

1. Core Area Research

A. Disturbances and Human Use

Work in this area is extensive. We divide this section into natural disturbances that create pattern in structure and influence processes in shortgrass steppe, and forces through past and present human landuse practices in this region that represent either exogenous or endogenous disturbances. Landuse in this region is currently 60% dryland wheat and 40% native rangeland or abandoned cropland grazed by cattle. Livestock production is a crucial part of the economic and social systems of the Great Plains, but has recently come under close scrutiny as an influence on ecosystems and their inherent biodiversity. Conversion to crop agriculture may be particularly unstable in this semiarid environment, as evidenced by the large abandonment of land during the 'dust bowl' period. Past and potential future shifts in landuse are perhaps one of the most critical factors affecting the integrity of the shortgrass steppe ecosystem.

1. Small Natural Disturbances

Recovery of shortgrass vegetation after smallscale disturbances:

Most studies of vegetation recovery in shortgrassdominated systems have focused on largescale disturbances, and in particular the cultivation and abandonment of agricultural fields. Small, patchproducing disturbances (ie., fecal pats of cattle, nest sites of western harvester ants, and burrows from small animals) are also important, but they have largely been ignored and have the largest potential effect on community structure. Our objective is to evaluate recovery of vegetation on naturallyoccurring and artificiallyproduced disturbances of different type, seasonality, size, and location by soil texture.

After one year of recovery, species composition on nest sites and animal burrows were similar to each other, yet different from artificially produced plots. High density and cover of perennials on nests and burrows indicates that perennial organs were not necessarily killed by the clipping activities of ants or burrowing activities of animals. Most cover on artificiallyproduced plots was annuals. One of the most important results from this study is the ability of *Bouteloua gracilis* to recover from seed on small disturbances. Previous studies had reported that this species can not recover after disturbance. Results from this field study as well as the old field study described below and our modeling exercises indicate that *B. gracilis* can recover after disturbance. Furthermore, recovery rates are dependent upon the characteristics of the disturbance, and in particular size and soil texture.

References: (Coffin and Lauenroth 1989)

Longterm recovery patterns of vegetation after patchy disturbances (1977 to present):

White grubs, including the larvae of June beetles (*Phyllophaga fimbripes*), are among the most destructive soildwelling insects, and have severely damaged large areas of grassland in North America. Our objective is to evaluate effects of white grubs on shortgrass steppe communities by determining the characteristics of patches of vegetation affected by

grubs, and monitoring plant recovery on these patches through time. We are also evaluating the importance of spatial heterogeneity in survival of *Bouteloua gracilis*, and effects of grazing by cattle on plant recovery patterns through time.

At the start of the study, patches in grazed pastures had more complete mortality of *B. gracilis* than patches in ungrazed exclosures. This difference likely resulted from indirect effects of grazing by cattle on white grubs rather than direct effects of grazing on plants. Successional dynamics of functional type composition was similar on patches affected by white grubs and areas affected by other types of disturbances. Annuals dominated initially followed by shortlived perennial forbs and grasses, and finally dominance by longlived perennial shortgrasses, and in particular *B. gracilis*. The rate of recovery was faster for areas affected by white grubs than for disturbance types of similar size, yet greater intensity. Spatial heterogeneity in survival of *B. gracilis* was only important to the recovery of this species. Linear relationships were found between spatial heterogeneity in survival of *B. gracilis* and cover of this species in each year of sampling. High r^2 values for ungrazed patches throughout the sampling period indicate the importance of initial conditions to recovery of *B. gracilis* for as many as 13 years after the start of recovery. Low r^2 values after 1979 for grazed patches indicate the increasing importance of grazing and decreasing importance of initial conditions to recovery of *B. gracilis* on these patches. The infrequent importance of grazing to the recovery of other functional types is similar to the effects of grazing on other structural and functional aspects of shortgrass steppe ecosystem, and reflects the long evolutionary history of grazing by large herbivores in these systems.

The persistence and stability of shortgrass ecosystems, in spite of disturbances such as white grubs, is determined at least in part by the characteristics of the disturbance interacting with the ability of plants to respond, and in part by the evolutionary history of the system. Management of shortgrass ecosystems must account for aspects of the current systems as well as past history.

References: Coffin et. al. submitted

The effects of cattle fecal pats on plant mortality and recovery:

We also evaluated the effects of cattle fecal pats, the most frequently occurring small disturbances of sufficient size (0.10.3 m diameter) to kill *B. gracilis* plants, on plant mortality and recovery. The time required for pats to decompose indicates the cumulative effect of pats through time; both in terms of the probability of plant mortality and the length of time the area is disturbed before plant recovery can begin. Two years were required for most (90%) pats to decompose; slow decomposition occurred after that time. Plant recovery by *B. gracilis* on areas killed by pats occurs within two years; this species dominated plant cover on disturbed areas within three years for both types of plant communities where the study was conducted. *Buchloe dactyloides* (buffalograss) was also an important perennial grass to recover within two years after the disturbances occurred.

References:

Response of individual *B. gracilis* plants to small disturbances:

In 1991 we initiated a field study to evaluate the response of individual *B. gracilis* plants to small (0.1 to 0.3 m diameter) disturbances. We selected six sites at the CPER to represent three soil textures (clay loam, silt loam, and sandy loam). At each site, a total of 100 *B. gracilis* plants were selected, half of which were protected from grazing by cattle and half were unprotected. Effects of small disturbances were simulated either by shading portions of each plant to represent cattle fecal pats or by removing above and belowground parts of each plant to represent digging and removal by small animals. Ten plants in each grazing treatment were randomly assigned to five mortality treatments: 0, 50, 75, 90, and 100% of each plant either shaded or removed. Treatments began in July (1991) when plant size and number of live tillers in the undisturbed part of each plant were recorded. Survival of each plant based on remaining number of live tillers was recorded in June and August (1992). We also established permanent plots at each site for demographic analyses. Plots will also be established at the sites representing the old and new grazing treatments. (see [Figure 2.8](#))

References: Fair 1995 (thesis)

2. Human Use Grazing

Defoliation effects on plant morphology, aboveground biomass, tissue N, and phenology in longterm grazed and longterm protected pastures:

This study investigates how the morphology, biomass, and aboveground nitrogen dynamics of *Pascopyrum smithii* (western wheatgrass) and *Bouteloua gracilis* (blue grama) plants are affected by defoliation and grazing history. A field experiment was carried out in four grazing treatments (long and short term grazing and long and short term protection) during the 1992 and 1993 growing seasons. We conducted a parallel greenhouse study to examine whether morphological and chemical differentiation due to longterm grazing has occurred. We also compared phenological development between grazed and protected populations of functional groups of graminoids, forbs, and half-shrubs. Longterm protection has resulted in plants with taller tillers and longer leaf blades in both species. Defoliation enhanced tillering in western wheatgrass plants under moderate defoliation intensity (clipped at 6 cm height) in longterm grazed plants, and under severe defoliation (clipped at 3 cm height) in longterm protected plants. Tillering was enhanced in the greenhouse by defoliation only in protected populations. Defoliation also reduced tiller density of greenhousegrown blue grama plants in longterm grazed populations.

Although biomass of western wheatgrass and blue grama plants was reduced by defoliation in the field and in the greenhouse, aboveground tissue N concentration and N yield were increased. A similar inverse relationship was observed between biomass and N yield in the greenhouse. Some differences in chemical and morphological characteristics between shortterm grazing and shortterm protection (two years in both cases) were also observed. No biomass or tissue N differentiation was observed in both species as a result of longterm grazing. With little difference in graminoid phenology (mainly as a result of more vegetative growth of longterm grazed western wheatgrass and

needle leaf sedge populations), there was no significant difference in growth within and between functional groups in grazed and protected populations. Some of our results are consistent with previous findings regarding plant morphology, biomass and tissue N dynamics response following defoliation. However, comparisons of morphology, biomass and N dynamics, and phenological development across grazing treatments and between tiller and plant organization has provided a broader view of defoliation and grazing history effects in the shortgrass steppe.

References:

Plant responses to defoliation and competition at two landscape positions:

Experiments were conducted in 1989 and 1990 to determine whether landscape position modifies the effects of defoliation and competition by *Bouteloua gracilis* (H.B.K.) Griffiths on established tillers of *Pascopyrum smithii* (ryd.) A. Love. During the first year, tiller survival, total growth in height, and number of green leaves per tiller were not significantly affected by topographic position. However, competition reduced those variables and defoliation reduced tiller survival and green leaves, but growth in height was increased almost five times by defoliation. Variables recorded in 1989 responded similarly to competition and defoliation between topographic positions. However, during 1990 with a drier growing season, individual tiller biomass, total growth in height, number of green leaves, total leaves produced, tiller survival, and density were greater on hillsides than in swales. Competition reduced all of these variables, but defoliation causes no response in aboveground biomass and total leaves produced, in spite of negative effects on tiller survival and, most of the time, negative effects on number of green leaves. This study suggests that the highly positive response to defoliation of growth in height and tiller N concentration partially contributed to the exact compensation of aboveground net primary production (ANPP) per tiller, and consequently almost doubled nitrogen yield. Furthermore, the responses of tiller survival, number of green leaves per tiller, and tiller density to competition were stronger in swales than on hillsides. Moreover, a significant second order interaction on the final sampling date on tiller survival and on total leaves produced indicated that the interactive effects of competition and defoliation did not vary in swales, but the negative effect of defoliation on those variables were exacerbated by competition.

Finally, the response of over winter variables suggest that competition and defoliation acted additively in reducing tiller density and the proportion of parent tillers producing daughter tillers, and that their effects are similar between topographic positions. Furthermore, a negative effect of defoliation on height of tillers growing the next spring suggests that *P. smithii* would be at a disadvantage in competition with surrounding vegetation dominated by *B. gracilis*.

References: Ibarra Gil 1992 (dissertation)

Longterm grazing in the shortgrass steppe: leaf photosynthetic characteristics and water relations:

Growing season gas exchange patterns were measured in two shortgrass steppe species

growing on upland and lowland sites that were either protected or subjected to 57 years of heavy grazing. On average, net photosynthesis (A) and stomatal conductance (Gst) in *Elymus smithii*, a C3 grass, remained, respectively, 29% and 40% lower in plants growing on both upland and lowland ungrazed sites relative to grazed sites. Diurnal leaf water potentials were also lower, although infrequently, in plants from ungrazed sites. Conversely, A and Gst measured in *Bouteloua gracilis*, a C4 shortstatured grass, were not changed by grazing history or by topographic position. A clipping experiment with *E. smithii* revealed the sensitivity of this species to shortterm defoliation events as well, with A in clipped plants over 14% higher than unclipped plants during the week following clipping. Leaf age was also shown to be an important factor influencing plant carbon gain with 35% higher A in upper canopy leaves of *E. smithii* relative to lower canopy leaves and 35% higher A in leaf bases relative to leaf tips. These results have important implications for net carbon gain in plants subject to various levels and durations of herbivory. Moreover, the positive response of *E. smithii* to short and longterm defoliation may partially explain the persistence of this coolseason grass in shortgrass steppe dominated by *B. gracilis*.

References: Fahnestock and Detling

The role of *Opuntia polyacantha* in providing a refuge for plant species under longterm heavy grazing:

We evaluated the role of *Opuntia polyacantha* in providing a refuge for plant species under longterm heavy grazing. In previous work, we found that heavy grazing resulted in a decrease in species richness compared to ungrazed areas. This summer, we tested the hypothesis that there is a greater species richness inside patches dominated by *O. polyacantha* than outside, in grazed pastures, due to the protection from grazing afforded by the spines. Our results supported the hypothesis. We found greater species richness in the patches, suggesting that *O. polyacantha* is important for sustaining plant species richness under grazing. (see

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References:

Effects of grazing, topography, and precipitation on the structure of plant communities:

Structural aspects of the shortgrass steppe plant community, functional groups, and species populations were examined in response to longterm heavy grazing and exclosure from grazing, contiguous wet or dry years, and an environmental gradient of topography. Of the three factors, relatively greater differences in community similarity were observed between catena positions, particularly on the ungrazed treatments. Grazing was

intermediate between catena position and shortterm weather in shaping plant community structure. Grazed treatments and ridgetops had a less variable species composition through fluctuations in weather.

An increase with grazing of the dominant, heavily grazed species was observed. Basal cover and density of total species was also greater on grazed sites. The more uniform "grazing lawn" structure of the grazed plant communities had an influence on segregation of plant populations along topographical gradients. Segregation was less on grazed catenas, but diversity and the abundance of introduced and opportunistic colonizer species was also less.

Although the shortgrass steppe community was relatively invariant, less abundant species were dynamic and interactions occurred with respect to grazing, weather, and catena position. The effects of grazing may be mitigated by favorable growing seasons but magnified in unfavorable years in populations that are adapted to favorable sites. Grazing can be considered a disturbance at the level of the individual but it may or may not be a disturbance at the level of the population, and it is not a disturbance at the level of the community in this particular grassland. (see [Figure 2.6](#))

References: Milchunas et al. 1989

Community structure relationships across a perturbation gradient encompassing different types of disturbances:

We constructed a perturbation (response) gradient that encompassed several types of disturbances (causes) affecting shortgrass steppe communities and that was confounded by time scales of initiation and duration. The objectives were to (1) examine the type of disturbance and the relative magnitude of response in relation to the history of the shortgrass steppe, and (2) determine which attributes of the plant communities displayed relationships across the perturbation gradient, rather than across traditional successional-time gradients.

Comparisons of disturbance types indicated that longterm heavy grazing by cattle resulted in plant communities differing less from communities resulting from other disturbances than were longterm ungrazed sites. The removal of grazers from this system promoted attributes of earlier seral stages. Water addition, belowground grazing by white grubs, and waterplusnitrogen enrichment had distinct and large impacts on community composition. Nitrogen enrichment resulted in additions but not losses of species. The shortgrass steppe has a high degree of adaptation to both shortterm drought and aboveground grazing. Belowground grazing and semiaridity may be considered antagonistic pressures on the community.

Community attributes that displayed a relationship with increasing level of perturbation were decreasing dominance and increasing diversity, and fluctuation in species composition during shortterm wet/dry cycles. The level of perturbation was related to negative impacts on the two primary species and a corresponding increase of other warm-

season species, but was not related to densities of any other species, lifeform, or functional group. (see [Figure 1.2](#))

References: Milchunas et al. 1990

Threedimensional distribution of plant biomass in relation to grazing and topography:

The horizontal and vertical distribution of plant biomass was examined on shortgrass steppe communities that were heavily grazed or protected from grazing for fortyseven years. Uplands and swales were sampled along the gently rolling topography. Threedimensional distributions of plant biomass were generated by direct sidebyside coring whereby 0.5m X 0.5m X 20cm deep volumes were completely sampled.

Longterm grazing had no effect on total biomass of surface crowns and only small effects on total biomass of roots at 010 cm and 1020 cm depths. The effect of grazing on the vertical distribution of crown and root biomass was also smaller than the difference between topographical positions. In contrast, grazing had a large influence on the horizontal distributions of all vertical components of the plant community by producing smoother more uniform horizontal distributions. This was most evident for the more heavily grazed swale communities. The grazinglawn concept was extended to the belowground plant community and discussed in terms of possible herbivore mediated plantplant interactions rather than as an aboveground grazing avoidance mechanism.

References: Milchunas and Lauenroth 1989

Abiotic and biotic control, and direct and indirect effects of large herbivores on demography of opportunistic species:

The initial emergence and subsequent survival and growth of five opportunistic 'weeds' after seed addition was examined in relation to indirect effects of longterm grazing treatments (heavily grazed vs protected), direct effects of currentyear defoliation, and removal treatments designed to eliminate plant competition while either leaving vegetation and soil structure unaltered or disturbed. The treatments were applied on both upland and lowland topographic positions to assess the relative influence of macroenvironment versus plant competition.

The indirect effects of large herbivores on the initial emergence of seedlings were so great that they prevented the potential for direct effects of the grazers to manifest to any large extent. Very few individuals emerged on the longterm grazed treatments that were either grazed or ungrazed during the current experiment. Numbers of individuals emerging on the longterm protected treatments were greater or equal to those emerging on the no competitionundisturbed treatments, but numbers were greatest on no-competition disturbed treatments. The microenvironment amongst a livingplant canopy may in some cases increase emergence, but soil disturbance is of greater importance.

None of the seeded individuals on the longterm grazed, currently grazed treatments survived to the end of the growing season. There was a slightly greater endofseason biomass of seeded species and percentage of the total population reaching reproductive

status on the longterm ungrazed compared with grazed nondefoliated treatments, and very high survival, biomass, and proportions of reproductives on both nocompetition treatments.

