I. RESEARCH

During the period Nov. 1st 2002 to July 31st 2003, we produced 27 papers in refereed journals, 2 book chapters, 2 dissertations, 3 theses, and numerous abstracts from national and international meetings. Eleven graduate students and 51 undergraduate students worked on research related to the shortgrass steppe LTER. We continue to sample our long-term projects, as well as initiate some new short-term experiments. Following are key research results in each of our three core areas: population dynamics, biogeochemical dynamics, and land-atmosphere interactions.

1. Population Dynamics

Plants

Invasive Plants

In the past, concern about plant invasions in northeastern Colorado has been largely hypothetical, because there were essentially no instances of invasive plants having influenced the native grasslands. That has changed substantially in the last several years and especially in 2001. Dalmatian toadflax (*Linaria dalmatica*), a very aggressive introduced perennial plant, has begun to become established and spread on a wide variety of upland shortgrass steppe locations throughout the SGS LTER site. Based on accounts of invasions by toadflax in other regions, there is every reason to believe that this invasion could prove to have substantial influences on native plant communities and ecosystems.

In 2002 we began a long-term demographic study of established toadflax patches. The objective of this work is to understand controls on the rate and extent of vegetative spread of established patches. The initial work is focused on characterizing the patches. The subsequent steps will involve manipulating water and nitrogen availability and the presence of the dominant species blue grama (*Bouteloua gracilis*). These manipulations will be performed around the expanding edges of the patches. The objective of the manipulations is to understand controls on rate and direction of spread.

In the fall of 2001, we located 12 patches of toadflax ranging in size from 1 to 7 m^2. For each patch, we counted the number of toadflax tillers, collected global positioning system coordinates for the center of each patch, and surveyed the boundaries of each patch. The data will be entered in to a geographic information system database and updated annually. Tiller numbers per patch ranged from 200 to 1000 varying with patch size and location.
Future work will include investigation of the ecosystem consequences of the presence of toadflax in terms of water, nitrogen and carbon balance.

Demography of Pinus flexilis

An outcropping of the Ogallala formation which occurs as an escarpment in the northern portion of the SGS LTER site contains woodlands dominated by *Pinus flexilis* and *Juniperous scopulorum*. While we have evidence from stumps and packrat middens that *Pinus flexilis* has been present on these sites since approximately 300 AD, all of the current trees are less than 160

years old. Our assumption is that essentially all of the trees were cut as settlers, especially homesteaders, moved into the area following the Civil War. Age-height relationships suggest that a few of the smallest trees may have escaped this harvest event. The relationship between age and height from 1900 to 1994 has a positive coefficient, indicating that older trees are taller than younger ones. The opposite is found for trees established before 1900, suggesting that a few old short trees were dominating the dataset. These were likely stunted trees that were passed over by the homesteaders as unusable. As a further indication of how different these sites are from the shortgrass steppe locations that dominate the vast majority of the LTER site, the understory in these stands was surveyed. *Bouteloua gracilis* accounts for 25 to 80% of the basal cover of most shortgrass locations. It accounted for only 6-21% of the basal cover under the *Pinus flexilis* woodlands. The dominant understory grasses are *Schizachyrium scoparium* and *Bouteloua curtipendula*, two species that are characteristic of grasslands found 300 km east of the SGS LTER site

Animals

Animal Monitoring Programs

Since 1994, we have estimated population sizes of nocturnal small mammals, rabbits, and terrestrial carnivores on the SGS-LTER site. These monitoring programs continued in 2002 and 2003, including live-trapping studies in May and roadside counts of rabbits and canids in October, 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. In addition, we continued arthropod pitfall trapping studies on trapping webs established for monitoring abundance of small mammals. Arthropods are important food items for rodents on the shortgrass steppe. Twenty traps are placed on each of three upland grassland and three saltbush sites. Pitfall traps are run for 4-5 consecutive days on three occasions during summer months to track temporal changes in abundance of arthropods as a possible determinant of trends in rodent numbers.

Beginning in July 1997, we modified our roadside census route to include areas of the Pawnee National Grassland (PNG), taking advantage of the 1996 SGS-LTER site expansion. We have continued to utilize this new route which includes more upland prairie habitats used by white-tailed jackrabbits (*Lepus townsendii*) and swift foxes (*Vulpes velox*), while continuing to allow us to monitor rabbit and canid populations on portions of the Central Plains Experimental Range (CPER).

