PROJECT SUMMARY

The Project Summary should include a statement of objectives, methods to be employed, and the significance of the proposed activity to the advancement of knowledge or education. Avoid use of first person to complete this summary. DO NOT EXCEED ONE PAGE. (Some Programs may impose more stringent limits.)

Project Summary

A comprehensive long-term ecological research program will be continued and expanded at the Konza Prairie LTER site in NE Kansas. Konza Prairie, a pristine tallgrass prairie is, arguably, the most intensively studied grassland site on earth. The 15 year old, broadly-based research program encompasses studies from the organismic through population, community, ecosystem and landscape ecology levels. These studies are thematically linked via an overarching theme that includes the major abiotic and biotic factors influencing this ecosystem. **Our central hypothesis is that fire, grazing and climatic variability are essential and interactive factors responsible for the structure and function of tallgrass prairie.** In contrast to many other grasslands where ecological processes are constrained by chronic limitations of a single resource (e.g., water), organismic to ecosystem processes and dynamics in tallgrass prairie are products of spatial and temporal variability in multiple limiting resources (water, light, N). Variability in, and switching among, these primary limiting resource(s) are caused by both extant and historical fire, grazing and climatic regimes. Moreover, responses to these factors are strongly dependent on topographic and landscape position. As a result of this complexity, and because grazing and fire regimes are managed in grassland systems worldwide, data from the Konza Prairie LTER program have relevance not only for understanding this grassland, but for broader ecological issues such as stability-diversity questions and interactions between land-use, biodiversity and climate change.

The proposed research will continue to build upon a long-term database on ecological patterns and processes derived from a fully-replicated watershed-level experimental design, in place on Konza Prairie since 1980. This design includes fire (annual fire to fire exclusion) and grazing treatments (grazed by native ungulates vs. ungrazed). In addition, short-term studies focused on key processes and mechanisms will continue to be a critical part of the Konza LTER program. Proposed new research for LTER IV includes studies of the effect of fire season (in addition to fire frequency) in tallgrass prairie, a fire-treatment reversal experiment in which watersheds that have been annually burned or unburned for 20 years will have their treatments reversed, comparative studies of bison vs. cattle as the dominant grazers, and a long-term study of how grazing, fire, climatic variability and agriculture affect annual C, H_2O and energy budgets in tallgrass prairie. A key question addressed by the latter study is whether or not tallgrass prairie soils are a sink or source for C and how land-use (fire, grazing) and climate affects the C budget. Interdisciplinary synthetic efforts are proposed to integrate results from short and long-term experiments

LTER IV
Long-Term Ecological Research in Tallgrass Prairie:
The Konza Prairie LTER Program

Investigator	**Department** (KSU unless otherwise indicated)	**Expertise**
John Blair, Ph.D.	Biology	Soil/Ecosystem Ecology
John Briggs, Ph.D.	Biology	Data Mgmt, Landscape Ecology
Scott Collins, Ph.D.	NSF, Ecology Program	Community Ecology
Jack Culley, Ph.D.	NBS Coop Unit	Wildlife Ecology
Walter Dodds, Ph.D.	Biology	Aquatic Ecology
Phil Fay, Ph.D.	Biology	Plant/Insect Ecology
Elmer Finck, Ph.D.	Biology (Emporia St. Univ.)	Mammalogy/Avian Ecology
Jonathan Frye, Ph.D.	Biology (McPherson Coll.)	Plant Ecology
Phil Gipson, Ph.D.	NBS Coop Unit	Wildlife Ecology
Doug Goodin, Ph.D.	Geography	Climatology, Remote Sensing
Larry Gray, Ph.D.	Biology (Ottawa Univ.)	Aquatic Ecology
Chris Guy, Ph.D.	NBS Coop Unit	Aquatic Ecology
Jay Ham, Ph.D.	Agronomy	Micrometeorology
David Hartnett, Ph.D.	Biology	Plant Population Ecology
Geoff Henebry, Ph.D.	Biology	Spatial Modeling
Robert Holt, Ph.D.	Ecology (Univ. Kansas)	Theoretical Ecology
Loretta Johnson, Ph.D.	Biology	Plant/Ecosystem Ecology
Donald Kaufman, Ph.D.	Biology	Mammalian Ecology
Glennis Kaufman, Ph.D.	Biology	Mammalian Ecology
Alan Knapp, Ph.D.	Biology	Plant Ecology
James Koelliker, Ph.D.	Civil Engineering	Hydrology
Wendy Macpherson, Ph.D.	Geology (Univ. Kansas)	Geochemistry
Duane Nellis, Ph.D.	Geography	Remote Sensing/GIS
Jack Oviatt, Ph.D.	Geology	Geomorphology
Rosemary Ramundo, B.S.	Biology	Lab Coordinator
Charles Rice, Ph.D.	Agronomy	Soil Microbial Ecology
Tim Seastedt, Ph.D.	EPO Biology (Univ. Colorado)	Ecosystem Ecology
Timothy Todd, M.S.	Plant Pathology	Nematology
Gene Towne, Ph.D.	Biology	Range Science
Mary Ann Vinton, Ph.D.	Biology (Creighton Univ.)	Ecosystem Ecology
Gail Wilson, M.S.	Plant Pathology	Mycorrhizal Ecology
John Zimmerman, Ph.D.	Biology	Avian Ecology

Clockwise from top left: (1) Fire was an inherent feature of tallgrass prairie in presettlement times. Today, watersheds on Konza Prairie are subjected to different fire regimes as part of the LTER experimental design. (2) Fire is important for maintaining tallgrass prairie and reducing woody species. The area on the right is not burned, the area on the left is frequently burned. In NE Kansas, forest occurs where fire is suppressed. (3) Large native ungulates (bison) were reintroduced to Konza Prairie in 1987. (4) Kings Creek on Konza Prairie is the only stream in the USGS benchmark system to drain pristine tallgrass prairie.

