I. RESEARCH

During 2000 and 2001 we produced 70 papers in refereed journals, 20 book chapters, 9 theses and dissertations, and numerous abstracts from national and international meetings. Fifteen graduate students and 20 undergraduate students work 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 results for 2000-2001 in each of our core areas including: Populations and Processes, Biogeochemistry, Paleoecology/Paleopedology, Disturbance, and Water and Energy Dynamics.

1. Populations and Processes

Plants

Invasive Plants

Results of a survey of invasive plant species in the western section of the Pawnee National Grasslands indicated that while invasive species were found along roadsides, few were found in the native steppe. We asked two questions in an attempt to understand why so few invasives were found in the steppe: 1) Is invasion limited by seed availability? 2) Is invasion limited by resource (water and nitrogen) availability? Samples of the soil seed bank indicated that availability of invasive seeds declined exponentially from the roadsides to 25 meters into the steppe suggesting that the presence of invasive species in the steppe is limited by seed dispersal. Experimental additions of water and nitrogen to plots in which the invasive annual grass *Bromus tectorum* was seeded indicated that increased availability of water combined with nitrogen had a significant positive effect on survivorship, and that nitrogen alone and in combination with water significantly increased aboveground biomass. Both seed and resource availability are apparently influencing the current success of invasive plants in the shortgrass steppe. Our results suggest that anything that increases the dispersal of invasive propagules into the steppe in combination with increased water and nitrogen availability could result in a plant invasion. Because the current disturbance regime results in a continuous supply of microsites with increased water and nitrogen availability, a substantial plant invasion may only be awaiting the introduction of a species with an effective long distance seed dispersal mechanism.

Demography of *Pinus flexilis*

There are few places outside of riparian areas on the Great Plains that support trees. The presence of xeric tree stands tends to coincide with specific topographical features, though the reason for this relationship is the topic of some debate. The presence of *Pinus flexilis* James (limber pine) stands along the Ogallala escarpment on the SGS LTER site represents such an occurrence and is one of only two areas in the Great Plains where *Pinus flexilis* occurs. Essentially nothing is known about these stands, and our initial efforts were focused on understanding whether these are relicts of a past environment or recent additions to the landscape. Data from 6 stands and approximately 350 trees indicated that most of the trees were recruited at the end of the 19^{th} or beginning of the 20^{th} century. A few small trees were older than this, suggesting that these individuals were passed over in late 19^{th} century harvesting by settlers. The relatively large number of trees that are less than 2 meters in height suggests that recruitment is quite active up to the present. A survey of stumps indicated that *Pinus flexilis* has been present on the Ogallala escarpment at the SGS LTER site since 1452 AD and an accelerator ^{14}C date on a macrofossil from a packrat midden suggests that it has been on the escarpment since 300 AD +/- 60. Future work on these stands will include sampling the understory as well as the

demography of *Juniperus scopulorum*, the other tree species that occurs in these stands.

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 2000-2001, 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. Twenty traps were 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, which are important food items for rodents in the shortgrass steppe, 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 Grasslands (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.

Cattle Utilization of Prairie Dog Towns

Studies on mixed-grass prairie have found that native large herbivores preferentially graze on prairie dog towns. We investigated use of prairie dog towns by cattle on the Shortgrass Steppe LTER site from June to August. Twelve pastures containing 15 black-tailed prairie dog (*Cynomys ludovicianus*) towns were surveyed three times a week, and the number of cattle on the towns and their behavior was recorded. Three pastures were intensively surveyed twice weekly wherein the habitat and activity of a randomly chosen focal animal was recorded every six minutes for 3-4 hours. Bite and step counts of other individuals were recorded for five-minute intervals. Vegetation height and cover data were collected monthly. Vegetation of prairie dog towns was significantly shorter on towns than that off prairie dog towns. Cattle randomly used the prairie dog towns observed on driving surveys. Towns occupied an average of 3% of pastures, and cattle were present on them an average of 3.5% of the time. The intensively surveyed pastures yielded similar results. This research indicates that cattle do not prefer, but also do not avoid, prairie dog towns on the shortgrass steppe LTER.