In May 2003, SGS-LTER researchers began field work as part of new research to assess the use of cattle grazing as a tool to create nesting habitat for the threatened Mountain Plover. This project includes determining the effects of different grazing regimes on arthropods and small vertebrates, which may indirectly influence the suitability of grazing-modified areas for plovers.

Small Mammal Plague Testing

Trapping of small mammals for plague surveillance was commenced during summer 2002. We trapped small rodents in 0.99 ha grids on and off prairie dog colonies on the CPER

and PNG (fall 2001, summer 2002) and on a colony experiencing a plague outbreak in the valley bottom of the S. Platte River near Red Lion Wildlife Area in Logan County in extreme northeastern Colorado (autumn 2002). Sampling of the most commonly captured rodents is summarized below; all animals were tested for plague antibodies from blood samples and fleas were tested by PCR. The only plague positive result was from a prairie dog flea, *Oropsylla hirsuta*, collected from a rabbit (*Sylvagus floridanus*) at Red Lion. None of the deer mice or their fleas from Red Lion tested positive, which brings into question whether deer mice act as a reservoir of the disease.

Number tested per species (# flea spp., # fleas tested)	*Peromyscus maniculatus*	*Onychomys leucogaster*	*Spermophilus tridecemlineatus*
CPER	5 (1,5)	41 (5,212)	70 (4,194)
Red Lion outbreak	46 (2,18)	1 (0)	5 (1,5)

In addition, we sampled fleas from black tailed prairie dogs (*Cynomys ludovicianus*) that were trapped in fall 2001 as part of an ongoing study of their metapopulation genetics on the PNG (L. Savage, unpubl.). 104 prairie dogs were tested for serology, they carried an average of 3.6 *O. hirsuta* (and no other fleas), and none of these tested positive for plague. We initiated visual counts of prairie dogs on the six colonies on the CPER to be able to monitor densities of animals on the CPER/PNG. These counts, in addition to determining the area of prairie dog colonies from GPS measurements, have demonstrated that prairie dogs colonies continued to exponentially expand in area, but not density.

Belowground Food Webs

Modeling studies addressed how changes in trophic interactions induced by disturbances affect food web stability, and how the belowground food web affects the dynamics and stability of the aboveground food web. The current debate has centered on how best to measure interaction strength, the per capita effects of species on the dynamics of other species. We developed an approach that relies on field estimates of the biomass of all species or groupings of species within the food web accompanied by estimates of their birth and death rates, feeding rates, and energetic efficiencies. We then assess the stability of the system through an analysis of the eigen values of the system's Jacobian matrix.

The empirical studies include the following: 1) the effects of reduced UV-B radiation and elevated CO_2 on plant growth, soil food web structure and the decomposition of grass litter, 2) the impact of prairie dogs and plague on the structure and stability of the belowground food web, and 3) the impact of cattle grazing on the structure and stability of the belowground food web. To date, we have observed significant shifts between the decomposer pathway dominated by bacteria and their consumers and the pathway dominated by fungi and their consumers. The shifts appear to be governed by changes in the C:N ratio of plant materials and the degree of disturbance to the soil. Models of these changes indicate that shifts towards either pathway lead to dynamic instabilities.

2. Biogeochemical Dynamics

Effect of Heavy Grazing on Carbon Flux

Here we report preliminary findings from a Bowen ratio/energy balance system monitoring CO_2 fluxes at the USDA-ARS Central Plains Experimental Range to investigate the effect of heavy grazing by cattle (75% forage removal) vs. the recommended grazing pressure (40% removal), and an ungrazed pasture. The study was begun in 2001, and will continue through 2003. The years 2000-2002 mark a period of major drought for the region. In 2001, precipitation was 80% of the long-term average, but there was no detectable effect of grazing intensity on C flux. These null responses are characteristic of previous work that has shown little to no significant effects of stocking rate on seasonal CO_2 fluxes. However, a different picture emerged in 2002. Precipitation was only about 50% of average in 2002, and as a result, cattle were removed from the pastures in mid-July. Nevertheless, CO_2 exchange was strongly affected by grazing treatment. Net CO_2 assimilation was lowest in the heavily grazed pasture, and highest in the ungrazed pasture; CO_2 assimilation in the moderately grazed pasture was intermediate between the other two treatments. Heavy grazing seemed to cause a net loss of C from the ecosystem. These results suggest that while the SGS may be resilient in the long-term to grazing, in the short-term, livestock removal or reductions in stocking rate may be important for maintaining a positive C balance in the face of drought.