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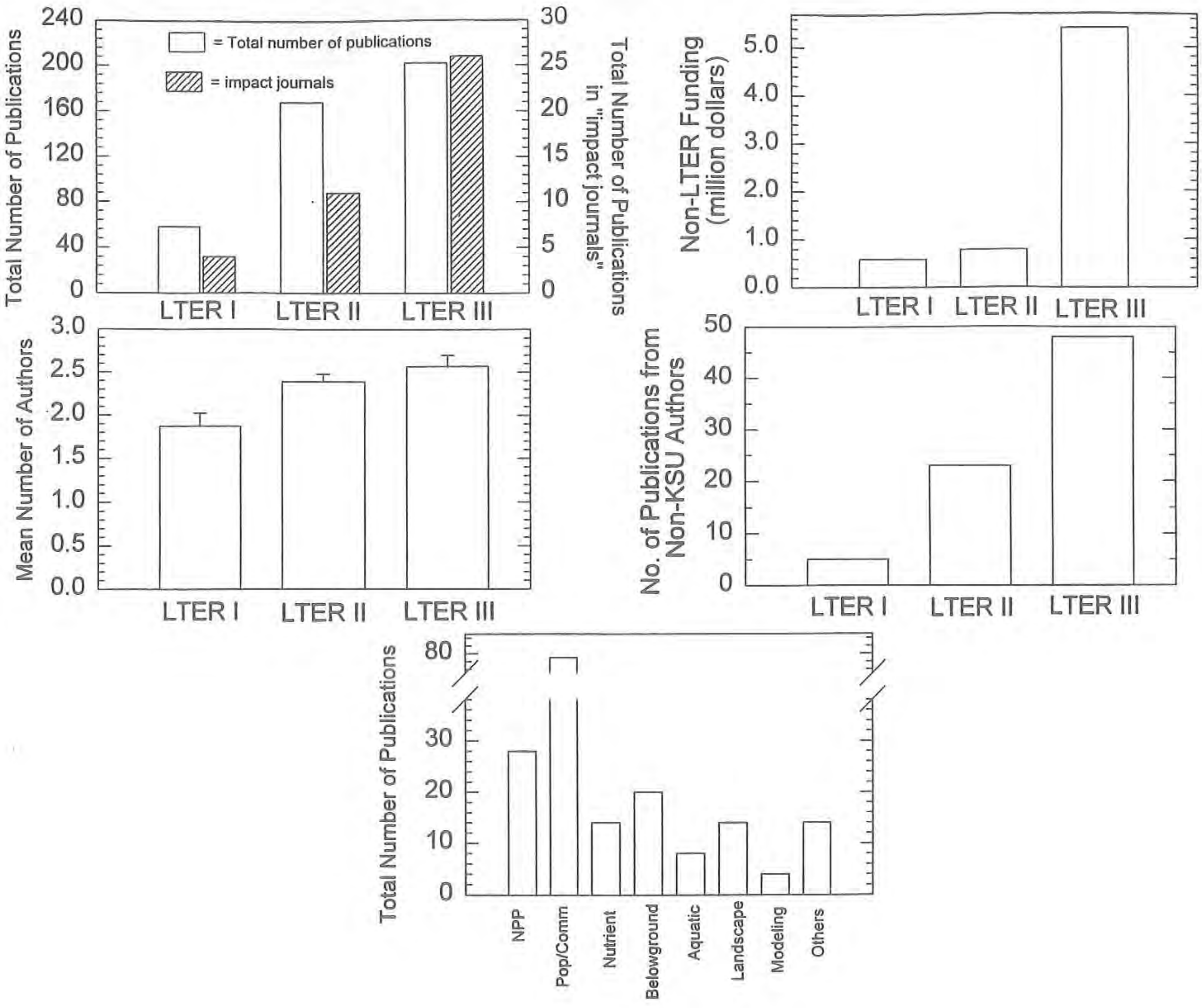


Fig.1. Top left: Trends in the total number of publications from each of the LTER funding cycles for the Konza Prairie LTER Program. In addition, the number of publications in "impact journals" (i.e., Ecology, Ecological Monographs, Ecological Applications and Oecologia) are shown.

Middle left: Trends in the mean number of authors per publication for each of the LTER funding cycles.

Top right: Trends in extramural research dollars (in millions), in addition to the core LTER funds, for each of the LTER funding cycles.

Middle right: Trends in the number of Konza LTER publications generated by non-Kansas State University authors.

Bottom middle: The distribution of publications during the LTER III funding cycle according to major research groups.

1. Results from LTER III

Knapp, A.K., J.M. Briggs, D.C. Hartnett and D.W. Kaufman. 1991-1996. Fire, Grazing, and Climatic Interactions in Tallgrass Prairie. NSF LTER Program. $3,300,000 (original request).

The six years encompassed by the Konza Prairie LTER III proposal included significant advancements in our understanding of grassland ecology, as well as more general ecological principles, a broadening of research expertise, an increase in multidisciplinary efforts, and turnover in scientific personnel associated with the Konza LTER program. The LTER III proposal was authored primarily by T.R. Seastedt (then PI), but both he and C.M. Tate (a co-PI) left Kansas State University shortly after LTER III began. Seastedt maintained a modest level of involvement throughout LTER III and continues today with selected ongoing studies. A.K. Knapp assumed PI duties in 1991, Walter K. Dodds, an Aquatic Ecologist, and John M. Blair, an Ecosystems Ecologist, joined the KSU faculty in 1991 and 1992, respectively. In 1995, Loretta Johnson, a Plant Ecologist with Ecosystem and Landscape Ecology interests, joined the faculty. With Seastedt's continued activity and the efforts of these new scientists, our LTER research group has grown substantially during this period.

Research productivity and quality, measured as peer-reviewed publications, invited book chapters, books and extramural funding grew concomitantly during this period (Fig. 1). From 1991 to present, Konza Prairie LTER scientists have published (or have in press) over 200 research articles and book chapters (these are marked with an "*" in the Literature Cited section). Most of these involved multiple authors and reflect the high degree of interaction within the Konza LTER program, as well as the interdisciplinary nature of much of our research. The books and invited book chapters (Zimmerman, 1993; Briggs and Su, 1994; Collins and Glenn, 1995; Hartnett and Keeler, 1995), along with several journal publications (Seastedt and Knapp, 1993; Briggs and Knapp, 1995; Gray, in press), represent real progress in the synthesis of our results. In addition to synthetic progress, we have also secured additional financial support for shorter-term studies. Such studies are integral to our long-term goals. We view the core LTER grant as the backbone of our program from which we have successfully competed for funds from a variety of other sources (Fig. 2), further broadening our research base. Currently, over $2.2 million in term-of-award support (in addition to LTER funding) funds tallgrass prairie ecological research at Konza Prairie. Finally, our success in attracting additional (non-Konza LTER) investigators to our site increased dramatically during LTER III, further strengthening and diversifying our research program (Fig. 1).