Equal compensation to currentyear herbivory occurred on longterm heavily grazed treatments even though aboveground production, and soil carbon and nitrogen, was much greater on longterm protected sites. Productivity and soil nutrients varied with topography, but very few topographical main effects or interactions occurred with demographic variables of seeded species, suggesting that macroenvironmental effects were of minor importance compared with grazing and plant competition. (see [Figure 1.18, Figure gz1.a](#))

References: Milchunas et al. 1992

Production and rain use efficiency in shortgrass steppe: grazing history, defoliation, and precipitation:

Grassland, subjected to fifty years of heavy, light, and no grazing intensity was clipped to simulate the natural pattern and intensities of defoliation by cattle or not clipped to simulate no grazing. A level of water resource treatment was superimposed upon the grazing and clipping treatments. Half of the plots were supplemented with additional water to simulate a wet year and half were not supplemented in a year of average precipitation. All three treatments interactively determined aboveground production. Water treatment had the largest overall effect on aboveground production. Currentyear defoliation had no direct significant effect on production, but mediated differences between both longterm grazing and watering treatments. Longterm ungrazed compared to grazed grassland was capable of responding to high amounts of precipitation, but was also most affected by low amounts of precipitation and, therefore, displayed greater variability in aboveground production and rain use efficiency. Only in the year of average precipitation, defoliation increased rain use efficiency in longterm lightly, but not heavily, grazed treatment. This suggests a water conservation mechanism of defoliation that is diminished with heavy grazing. (see [Figure 2-8b](#))

References: Varnamkhasti 1991, Varnamkhasti et al. 1995, Milchunas et al. 1995

Forage quality in relation to longterm grazing history, currentyear defoliation, and water resource:

Forage nitrogen concentrations, nitrogen yields, and invitro digestibilities were assessed in shortgrass steppe that had been ungrazed, lightly, or heavily grazed for 50 years. Caged plots were not defoliated or defoliated based upon removals observed in naturally-grazed reference plots. This was done in a year of average precipitation and with a supplemental water treatment to simulate a wet year. In general, currentyear defoliation had positive effects, and longterm grazing and supplemental water had negative effects, on forage nitrogen concentrations and digestibilities. However, defoliation interacted with longterm grazing in determining forage nitrogen concentrations, and with grazing and with watering in determining digestibilities. Nitrogen concentration and digestibility increased with defoliation in lightly, but not in heavily, grazed treatments. The dilution

effect of supplemental water on digestibilities through increased plant growth was offset by defoliation. The negative effects of longterm grazing on forage quality were small, equally or more than compensated for by defoliation in a year of average precipitation, but more pronounced in the simulated wet year.

Nitrogen yields and digestible forage production were usually increased by defoliation, but this depended upon grazing and watering treatments. Increased nitrogen and digestible forage yields and concentrations in response to defoliation were greater than the biomass response in lightly grazed grassland. For both nitrogen and digestibility, yields were greater in grazed than ungrazed treatments in the year of average precipitation, but less in the simulated wet year. Optimizing quantity and yeartoyear stability of nitrogen and digestible forage yield may best be achieved with light grazing rather than no or heavy grazing.

Clipping was conducted in a manner closely resembling the natural pattern and intensity of defoliation by the cattle, and confirm the potential for a positive feedback of increased forage quality with defoliation observed in pot experiments. Longterm heavy grazing can diminish this response. Quantity (ANPP), quantity of quality (digestible and N yields), and quality (concentrations) do not necessarily respond similarly in interactions between currentyear defoliation, longterm grazing history, and level of water resource. (see [Figure gz2a](#))

References: Milchunas et al. 1995

Aboveground primary production across fifty years of grazing intensity treatments:

Estimates of forage production for longterm ungrazed, lightly, moderately, and heavily grazed treatments (0, 20, 40, 60 % removal of annual forage production) established in 1939 in shortgrass steppe communities were subjected to multiple regression analyses to assess longterm temporal trends resulting from grazing and shortterm sensitivities to abiotic factors. Average production based upon all data from 1939-1990 was 75, 71, 68, and 57 g m² yr⁻¹ for ungrazed, lightly, moderately, and heavily grazed treatments, respectively. Variability in forage production was explained mostly by coolseason precipitation, and magnitude of forage production was more sensitive to annual fluctuations in precipitation than to longterm grazing treatments. Production per unit increase of precipitation was greater for coolseason than warmseason precipitation, but only when coolseason precipitation was above average. This was attributed to differences in evaporative demand of the atmosphere resulting in different utilization efficiencies of small and large rainfall events in the two seasons. Based upon a regression model constructed using data from 1939 through 1962, forage production was not affected by grazing at 20 to 35 % removal. For pastures of average relative productivity, grazing at 60 % level of consumption for 25 yrs resulted in a 3 % decrease in forage production in wet years and a 12 % decrease in dry years. Estimates of productivity after 50 years of heavy compared to light grazing treatment were 5 and 18 % for wet and average years of precipitation, respectively. (see Estimates of forage production for longterm ungrazed, lightly, moderately, and heavily grazed treatments (0, 20, 40, 60 % removal of annual forage production) established in 1939 in shortgrass steppe communities were subjected

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References: Milchunas et al. 1994

Impact of cattle grazing on nematode communities:

Nematode populations were 41% greater in underplant soils than in inter plant soils, with any differences between the four grazing treatments having yet to be detected. In this study, 119 taxa (109 genera, eight subfamilies, one family and one unidentified nematode taxa) in 45 families and nine orders were identified from five sites across the CPER. Nematode communities were dominated by three genera, Acrobeles, Tylenchorhynchus and Helicotylenchus, which represented 51% of the population. Another 16 taxa occupied 34% of the population, 37 taxa comprised 13%, and 63 other taxa 2%. Based on percentages, bacterial feeders were a greater proportion of communities in long term ungrazed (UU) than in long term grazed soils (GG), whereas plant parasites were a greater proportion of the community in long term grazed treatments. There were more omnivores in shortterm grazed (GU) than in short or longterm ungrazed treatments (UG and UU), and more fungal feeders in interplant (I) than in underplant (P) soil. Indices of diversity, evenness, richness, and dominance indicated no differences in nematode communities in the four grazing treatments (GG, GU, UG and UU). However, principle component analysis (PCA) using relative abundance data grouped the grazed treatments (GGP, GUP, GGI and GUI) separately from the ungrazed treatments (UUP, UII, UGI, and UGP). Trophic group data in PCA clustered four grazed treatments over the zero level of second component, and four ungrazed ones below the level, and distinguished the interplant and underplant treatments.

References: Haung and Freckman 1995

Livestock grazing: consumer and plant biodiversity and the relationship to ecosystem function:

We synthesized published and unpublished data from longterm grazing treatments in the

shortgrass steppe on the diversity and abundance of plants, lagomorphs, rodents, birds, aboveground and belowground macroarthropods, microarthropods, and nematodes. The relatively invariant nature of the shortgrass steppe plant community in response to grazing provides an opportunity to address some broad questions concerning relationships between responses of various structural and functional aspects of systems in general. Are there consistencies in diversity and abundance responses to grazing between groups of organisms? Are some groups more sensitive than others, or do responses mirror that of vegetation? Are the responses in terms of biodiversity related to functional responses?

Responses to longterm grazing intensity treatments in term of diversity, abundance, dominance, and dissimilarity were highly variable across classes of organisms. Some groups of consumers displayed large differences between grazing treatments even though differences in plant community attributes were relatively minor. Some responses were large even when comparing ungrazed to lightly grazed, or lightly to moderately grazed treatments. Birds appeared to be a particularly discriminating group to the grazing intensity treatments. Differences among grazing treatments in richness of groups other than plants and birds were relatively minor, especially when compared to large declines in abundance of some groups with increasing grazing intensity. For the wellstudied groups (plants and birds), shifts in species in terms of 'quality' factors, such as exotic, endemic, rare, generally suggest that livestock grazing may be more similar to conditions this particular system was exposed to in recent evolutionary time than would be the removal of the exotic, domestic grazers that functionally serve as a surrogate to bison.

Trophic structure composition did not vary greatly across grazing treatments. Further, large effects of grazing on some consumer groups did not translate into similarly large effects on ecosystem processes such as primary production or soil nutrient pools or cycling rates. (see [Figure 1.19](#), [Figure 2.8a](#))

References: Milchunas et al. 1995

3. Human Use Cultivation

Soil Organic matter recovery in semiarid grasslands: implications for the Conservation Reserve Program:

Although the effects of cultivation on soil organic matter and nutrient supply capacity are well understood, relatively little work has been done on the longterm recovery of soils from cultivation. We sampled soils from 12 locations within the Pawnee National Grasslands of northeastern Colorado, each having native fields and fields that were historically cultivated but abandoned 50 years ago. We also sampled fields that had been cultivated for at least 50 years at 5 of these locations.

Our results demonstrated that soil organic matter, silt content, microbial biomass, potentially mineralizable N, and potentially respirable C were significantly lower on cultivated fields than on native fields. Both cultivated and abandoned fields also had significantly lower soil organic matter and silt contents than native fields. Abandoned

fields, however, were not significantly different from native fields with respect to microbial biomass, potentially mineralizable N, or respirable C. In addition, we found that the characteristic smallscale heterogeneity of the shortgrass steppe associated with individuals of the dominant plant, *Bouteloua gracilis*, had recovered on abandoned fields. Soil beneath plant canopies had an average of 200g/m² more C than betweenplant locations.

We suggest that 50 years is an adequate time for recovery of active soil organic matter and nutrient availability, but recovery of total soil organic matter pools is a much slower process. Plant population dynamics may play an important role in the recovery of shortgrass steppe ecosystems from disturbance, such that establishment of perennial grasses determines the rate of organic matter recovery. (see [Figure 1.16](#))

Reference: Burke et al. 1995

Recovery of soil organic matter and nutrient availability on Conservation Reserve Program fields:

Large reductions in soil organic matter (SOM) due to cultivation have been widely investigated, but the short term (<10 year) dynamics of SOM recovery following cultivation are far less clear. In two experiments, we measured the recovery of SOM pools (coarse particulate organic matter (coarse POM), fine POM and total SOM) and nutrient availability (mineralizable C and N) on 6 year old Conservation Reserve Program (CRP) fields relative to baseline SOM levels in adjacent, conventionallytilled, wheatfallow fields. We also tested plant life form effects on SOM recovery by measuring microsite (<10 cm) SOM patterns, where we expected labile SOM to be larger under plants than between plants and to be larger under plants that produced more labile tissue.

In the first study, CRP fields seeded with rhizomatous grasses contained higher fieldscale (~ 20 ha) rates of C and N mineralization than wheatfallow fields, but none of the other SOM pools were altered. At the microsite scale, only coarse POM N was higher under grasses than in plant interspaces, indicating that the soil heterogeneity associated with native arid grasslands was only weakly restored on these fields.

In the second study, we tested CRP management and plant life form effects on SOM recovery using 3 treatments: wheatfallow, 20% legume / 80% grass (LL CRP) and 80% legume / 20% grass (HL CRP). The net impact of increased plant inputs and cessation of tillage generally increased pools on mineralizable and coarse POM C and N by factors of 24 relative to wheatfallow fields, but had negligible effects on fine POM and total SOM pools. Recovery of soil heterogeneity was accelerated under legumes, which produced more labile tissue than grasses, in that soils under legumes contained larger pools of coarse POM C and higher net N mineralization rates than soils under grasses or in plant interspaces.

Grasses growing in HL CRP soils, which contained the highest rates of potential net N mineralization, produced more labile tissue than the grasses in the more nutrient depleted LL CRP soils, suggesting that plant/soil feedbacks were important. Recovery of labile

soil and plant N was thus enhanced when the proportion of legumes was high, and this may lead to improved grain or animal N nutrition if these CRP fields are subsequently cropped or grazed.

References: Robles and Burke 1995, Robles 1995 (thesis), Robles and Burke 1995a (submitted), Robles and Burke 1995b (submitted)

Patterns of N availability among dominant land uses in the shortgrass steppe:

We conducted a set of in situ incubations to evaluate patterns of N availability among dominant land uses in the shortgrass steppe region of Colorado and to assess recovery of soil fertility in abandoned fields. Replicated 30 d incubations were performed in 3 sets of native (never cultivated), abandoned (cultivated through ca. 1937), and currently cultivated, fallow fields. Net N mineralization and the percentage of total N that was mineralized increased in the order: native, abandoned, cultivated. Higher soil water content in fallow fields is the most likely reason for greater mineralization in cultivated fields, while higher total organic C and C/N ratios in native and abandoned fields may explain differences between these land uses. Recovery of soil organic matter in abandoned fields appears to involve accumulation of soil C and N under perennial plants, but probable methodological artifacts complicate evaluation of the role of individual plants in recovery of N availability. Higher N mineralization and turnover in cultivated fields may make them more susceptible to N losses; recovery of N cycling in abandoned fields appears to involve a return to slower N turnover and tighter N cycling similar to native shortgrass steppe.

References:

Separation of the processes of cultivation that cause SOM loss:

Cultivation decreases soil organic matter (SOM) due to fewer plant residue inputs and greater outputs such as decomposition and erosion, but the relative effects of these processes are unknown. We designed a study to separate the effects of alteration of inputs and outputs on total and active SOM pools. We sampled four different SOM manipulations: high litter inputs (beneath live plants); low litter inputs (interspace); lack of litter inputs (antinduced bare area); and higher erosion, high decomposition, low litter inputs (wheatfallow agriculture) at two sites in and near the Pawnee National Grasslands. A cultivated system and a native system with 90% of all plant removal were simulated using the Century Ecosystem Model. Both active and total pools decreased in response to decreasing litter inputs, and the highest losses were found in cultivated treatments. Our study suggests that 1) depending on topographic position, erosion may both increase SOM inputs to and increase SOM outputs from a cultivated system, 2) plant absence in native areas confers comparable variability to land use management practices, and 3) when comparing Century simulations to our field data, we found that Century overestimates the amount of loss in SOM due to increased erosion and decomposition and underestimates the amount of SOM loss due to reduced plant litter inputs. (see [Figure SOM loss](#))

References: Bisbee et. al 1995

Recovery of shortgrass vegetation on abandoned agricultural fields:

Plowing and subsequent abandonment of semiarid grasslands in the shortgrass steppe region of North America results in both short and longterm changes in plant community structure. The traditional Clementsian model of succession in which shortgrasses rapidly dominate the vegetation was modified for these grasslands in the 1970's to predict a prolonged stage characterized by the dominance by the bunchgrass, *Aristida purpurea*, followed by a very slow recovery of shortgrasses after largescale disturbances. Because neither the Clementsian nor the modified model was supported by results of recent scale-dependent field experiments and simulation analyses, we designed a study to evaluate recovery of shortgrass communities on old fields abandoned for 53 years in the CPER and in the adjoining Pawnee National Grasslands of northeastern Colorado. Our objectives are: (1) to compare species composition on abandoned fields with adjacent, unplowed areas; (2) to compare vegetation on these fields with predictions from the prevailing conceptual models; and (3) to evaluate the relationship between recovery patterns within fields and distance from the source of propagules at the edge of a field. Dynamics of soil processes are also being studied on the same fields and are described elsewhere in this report.

For data collected in 1990, we reached different conclusions based upon the choice of indicator of recovery. For most fields (9 of 13), relative shortgrass cover did not fit predictions of either the Clementsian model or the modified model. High shortgrass cover on two of the remaining fields was similar to that expected by the Clementsian model, and low shortgrass cover on the remaining two fields was similar to that expected by the modified model. Two fields with high shortgrass cover were dominated by the less drought and grazingresistant species, *Buchloe dactyloides*, compared to *Bouteloua gracilis*, the dominant species in undisturbed communities. Uniformity in cover of other perennial graminoids and density of perennial forbs and annuals on and off fields indicated that these groups had recovered on most fields. However, differences in similarity in species composition on and off fields indicated that none of the fields had recovered. High variability in recovery of vegetation among fields with similar annual climatic variables and soil textures may be attributed to differences in initial conditions, management practices through time, finescale climate, and/or other site characteristics that were not measured in this study.

We found *B. gracilis* on all fields sampled, and it dominated basal cover on two fields. Four groups of fields were distinguishable based on the relationship between *B. gracilis* cover and distance from the edge with unplowed vegetation: (1) fields with uniformly high cover of *B. gracilis*; (2) fields with a decrease in cover with distance, and cover dominated by *B. gracilis*; (3) fields with a decrease in cover with distance, and cover dominated by *B. dactyloides* and (4) fields with uniformly low cover of *B. gracilis* and *B. dactyloides*, and dominated by other perennial graminoids indicating a mid to late successional stage had been reached.

