Annual Report 2004: Activities and Findings

This has been a year of building new collaborations within and among other institutions, while remaining focused on studying the structure and function of the SGS ecosystem and addressing broader scientific initiatives. This annual report provides a summary of our A) Research Activities, B) Information Management, C) Education, Outreach and Training Activities, and D) Project Management.

A) RESEARCH ACTIVITIES

During the last year, we produced 24 papers in refereed journals, three book chapters, two dissertations, and 15 abstracts from national and international meetings. **Twelve graduate students and 17 undergraduate students** (including five REU students) worked on research related to the shortgrass steppe LTER. We continue to sample our long-term projects, as well as initiating some new short-term experiments. Following are key research progress and results in each of our three core areas: population dynamics, biogeochemical dynamics, and land-atmosphere interactions.

1. Population Dynamics

Plants

<u>*Ecology and genetics of Linaria dalmatic*</u>*:* In 2001, we located patches of toadflax at the Central Plains Experimental Range (CPER) of different sizes with the objectives of studying the genetic relationships among plants and patches and the conditions under which toadflax could rapidly expand its population. The severe growing season drought of 2002 had no effect on data collection for the genetic analysis and a huge negative effect on field experiments, but provided an opportunity to evaluate how toadflax would respond to drought. Here we want to focus on the genetics results, but before doing so we want to mention that preliminary analyses suggest that while toadflax was negatively affected by the drought it 2002, patch density (number of tillers per patch) increased 30% during the more normal growing season of 2003.

The genetic analysis of toadflax patches entailed collecting plant material from 14 patches or populations. The analysis was accomplished using the inter simple sequence repeat markers (ISSR) genotyping approach. The questions we are interested in exploring in this part of the research are whether or not the plants in each population are all descendants of a single genotype suggesting that the populations began with a single individual and have spread vegetatively, and whether there are relationships among the 14 populations. Results to date indicate that the populations are composed of genotypically diverse individuals. This suggests that at least part of the population spread has been the result of sexual reproduction. Eleven of the populations are considered small, with fewer than 15 individuals. In these small patches, approximately 50% of the individuals have unique genotypes. The existence of different genotypes within a patch indicates recruitment by seeds rather than by clonal spread. Of the 14 populations, three related groups arise using a dendrogram. The geographic pattern of these groups suggests that grazing animals and/or vehicles are the likely modes of dispersal. The patterns do not seem to be related to patterns of wind and water movements suggesting those modes of dispersal are not the most important. Further, there is not a distance-based pattern to the relationships, again indicating wind and water dispersal may not be controlling dispersal. Additional data analysis and follow-up research will be required to identify the most likely dispersal mechanism.

Grazing Experiments: The long-term grazing experiment that was established in 1991, together with a LTER cross-site grant that constructed small-plus-large mammal exclosures, was one of seven grassland sites (3 sites in Utah, Konza, Cedar Creek, The Netherlands, and SGS) used to compare the effects of large and small herbivores on plant diversity. A reversal of herbivore impact on plant species richness from negative to positive over an increasing productivity gradient was found. However, the effect of herbivore grazing depended on body size. The positive effects at high production were mainly due to large herbivores, whereas the negative effects at low production were mainly caused by small herbivores. Results indicate that large herbivores increased plant species richness at high plant production through relieving subordinates from intense light competition and through selective grazing on dominant grasses. Small herbivores on the other hand reduced plant species richness presumably through selective grazing on subordinate forbs. Large and small herbivores had therefore predominantly compensatory effects on plant species richness. The productivity of the site determined whether the negative effects of small herbivores were outweighed by positive effects of large herbivores. Progress has been made on a second manuscript from this work on nutrient cycling.

The role of cactus in structuring grazed SGS plant communities was further analyzed (Rebollo et al. 2004), based on earlier sampling (Rebollo et al. 2002). Cattle do not graze inside cactus clumps, resulting in small refugia scattered across the grazed landscape. The study was conducted in eight long-term grazed pastures and their respective ungrazed controls that were established 60 yrs ago. Refuge effects were mainly influenced by grazing intensity, plant community productivity, and growth form of cactus. Heavy grazing intensities were necessary for some positive effects of cactus to manifest, and some refuge effects changed to negative effects under lower grazing pressure. Refuge effects increased with plant community productivity due to greater abundances of grazing-sensitive species, and greater grazing intensities in the more productive areas. Cover of cactus cladodes inside clumps appeared to be the main limiting factor for refuge effects, probably by limiting available space for grazing-sensitive species. Other factors such as size and density of cactus clumps, and the presence of large refuges in the proximity of clumps had minor influence in the effectiveness of cactus refuges.

CO_2 Experiment: Data from the CO_2 field experiment for root production and belowground tissue quality, and aboveground forage quality were compiled and two manuscripts submitted (Milchunas et al. 2004 a, b). Progress has also been made in compiling mini-rhizotron data from this experiment.

A modified root in growth method was developed to minimize destructive sampling in experiments with limited space, and used to estimate belowground net primary production and root tissue quality in a native semiarid grassland exposed to elevated CO_2 for five years. Increases in root production of over 60% were observed with elevated CO_2 during years of intermediate levels of precipitation, with smaller effects in a very wet year and no effects in a very dry year. Aboveground to belowground production ratios, and the depth distribution of root production, did not differ between ambient and elevated CO_2 treatments. Root soluble concentrations increased an average of 11% and lignin concentrations decreased an average of 6% with elevated CO_2, while nitrogen concentrations decreased an average of 21%. However, most tissue quality responses to CO_2 varied greatly among years. Estimates of root production by the ingrowth donut method were much lower than previous estimates in the shortgrass steppe based on ^{14}C decay.

The effects of elevated CO_2 on ruminant forage quality and nutrient yields were assessed during four years. CO_2 effects on forage soluble and fiber (celluloses, lignin) constituents were small, even though mid-growing season yield and end of season production increased. However, large negative effects of elevated CO_2 were evident in crude protein concentrations and digestibility of forages. While the effects were more negative mid-growing season than autumn, a reduction in already poor quality autumn forage may be more critical to animals. Crude protein concentrations of autumn forage on the elevated CO_2 treatment fell below critical maintenance requirements 3 out of 4 years, compared to 1 of 4 for ambient and control treatments. Forage digestibility declined 14% mid-season and 10% in autumn with elevated CO_2 Low protein and digestibility can slow passage through the rumen and inhibit voluntary intake. Negative effects of elevated CO_2 on animal performance mediated through forage quality are likely to be greater than the positive effects of increased quantity, because quality drops to critically low levels that can inhibit utilization. Further, elevated CO_2 shifted the proportional availability of protein and energy to a species of lower overall quality and the species most negatively affected by drought. Current-year defoliation increased both quality and production of protein and energy compared to non-defoliated plots, but no CO_2 by grazing treatment interactions were observed. Nitrogen fertilization increased crude protein concentrations and digestibilities, but not in the least nutritious species that increased with elevated CO_2 or in autumn when quality was lowest, but fertilization results were limited to dry years.