The central hypotheses for the Konza LTER program identify fire, grazing and climatic variability as key forcing factors that alter the structure and functioning of this grassland. These can lead to multiple ecosystem states (from those resembling shortgrass prairie to closed forest) depending on topographic position and climatic history. LTER III represented a significant expansion in research scope relative to LTER I and II. In LTER I, our focus was primarily on understanding the impacts of extremes in fire regimes (annual fire vs. no fire) on an array of ecological patterns and processes in tallgrass prairie. In LTER II, the program was expanded to include additional fire frequencies (1, 2, 4 and 10 year fire intervals) and, with the NASA-FIFE program, the range of spatial scales encompassed by our studies was increased. In LTER III, large native herbivores (bison) were introduced as an experimental variable and we expanded our landscape-level efforts to explicitly include the influence of topoedaphic gradients on ecological processes. Throughout all of these funding cycles, the important and interactive role that climate plays in constraining or

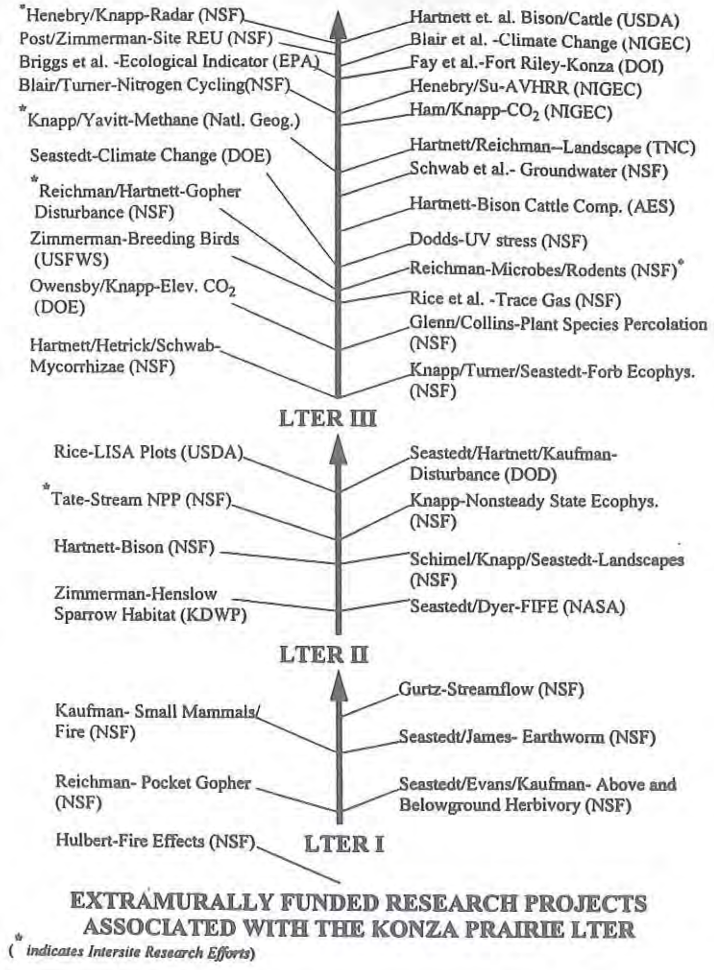


Fig. 2. Trends in the numbers and types of extramural projects funded to conduct grassland ecological research at Konza Prairie from LTER I through LTER III. We view LTER funding as the backbone of a much larger and more diverse research program in tallgrass prairie ecology.

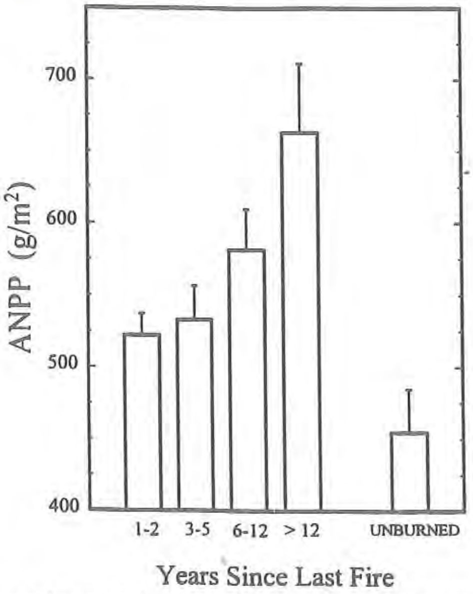


Fig. 3. ANPP in a variety of burned watersheds on Konza that differed in fire history. All watersheds (except the unburned) were burned in the same year. Note that in watersheds burned for the first time in 6+ years, there is a significant "pulse" in ANPP relative to frequently burned watersheds. Vertical lines represent standard error of the mean.

enhancing fire and grazing impacts across the landscape has been implicit within our studies. However, the "sample size" (i.e., years) for studying climatic interactions is only now approaching a level where statistically robust analyses are possible. Below we provide an overview of some of our research accomplishments during LTER III.

Patterns of aboveground net primary productivity (ANPP) have now been documented for 20 years in burned and unburned sites on Konza. We recently published a synthesis of these data that included an assessment of the key controls of ANPP (Briggs and Knapp, 1995). ANPP varied by 4-fold, and annual precipitation by 3-fold, during this period, but in contrast with most grasslands, precipitation was not correlated with variability in ANPP in unburned sites. In burned sites, where ANPP is often higher relative to unburned sites, growing season precipitation was strongly correlated with ANPP, but only on uplands. Previous evaluations of landscape patterns of ANPP at Konza (Schimel et al., 1991; Knapp et al., 1993) indicated that in unburned watersheds, light limitations may occur at all topographic positions, muting the impact of spatial and temporal variability in soil moisture and N. In burned watersheds, water is the primary limitation to ANPP in uplands only, whereas water, light and N may all limit ANPP in lowlands.

