Research

During 1996 and 1997 we produced 57 papers in refereed journals, 16 book chapters, 2 dissertations and 18 abstracts from national and international meetings. 17 graduate students and 19 undergraduates work on research related to the shortgrass steppe LTER. Scientists at our site are involved in a number of new experiments in addition to continuing our long term projects. This section is organized by a modified version of the LTER core areas. An online version of this document is also available at our website (http://sgs.cnr.colostate.edu/proposal/nsfindex.html).

1. Populations and Processes

Our work since our last progress report has focused on continuing to sample our long term projects and to initiate several new long term studies of both plants and animals. The new plant work involves a new study and a data rescue effort. The new project is designed to investigate the dynamics of individual plants on permanent plots located in conjunction with our long-term exclosure experiment. The data rescue effort involved chart quadrat data that had been collected at Hays, Kansas from 1932 until 1972. The new animal work involved expanding the monitoring program we began in 1994 and initiating work on prairie dogs.

Plants

Chart quadrat study: The only way to be able to understand the demography of herbaceous plants is to identify individuals and follow them throughout their lives. In 1997, we established twelve 1x1 meter plots on which we plan to map annually the size and location of every individual. The mapping will be accomplished with a pantograph. Six of the plots are located in an exclosure and six are in a grazed pasture. All of the plots are located in conjunction with our long-term exclosure experiment.

Hays chart quadrat data rescue: In 1932, as part of his doctoral dissertation research at the University of Nebraska under John Weaver, Fredrick W. Albertson began a study involving approximately 70 $1m^2$ quadrats. Most of these quadrats were mapped every year from 1932 until 1972. In 1996, Gerald Tomanek moved from Hays to Kansas City

effectively removing the last person who cared about the future of the original maps from the immediate environment. Additionally, since Gerald is now in his 70s, when he dies all living record of the history of the chart quadrats will be lost. Our interest in the demography of grassland plants lead us to propose under supplemental funding that we obtain and digitize all of the Hays quadrat maps and make them available to the ecological community over the world wide web and on CD. We are nearing completion of that effort. All of the maps have been digitized and checked. We are currently creating a photographic archive of the original maps and preparing the final copies for the web. We plan to publish an analysis of some of the data as a way to advertise their availability. A draft of the paper has been written and should be submitted by this fall.

Animals

Animal Monitoring Programs**:** Since 1994, we have estimated population sizes of nocturnal small mammals, rabbits, and, to a lesser degree, terrestrial carnivores, on the SGS-LTER site in north-central Colorado. These monitoring programs continued in 1997, including live-trapping studies in May and roadside counts of rabbits and canids in January, April, and July. We continued monthly warm-season surveys of terrestrial macroarthropods, studies that were also initiated in 1994. Captures of major insect taxa are counted in 90 pairs of pitfall traps placed along a 1 km topographic gradient as part of new long-term monitoring studies.

Additional small mammal surveys will be conducted in September and October 1997. Beginning in July 1997, we modified our roadside census route to include areas of the Pawnee National Grasslands (PNG), taking advantage of the 1996 SGS-LTER site expansion. The new route includes more upland prairie habitats used by white-tailed jackrabbits *(Lepus townsendii)* and swift foxes *(Vulpes velox)*, while continuing to allow us monitor rabbit and canid populations on portions of the Central Plains Experimental Range.

Prairie Dog Studies: Black-tailed prairie dogs *(Cynomys ludovicianus)* are thought to influence a number of important ecological processes in North American grasslands, yet relatively little is known of their effects on the shortgrass-steppe ecosystem. In the 1996 proposal, we outlined new research that investigates the role of prairie dogs on the SGS-LTER site. In June 1997, we identified 5 active prairie-dog colonies and 5

nearby uncolonized sites with similar soils, topography, vegetation, and land-use history. Research plots (1.2 ha) are centered on colonies and include a 0.4 ha grid for possible long-term studies of animal populations. Pilot studies to determine the effects of prairie dogs on other small mammals were conducted in June-July 1997 (Fig. 1) and are ongoing. Additionally, two related Master's research projects were initiated in 1997 under the direction of Dr. B. Van Horne in the Department of Biology at Colorado State University. J. Junell is investigating the effects of prairie dogs on insect populations and J. Roach is using molecular techniques to determine the genetic structure of prairie-dog populations on the PNG.