Effects of reduced nitrogen availability on exotic plant invasion

We tested the hypothesis that adding carbon amendments in the form of humus precursors and sucrose would reduce the prevalence of exotic species, and increase native species, on a disturbed area within the Shortgrass Steppe LTER research site. We superimposed six new carbon treatments (control, sugar, lignin, sawdust, lignin and sugar, and sawdust and sugar) on a historic study site that received nitrogen, water, or the combination from 1970-1975, resulting in a dramatic increase in exotic species on the water plus nitrogen amended plots, a community change that persists into today. All of the new carbon treatments significantly reduced exotic species density on the historic plot which had the highest pre treatment density of exotic plants. The lignin and sugar treatment was the most effective, reducing exotic density by 90%. Our results show that the addition of carbon amendments can reduce exotic species density on the shortgrass steppe, at least over short time scales. While this has been recognized in the past, our goal over the next several years is to address the ability of our various treatments to maintain their influence over longer (decade to longer) times spans.

CO_2 effects on forage quality

Fiber composition of aboveground plant tissue is a partial index of potential digestibility by consumers, and also has implications for the rate at which forages can be processed through the digestive tract (rate of passage) that is important for bulk-limited consumers. Compared to ambient, elevated CO_2 had small effects on mid-summer cell soluble contents. Some decreases were evident, but this was species dependent. *Stipa comata* (STCO) always had lower cell soluble content when grown under elevated CO_2, whereas *Pascopyrum smithii* (PASM) never

displayed significant differences. *Bouteloua gracilis* (BOGR) response was variable between years. All differences among CO_2 treatments disappeared by the fall harvest, regardless of whether plants had been clipped that summer or not. Differences among species regardless of CO_2 treatment reflect the differences in palatability of these species. PASM is highly selected for by ruminants, and it is often a component of the diet of small mammals far in excess of its availability. STCO is a relatively unpalatable species, and BOGR is consumed in quantities about equal to its abundance.

At the other extreme of fiber quality, mid-summer lignin content also generally declined in elevated compared to ambient CO_2 treatments. PASM displayed the greatest declines and STCO the least. Differences between elevated and ambient CO_2 treatments disappeared by fall harvest for plants not clipped in the summer, and only small declines were observed for fall harvest plants clipped in the summer. The low palatability of STCO is also evident in lignin contents among species.

Celluloses make up the third primary class of fiber components, and are often the largest component of native forages. Since both cell solubles and lignins generally decreased, celluloses increased relative to the decreases in the other two components with elevated compared to ambient CO_2 treatments. The decreases in both cell solubles and lignins may be considered somewhat offsetting in terms of tissue quality. However, increases in celluloses would suggest a lowering of quality for mongastrics, and a potential lowering for ruminants depending on plant species specific factors and the rate at which the celluloses may be processed. In-vitro digestible dry matter is a good predictor of in-vivo digestible energy for ruminants. It integrates over forage nitrogen and fiber contents, as well as over other potential macro- and micro-nutrient limitations and the inhibition of microbial processes imposed by toxic allelochemicals. It is not necessarily a good predictor of rate of passage, but higher digestibilities generally translate into a greater potential for more rapid passage through the rumen depending to some extent on the rate of digestion. Mid-summer digestibilities were similarly lower in BOGR, PASM, and STCO in elevated compared to ambient CO_2 treatments. Other species (lumped together) did not display differences between the CO_2 treatments, possibly due to the variable mix of species. STCO was the least digestible species regardless of treatment.