Our results contrast with the conventional view of shortgrass community response to disturbances, and suggest an alternative view of the recovery process that focuses on interactions between individual plants and their environment to explain recovery patterns

that vary in time or space. Accounting for this variability in recovery is critical to the management of these systems, especially under conditions of changing climate and land use.

Results from this study, and in particular the large variability in recovery rates and patterns, led us to expand our sampling of old fields at the CPER. Approximately 25% of the CPER was plowed and abandoned prior to 1937. These fields are of similar abandonment age, climate, and grazing regime since at least 1969, yet differ in soil texture and most likely in past management practice. In 1994, we sampled vegetation and soils for 6 of these fields. Our plan is to continue sampling old fields at the CPER until all fields have been sampled once. We will then repeat the sampling of all fields at a 5 year interval. In addition, we plan to resample the 13 fields in the PNG at approximately 5 to 10 year intervals. (see [Figure 1.16](#), [Figure 2.30](#), [Figure 2.31](#))

References: Coffin et. al 1993, Burke et. al 1995, Ihori et. al 1995, Coffin et. al 1995 (in press)

Influence of plant presence and land management practices on nematode communities in shortgrass steppe:

Previous research in shortgrass steppe has shown that soil organic matter dynamics are extremely dependent upon both the spatial patterning of individual plants, and upon land-use management history. We conducted a study to evaluate the extent to which plant presence and landuse management control nematode community structure. We sampled soils in native shortgrass steppe, cultivated wheat fallow, and 8year old Conservation Reserve Program (CRP) land. We found that there were significantly more bacterial and fungalfeeding nematode under individual bunchgrasses than in the bare soil interspaces in both native and CRP fields. Total numbers of all nematodes were similar on CRP and native fields, demonstrating that 8 years was sufficient for recovery of these populations. Nematode populations were lowest on fallow wheat fields, and highest in currentyear wheat fields immediately following harvest. Our data suggest that nematode populations are highly responsive to litter inputs, resulting in strong spatial and seasonal patterning in shortgrass steppe.

References: Ortiz et. al 1995

Inertia in plant community structure: deflection after cessation of nutrient enrichment stress:

Water, nitrogen, and waterplusnitrogen at levels beyond the range normally experienced by shortgrass steppe communities were applied from 1971-75. Plant populations were sampled through 1977 and sampling was reestablished in 1982 to follow recovery. Although productivities increased, dissimilarities in plant species composition at the end of the five years of nutrient treatments were not significantly different from controls. Two years after cessation of the treatments exotic "weed" species were increasing in water plusnitrogen treated communities, and community dissimilarities were diverging in water and waterplusnitrogen treated communities. Seven years after cessation of treatments all communities were significantly different from controls. Exotics were more than ten times

more abundant in waterplusnitrogen and nitrogen treated communities than they had been two years post treatment. A consistent trend in recovery of all treated communities was evident over the next five years. However, the trend towards recovery reversed over the next four consecutive years in the previously waterplusnitrogen and water treated communities. The fourtofive year cycles in species composition and abundance of exotics towards, and then away from conditions in undisturbed, control communities were not related to weather, but large accumulations of litter suggested biotic regulation.

Inertia of existing plant populations, or the tendency to continue to occupy a site when conditions become unfavorable, can mask future deterioration in ecosystem condition and unstable behavior resulting from environmental stressors. Timelags in initial response mean that an ecosystem can pass a threshold leading to transitions to alternate states before it is evident in structural characteristics such as specie composition. Global climate change and sulfur and nitrogen oxide pollutants also have the potential to act as enrichment-stressors with initial timelags and/or positive effects and cumulative, subsequent negative effects, rather than as disturbance forces with immediate negative impacts. Sociopolitical systems, however, often require change in biological variables or negative impacts before acting to ameliorate environmental problems. The manner in which conclusions changed at various periods in time, and the potential for timelags in responses of species populations raises questions about which variables are most useful for detection of stress and how long studies must last to be useful. (see [Figure 1.17](#))

References: Milchunas and Lauenroth 1995

B. Biogeochemical Dynamics:

Our research in this area encompasses primary productivity , spatial patterns of carbon and nutrient cycling processes in unmanipulated grassland, responses to manipulations and landuse practices (see Disturbances/Human Use section), and fluxes of trace gasses. Because the inputs and movements of nutrients are closely tied to the inputs and fate of soil organic matter in semiarid regions, our approach is to deal with them together. We have focused on spatial heterogeneity and its causes at a range of scales, from individual plants to catenas, and physiographic units. We have also explicitly addressed the influence of recovery from disturbance on soil organic matter and nutrient dynamics.

1. Primary Production

The effects of increased temperature, water availability, and N availability on the relationship between ecosystem structure and function:

A prediction of our conceptual framework is that there are twoway interactions between the structure and function of shortgrass steppe ecosystems. Results from analyzing a longterm data set on aboveground net primary productions(ANPP) suggested that ecosystem structure constrained ANPP. Production was greater in dry years and less in wet years than expected by comparison with sites with mean annual precipitation corresponding to the wet and dry conditions. This leads us to the question: How does the

relationship between ecosystem structure and function change under altered climate and resource availability?

We initiated a new longterm experiment that addresses questions about the effects of increased temperature, increased water availability, and increased N availability on the relationship between ecosystem structure and function. A portion of the experiment (temperature and water manipulations) is also being conducted in the Patagonian steppe in Argentina with our collaborator Dr. Osvaldo Sala. In each of two blocks, we have implemented 4 treatments that each cover 0.12 ha (1200 m²): irrigated, control, N fertilization, and N fertilization plus irrigation. In the control and irrigated treatments, we have installed 60 warming chambers, so that we can assess a total of 6 treatments (the prior 4 plus warmed, and warmed and irrigated). We are measuring the responses of vegetation structure (species composition and numbers of tillers), ANPP, and decomposition (leaf and root litterbags) to these treatments, which we plan to sample intensively for the next several years, and less intensively for 20 years or more. (see [Figure 1.6](#))

References: Lauenroth and Sala 1992

Longterm monitoring of aboveground production:

We are continuing to monitor aboveground production on six sites selected to represent topographic positions and soil textures. Four sites have been sampled since 1983, and two since 1991. Production in the sandy lowland site was consistently greater than a more loamy lowland site, and the least productive site was the clay loam lowland. Grasses contributed nearly 100% of the production in the clay loam lowland, and shrubs and forbs were a relatively greater proportion of the production in ungrazed uplands compared to grazed uplands. In addition, nitrogen concentrations and yields are determined for all longterm ANPP sites. As a result of an experiment started in 1992 to study the effects of grazing and protection from grazing on shortgrass ecosystem structure and function, we are sampling net primary production in each of four treatments at five sites. These sites will be sampled as part of this longterm exclosure study, and will complement other data being collected at the same sites, as well as add to our longterm production data set. We are also continuing to evaluate belowground production using a radioisotope technique. (see Figures [1.5](#), [NPP.a](#))

References: Milchunas and Lauenroth 1992, Zak et al. 1994, Singh et al. (1996)

Longterm 14C plots, belowground production, and root biomass dynamics:

Large areas of native shortgrass steppe were heavily labeled with 14C for the purpose of assessing the implications of short and longterm carbon dynamics on estimates of aboveground, crown, and root production using 14C dilution, 14C turnover, and traditional harvest methods. Stabilization of plant labile 14C via translocation, incorporation into structural tissue, and respiration and exudation required one growing season. Respiration was 73% of initial uptake, and exudation was 17% of plant 14C after stabilization of labile 14C. Turnover estimates for leaves, crowns, and roots by 14C turnover were 3, 5, and 8 years, yielding estimates of belowground production that were

much lower than previously thought. Estimates of aboveground production by ^{14}C turnover were close to those obtained by harvest of peakstanding crop, but lower than reported values obtained by harvest maximum/minimum. Estimates of root production by harvest maximum/minimum were zero in 2 of 4 years. ^{14}C turnover appeared to provide reliable estimates of above-ground, crown, and root production, although they are an integration over many years. Annual estimates of production by ^{14}C turnover are biased by the difference in decomposition during a particular year from the average decomposition rate over the complete turnover period.

Anomalous estimates of root production by ^{14}C dilution were attributed to a nonuniform label resulting in differential decomposition of ^{14}C : ^{12}C through time, as well as movement and loss of labile ^{14}C through the first growing season. Based on ^{14}C turnover, eight years of labeling would be required to uniformly label the rootmass with ^{14}C . Isotope dilution methodologies may be unreliable for any estimate of pool turnover when the labeling period is not as long as pool turnover time. This does not similarly apply to isotope turnover methodologies when the labeled portion of the pool temporally progresses through all states, but assumes the proportion labeled within a defined pool, but not the quantity, at a pulse labeling is the same that would be labeled through all potential times of pulsing during the pool turnover time.

This spring was the 11th year of sampling on our longterm C^{14} plots. Several interesting developments have occurred since the initial publication of results from this experiment. First, the amount of C^{14} activity in aboveground, crown, and root tissue has held constant for several years, after a previous steady, linear decline. Second, all plant tissue-types appear to be converging to similar activities. Third, live roots (only those obviously live) were separated from dead detrital material in the previous year's sample, and no difference in activity between the two were found. These results suggest some type of internal cycling of carbon in this system. We took separate samples of new, green leaves in 1995 in addition to the usual aboveground leaf plus litter samples in order to further assess these unusual phenomena.

A minirhizotron was obtained through an Agricultural Experiment Station equipment grant. This year we began installing tubes adjacent to the C^{14} plots and the root harvest plots, where we have 11 yrs of root biomass data collected through the growing season. Minirhizotron tubes will also be installed at our new six-site, four-treatment grazing experiment. (see Figures A minirhizotron was obtained through an Agricultural Experiment Station equipment grant. This year we began installing tubes adjacent to the C^{14} plots and the root harvest plots, where we have 11 yrs of root biomass data collected through the growing season. Minirhizotron tubes will also be installed at our new six-site, four-treatment grazing experiment. (see Figures [2.17](#), [NPP.b](#), [NPP.c](#))

Reference: Milchunas and Lauenroth 1992

Errors in estimating production:

Simulation modeling has demonstrated the potential for large errors of estimating production when using traditional methods. We developed an analytical solution to the

problem of calculating production. Random errors associated with estimates of biomass used in calculation of net production always have the effect of overestimating net production. The overestimation was related to sampling effort in such a way that the more times biomass was estimated, the higher the overestimate. A method was also developed to correct net production values for the overestimation. This problem has been addressed by developing isotopeturnover methods of estimating ANPP, BNPP, and crown production.

References: Boindini et al. 1991, Milchunas and Lauenroth 1992

How can net primary productivity be measured in grazing ecosystems?:

The majority of studies that measure grassland aboveground production use peak biomass in yearlong temporary caged exclosures as estimates of production, and calculate consumption as the difference between standing crop in grazed plots. However, this method does not account for compensatory responses by grazed plants; production and consumption values may be systematically biased. We review four alternative methods: (1) animal metabolic models, (2) moveable exclosures, (3) clipping inside exclosures to simulate grazing, and (4) moving herbivores onto and off of pastures. Methods 2, 3, and 4 are designed to account for compensatory responses; however, they too may be subject to errors and biases. Selecting an appropriate method to measure grassland production and consumption requires understanding the limitations of the available methods.

References: McNaughton et al. 1995

2. Spatial Heterogeneity

Spatial patterns of root biomass and plant cover:

We quantified spatial patterns of root biomass and plant cover in 10 late successional, shortgrass steppe communities in which a large proportion of soil is bare and regeneration is frequently limited by soil water. Our main objectives were to evaluate patterns of root density associated with previously documented variation in recruitment in canopy openings of different sizes and to estimate the abundance of openings with low root density. Root biomass in the top 30 cm of soil was much lower in openings of all sizes than under plants and declined steeply as opening size increased. Biomass of light roots presumed to be functional was 62, 33 and 4% as much as under plants in centers of 10, 20, and 60 cm openings, respectively. Openings more than 5 cm across made up 34% of the surface. Most were small: 86% of openings were <20 cm across, a size at which strong interference between established plants and seedlings has been demonstrated. Openings without signs of disturbance were 88% of the openings. Only 2% of openings, equivalent to 2% of the area, were more than 50 cm across, a size supporting enhanced regeneration and having low root density. Nearly all of these large openings were caused by disturbance. However, many openings caused by disturbance were 30-50 cm across, a size range of transition from strong to weak interference, or smaller. Less than 0.5% was beyond *B. gracilis* root systems. We infer that most openings large enough to support enhanced recruitment are explored by roots of dominant bunchgrasses and that gap dynamics in shortgrass steppe involves constraints on water use in *B. gracilis* root

systems. Because large openings are rare, variation in belowground competition in abundant, smaller openings may be important to regeneration.

References: Hook et al. 1994

Evaluating spatial heterogeneity in aboveground biomass:

Our remote sensing research activities are evaluating spatial heterogeneity in aboveground biomass using the CENTURY model for comparison. Our objectives were to 1) compare the spatial heterogeneity of remote sensing indices and models and CENTURY models of aboveground biomass estimates. 2) to test the spatial independence of modeled estimates, and 3) to determine if spatial information could improve model estimates. Multiple regression models of the tasseledcap soil brightness index used in conjunction with vegetation indices has improved site level biomass estimation relative to univariate regression models. Soil texture, precipitation, and temperature were used as driving variables for aboveground biomass estimates in the CENTURY model. Holding weather variables constant, soil texture drives the heterogeneity of CENTURY model estimates at this site. An appropriate textural and spatial resolution for model and remote sensing data comparison were determined from canonical discriminant analysis. Ten soil texture groups were formed from the original sixteen soil texture classes. We compared linear, quadratic, and cubic regression models of modeled biomass as a function of remote sensing soil brightness index (SBI), soil wetness index (SWI), and green vegetation index (GVI) as well as elevation, stream proximity, and slope for two dates. Similar patterns of remote sensing indices as a function for percent sand were associated with texture group means for both years. Results indicated a poor correlation between model estimates and remote sensing, elevation, and 1st and 2nd order, 3rd and 4th order, and 1st through 4th order stream proximity. The mean remote sensing biomass estimates for two soil groups with relatively low sand content were higher than CENTURY estimates. High negative residuals (TM estimates higher than CENTURY) were associated with some but not all stream drainages.

References: Todd et. al 1993

Soil heterogeneity following death of individual plants:

The shortgrass steppe of northern Colorado is characterized by patchy plant cover and associated spatial heterogeneity of soil resources. Plant-associated zones of relatively high soil organic matter (SOM) and nutrient availability are likely the result of direct organic inputs through root death and exudation, as well as wind induced redistribution of soil. We studied the duration of plant-associated enrichment following plant death in labile, intermediate, and total pools of SOM. We sampled plant-associated microsites 0, 1, 9, and 36 months following plant death, and compared these values to betweenplant microsites. Soils associated with live plants and dead plants of all ages were enriched in total C and N relative to bare microsites. Labile and intermediate pools of SOM, however, were not enriched relative to bare microsites 36 months after plant death. We found a general pattern following plant death that is characterized by an initial phase of increased SOM and nutrient availability due to greater litterfall than decomposition. Shortly thereafter, there is a decrease in SOM and nutrient availability when substrate supplies decline and

decomposition continues. Though decomposition and nutrient release provide important resources to maintain plant-associated zones of enhanced SOM and nutrient availability for the first several months following plant death, our results suggest that enriched nutrient supply zones under dead plants do not persist beyond several months to provide resources to subsequently colonizing individuals. (see [Figure 1.8](#))

References: Kelly and Burke 1995 (submitted), Kelly 1995 (thesis)

Smallscale spatial heterogeneity in soil nutrients associated with the presence of *B. gracilis* individuals:

During 1990, we conducted a study on the smallscale spatial heterogeneity in soil nutrients associated with the presence of *B. gracilis* individuals. Field and laboratory analysis suggest that 1) plant-associated C and N are distributed concomitantly with the presence of *B. gracilis* individuals, 2) total soil C and N are higher under individual *B. gracilis* plants than between, and 3) available and potentially mineralizable C and N are higher under than between individual *B. gracilis* plants. These results have a great deal of significance for our understanding of shortgrass steppe ecosystems because they suggest that semiarid grasslands are subject to the same kind of plant-induced heterogeneity that is often recognized as occurring in semiarid shrublands.