Animals

Mountain Plover Habitat: This year we initiated a new project related to current SGS-LTER interests, in addition to continuing our long-term studies of mammal populations, which are entering their 10th year of field sampling. We began field sampling on a project to determine whether grazing and varying degrees of grazing intensity can be used to create habitat for the threatened Mountain Plover. In addition, we are monitoring the biogeochemical properties (C and N), soil moisture and surface characteristics of the experimental plots to determine the broader environmental impacts. We began studies of small mammal and arthropod populations in other plots with similar grazing intensities last summer, and continued the project through the 2004 season as part of our supplement request.

The Ecology of Plague in Prairie Dog Colonies in northern Colorado: We began field research on the project in May 2004, which includes sampling and testing for plague in small mammals and fleas in prairie dog colonies with different histories of plague. We recently published a paper on this research in *Frontiers in Ecology and the Environment* (Stapp et al. 2004).

Outbreaks of many vector-borne human diseases are broadly correlated with climatic variation, but evidence of similar fluctuations in disease in natural host populations is rare. Here, we use 21 years of monitoring of black-tailed prairie-dog (*Cynomys ludovicianus*) colonies in northern Colorado to demonstrate a link between extinctions of colonies attributed to plague (*Yersinia pestis*) and climatic fluctuations associated with El Niño Southern Oscillation events that promote the growth of flea vector and rodent host populations. Logistic regression revealed that rates of extinction of the largest colonies (>16 ha) during epizootics were nearly as high (>60%) as for the smallest ones (<3 ha), whereas only a third of intermediate-sized colonies were extirpated. The probability of extinction was influenced by the size and fate of nearby colonies, but there was no predictable relationship between extinction probabilities and inter-colony distance, indicating that spatial isolation may not reduce the vulnerability of colonies to plague. By causing sporadic extinctions of colonies, plague creates a metapopulation structure that has altered the dynamics of prairie-dog colonies as they respond to a century of human persecution and habitat loss.

Belowground foodweb interactions on Black-tailed prairie dog mounds on shortgrass steppe: There are two main components of this research in prairie dog ecology. 1) this year, an initial examination on prairie dog colonies was conducted in order to identify types of landscape effects with respect to prairie dog activity on belowground food web interactions. 2) in years two and three, the goal is to differentiate changes in belowground food web interactions at the microcosm level within inactive and active prairie dog mounds. Specifically we are examining variations among different type of mounds (crater, dome and other) within inactive and active areas of two black-tailed prairie dog towns located on the Pawnee National Grasslands (PNG).

This study has been taking place on the CPER and the Pawnee National Grasslands (PNG) in Nunn, CO. Six sites were chosen for year one sampling (three on CPER and three on PNG). Due to landscape variations observed in year one data, we will sample exclusively on PNG for years two and three, sites 69 and 79.

Preliminary data of fungal hyphal densities from year one indicates that not only are there seasonal differences among the sites but there is also a block effect indicating a possible landscape effect. (Wyant et al., 2004). Since the data from year one indicated an effect from the landscapes on both the PNG and CPER, years two and three will be devoted to an examination on-and-off mound exclusively on the PNG. The overall goal of this study is to obtain a better understanding of the effects of prairie dog activity on productivity and trophic structure in belowground food webs. An examination directly on and off the various types of prairie dog mounds (dome, crater, and other) will help isolate these interactions. In year two (2004) we are continuing, in coordination with the LTER field crew, to locate mounds on the PNG through the GPS system. We sampled mounds in May, 2004, and plan to sample in Oct. 2004, May and Oct. 2005.

Prairie Dog – Vegetation Interactions: Since 1997, we have estimated peak aboveground plant biomass annually from on and off each of five black-tailed prairie dog (*Cynomys ludovicianus*) colonies that had been inhabiteded for 3-5 years when the study was initiated.. Over the course of the study, mean biomass of the dominant grass, *Bouteloua gracilis*, has been about 30% lower on prairie dog colonies than at off colony sites. In contrast, over the same period, forb biomass on the active prairie dog colonies averaged nearly three times more than off the prairie dog colonies. These trends towards lower grass biomass and greater forb biomass on prairie dog towns are in the same directions as those observed in mixed grass prairie. However, the magnitude of the differences between on and off town sites were considerably less in the shortgrass steppe, supporting the notion that the shortgrass steppe is highly adapted to grazing. Late in 1998 and early in 1999, prairie dogs in two of the colonies died off, apparently from plague. Since then, graminoid biomass on the extinct prairie dog colonies has increased to values similar to those off the colonies, and forb biomass on extinct colonies had decreased to values similar to those off the coloniess. These results suggest that the effects of prairie dog grazing on aboveground plant biomass are reversed quickly following their disappearance at our shortgrass steppe site.

A related study was initiated during summer, 2002, and is continuing through the 2004 field season. The objective of this study is to determine the time course of vegetation change and nutrient dynamics following colonization or abandonment by prairie dogs. We are monitoring plant biomass, species diversity, N concentratrion, and N supply rates on and off prairie dog colonies of different ages. Three colonies were about four years old in 2002 ("young colonies"), three were >15 years old in 2002 ("old colonies"), and three had recently died off from plague in 2002 ("extinct colonies"). Averaged across 2002 and 2003, aboveground grass biomass was 38-40% as great on the new and old colonies as their off colony control sites. Biomass on extinct colonies was 76% as great as at their control sites, again indicating that vegetation rebounds quickly following loss of prairie dogs from the system. Soil N supply rates were not different on and off prairie dog colonies, regardless of whether active or extinct.