Silica Biogeochemistry

Over geologic timescales, biologically mediated weathering processes influence atmospheric carbon dioxide content and global climate because the net effect of silicate weathering is the transfer of atmospheric carbon dioxide to bicarbonate. These weathering processes further influence atmospheric carbon dioxide due to a net transfer of dissolved silica to the oceans which promotes diatom production and sedimentation thereby adding carbon to the oceanic reservoir. There is a substantial body of evidence that suggests that plants may transform silica into more stable or labile forms thus acting as potential sinks or sources of silica thus influencing estimates of terrestrial weathering rates derived from riverine systems. To ascertain the range in variability we conducted research that investigates the changes in the biogeochemistry of silica along a bioclimatic gradient and soil chronosequence in grasslands of temperate regions. The goal of this research was to use a systematic approach to identify the possible effects of plant type and production on the losses, gains and compartmentalization of silica during soil development

Our results suggest that grassland ecosystems have considerable variation in biogenic silica production and storage as a function of landscape age and bioclimatic conditions In general our chronosequence studies suggest that Holocene aged soils of temperate grassland ecosystems have a net accumulation of silica while soils of Pleistocene age have experienced a net loss of silica. However, all soils in grassland systems across the chronosequence accumulate biogenic silica. In our studies that evaluated different grassland systems our results suggest that shortgrass steppe ecosystems have greatest accumulations of biogenic silica in soil and the lowest storage in biomass, whereas, tall grass systems have greatest biomass silica and lowest biogenic Si accumlation in soil. The silica transformations with each system are quite different and our data suggest that in wetter more productive grassland systems biogenic silica not removed from the system through leaching processes may be stored in the clay fraction of soils.

Phosphorous Biogeochemistry

We have sampled and characterized six alluvial terraces that date back to 600K years and are currently evaluating mineralogical and isotopic data. We are also applying our current working model of Holocene landscape development to this portion of the grasslands and have selected and sampled two stratigraphic sites that will allow us to evaluate a continuous record of Holocene paleoclimate in the eastern margins of the SGS.

The primary phosphate fraction (P_{Ca}) declines over time, from 75% of the total P at 2000 years to 50% at approximately 600,000 years. The occluded P fraction increases from around 7% of the total to 10% while organic P increased approximately 23% over time, with the highest value present at the EBL (350,000 years) site. Organic P rose 14% in the time period from 2ka to 10ka, a rapid initial increase that continued over time, reaches a maximum at about 190 ka to 300 ka, then begins to decline in Pre-Bull Lake time. The non-occluded P (labile inorganic pool) remained a very small percentage of the total P over time, with values ranging from 1 to 6%. Non-occluded P, increasing up to EBL and then declining, behaves similarly to the organic P fraction. Total P varies between sites but shows an overall declining trend over time.

3. Land-Atmosphere Interactions

Atmospheric-biogeochemical model

The application of the coupled atmospheric-biogeochemical model continues, with the plan to validate its skill at simulation using the observational data for different levels of grazing intensities and for different years. The comparison of the interaction between the atmosphere and the short grass steppe during the three years of data (which includes a serious 1 year drought) will be a major emphasis of the work. The role of land use type is also being investigated using the coupled modeling system.

DAYCENT modeling

We used DAYCENT to investigate the effects of elevated atmospheric [CO_2] on plant

growth, soil water levels, and soil respiration rates at the shortgrass steppe. Model results agreed with data collected from open top chamber plots at the shortgrass steppe showing higher NPP and higher soil respiration under elevated [CO_2] largely due to higher soil water contents for this treatment. In collaboration with a group from Australia using the G'DAY model, DAYCENT was applied to study long term effects of elevated [CO_2] and climate change for the shortgrass steppe, the tallgrass prairie, and a boreal forest. Results have been submitted to *Tellus* and included in the LTER book. DAYCENT simulations of N gas emissions from cropped and grazed soils for 27 counties in the Front Range of Colorado were compared with N emissions from industry and vehicles in the same counties.

