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1. Brief summary of progress to date and work to be performed during the succeeding period;
2. Statement of funds estimated to remain unobligated —if more than 20%— at the end of the period for which NSF currently is providing support (not required for participants in the Federal Demonstration Project);
3. Proposed budget for the ensuing year in the NSF format, only if the original award letter did not indicate specific incremental amounts or if adjustments to a planned increment exceeding the greater of 10% or \$10,000 are being requested;
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P.I. Signature: Ingrid C. Burke

## **Central Plains Experimental Range Long Term Ecological Research Project 1993-94 Annual Report**

This is the 1993-94 progress report for the project entitled "Long term ecological research program - Shortgrass Steppe" (BSR 9011659) funded to Colorado State University. We had a successful year, and continue to make very good progress in furthering our understanding of the shortgrass steppe. The project produced 25 total papers and 15 papers in refereed journals since our last report. We supported a large number of graduate, undergraduate, and post doctoral fellows for research at the site. In addition, five senior-level scientists were added to our LTER in order to expand the breadth of scientific expertise and research being conducted at the site: Drs. Mike Coughenour (ecophysiological modeling, plant-animal interactions), Bill Hunt (soil food web ecology), Diana Freckman (nematode ecology), Jeff Welker (ecophysiology), and Chuck Grier (root ecology). Scientists at our site are involved in a number of LTER network activities, through comparative modeling studies, database management, international collaborations, and development of new cross-site experiments.

The report contains two sections: Summary and Overview, and a Detailed Report. We organized both sections into four key areas: Core Area Research, Synthesis Activities, Current International Collaborations, Data Management. A List of Publications is contained at the end of the Detailed Report.

### **I. SUMMARY AND OVERVIEW**

#### **1. CORE AREA RESEARCH**

##### **a. Pattern and control of primary production**

In an analysis of long-term forage production from 1943 to 1990, we found that average production was 75 (ungrazed), 71 (lightly), 68 (moderately), and 57 (heavily)  $\text{g m}^{-2} \text{y}^{-1}$  under the different grazing treatments. Variability in forage production was explained mostly by cool-season precipitation, and magnitude of forage production was more sensitive to annual fluctuations in precipitation than to long-term grazing treatments. Based upon a regression model constructed using data from 1939 through 1962, forage production was not affected by grazing at 20 to 35 % removal.

In an analysis of spatial patterns of root biomass and plant cover, we found that root biomass in the top 30 cm of soil was much lower in canopy openings of all sizes than under plants and declined steeply as opening size increased. Biomass of functional roots was 62, 33 and 4% more under plants than in centers of 10, 20 and 60 cm openings, respectively. Openings more than 5 cm across made up 34% of the surface, and most were small (<20 cm-diameter), a size at which strong interference between established plants and seedlings has been demonstrated. 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.

## **b. Spatial and temporal distribution of populations selected to represent trophic structure**

### **Plant populations**

In a study of intra- and inter-specific competition between *Bouteloua gracilis* and *Buchloe dactyloides* where water and nitrogen were added to plots in a factorial design, we found that competition was the dominant factor explaining total variability with no differences between intra- and inter-specific competition. The addition of water increased plant biomass 23%, while nitrogen increased biomass 17%; there was no interaction between the effect of both resources. Based upon the first year's results, we speculate that belowground competition is intense and important in the shortgrass steppe, and its role does not change with the differences in resources found in a major east-west gradient of precipitation. Morphological and ecophysiological similarities between *B. gracilis* and *B. dactyloides* hamper the role of competition as the main force determining relative success of these two species. Relative abundance of the two species should be the result of other ecological processes such as tolerance to herbivory, response to drought, response to disturbance, etc..

We evaluated the ability of *B. gracilis* to exploit resources in central and outer portions of root systems. 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. 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.

### **Animal populations**

We investigated the relative roles of species interactions, vegetation structure, and resource availability as determinants of habitat use and community organization of rodents at the CPER, including a detailed examination of the habitat use and movement patterns of the northern grasshopper mouse (*Onychomys leucogaster*). Preliminary analyses of microhabitat use data from fluorescent powder tracking confirm that the movements of deer mice are influenced by the distribution of shrub cover. A large proportion of the movement pathways of grasshopper mice were in areas with considerable soil disturbance by pocket gophers and harvest ants, and numerous rodent burrows. We speculate that grasshopper mice preferentially use these areas because prey availability is higher in these microhabitats. In an experiment to test the hypothesis that deer mice directly avoid grasshopper mice, wild deer mice were provided with a choice of traps containing fecal and urinary odors of grasshopper mice, odors of western harvest mice, and clean traps. Contrary to expectations, deer mice did not avoid traps containing grasshopper mouse odors.

## **c. Pattern and control of organic matter accumulation and of inorganic inputs and movements of nutrients**

### Spatial heterogeneity

We examined the importance of plant species and plant cover (ie. plant covered microsites vs. bare soil) on nutrient cycling at the CPER by using an area that had undergone nitrogen and water additions from 1971-1974, resulting in significant shifts in plant species composition. Soils under plants had consistently higher C and N mineralization rates, and in some cases, higher total and microbial C and N levels, than soils from bare soil. Four native grasses, one sedge and one shrub differed from one another in the quantity and quality of above- and belowground biomass, but differences among the six species in soil nutrient cycling under their canopies were slight. Plant cover patterns had larger effects on ecosystem-scale estimates of soil properties than the attributes of a particular plant species likely as a result of the semi-arid nature of this grassland in which plant cover is discontinuous and decomposition and nutrient availability are primarily limited by water, not by plant species-mediated characteristics such as litter quality. That local plant-induced patterns in soil properties significantly affected ecosystem scale estimates indicates that consideration of structural attributes, particularly plant cover patterns, is critical to estimates of ecosystem function in shortgrass steppe.

We quantified C and N pools and monitored seasonal patterns of N mineralization in 8 paired upland and lowland plots representing 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 2-3 times greater in the 3 alluvial lowlands than on adjacent uplands. Soil C and N pools were consistently greater under than between bunchgrasses, and these differences were generally similar to or greater than topographic differences. For most landscapes, topographic variation in C & N appears to be less consistent than microscale heterogeneity related to patterns of plant cover, probably because runoff and associated material transport is limited.

We are continuing our research on soil-climate interactions in order to understand the climatic and biological conditions that existed during the Holocene. We use the stable C isotope composition of paleosols to provide a record of paleovegetation from which inferences to climate change can be made. Surficial geologic deposits at the CPER which bury Holocene paleosols include multiple types and ages of both alluvium and loess. None of the parent materials sampled were clearly eolian; several deposits thought to be fluvial had loessal characteristics and no deposits resemble dunes. Published  $^{14}\text{C}$  dates for CPER paleosols indicated three periods of soil formation during the Holocene: 10000-8000, 5000-3000, and 1500-0 ybp. Early Holocene paleosols were the most well-developed, and appeared to contain more organic C than soils of subsequent soil-forming intervals. In general, morphologic evidence suggests the early Holocene environment was conducive to more rapid pedogenesis than subsequent soil-forming intervals.

### Recovery from disturbance

In 1991, we began a new experiment on the influence of grazing on shortgrass steppe ecosystem structure and function. We manipulated the boundaries of 6 exclosures to produce 4 treatments: 1) long-term grazed, currently grazed; 2) long-term grazed, currently ungrazed 3) long-term exclosed, currently exclosed; and 4) long-term exclosed, currently grazed.

Two years following the new manipulations, we sampled soil organic matter for total and more active indices such as mineralizable C and N. Our results indicate that there is significantly less

total C, total N, and mineralizable N in the long-term grazed than the long-term exclosed treatments. For the more active pools, both short-term treatments were statistically indistinguishable from both long-term treatments. Thus, exclosure increases soil organic matter and grazing decreases it. However, the patterns created by grazing and by exclosure are much less pronounced than the small-scale patterns created by plant presence and absence. Our results support the hypothesis that grazing management (either grazing or exclosure) has minimal impact -- though statistically significant -- on shortgrass steppe ecosystems. Our interpretation is that grazing primarily influences aboveground portions of the ecosystem via removal of biomass. Since greater than 90% of the organic matter in these systems is belowground, the influence of grazing on total carbon storage is relatively small. In addition, the species of shortgrass steppe do not change in composition with grazing, such that community structure remains stable. Disturbances such as cultivation that target the major pool of elements in shortgrass steppe, which are belowground, are more likely to impact soil organic matter.

#### **d. Water dynamics**

We evaluated long-term (1985-1992) dynamics and landscape variations in soil water in the soil profile below the evaporative zone for the CPER. Soil water through the profile averaged across all years and slope positions was maximum in the clay loam site ( $\bar{x} = 12.3$  cm) and minimum in the sandy loam site ( $\bar{x} = 8.8$  cm). Stored soil water did not vary systematically among slope positions. Linear combinations of precipitation and soil texture parameters associated with the A horizon, the specific soil layer, and the overlying layers explained a significant amount of variability in the soil water content of a particular layer. For the total soil water of the profile, average clay content of the profile, clay content of the A horizon, and precipitation were the important explanatory variables. The analysis also showed that the previous water content of a particular layer or of the profile could by itself explain a significant amount of variability in the current water content of that layer or the profile; the importance of the previous water content in accounting for variability in the current water content of a layer increased with depth. Soil water in all layers exhibited marked seasonality; the seasonal dynamics were, however, more conspicuous for the upper layers, and during wet years. The depth-pattern of soil water depletion was consistent with the depth-distribution of roots.