Because prairie dogs change vegetation towards higher herbaceous dicot coverage, reduced canopy height, and increased bare ground, we initiated a new study in 2003 to evaluate the consequences of such changes on insect pollinator populations and assemblages. Prairie dog colonies represent large patches within the shortgrass steppe matrix that contain a higher density of floral resources, which pollinating insects may perceive or utilize as a different habitat type. In the first of three consecutive years of study, four large colonies and paired off-colony areas were sampled for floral resources and insect visitation rates. In May – July, 2003, approximately twice as many inflorescences and open flowers were found on colonies as off. Concomitantly, over two times more insect visitors were observed foraging on the colonies during the same period. Both of the dominant pollinator orders in this system, Hymenoptera and Lepidoptera, were observed foraging 2-3 times more frequently at on-colony sites. The Hymenoptera, but not the Lepidoptera, showed differing relative abundances and community structure on-colonies compared to off-colonies. These data suggest that prairie dogs may be an important driver of patch heterogeneity in this system, and affect floral resources that influence pollinator abundance and community structure on the shortgrass steppe.

2. Biogeochemical Dynamics

Biogeochemistry of Silica in Grasslands: On land, most silica is stored in relatively inert mineral forms. However, a substantial body of evidence suggests that higher plants create a highly dynamic and biogeochemically important reservoir of biogenic silica In terrestrial environments, most biogenic silica takes the form of plant opal phytoliths, micron-size bodies of silica precipitated within plant tissues mainly around stomatal cells. Recent estimates suggest that the global uptake of biogenic silica stored in the terrestrial biomass ranges from 60 to 200 Tmol yr^{-1} and rivals quantities stored in the biologically active portions of the ocean systems. Importantly, the *largest* reservoir of biogenic silica in terrestrial systems resides not in living biomass but in soils, as biogenic silica is deposited upon death and decomposition of the plant materials. Estimates of biogenic silica stored in soils are 500 to 10,000 times greater than above-ground annual uptake, with grassland ecosystems occupying the higher range of these estimates. This large, but currently poorly defined, reservoir of biogenic silica is potentially of great importance in global biogeochemical cycles.

Preliminary results for this year were obtained by sampling and characterizing biogenic Si from a published bioclimatic gradient in the Great Plains of North America (McCulley et al, 2005). Our initial results show an increase in annual net primary production (ANPP) with increasing mean annual precipitation (MAP) as vegetation changes from short grass steppe to mixed grass prairie to tall grass prairie systems. With increasing ANPP biogenic silica stored in the above ground materials increase as expected. Biogenic silica storage in the soils is inversely related to aboveground production suggesting transformations or loss of this biogenic material occurs at higher MAP zones. These results suggest that grassland ecosystems have considerable variation in biogenic silica production and storage as a function of bioclimatic conditions. In general Holocene aged soils of temperate grassland ecosystems have a net accumulation of biogenic silica. 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 silica accumulation in soils.

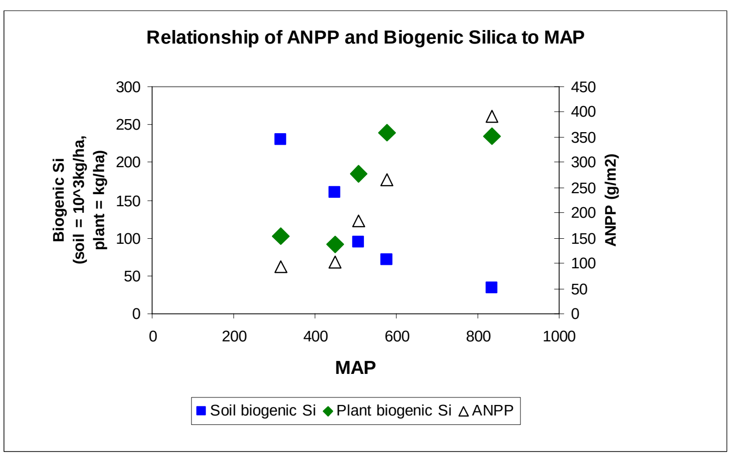

Figure 1. The Production and Biogenic Silica along a) bioclimatic gradient. Biogenic Silica in soils (squares); b) Biogenic Silica in plant material (diamonds) , c) ANPP (triangle) adapted from McCulley et al, 2005.

As a preliminary set of observations, we obtained Ge/Si data from soil size fractions and soil, stream and well waters from several sites within the LTER framework. Ge/Si in size fractions show highest ratios in the clay fraction. Lower values in the silt and sand fractions primarily reflect the presence of quartz, which typically has Ge/Si ≤ 1, but also probably contain some feldspar with intermediate Ge/Si.

Phytoliths extracted from local grass species have Ge/Si from ca. 0.2 to 0.4 µmol/mol. Soil waters (saturation pate method, equilibrated for 7 days) have Ge/Si much lower than that of bulk soils or any of the soil size fractions, but close to that of the plant phytoliths. The low Ge/Si values for soil water could reflect either the production of low Ge/Si fluids to balance high Ge/Si clays produced during weathering reactions, or direct dissolution of biogenic silica. We hypothesize that, in most cases, biogenic silica will be the source of low Ge/Si soil solutions. We can test this hypothesis by making major element and Ge/Si measurements on separated soil minerals and of coexisting waters. Major element and Ge/Si mass balances will permit a direct estimation of Ge/Si produced by mineral reactions (as described for the Luquillo regolith study). These results will be compared to the Ge/Si in soil solutions. We predict that mineral transformations (such as feldspar or mica to clays, or dissolution of quartz) will produce dissolved Si with a higher Ge/Si (ca. 0.6 to 1.0 µmol/mol than direct dissolution of biogenic opal (0.2 to 0.4 µmol/mol). These predictions are directly testable using the coupled elemental and Ge/Si mass balances. We will separate and analyze mineral fractions by density fractionation, electromagnetic separation, and hand picking. XRD, TGA and elemental data from the < 2µm fraction will be used to determine the identity and abundance of clay minerals. Ge/Si and major element analysis of the quantitatively important mineral species will be used with co-existing soil solution data to determine the contributions of silica and Ge/Si from weathering reactions. Analysis of phytoliths and soil solutions from zones dominated by biogenic silica will determine the Ge/Si characteristics of biogenic silica dissolution.

