at SGS-LTER





SECTION 5: Outreach

The SGS-LTER has focused on community outreach, interactions with federal land management agencies, non-profit organizations, and K-12 education through student mentoring, curriculum development, teacher professional development, community partnerships, and education research. Our informal activities include interactions with federal land management agencies, partnerships with local not-for-profit organizations, interactions with the news media, and the presentation of programs to local schools and community groups. Our formal programs include Schoolyard LTER, the GK-12 Graduate Fellowship Program, Research Assistantships for Minority High School Students (RAMHSS), The Center for Learning and Teaching (CLT), Teacher Enhancement (TE), and Research Experience for Undergraduates (REU).

Land Management Agencies

We have very strong interactions with the Agricultural Research Service (ARS); the lead Range Scientist Research Leader, Jack Morgan, is a Co-PI on the project. As a mission-oriented research agency, our interactions with Jack and Arvin Mosier (also ARS) lead to a much enhanced interaction with both federal and private land owners. The ARS Range Unit has a very strong outreach program of interaction with ranchers in Colorado and Wyoming, and we plan to participate in their field days to communicate with this important group on the shortgrass steppe.

We continue to have very strong ties to our partners at the U. S. Forest Service Pawnee National Grasslands (PNG), including their management staff/rangers, wildlife and plant ecologist, and interpretation staff. This includes very frequent interaction with respect to management decisions, especially regarding prairie dogs and fire. The PNG uses our data and cites our publications for their grazing management policies. We have been developing a joint geographic database with the PNG for several years now, and plan to expand our geographic database of research experiments that we developed with the Agricultural Research Service (ARS) for the PNG within the next several years.

Informal Outreach to the Public: Nonprofits and News Media

One of the most important outreach contributions we make is to lead field trips for interest groups to our research site. Recently, we had great attendance at a field day aimed at members of non-profit organizations and federal agencies. These groups include the Audubon Society, Sierra Club, Southern Plains Land Trust, Colorado Division of Wildlife, National Wildlife Federation, Agricultural Research Service, Defenders of Wildlife, Nature Conservancy, Forest Service, Boulder County Open Space, Weld County Open Space, Rocky Mtn Bird Observatory, Colorado Wildlife Society, Colorado Natural Heritage Program, and the Crow Valley Grazing Association. We participated in the National Wildlife Foundation's 2001 Prairie Summit. The site receives visits from the recreational public, including a large number of birdwatchers. We plan to increase our visibility with these groups and individuals over the next funding cycle.

During two of the past 6 field seasons, we participated in Landmark Volunteer's program, hosting 10-15 high school students. Students spent one week in the field and one in the lab assisting with various duties.

The news media has covered a great deal of our work during the past cycle, including coverage in local and national newspapers on the Alward et al. Science article, articles on prairie dogs, and on our grazing research. Channel 9 news of Denver and the Rocky Mountain News each released a story detailing our grazing work in 1997, the story was released to AP, and was picked up by many local newspapers throughout CO and the Rocky Mtn region. The Denver Museum of Natural History made a video of the shortgrass steppe that focused on our site.

Visiting Scientists

In addition, we have a very large number of visitors from universities and other organizations around the world. We host these individuals as they contact us, for either field trips or research collaborations (far too many to list here, but including every continent). In many cases, we host these individuals at our field station.

Education

The SGS-LTER has a very strong program in both formal and informal education, with a strong emphasis on serving first generation and low income (FGLI), female, and rural school students. In Colorado the majority of FGLI students are students of color. Our focus addresses the national need to involve under-represented groups in math and science disciplines.

Formal Programs:

Below, we list our formal education programs associated with SGS-LTER. All but the REU

program are directed by Dr. John Moore.

Schoolyard LTER: In 1996, we received NSF funding to explore the feasibility of establishing small-scale research plots on school grounds. This project led to the development of the LTER-Schoolyard Ecology program (SLTER). Nine schools in 6 cities and 4 counties have participated in this program to date. Students and teachers at these schools have created authentic research projects that involve students and scientists from SGS-LTER. Examples of SLTER projects include: the effects of disturbance on invasive plant seedling establishment; biogeochemistry on urban and rural prairie dog towns, and an analysis of the Conservation Reserve Program success in restoring native vegetation and soils. Several of our students showcased their SLTER research at the Colorado State Science Fair. We also met with members from SLTER at Jornada LTER, Andrews LTER, and the LTER Network to begin collaborations between students at our respective schools.

NSF-RAMHSS-Research Assistance for Minority High School Students Program: Between 1997 and 2000, RAMHSS at the SGS-LTER involved 23 high school students from groups under-represented in ecology. All of 1997 to 1999 scholars have graduated and entered college. All those from 2000 are juniors now and have been accepted or applied to college at this time.

<u>DOE-Upward Bound:</u> The inclusion of SGS-LTER activities has greatly enriched our DOE-funded Math and Science Upward Bound program, curriculum development (Moore et al. 2000), and research agenda (Miller et al. 1999, Moore et al. 2000, Rham 2001, Rham et al. submitted).

NSF-GK-12-Graduate Fellowship Program: The goal of this program is to establish SGS-LTER PI/Graduate Student/K-12 teacher partnerships that place teachers on a research team and graduate students in the K-12 classroom. In 2001, approximately 650 GK-12 students interacted with LTER graduate students, field staff and scientists through classroom presentations, site activities and workshops.

<u>NSF-CLT-Center</u> for <u>Learning and Teaching</u>: This new program will provide teacher professional development, and research on how the different ways of knowing and learning for students from different backgrounds influence teaching and learning

students from different backgrounds influence teaching and learning.

NSF-TE-Teacher Enhancement: This program establishes a summer research internship program for K-12 teachers, in collaboration with Portland State University, Oregon State University, and the Andrews-LTER, to compliment our Schoolyard LTER activities.

<u>REU</u>: Our REU Program was begun 1996 and has attracted over 15 stellar students from colleges and universities throughout the U.S. Students researched topics such as invasive plant species on the SGS, dendroclimatology of pines, and metapopulation genetics of prairie dogs.

Assessments of our formal programs have been used to study authentic research in the classroom, factors affecting student attitudes and career aspirations toward ecology, curriculum development, and the state of K-12 science education (Endicott et al 1997, Miller et al 1999, Moore 2000, Moore et al. 2000a,b, Rham 2001, Rham et al submitted).

Informal Activities:

In addition to formal programs we are increasing our partnerships with local organizations, including the Rocky Mountain Bird Observatory, the Central Mountains & Plains Section of the Wildlife Society, the Denver Museum of Nature and Science, the Discovery Science Center in Fort Collins, the Environmental Learning Center and the Center for Life Sciences at CSU, and the Science Coordinators at two local school districts.

Summary

We plan to continue to have a very active outreach and education program, which is now well-funded from the initiatives above, led by John Moore. All of our education activities and plans do not fit into this two-page document. Please see the <u>Outreach</u> link under Proposal 2002 on our home page (http://sgs.cnr.colostate.edu/).