References: Hook

Soil organic matter and nutrient availability responses to reduced plant inputs: an assessment of turnover characteristics:

It is difficult to obtain an understanding of the temporal dynamics of soil organic matter (SOM) because of the multiple pools and processes that interact to determine SOM content. Many simulation models subdivide SOM into pools based on turnover characteristics. Common to most of these models is the separation of an active pool responsible for nutrient supply, an intermediate pool, and a pool of stable SOM with an extremely long turnover time. Almost all of these separations are theoretically based on kinetic characterization, not empirically based on measurable pools. Through a finer separation and better understanding of decay characteristics of conceptual pools, we may be able to improve our ability to predict ecosystem response to disturbance.

Many studies attribute levels of SOM to levels of root biomass, but few, if any, go beyond a theoretical relationship to a quantitative measurement of the connection between root biomass and SOM. By examining this relationship over time, we will better understand the temporal dynamics of SOM in the region. We designed an experiment to assess the effects of reduced plant inputs on SOM based upon naturally occurring zones of plant removal across a spatial gradient in root biomass and a temporal gradient of disturbance age. In addition, we compared our field estimates to simulation modeling results, cultivation studies, and theoretical concepts of SOM pool size and turnover.

We found a tight connection between root biomass and SOM, especially in the active pools of microbial biomass and mineralizable C and N. Over time, a reduction in plant inputs led to large initial decreases in active and total SOM, but loss rates leveled off

following the initial period of approximately 10 years. Based upon our temporal measurements, we calculated turnover rates (kvalues) that were somewhat similar to theoretical abstractions of SOM turnover dynamics, except that we found passive SOM to be more tightly coupled to environmental changes than previously reported in the literature.

References: Kelly 1995 (thesis), Kelly et. al submitted

Influence of grazing on soil organic matter in U.S. shortgrass steppe:

Grazing-induced soil degradation has been cited as a major cause of ecological changes and reduced primary and secondary productivity in the world's dry regions. However, few controlled studies have been conducted to evaluate the effects of grazing on soil biogeochemistry. The shortgrass steppe of eastern Colorado provides an excellent location to evaluate the biological and physical effects of livestock grazing on soils. The composition of the dominant native bunchgrass community is not altered significantly by grazing, even under high levels of biomass removal.

We initiated an experiment to determine short(2y) and longterm (53y) effects of grazing on C and N dynamics at the Central Plains Experimental Range (CPER). Total soil C and N pools were unaffected by moderate grazing or enclosure following both 2 and 53 years of treatment. Particulate organic matter (POM) and microbial biomass were also unaffected; these pools represent recent belowground litter inputs and substrate available for decomposition. However, mineralizable C and N, representing the most active pools of soil organic matter, were significantly higher under longterm enclosure than longterm grazing, but only in bare soil areas between plants. Previous work reported increases in N mineralization in response to herbivory due to decreases in litter, decreases in immobilization potential, faster recycling of nutrients via feces and urine, higher ammonia volatilization, and increased soil temperatures. Our animal densities were lower than those reported upon due to lower primary productivity, thus, cycling rates are not as accelerated. Additionally, the basal cover of the dominant grass, *B. gracilis*, increases with grazing, ameliorating the thermal effects of reduced aboveground litter.

Bulk density was significantly higher in grazed treatments compared to the longterm ungrazed treatment (UU). Soil compaction is commonly cited as a factor that promotes runoff and, therefore, erosion on grazed lands, but soil C and N data suggest that erosion did not differ substantially among treatments. The small decreases in mineralizable C and N in bare areas may reflect slight erosion due to reduced canopy and litter cover or compaction by cattle.

Effects of grazing on soils were much smaller than localized differences imposed by individual plants. Individual bunchgrasses influenced all indices of soil organic matter strongly, indicating important effects of plants on organic matter accumulation and protection from erosion. This result is consistent with recent work on shortgrass steppe and other semiarid regions. Our results suggest that individual plants impose greater variation and are more important to system function than grazing management.

Grasslands are widely recognized for the large proportion of total carbon and nutrient capital that is stored in relatively recalcitrant organic matter pools. Carbon distribution and turnover to a 1 m depth at the CPER demonstrates that less than 1% of the C is present aboveground, and only 12% is present as roots. Previous work at the CPER indicated that grazing has a minor effect on roots, although work in other areas has shown grazing induced reductions in root biomass sufficient to increase net N mineralization. In our experiment, longterm removal of plant biomass by cattle did not reduce soil organic matter pools or processes, indicating that most organic matter originates from root litter. While our grazing intensities were not as high as may occur in heavily overgrazed areas, plant basal cover and rooting patterns in a pasture that has been grazed heavily for 53 years (50% higher forage removal than this study) provide no evidence that a threshold response in soils would occur under heavy grazing, short of denudation. (see [Figure 1.21](#))

Reference: Burke et al. 1994, Burke et al. in prep

The role of *Opuntia polycantha* and *Bouteloua gracilis* on conserving SOM in grazed and ungrazed pastures:

We are measuring microtopographic variation as an estimate of net erosion rates, and sampling material that accumulates under these species to assess the relative roles of organic and mineral deposition. We plan to regularly sample, at decadal intervals, to assess the actual rates of accumulation of material. Thus far, we have analyzed data on net erosion. Our data demonstrate that 1) there is substantial accumulation of material under both *B. gracilis* and *O. polycantha*, with the highest accumulation under *O. polycantha*; 2) grazing increases the redistribution of materials from interspaces to under these plants; and 3) the highest levels of redistribution occur in summit and midslope positions. (see Figures [2.13](#) [2.21](#))

References: Brannen

Long term ^{15}N studies in a catena of the shortgrass steppe:

A set of long term ^{15}N studies was initiated during the summers of 1981 and 1982 on the backslope and footslope, respectively, of a catena in the CPER. Microplots labeled with ^{15}N urea were sampled for ^{15}N and total N content in 1981 and 1982 and again in 1992. In November, 1982, 100% of the added N was recovered in the soilplant system of the finertextured footslope, compared to 39% in the coarsertextured backslope microplots. Ten years later, ^{15}N recovery of the applied N decreased at both topographic positions to 85% in the footslope and 29% in the backslope. Average losses since the time of application were 3.5g N m²yr⁻¹ in the back slope and 0.8g N m²yr⁻¹ in the footslope. In 1992, soil organic matter was physically fractionated into particulate (POM) and mineral associated (MAON) fractions and 21day mineralization incubations were conducted to assess the relative amounts of ^{15}N that were in the slow, passive and active soil organic matter pools, respectively, of the two soils. Our findings confirm the assumptions that POM represents a large portion of the slow organic compartment and that the MAON represents a large fraction of the passive compartment defined in the Century model. The N located in the MAON had the lowest availability for plant uptake. Isotopic data were

consistent with textural effects and with the Century model compartmentalization of soil organic N based on the residence time of the organic N.

References: Delgado et. al (in press)

Controls of soil carbon and nitrogen dynamics in semiarid grasslands:

Geomorphic processes, effects of individual plants, and seasonal variation in weather are thought to be important controls of soil carbon and nitrogen dynamics in semiarid grasslands, but their relative importance and interactions are not known. We quantified C and N pools and monitored seasonal patterns of N mineralization in 8 paired upland and lowland plots in shortgrass steppe. Plots represented diverse geomorphic settings, with lowlands ranging from minor swales to alluvial surfaces of ephemeral streams. Total C and N and mineralizable C in the top 15 cm of soil varied relatively little among upland sites but were 23 times greater in the 3 alluvial lowlands than on adjacent uplands; C and N in nonalluvial lowlands ranged from no greater to 1.8 X greater than adjacent uplands, with no clear pattern related to landscape position. Soil C and N pool were consistently greater under than between bunchgrass plants, and these differences were generally similar to or greater than topographic differences. Neither large nor small scale spatial patterns of N mineralization were as clear as C and N pool results. For most of the landscape studied, topographic variation in C and N appears to be less consistent than microscale heterogeneity related to patterns of plant cover, probably because runoff and associated material transport is limited. (see [Figure 1.7](#), [Figure 2.5](#))

References:

The influence of individual plants on soil nutrient dynamics in the central grassland region of the United States:

The extent to which plant community structure influences ecosystem nutrient cycling is an important but poorly understood element of ecosystem ecology. We studied the effects of two aspects of vegetation structure, plant cover patterns and plant species composition, on nutrient cycling in soils of shortgrass steppe, mid and tallgrass prairie, and desert grassland in the Great Plains. The general objective was to identify the importance of plant cover patterns and species composition, especially in the context of other environmental variables, to soil nutrient dynamics in these grasslands.

In the dry shortgrasssteppe and desert grasslands, plant cover patterns were very important in determining patterns of soil nutrient dynamics. Soils under plants had generally higher rates of carbon and nitrogen pool sizes and turnover rates than soils from adjacent bare ground areas between plants. Individual plant characteristics, such as lifespan and growth form, explained the degree of soil heterogeneity in some cases, with the most longlived, productive species fostering the most plantinterspace soil heterogeneity. Also, abiotic environmental variables explained patterns in plantinduced soil heterogeneity. The desert grassland with the largest proportion of bare ground, and thus possibly the most soil erosion, had the largest plantinterspace soil heterogeneity. The wet grasslands, the mid and tallgrass prairies, had more continuous plant cover; thus plant cover did not impose strong control over soil nutrient patterns in these ecosystems.

Plant litter quantity and quality of tissue for decomposers differed between species and grassland ecosystems and, in some cases, affected soil nutrient cycling. *Kochia scoparia*, an introduced species in shortgrass steppe, had high quality tissue (low carbon:nitrogen and lignin:nitrogen) and had relatively high rates of nitrogen and carbon mineralization in its soils. Precipitation affected plant tissue quality, with a general decrease in average quality and increase in interspecies variation in quality from dry to wet grasslands.

Vegetation structure, and its interaction with site-based abiotic variables such as precipitation, had important effects on soil carbon and nitrogen dynamics in these grassland ecosystems. Results indicate that information about plant community structure may be critical to large-scale estimates of ecosystem function. (see [Figure 2.20c](#))

References: Vinton et al. submitted, Vinton 1994 (dissertation)

3. Gas Flux

Nitrogen biogeochemistry and N gas emissions in the shortgrass steppe:

Recent studies in grasslands have found that gaseous N losses may be a keystone process regulating biogeochemistry of these ecosystems. Results from our studies at the CPER and data from other research indicate that rates of N₂O loss from grasslands are similar to rates of atmospheric N inputs, suggesting that exports of N in gaseous form may well be the principal control on long-term grassland N balance and productivity. Along with its role in regulating primary productivity, the N cycle of terrestrial ecosystems interacts with atmospheric trace gas chemistry in important ways. Keys to understanding the dynamics and magnitudes of N₂O fluxes are the relative and absolute magnitude of processes and biological properties which regulate N turnover.

From the 24 sites where trace gas studies have been or are being conducted in the CPER five were selected with differing textures, landscape positions and management. Within these sites simulated rainfall intensity was varied and the effect of various rainfall episodes on nitric oxide (NO) and N₂O, CH₄ and CO₂ fluxes were assessed. Concurrently, soils were analyzed for microbial biomass, net and gross N mineralization and immobilization estimates were made using ¹⁵N dilution and other soil parameters.

In the grassland sites, simulated light and heavy rain storms resulted in large and rapid responses in NO (10200 UG N m² hr⁻¹) and N₂O (150 UG N m² hr⁻¹) flux rates. Maximum rates were obtained in 30 minutes to 4 hours after wetting. NO flux rates were typically >10 times higher than N₂O flux rates in coarse-textured soils but were lower in fine-textured soils. The magnitude of the NO flux appeared to be related to the substrate availability and was well correlated with soil CO₂ fluxes. The duration of the flux was more closely controlled by the soil water filled pore space (WFPS). The NO flux rate peaked at approximately 35% WFPS for coarse-textured soils but were relatively lower and showed less marked response to WFPS in finer textured soils. N₂O fluxes continued to increase with increased WFPS. NO and N₂O fluxes are highly correlated following moderate size wetting events but are not correlated following large rain events. Microbial

biomass values for soils collected in early June show highest correlation with the anaerobic N mineralization and NO fluxes.

References:

Soil atmosphere exchange of CH₄, N₂O and CO₂: importance of yearround measurements:

Most tracegas budgets assume that tracegas exchange between the soil and the atmosphere stops when soil is snow covered or soil temperatures drop to about 0°C. In systems where soils are not typically snow covered, like the grasslands and cultivated fields of eastern CO and western NE, the soilatmosphere exchange of CH₄,N₂O and CO₂ were measured yearround at 2030 locations using closed chamber techniques. In subalpine systems gas fluxes were measured by measuring gas concentration gradients within the snow and calculating the fluxes using diffusion equations.

In the subalpine systems, soils beneath the snow pack emit CO₂ and N₂O and take up atmospheric CH₄ throughout the snowcovered period. Soil respiration under the snow represents oxidation of more than 25% of the estimated carbon fixed in the ecosystem during the growing season. About 30% of the annual CH₄ consumption and 32% of the N₂O emission in the subalpine system occurred during the snowcovered period. In the grasslands, Nov.Feb. fluxes of NO and N₂O comprise 1050% of the annual mean flux. There are times during the winter when surface soils thaw and moisture content of the thawed surface is high when N₂O fluxes are at the peak for the year at some sites. These data clearly show that gas fluxes that are controlled by soil microbial processes cannot be assumed to be negligible even when soil temperatures are near zero. Fluxes of N₂O, CH₄ and CO₂ during the four months of Nov.Feb. comprised 1556% of these gas fluxes. Using the assumption that Nov.Feb. CH₄ uptake rates were zero underestimate the mean annual CH₄ uptake rate by 2530%. (see [Figure 1.9](#))

References:

Soilatmosphere exchange of CH₄, N₂O and CO₂: agricultural systems in northeastern Colorado:

The influence of agriculture and agricultural management practices on N₂O emissions and CH₄ consumption in soils are not well known. We measured fluxes in native grassland (NG), grassland that had been N fertilized from 1976 to 1989 (FG), grassland that was first plowed in 1992 (PG), wheatfallow fields (one placed in the conservation reserve program in 1985 (CRP), one planted to wheat in September, 1993 (WHT), and one planted to wheat in September, 1994 (FAL)), and an irrigated wheat field (where no fertilizer was added (IWC) and another where 90 kg N ha⁻¹urea N was applied (IWN))

We observed the following trends: (1) in NG there is a longterm effect of N addition and plowing on both N₂O emission and CH₄ uptake (N₂O emissions increased 160% and CH₄ uptake decreased 25%); (2) in CRP N₂O fluxes remain 170% higher and CH₄ uptake 30% lower than NG; (3) N₂O emissions were 50% lower from the WHT than from the NG or the FAL while CH₄ uptake rates averaged 35 and 44%,respectively; (4)

N₂O emissions in IWC and IWN were 304 and 945% that of the NG while CH₄ uptake was 6 and 4% of the NG, respectively. Generally, as cropping intensity increased N₂O flux increased and CH₄ consumption decreased.

References:

Importance of aerobic soil consumption of CH₄ on the global CH₄ budget and relative effect on the global warming potential of trace gases in shortgrass steppe:

Considerations of global budgets of atmospheric methane have typically focused on production sources. Consumption of CH₄, other than through hydroxyl radical reaction in the atmosphere, has been given little attention in spite of a few measurements which indicated that aerobic soils potentially served as sinks for atmospheric methane. Our research was initiated partially to determine the soil sink strength for atmospheric CH₄ in a large variety of ecosystems. Longterm field campaigns for trace gas flux measurement were initiated two to four years ago in managed grasslands in AK and PR, in native and managed agricultural systems in CO, in subalpine forests and a managed grassland in WY, and in a long term tillage experiment in western NE. Weekly or more frequent flux measurements were made at most sites.

These studies are providing information which confirms that aerobic soils are an important sink for atmospheric CH₄. These and other studies around the globe led to a reassessment of the soilsink strength by the latest IPCC assessment, which concluded that the total global soil sink for atmospheric CH₄ is about 40 Tg C yr⁻¹. The soil CH₄ sink appears to be intimately tied to soil nitrogen dynamics and is strongly inhibited by fertilization or cultivation in some systems. This sink is similar in magnitude to other much more intensively studied terms of the global CH₄ budget, including emissions from rice paddies and enteric fermentation, and the rate of increase in the atmospheric CH₄ pool. Although it is clear that aerobic soil consumption of CH₄ is an important part of the global budget, how does a land area like the CO shortgrass steppe for example, impact the net green house gas flux? Since the grasses fix CO₂ we assume a net balance between fixation and respiration. The grasslands produce N₂O and are used for cattle grazing part of the year. The cattle produce CH₄ through enteric fermentation. Based on CPER stocking rates, animal size and diet, cattle produce about 0.16 kg CH₄ day⁻¹ cow⁻¹. A pasture stocked at the moderate rate of 20 animals for a 130 ha pasture and 130 stocking days emits about 420 kg of CH₄ yr⁻¹. The pasture produces about 40 kg of N₂O yr⁻¹ and consumes about 610 kg⁻¹ of CH₄ yr⁻¹. Using IPCC1994 global warming potential factors for CH₄ and N₂O, calculations indicate that because of the soil CH₄ sink, the shortgrass steppe has a net global warming capacity of 1100, ie is a net sink for greenhouse gases. Long term studies at selected sites will continue.