Black-tailed Prairie Dog Mounds and nitrogen cycling

One LTER graduate student is investigating the effect of prairie dogs (*Cynomys ludovicianus)* mounds on nitrogen cycling and plant species diversity across a North South transect of prairie dog habitat, including prairie dog colonies at the Shortgrass Steppe LTER research site. During the summer of 2000, he took vegetation cover measurements and collected plant samples from mound, inter-mound, and off-town plots on 3 active prairie dog towns. At the SGS LTER, several species of forbs (*Sphaeralcea coccinea* and *Solanum triflorum*) exhibit significantly greater percentage cover on prairie dog mounds than on inter-mound and off-town areas, while the grasses *Bouteloua gracilis* and *Buchloe dactyloides* showed the opposite trend of greater

cover off town and inter-mound than on mound. *Agropyron smithii* showed only marginal differences between on-mound sites and inter-mound and off-town sites.He is currently statistically analyzing the plant tissue samples for frequency, biomass and nitrogen content.

Belowground Processes:

Belowground primary production by carbon isotope decay and long-term root biomass dynamics.

The isotope-decay method of estimating belowground net primary production (BNPP) potentially overcomes assumptions and biases associated with traditional methods. Isotope loss through *in-situ* decomposition after pulse labeling is considered the inverse of production, and turnover times are estimated by regression to time of zero remaining isotope. Method development and estimates of production were previously published using four years of data, which showed a clear linear loss rate over time. A slow, distinctly different phase in isotope loss developed 5 - 10 years post-labeling.

2. Biogeochemistry

CO_2 Fertilization Study

Four years of conducting the Open Top Chamber CO_2 Project on the Colorado Shortgrass Steppe has revealed several new and important findings. First and foremost, doubling ambient CO_2 concentration consistently leads to enhanced production on the shortgrass steppe. Relative enhancements of aboveground phytomass determined at the time of peak phytomass production range from a 20% enhancement in 1998 (NS) to a 71% enhancement in 2000. Both the degree of enhancement as well as the magnitude are the highest observed in grassland CO_2 enrichment studies. Gas exchange and plant and soil water measurements suggest that improved water relations and higher water use efficiency are the major driving forces behind CO_2-induced production increases. The significant enhancement of growth from CO_2 enrichment was detected for both C_3 and C_4 plants; after three years of CO_2 enrichment, there has been no change in the percentage composition of C_3 and C_4 aboveground vegetation. These general trends have continued through the 2000 growing season.

Large increases in root production have been observed in response to CO_2 enrichment, averaging 59% based on minirhizotron methods and 43% based on root ingrowth cylinders. production to decomposition ratios from minirhizotron root observations indicate that values have not yet reached an oscillating equilibrium about a ratio of one more than three years after installation of tubes. These data also suggest a long turnover time for roots in this system.

From weekly measurement of trace gas exchange in control, ambient CO_2 and double ambient CO_2 OTCs, we observed no detectable CO_2 enrichment effect on ecosystem respiration, oxidation of atmospheric CH_4, or emissions of NO_x or N_2O.

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 richness and aboveground biomass compared to

the controls, regardless of the historic treatment. The new carbon treatments, with the exception of lignin alone, reduced exotic species density by an average of 50% on the historic water plus nitrogen plots. 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. .

3. Paleoecology/Paleopedology

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.

Mass balance calculations of soils along the terrace chronosequence indicate substantial changes in chemical constituents over geologic timescales. The accumulation of carbonate over time from Stage I to early Stage III reveals a morphogenetic sequence that positively associates soil development with age. The build up of secondary carbonates is a good indicator of soil age in arid and semi-arid areas. Organic C exhibited variability over time and showed no increasing or steady state trend with soil age. The variability in the 600,000 year old site is most likely due to erosion of the surface layer. Total P was reduced over time, but the primary calcium-phosphate fraction has not been exhausted in soils from the late Pleistocene, indicating a slow rate of primary mineral weathering compared to that of the Hawaii studies

Gains and losses of major soil forming elements were quantified using mass-balance analysis. The dominant processes identified with pedogenesis include the accumulation of Ca, P, and metals (Fe and Al). Although Mg and K did not show similar transport trends with any other elements, baseline information was gathered about the behavior of these elements over time in soil profiles of the shortgrass steppe. One of the notable trends was that of relative inactivity or little elemental net gains or losses in the Holocene soils. It is apparent from the strain calculations that collapse, or volume compaction, is occurring to greater degree in progressively older soils with respect to all three immobile index elements Zr, Ti and Al. This is likely due to an increase in bulk density accompanied by the dissolution of minerals containing mobile elements that leave the weathered soil enriched in immobile elements

4. Disturbance

The role of a spiny biogenic refuge in structuring grazed shortgrass steppe plant communities

This study evaluated the hypothesis that biological grazing refuges have an important role in plant-grazer interactions in grasslands with a long history of grazing. We assessed the hypothesis that clumps of the spiny cactus *Opuntia polyacantha* provide biological refuges from cattle grazing, affecting cover and seedhead production of associated vascular plants in the shortgrass steppe of the North America. The study was based on sampling inside and outside the biological refuges in eight long-term moderately grazed pastures established 60 yrs ago and their respective ungrazed controls.