Another aspect of tallgrass prairie that makes it unique among Great Plains grasslands is that "pulses" in ANPP occur after drought years or in sites burned following an extended period of fire exclusion (Fig. 3; Seastedt et al., 1991; Briggs et al., 1994). These non-sustainable periods of high ANPP are characteristic of this ecosystem and result when release from more than one limiting resource occurs simultaneously (Seastedt and Knapp, 1993). For example, light limits ANPP in unburned grassland due to the shading effect of the previous years' detritus (Knapp and Seastedt, 1986) and concomitantly, soil N pools may increase. After several years of fire exclusion, burning the site results in release from light limitation which coincides with increased N availability (Seastedt et al., 1991). As a result, ANPP in the year immediately following fire is higher in these sites than in either annually burned or unburned sites (a pulse). Because of these pulses, and the multiple resource constraints that limit energy flow into this grassland, our understanding of the controls of patterns of ANPP must include the complex interactions among spatial and temporal variability in light, water and N that are driven by a combination of topography, fire history and climate (Briggs and Knapp, 1995).

Terrestrial nutrient cycling research during LTER III focused primarily on N, since it is the nutrient with the greatest potential to limit productivity in tallgrass prairie (Seastedt et al., 1991; Ojima et al., 1994). However, we also continued to document patterns of P input and export, and have in place long-term fertilization experiments (the "Belowground Plots") to examine the effects of N, P and N+P additions in these grasslands. During LTER III we continued to develop and refine a conceptual model of N cycling (Fig. 4), which built upon earlier LTER efforts summarized in Seastedt and Ramundo (1990). We added new information on different pathways of N loss from tallgrass prairie ecosystems. Volatilization of plant and litter N during fire represents the most significant N loss in tallgrass prairie (Ojima et al., 1994). During this period we also began to examine the potential importance of denitrification losses of N. Although denitrification losses historically have been considered to be insignificant in grasslands (Woodmansee, 1978; Seastedt and Hayes, 1988), laboratory-based measurements in cores taken from different landscape-positions and land-use types across Konza (Groffman et al., 1993) suggest that denitrification losses can be significant in tallgrass prairie. Extrapolation of measured denitrification rates suggest losses of up to 1 g N m^{-2} yr^{-1} in fertile sites with deep soils (Groffman et al., 1993; Groffman and Turner, 1995).

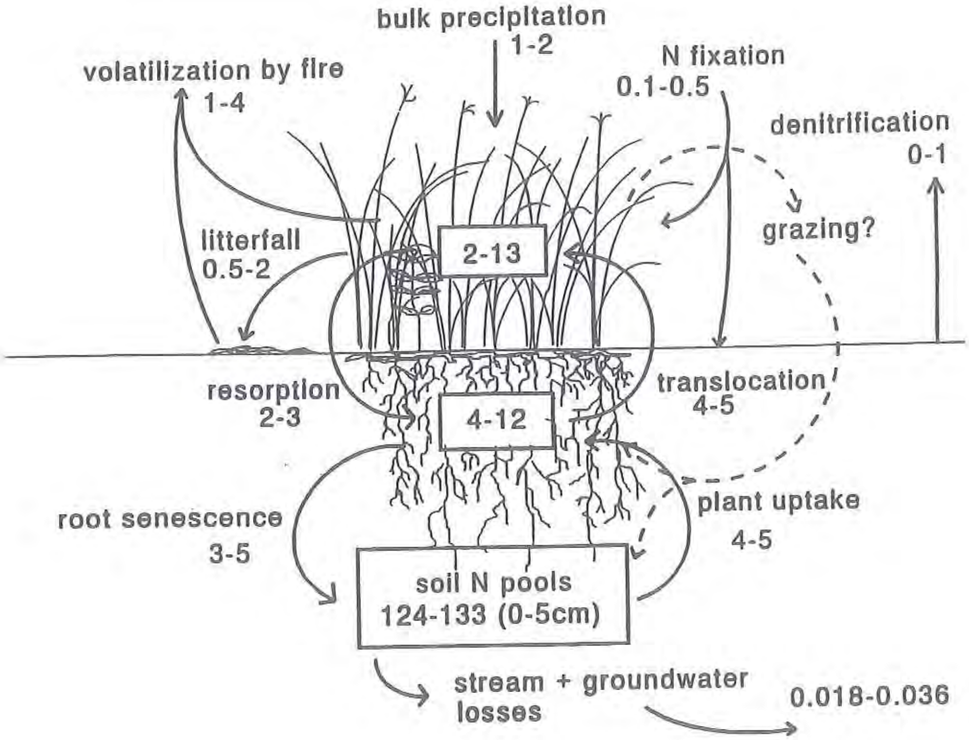


Fig. 4. A conceptual model of N cycling in tallgrass prairie. Standing stocks (boxes) are reported as g N/m^2 and fluxes (arrows) as g $N/m^2/yr$. The wide ranges of values for aboveground N mass and volatilization losses are due to differences in fire frequency (annual vs. infrequent fires). Recent studies also confirmed the importance of N resorption as a N conserving mechanism in the dominant grasses (Heckathorn and DeLucia, 1994), and provided new data on ammonia volatilization losses from leaf surfaces (Heckathorn and DeLucia, 1995; not included in this figure). More detailed analyses of soil N pools (Rice and Garcia, 1994; Garcia and Rice, 1994; Zak et al., 1994) and fluxes (Ojima et al., 1994; Turner et al., submitted) were also obtained during LTER III. Effects of grazing will be a new focus during LTER IV.

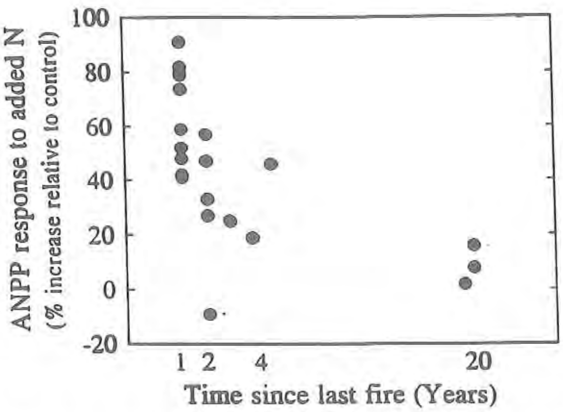


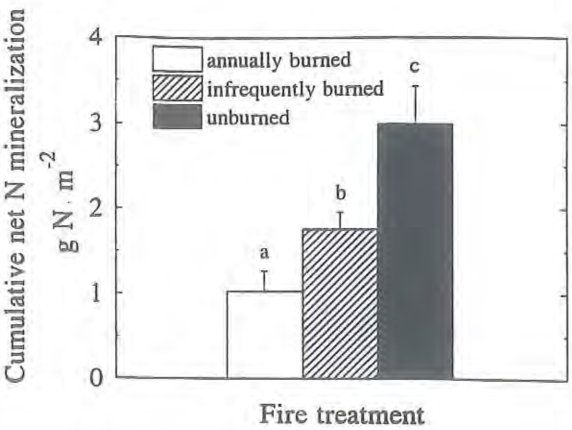
Fig. 5. The effect of time since last fire on the aboveground productivity response of tallgrass prairie to added N (from Seastedt et al., 1991). Tallgrass prairie which was burned annually averaged a 68% increase in ANPP in response to added N, while long-term unburned prairie burned in the year of measurement responded least (average increase of 9%) to added N.