Habitat selection and community structure of small mammals and terrestrial insects:
Detailed investigations of habitat selection and movement patterns of the two most common nocturnal rodents in shortgrass steppe (the deer mouse and northern grasshopper mouse) were completed in 1997 (Stapp in press a, Stapp and Van Horne in press, see also Stapp submitted ms). This information was used to examine the role of competitive and predatory interactions between these species and in determining patterns of local distribution and abundance in shortgrass steppe (Stapp 1997a, see also Stapp 1996a). Additionally, studies of the abundance of insect prey consumed by grasshopper mice provided information on microhabitat preferences and species composition of darkling beetles among sites with different soil types and shrub characteristics (Stapp 1997b, Stapp in press b).

2. Biogeochemistry

In the past year, we have continued our long-term investigations into the controls over biogeochemical pools and fluxes, at several temporal and spatial scales. Below, we summarize our most recent results, and particularly highlight those that resulted in publications this year.

Influence of resource availability on biogeochemical pools and processes

We are in the second year of treatment in our cross-site project, in which we have applied 6 separate treatments (increased temperature, added water, increased nitrogen, control, and interactions except temperature + N) to assess the effects on above- and below-ground net primary productivity, decomposition, trace gas flux, and soil organic matter pools. Several differences are becoming apparent. Nitrogen trace gas

fluxes (NO and N_2O) are clearly increased by increased moisture and N, with thus far an unclear influence of temperature; methane uptake is significantly decreased by N additions. We are collecting minirhizotron data for belowground primary productivity, and using both clipping and digital photography for aboveground primary productivity.

In addition, we have just initiated a rainout experiment in the same exclosure, led by an LTER Ph.D. student (with equipment support from Burke's PFF). Two shelters with humidity sensors have been constructed, and treatments will be initiated this coming spring.

Influence of topography, texture, and grazing on biogeochemical pools and processes

We recently completed a study on the interactions between topography and soil texture as they influence N cycling and availability (Hook et al in revision) (Fig 2). Our results demonstrated that soil texture is responsible for most if not all of the influence of landscape-scale patterns in N cycling. This summer we are also completing a study of the interactions of topography and grazing on soil organic matter and soil erosion. This work consists of 4 key pieces, 3 of which have been contributed by either REUs or undergraduate thesis projects: the influence of grazing and topography on 1) soil microtopography (Brannen thesis); 2) soil organic matter pools (Madigan thesis), 3) C and N cycling (Burke 1996 ESA presentation), and 4) in situ soil respiration (Beard, one of this year's REU projects). Results thus far indicate that both topography and the location of individual plants have a very strong influence on soil erosion and organic matter, and that grazing has relatively minor effects.

The influence of plants on soil pools and processes

Five studies were completed this year that evaluate the effects of plant species or plant location on soil pools and processes. In a first set, we found that the strong plant-interplant patterns with soil organic matter are primarily due to root gradients (Kelly et al. 1996), and that the enrichment with respect to N availability caused by individual plants is quite short-lived (less than 3 years) (Kelly and Burke 1997). We found that soil recovery in recently plowed grasslands that are returned to perennial grasslands is hastened by the presence of N-fixing species (Robles and Burke 1996). Epstein et al (accepted) documented a significant influence of plant functional type (C_3 vs. C_4 type) on trace

gas flux from shortgrass steppe, and Epstein et al. (in prep) found that total retention is significantly different between vegetation types dominated by C_3 and C_4 species. Finally, Vinton and Burke (1997) demonstrated that in the shortgrass steppe, the location of individual plants is a more important contributor to soil organic matter than species identity, but that this relative importance reverses with increasing average annual precipitation across a gradient. Studies of biogeochemical pools and processes that involve simulation and regional analysis are listed under Synthesis/Cross Site studies.

3. Paleoecology/Paleopedology

Progress to Date

Research activities relating to the paleoecology and paleopedology of the LTER site during 1996-1997 have centered on three areas: 1) the summarization of existing data sets; 2) preparation for expanding our paleoinvestigation beyond the CPER to the entire Pawnee national grasslands; and 3) initiation of a stable Si isotope study for evaluating stable Si isotope ratios of biogenically produced minerals.