Opuntia clumps had refuge effects on seedhead production of the dominant grass (*Bouteloua gracilis*) and on cover and seedhead production of many functional groups. They had refuge effects on species sensitive to grazing ("decreasers") and barrel-cacti, but not on species preferred by cattle, exotics or weeds. Our results suggest that indirect refuge effects were more common than direct effects even though all potential indirect effects could not be measured. Indirect effects appeared to be mediated through changes in litter cover and, to a lesser extent, soil texture.

5. Water and Energy Dynamics

Effects of irrigated corn and dryland wheat agriculture on carbon and nitrogen

We investigated the effects of irrigated and fertilized corn agriculture on soil C, N and P in northeastern Colorado as they compare to dryland wheat-fallow fields and native rangelands. Three replicates each of native rangeland, dryland wheat-fallow, and irrigated corn fields located in or adjacent to the Pawnee National Grasslands were selected for this study. We measured potentially mineralizable C and N from 0-15cm in the soil profile, particulate organic matter (POM) C and N in the upper 30cm, total and $NaHCO_3$-P to a depth of 105cm, and total soil C and N to a depth of 195cm in the soil profile.

Irrigated corn fields contained significantly lower mineralizable, POM, and total C and N than rangelands in the upper 5cm of soil. Corn fields also had significantly greater $NaHCO_3$-P content than rangelands or wheat-fallow fields to a 1-meter depth in the soil. Wheat-fallow fields had significantly less potentially mineralizable and POM C and N than rangelands or corn fields in the upper 5cm of soil. Cumulative losses of total C and N in wheat-fallow fields extended to depths of 75cm or more. There were no significant differences in total P among landuse types. Differences in C and N between corn and wheat-fallow fields are likely due to differences in the quantity of plant residue inputs. These results indicate that irrigated and fertilized corn crops in this region of the semiarid shortgrass steppe depletes pools of C and N at the soil surface but does not cause a change in C or N below the 5cm layer of soil.

Intra-annual and interannual variability of ecosystem processes in shortgrass steppe

We used a daily time step ecosystem model (DAYCENT) to simulate ecosystem processes at a daily, biweekly, monthly, and annual time step. The model effectively represented variability of ecosystem processes at each of these timescales. Evolution of CO_2 and N_2O, NPP, and net N mineralization were more responsive to variation in precipitation than temperature, while a combined temperature-moisture decomposition factor (DEFAC) was a better predictor than either component alone. Having established the efficacy of CENTURY at representing ecosystem processes at multiple timescales, we used the model to explore interannual variability over the period 1949-1996 using actual daily climate data. Precipitation was more variable than temperature over this period, and our most variable responses were in CO_2 flux and NEP. Net ecosystem production averaged 6 g C m^{-2} yr and varied by 100% over the simulation period. We found no reliable predictors of NEP when compared directly, but when we considered NEP to be lagged by 1 year, predictive power improved. It is clear from our study that NEP is highly variable and difficult to predict. The emerging availability of system-level C balance data from a network of flux towers will not only be an invaluable source of information for assessments of global

carbon balance but also a rigorous test for ecosystem models.

Effects of grazing on regional climate

Before European settlement, the Great Plains of the United States contained vast herds of bison. These bison altered the landscape trhough their grazing. Measurement data of the disturbance that such grazing could produce, when scaled for the large population of bison, were used with a coupled atmospheric-ecosystem model to evaluate the likely effect that this grazing had on the growing season weather in the Great Plains. A dynamically coupled meteorological and plant growth model was used to investigate the regional atmospheric conditions over a single growing season. A 50 km horizontal mesh was implemented, covering the central plains of the United States. The modeling system was then integrated, with a time step of 90 s, for a period covering 1 April 1989 through 31 August 1989 using boundary conditions obtained from an objective analysis of gridded archive data. This integration was performed with and without grazing to assess the effects on regional atmospheric and biological processes. The grazing algorithm was employed to represent presettlement North American bison and was switched on and off for different simulations. The results indicated a cooling response in daily maximum temperatures to removal of grazing. The opposite trends were found for the minimum daily temperature. It was also found that grazing produced significant perturbations in the hydrological cycle.

II. INFORMATION MANAGEMENT

Our data management team continues to make our datasets accessible to the public, as well as providing a method for the smooth continuation of data through field collection to final long-term storage. We have also added a new file server.