A major emphasis during LTER III was the development of a better mechanistic understanding of the effects of fire frequency and history, climatic variability and topographic position on N cycling processes. Results from LTER II demonstrated the importance of fire extremes (annually burned vs. unburned) in affecting N availability and plant response in tallgrass prairie (Knapp and Seastedt, 1986; Ojima et al., 1990; Seastedt and Ramundo, 1990), and these responses were incorporated into CENTURY modeling efforts (Ojima et al., 1990, 1994; Seastedt et al., 1994). Most prior studies of N limitation in tallgrass prairie had been based on plant tissue chemistry as an index of N availability (Schimel et al., 1991) or on growth responses of plants to added N (Seastedt et al., 1991; Benning and Seastedt, 1996). During LTER III, we determined the effects of fire on biologically active soil N pools (Garcia and Rice, 1994; Rice and Garcia, 1994) and in situ N mineralization rates (Ojima et al., 1994; Turner et al. submitted). Higher rates of N mineralization and greater availability of inorganic N in unburned prairie, relative to annually burned prairie, were documented (Ojima et al., 1994; Turner et al. submitted), and new studies were begun using ^{15}N to assess the effects of fire on plant-microbial competition and the fate of added N (Dell and Rice, 1995). As noted above, fire history affects N limitation (Seastedt et al., 1991; Fig. 5) providing a link between "pulses" in ANPP and enhanced N availability after fire in infrequently burned prairie (Seastedt and Knapp, 1993). Indeed, net N mineralization rates are greater in infrequently burned prairie, compared to annually burned prairie (Blair and Knapp, in prep; Fig. 6) in support of this hypothesis.

Studies during LTER III also focused more explicitly on how N cycling processes vary with position in the landscape. In general, N is most limiting at annually burned, lowland sites, since water limitations become relatively more important than N availability in the drier, shallow soils of upland sites (Schimel et al., 1991; Benning and Seastedt, 1996). Turner et al. (submitted) measured soil N availability and plant response to added N at different landscape positions and under different fire frequencies. Both fire treatment and topography affected soil N availability, with greater N mineralization on unburned than on burned sites, and at upland sites relative to lowland sites. Studies of belowground decomposition also demonstrated significant topographic effects, with faster decay and net N mineralization rates at upland sites (O'Lear et al., 1996). In general, it appears that patterns of ANPP across the prairie landscape (higher in annually burned sites and in lowland areas), are not correlated with patterns of soil N availability (higher in unburned sites and in upland positions; Fig. 7), indicating that different factors may control soil N cycling processes and plant productivity across the prairie landscape.

Tallgrass prairie soils are noted for their high organic C content. An ongoing research focus on Konza (from LTER I through IV) is to determine how land management (fire, grazing) and climatic factors affects soil organic matter (SOM) dynamics. However, changes in SOM occur slowly and are difficult to detect in this grassland. We have measured responses to burning in the more dynamic fractions of the SOM pool and found increases in the active organic C fraction compared to unburned sites (Rice and Garcia, 1994). Annual burning also results in increased nitrogen use efficiency (NUE) of plants (Knapp, 1985) and thus a lower C:N ratio of root inputs (Ojima et al., 1994) which affect both N and SOM dynamics. Soil microbial biomass, part of the "active" fraction of SOM, follows a seasonal pattern of low biomass in the spring and recovery by late summer and early fall (Garcia and Rice, 1994). Soil microbial C is positively related to plant production. Thus, microbial biomass is generally greater under annual burning unless production is limited by drought. In contrast, microbial biomass N responds negatively to plant production and drought.

Fig. 6. Cumulative net N mineralization (May-October 1994) calculated by summing values from 30 day in situ covered core incubations (Raison et.al., 1987) in plots that were annually burned, unburned, or infrequently burned (unburned prior to a spring 1994 fire). Seasonal net N mineralization was significantly affected by fire frequency (*P*=0.004). Soils in unburned plots mineralized approximately 3x more total N over the growing season than soils in annually burned plots. Net N mineralization in infrequently burned plots was intermediate, but was greater than in annually burned plots.



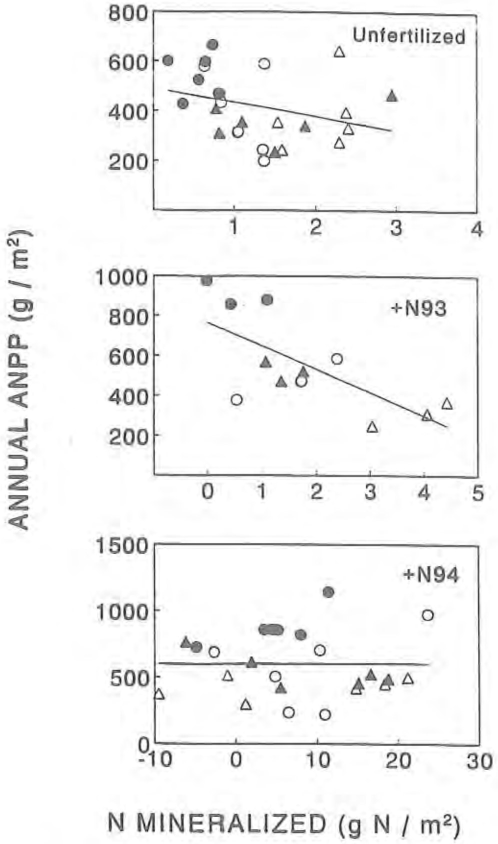
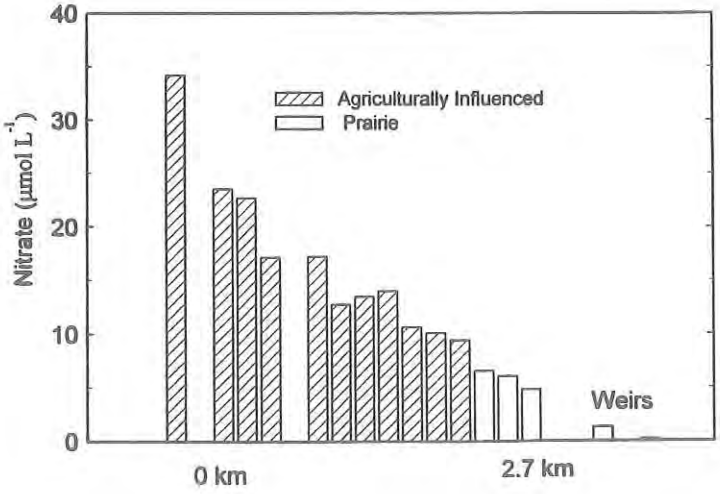