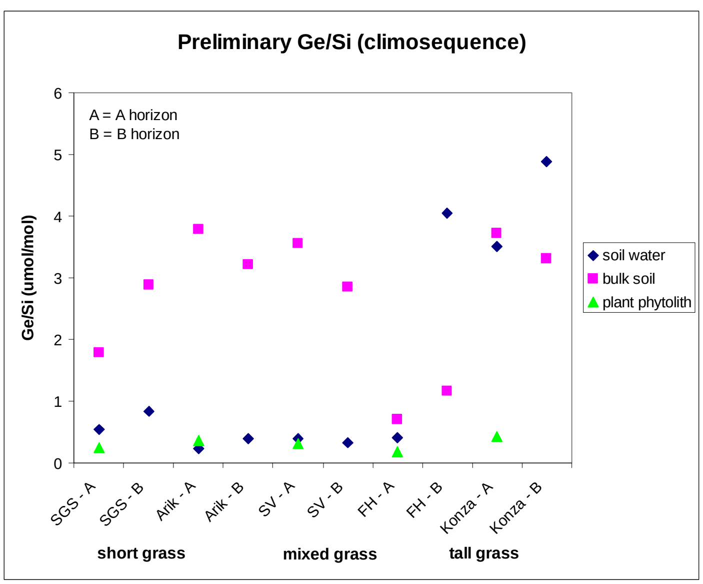

Figure 2. Ge/Si ratios along bioclimatic gradient in Great Plains. Ge/Si ratios of a) bioclimatic gradient. Biogenic Silica in soils (squares); b) Biogenic Silica in plant material (diamonds) , c) ANPP (triangle) adapted from McCulley, 2002.

Once we have established the sources of Si in the grassland soil waters, we can use this information to estimate the proportion of stream export of Si from biogenic sources. Preliminary water data from streams at the Konza site yield a mean Ge/Si = 0.28 µmol/mol (std. dev. = 0.08, n=11), while well waters have mean Ge/Si = 0.65 µmol/mol (std. dev. = 0.10, n = 6). The low values from the stream waters strongly suggest that biogenic Si is a major component of stream export from the Konza site, while the higher values from well waters imply that mineral dissolution reactions may be the dominant source of dissolved Si in deep groundwaters, well-removed from the biologically active part of the soil. Once the Ge/Si characteristics of the mineral and biogenic sources are defined, it is relatively straightforward to determine the fractions of each which contribute to stream export (as in our work in Hawaii). The key is to combine careful measurements of the relevant phases with simple reaction modeling to establish how mineral and biogenic silica reactions contribute Si and Ge to solution. We note that we have carried out all the relevant measurements at other study areas – we have direct experience with both the analytical and modeling methods.

An important result from this part of the study will be the first estimate of the importance of biogenic silica sources in the export flux from grasslands, across a range of modern climates. We anticipate that biogenic silica will prove to be the dominant source of the export flux from grasslands, as we found for tropical forested watersheds in Hawaii, but for different reasons. While Hawaiian soils are silica poor, permitting a modest biogenic pool to play a large role, the grassland soils we sill study are not silica poor, and have a very large biogenic pool. These hypotheses are fully testable with the data we plan to collect.

Interannual and regional patterns in C cycling of grasslands: The large organic carbon (C) pools found in non-cultivated grassland soils suggest that historically these ecosystems have had high rates of C sequestration (McCulley et al, 2005). Changes in the soil C pool over time are a function of alterations in C input and output rates. Across the Great Plains and at individual sites through time, inputs of C (via aboveground production) are correlated with precipitation; however, regional trends in C outputs and the sensitivity of these C fluxes to annual variability in precipitation are less well known. To address the role of precipitation in controlling grassland C fluxes, and thereby soil C sequestration rates, we measured above- and belowground net primary production (ANPP-C and BNPP-C), soil respiration (SR-C), and litter decomposition rates for two years, a relatively dry year followed by a year of average precipitation, at five sites spanning a precipitation gradient in the Great Plains. ANPP-C, SR-C, and litter decomposition increased from shortgrass steppe (36, 454, and 24 g C m^{-2} yr^{-1}) to tallgrass prairie (180, 1221, and 208 g C m^{-2} yr^{-1} for ANPP-C, SR-C, and litter decomposition respectively). No significant regional trend in BNPP-C was found. Increasing precipitation between years increased rates of ANPP-C, BNPP-C, SR-C, and litter decomposition at most sites. However, regional patterns of the sensitivity of ANPP-C, BNPP-C, SR-C, and litter decomposition to between year differences in precipitation varied. BNPP-C was more sensitive to between year differences in precipitation than the other C fluxes, and shortgrass steppe was more responsive than mixed grass and tallgrass prairie.

Long Term Study of Land Use on N Retention: Using supplement money from NSF we re-sampled permanent ^{15}N addition plots originally established in 1988 in both grazing and dryland agricultural experiments located in northeastern Colorado. The main objective of this re-sampling effort was to assess the effects of land use (i.e., grazing and cropping regime) and topographic position on soil N retention. The re-sampling occurred in mid-May 2003 and consisted of taking one randomly placed soil core from within the permanent plots, sectioning the core longitudinally into 0-10 cm and 10-30 cm depth increments, and processing the depth increments for particulate organic matter (POM), ^{15}N, and %N. In both the grazing and agricultural treatments, majority of the ^{15}N remaining 15 years after the initial application resided in the top 0-10 cm of soil. At the SGS-LTER, heavy grazing significantly reduced soil N retention (0.78 g ^{15}N m^{-2} in heavy grazing areas versus 1.05 g ^{15}N m^{-2} in ungrazed, p-value = 0.0181). Both the coarse (> 53 µm) and fine (< 53 µm) POM size classes retained similar quantities of ^{15}N. Despite differences in soil texture between upland summits and lowland footslopes at this site, there were no significant differences in soil N retention related to topography. At the dryland agricultural sites, more ^{15}N was retained in fine versus coarse POM fractions in both depth increments. Despite no-till practices being implemented at these sites, cropping regimes of wheat-fallow (WF), wheat-corn-fallow (WCF), and wheat-corn-millet-fallow (WCMF) all had significantly less ^{15}N retained in the soil than the treatment of planting perennial grasses (0.41, 0.37, and 0.52 g ^{15}N m^{-2} in WF, WCF, and WCMF, respectively, versus 1.85 g ^{15}N m^{-2} in perennial grasses, p-value < 0.001). Moreover, there were no significant differences between the various cropping intensities (WF, WCF, or WCMF). Heavy grazing and rotational cropping increased losses of ^{15}N by 27 and 23.4%, respectively, over levels experienced in the ungrazed and perennial grass treatments. These results indicate that land use management decisions play a primary role in determining the ability of shortgrass steppe to retain N.