We have several important goals for the next year including: providing information for database management modules, supporting and participating the LTER Network's effort to establish metadata standards, support and participate in the Network's efforts to distribute data to teachers and students in a user-friendly format for the classroom, to collaborate with other research agencies in relation to data management, and to continue to work with scientists to make new datasets available to the public.

We have georeferenced about half of the study sites on the Shortgrass Steppe LTER, as well as georeferencing roads, fencing, and human made land features. We have also created spatial databases of historical prairie dog data from 1980 to present, historical pasture locations and associated management methodologies, historical herbicide application areas, historical cropland areas, and historical burned areas within the Shortgrass Steppe LTER research site.

III. OUTREACH ACTIVITIES

Education

In the past year, we have continued our Research Experience for Undergraduate (REU) program with two students working on the following projects : 1) Investigations of the relationship between prairie dog metabolism and environment. 2) Development of a non-invasive DNA extraction technique for prairie dogs.

The Research Assistantships for Minority High School Students (RAMHSS) program was highly successful this year, providing minority students with an opportunity to participate in scientific research, learn about how science really works, and to prepare and present scientific results.

The Schoolyard LTER program made significant progress this year. There are six schools currently

involved in the schoolyard LTER program. Teachers from these schools met with LTER scientists to visit the SGS LTER site and the demonstration plots at UNC in July 2000. The group held a two-day workshop to discuss potential experiment designs, data collection, and protocol on maintaining databases. All data collected will be maintained as part of the SGS-LTER database and made available to the teachers and students. LTER scientists and the teachers worked to incorporate the schoolyard LTERs into curricula. We used the guidelines proposed by NSF and the National Science Education Standards to develop curricula and lab modules that are age-appropriate and inquiry-based.

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

Every year we have many visitors to the Shortgrass Steppe LTER research site including many K-12 students, undergraduate students, graduate students, researchers and faculty from different universities and organizations, and the public. This year our visitors came from such diverse places as Africa, Australia, and South America. LTER scientists hosted a site visit at the Shortgrass Steppe in July 2000 and May 2001 for schoolyard LTER teachers and other interested parties. The objectives of the visits are to familiarize the teachers with the LTER site and experiments, and provide an example of how a field experiment can be scaled-down to a schoolyard setting.

IV. CROSS-SITE, SYNTHESIS, and NETWORK-LEVEL ACTIVITIES

Cross-Site and Regional Analysis Research Highlight

Nitrogen mineralization across a Great Plains precipitation gradient

Regional analyses and biogeochemical models predict that ecosystem nitrogen (N) pools and N cycling rates increase from the semi-arid shortgrass steppe to the sub-humid tallgrass prairie of the Central Great Plains, yet few field data exist to evaluate these predictions. We hypothesized that *in situ* net N mineralization would increase with increasing N pool sizes across this grassland community gradient and track interannual and regional differences in precipitation and temperature. We measured *in situ* net N mineralization monthly during two growing seasons at five sites across a precipitation gradient in the Great Plains region. Growing season precipitation varied more than two-fold across the gradient and by >25% at each site between years. Respectively, soil N pools and the N content of aboveground net primary production (ANPP-N) increased significantly from the shortgrass steppe (208 and 1.76 g N m^{-2}) to the tallgrass prairie (409 and 3.27 g N m^{-2}), and ANPP-N at the shortgrass steppe sites tracked the differences in interannual precipitation (0.88 g N m^{-2} in a dry year to 2.12 g N m^{-2} in a wet year). However, measured *in situ* net N mineralization rates did not increase across the community gradient or reflect regional and/or interannual differences in precipitation and temperature. These data suggest that current methods of measuring *in situ* net N mineralization may not be effective for soils with large immobilization potentials.

Synthesis

We continue to work on our synthesis book, Ecology of the Shortgrass Steppe: Perspectives from Long-Term Research. In addition, our scientists have continued to publish numerous modeling papers and synthesis papers. For instance, we have recently published a new model of trace gas fluxes for the shortgrass steppe, submitted papers reviewing the regional balance of nitrogen for the shortgrass steppe and central grasslands region, we published a model analysis of the role of grazing in influencing regional climate, a paper , and have two review papers accepted that evaluate the relationship between

root production and environmental variables.

Network Activities

We continue to be very active in network activities. One of our PI's, Roger Pielke, is taking the lead on a cross-site modeling project with the San Diego Computer Center. Indy. Burke served on the Coordinating Committee and the Executive Committee.

2000-2001 Publications

Journal Articles

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