Fig. 7. The relationship between annual aboveground net primary productivity (ANPP) and cumulative net N mineralization in burned (solid symbols) and unburned (open symbols), upland (triangles) and lowland (circles) prairie that was unfertilized, fertilized in 1993 (+N93) or fertilized in 1994 (+N94) (from Turner et al., submitted). The general lack of relationship suggests that the controls of plant productivity and soil N availability operate somewhat independently across the tallgrass prairie landscape.

Fig. 8. Spatial trends in nitrate concentration in Kings Creek, from where Kings Creek enters the larger McDowell Creek off Konza to the upper reaches of the gallery forest 2.7 km upstream. The figure shows where the influence of agricultural activity begins and the associated increase in nitrate downstream from this activity. The upper extent of the sampling is at the weir on N04D watershed. Figure 36 extends the sampled area to the headwaters.



Aquatic and hydrologic studies provided estimates of watershed-level hydrologic export of N during LTER III. Streamwater N concentrations at Konza are low, typically <150 μg total N L^{-1} (Tate, 1990), and the first four years of measurement on gauged watersheds indicate very little annual hydrologic export of dissolved N, which does not appear to be strongly influenced by fire or grazing (Dodds et al., submitted). This represents only a small proportion of incoming precipitation N (0.01-6%). Groundwater losses of N are similarly small. The prairie is more retentive of N than most terrestrial systems (Dodds et al., submitted) and comparative measurements of stream inorganic N downstream from pristine watersheds vs. agricultural areas indicate an increase in N export with land use change (Fig. 8). Because stream-aquifer interactions are important on Konza, groundwater well and lysimeter transects have been established. Groundwater community dynamics have also been documented, including stimulatory effects of isopods on bacteria (Edler and Dodds, 1992), and inhibitory effects of protozoans on nitrifying bacteria (Strauss, 1995).

Community and population structure and dynamics continued to be areas of emphasis in LTER III (Fig. 1). Analyses of long-term patterns from permanent transects on Konza have yielded significant insights into tallgrass prairie plant community structure and dynamics. Spatial and temporal distributions of species show bi-modal patterns consistent with the "core-satellite" hypothesis, including a matrix of widely distributed, temporally stable and abundant core species (mostly dominant warm-season grasses) and a second group of localized, less abundant, and temporally unpredictable interstitial satellite species (Collins and Glenn, 1991). The rarer satellite species are responsible for the non-equilibrium dynamics of this system and determine the patch structure of the community (Glenn and Collins, 1992, 1993). We have also shown that plant species diversity and spatial heterogeneity vary with fire frequency (Collins, 1992) and that the effects of fire on both sexual and vegetative reproduction of grasses and forbs underlie fire-induced shifts in species densities and composition (Towne, 1995; Hartnett, 1991).

Bison grazing increases plant species diversity and community heterogeneity in tallgrass prairie (Hartnett et al., in press). These changes in diversity result from effects of selective grazing on species relative abundance, and heterogeneity generated by effects of non-grazing activities such as urine deposition (Steinauer and Collins, 1995). At the landscape-level, changes in spatial patterns of vegetation in response to bison are influenced by fire and topography, and in turn, vegetation composition influences the seasonal distribution of bison grazing (Vinton et al., 1993). Fire also influences small-scale bison dietary selection patterns (Vinton et al., 1993; Pfeiffer and Hartnett, 1995). Bison preferentially graze where C_4 grasses are dominant and these grasses show significant short-term compensatory growth following defoliation. However, longer-term reductions in growth and tillering were measured after repeated defoliation over several seasons (Vinton and Hartnett, 1992; Turner et al., 1993). Recent results indicate positive relationships between plant species richness and the stability of primary production and species composition in tallgrass prairie (Collins, 1995; Hickman et al., in press). Thus, effects of large ungulate grazers and fire on plant diversity may have important implications for the ecological stability of tallgrass prairie plant communities.

Ongoing studies of the population dynamics of small mammals indicate that there are strong topographic-fire interactions affecting the distribution and abundance of most species (Kaufman et al., 1995; Brillhart et al., 1995; Fig. 9). However, interannual variability in abundance of small mammals does not appear to be driven by any single environmental factor. In contrast, abundances of birds that are grass/forb dependent are strongly and negatively impacted by