The effect of urbanization on Shortgrass steppe ecosystems: Urban ecosystems are expanding globally and a mechanistic understanding of the ecological consequences of urbanization is critical to understanding the biology of global change related to land use. We measured carbon (C) fluxes, nitrogen (N) cycling, and soil microbial community structure in a replicated (n = 3) field experiment comparing urban lawns to irrigated corn, dryland wheat-fallow, and unmanaged shortgrass steppe ecosystems in northern Colorado (Kaye et al, submitted). Aboveground net primary productivity in urban ecosystems (383 $\pm$ 11 C m^{-2} y^{-1}) was four to five times greater than wheat or shortgrass steppe, but significantly less than corn (537 $\pm$ 44 C m^{-2} y^{-1}). Soil respiration (2777 $\pm$ 273 g C m^{-2} y^{-1}) and total belowground C allocation (2602 $\pm$ 269 g C m^{-2} yr^{-1}) in urban ecosystems were both 2.5 to 5 times greater than any other land-use type. We estimate that for a large (1578 km^2) portion of Larimer County, Colorado, urban lawns occupying 6.4% of the land area account for up to 30 % of regional ANPP and 24% of regional soil respiration from land use types that we sampled. Managed biomass N fluxes were comparable in urban and corn ecosystems (~ 12 to 15 g N m^{-2} y^{-1}), but most urban biomass management enhanced internal N cycling while corn harvesting resulted in large N exports. A one-time measurement of microbial community structure via phospholipid fatty acid analysis suggested that land-use types had a large impact on microbial biomass and a small impact on the relative abundance of broad taxonomic groups of microorganisms. Our data are consistent with several other studies suggesting that urbanization of arid and semi-arid ecosystems leads to enhanced C cycling rates that alter regional C budgets.

Effect of cropping in the Great Plains on carbon dynamics: Land use and altered carbon dynamics are two of the primary components of global change. Consequently, the effect of land use on carbon cycling is a crucial issue in regional scale biogeochemistry. Previous studies have shown that climate and soil conditions control net primary production (NPP) at regional scales, and that agricultural land-use can influence NPP at local scales through altered water availability and carbon allocation patterns. However, few studies have attempted to quantify the effect of cultivation on NPP at regional scales, and no studies have examined this relationship for the most heavily cultivated region of the U.S.: the Great Plains. We quantified (Bradford et al., submitted) current regional above- and belowground productivity (including cultivation) for nine years on a county basis from two sources: 1) USDA agricultural census data and 2) STATSGO range site production values. By comparing these data with values of native vegetation NPP (pre-cultivation) derived from STATSGO, we estimated that cultivation is increasing regional NPP by approximately 10%, or 0.046 Pg C $year^{-1}$. In addition, we examined the relationship between cultivation of particular crops and NPP change between counties and characterized the influence of individual crops on primary productivity.

Controls over ecosystem processes: the role of land-use: Identifying the conditions and mechanisms that control ecosystem processes is a central goal of ecosystem ecology. Ideas have ranged from single limiting-resource theories to co-limitation by nutrients and climate, to simulation models with edaphic, climatic and competitive controls. Although some studies have begun to consider the influence of land use practices, especially cropping, few studies have quantified the impact of cropping at large scales relative to other known controls over ecosystem processes. We utilized a 9-year record of productivity, biomass seasonality, climate, weather, soil conditions and cropping in the U.S. Great Plains to quantify the controls over spatial and temporal biomass patterns and estimate sensitivity to specific driving variables. We considered climate, soil conditions and long-term average cropping as controls over spatial patterns and weather and interannual cropping variations as controls over temporal variability. We found that variation in primary production is primarily spatial, whereas variation in seasonality is more evenly split between spatial and temporal components. Our models explained more of the variation in primary production than in seasonality, and more of the spatial than the temporal patterns. Our results as reported in Bradford et al. (submitted) indicate that although climate is the most important variable for explaining spatial patterns, cropping explains a substantial fraction of the residual variability. Soil texture and depth contributed very little to our models of spatial variability. Weather and cropping deviation both made modest contributions to the models of temporal variability. These results suggest that the controls over seasonality and temporal variation are not well understood. Our sensitivity analysis indicates that production is more sensitive to climate than to weather and is very sensitive to cropping intensity. In addition to identifying potential knowledge gaps, these results provide insight into the probable long- and short-term ecosystem response to changes in climate, weather, and cropping.

Water Use by Woody Plants: We examined whether limber pine and skunkbush sumac individuals co-existing on the Pawnee Buttes of northeastern Colorado have the ability to access and utilize deep soil water resources. The $\delta^{18}O$ signature of source water to the plants (deep soil water and precipitation) and plant cell water were measured in June 2000. The $\delta^{18}O$ signatures of the two woody plant species were not significantly different from each other. However, the average $\delta^{18}O$ signature of skunkbush sumac (-9.4‰) differed from the $\delta^{18}O$ signature of deep soil water (-13.0‰), while the average $\delta^{18}O$ signature of limber pine (–11.3‰) did not. Variability in the $\delta^{18}O$ signature across plots and between individuals within a plot was relatively high for both species. These results suggest limber pine and some individuals of skunkbush sumac are able to access and utilize deep soil water resources at this site. This ability may confer an ecological advantage to these plants given the semiarid climate of the site. This paper is in press in American Midland Naturalist (Roberts et al., 2004).

3. Land-Atmosphere Interactions

Grazing Intensity Research: The final year of a grazing intensity study was completed in 2003 in which a Bowen ratio/energy balance (BREB) micrometeorological system was utilized to monitor CO_2 fluxes to investigate the effect of heavy grazing (75% forage removal) by cattle vs. the recommended grazing pressure (40% removal) and an ungrazed pasture. The study was conducted from 2001 through 2003, a period of drought for the experimental site at the CPER. Annual CO_2 fluxes indicated a net gain of C in years 2001 and 2003 for all grazing intensities, but losses of C in the heavily-grazed pasture in 2002, the driest year of the study when only 50% of the long-term MAP was received. These results support previous work that suggest the SGS is resilient in the long-term to grazing, but also indicate that 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.

A new grazing intensity study was initiated in 2003 to evaluate the responses of shortgrass steppe vegetation and soils to extreme over-grazing, and also as an exploratory management option for the creation of Mountain Plover habitat. The Land Atmosphere Group is focusing on the effects of these grazing practices on energy, water and CO_2 fluxes. An additional aspect of this investigation is to evaluate different technologies for monitoring CO_2 fluxes. BREB stations were established in pastures with current recommended moderate grazing practices (the Control; approximately 40 % forage removal), a heavily spring-grazed pasture, and a season-long heavily-grazed pasture. On the Control, moderately-grazed pasture, year-round CO_2 fluxes are also being measured with an eddy covariance tower by collaborator Peter Blanken (CU, Boulder), plus periodic chamber measurements of CO_2 fluxes are being undertaken to compare with the BREB and eddy covariance fluxes. Energy, water and CO_2 fluxes from these towers on the shortgrass steppe will be compared to results obtained from micrometeorological flux towers established in near-by Conservation Reserve Program (CRP) and cropped shortgrass steppe agro-ecosystems.