#### **e. Patterns and frequency of disturbance**

##### **Small, patchy disturbances**

Using a laser surveying instrument, we compared the microtopography inside and outside of small disturbances by measuring the heights of plants and bare soil openings located within each disturbance and in the surrounding undisturbed landscape. Site microtopographic differences were statistically significant regardless of disturbance size and soil texture. Heights of plants and bare soil openings were significantly less on disturbances than for the undisturbed landscape for all treatments indicating the net loss of soil material of the disturbed areas through time. Coarse soils were more erodible as a result of higher vegetation cover on the fine- than the coarse-textured soils. The differences between heights of plants and bare soil openings were similar for both locations indicating that microtopography of the landscape had recovered within 8-9 years after the disturbances occurred.

## Large disturbances

We used treatment plots (water addition, nitrogen addition, and water+nitrogen addition) started in the 1970's to evaluate the importance of inertia to plant community response. Two years after cessation of the treatments, exotic "weed" species were increasing in water-plus-nitrogen treated communities, and community dissimilarities were diverging in water and water-plus-nitrogen treated communities. Seven years after cessation of treatments all communities were significantly different from controls. A consistent trend in recovery was evident over the next five years; however, the trend reversed over the next four consecutive years in the previously water-plus-nitrogen and water treated communities. The four-to-five 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 rather to large accumulations of litter, suggesting 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.

We evaluated the biomass, nitrogen yield, and morphological responses to defoliation of western whategrass in long-term grazed and long-term protected plants. Results indicated that defoliation decreased biomass (g/tiller) by the same amount in long-term grazed and long-term protected plants. N yield (mg/tiller) was significantly higher in long-term protected plants than in long-term grazed plants following defoliation. No significant difference was observed between grazed and protected plants regarding new growth in length and number of new tillers per mother tiller following defoliation.

## Plant community modeling

We used the STEPPE model to evaluate the relative importance of soil texture and disturbance to plant recovery dynamics. Soil texture effects on seedling establishment were found to be more important than disturbance size in determining recovery patterns through time and space.

## **2. SYNTHESIS ACTIVITIES**

### Field experiments

We investigated the relative roles of plant species and plant cover in influencing soil C and N cycling at three sites along a precipitation gradient (CPER, Hays, Kansas, and Konza). Konza and Hays had higher levels of total soil C and N and higher ratios of C:N than did the CPER. Konza and Hays had more continuous plant cover, resulting in less plant cover-induced variation in soil C and N, than did CPER. Plant species at Konza and Hays had higher and more variable levels of tissue C:N and potential soil C:N mineralization rates in associated soils than did plant species at CPER. These results indicate that plant cover is most important at the dry end and plant species most important at the wet end to soil C and N cycling.

We also investigated plant community-ecosystem interactions along a temperature gradient in arid and semi-arid grasslands through a project funded by an LTER Supplemental grant to Debra Coffin, Bill Lauenroth, and Indy Burke. We started our investigation in 1993 of the relationship between individual plants of *B. gracilis* and *B. eriopoda* and soil processes at three LTER sites (CPER, Sevilleta, and Jornada) in order to determine and predict the geographic distributions of

these two species, and to obtain a better understanding of the importance of environmental factors and feedbacks between plants and soil processes in structuring arid and semiarid grasslands. Our plans to follow up on these initial field studies and simulation analyses with a more thorough investigation of these plant-soil interactions through a proposal to NSF Ecosystem Studies. A workshop is being planned for October (1994) where interested scientists from all three sites will meet at CSU to develop this proposal.

During the summer of 1993, we compared morphological characteristics and response to small scale disturbance by the two species at all three LTER sites. We found more bare ground at the two southern LTER sites than at the CPER. *B. gracilis* was larger in basal area at the Sevilleta than at the CPER. *B. eriopoda* genets were larger in basal area at the Jornada than at the Sevilleta while ramets were not significantly different in basal area between the two sites. We also tested the relative roles of biotic, ie. plant species, and abiotic factors in plant-induced soil properties at these three LTER sites by sampling soil under and between plants. Total soil carbon increased from Jornada to CPER, probably as a result of increased decomposition rates at the warmest site (JRN). Soils under plants had generally higher pool sizes, particularly labile pools, of carbon and nitrogen than did soils between plants in all systems. Within Sevilleta, the two species growing together in mixed stands did not differ from one another in their effects on soils. However, soils associated with the species growing in pure stands differed from the soils associated with their conspecifics growing in mixed stands at Sevilleta.

### Simulation modeling

We have been involved in a global change simulation analysis funded by a LTER Supplemental grant led by Bill Parton. We predicted changes in soil carbon storage across 11 LTER sites in response to 2xCO<sub>2</sub> climate change predicted by the MM4 GCM.

In conjunction with another NSF-supported project (BSR 9013888), we used the new version of STEPPE to simulate the dynamics of grasslands at nine sites selected to represent the different types of grasslands found in the Great Plains region of the U.S. Although vegetation at the sites responded differently to climate change, shifts in functional types occurred within 40 years of the start of the climate change. C<sub>4</sub> grasses increased in dominance or importance at all sites with a change in climate, primarily as a result of increases in temperature in all months at all sites. The coolest sites that are currently dominated by C<sub>3</sub> grasses were predicted to shift to a dominance by C<sub>4</sub> grasses, whereas sites that are currently dominated by C<sub>4</sub> grasses had an increase in importance of this functional type with a change in climate.

### Regional analysis

Our regional analysis efforts are in conjunction with another NSF-supported project (BSR 9106183) that provides the funding for these efforts.

We collected data for the Central Grasslands of the U.S. on land use, soils, and climate, from Montana to Texas and the Front Range of the Rockies to the eastern plains to conduct a regional analysis of land management. We found that the likelihood an area will be cropped increases with the proportion of silt+clay and mean annual precipitation; this relationship is strongly influenced by mean annual temperature. We then imposed a climate change scenario upon our region, and using the predictive relationships described above, predicted changes in land use patterns. The total area cropped in the region decreased as a result of increased temperatures, and major crops

shifted in their distribution. Finally, we used the Century model to simulate across the region the influence of long-term cultivation on carbon storage and grain production, and to simulate the influence of altered climate. Carbon storage across the entire Central Grasslands decreased significantly as a result of cultivation.

We used the SOILWAT model to investigate the potential effects of changes in temperature and precipitation on soil water dynamics in the central grassland region of the U.S. Soil water patterns under current climatic conditions reflected the large scale west-east precipitation and south-north temperature gradients. Bare soil evaporation accounted for a large proportion of water loss in the driest areas and was replaced by canopy interception in the wettest areas. Transpiration water loss reflected the regional pattern of net primary production, highest in the warm and wet areas and lowest in the warm and dry areas. Increased temperature affected both evaporation and transpiration losses largely by increasing the length of time when evaporative demand of the atmosphere was high. Increases and decreases in precipitation affected water supply directly. Interactions between changes in elevated temperature and increased or decreased precipitation depended upon the balance of changes in water supply and demand.

We evaluated the recruitment potential by seedlings of *B. gracilis* for the central grassland region of the U.S. under current climatic conditions and for changes in climate using the SOILWAT model. 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.

We evaluated ecologically similar regions in the temperate zones of North and South America using analyses of climatic data in order to identify sites that could be used to compare the responses of grassland and shrubland ecosystems on each continent to global change. We used multivariate statistical methods and monthly precipitation and air temperature in our analyses. Our results showed good correspondence for areas in which the native vegetation still exists on both continents as well as good agreement for areas that are in similar crops. The analyses also pointed out some important differences between the two continents related to the comparative small size of the temperate zone in South America.

### **3. CURRENT INTERNATIONAL COLLABORATIONS**

We are continuing our very fruitful collaboration with Dr. Osvaldo Sala from the University of Buenos Aires. We were funded through our 1993 LTER Supplemental Award to bring Dr. Jai Singh from India to CSU for six months. A number of publications are expected to result from Dr. Singh's visit, including a manuscript recently submitted to *Ecology* (Singh et al. submitted). 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 long-term biodiversity research.

### **4. DATA MANAGEMENT**

We recently ordered an Oracle data base system. Our goal for the coming year is 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. This system is meant to compliment our current



methodology, not to replace it entirely. We completed development of the Distributed Processing Interface Library (DPIL), a library of Interprocess Communication functions to implement file transfer procedures directly using Remote Procedure Call methods. A server designed to access the Konza Prairie SQL climate database is now being developed. The bibliographic routines developed at CPER have been converted from FORTRAN to C++, and support has been provided to generate FrameMaker documents as well as ASCII files. A Motif user interface has been added to facilitate searches of the database, and for creating new entries in the database. Internet access to the CPER bibliography will be provided, through either a Mosaic interface or an interface developed from the DPIL. The new bibliographic system will be linked to the data retrieval system through hypertext links.