The summarization of existing data sets resulted in the publication of two manuscripts (Blecker et al., 1997;Kelly et al.,1997). New findings include a comparison of Holocene paleosol phytoliths between sites in northeastern Colorado and southwestern Nebraska. This comparison provided a test of our conceptual Holocene paleoclimate model (Kelly et al., 1993), which is based on data from northeastern Colorado alone. Results indicated that climatic variations detected in paleosols by isotopic techniques may be masked by topographic variations. Perhaps the most significant outcome of this portion of our research was that it clearly indicated the need to expand the geographic extent of our analyses.

Expansion of the LTER site beyond the confines of the CPER will allow for the identification and characterization of more paleosols and the delineation of major stratigraphic units, both of which will allow for the more robust interpretation of our paleoclimate model. Preparation for such expansion involves the compilation and interpretation of existing soils, geologic, topographic and land use maps, and aerial photography. A suitable base map must be prepared prior to the commencement of additional field investigations.

The analyses of Si isotopes in plant opal phytoliths are currently in the experimental phase. We are hopeful to be able to quantify the biological fractionation of Si when plants take it up from the soil solution. We have initiated greenhouse studies growing both C_3 and C_4 grasses in hydroponic solutions. Isotopic analyses and sample preparation is being conducted with cooperators at University of California at Santa Barbara. Implications for establishing terrestrial "biomarkers" are exciting. Also we have been contacted by NASA scientists about other collaborative work regarding Mars.

Expanded role of Pedology Group

We have expanded our sphere of influence on the project by exploring some unique aspects of the biogeochemistry of the shortgrass steppe. We are studying the relationship between weathering (Si and Sr isotopes) and atmospheric inputs (Blecker Ph.D.), the distribution of C across landforms (Kelly, Yonker, Chadwick, Gessler, Elliott, Paustian), and the geochemical coupling of hydrological and biological processes (C and O isotopes) for scaling of soil respiration flux measurements (Sulzman Ph.D.). To date we have initiated field campaigns in each of these areas. Both Ph.D. candidates Blecker and Sulzman are conducting field studies on sites at the Pawnee as part of a bioclimatic transect from the alpine to grassland ecosystems.

4. Disturbance

Small scale disturbance studies

We continue to monitor plant recovery on small, patchy disturbances similar in characteristics to cattle fecal pats, Western harvester ant nest sites, and burrows from small animals. Furthermore, we are studying the importance of the removal of *Bouteloua gracilis* from 1.75 m^2 plots on a fine- and coarse-textured soil (Martinez-Turanzas 1997). This study will allow us to determine the species expected to dominate shortgrass steppe communities in the absence of the current dominant. C_3 perennial graminoids dominated the plots in 1993 after the removal of *Bouteloua gracilis*. However, density of these grasses decreased through time as density of annuals and perennial forbs increased. In addition, density was higher on fine compared to coarse-textured soils, and grazing did not have significant effects on plant density. These plots will be followed in the long-term to determine species composition in the absence of

Bouteloua gracilis. We are also studying the effects of the removal of individual *Bouteloua gracilis* plants on plant recovery compared to the removal of individuals of other species common in these communities (Martinez-Turanzas 1997). Removal of *Bouteloua gracilis* plants had significant effects on both gap size and gap colonization, suggesting that the death of *Bouteloua gracilis* plants are the most suitable habitats for plant colonization. Grazed plots had higher rates of colonization than ungrazed plots.

Large scale disturbance studies

In 1991, we initiated a long-term grazing study, whereby half of each of six (>50y) exclosures were opened to grazing and new large exclosures were constructed. This resulted in four treatments: previously ungrazed - now grazed, previously grazed - now ungrazed, long-term ungrazed, and long-term grazed. Sampling by a number of LTER investigators continues under the new LTER cycle. We also started monitoring root production and turnover using minirhizotrons this year. Results from the vegetation sampling indicate that small-scale (within a 1200 m^2 area) heterogeneity in soil texture plays a large role in local plant diversity and species distributions in ungrazed shortgrass steppe, but that grazing by large herbivores smoothes this heterogeneity. Plant species diversity increases with increasing sand content in ungrazed treatments but remains low and constant over texture gradients in grazed treatments (Fig. 3). We have also found that selectivity of a particular species by herbivores is not necessarily related to increases or decreases in that species with grazing. Some species that are selected by cattle were found to increase with grazing and some that are not selected by cattle decrease with grazing. This is contrary to current general perceptions of plant-animal interactions, and suggests that the indirect effects of herbivores on plant-plant interactions may be as important as the direct effects of defoliation in structuring plant communities. In conjunction with an LTER-cross site grant, small mammal exclosures were constructed this year at three of the six large-herbivore exclosure sites. This will allow us to compare the roles of small selective herbivores to large generalist herbivores in the shortgrass steppe, and across sites that differ in productivity and evolutionary history of grazing.