References:

C. Population and Trophic Dynamics:

Work in this area encompasses short and longterm population dynamics studies, food web structure, as well as competition, ecophysiological, demographic and phenological,

and genetic structure studies. Some of this research is reported in the Disturbance/Human Use or Biogeochemical Dynamics sections of this report.

1. Plant Populations

Competition between dominant species within a guild of short warm season grasses:

Bouteloua gracilis and *Buchloë dactyloides* are dominant and subdominant species in the shortgrass steppe and together constitute a guild of warmseasonperennial shortgrasses. Our general objective was to study the competition between these two species when resources are added. Our results indicated that competition can be very intense and important under both low and high availability of resources. Addition of water and nitrogen did not change the intensity of either intra or interspecific competition. Addition of resources did not reduce the intensity of belowground competition or significantly increase the shading (aboveground competition) among plants.

We also studied factors other than competition to explain the difference in the relative importance of these two species: recruitment differences, disturbance regime and drought tolerance. Longterm data suggest that *B. dactyloides* is less tolerant to drought than *B. gracilis*. The results indicated that differences in drought tolerance and recruitment probabilities along with their interactions with disturbance regime exert a major control on the biomass of the species. Biomass of each species increased with the relative superiority in recruitment. Disturbance favored *B. dactyloides*, while the intolerance to drought in *B. dactyloides* favored *B. gracilis*. In absence or with intermediate disturbance, a higher recruitment probability and greater tolerance to drought of *B. gracilis* than *B. dactyloides* yielded relative abundance of these species similar to the patterns observed in the shortgrass steppe.

References: Aguiar et. al 1994, Aguiar et. al submitted, Aguiar 1995 (dissertation)

The ability of *B. gracilis* roots to exploit resources:

We evaluated the ability of *B. gracilis* to exploit resources in central and outer portions of root systems. Morphological constraints were hypothesized to explain scales of strong neighbor interaction and gap dynamics observed in shortgrass steppe. Water or water plus nitrogen were supplied at horizontal distances greater or less than 10 cm from tillers in containers. Growth was significantly less when water was supplied only to the outer root system than when water was supplied only to the central root system. Reduced growth was associated with asymmetrical distribution of roots relative to direction of tiller growth. N addition did not affect plant growth. Although adventitious roots were mostly <10 cm from crowns, root length density and water use were similar in central portions of root systems and at distances >10 cm from leading ends of tillers, which corresponded to distances >10 cm from intact plants. Given typical plant spacings in shortgrass steppe (<15 cm), established *B. gracilis* individuals are likely to compete strongly and preempt resources in most openings. Results suggest that enhanced resource availability and colonization in small gaps (=50 cm) in shortgrass communities do not reflect strong morphological constraints on the outer root system of *B. gracilis* plants.

References: Hook

Plant species effects on temporal patterns of nutrient cycling:

We conducted an experiment to examine the impact of species with different phenologies on nutrient cycling patterns in the shortgrass steppe. Species having the C3 or C4 photosynthetic pathway have different optimum temperatures for photosynthesis and thus have periods of offset growth during a growing season. These differential growth patterns are expected to yield temporal differences in nutrient cycling for communities dominated by C3 species, C4 species or mixed communities. We conducted experiments at three time periods throughout a growing season; spring, summer and fall. During each time period we plan to examine nitrogen availability, nitrogen uptake by plants and movement through the soil profile, and atmospheric fluxes of NO, N₂O, CO₂ and CH₄. We will analyze these response variables for C3, C4 and mixed plots at two locations at the CPER.

During each time period, initial soil cores were taken for ammonium and nitrate extractions, and cores with resin bags were left in the field to analyze ammonium and nitrate levels at the end of the monthlong experiments. These data are currently being analyzed. ¹⁵N was added to plots to trace nitrogen use by plants and movement through the soil profile. Soil samples in the ¹⁵N plots were taken to 50cm after one month. Lab work is currently underway for analyzing soil and biomass samples for ¹⁵N. Gas fluxes were sampled on a weekly basis. (see [Figure 2.20](#))

Seed production in relation to soil texture and grazing:

We are continuing to sample seed production of individual *B. gracilis* plants each year on 10 sites selected to represent a range in soil textures as well as grazing intensities. Seed production as well as other morphological characteristics have been sampled from 108 plants at each site since 1989. Our data indicate that temporal and spatial variability in production of viable seeds are important constraints on the ability of *B. gracilis* to recover after disturbances. (see [Figure 1.1](#))

References: Coffin and Lauenroth 1990

Vectors of seed dispersal for two important grass species:

Plant recovery following disturbance is affected by interactions between disturbance characteristics and life history traits of plants in the community. Seed dispersal into a disturbed area is an important method of plant colonization during recovery. This project investigates vectors of seed dispersal for two dominant grasses at the CPER: *Bouteloua gracilis* (blue grama) and *Buchloe dactyloides* (buffalo grass). These two species vary in life history traits associated with recruitment that may affect their dispersability and recovery after disturbance. Specifically, we are evaluating the importance of cattle as vectors of dispersal of *B. gracilis* and *B. dactyloides* seeds. We will also investigate the wind dispersal patterns of these two species. Results from this study will aid in our understanding of the persistence and dominance by *B. gracilis* and *B. dactyloides* in the presence of disturbances of different sizes, and the role of cattle in the plant recovery process.

Approximately 225 recently deposited cow fecal pats were located and mapped in each of four halfsection pastures at the CPER in late Sept to early Oct 1994 after both *B. gracilis* and *B. dactyloides* had produced mature seed. These pats will be used to test for the presence of viable seed and examine changes in seed viability over time. Collection of 15 soil samples in June, July, and September from each pasture will be used to evaluate the seed availability in pats as compared to the soil seedbank. Wind dispersal of seed will be estimated by marking seed of isolated *B. gracilis* and *B. dactyloides* plants with fluorescent dye in July and August/September. Dispersal distances of seeds will be measured to determine the relationship between seed density and distance as well as maximum dispersal distance under natural conditions. In addition, wind tunnel studies will be conducted to measure seed dispersal distances for both *B. gracilis* and *B. dactyloides* at several wind speeds and release heights to determine the pattern of seed sinking velocity of each species.

References:

Development of microtopographic relief in a semiarid grassland: effects of disturbance size and soil texture:

Our objective was to evaluate effects of disturbance size (50, 100, 150 cm diameter created in 1984 to 1985) and soil texture (sandy loam, clay loam) on development of microtopographic relief for a shortgrass plant community. Disturbed plots were not manipulated after being created, and recovery occurred until microtopographic relief was measured in 1993.

Crown heights of plants were significantly higher than bare soil openings both for the undisturbed landscape and inside disturbances. Differences between crown heights of plants and bare soil openings were similar for both locations, indicating that smallscale microtopographic relief had recovered within nine years after disturbance occurred. However, complete recovery to the undisturbed state had not occurred, because crown heights of plants and bare soil openings were significantly less on disturbed than undisturbed microsites. These differences between locations and between microsites may indicate a net loss of soil material from bare soil interspaces, and a net accumulation of soil material under plants on disturbed areas.

Differences in height between plants and bare soil openings on disturbed plots increased as disturbance size increased, indicating greater soil erosion with increasing plot size. Larger differences in height were also found on plots on fine than coarse textured soil indicating the importance of soil particle size to the development of the microtopography.

Plant cover was also important to microtopographic relief. Differences in height between microsites were positively related to total plant cover and to cover of *B. gracilis*. Larger differences between plants and bare soil openings may be explained by the patchy characteristic of plant cover.

In this semiarid grassland, the topography at a large spatial scale is characterized by flat uplands and low-lands connected by gentle slopes. At a small scale, microtopographic

relief is heterogeneous, likely as a result of the smallscale redistribution of soil between bare openings and *B. gracilis* plants through time. We conclude that the microtopographic relief of shortgrass communities can become reestablished within a short time (<9 years) after disturbance.

References: MartinezTuranzas et. al submitted

Effects of the death of a single plant by disturbances on community structure and productivity:

This study was designed to address the following questions: 1. Will the death of individuals of different plant species have a differential effects on plant community structure? 2. Does grazing by cattle affect plant recovery for these patches? The experiment consists of twelve treatments (2 grazing levels: grazed and protected X 6 species: *B. gracilis*, *E. effusum*, *A. longiseta*, *Stipa comata*, *O. polyacantha*, *S. hystrix*). Individual plants were killed by clipping at ground level to keep soil disturbance to a minimum. Half of the plots were protected from grazing by using temporary exclosures. Plant community composition and basal cover from the target and neighboring plant species at the disturbed area and the surrounding area were measured before treatment application. The time of recolonization or recovery by seedling or vegetative propagules has been recorded at the end of each growing season of 1993, 1994 and 1995. Both plant community composition and basal cover of the plant species in the disturbed plots will be evaluated. Effects of small scale disturbances on shortterm recovery of plants will be evaluated by comparing simulation results from the Steppe Model and results from experimental field data.

Recovery patterns of *B. gracilis* on old agricultural fields:

Our objective was to determine the relationship between the recovery patterns of *B. gracilis* on old agricultural fields and the soil texture characteristics of these fields. Specifically this experiment is designed to address the following specific objectives: 1. To determine the degree of recovery of *B. gracilis* on the abandoned agricultural fields. 2. To determine the relationship between *B. gracilis*'s recovery patterns on abandoned agricultural fields and the distance from the edge of undisturbed vegetation. *B. gracilis* plants were sampled at each field in July of 1994 using transects (100 m long) spaced 10 m apart and located perpendicular to the edge of the field in order to determine the relationship between cover or density and the distance from the edge.

References:

Correlations between temperature and vegetation:

We analyzed longterm weather records from the CPER to identify patterns in T_{min} and T_{max} during warming trends. Correlation analyses between temperature trends and vegetation patterns were conducted to identify specific hypotheses to be addressed in fieldwarming experiments described below. Analysis of CPER weather records revealed a general warming trend in average annual temperatures from 1964 1992. This was largely the result of a significant increase in mean annual T_{min} . These changes in annual T_{min} are largely driven by increases in spring and summer average T_{min} . There was

considerable interannual variation in Tmax and precipitation; however, there was no significant trend in either of these variables during 1971-1991.

Permanently marked vegetation quadrats have been monitored annually at the CPER between 1971 and 1991, inclusive (with some gaps in data collection). We used this data on plant densities and aboveground net primary production (ANPP) along with annual and seasonal temperature and precipitation data to construct linear correlation models and assess the relationships between climate and vegetation. Positive correlations between vegetation response variable and Tmin included: (a) tiller densities of the dominant grass, *Bouteloua gracilis*, with mean annual Tmin; (b) stem densities of all other warm season grasses with spring Tmin; and (c) ANPP of a sedge with fall Tmin. Negative correlations with Tmin included: (a) forb stem densities and winter Tmin; (b) forb ANPP and spring Tmin; and (c) density of a dwarf shrub with summer Tmin.

Other vegetation response variables were correlated with Tmax (i.e., densities of shrubs, an exotic annual forb, and a cool season native grass; ANPP of a native forb; and total basal cover. Only densities of a cactus and species diversity were strongly correlated with precipitation. The evidence suggests that different species and functional groups are sensitive to variation in Tmin versus Tmax. One objective of climate change research is to improve our ability to predict the consequences of climate change on the structure and dynamics of real ecosystems. These analyses highlight the importance of conducting temperature manipulations that mimic the mechanism of documented warming trends in order to meet that objective.

References:

Effects of increased nocturnal temperatures on plantherbivore interactions:

In field experiments, we are manipulating nocturnal temperatures and grasshoppers to evaluate hypotheses that address four objectives: (i) determine the direct effects of increased nocturnal temperatures on plants, (ii) quantify the responses of plants to herbivory, (iii) assess the existence of interactive effects between temperature and herbivory on native grassland species assemblages, and (iv) evaluate the response of native grasshoppers to host plants growing at increased temperatures. During the latter half of the 1994 growing season, a pilot study on the feasibility of manipulating nocturnal temperatures was conducted by passively reducing soil to air reradiation. This pilot study was necessary since no similar apparatus for reducing soil heat loss has been discussed in the literature. The design incorporates a horizontally mounted polypropylene fabric curtain suspended from cables 0.8m above the ground and the sides of the angle down to within 0.15m of the ground. The warmed plot is 7m long by 6m wide. Measurements and herbivory treatments are restricted to a central 4x4m plot to avoid potential edge effects due to temperature gradients. The fabric curtain is pulled back and forth along its cable supports by a industrial garage door opener. The opener is connected to a timer to automatically cover the plot one-half hour before sunset and uncover the plot one-half hour before sunrise. This technique successfully elevated nocturnal soil temperatures by 1-1.5°C to a depth of 30cm over the several months of the study.

References:

N uptake by grasses and shrubs:

Plots containing both grass (*B. gracilis*) and shrub (*Atriplex canescens*) plants were labeled with ¹⁵N injected at four depths in the soil profile (5, 25, 45, and 65 cm), and plots containing grasses from around which shrubs were killed or shrubs from around which grasses were killed two years prior to labeling were injected with ¹⁵N at 5 and 65 cm in the soil profile. Shrubs exploited nitrogen where ever it was located, but grasses were relatively more constrained to exploiting surface pools. Shrubs tended to affect grasses, but grasses had little effect on shrubs. No difference in internal recycling abilities of the two lifeforms was observed, and soil nitrogen concentrations did not differ under versus between shrubs.

References:

2. Consumer Populations

Ecological investigations of the swift fox (*Vulpes velox*):

A total of 68 swift foxes have been captured. Fiftyfour of them have been radiocollared and ear tagged. An additional 14 have been eartagged only. Thirty four of the animals (14 adult males, 3 male pups, 12 adult females, 5 female pups) have been captured on the LTER site, the other thirtyfour individuals (16 adult or yearling females; 18 adult or yearling males) were captured on the Pawnee National Grasslands (PNG) within 40 km of the LTER. Nine females and 11 males captured on the PNG have been radiocollared, the other 14 animals were ear tagged. Trapping success compared to the late 1970's suggests that there are more swift fox present on the study sites than there were over a decade ago.

Seven (13%) of the 54 radiocollared animals, 4 males and 3 females have been killed. Four of the dead animals have been killed by coyotes, one from a motor vehicle, and two from causes undetermined. Two of the dead animals were recovered from cultivated areas adjacent to native prairie, one from a roadside, and four from prairie upland sites. One animal killed by a coyote was a lactating female her single pup was found dead near the den. The pup died from hypothermia or starvation. Pups of the year are just beginning to emerge from natal dens with a total of six dens located. Pup counts are lower (1.2 average) than counts made in the late 1970's and early 1980's (3.4 average).

Radio tracking and traprecapture data indicate that most animals are occupying home ranges of 45 km². A few individuals have moved over 7 km from their points of capture. Foxes are not utilizing saltbush communities during most of their foraging activity, possibly because of the potential for increased predation by coyotes in the denser habitat.