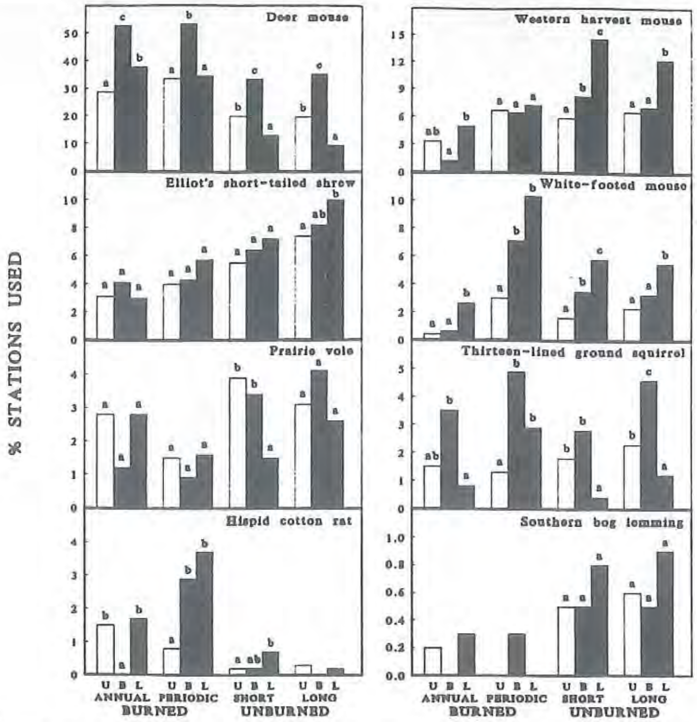
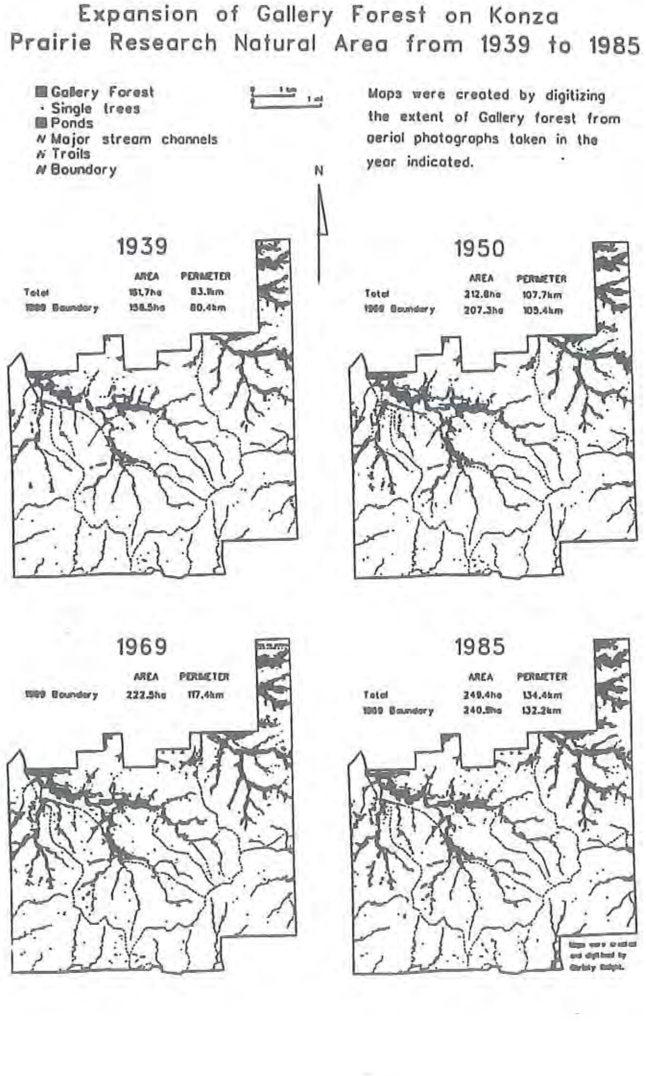


Fig. 9. Percent of stations used in upland (U), limestone-breaks (B) and lowland (L) prairie in annual and periodic burns, and short-term (burned in last 2-4 years), and long-term (5-20 years) burns by eight common species of small mammals on KNZ. Within each fire treatment, different letters above bars indicate significant differences in each panel.

Fig. 10. GIS representation of gallery forest expansion, digitized from aerial photographs taken in 1939, 1950, 1969 and 1985. (From Knight et al., 1994)



drought in burned, but not unburned watersheds (Zimmerman, in press). This may be due to the greater effect of drought on ANPP in burned relative to unburned sites (Briggs and Knapp, 1995).

Landscape-level research has demonstrated the importance of topographic position and landscape-level analysis for understanding spatial and temporal patterns in tallgrass prairie. Throughout LTER III, we utilized remote sensing and geographic information systems (GIS) to capture, manipulate, process, and analyze spatially explicit, geo-referenced data for these purposes. Examples include the use of NDVI measurements to quantify changes in vegetation patterns in response to fire and the reintroduction of bison on Konza Prairie (Briggs and Collins, 1994; Henebry, 1993). In addition, Henebry and Su (1993) demonstrated how the litter layer affects the spatial dynamics of NDVI during the growing season, as well as the robustness of measures of spatial dependence for comparing images from different dates.

One of the most substantial landscape-level changes to occur on Konza Prairie within the past 100 years has been the increase in forested area; GIS was used for a detailed spatial analysis of gallery forest dynamics on Konza (Fig. 10). Knight et al. (1994) found that, while only 5 ha of forest were noted in 1859 (Abrams, 1986), by 1939 over 159 ha of forest were present on Konza, a 97% increase. Furthermore, since 1939 the area of forest has continued to increase, with a total of 250 ha of forest noted in 1985. Knight et al. (1994) concluded that the expansion of gallery forest on KPRNA was not limited by the landscape positions available, since only 10-15% of the alluvial-colluvial deposits along stream channels (the best landscape unit for forest on Konza) are forested. Thus, other factors such as past land-use practices (i.e., fire, grazing, etc.) or hydrologic constraints may limit forest expansion.

The major *modeling* efforts during LTER III have taken two forms: (1) top-down representations of spatio-temporal dynamics at the landscape level and (2) bottom-up representations of ecosystem processes at the stand level. The effects of species interactions on community dynamics have also been explored through a modeling approach (Dodds and Henebry, 1995, 1996). Major achievements included the development of a robust procedure for spatial model error analysis using autocorrelation indices (Henebry, 1995) and the development of a scene modeling framework to perform spatio-temporal analyses on image time series (Henebry, 1993; Henebry and Su, 1993, 1995; Henebry and Kux, 1995; Fig. 11). Process modeling efforts included the use of CENTURY to explore ecosystem processes (Seastedt et al., 1992) and potential responses to climate change (Seastedt et al., 1994) and the ongoing development of a new model that explores the consequences of variations in multiple limiting resources in tallgrass prairie. This model will be discussed in greater detail in the main body of the proposal. Overall, these modeling efforts have enhanced our ability to formulate testable hypotheses about tallgrass prairie dynamics, as well as to identify additional research needs.

Other accomplishments of note during LTER III include the development of a WWW "home page" to provide access for scientists and the public to information about our program and database (see next section); participation of Konza Prairie LTER scientists in workshops and other LTER network activities; and the initiation and near completion of a synthesis volume summarizing and integrating 15 years of Konza Prairie LTER research. Additional information on this latter activity can be found in the main body of the proposal.