**Central Plains Experimental Range Long Term Ecological Research Project  
1993-94 Annual Report**

**II. DETAILED REPORT**

**1. CORE AREA RESEARCH**

**a. Pattern and control of primary production**

1) We are continuing to monitor aboveground production on five sites selected to represent topographic positions and soil textures. Four sites have been sampled since 1982, and the fifth since 1986. 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. In addition, 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 long-term enclosure study, and will complement other data being collected at the same sites, as well as add to our long-term production data set. We are also continuing to evaluate belowground production at a single site using a radioisotope technique.

2) We recently conducted an analysis of long-term forage production from 1943 to 1983 collected from grazing treatments established in 1939 (Milchunas et al. 1994). Estimates of forage production for long-term 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 long-term temporal trends resulting from grazing and short-term sensitivities to abiotic factors. Average production based upon all data from 1939-1990 was 75, 71, 68, and 57 g m<sup>-2</sup> yr<sup>-1</sup> for ungrazed, lightly, moderately, and heavily grazed treatments, respectively. Variability in forage production was explained mostly by cool-season precipitation, and magnitude of forage production was more sensitive to annual fluctuations in precipitation than to long-term grazing treatments. Production per unit increase of precipitation was greater for cool-season than warm-season precipitation, but only when cool-season 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.

3) We also clipped shortgrass steppe communities subjected to fifty years of heavy, light, and no grazing intensity to simulate the natural pattern and intensities of defoliation by cattle or not clipped, and supplemented with additional water to simulate a wet year or not supplemented in a year of average precipitation (Varnamkhasti et al. submitted). When not exposed to current-year defoliation, aboveground net primary production (ANPP) response to long-term grazing history depended upon water treatment; ungrazed were more productive than grazed communities under wet-year conditions, but less productive in the year of average precipitation. ANPP was greater in the long-term lightly than heavily grazed treatment only when defoliated under

conditions of relatively greater water stress. The only instance where less precipitation did not result in less ANPP was in the lightly grazed treatment with current-year defoliation; suggesting a water conservation mechanism due to defoliation under water stress conditions. However, water treatment generally had the greatest effect on ANPP among the three factors. Rain-use efficiency of nondefoliated grassland differed between water treatments only in long-term ungrazed grassland, and differed between lightly and heavily grazed treatment only when defoliated. Long-term ungrazed 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 ANPP.

4) We also quantified spatial patterns of root biomass and plant cover in 10 late-successional, shortgrass steppe communities in which a large proportion soil is bare and regeneration is frequently limited by soil water (Hook et al. 1994). 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 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% of the area 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.

5) Our remote sensing research activities are evaluating spatial heterogeneity in aboveground biomass using the CENTURY model for comparison (Todd et al. in prep). 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 tasseled cap soil brightness index used in conjunction with vegetation indices has improved site level biomass estimation relative to univariate regression models, on the shortgrass steppe. We used the CENTURY model as an independent measure of aboveground biomass on the CPER. Soil texture, precipitation, and temperature were used as driving variables for aboveground biomass estimates in the CENTURY model. With weather variables consistent at the CPER, soil texture drives the heterogeneity of CENTURY model estimates at this site. Fractions of sand, silt, and clay were calculated using soil texture triangle information, and soil profile descriptions. An appropriate textural and spatial resolution for model and remote sensing data comparison were determined from canonical discriminant analysis, resulting in 142 polygons. 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, June, 1984 and July, 1991. Similar patterns of remote sensing indices as a function of 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 highest single variable regression correlations were elevation ( $R^2 = 0.02$ ,  $F > 0.07$ , 1984), and SWI ( $R^2 = 0.08$ ,  $F > 0.001$ , 1991). The best two variable models were SBI<sup>3</sup> plus elevation ( $R^2 = 0.04$ ,  $F > 0.08$ , 1984), and SWI<sup>3</sup> plus GVI ( $R^2 = 0.09$ ,  $F > 0.001$ , 1991). The 1991 data produced one significant three variable model: GVI, SWI<sup>3</sup>, and elevation ( $R^2 = 0.11$ ,  $F > 0.0003$ ). Residuals of regression models were spatially autocorrelated using Moran's univariate I statistic. The inclusion of spatial autoregressive error terms improved  $R^2$  values. The residuals between CENTURY and TM derived biomass models were also spatially autocorrelated. The mean remote sensing biomass estimates for two soil groups with relatively low sand content were much higher than CENTURY estimates. High negative residuals (TM estimates higher than CENTURY) were associated with some but not all stream drainages.

## **b. Spatial and temporal distribution of populations selected to represent trophic structure**

### Plant populations

Because physiognomy as well as trophic structure of shortgrass steppe ecosystems are dominated by the perennial bunchgrass, *Bouteloua gracilis*, our plant population work has focused on the interactions of disturbances with recruitment and mortality of *B. gracilis* as well as abiotic and biotic controls over demographic variables of this and other species.

1) We studied the intra- and interspecific competition between *Bouteloua gracilis* and *Buchloë dactyloides* under natural conditions at the CPER and under conditions of added water and nitrogen (Aguilar et al. 1994). These species are the dominant and subdominant species throughout the shortgrass steppe, and share ecophysiological and morphological characteristics that group them into a guild of warm season grasses. We planted a garden with both species in order to get the combination required for studying intra- and interspecific competition. The garden resembled the plant distribution in the field. We added water and nitrogen in a factorial combination at two levels. We added water weekly up to doubling the current precipitation at the CPER. Nitrogen (10 g/m<sup>2</sup>) was added at the start of the growing season. During the first year, competition was the dominant factor explaining a large proportion of the total variability (Aguilar et al. 1993). There were no differences between intra- and interspecific competition. The addition of water increased the plant biomass 23%, while nitrogen increased the biomass 17%. There was no interaction between the effect of both resources, yet plants that received both achieved the largest biomass. Plants that grew with competition did not increase their biomass when resources were added. Based upon the first year's results, we speculate that belowground competition is intense and important in the shortgrass steppe, and its role does not change with the differences in resources found in a major east-west gradient of precipitation. Morphological and ecophysiological characteristics of the species are good predictors of ecological features such as competitive abilities. Inside this guild competition is an important structuring force, but similarities between *B. gracilis* and *B. dactyloides* hamper its role as the main force determining success. Relative abundance of the two species should be the result of other ecological processes such as tolerance to herbivory, response to drought, response to disturbance, etc..

2) We used a simulation analysis to evaluate the effects of soil texture on the probability of establishment of *B. gracilis* seedlings (Lauenroth et al. 1994d). A multi-layer daily time step model of soil water dynamics (SOILWAT) was used to simulate the conditions required for establishment of *B. gracilis* seedlings on eleven soil textures. The probability of establishment was found to increase as the silt content of the soil increased.

3) 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.

4) We evaluated the ability of *B. gracilis* to exploit resources in central and outer portions of root systems (Hook and Lauenroth 1994). 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.

#### Animal populations

1) We used roadside censuses along a permanent transect to evaluate seasonal and interannual fluctuations in bird populations. Nesting behavior of the Horned Lark, McGown's Longspur, and Lark Bunting as well as movement patterns of McGown's Longspur and their important prey item (grasshoppers) were also studied.

2) We are also investigating of the relative roles of species interactions, vegetation structure, and resource availability as determinants of habitat use and community organization of rodents at the CPER. This research includes a detailed examination of the habitat use and movement patterns of the northern grasshopper mouse (*Onychomys leucogaster*). Because of its predatory habits, this species occurs at relatively low population densities, and individuals have large area requirements. Grasshopper mice therefore likely respond to habitat characteristics across a range of spatial scales. Regular censuses of arthropods on different soil and microhabitat types allow for the examination of variability in the distribution of prey. We are also conducting a species removal experiment to examine the potential effects of grasshopper mice on the abundance, diet, movements, and patterns of microhabitat use of deer mice (*Peromyscus maniculatus*). Grasshopper mice may both compete with and prey upon deer mice and other prairie rodents, and therefore may play an important role in determining community organization. Finally, we are investigating the response of deer mice to the distribution and dispersion of shrub cover. Deer mice are most abundant in areas of high shrub cover, and appear to orient their movements

toward large shrubs. Movement pathways from deer mice on areas with varying shrub densities will be analyzed to develop a predictive model. Predictions will be tested with movement pathways from additional sites, and on a site where shrub cover is manipulated.

Preliminary analyses of microhabitat use data from fluorescent powder tracking confirm that the movements of deer mice are influenced by the distribution of shrub cover (Stapp 1993a; Stapp et al. 1994). A large proportion of the movement pathways of grasshopper mice were in areas with considerable soil disturbance by pocket gophers and harvest ants, and numerous rodent burrows. We speculate that grasshopper mice preferentially use these areas because prey availability is higher in these microhabitats. Radiotelemetry data also suggest a relationship between grasshopper mouse activity and soil disturbances, which will be explored with data from the Spring and Summer 1994 field seasons. Data collection for the removal experiment began in May 1994 and will continue through August 1994. In 1993, a companion experiment was performed to test the hypothesis that deer mice directly avoid grasshopper mice. Wild deer mice were provided with a choice of traps containing fecal and urinary odors of grasshopper mice, odors of western harvest mice, and clean traps (Stapp 1993b). We examined variation in capture rates among odor types across seasons, between sexes, and between sites with different abundances of grasshopper mice. Contrary to expectations, deer mice did not avoid traps containing grasshopper mouse odors. These results will be compared to those from the removal experiment.