References:

Longterm canid monitoring:

In addition to monitoring populations of small mammals, we collect scats during January,

April, July, and October along the lagomorph survey route to track relative numbers of coyotes (*Canis latrans*) and swift foxes (*Vulpes velox*) on the Central Plains Experimental Range. All scats are removed from the lagomorph survey route ca. 10 d prior to the sampling period. During sampling, the route is driven slowly and the location, species and approximate age of all scats are recorded. These data currently serve only as an index to the relative abundance of these species; concurrent population studies using more reliable methods for estimating abundance (e.g., trapping) are needed to establish the relationship between scat counts and density. (see [Figure 2.16](#))

References: Stapp 1996 (dissertation)

Longterm monitoring of rodents and lagomorphs:

Small mammals (rodents and lagomorphs) influence the structure and function of grassland ecosystems as consumers of plants and arthropods, as movers of soils and soil nutrients, and as the primary prey of raptors and carnivorous mammals. Because of their intermediate trophic position, populations of small mammals may track changes in vegetation and the abiotic environment that may result from shifts in land use and other anthropogenic disturbances. These populations are variable over space and time, however, and their response to environmental changes may not be immediately apparent, given their behavioral plasticity and relatively long life span and generation times. Long-term studies of population and community dynamics, therefore, are needed to fully understand the role of small mammals in grassland ecosystems. In 1994, we began censusing populations of nocturnal rodents and lagomorphs. Our objective was to establish programs to assess spatial and temporal patterns of abundance and community composition of small mammals among representative vegetation types. These efforts will provide baseline information for future work on the site and for comparative studies among other sites in the LTER network. In April 1995, we completed our first year of sampling of small mammal and lagomorph populations on the site. Rodent densities are estimated in midspring (April/May) and late summer (August/September) on three 3.14ha trapping webs on upland prairie (dominated by *Bouteloua gracilis* and with little vegetative structure) and three webs on shrub grasslands (containing abundant *Atriplex canescens* and a variety of small shrubs). Our first year of results suggests that rodent diversity may be similar on prairie and shrubgrassland sites, but that rodents are more abundant on shrubdominated lowlands. Northern grasshopper mice and diurnal thirteen-lined ground squirrels (*Spermophilus tridecemlineatus* not currently monitored) are the only rodents consistently captured on upland prairie. Fifteen rodent species have been captured or seen on the study area, but four species [(grasshopper mouse, deer mouse, Ord's kangaroo rat (*Dipodomys ordii*), western harvest mouse (*Reithrodontomys megaliths*)] comprise most of our captures. In general, rodent diversity and abundance was much higher on shrubdominated lowland sites than open grassland, and rabbits showed marked seasonal variation in density.

We spotlight rabbits along a 32km route on one night in January, April, July, and October. The route consists of gravel roads and unimproved trails along pasture fences. Censused begin at dark and last ca. 4 hr. Perpendicular distances from the vehicle to rabbits are recorded; these data are used to calculate density in DISTANCE. Three

species of lagomorphs are present on our site. Blacktailed jackrabbits (*Lepus californicus*) and desert cottontails (*Sylvilagus audubonii*) are the most abundant species, particularly in saltbushdominated areas. Whitetailed jackrabbits (*L. townsendii*) are relatively uncommon and occur primarily on upland prairie. All species were least abundant during January in our first sampling year. (see [Figure 2.15](#))

References: Stapp 1996 (dissertation), Lindquist et al. 1995

Determinants of thirteenlined ground squirrel (*Spermophilus tridecemlineatus*) abundance:

We conducted a study to determine squirrel abundance on upland prairie and shrub-dominated lowlands and to identify factors affecting squirrel abundance on shortgrass steppe. Squirrels were livetrapped on three upland and lowland sites during June and July 1995. These data were compared to vegetation characteristics and prey abundance (arthropods). Squirrels were significantly more abundant in shrubdominated lowlands; adults were more numerous in June prior to juvenile emergence, whereas populations in July were dominated by youngoftheyear. Squirrels tended to be captured more often at trap stations with low, shortgrass vegetation, reflecting this species' preference for open habitats. Multipleregression models indicated that the abundance of orthopterans and density of small shrubs were the best predictors of squirrel abundance. On a broad scale, squirrels apparently respond to the presence of shrubs and associated edaphic conditions, but that other factors such as prey abundance may also be important.

References: Higgins and Stapp 1995

Determinants of habitat use and community structure of rodents:

We examined the relative roles of habitat structure, resource availability, and interspecific interactions as determinants of habitat use and community structure of rodents. This work has focused largely on two nocturnal murids (deer mice, *Peromyscus maniculatus*, and grasshopper mice, *Onychomys leucogaster*) and addresses 3 questions. First, what factors influence the distribution, abundance, and surface activity of grasshopper mice and at what scales are these elements important? This work has focused on movements of these mice with respect to the distribution of habitat characteristics and microhabitat distribution of insect prey. Second, how does the distribution of shrub cover influence movements, habitat use, and population size of deer mice? Like many quadrupedal rodents, deer mice prefer shrub cover, and this study examined how deer mice respond at both behavioral and population levels to the dispersion of shrubs. Third, how do grasshopper mice affect habitat use and local abundance of deer mice? Grasshopper mice prey on other rodents and their presence may influence population size and surface activity of deer mice and other rodents.

Unlike deer mice, grasshopper mice showed no affinity for shrubs on a microhabitat scale, even though arthropods tended to be captured most often in traps beneath shrubs. Powder tracking revealed that grasshopper mice prefer areas of soil disturbances, especially pocketgopher (*Thomomys talpoides*) mounds. Activity areas also had more soil disturbances than randomlychosen points. On a macrohabitat scale, the abundance of

grasshopper mice was positively correlated with soil texture, although mice were more numerous in areas with both coarsely textured soils and large shrubs. Because diversity and abundance of arthropods also tended to reflect gradients in soil texture, grasshopper mice may respond directly to structural habitat elements or to prey availability.

We live-trapped rodents across a range of shrub densities to investigate the relationship between the dispersion of shrubs and deer mouse abundance. Movements were significantly more directed and less tortuous in areas where shrubs were far apart and more regularly spaced. Densities of deer mice increased with increasing shrub density and shrub clustering. Integration of the responses to shrubs at individual and population scales will provide a mechanistic link between individual behavior and patterns of abundance and distribution.

We conducted a behavioral experiment to test whether deer mice avoid grasshopper mice using olfactory cues. Results indicated that olfactory cues may not be important. A removal experiment to examine the effects of grasshopper mice on habitat use and population size of deer mice indicated that deer mouse numbers declined on both control and removal sites, but the decline was more marked on control areas, where grasshopper mouse numbers increased. Deer mice also increased their use of shrub microhabitats on control sites; shrub microhabitats may be safer because they typically are not used by grasshopper mice. Results of a concurrent diet study will help to clarify whether interactions between these species are competitive or predatory.

References: Stapp 1995a, Stapp 1995b, Stapp 1994, Stapp et al. 1994, Stapp and Van Horne 1995.

Owl predation on small mammals:

We collected and analyzed pellets from known roosts of great horned owls (*Bubo virginianus*) during 1992-1994 to examine seasonal trends in owl predation on small mammals. We also compared species composition of small rodents in the diet to the relative abundance of rodents. In all seasons, lagomorphs comprised most of the diet in terms of biomass, although most individual prey items taken were rodents (primarily deer mice). Pocket gophers (*Thomomys talpoides*) were also preyed upon in all seasons, with the highest percentage consumed in spring. Comparisons of diet with information on rodent abundance suggested that owls hunted in a relatively restricted part of our study area, especially in winter. Most prey apparently were taken from roadsides, buildings, and an adjacent saltbush (*Atriplex canescens*) floodplain, where rodent densities remained relatively higher in all seasons than in the surrounding vegetation. We speculated that the use of these foraging habitats may reflect the availability of suitable hunting perches on the site. (see We collected and analyzed pellets from known roosts of great horned owls (*Bubo virginianus*) during 1992-1994 to examine seasonal trends in owl predation on small mammals. We also compared species composition of small rodents in the diet to the relative abundance of rodents. In all seasons, lagomorphs comprised most of the diet in terms of biomass, although most individual prey items taken were rodents (primarily deer mice). Pocket gophers (*Thomomys talpoides*) were also preyed upon in all seasons, with the highest percentage consumed in spring. Comparisons of diet with

information on rodent abundance suggested that owls hunted in a relatively restricted part of our study area, especially in winter. Most prey apparently were taken from roadsides, buildings, and an adjacent saltbush (*Atriplex canescens*) floodplain, where rodent densities remained relatively higher in all seasons than in the surrounding vegetation. We speculated that the use of these foraging habitats may reflect the availability of suitable hunting perches on the site. (see [Figure 1.3](#))

References: Zimmerman et. al (submitted)

Longterm arthropod monitoring:

In accordance with the longterm research framework at the CPER/LTER site, we have initiated and implemented a system for monitoring arthropod population densities and community diversities. We have collected such data for the past two years and will continue to do so for at least two more, which will result in baseline density and diversity data for an abundant and understudied faunal component of the CPER. In addition, a reference collection will be compiled of some of the more abundant arthropods. These data and the established protocol may then act as the foundations for future arthropod research at the site.

Six 638m² live pitfall trapping webs are located in six areas of the CPER. Each web consists of 80 pitfall traps. Traps are arranged in 8 rays radiating out from a central spot, with 10 traps per ray. Trapping is conducted once a month from late May to late August (4 trapping sessions), regardless of weather, in which all 480 traps are checked once daily for six consecutive days. The contents of each individual trap are recorded and released.

Longterm June beetle (*Phyllophaga* sp.) population monitoring:

June beetles (*Phyllophaga* sp.) represent one of the most important populations of herbivores because of their effects on the system rather than as a result of their abundance. The larval stage of *Phyllophaga* feeds on roots of *B. gracilis*, which in certain years results in widespread but patchy death of individuals. Populations of adults have been monitored since 1986 using light traps. Year to year fluctuations in density of adults are large, ranging from peaks of 40 to 360/week.

Microhabitat selection and community structure of darkling beetles (Coleoptera: Tenebrionidae):

We conducted pitfall trapping studies between 1992 and 1995 to evaluate the effects of vegetation structure and soil texture on seasonal variation in relative abundance and species composition of darkling beetles (Coleoptera: Tenebrionidae) on shrubdominated lowland areas. In spring and summer, we recorded captures of beetles in traps placed in shrub, cactus, grass, and bareground microhabitats. These data were used to assess seasonal and diel timing of activity, document changes in beetle abundance, and to compare patterns of community structure among vegetation/soil types. Beetles were most numerous in summer on all sites, although some species showed peaks of activity in late spring. All but one species (*Eleodes sextricata*) preferred traps beneath shrubs, revealing the importance of these microhabitats for thermal cover, food, or protection from predators. Furthermore, on shrublands, beetles were more nocturnal than had been

reported previously for adjacent open grassland, suggesting that shrubs kept temperatures on lowlying areas warmer at night than on upland prairie. Fourteen tenebrionid species were captured, and on average more species were captured beneath shrubs than in other microhabitats. Each site had a suite of five resident species, of which only *E. obscura* and *Embaphion contusum* were captured on all sites during all trapping periods. Species richness and diversity and beetle abundance, especially of the most common species (*E. obscura*), were inversely related to shrub density but increased with increasing soil coarseness. Overall, tenebrionid communities on shrubdominated areas were similar to those reported for open grasslands, but small species tend to be dominant on uplands, perhaps because most refuges are relatively small. The prevalence of larger beetles in areas with coarse soils and large shrubs may reflect the abundance of suitable refuges, both below ground and under vegetation, as well as the availability of feeding and oviposition sites.

Another related project includes a study of the effects of landscape structure on the movement patterns of beetles. This is an ongoing, relatively shortterm project (expected completion date: 1998) that entails measuring beetle movement paths in areas with different habitats and correlating path metrics (e.g. net displacement, fractal dimension) with habitat structure. Two or three more field seasons of data will be collected that will focus on elucidating the processes (primarily pertaining to food distributions) accounting for the movement patterns observed. (see [Figure2-17n](#))

References: Stapp 1995, Stapp submitted

A comparison of two arthropod collection techniques:

The efficacy of two arthropod collection techniques (live pitfall trapping and kill pitfalling with propylene glycol) were compared. Kill pitfall traps caught significantly more species and individuals overall than did live pitfalls, but this effect was mediated by species-specific capture events. Differences between the two trap types were attributed to attractant properties of the propylene glycol, because the same number of individuals per species was caught in both trap types for those species that were collected in both trap types. This indicated that better retention of captured arthropods by the killing agent was not responsible for the observed differences. Because of species-specific differences in trap efficiency from nonneutral properties of the killing agent and because kill pitfalling indiscriminately eliminates more than just the target taxa, live pitfall trapping is recommended over kill pitfalling with propylene glycol.

References: Weeks and McIntyre submitted

Methamidophos application effects on *Pasimachus elongatus* (Coleoptera: Carabidae):

Population densities of a predatory ground beetle, *P. elongatus* (Coleoptera: Carabidae), were examined at the site. Using distance sampling theory, we analyzed density estimates dating from before an application of the insecticide methamidophos (1988) and three beetle generations afterward (1994) to address the following questions. Have population densities of *P. elongatus* recovered to prespray levels? Are current population densities of *P. elongatus* in areas exposed to methamidophos in 1988 equal to those not exposed in

1988? How do population densities of *P. elongatus* vary with habitat type in methamidophos exposed and unexposed areas? This work updates earlier findings that *P. elongatus* population densities decreased after methamidophos applications. Lingering differences in *P. elongatus* densities were found among areas differing in methamidophos exposure; these differences were also related to habitat type. Higher population densities were found in methamidophos exposed than in control areas; higher densities were also found in shrub dominated than in grass dominated sites, regardless of past methamidophos exposure and nonexposed areas and despite the greater abundance of the carnivorous *Pasimachus* in treatment areas. *P. elongatus* density patterns are discussed in relation to possible longterm disruption of the arthropod prey community by methamidophos.

References: McIntyre 1995

Spider community response to manipulated microhabitat structure:

We have just begun the first portion of a two year study investigating the diversity of spiders on the CPER. An additional component of this work will be to investigate spider community response to manipulated microhabitat structure. The relative proportions of grass to bare ground patches will be manipulated into a microhabitat patch mosaic.

D. Paleoecology/Paleopedology:

Paleoecological Analysis of the Semiarid Shortgrass Steppe:

Our research, to date, has focused on reconstructing the evolution of Holocene landforms, vegetation and climate at the Central Plains Experimental Range (CPER). We use the stable C isotope composition of paleosols to provide a record of paleovegetation from which inferences to climate change can be made. Seven paleosols have been dated to provide chronologic control. We are currently investigating the shape and area of paleosols and expanding our investigation beyond the boundaries of the CPER to test our conceptual model of Holocene shortgrass steppe evolution.

CPER paleosols appear to have been preserved as small "patches" (< 1 km²) rather than as extensive, continuous surfaces. It is unclear, given their contemporary landscape positions, what positions they occupied on the paleolandscape. A robust interpretation of the Holocene paleoenvironment requires the determination of paleosol area and morphometry. Extensive coring must be done to determine if these relic features were isolated depressions or part of a more extensive landscape. A paleosol dated at 7980±100 y.b.p. was surveyed at 3 m intervals. It was apparently crescent shaped with a total area of <100 m², suggestive of an oxbow lake.

We are entering into collaborative research with Dr. Richard Madole of the United States Geological Survey, testing our Holocene conceptual model with a detailed investigation of the stratigraphy and geomorphology of that portion of the shortgrass steppe which encompasses the Colorado Piedmont and High Plains physiographic provinces of the Platte River drainage. The objective of this research is to identify and characterize paleosols according to the protocols developed for the CPER, linking paleosurfaces

chronologically as well as spatially. Our goal is to develop a model of Holocene shortgrass steppe evolution that is linked to regional and climatically driven geologic episodes.

We are also entering into collaborative research with Dr. Rosemary Capo of the University of Pittsburgh, using Sr isotope measurements as a proxy for Ca in quantifying the amount of weathering versus atmospheric inputs of nutrients to the shortgrass steppe ecosystem. Our goal is to develop a better understanding of mineral weathering in this semiarid environment, and to develop a conceptual model which evaluates the resilience and recovery potential of the shortgrass steppe nutrient reserve to climatic disturbance. (see [Figure 1.10](#))

References: Kelly 1994, Blecker et. al 1995

E. Water and Energy Dynamics

Longterm dynamics and patterns of soil water:

Soil water at 30, 45, 60, 75, and 90 cm depths were monitored on four sites at the CPER from 1985-92, using a neutron probe. Each site comprised an upland, a midslope and a lowland position. The study focused on the soil water dynamics in the portion of profile which is beyond the influence of bare soil evaporation. The clay loam site was the wettest and the sandy loam site was the driest, while the two sandy clay loam sites were intermediate. Soil water did not vary systematically among the slope positions. Across all sites, slope positions and years, the water content of each soil layer was related to that of all other layers; the correlation coefficient between any pair of soil layers declined with increasing distance between the layers. Linear combinations of soil texture and precipitation terms explained a significant amount of variability in water content of different soil layers. Current water content of a soil layer was also related with the previous water content of that layer; this relationship strengthened with depth. Soil water showed a marked seasonality, a recharge during the winter and a depletion during the growing season. The deeper soil layers were more dynamic in terms of soil water during the wet years compared to the dry years. NPP had an inverse nonlinear relationship with growing season mean soil water content of different layers, indicating water use even from the deepest layer investigated.