Soil-atmosphere exchange of CH_4, CO_2, NO_x, and N_2O in the Colorado Shortgrass Steppe under Elevated CO_2

In late March 1997, an open-top-chamber (OTC) CO_2 enrichment study was begun in the Colorado shortgrass steppe. The main objectives of the study were to determine the effect of elevated CO_2 (~720 µmol mol^{-1}) on plant production, photosynthesis, and water use of this mixed C_3/C_4 plant community, soil nitrogen (N) and carbon (C) cycling and the impact of changes induced by CO_2 on trace gas exchange. From this study we report here our weekly measurements of CO_2, CH_4, NO_x and N_2O fluxes within control (unchambered), ambient CO_2 and elevated CO_2 OTCs. Soil water and temperature were measured at each flux measurement time from early April 1997, year round, through October 2000. Even though both C_3 and C_4 plant biomass increased under elevated CO_2 and soil moisture content was typically higher than under ambient CO_2 conditions, none of the trace gas fluxes were significantly altered by CO_2 enrichment. Over the 43 month period of observation NO_x and N_2O flux averaged 4.3 and 1.7 in ambient and 4.1 and 1.7 µg N m^{-2} hr^{-1} in elevated CO_2 OTCs, respectively. NO_x flux was negatively correlated to plant biomass production. Methane oxidation rates averaged -31 and -34 µg C $m^{-2}hr^{-1}$ and ecosystem respiration averaged 43 and 44 mg C $m^{-2}hr^{-1}$ under ambient and elevated CO_2, respectively, over the same time period.

II. INFORMATION MANAGEMENT

The SGS-LTER Information Management (IM) team accomplished their goals to focus more resources on information management. SGS-LTER now has the equivalent of a full time Information Manager who is assisted by many students with Computer Science majors who help design, develop, and implement new tools for the SGS-LTER database and web site. The flow of data and metadata were streamlined from the field to release on the web site. We have set new goals to accomplish during the next funding cycle, including the implementation of a more centralized and flexible IM system, participation in Network wide IM activities and continued professional development for IM staff.

SGS-LTER continues to participate in cross site and other community driven IM activities. Nicole Kaplan, Information Manager, participated in a DataBank workshop at The

Evergreen State College in May 2003 with 4 other Information Managers (IMs) from LTER sites (http://canopy.evergreen.edu/bcd/home.asp). At the workshop, IMs developed templates for database designs, statistical analysis and visualization tools for data collected on the growth of roots belowground. Other grassland ecology sites within the LTER Network that collect similar data will be able to implement these IM tools. IMs and Principal Investigators from the Jornada and Sevilleta sites are interested in continuing to develop these tools. Future workshops and a presentation at the 2003 All Scientists Meeting are being planned. In addition, SGS-LTER has contributed to a "data cooperative" to accelerate the sharing, standardization, completeness, and accessibility of data on the distribution and abundance of non-native plants, animals, and diseases across the United States. Strong partnerships between government and non-governmental organizations administratively housed in the U.S. Geological Survey's Fort Collins Science Center in Colorado have demonstrated the importance and success of data synthesis. Participants plan to present this project, which is part of the National Biological Information Infrastructure (http://www.nbii.gov/issues/invasive/home.html), at a data synthesis workshop at ASM in Seattle this September.

III. EDUCATION AND OUTREACH ACTIVITIES

REU Program

In 2002 we received funding for two REU students who completed research projects at the Shortgrass Steppe (SGS) LTER site. Two additional REU students funded through a separate NSF award to Drs. Keith Paustian and Gene Kelly participated in our REU activities and completed projects on the SGS. A fifth undergraduate student funded by the Department of Biology also participated in the SGS REU programs. All five students attended a weekly lecture and gave oral presentations of their work. Topics covered in the weekly meetings included: Database searches, What is science, How to write a scientific proposal, , Current issues in science, Ethics in science, Careers in science, and Gender issues in science. Students presented their proposals and their final results orally to the group, as well as to other members of the SGS-LTER community. Below is a short summary of each student's research project.

Linsdey Bach, Clemson University student (SGS-LTER-funded)

Ms. Bach worked with Dr. William Lauenroth to investigate the relationship between canopy reflectance in the visible and near infrared wavelengths and leaf area and biomass. Ms Bach worked on a site that has two radiometers: one in an cattle exclosure and one in a grazed pasture. The radiometers collect reflectance data every minute and a data logger stores hourly averages. Green and brown leaf area were estimated using the point frame technique and aboveground biomass by harvesting vegetation. The long-term goal of this work is to correlate satellite or aerial photo data with real vegetation data.