### **c. Pattern and control of organic matter accumulation and of inorganic inputs and movements of nutrients**

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.

#### **Spatial heterogeneity**

1) The effect of plant community structure on nutrient cycling is fundamental to our understanding of ecosystem function. We examined the importance of plant species and plant cover (ie. plant covered microsites vs. bare soil) on nutrient cycling at the CPER (Vinton and Burke in review). We tested the effects of both plant species and cover on soils in an area of undisturbed shortgrass-steppe and an area that had undergone nitrogen and water additions from 1971-1974, resulting in significant shifts in plant species composition. Soils under plants had consistently higher C and N mineralization rates, and in some cases, higher total and microbial C and N levels, than soils from bare soil. Four native grasses, one sedge and one shrub differed from one another in the quantity and quality of above- and belowground biomass but differences among the six species in soil nutrient cycling under their canopies were slight. However, soils under bunchgrasses tended to have higher C mineralization and microbial biomass C than soil under the rhizomatous grass, *Agropyron smithii*. Also, the one introduced annual in the study, *Kochia scoparia*, had soils with less plant-induced heterogeneity and higher rates of C and N mineralization as well as higher levels of microbial biomass C than soils associated with the other species. This species was abundant only on the historical water and nitrogen addition plots, where it has persisted in the absence of resource additions for 20 y, suggesting a positive feedback between plant persistence and soil nutrient status.

Plant cover patterns had larger effects on ecosystem-scale estimates of soil properties than the attributes of a particular plant species. This result may be due to the semi-arid nature of this grassland in which plant cover is discontinuous and decomposition and nutrient availability are primarily limited by water, not by plant species-mediated characteristics such as litter quality. That local plant-induced patterns in soil properties significantly affected ecosystem scale estimates indicates that consideration of structural attributes, particularly plant cover patterns, is critical to estimates of ecosystem function in shortgrass steppe.

2) The role of roots in soil organic matter formation and recovery is an important and poorly understood component of disturbance dynamics in the shortgrass steppe. We conducted field and laboratory studies on the role of roots in soil organic matter (SOM) dynamics using Western Harvester ant (*Pogonomyrex occidentalis*) nests to provide a root input gradient (Kelly and Burke 1994). The nests have a "disk" area that surrounds the central mound and is maintained with no aboveground and few belowground inputs for many (29-58) years, with minimal physical disturbance to soil structure. Root biomass decreases from the outside edge to the center of the disk. A nest can be aged by its morphology, allowing us to examine soil organic matter dynamics over gradients of root density and disturbance age. Active soil organic pools, indexed by potentially mineralizable C and N, responded with greater proportionality to both disturbance age and the root gradient than total C and N pools, because they are dependent upon inputs over a short period of time. Results of this study allow us to test the temporal and spatial predictions of current models of SOM formation and mineralization.

3) 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 (Hook and Burke 1994). 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 2-3 times greater in the 3 alluvial lowlands than on adjacent uplands; C and N in non-alluvial 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 pools 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 & N appears to be less consistent than microscale heterogeneity related to patterns of plant cover, probably because runoff and associated material transport is limited.

4) We compared several *in situ*, open tube incubation methods for estimating net N mineralization at the CPER (Hook and Burke submitted). Our objectives were to evaluate (1) effects of root death, spatial heterogeneity of roots, and length of incubations on artifacts involving N immobilization, (2) changes in soil water dynamics, and (3) similarity of incubation results to other indices of N availability. Mineralization estimates depended on length of incubations, soil handling, and microsite. Results suggested that net mineralization was affected by transient N release and immobilization involving active organic matter, especially in sieved soil. Net N mineralization was highest 15-30 d after starting incubations; generally no additional net mineralization occurred after day 30, and net immobilization often occurred. Inorganic N increased and decreased more rapidly in sieved samples than intact cores, which were less prone

to immobilization. Removal of roots did not enhance net mineralization consistently. Net N mineralization was greater under *Bouteloua gracilis* plants than in bare soil. Thus root death was not a dominant control of net N mineralization, and sieving to remove roots was counterproductive. Water content in open core incubations responded to weather but was higher than ambient during moist periods. Patterns of plant N uptake estimated from long incubations were not plausible, featuring periods "negative uptake". Patterns of N capture on ion exchange resins were consistent with incubation results in some respects but not others. We recommend 15-30 d incubations of intact cores to minimize artifacts and capture effects of environmental variation.

5) We are continuing our research on soil-climate interactions in order to understand the climatic and biological conditions that existed during the Holocene. Our research focuses on the Holocene paleoenvironment, including reconstruction of landforms, vegetation and climate over the last 10,000 years. We use the stable C isotope composition of paleosols to provide a record of paleovegetation from which inferences to climate change can be made. Paleosols are carbon dated to provide chronologic control. The carbon isotopic composition of soil organic matter, carbonate and opal phytoliths (biogenic silica) varies as a function of the relative proportion of C3 and C4 plants growing at that locality. This relationship provides important information regarding vegetative composition and prehistoric climate in terrestrial ecosystems. Isotopic equilibrium between soil organic matter and carbonate is evident in Holocene paleosols. Isotopic signatures of various soil constituents indicate the dominance of C4 vegetation in the latter part of the Holocene. These isotopic techniques, usually applied to more ancient environments, appear useful in evaluating Holocene paleoclimatic conditions (Kelly et al. 1993).

Surficial geologic deposits at the Central Plains Experimental Range which bury Holocene paleosols include multiple types and ages of both alluvium and loess. The number and distribution of these deposits is evidence of instability in the region, but inferences to climate based on mode of deposition alone are suspect, as it is often difficult to reliably discriminate between alluvial and eolian deposits. Particle size frequency statistics were applied to CPER surficial geologic deposits (soil parent materials) to discern their mode of deposition. This technique is used to differentiate between eolian and fluvial deposits in geologic settings and, to our knowledge, has not been applied in a pedologic setting. Bivariate analysis of particle size frequency statistics indicated none of the parent materials sampled are clearly eolian; several deposits thought to be fluvial had loessal characteristics and no deposits resemble dunes. CPER fluvial deposits have smaller mean grain size and are better sorted than averages reported in the literature (Bleeker 1993).

Published <sup>14</sup>C dates for CPER paleosols indicated three periods of soil formation during the Holocene: 10000-8000, 5000-3000, and 1500-0 ybp. Because these intervals are of the same approximate length, morphologic differences between contemporary soils and paleosols may infer differences in climate during the time of soil formation. The relative developmental stage of diagnostic soil horizons, and the distribution of organic carbon and phytoliths, were determined for contemporary soils and paleosols. The presence of horizons enriched with illuvial clay and carbonate are the result of eolian influx of material, as opposed to in-situ weathering and translocation. Early Holocene paleosols appear to contain more organic C than soils of subsequent soil-forming intervals. Early Holocene paleosols are also the most well developed. Early and mid-Holocene paleosols contain at least a 2-fold increase in phytolith over their contemporary counterparts. In general, morphologic evidence suggests the early Holocene environment was conducive to more rapid pedogenesis than subsequent soil-forming intervals (Bleeker 1993).



## Recovery from disturbance

1) Livestock production is a crucial part of the economic and social systems of the Great Plains. In recent years, the influence of livestock grazing on ecological systems in the American West has come under close scrutiny, with important new political debates focusing on management of federal lands. The CPER-LTER has been conducting research on grazing effects since our site was funded (e.g. Milchunas et al. 1988, and many others). Our past work has indicated that shortgrass steppe systems evolved in the presence of grazing by large, generalist herbivores, and that shortgrass steppe vegetation is extremely well-adapted to grazing, and only small changes in species composition were be seen as a result of grazing. All of this work utilized a network of long-term exclosures (since 1938) on the CPER.

In 1991, we began a new experiment on the influence of grazing on shortgrass steppe ecosystem structure and function. Our idea was that interpretation of long-term exclosures may not be appropriate for truly testing the effects of grazing in a system that evolved under grazing. Are differences due to exclosure or to grazing? What are the transient effects of grazing or of exclosure? We manipulated the boundaries of 6 exclosures to produce 4 treatments: 1) long-term grazed, currently grazed; 2) long-term grazed, currently ungrazed 3) long-term exclosed, currently exclosed; and 4) long-term exclosed, currently grazed.

We have sampled the new treatments for a number of factors, including vegetation, small-scale disturbances, soil organic matter, biomass, and trophic structure. Below, we present the most recent data from the soil organic matter study.

Two years following the new manipulations, we sampled soil organic matter for total and more active indices such as mineralizable carbon and nitrogen. Our results indicate that there is significantly less total carbon, total nitrogen, and mineralizable nitrogen in the long-term grazed than the long-term exclosed treatments. In addition, the short-term effects of the treatments are beginning to be evident in the more active pools, such that both short-term treatments are statistically indistinguishable from both long-term treatments. Thus, exclosure increases soil organic matter, and grazing decreases it. However, the patterns created by grazing and by exclosure are much less pronounced than the small-scale patterns created by plant presence and absence.