References: Singh et al. 1996

Patterns of controls of water dynamics in the shortgrass steppe:

We integrated our longterm meteorological records with simulation analysis to evaluate a longterm estimate of soil water dynamics. This work represents a major step toward (1) systematically describing the temporal variability in precipitation and soil water between years and within growing seasons and (2) describing differences in dynamics of water at different soil depths and their relation to precipitation. In other words, it summarizes our understanding of patterns and controls of water dynamics in the shortgrass steppe. Precipitation is concentrated during the growing season. Small precipitation events which wet surface soil are most frequent and occur in similar amounts in most years. Water

from small rains is lost rapidly. Consequently, surface soil is usually dry and shows no seasonal pattern. Large rainfall events, which can infiltrate deeper, occur infrequently and are responsible for most of the difference between wet and dry years. Intermediate soil layers have highest soil water availability over the year and show a strong seasonal pattern related to spring and summer precipitation. Soil water is concentrated very near the surface in dry years and percolates up to 1.3m deep in wet years. The shallow modal distribution of soil water matches the distributions of roots of the dominant grass, *B.gracilis*, providing support for the hypothesized basis for dominance of *B. gracilis* and its coexistence with other species. Interaction of soil water and biotic constraints may determine the distributions and rates of ecosystem processes controlling organic matter and nutrients. Results demonstrate the need to focus efforts on understanding water dynamics near the soil surface, which has historically been very difficult to do with available technology. The results also provide a longterm context for studies conducted in any particular period and a basis for experimental manipulations of water to mimic dry, average, and wet years.

Reference: Sala et. al 1992

Seasonality of soil water loss in shortgrass steppe:

We completed a study of seasonality of soil water loss in shortgrass steppe. This study contributes to development of simple methods for estimating energy balance and evapotranspiration in areas with high proportions of bare soil. Microclimatic data commonly used to estimate water and energy balance were compared with weighing lysimeter data, which provided a direct estimate of water balance. Consistent relationships were found (1) between sensible heat flux and the midday difference between soil and air temperatures and (2) between total and net solar radiation. Evapotranspiration estimated from these relationships compared favorably with lysimeter data. This approach may provide a basis for estimating regional patterns of evapotranspiration from remotely sensed data and standard meteorological station data. It could also allow estimation of water balance in site specific research where weighing lysimeters, which are rare and expensive, are not available. Comparison of precipitation and lysimeter records also implied that dew formation may be common during the growing season; dew may be important to sustaining biological activity in surface soil between rains.

Reference:

Soil water patterns associated with a shrubland site:

We found increasing soil water content with depth at the Owl Creek enclosure site, associated with a substantial change in soil texture (from loamy sand to loam) at approximately 90 cm depth. This was in contrast to local areas of grassland where water content decreased with depth. This deep water resource is stable seasonally and in the longer term, affected only by very large precipitation events. It may account for the co-dominance of *Atriplex* and various grasses at this site, since it is only available to the deeprooted shrubs. (see [Figure 1.11](#))

References:

Lysimeter and microclimate data:

During the last year we have also worked extensively on analyzing and cleaning up data from the lysimeter microclimate site. The data from 1986 to 1992 has been checked and is available in a file that includes daily summary of all of the variables measured at the microclimate site. The variables include: daily net and total solar radiation, daily actual evapotranspiration water loss, precipitation inputs from several gauges, maximum and minimum air and soil temperatures, etc. A paper describing the microclimate data has recently been accepted in Agricultural Meteorology and another paper is being written to describe the winter water budgets at CPER from 1986-92. We are also working on a paper which compares the efficiency of different rain gauges. The results show that precipitation inputs are being underestimated by 30 to 50 cm during the winter. (see [Figure 2.24](#))

References:

Spatial patterns of soil water associated with smallscale disturbance:

We have documented spatial patterns of soil water associated with smallscale disturbance. The spatial scale of soil water heterogeneity is consistent with the scale of gap dynamics. This result supports one of the basic assumptions of the individual plantbased models that we are using in analyses of vegetation and ecosystem dynamics involved in recovery from disturbance and in analyses of regional controls of vegetation and ecosystem patterns. This study also demonstrated the feasibility of using time domain reflectometry to resolve soil water dynamics near the surface.

References: Hook and Lauenroth

2. Synthesis Activities

A. Field Experiments

Consequences of patterns in food webs on stability:

Data collected from the CPER has been used in conjunction with data from other sites as part of an across site comparison in search of patterns in food webs and the effects that disturbance has on these patterns and system stability. The work has resulted in 6 publications. The more significant results of the project have been reached by coupling the models traditionally used by community ecologists with those used by ecosystem ecologists. The studies listed below have provided insight into the roles of productivity and dynamics in structuring ecosystems, the calculation of interactions strength using field data, and common features of agricultural practices on the structure and function of soil communities.

We previously demonstrated that the resilience of simple food chains was directly related to the level of primary productivity and the rates of detritus inputs from external sources. The key to this study was in the development of Lotka Volterra based models that were

expressed in terms of ecological energetics. This result would seem to support the "dynamics hypothesis" that proposes that food chain length was a function of the limitations that increased length placed on the likelihood of the system recovering from a minor disturbance. A second important result was the finding that the feasibility (ability of the system to maintain positive population densities at steady state) of the food chains was a function of the level of productivity and detritus inputs. Higher levels of productivity were able to sustain longer food chains. This finding had been hypothesized G.E. Hutchinson (1959 Am. Nat. 93:145) and subsequently termed the "energetics hypothesis." The conclusion of our work was that system dynamics and energetics were inextricably interrelated. Food chain length was a function of both energetics and dynamics.

Considerable progress has been made in the development of procedures used to estimate the interaction strength among organisms with a food web. Paine (1992 Nature 355:73) proposed measuring interaction strengths among species through a series of species removal experiments. As an alternative, we estimated interaction strength with models. The population dynamics of species within the community were described after Moore et al. (1993) and DeRuiter et al. (1994), and the field average population densities, were substituted for the theoretical equilibria. The elements of the community matrix (interaction strengths) are estimated by sampling physiological parameters, consumption coefficients and population densities, from ranges established by microcosm and field data.

An interesting pattern emerged when we estimated the interaction strengths (as above) and the trophic position of each consumer-prey interaction within food webs in North America and Northern Europe. The negative effects of consumers on prey decreases with increased trophic position and the converse was true for the positive effects of prey on consumer. De Ruiter et al. (Science, in review) demonstrated that communities that possess this asymmetric patterning of interaction strength with increased trophic position are more likely to be stable than matrices depicting the same trophic structure but no pattern in the distribution of interaction strength.

The conclusion of our work with food chain length and interaction strength is that the energetic organization of communities forms the basis of ecosystem stability. In 1995-1996 the work will be directed towards empirical tests of these findings. (see [Figure webs](#))

References: Moore et. al 1993, Moore et. al 1993, Moore and DeRuiter 1993, Moore 1994, Moore et. al 1995 (accepted), DeRuiter, et. al 1995 (in review)

A quantitative assessment of the effects of grazing on vegetation and soils over a global range of environments:

Multiple regression analyses were performed on a worldwide data set compiled from

studies that compared species composition, aboveground primary production (ANPP), root biomass, and soil nutrients of grazed versus protected, ungrazed sites.

Changes in species composition with grazing were primarily a function of ANPP and evolutionary history of grazing of the site, with sensitivity to level of consumption third in importance. Changes in species composition increased with increasing productivity and with longer, more intense evolutionary histories of grazing. These three variables together with latitude explained 50% of the variance in composition of grasslands, and precipitation, evolutionary history, and years of protection explained 72% of the variance for shrublands, even though methods of measurement and grazing systems varied between studies. The response of shrublands was different from that of grasslands, with a change in evolutionary history of grazing of shrublands resulting in less effect on change in species composition than in grasslands.

Similar variables entered models of change in the dominant species with grazing, but explanatory power was less than for species composition. Increases of the dominant species were more likely to occur in shrublands than grasslands, and decreases more likely among bunch grasses than other lifeforms and among perennials than annuals.

Percentage differences in ANPP between grazed and ungrazed sites decreased with increasingly long evolutionary histories of grazing and increased with increasing ANPP. Although most effects of grazing on ANPP were negative, the statistical models predicted increases in ANPP with grazing under conditions of long history, low consumption, low ANPP, and large range in annual temperature for grasslands plus shrublands. The data and the models support the controversial hypothesis that grazing can increase ANPP in some situations.

Counter to the common held view that grazing negatively impacts root systems, there was no relationship between difference in ANPP with grazing and difference in root mass; as many positive as negative differences occurred even though most ANPP differences were negative. Further, there was a weak relationship between change in species composition and change in ANPP, and no relationship with root mass, soil organic matter, or soil nitrogen. All three belowground variables displayed both positive and negative values in response to grazing. Current management of much of the worlds grazinglands based on species composition criteria may lead to erroneous conclusions concerning the longterm ability of a system to sustain productivity. (see Figure [2.20b](#))

References: Milchunas and Lauenroth 1993

B. Simulation Modeling

STEPPE model:

We are continuing to use models of soil water dynamics (SOILWAT), plant community structure (STEPPE), and production and turnover of soil organic matter (CENTURY) to better understand various aspects of shortgrass steppe structure and function. We are continuing to use these models both independently and as linked, interacting models to

aid in the formulation of questions and hypotheses, and in the interpretation of field and laboratory data.

References: Parton et al. 1988, Coffin and Lauenroth 1990

Species recruitment across an environmental gradient:

We evaluated the effects of precipitation and temperature on the recruitment of two dominant perennial C4 grasses along an environmental transect from the Central Plains Experimental Range in northern Colorado to southern New Mexico. *Bouteloua gracilis* ranges from Canada to Mexico, and dominates the shortgrass steppe. *B. eriopoda* is limited to the southern United States and Mexico, and dominates the desert grasslands. Successful sexual reproduction is rare in these species, but may be important in explaining the species geographic ranges. We evaluated the probabilities of recruitment for these two species at 16 sites in Colorado and New Mexico, including three LTER sites, the Central Plains Experimental Range, the Sevilleta, and the Jornada, using a daily time step, multi layer soil water model (SOILWAT). We used 30 years of climatic data from weather stations to produce 5000 years of weather data for each site using a Markov weather generator. Both the environmental factors of most importance to the two species and probability of recruitment along the transect differed. Precipitation was more important to the recruitment of *B. gracilis* while temperature was more important to the recruitment of *B. eriopoda*. Probability of recruitment decreased from north to south for *B. gracilis* while increasing from north to south for *B. eriopoda*. These results suggest that recruitment is important in the distribution and dominance of these two species.

References: Minnick, T.J. and D.P. Coffin 1995

The importance of soil water in the recruitment of *Bouteloua gracilis* in the shortgrass steppe:

In the shortgrass steppe region of North America there is a controversy about the ability of the dominant species to recruit from seedlings. The prevailing view is that *B. gracilis* is incapable of recruitment from seedling in areas receiving <380 mm of annual precipitation. A common explanation for this situation is that environmental conditions permitting seedling establishment are infrequent. To assess the frequency of environmental conditions appropriate for the recruitment of *B. gracilis* we used a soil water simulation model and longterm climatic data in conjunction with detailed information about the ecophysiological requirements for seed germination and growth of seminal and adventitious roots.

We found that recruitment events occur as frequently as every 30 50 yr. on silty clay, silty clay loam, and silty loam soils, but less than once in 5000 yr. on sandy soils. Simulated frequencies of recruitment were sufficient to account for the observed abundance of *B. gracilis* in 7 or 11 soil textures evaluated. The differences in silt content and available water occurrence of recruitment events. Therefore, soil texture variability may explain the spatial pattern of recruitment and of population recovery after disturbance that occur at the soil type and microsite scales.

Annual precipitation explained a large fraction of the temporal variability in recruitment. On average, recruitment occurred in years when precipitation was above the mean. The occurrence of recruitment events in some dry years (precipitation < mean), and their absence during some wet years (precipitation > mean), emphasizes the importance of the intraseasonal distribution of precipitation.

The sensitivity of recruitment to soil water availability suggests that climate change, particularly changes that increase or decrease the amount or the effectiveness of soil water, could have important effects on the future of populations of *B. gracilis*. (see [Figure pop_b](#))

Reference: Lauenroth et al. 1994

Seedling recruitment potential of *Bouteloua gracilis* in the central grassland region:

We evaluated the recruitment potential by seedlings of the perennial C4 grass, *Bouteloua gracilis* (blue grama) for the central grassland region of the U.S., including the Central Plains Experimental Range, under current climatic conditions and for changes in climate. Four grassland types are found within this large region. *B. gracilis* dominates the vegetation for one grassland type found at the CPER, the shortgrass steppe, and is common in the other three types (northern and southern mixedgrass, and tallgrass prairies). The geographic distribution of abundance of this species may be explained by its potential for recruitment by seedlings. We used a multilayer daily time step soil water model to evaluate the probability of recruitment of *B. gracilis* seedlings for a range of soil textures and a range of current and expected changes in climatic conditions representative of the region. Simulations were conducted using daily precipitation and temperature data for > 200 weather stations. Probability of recruitment increased with increasing temperature and precipitation, and was also positively related to silt content of the soil. Probabilities were lowest in the coolest and driest areas, including parts of the shortgrass steppe. The effects of climate change on recruitment was dependent upon the balance between increases in temperature and decreases in precipitation. Sites most susceptible to change in climate were the shortgrass steppe and northern mixedgrass prairie where *B. gracilis* is most important to plant community structure and ecosystem processes.

Simulations conducted with the STEPPE model also indicated the importance of soil texture to the recovery of *B. gracilis* after disturbances of various sizes. Average probabilities of seedling establishment from the SOILWAT simulations were used in STEPPE based on silt and content. Disturbances on the soil with a large silt content (silt loam) had large *B. gracilis* biomass through time compared to soils with low silt content (sandy clay loam, loamy sand). Additionally, recovery was dependent upon disturbance size, where small disturbances recover faster than large disturbances. A nonlinear relationship was found between the proportion of plots recovered by *B. gracilis* in year 500 and silt content of the soil. Disturbance size was less important than soil texture in determining plant recovery. (see Figures [1.15](#) [2.33](#))

References:

CENTURY model:

We used the Century model to simulate the impact of climatic change and increased atmospheric CO₂ on dynamics of the shortgrass steppe. The results showed that increasing air temperature resulted in increased plant production and reduced soil organic matter levels. Increasing atmospheric CO₂ levels caused plant production and soil carbon levels to increase. The combined impact of increasing atmospheric CO₂ and climatic change is to reduce the decrease in SOM level caused by increasing air temperatures and to further increase the plant production. As part of the ecosystem modeling work, we compared the Century model (monthly time step simplified model) with the Grass model (daily time step process oriented model) and found that the Century and Grass models both did a good job of simulating annual plant production and seasonal patterns of live biomass at CPER. Results from the modeling work are described in five papers (see attached references).

During the last year we have worked on improving the soil water and soil temperature model (SOWAT) and have developed a new model for simulating snow melt, sublimation and bare soil evaporation during the winter. The SOWAT model was tested using data from the PILPS soil water comparison workshop in Australia and compared to 12 other water flow models. A paper describing this work was written and submitted for publication. A paper describing the new winter water budget model has been written, however, it has not yet been submitted for publication. The winter water budget model has been developed using data from the CPER lysimeter and microclimate station. (see [Figure 2.34](#))

References:

Soil-atmosphere exchange of CH₄, N₂O and CO₂: using field flux measurements for development of process-based gas flux models for CH₄ and N₂O:

Using the information collected during the past four years from a wide variety of research sites, we developed a set of first generation, process based models which describe the oxidation of CH₄ and production of N₂O in the soil. A general model was developed to simulate N₂ and N₂O fluxes from nitrification and denitrification. N₂O flux from nitrification is a function of the soil water filled pore space (WFPS), soil temperature and the maximum nitrification rate (soil specific parameter). The effect of WFPS on nitrification is a function of soil texture with the optimum value for nitrification occurring at higher WFPS for fine textured soils. Total N₂ and N₂O gas fluxes from denitrification are a function of the soil NO₃ level, soil respiration rate at 0.6 WFPS (index of available soil C) and soil WFPS. The maximum N gas flux from denitrification is calculated as the minimum of the soil respiration and soil NO₃ functions and reduced by WFPS function. Denitrification rates decrease as WFPS decreases below 0.9, with the rate decreasing most rapidly in the fine textured soils. The ratio of N₂:N₂O gas fluxes from denitrification is a function of soil respiration rate, soil NO₃ level and soil WFPS. The highest N₂:N₂O ratios occur for soils with low soil NO₃ levels, and high values of soil respiration and WFPS. The model is used to relate field measured fluxes to the processes which drive the fluxes.