Katherine McAnelly, Colorado State University student (SGS-LTER funded)

Ms. McAnelly worked with Dr. Mike Antolin on black-tailed prairie dogs. Katie developed her

own study comparing the reactions of black-tailed prairie dogs in different habitats to different types of human disturbance. She hypothesized that prairie dogs living close to humans in urban areas would see humans as non-predators, while those living on the SGS may or may not have that view of humans. Katie observed prairie dog towns close to established human dwellings, those far from dwellings on the SGS, and those in a protected city park site. She subjected each town to disturbances from a bicyclist and a runner, and monitored the behavior of the prairie dogs. Her observations suggested that prairie dogs living near human activity adapt more readily to runners or bicyclists traversing their towns.

Ted Zbacnik and Derek Godsey, Colorado State University students (other NSF REU funding)

Mr. Zbacnik and Mr. Godsey investigated soil aggregate properties and soil organic matter fractions across a soils chronosequence on the Pawnee National Grasslands under the direction of Dr. Keith Paustian and Dr. Gene Kelly. Ted and Derek worked at locations east of the main CPER-LTER study site. Their objective was to examine soil aggregate and organic matter amounts and distribution across a soil chronosequence, where the main variable was believed to be soil age, and hence time of soil development. They found that aggregate distributions as a function of soil age were consistent with our hypothesis of increasing aggregation and stability as a function of soil age, but differences were less than originally anticipated. The results of this work have been presented as a poster at the ASA-CSSA-SSSA 2003 annual meeting in Denver, CO, and are included in a manuscript in preparation for *Geoderma*.

Andra Savage, Colorado State University student (Department of Biology funding)

Ms. Savage conducted population studies of four prairie dog towns on the SGS under the direction of Dr. Mike Antolin. For a two week period, pairs of observers counted prairie dogs within marked areas surrounding towns. Observations were done at the same time each dusk. Each town was counted by different pairs of observers to determine any observer biases. The final results indicated that the scoring and timing of the counts was independent of the observers, and that the counts are representative of the actual populations. Andra received assistance from Katie, Lindsey, and several other SGS-LTER students in counting above-ground animals at timed intervals. The protocol used in this project is that now being used by Dr. Antolin's group to monitor prairie dog populations during their study of plague outbreaks on the SGS.

Education

The SGS-LTER educational activities are coordinated through the Math and Science Teaching (MAST) Institute at the University of Northern Colorado. The projects support research for K-12 students, professional development for K-12 teachers, and research opportunities for science educators on various aspects of K-16 education.

Schoolyard Ecology: The project is funded by annual supplements to the SGS-LTER. Currently, funds are used to support programs at 7 schools in NE Colorado (1 elementary, 1 middle school, and 5 high schools). The programs include formal research plots to science fair programs.

Research Assistance for Minority High School Students (RAMHSS): The RAMHSS program works closely with the UNC Math and Science Upward Bound (COSMOS) and the UNC Frontiers of Science Institute (FSI) operated through MAST. In 2002-2003 23 supported nine students from the across the state of Colorado. Students are recruited for a six-week residence summer internship program, and for those living within commuting distance to UNC, an academic year research internship. Funds were used to house students, transportation to the site, graduate stipends for supervision, stipends and wages for the students, tuition monies for the credit that they earned, and supplies.

GK-12: The project is by NSF through the GK-12 program. The projects theme is "Human Impact Along the Front Range of Colorado." This dovetails nicely with current emphasis at the SGS-LTER. The SGS-LTER serves as a hub for the GK-12 project, in terms of research, faculty interaction, and graduate students. The GK-12 project supports 2 SGS-LTER graduate students and has adopted the LTER schoolyard ecology model.

CLT-W: The Center for Learning and Teaching in the West, funded by NSF through the CLT program, provides GRA appointments for graduate students, on-line course development for K-12 teachers and graduate students on topics ranging from traditional courses on teaching and learning theory, diversity and equity to practical topics such as lab and field safety. The CLT-W is developing a M.A. program in Natural Sciences for teachers. SGS-LTER scientists are assisting in the development of content courses in ecology, and will serve as advisors for prospective teachers.

Teachers on the Prairie: The project is funded by NSF through Teacher Enhancement grant to Portland State University, and patterned after the Teacher in the Woods program at PSU and the H.J. Andrews LTER. The project offers K-12 teacher professional development opportunities through workshops and research internship on topics germane to the SGS-LTER. Much of 2002-2003 was spent making contacts throughout NE Colorado and planning for the workshops, the first of which were planned for June 2003.