Our results support the hypothesis that grazing management (either grazing or exclosure) has minimal impact -- though statistically significant -- on shortgrass steppe ecosystems. Our interpretation is that grazing primarily influences aboveground portions of the ecosystem via removal of biomass. Since greater than 90% of the organic matter in these systems is belowground, the influence of grazing on total carbon storage is relatively small. In addition, the species of shortgrass steppe do not change in composition with grazing, such that community structure remains stable. Disturbances such as cultivation that target the major pool of elements in shortgrass steppe, which are belowground, are more likely to impact soil organic matter. These results will be presented at ESA this summer (Burke et al. 1994), are reviewed in a current review manuscript (Burke and Lauenroth submitted), and will be submitted for publication this year. See also Figure 1.

2) 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 (Ihori et al.1994). 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.

#### **d. Water dynamics**

We have designated Water Dynamics as an additional core topic because we consider it to be fundamental for understanding the origin, structure, function, and sustainability of the shortgrass steppe. Research under other core topic areas includes analyses of the interactions between water and primary production, organic matter and nutrients, vegetation structure and dynamics, and effects of disturbance. Our focus on water dynamics is concerned both with variation in the major external control of water (precipitation) and with variation in the major, proximate control on ecosystem processes (soil water).

We evaluated long-term (1985-1992) dynamics and landscape variations in soil water in the soil profile below the evaporative zone for the CPER under low and markedly variable precipitation regime (Singh et al. submitted). Data were collected using the neutron probe technique through permanent access tubes in four sites. Each site comprised a toposequence with an upland, a midslope and a lowland position. One was a predominately sandy loam site, another a clay loam, and the remaining two sandy clay loam sites. Soil water was monitored at 15 cm intervals providing estimates covering 22.5 to 97.5 cm depths.

Depending upon the scale, two spatial patterns in soil water storage were indicated. Soil water through the profile averaged across all years and slope positions was maximum in the clay loam site ( $\bar{x}$  = 12.3 cm) and minimum in the sandy loam site ( $\bar{x}$  = 8.8 cm). Stored soil water did not vary systematically among slope positions. While the clay loam site exhibited the expected gradient of more soil water in the lowland position, more sandy sites stored greater amounts in the upslope positions. The deeper layers of the profile held more water in the finer-textured sites while the reverse was true for the sites with relatively greater proportion of coarse particles. Soil water storage of each layer was related to that of all other layers examined; this relationship weakened with the vertical distance between the layers. Linear combinations of precipitation and the texture parameters of A horizon, of the specific soil layer, and of the overlying layers explained a significant amount of variability in the soil water content of a particular layer. For the total soil water of the profile, average clay content of the profile (positive  $\beta$ ), clay content of the A horizon (negative  $\beta$ ) and a precipitation term (positive  $\beta$ ) were the important explanatory variables. This is consistent with the expected role of soil texture in the precipitation-infiltration-retention part of the hydrological cycle. The analysis also showed that the previous water content of a particular layer or of the profile could by itself explain a significant amount of variability in the current water content of that layer or the profile, and the importance of the previous water content in accounting for the variability in the current water content of a layer increased with depth. Thus

while the previous season's water content alone explained 40-47% variability in the current season's water content of the 30 cm layer, it accounted for 55-96% variability in 60 cm layer and 94-99% variability in 90 cm layer in different seasons.

Soil water in all layers exhibited marked seasonality; the seasonal dynamics were, however, more conspicuous for the upper layers, and during wet years. Since the soil layers studied were beyond the influence of bare soil evaporation, these dynamics are interpreted to reflect the plant use (soil water depletion during the growing season) and net recharge of the profile (conservation of the cool season precipitation). Across all sites, 6-28% of the non-growing-season precipitation was conserved in different years in the 22.5-97.5 cm profile. The depth-pattern of soil water depletion was consistent with the depth-distribution of roots. More water was used in the wet years compared to dry years; this is also consistent with the expected behavior of plant growth and consequent enhanced demand for water in the wet years. There was an inverse relationship between aboveground net primary production and mean soil water content of the 30, 45 and 60 cm layers during and following the active growth period, indicating the feedback effect of NPP on soil water. Root distributions through the profile did not, however, vary with soil texture or the different soil water profiles controlled by soil texture.

In this semiarid shortgrass steppe, the spatial pattern of soil water storage is determined by soil texture and the temporal pattern by precipitation and plant use. The less variable water content of the deeper layers is a resource which potentially buffers the impact of pronounced variability in precipitation and thus contributes to the stability of the shortgrass cover which obtains water from these layers in addition to the more variable storage in the upper layers subjected to the influences of the bare soil evaporation.

#### **e. Patterns and frequency of disturbance**

Most of our disturbance work can be placed into two broad categories, small to intermediate-sized patchy disturbances and large disturbances. We continue to use both experimental studies and simulation modeling to improve our understanding of the effects of disturbance on shortgrass ecosystems.

##### **Small, patchy disturbances**

We are continuing to monitor the response of shortgrass steppe plant communities to small scale disturbances that were produced in 1984. Plant cover and density are estimated by species for disturbances of different sizes, locations by soil texture, and seasonality. Annuals were important colonizers of the disturbed areas and perennial grasses rapidly became important within 5 years after recovery began. In addition to monitoring successional dynamics, we also evaluated the effects of disturbance size and soil texture on the microtopography of the landscape using these plots. In 1993, by using a laser surveying instrument, we compared the microtopography inside and outside of disturbances by measuring the heights of plants and bare soil openings located within each disturbance and in the surrounding undisturbed landscape (Martinez-Turanzes and Coffin in prep). Our results indicate that the site microtopographic differences were statistically significant ( $p < 0.01$ ) regardless of disturbance size and soil texture. However, heights of plants and bare soil openings were significantly less on disturbances than for the undisturbed landscape for both soil textures and all of the three disturbance sizes indicating the net loss of soil material of the disturbed areas through time. Although coarse-textured soils are typically less erodable than fine soils due to particule size differences and physical factors such as wind, our results showed that coarse soils were more erodable as a result of higher vegetation cover on

the fine- than the coarse-textured soils. Heights of plants were significantly higher than bare soil openings both for the undisturbed landscape and inside of each disturbance. The difference between heights of plants and bare soil openings were similar for both locations (1.68 cm undisturbed; 1.85 cm disturbed) indicating that microtopography of the landscape had recovered within 8-9 years after the disturbance occurred. We concluded that the microtopography of the landscape of shortgrass communities can become re-established within a short time (<9 years) after a disturbance, and that the plant-soil microtopography is an interaction between soil erosion, deposition, plant cover and soil plant accumulation.

### Large disturbances

1) We are using treatment plots started in the 1970's to evaluate the importance of inertia to plant community response (Milchunas and Lauenroth 1994). Water, nitrogen, and water-plus-nitrogen 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 re-established 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-plus-nitrogen treated communities, and community dissimilarities were diverging in water and water-plus-nitrogen treated communities. Seven years after cessation of treatments all communities were significantly different from controls. Exotics were more than ten times more abundant in water-plus-nitrogen 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 water-plus-nitrogen and water treated communities. The four-to-five 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. Time-lags in initial response means 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 time-lags 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 time-lags 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.

2) We are continuing to study the long-term effects of grazing and recovery on shortgrass ecosystems using the exclosure study that we started in 1991. In this study, we moved 50-year-old exclosure boundaries in 6 locations across a soil texture gradients in order to create 4 treatments: long term grazed/currently grazed, long term grazed/recently exclosed, long term exclosed/ currently exclosed, and long term grazed/recently grazed. We have been investigating a large number of characteristics of shortgrass structure and function on these treatments, and will continue to do into the future. Below we describe our findings from 1993. Additional results

were presented under Pattern and control of organic matter accumulation.

We evaluated the biomass, nitrogen yield, and morphological responses to defoliation of two species in long-term grazed and long-term protected plants (Atsedu and Detling in prep). Field investigation was initiated in the summer of 1992 in long-term grazed and protected (GU) and long-term protected and protected (UU) sites at the CPER. Biomass, N yield, growth, and tillering of western wheatgrass (*Pascopyrum Smithii* Rybd. A. Love) plants in response to defoliation was studied. Results indicated that defoliation decreased biomass (g/tiller) by the same amount in long-term grazed and long-term protected plants. N yield (mg/tiller) was significantly ( $p < 0.05$ ) higher in long-term protected plants than in long-term grazed plants following defoliation. No significant difference was observed between grazed and protected plants regarding new growth in length and number of new tillers per mother tiller following defoliation. In the summer of 1993 blue grama (*Bouteloua gracilis* (H.B.K. Lag) was included in the experiment and the 1992 study on western wheatgrass was repeated in four grazing treatments (UU, UG, GU, and GG). A greenhouse study was also established to examine whether biomass, chemical, and morphological characteristics exhibited in the field are maintained in a control environment. Both blue grama and western wheatgrass were studied in the greenhouse. Results of the field and greenhouse data for the summer of 1993 are currently under analysis.