The CH₄ uptake model is based on the observation that CH₄ uptake rates are limited by diffusion, and can thus be modeled based on Fick's first law of diffusion in which flux is proportional to the concentration gradient with respect to soil depth. Diffusion coefficients are estimated as functions of pressure, temperature, soil bulk density, texture and moisture. A factor relating soil N turnover to CH₄ uptake is also included.

Further refinement of these models and linkage to the CENTURY model is planned. Once that phase is accomplished, then the model package will be linked with GIS systems to develop regional flux models.

References:

C. Regional Analysis

Our regional analysis efforts are in conjunction with another NSF-supported project (BSR 9106183) that provides the funding for these efforts. Below we summarize a few of our important findings from that project that are relevant to our site-level research at the CPER.

Aboveground net primary productivity across a precipitation gradient in the Central Grassland region:

Controls on aboveground net primary productivity (ANPP) and vegetation structure at the CPER and at 12 satellite sites were studied across a precipitation gradient through the Central Grassland region. Patterns of productivity across the gradient may be explained by the inverse texture hypothesis which predicts that in arid and semiarid regions, plant communities on coarse-textured soils should have higher aboveground net primary productivity (ANPP) than those on fine-textured soils, while the reverse should occur in humid regions. The first objective was to test these predictions by measuring ANPP in 1993 and 1994 at 14 natural grassland sites (CPER + 12 satellite sites), equally divided between coarse and fine-textured soils, along a regional precipitation gradient (333 mm/y to 759 mm/y) where mean annual temperature remains constant. Below 400 mm of mean annual precipitation (MAP), coarse-textured sites were significantly more productive than fine-textured sites in 1993 but not in 1994. For all sites, ANPP was significantly correlated with both MAP and precipitation for the 12 month period preceding sampling. Soil texture explained a significant proportion of variability in ANPP of graminoids and forbs but not total ANPP.

The second objective was to quantify aboveground canopy structure of natural grasslands along the precipitation gradient to examine the consequences of increases in the importance of aboveground competition with increased productivity. We found abrupt shifts in maximum canopy height and in PAR transmission at the transitions between vegetation types. Transmission of PAR through the canopy decreased with increasing precipitation. With increasing precipitation, total biomass and LAI increased, but the proportion of biomass and leaf area near the soil surface decreased. Overall, these results revealed discontinuous changes in canopy structure between different vegetation types.

The third objective was to examine longterm precipitation dynamics and long term soil water dynamics for two contrasting soil textures to understand potential mechanisms for observed patterns in ANPP and canopy structure across the precipitation gradient. We used a daily time step multilayer soil water simulation model to examine these dynamics. With increasing total precipitation, the proportion of growing season (April 1 October 1) precipitation accounted for by large events (> 30 mm) increased significantly. Distribution of precipitation interacted with soil texture in determining transpiration and evaporation. Transpiration from the sandy soil was higher than from the clay loam at the four driest sites, while the reverse was true at the two wettest sites. For the clay loam, the deep 30100 cm soil layer represented a consistently important water resource only for the two wettest sites. Simulation results suggest that across this precipitation gradient the relative success of plant functional types with different rooting distributions and phenologies may vary according to soil texture.

Results presented here demonstrated that effects of abiotic driving variables on ecosystem dynamics may be mediated through vegetation structure. These results indicate the importance of including vegetation structure in regional analyses of ecosystem structure and function.

References:

A regional analysis of N mineralization in coarse and fine textured soils along a precipitation gradient in the Central Grasslands of the U.S:

We estimated field and laboratory N mineralization rates for seven paired sites of fine and coarse textured soils along a precipitation gradient extending from the semiarid shortgrass steppe of Eastern Colorado through the mesic tallgrass prairie of Nebraska.

No clear trend in field or laboratory rates of N mineralization was evident along this precipitation gradient. Laboratory rates were generally higher than field rates, especially toward the dry end of the gradient. Fine textured soils generally supported higher rates of N mineralization than did coarse textured soils.

References: Barrett et al. 1995

N retention in the northern mixedgrass prairie and shortgrass steppe:

Anthropogenic sources of fixed N contribute to a suite of environmental problems including acid deposition, groundwater pollution and accumulation of greenhouse and photochemically active grasses. Additions of fixed forms of N in excess of plant demand, may stress native terrestrial systems. We are developing an experiment to study the effects of elevated levels of N on native grassland systems along a temperature gradient of the Central Grasslands. We have collected soils from five sites along this gradient, extending from SE Montana, through Wyoming and Colorado, to the Panhandle of Texas. Preliminary analysis will include estimates of gross and net rates of N mineralization, potential C mineralization and SOM. Plans to initiate a fertilization experiment and monitor N trace gas flux are being developed.

References:

Regional patterns of NDVI in North American shrublands and grasslands:

We characterized the seasonal pattern of the Normalized Difference Vegetation Index (NDVI) of 49 grassland and shrubland sites corresponding to areas with low human impact. Each site was characterized as a vector of 21 elements, where each element corresponded to the average NDVI for one date. We used the integral of the NDVI as an estimate of the total production, and the difference between the maximum and minimum NDVI over the year as a measure of the seasonality.

Based on a Principal Component Analysis, the integral of the NDVI accounted for 63% of the variability of the SITEXDATE matrix. The difference between the maximum and minimum NDVI throughout the year accounted for 19%. Mean annual precipitation explained 67% of the variability of the integral of the NDVI curves ($p < 0.01$). The slope of the relationship between precipitation and integrated NDVI was significantly steeper for grasslands than for shrublands. The difference between the extreme values of NDVI increased with mean annual precipitation and the thermal amplitude, and decreased with mean annual temperature ($p < 0.01$). (see [Figure 2-20a](#))

References: Paruelo and Lauenroth 1995

Effects of grazing on ecosystems of the Great Plains:

Grazing by large herbivores has been part of the evolutionary and developmental environment of the Great Plains for the past 10,000 years. There is evidence that past grazing has had an important positive effect on the ability of the ecosystems of the Great Plains to withstand grazing by domestic livestock. Settlement of the region by European agriculturalists in the past 150 years has had major impacts, but there is no conclusive evidence that the change from wild ungulates to properly managed domestic livestock has had detrimental ecological impacts.

The major westeast and southnorth climatic gradients provide the best explanations for differences in the responses of ecosystems to grazing. Experiments conducted in the western, driest portion of the region suggests that plant communities in these areas are the least susceptible to detrimental impacts of improper grazing management. These areas also have the lowest productivity both of plants and animals. By contrast, plant communities in the eastern, wettest part of the plains has the capacity to support the largest number of animals per unit area but they are most susceptible to changes in community composition, diversity, and physiognomy under well managed light to moderate grazing. These communities are also potentially the most vulnerable to the detrimental impacts of poor management. Aboveground net primary production generally declines with grazing, although increases in the wettest areas have been attributed to opening dense canopies and reducing litter layers.

Interactions between livestock grazing and wildlife is a complex issue in the Great Plains as it is every where else. The same grazing management system can have positive impacts for one wildlife species and negative for others. Furthermore, it is clear in may

cases that the effects of one management system on a single species can be a mixture of positive and negative impacts.

Despite the fact that grazing by domestic livestock does not have simple relationships to the other elements of the structure and function of Great Plains ecosystems, management of grazing animals using current technology appears to be a sustainable resource use. The conversion of rangeland to cropland has many implications for both sustainable resource use and global environmental issues. (see [Figure 2.20d](#))

References: Lauenroth et al. 1994

ANPP estimates from NDVI for the Central Grassland region of the US:

The lack of a quantitative ecological interpretation of remotely sensed data is a major constraint for the use of satellite imagery in environmental studies. The ability to translate spectral data to biologically meaningful variables is a key step in increasing the use and value of satellite information. In this paper we present an empirical calibration of the relationship between the integral of the Normalized Difference Vegetation Index (NDVI) and aboveground net primary production (ANPP) for the Central Grassland Region of the United States. We calibrated a three year average of the NDVI integral (NDVII) (AVHRR/NOAA 1.1 km dataset) using spatially aggregated values of ANPP from rangeland survey data obtained from the Soil Conservation Service. This is the first attempt to calibrate a standard NDVI product for temperate grasslands.

For grassland areas with mean annual precipitation between 280 mm and 1150 mm, and mean annual temperature between 4°C and 20°C, the NDVII and ANPP showed a strong and statistically significant relationship ($r=0.93$, $n=19$, $p<0.001$). NDVII was positively related to the ANPP. The relationship found is based on NDVII and ANPP data averaged over time and aggregated at the same spatial scale.

References: Paruelo et al. submitted

Climatic controls of the relative abundance of plant functional types in grasslands and shrublands of North America:

It has been widely accepted that temperature is the principal control of the distribution of the number of C3 and C4 species. Our results showed that at a regional scale and based on data of relative abundance, precipitation and its seasonal distribution are important controls, in addition to temperature, of the distribution of C3 and C4 grasses. Latitude and longitude explained a substantial portion of the variability of the distribution of shrubs, C3 grasses, and C4 grasses (55%, 46%, and 62% respectively). Along a given longitude, C3 grasses increased with latitude. As one moves westward there is a replacement of C4 grasses by shrubs. The relative abundance of C4 grasses reached a maximum at southern latitudes and eastern longitudes. Succulents showed a marginal decreasing trend with latitude. For forbs, no relationship with geographic variables was detected. C4 grass distribution was positively related with three climatic variables: mean annual precipitation, mean annual temperature, and the proportion of the precipitation falling in summer. These variables accounted for 66% of the total variability of this

functional type. C3 grass abundance decreased with mean annual temperature and increased with the proportion of the precipitation falling during winter ($r^2 = 0.37$). Sixty two percent of the relative abundance of shrubs was explained by climate. The abundance of this functional type decreased with mean annual precipitation and increased with the proportion of water falling in winter.

References: Paruelo and Lauenroth 1995

Cross LTERsite comparison of factors that control decomposition: Effects of *Bouteloua gracilis* and *Bouteloua eriopoda* and indigenous microbes on rates of decomposition and soil organic matter formation:

We initiated a litter bag root decomposition experiment using transplanted soils from the Jornada and CPER longterm ecological research sites. Roots of the species *Bouteloua gracilis* and *Bouteloua eriopoda* were placed in both types of soils. The experiment began in late January 1994. We will harvest litter bags and soils in early July of this year, and calculate mass loss of the root litter.

Generating and testing daily weather data using a regional grassland data set:

Water balance will be a key aspect of ecosystem function in grasslands in response to global change. Most soil water balance models need daily weather data to generate reliable patterns. Those data are scarce for many regions of the world. We developed a procedure that generates daily data from a global data base of monthly precipitation and temperature on a 50 x 50 (lat., long.) scale. We tested the procedure by simulating daily data for the Central Grasslands USA and comparing them to actual data for 300 weather stations collected over a twenty year period. The generated data reproduced the regional and seasonal patterns of climate of the region. Multiple regression analysis showed that monthly averages of temperature, maximum temperature, minimum temperature, precipitation and number of rainy days were associated with geographic variables (lat., long.) for both generated and actual data ($p < 0.0001$) in a similar manner.

3. Current International Collaborations

Comparison between semiarid systems in North and South America:

During the last 15 years, the LTERCPER project has maintained a fruitful relationship with the Department of Ecology in the School of Agronomy, University of Buenos Aires. This relationship has grown in the last years through several projects of comparison between the shortgrass steppe ecosystem with the Patagonian steppe in South America. Currently, studies involve a comparison of grazing as an important driving force in the two systems. The shortgrass steppe has evolved under the impact of grazing, while the Patagonian steppe lacks a long evolutionary history of grazing. The consequence of this is that grazing has large impacts on plant communities in

the Patagonian steppe. We studied the consequences of these vegetation changes for the Patagonian steppe ecosystem.

Grazing promotes changes in the plant functional type composition of the Patagonian steppe, grasses are replaced by shrubs. This modification promotes differences in the soil water dynamics, through changes in the seasonality of the water losses through transpiration. Evaporation was maximum in intermediate situations where neither grasses nor shrubs dominate the community. We evaluated the primary and secondary production along the grazing gradient. Overgrazed systems, dominated by shrubs, had less primary and secondary production than ungrazed ecosystems dominated by grasses. We also studied the changes that occur in the albedo and roughness, two key parameters for predicting the feedbacks of the ecosystem to the atmosphere.

References: Aguiar et al. in press

Regional analyses of the structure and function of grassland and shrubland ecosystems:

We performed an analysis of the climatic patterns of the temperate zones in North and South America using a global database of monthly precipitation and temperature. Three synthetic variables, identified by a Principal Component Analysis of the monthly data, were used: mean annual precipitation, mean annual temperature and the proportion of the precipitation falling during summer. We displayed the spatial gradient of the three variables by constructing a composite color raster image. We used a parallelepiped classification algorithm to locate areas in both continents that are climatically similar to five North American Long Term Ecological Research sites and to two South American long term ecological research sites. The same algorithm was used to identify areas in South America which are climatically similar to some of the major grassland and shrubland types of North America.

There is substantial overlap between the climates of North and South America. Most of the climatic patterns found in South America are well represented in North America. However, there are certain climates in North America that are not found in South America. An example is a climate with relatively low mean annual temperature and high summer precipitation. The climatic signatures of three North American LTER sites (Cedar Creek, CPER and Sevilleta) were not found in South America. The climatic signatures of two LTER sites (Konza and Jornada) had some representation in South America. Two South American research sites (Rio Mayo and Las Chilcas) were well represented climatically in North America. The climates of six out of seven selected North American grassland and shrubland types were represented in South America. The

northern mixed prairie type was not represented climatically in South America. Our analysis suggests that comparisons of North and South America can provide a powerful test of climatic control over vegetation.

References:

Collaboration between Hungarian and LTER scientists:

As part of a project funded by NSF International Programs to Diana Freckman and Debra Coffin, we are investigating areas of collaboration between Hungarian scientists and LTER scientists with a focus on longterm biodiversity research.

4. Data Management

A. Longterm Storage and Maintenance

The primary goal of data management is to provide long term storage and maintenance of the LTER data. The design of our archival procedures, data base, and data base access system are all oriented toward achieving this goal. The second goal for data management is to provide assistance in the analysis of the data and the use of the data in modeling activities.

Over the last year a committee of scientists associated with the LTER program reviewed and amended the data management plan for the project. The committee developed a statement of the objectives for data management and policies for implementation of those objectives. The data management policies list the responsibilities of the scientists and the data management staff, and also give guidelines to ensure that data collected for the project become publicly accessible on a timely basis.

Our goal for this year was to get much of our data installed in the data base system, and to provide the project scientists with the tools and interfaces necessary to access the data. The tools for accessing the data are essentially completed, with the exception of updating of the manuals to reflect recent changes in the software. We have completed converting our system for handling bibliographic data from Fortran to C++, and have added an Xwindows interface (Motif) for entering and keywording references. We have also added an interactive tool for searching the bibliographic data base. The system enables one to save results of searches as ASCII files, WordPerfect files or FrameMaker files.

Our current system enables scientists from anywhere on the internet to access our publicly available data using the LTERMENU program that we developed. We have also developed a Mosaic "page" to provide access to our data. The data and data description files can be browsed with Mosaic. The advantage of LTERMENU over Mosaic is that it enables one to plot or to extract in tabular form specific columns of data from the data files. The Mosaic interface provides easy access to the files, but does not provide a way of easily extracting data. The data files are often hard to browse with Mosaic because most of our tabular data are stored in fixed field, card image formats.

B. LTER GIS Support and Development

GIS support continued through collection of new data, refinement of the current spatial data and metadata, additions to the CPER map atlas, further development of a computer interface to view these data, and GIS analysis in support of current and potential research. New digital map library layers include (1) a more spatially detailed soil survey with soil properties, (2) aerial photo indices, (3) new field study sites, and (4) acquisition through a cooperative project of Digital Elevation Models (DEMS) for watersheds surrounding the CPER.

Two major refinements of existing data have been accomplished. A new format for access and retrieval of historical field study sites was developed. This new format allows scientists to more easily identify past research, based on plant or animal species key words, soils key words if appropriate, researchers names, dates of study, and, of course, geographic proximity. The second refinement to existing data is the expansion of metadata and modification to the format allowing these data to be more easily shared with other data management software.

The CPER map atlas is a collection of color maps that can be viewed onscreen or printed out on a color printer. The atlas has been expanded to include new data layers, new combinations of data as requested by researchers, and black-and-white versions of most maps.

Modifications to the interface were driven by additions of new data to the digital map library and the expansion of metadata. GIS analysis covered a broad spectrum of needs. Basic support such as the generation of reference field maps or location of study sites was provided. More complex types of analysis such as logical queries using multiple map layers or determining the shape and orientation of certain landscape features were also provided.