UV radiation Experiment: Potential changes in levels of UV radiation are another aspect of climate change. As an extension of the CO_2 experiment, plant materials grown under the ambient and elevated treatments of different quality were decomposed in a field experiment using shelters that blocked or passed UV radiation (King et al. 2003). Wet and drought year precipitation scenarios were applied under the shelters, whereby abiotic (photo-oxidation) versus biotic components of decomposition could be assessed. Production plots were also established, because UV radiation can affect plant growth and the production of UV-blocking compounds that are allelopathic. Subplots were either non-defoliated or defoliated to simulate grazing by livestock (Milchunas et al. 2004).

Litter decomposition was affected by UVB exposure, the CO_2 growing conditions, and precipitation level. Under dry conditions, UVB radiation tended to increase litter decomposition, as measured by mass loss. There were no clear initial effects of UVB treatment on soluble and fiber constituents of litter. Litter arthropod density was lower with exposure to UVB and also lower under drought conditions. Microorganisms and fungal hyphae were not affected by UV treatment.

Productivity and seasonal standing biomass of the dominant grass species were negatively affected by passing versus blocking UV, but only in the dry year. Another species was negatively affected by passing UV in the wet year, indicating the potential for future shifts in species composition. Forage quality for ruminants increased when UV was passed compared to blocked, as determined by *in vitro* digestible dry matter, depending on species and precipitation. Nitrogen concentrations and soluble and fiber components of vegetation also displayed some UV effects, but they were generally small and depended on species, season and/or amount of precipitation. Grazing treatment had large positive effects on current-year productivity only in the wet year, and some small positive effects on quality in both wet and dry years. Interactions between UV and grazing treatment were not observed.

Paleopedology/paleoecology: The parent material of the eolian aggradational part of the SGS area is loess with large areas of stabilized sand dunes. Our sampling this year focused on a wide array of loess deposits. Throughout eastern Colorado, northern Kansas, and western Nebraska three major loess units have been recognized: the Gilman Canyon Formation, Peoria, and Bignell loess. Beecher loess, an additional late glacial unit, is recognized in eastern Colorado. Peoria loess, which is younger than the Gilman Canyon, but older than the Bignell was deposited in western Nebraska between about 25,000 and 14,000 OSL yr BP. Bignell loess, the youngest recognized in this region, is Holocene in age and was deposited starting approximately 11,000 to 9,000 yr BP and deposition continued episodically until less than 1000 yr BP. Bignell loess traditionally has been thought derived from floodplain sources, in part from the alpine glaciers in the Rocky Mountains, but new work demonstrates that Bignell loess is thickest downwind of inactive dune fields, strongly suggesting that Bignell loess resulted from climatically driven episodes of Holocene dune activity.

We have sampled a well-dated sequence of Holocene Paleosols along a precipitation gradient from the shortgrass steppe to the mixed grass praire (Figure 3) and will utilize the stable isotope signatures of soil organic matter and biologically produced minerals (carbonates and Phytoliths) and determine their paleoenvironmental significance. We are utilizing a more precise technique for documenting changes in the biotic composition of these regions. Our new approach is to utilize the carbon isotopic compositions of specific biomarkers (“compound specific isotope analyses”, CSIA) derived from higher plants. We will extract and measure the carbon isotopic compositions of long-chain *n*-alkanes and lignin phenols from modern soil and paleosols to evaluate the organic carbon input from vascular plants.

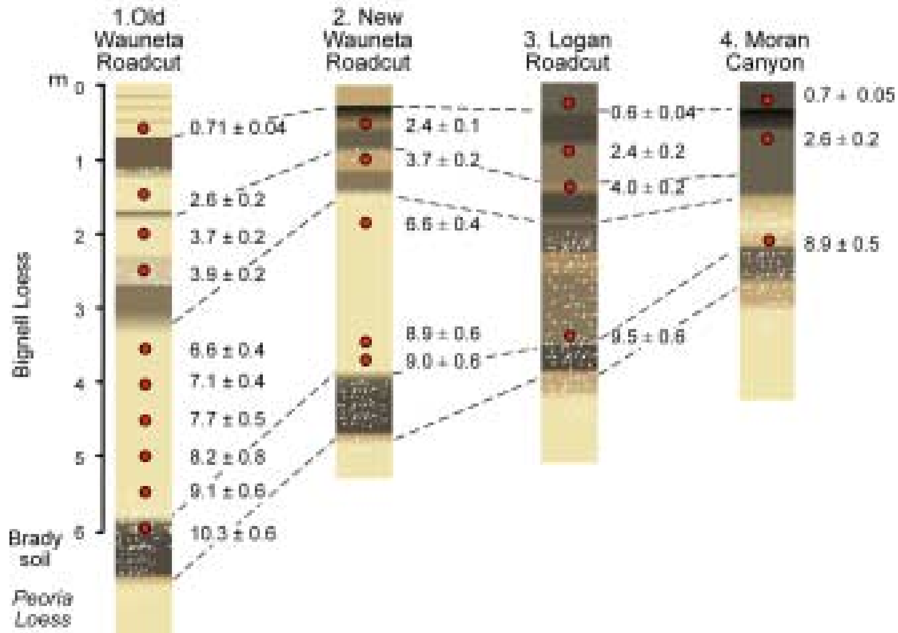

Figure 3. The sequence of paleosols sampled in 2003-2004 for paleoclimatic studies.

4. Integrated and Synthetic Research

<u>*Detritus, Changes in Below-ground Allocation and Food Web Stability:*</u> Human activities alter the availability of labile SOM and shift the plant community towards weedy species or accelerates root growth and turn-over (narrows C:N ratios of SOM and plant materials). We predict that areas liberated from cattle grazing and the extinction of prairie dogs will induce a shift in nutrient cycling and community structure towards the fungal "slow" pathway, while areas that are newly grazed and/or recently colonized by prairie dogs will shift toward the bacterial "fast" pathway (Figure 1) We expect that an analysis of the models developed for each site will reveal that sites that retain nitrogen will be more likely to be dynamically stable than sites that retain less nitrogen (Figure 2). A prediction from the hypothesis is that native sites will possess soil food webs that are dynamically more stable than occupied sites, and that after plague epizootics remove prairie dogs, those sites will quickly converge in community composition to the native sites. The ideas are presented in Moore et al. 2003 and Moore et al. 2004.