3) We also evaluated forage nitrogen concentrations, nitrogen yields, and in-vitro-digestibilities in shortgrass steppe that had been ungrazed, lightly, or heavily grazed for 50 years (Milchunas et al. submitted). Caged plots were defoliated based upon removals observed in naturally-grazed reference plots or not defoliated. This was done in a year of average precipitation and with a supplemental water treatment to simulate a wet year. In general, current-year defoliation had positive effects, and long-term grazing and water had negative effects, on forage nitrogen concentrations and digestibilities. However, defoliation interacted with long-term 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 watering on digestibilities through increased plant growth was offset by defoliation. The negative effects of long-term grazing on forage quality were small, equally or more than compensated for by defoliation in a year of average precipitation, but more pronounced with increased precipitation. 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 year-to-year 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. Long-term 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 current-year defoliation, long-term grazing history, and level of water resource.

#### Plant community modeling

We are continuing to use an individual plant-based approach to understanding controls

on plant community dynamics. The STEPPE model simulates the recruitment, growth, and mortality of individual plants on a small plot through time at an annual time step. We have used the STEPPE model to simulate small to large disturbances of different soil textures and climatic regimes. In our most recent analysis, we evaluated the relative importance of soil texture and disturbance to plant recovery dynamics (Coffin and Lauenroth 1994b). Soil texture effects on seedling establishment were found to be more important than disturbance size in determining recovery patterns through time and space.

## 2. SYNTHESIS ACTIVITIES

We are involved in three different and complementary aspects of cross-site integration and synthetic activities. The first focuses on field experiments, the second on simulation modeling, and the third on regional analysis.

### Field experiments

1) We conducted an analysis of population-ecosystem interactions in grasslands. We investigated the relative roles of plant species and plant cover in influencing soil C and N cycling at three sites along the precipitation gradient from the eastern Colorado shortgrass-steppe, in the rain shadow of the Rocky Mountains, to the tallgrass prairie in eastern Kansas (Vinton and Burke 1993). This project was funded by an NSF Dissertation Improvement Award to Indy Burke and Mary Ann Vinton. The two sites on the extremes of the gradient were LTER sites, the CPER and the Konza Prairie Research Natural Area (KPRNA). The third site was Hays, Kansas, located between the LTER sites. The wet, tall- and midgrass prairie sites, KPRNA and Hays, had higher levels of total soil C and N and higher ratios of C:N than did the dry shortgrass-steppe site in northeastern Colorado, CPER. KPRNA and Hays had more continuous plant cover, resulting in less plant cover-induced variation in soil C and N, than did CPER. Plant species at KPRNA and Hays had higher and more variable levels of tissue C:N and potential soil C:N mineralization rates in associated soils than did plant species at CPER. These results indicate that the relative importance of plant cover patterns and plant species to soil C and N cycling varies over this gradient of increasing precipitation, with plant cover being most important at the dry end and plant species being most important at the wet end.

2) We are also involved in investigating plant community-ecosystem interactions along a temperature gradient in arid and semi-arid grasslands. This project is funded by an LTER Supplemental grant to Debra Coffin, Bill Lauenroth, and Indy Burke. The objectives of the project are: (1) to evaluate factors controlling the geographic distribution and relative dominance of *Bouteloua gracilis* and *Bouteloua eriopoda*; and (2) to evaluate small-scale heterogeneity in plant structure and ecosystem processes by studying interactions and feedbacks between individual plants and soil processes. We started our investigation in 1993 of the relationship between individual plants of *B. gracilis* and *B. eriopoda* and soil processes at three LTER sites (CPER, Sevilleta, and Jornada) in order to determine and predict the geographic distributions of these two species, and to obtain a better understanding of the importance of environmental factors and feedbacks between plants and soil processes in structuring arid and semiarid grasslands. Our plans to follow up on these initial field studies and simulation analyses with a more thorough investigation of these plant-soil interactions through a proposal to NSF Ecosystem Studies. A workshop is being planned for October (1994) where interested scientists from all three sites will meet at CSU to develop this proposal.

During the summer of 1993, we compared morphological characteristics and response to small scale disturbance by the two species at all three LTER sites. Study areas were selected at each LTER site that were dominated by either *B. gracilis*, *B. eriopoda* or a mixture of the two species. To confirm the dominance patterns, we did vegetative surveys and characterized the areas for soil texture. All areas were dominated by the appropriate species and were approximately 75% sand, 15% clay and 10% silt. We found more bare ground at the two southern LTER sites than at the CPER. Also, the Sevilleta had slightly more bare ground than did the Jornada. We measured morphological characteristics of *B. eriopoda* and *B. gracilis* in each of the study areas. *B. gracilis* was larger in basal area at the Sevilleta than at the CPER. *B. eriopoda* genets were larger in basal area at the Jornada than at the Sevilleta while ramets were not significantly different in basal area between the two sites. The higher amount of bare ground in *B. eriopoda* dominated areas at the Sevilleta than at the Jornada may be explained by the larger plant size at the Jornada. We began a study involving the effects of small scale disturbance. In each study area, we removed ten plants and ten half plants of *B. eriopoda* and/or *B. gracilis*. In the future, we will measure growth into the disturbed areas by surrounding plants and the course of succession.

Because plant-induced soil heterogeneity is an important feature of arid and semi-arid ecosystems, and changes in this soil heterogeneity are associated with disturbances and ecosystem stability, we also tested the relative roles of biotic, ie. plant species, and abiotic factors in plant-induced soil properties at these three LTER sites (Vinton et al. in prep). The two species, *Bouteloua eriopoda* and *Bouteloua gracilis*, are both warm-season, perennial bunchgrasses but may have significantly different lifespan and dispersal characteristics and responses to grazing. We sampled these species and associated soils at the three sites, capturing the extremes and the shared sites in the geographical distribution of the two species. We sampled soils and plants of 1) *B. eriopoda* at the Jornada Experimental Range 2) *B. eriopoda* and *B. gracilis* in both pure and mixed stands at the Sevilleta and 3) *B. gracilis* at the CPER. Total soil carbon increased from the southern site, Jornada, to the northern site, CPER, probably as a result of increased decomposition rates at the warmest site, Jornada. Soils under plants had generally higher pool sizes, particularly labile pools, of carbon and nitrogen than did soils between plants in all the systems. This plant-induced soil heterogeneity was larger at Sevilleta than at either Jornada or CPER for soil carbon. Sevilleta also had the largest bare ground cover, so erosional processes between plants may have contributed to the under plant vs. between plant contrast in soil carbon at this site to a greater degree than at the other sites. Within Sevilleta, the two species growing together in mixed stands did not differ from one another in their effects on soils. However, soils associated with the species growing in pure stands differed from the soils associated with their conspecifics growing in mixed stands at Sevilleta. This result may have been due to differing successional age between stands. Since *B. eriopoda* may be shorter-lived and recruit more frequently than *B. gracilis*, the *B. gracilis* stands were likely the oldest stands. This may explain the significantly higher rates of soil carbon and nitrogen cycling in the pure *B. gracilis* stands than in the other stands. Individual plants clearly affected soil nitrogen and carbon dynamics at all sites. Also, the abiotic factors varying with site interacted with the biological factors associated with *B. eriopoda* and *B. gracilis* to significantly influence soil properties. In particular, abiotic factors that determine lifespan, productivity and erosional characteristics are all important in determining patterns in plant-soil heterogeneity in these desert- and shortgrass-steppe grasslands.

### Simulation modeling

We are continuing to use models of soil water dynamics (SOILWAT; Parton 1978), plant

community structure (STEPPE; Coffin and Lauenroth 1990), and production and turnover of soil organic matter (CENTURY; Parton et al. 1988) 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.

1) We have been involved in a global change simulation analysis funded by a LTER Supplemental grant led by Bill Parton. Uncertainties related to ecosystem response to climatic change in North America have made realistic decisions related to natural resource management almost impossible. Questions related to carbon storage, sustainable ecosystem productivity, and habitat availability are unresolved. Many regions of North America lack ground based information of ecosystem functioning and ways of projecting modifications to these ecosystems with different scenarios of climate change. The LTER network provides a unique opportunity to address the complex issue of climate change impact on a variety of ecosystems because of their extensive data base on ecosystem functioning under current environmental conditions. Our project (Supplement to NSF BSR- 901659) used the ecosystem model, CENTURY, to study the impact of climate change across the network of LTER sites (Pulliam et al. in prep). These analyses of ecosystem response to changing environmental factors provided further insight into the sensitivity of ecosystem processes at a variety of ecosystems across North America. The project used the core data sets from the different LTER sites to parameterize and validate CENTURY across a wide range of terrestrial ecosystems present in the network. The project also trained investigators at these sites in the use of a predictive, systems model. We have assisted investigators from the different LTER sites to use CENTURY for specific site-level questions that will benefit their own research and further development of CENTURY.