5. Water and Energy Dynamics

In addition to continuing to monitor soil water at a number of long-term sites we conducted a new study and a new data analysis since our last report. The new study focused on an area in which we had very little previous information, bare soil evaporation. The new analysis used data from our network of rain gages over the CPER.

Bare soil evaporation: Bare soil evaporation is an extremely important process in semiarid and arid regions. It can account for a very large fraction of the total water loss from the soil and it is very poorly understood. We conducted an experiment to evaluate the effects of soil texture on bare soil water loss (Wythers 1996). The study utilized minilysimeters, four soil textures and 15 replicates of each texture. Evaporation influenced soil water content to a depth to 40 cm in all textures. Our previous assumption had been that bare soil evaporation only influenced the top 10-20 cm of the soil. The depth to which evaporation had its maximum influence varied among textures. The depth of most rapid change in soil water was greater for a clay loam than for a sandy loam which fit our previous model of the effects of bare soil water loss. Using these data we found that our previous parameter values for our soil water simulation model resulted in a 50% underestimate of bare soil evaporation over 10 days. These new results will be very valuable in future soil water simulation exercises.

Spatial and temporal variability in summer rainfall: The SGS-LTER maintains a network of 10 recording rain gages over a 10 km^2 at the CPER. Five of the gages have been in place since 1988 and the remaining five since 1994. We used these data to investigate the answers to two questions: What is the relationship between the amount of rain collected by two gages and their distance? and Over what time period do the cumulative amounts collected by two gages become indistinguishable? We performed kriging analysis on the intergage correlation coefficients and a multiple regression analysis on the intergage distances and azimuths. Correlation decreases linearly with distance and with variation from a northwest-southeast orientation. Records were aggregated into intervals of 2, 3, 4, 7, 14, 21, 28, 42, 56 and 70 days and a correlation analysis was preformed. Correlation increased asymptotically such that it was close to one on a seasonal basis and statistically indistinguishable from one after 3 weeks.

Data Management

Progress To Date

In a continuing effort to bring all of our datasets in line with NSF's 2 year public accessibility guidelines, we have opened 10 datasets to the public. Currently 114 of 209 datasets are open to the public and nearly all of the closed datasets were received by the data management staff in the past two years. These datasets are available via our website at http://sgs.cnr.colostate.edu. We continue to contact principal investigators on a regular basis regarding the status of their datasets. Along with this effort we have uncovered metadata for older datasets from the International Biome Project (IBP). In this ongoing project we are attempting to locate all of the metadata related to these datasets. To date we have located complete metadata for 17 of the 65 IBP datasets and partial metadata for all 65 IBP datasets.

One of the goals of the SGS data management program is to utilize our website as our primary communication tool within our group and to the public. To this end we have redesigned the data access portion of our website to include more flexible searching tools and easier access to our datasets and metadata. In addition, we are currently building a link between our datasets and our bibliography. Last, we have entered over 350 abstracts into our bibliographic database and plan to have these available via our website.

Goals for the Upcoming Year

In the upcoming year we plan to focus on three aspects of data management: improving the presentation and storage of weather data, linking the bibliography and datasets, and improving the information content of our website. First, we plan to provide tools to access monthly summary values of our meteorological data along with graphs of the most widely used parameters. This will be an important addition to our data management program, since these data are consistently used for modeling efforts which require monthly meteorological data. Second, we plan to enable the link between our datasets and our bibliographic database. This will allow visitors to our website the ability to search for information by either data or by publications. Lastly, we plan to rebuild the species database, develop searching tools, and link this new species database to the 452 images we have collected in the past year. Ongoing activities include: opening more datasets to public access, entering the abstracts of older publications, and improving our website.

Geographical Information Systems

Most of the Geographical Information Systems (GIS) work in the past year has focused on the Hays chart quadrat data rescue project described above in Populations and Processes - Plants. Additional work has included the identification and acquisition of new soil and topography data for the Pawnee National Grasslands.