Figure 1

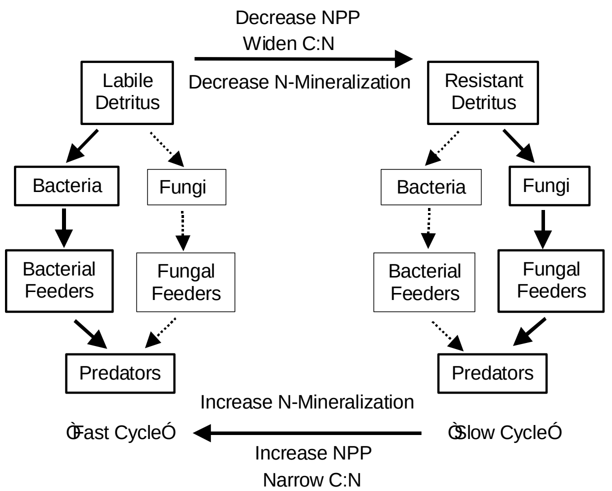

Figure 1. The soil food webs are compartmentalized into three interactive pathways – the root, bacterial and fungal energy channels. Empirical studies at the Toolik Lake and elsewhere have demonstrated that disturbance can induce changes in the relative flow of nutrients through these pathways and nutrient retention (Doles 2000, Moore et al 2003).

Figure 2

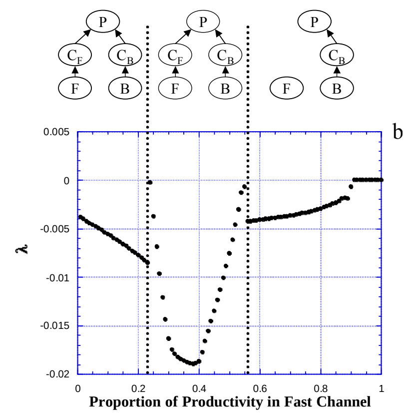

Figure 2. Simulations where the relative proportions of nutrients through the fungal and bacterial channels were altered. Stability is indexed by the most negative eigenvalue, λ. The more stable region occurs when neither the bacterial or fungal energy channel is dominant (Moore et al. 2004)

B) INFORMATION MANAGEMENT

The information management (IM) team at the Shortgrass Steppe LTER is composed of a full-time data/information manager, a part-time GIS technician and programer, and a part-time programer, systems and server manager. In the past year the IM team has focused on updating information technology (IT) equipment and systems, as well as data and information to support local and Network-wide research. In addition, the team is strengthening partnerships with other LTER and ecological research sites to leverage expertise and experience in database management, web development, and ecological metadata language (EML) implementation. We have supplied our field station and technical staff with new desktop, laptop and handheld computers to serve a growing number of scientists and students in residence. Mobile equipment and a distributed network of data loggers are used to collect data from study sites in the field. There is connectivity from the field station to the new SGS-LTER information network server on campus so data can be captured and backed-up in the system within twenty-four hours of collection and entry. We are revising legacy data quality control programs, originally composed in Fortran, for many of our data tables that support vegetation research and relate to over 60% of our studies. Our GIS technician/programmer has expanded this suite of programs, which we call the Matrix, to process meteorological data for submission to CLIMdb (http://www.fsl.orst.edu/climdb/). The SGS-LTER IM team will continue to work with researchers to develop tools that will more efficiently process and publish their data with high integrity. We have organized the GIS library and are developing search tools for spatial data discovery.

Our data manager continues to work closely with researchers and students to update the SGS-LTER and network-wide databases. Nine new data tables relevant to prairie dog and regional biogeochemical research were published on the SGS-LTER website (http://sgs.cnr.colostate.edu/Data/AcquisitionPlcy.htm). CLIMdb also was updated with SGS-LTER meteorological data from two weather stations. Our data manager continues to investigate and acquire more robust metadata content for legacy data sets to archive and create documents in EML. Our IM team has tested several tools that have been developed within the ecoinformatics community to create EML, including Morpho 1.5 (NCEAS), an EML MS Excel Spreadsheet Template (FCE), and an EML Relational Database Management System (RDBMS) conceptual model (Blankman, LNO). David Blankman and Marshall White from the LTER Network Office (LNO) visited the SGS-LTER IM office in October of 2003 to help our efforts to generate EML and improve the SGS-LTER website by making information more accessible and manageable. LNO staff and SGS-LTER IM team members discussed the importance of creating EML, improving access to information on LTER web sites, and partnering with sister sites and LNO staff to leverage expertise across the ecoinformatics community.

The IM team has focused their efforts to generate EML on redesigning and retrofitting the existing RDBMS to support EML implementation. The current RDBMS contains the necessary metadata to support the implementation of the “datatable” module of EML. However, these metadata are not related or normalized within the RDBMS. In the past, the SGS-LTER RDBMS was designed to support the logistical procedures necessary to approve applications to conduct experiments and manage project level information over time. Currently, this project level and dataset level information is published discretely using functions in the database and website. The IM team is working to establish new relationships between the tables that contain the necessary information to create a valid EML document. The IM team is exploring ways to generate XML from the more integrated RDBMS design and then convert this XML to EML using style sheet tools. In addition, we are working on GIS metadata documentation procedures and tools to generate EML.

We continue to collaborate with Judy Cushing and others at the Evergreen State College, information managers at other LTER sites, Kristin Vanderbilt (SEV), Ken Ramsey (JRN), Eda Meléndez-Colom (LUQ), and Jonathon Walsh (BES) on the Canopy Databank Project (http://canopy.evergreen.edu/). They will be presenting a poster at the Ecological Society of America 2004 meeting in Portland, entitled *Database Tools for Ecological Data Integration and Synthesis*. One focus of their work has been designing databases to integrate and synthesize annual aboveground primary production data from three grassland LTER sites that are employing different methodologies to measure productivity. Our information/data manager, Nicole Kaplan, remains closely connected to the LTER IM community as a member of the IM Executive Committee. She participated in several IM workshops this year, including the use of Web Services to integrate datasets, sponsored by the LNO and San Diego Supercomputer Center, and co-authored an article about the workshop in the Spring 2004 LTER Network Newsletter (http://intranet.lternet.edu/archives/documents/Newsletters/NetworkNews/spring04/spring04_pg06.htm).