This cross-site effort also contributed to the on-going modeling efforts of global environmental interactions with terrestrial ecosystems being conducted by national and international efforts of research groups such as the NSF-funded project at UCAR, the Climate System Modeling Project (CSMP), the Model Evaluation Consortium for Climate Assessment (MECCA funded by the private sector), the SCOPE Grassland and Forest Modeling Project, and the IGBP Global Analysis and Integrated Modeling Project (GAIM). We used GCM output provided by Tim Kittel (UCAR) to provide GCM-derived seasonal scenarios of climatic change for the different LTER sites. CENTURY incorporate these changes as monthly perturbations of temperature and precipitation. The enhanced CO<sub>2</sub> enrichment across sites were simulated by adjusting water use and nutrient use efficiencies of the simulated ecosystems. Figure 2. shows an example of these results, presenting the predicted changes in soil carbon storage across 11 LTER sites in response to 2xCO<sub>2</sub> climate change predicted by the MM4 GCM.

The project enabled us to work with the various LTER researchers, to collect data for model parameterization, and to conduct climate and CO<sub>2</sub> perturbations. For each of the sites we: (1) delivered a PC version and user's manual of CENTURY, (2) trained one or more individuals in the use of the model, and (3) work in close collaboration with the site researchers to insure that required modifications and changes in parameterization are adequately made. In September 1993, we held a workshop to review progress of the model simulations at the different LTER sites and presented the results at the LTER-ALL scientist meeting. We are preparing a paper entitled, "Potential consequences of climate change across North American Ecosystems" for publication in Science, BioScience or other appropriate journal. We also are preparing an LTER internal document that contains tables of initial conditions, drivers, and output predictions of selected variables so this information is available for subsequent comparative efforts.



2) We recently modified the STEPPE model developed for shortgrass steppe plant communities to allow the model to simulate the dynamics of all grasslands in the North American Great Plains region. This new version of STEPPE incorporates competition for light and nitrogen in addition to competition for soil water. The basic premise of the model is the same as the original STEPPE, although a much more detailed examination of temporal and spatial processes is included. In conjunction with another NSF-supported project (BSR 9013888), we used the new version of STEPPE to simulate the dynamics of grasslands at nine sites selected to represent the different types of grasslands found in the Great Plains region of the U.S.: tallgrass prairie, northern and southern mixedgrass prairies, shortgrass steppe, and desert grassland (Coffin and Lauenroth submitted). We used the new version of the STEPPE model linked with SOILWAT to evaluate effects of changes in climate on grassland vegetation at each site. Although vegetation at the sites responded differently to climate change, shifts in functional types occurred within 40 years of the start of the climate change.  $C_4$  grasses increased in dominance or importance at all sites with a change in climate, primarily as a result of increases in temperature in all months at all sites. The coolest sites that are currently dominated by  $C_3$  grasses were predicted to shift to a dominance by  $C_4$  grasses, whereas sites that are currently dominated by  $C_4$  grasses had an increase in importance of this functional type with a change in climate. Current annual temperature was the best predictor of changes in  $C_3$  biomass, and  $C_3$  and  $C_4$  biomass combined; current annual precipitation was the best predictor of changes in  $C_4$  biomass. These predicted shifts in dominance and importance of  $C_3$  versus  $C_4$  grasses would have important implications for the management of natural grasslands as well as the cultivation of crops in the central grassland region.

### 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.

1) Land management at a regional scale may have large impacts on terrestrial carbon storage, trace gas flux, and regional radiative and hydrologic balances. Over the past 100 years in the Central Grasslands of the U.S., land use has been dynamic, changing with short-term climate patterns and economic and policy trends. We collected data for the Central Grasslands of the U.S. on land use, soils, and climate, from Montana to Texas and the Front Range of the Rockies to the eastern plains. We overlaid the data in a geographic information system to conduct three analyses (Burke et al. 1994). First, we produced statistical relationships that allow us to predict land use from soils and climate data. The likelihood that an area will be cropped increases with the proportion of silt+clay and mean annual precipitation. This relationship is strongly influenced by mean annual temperature, with increases in temperature (and PET) decreasing the proportion of area that is cropped within a given soil texture and mean annual precipitation. Second, we imposed a climate change scenario upon our region, and using the predictive relationships described above, predicted changes in land use patterns. The total area cropped in the region decreased as a result of increased temperatures, and major crops shifted in their distribution. Finally, we used the Century model to simulate across the region the influence of long-term cultivation on carbon storage and grain production, and to simulate the influence of altered climate. Carbon storage across the entire Central Grasslands decreased significantly as a result of cultivation. Grain production was influenced both by the changes in total cropland and by the

changes in crop distribution.

2) We used a daily time step soil water model to investigate the potential effects of changes in temperature and precipitation on soil water dynamics in the central grassland region of the U.S. (Lauenroth et al. 1994a). We collected 20-years of driving variable data from each of 300 USGS weather stations throughout the region. Simulations were run for each station and the results were entered into a GIS database for analysis and display. Soil water patterns under current climatic conditions reflected the large scale west-east precipitation and south-north temperature gradients. Bare soil evaporation accounted for a large proportion of water loss in the driest areas and was replaced by canopy interception in the wettest areas. Transpiration water loss reflected the regional pattern of net primary production, highest in the warm and wet areas and lowest in the warm and dry areas. Increased temperature affected both evaporation and transpiration losses largely by increasing the length of time when evaporative demand of the atmosphere was high. Increases and decreases in precipitation affected water supply directly. Interactions between changes in elevated temperature and increased or decreased precipitation depended upon the balance of changes in water supply and demand.

3) We evaluated the recruitment potential by seedlings of *B. gracilis* for the central grassland region of the U.S. under current climatic conditions and for changes in climate (Coffin and Lauenroth 1994a). Four grassland types are found within this large region. *B. gracilis* dominates the vegetation for one grassland type, 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 multi-layer daily time step soil water model (SOILWAT) 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.

4) Identification of ecologically similar regions is the first step in selecting pairs of sites on different continents to conduct experimental comparisons of responses of ecosystems to global change. Our approach to this problem was to evaluate ecologically similar regions in the temperate zones of North and South America using analyses of climatic data (Lauenroth et al. 1994c). Our specific objective for this project was to identify sites that could be used to compare the responses of grassland and shrubland ecosystems on each continent to global change. We used multivariate statistical methods and monthly precipitation and air temperature in our analyses. Each point represented a cell of  $0.5^{\circ} \times 0.5^{\circ}$ . A total of 5048 sites were included. The specific variables used were chosen to reflect the seasonality and magnitudes of precipitation, water deficits, and temperature. A principal components analysis followed by a divisive cluster analysis were used to identify similar regions. The cluster analysis was conducted using three variables: mean annual temperature, and the scores on the first and second PCA axes.

Our results showed good correspondence for areas in which the native vegetation still exists on both continents as well as good agreement for areas that are in similar crops. The analyses also pointed out some important differences between the two continents. A number of the differences

were related to the comparative small size of the temperate zone in South America. The difference in size, in many cases, translated into poorly represented or missing climatic types in South America compared to North America. These differences in climatic types are closely related to differences in the distributions of ecosystem types.

### **3. CURRENT INTERNATIONAL COLLABORATIONS**

1) We are continuing our very fruitful collaboration with Dr. Osvaldo Sala from the University of Buenos Aires. Dr. Sala, a Co-Investigator on our project, continues to contribute to the project both through his direct involvement as well as through his students. Two students who are currently working on doctoral degrees at CSU received their Masters degrees from the University of Buenos Aires under Dr. Sala's direction.

2) We were funded through our 1993 LTER Supplemental Award to bring Dr. Jai Singh from India to CSU for six months. A number of publications are expected to result from Dr. Singh's visit, including a manuscript recently submitted to *Ecology* (Singh et al. submitted).

3) 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 long-term biodiversity research. Freckman and Coffin were part of a 10-member LTER delegation that visited long-term research sites in Hungary in May (1994). Our site will be one of four LTER sites that 16 Hungarian scientists will visit in September (1994). A workshop will be conducted in Budapest in February (1995) to establish collaborative links among scientists interested in biodiversity research.

### **4. DATA MANAGEMENT**

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. The data management staff currently includes Tom Kirchner, the data manager, and Steve Chaffee, the programmer for the LTER project.

We have just ordered an Oracle data base system. Our goal for the coming year is 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. This system is meant to compliment out current methodology, not to replace it entirely. In particular, the scheme we are currently using to document our data files and access data within the files will be used to develop an intersite exchange protocol. The LTER data managers agreed at the July, 1993 Data Manager's meeting to pursue methods to facilitate the exchange of data between the sites. The strategy to be employed is to use a common metadata format to describe the data being transferred. Tools will be developed to convert from the metadata format employed at each sites to the common format. Additional tools such as Itermenu will be developed to efficiently access and reformat the data. The common format to be used is the extensible metadata format we developed for the CPER database system.

We have completed development of the Distributed Processing Interface Library (DPIL) (Kirchner, submitted), a library of Interprocess Communication functions to implement file transfer

procedures directly using Remote Procedure Call methods. These functions are designed to facilitate the construction of distributed client and server applications. The applications can be written in either FORTRAN or C. Ltermenu, which makes use of the IPC library, has been ported to X-Windows under UNIX and to the PC under DOS. A server designed to access the Konza Prairie SQL climate database is now being developed. The server will accept a request for a data set (table) from Ltermenu or similar applications, retrieve the data, generate a metadata file to describe the format of the data, then send the metadata file and data to the client application. This server will also be used at the CPER once our Oracle data base system is functional.