Outreach Activities

Collaborations

Since our last progress report we have been involved with several local groups including the Denver Museum of Natural History, The Audubon Society, and The Nature Conservancy. In June, 1997, the Denver Museum of Natural History released an educational video entitled "The Last Place to Hide" about the rehabilitation work at the Rocky Mountain Arsenal. Dr. Bill Lauenroth was an important collaborator on this project providing ecological information about the shortgrass steppe ecosystem. Dr. Lauenroth also provided important ecological background information regarding the impacts of grazing on the shortgrass steppe for the article "The Plains Great Mirage" in the May/June 1996 issue of Nature Conservancy. Dr. Deborah Coffin was the editor of the 1996 report "Summary Report: Shortgrass Prairie/Mountain Plover Workshop" which summarized the Denver Chapter of the National Audubon Society workshop held March 1-2, 1996 in Fort Collins, CO. Dr. Lauenroth contributed a chapter entitled "Results of vegetation studies on Pawnee Grassland" to this summary report.

Education

In the past year we have continued our Research Experience for Undergraduate (REU) program with four students working on the following projects: 1) the effects of burning on shortgrass steppe plant communities, 2) dendroclimatology of the Great Plains, 3) the effects of grazing and topography on soil respiration, and 4) the effects of disturbance and increased water availability on seedling dynamics. This REU program has been extremely successful and we consider it an integral part of education at the shortgrass steppe LTER. In the coming year we plan to expand this program by applying for status as a NSF REU site.

Field Trips and Other uses of the Shortgrass Steppe LTER field site

One of the important contributions we make in the area of outreach is to lead field trips for interest groups to our research site. In addition, each year we host several non-LTER groups who are conducting classes or research at our field site. 1996-7 visitors included: students and professors from Utah State, University of Dayton- Ohio, University of Chicago, University of Miami-Ohio, University of Texas-Austin, University of Northern Colorado, University of Wyoming and West Greeley High School; professionals from the Colorado State Land Board, National Park Service, Colorado Division of Wildlife, US Department of Agriculture, US Geologic Survey, Smithsonian Institute, Niwot Ridge LTER, and the Boulder County Parks and Open Space department; and visiting scientists from Argentina, Spain, and Japan.

Cross-site, Synthesis, and Network-level Activities

We are currently funded to conduct several cross-site experiments. We were recently funded to evaluate the effect of mammal exclosures on ecosystem structure and function (Milchunas and Detling). We are also currently funded on several other cross-site projects, one assessing the within- and across-site variation in ant community structure at three semiarid LTER sites (Wiens et al), one comparing the controls over decomposition and net primary productivity in North American and South American steppe ecosystems (Lauenroth, Burke, and Sala), and one addressing the role of natural grazing refuges in grassland biodiversity in Israel and the US (Milchunas). We were just funded on a project that focuses much of the work on N sequestration in shortgrass steppe soils, but includes an experiment to compare soils from a large network of LTER sites (Burke, Maciel, and Lauenroth). All of these experiments are currently in progress.

We have successfully completed a number of synthesis and cross-site studies in the past year. We utilized our regional database to assess the factors that control plant species distributions (Epstein et al. 1996) and net primary productivity (Epstein et al. 1997a, b and c). We recently developed algorithms for assessing net primary productivity across the Central Grasslands using AVHRR satellite imagery (Paruelo et al. 1997). We tested regional models developed for the Central Grasslands and found that they are quite robust when applied cross-continentally to South America (Paruelo et al, in press). Finally, we used simulation models applied to a GIS to attempt to disentangle the covariance among

net primary productivity, annual precipitation, and net N mineralization across the Central Grassland region (Burke et al. 1996).

In addition, we recently produced a synthesis paper on the interactions between soils and plants in grasslands (Burke et al. in press). Our paper suggests that as resource-limitation switches from below-ground to aboveground with increasing precipitation in grasslands, the importance of species composition increases. The work synthesizes more than 20 recent publications from our group. We are well on the way to producing our Shortgrass Steppe synthesis volume. More than half the chapters have been submitted and we anticipate a completed volume within the year.

Finally, we are involved in a number of network level activities. We participate in the cross-site litter decomposition study directed by Mark Harman at Oregon State University. I. Burke serves on the Executive Committee for the Network, and C. Wasser serves on the network Data Management Coordinating Committee.