C) EDUCATION, OUTREACH AND TRAINING ACTIVITIES

REU: We sponsored one REU student last fall, Karl Wyant from the University of Northern Colorado. He worked with Dr. John Moore to study fungal hyphal densities in new, old and extinct prairie dog colonies. His data serve as the first year of a longer term study (see the section above on *Belowground foodweb interactions on black-tailed prairie dog mounds on shortgrass steppe*) and have shown seasonal differences among the sites and suggested a landscape effect.

We have combined the remainder of last year's REU funds with this year's award (and additional funds from our primary SGS LTER award) to sponsor four REU students this summer: Julia West, a junior from Middlebury College in Vermont; Chris Warren, a senior from Earlham College in Indiana; Josh Metten, a sophmore at CSU; and Martin Danglemar formerly at Front Range Community College and recently transferred to CSU. All four are actively involved in research efforts at this time.

Schoolyard Ecology: We will involve 8 schools (one K-6, one 6-12, one middle school and 5 High Schools) from school districts in the northern Front Range and eastern plains of Colorado. The following schools and science teachers have expressed an interest in the program:

School	Science Teacher
Akron High School, Akron, CO	Ms. Deanna Schrock
Frontier Academy, Greeley, CO	Dr. Sean Madden
Greeley West High School, Greeley, CO	Mr. Gary Prewitt
John Evans Middle School, Greeley, CO	Mr. Jason Mclaughlin
Rocky Mountain High School, Ft. Collins, CO	Mr. Dave Swartz
Rough Rock High School, Navajo Nation, AZ	Mr. William Rosenberg
S. Christa McAuliff Elementary School, Greeley, CO	Ms. Rebecca Rimerez
Union Colony Prep School, Greeley CO	Ms. Cathy Hoyt

Research Assistance for Minority High School Students (RAMHSS): The following students were supported with LTER RAMHSS funds in 2003. The students were participants in the UNC Upward Bound Math and Science program known as COSMOS. The students were supported with room and board, tuition and stipends for the six-week summer program, and provided stipends during the academic year.

Student	Gender	Ethnicity	High School
SaDune Quarles	M	African-American	Greeley West
Jaime Salazar	M	Hispanic	Greeley West
Lucio Smith	M	African-American	Greeley Central

GK-12: Human Impact along the Front Range of Colorado: The project is an NSF-funded collaborative between the University of Northern Colorado and Colorado State University. Graduate students in STEM disciplines are placed K-12 classrooms during the academic year to assist K-12 teachers with the transference of research. K-12 teachers work with the graduate students during the summer on research. The project promoted the schoolyard ecology program, and provided teachers with graduate credit hours, travel to National Meetings (e.g., the ESA in Savanna, GA in 2003). The following Graduate students were supported: Ms. Laurel Hartley, Department of Biology, Colorado State University: Ms. Meghan Quirk and Mr. Rodney Simpson, Department of Biological Sciences, Univ. of Northern Colorado

CLT-W: Center for Teaching and Learning in the West: The CLT-W is an NSF-funded collaborative between Montana State University, the University of Montana, Colorado State University, Portland State University, and the University of Northern Colorado with the objective of researching the achievement gap between students of color and whites, providing K-12 professional development for teachers in STEM, and providing graduate programs in science education. The project supported research in the nature of the student-mentor relationship, and initiated an outreach program with Native American Tribes in Arizona, Montana and South Dakota (2004 Environmental Education supplement).

*Teachers on the Prairie:*The project is an NSF-funded collaborative between Portland State University, Oregon State University and the University of Northern Colorado, designed to provide K-12 teachers with focused professional development in prairie ecology. The following workshops were offered during June – August 2003:

Topic	***Instructor(s)***
Bagging Big Bugs	Dr. Boris Kondratief
GIS Workshop	Dr. Melinda Laituri
Invasive Species	Mr. Greg Newman
Peakes to Prairie	Ms. Laurel Hartley and Ms. Angie Moline
Soil Ecology	Dr. John Moore
Soil Formation,	Dr. Gene Kelly

D) PROJECT MANAGEMENT

We continue to refine our management process as needed to facilitate efficient support of our research, outreach and reporting efforts. For this round of funding we have moved our management efforts from an executive committee composed of all local co-PI's to a smaller group representing each of our research areas. The executive committee has met this past year to discuss primarily science and research topics. One of the ideas presented was that the larger group missed the more regular contact that they had in past years as part of the management plan. They wished to meet more often for the scientific exchange and we will increase these meetings in the coming year.

For LTER V, Dr. Eugene Kelly (EFK) is serving as lead PI. Dr. Ingrid Burke (ICB) remains as lead co-PI for the first three years. Dr. Michael Antolin (MFA) will assume this position (lead co-PI) in years four through six. The small management group that includes EFK, ICB, MFA and the leads of our other two research areas, Dr. Jack A. Morgan (JAM) for Land-Atmosphere Interactions and Dr. William K. Lauenroth (WKL) for Plant Dynamics, meets more often to discuss issues affecting the project. Dr. Susan Stafford was originally included in this group as lead for information management, but has taken a position in Minnesota and is not able to participate directly any longer. We have requested that Dr. John C. Moore take her position in the NSF list of co-PI's and participate in the management group as lead for our education and outreach efforts.

We remain active in attracting new scientists to the project. This year Dr. Marilyn Banta at the University of Northern Colorado is working on silky pocket mice with seed money supplied from our supplement request. Drs. Justin Derner and Dana Blumenthal are new hires with the ARS in Fort Collins and both have become involved with LTER projects in the past year (mountain plover and invasive weeds, respectively).

This year we have also been host to a large international research group studying communication in swift foxes. This group is lead by a PhD student from the University of Copenhagen, and has brought a field crew of four to six (field technician, masters and undergraduate students) to the field station for eight months this year. The swift fox project will continue for two more years.

Our brown bag seminar series continues to be a venue for inviting new researchers to meet our investigators, and talk about collaborations. We are meeting twice monthly during the academic year and have heard presentations from visiting scholars at CSU, graduate students, senior researchers from ARS and USGS, and our own researchers. Within our own research community the feedback provided from those in one area has often given those in another area new ideas about interpreting data or setting up their next round of experiments. Specifically one graduate student in the fauna group studying prairie dog distribution saw an interesting trend that researchers in the biogeochemistry group could quickly link to differences in soil types. Further discussion of this correlation has lead to refinement in the student's hypothesis and an extra dimension to interpretation of the data.