The bibliographic routines developed at CPER have been converted from FORTRAN to C++, and support has been provided to generate FrameMaker documents as well as ASCII files. A Motif user interface has been added to facilitate searches of the database, and for creating new entries in the database. Internet access to the CPER bibliography will be provided, through either a Mosaic interface or an interface developed from the DPIL. The new bibliographic system will be linked to the data retrieval system through hypertext links.

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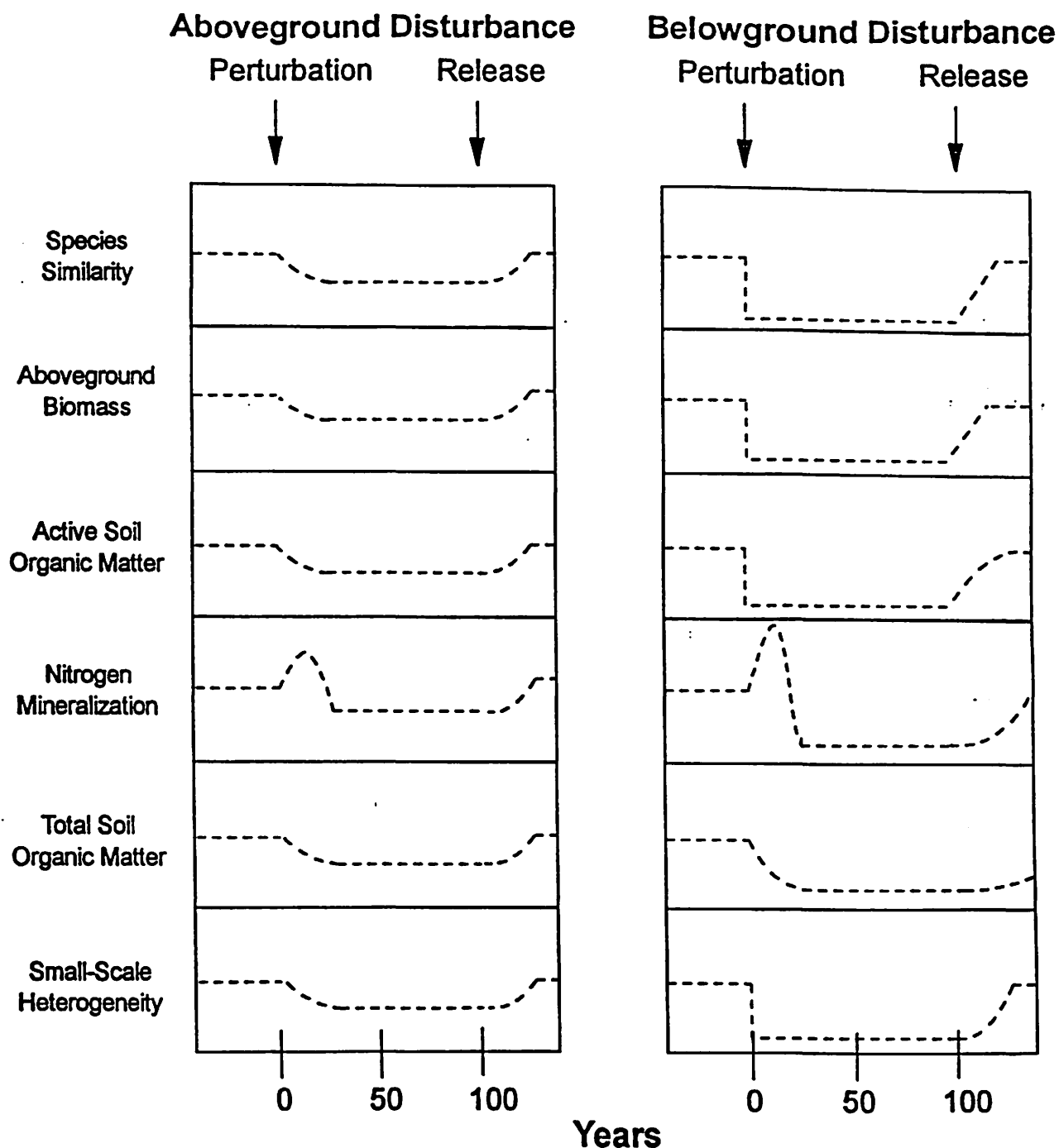
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#### FIGURE LEGEND:

Figure 1. Conceptual framework for the response of U.S. Great Plains grasslands to management practices. Management practices are viewed as a system level disturbance. Each plate in the figure represents the state of an ecosystem feature relative to a native grassland, its relative change in response to a disturbance and release from that disturbance. We have generalized disturbances into two types to capture the biogeochemical impacts, disturbances that directly influence only the aboveground components such as fire or grazing, and disturbances that directly influence the belowground compartments, such as cultivation.

# PREDICTED SOIL CARBON CHANGES CENTURY + MM4 MODELS

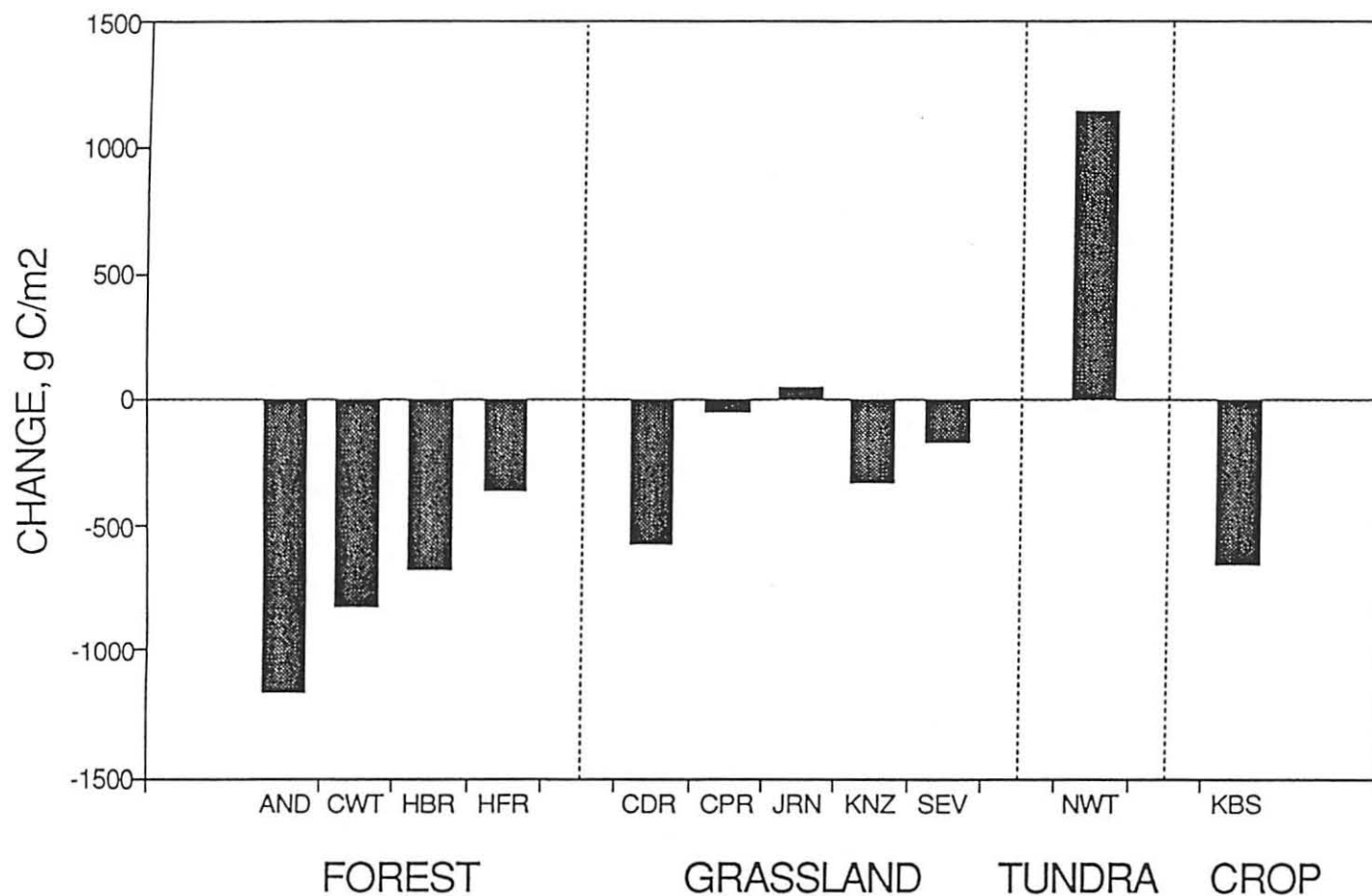


Fig. 2 Figure Legend:

Predicted changes in soil carbon storage in response to 2 x CO<sub>2</sub> induced climate change, using CENTURY model driven by MM4 predicted climate perturbations. Changes are difference between end points of 250 year runs with and without altered climate, and are shown for each LTER site grouped by ecosystem class.