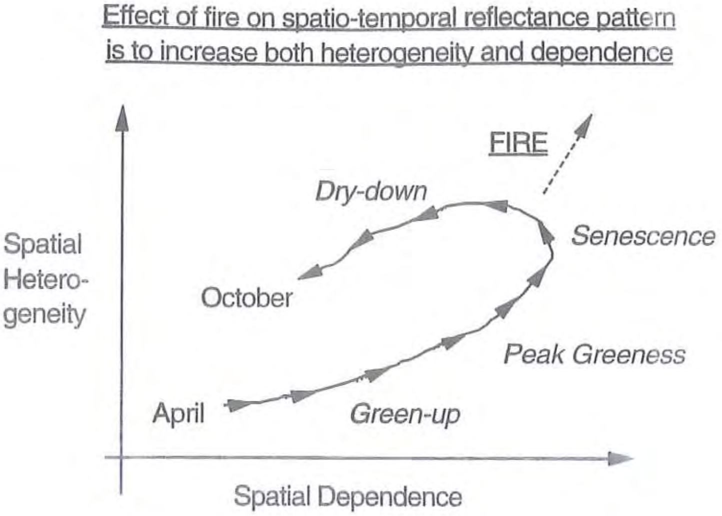
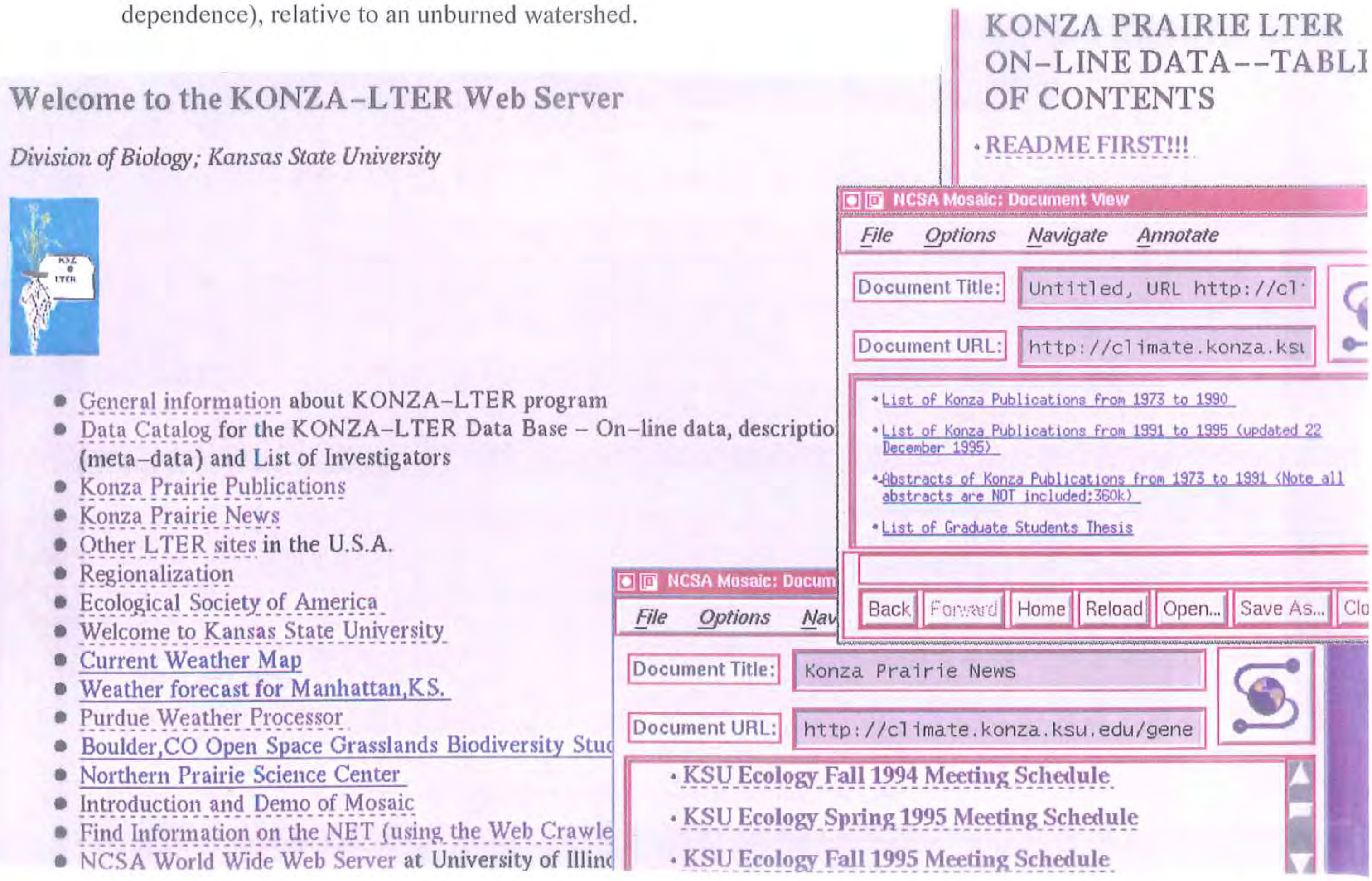

Effect of fire on spatio-temporal reflectance pattern is to increase both heterogeneity and dependence

Fig. 11. Time series of remote sensing images are a challenge to analyze. Conventional statistics are not robust in the face of autocorrelation but ecological processes generate autocorrelation in space and time which are observable in image time series. Canopy development generates changes in complementary aspects of spatial pattern (heterogeneity and dependence). We have developed techniques to quantify these changes and theory to understand them. Given a hypothetical "landscape trajectory" in the metric space defined by heterogeneity and dependence, we can further hypothesize the effects of disturbances on the nominal trajectory. Fire removes the litter layer that acts as a buffer against abiotic forcings, thus we would expect a burned watershed to exhibit increased heterogeneity and greater similarity within areas with similar soil moisture (increased dependence), relative to an unburned watershed.



KONZA PRAIRIE LTER
ON-LINE DATA--TABLI
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· README FIRST!!!

Welcome to the KONZA-LTER Web Server

Division of Biology; Kansas State University

- General information about KONZA-LTER program
- Data Catalog for the KONZA-LTER Data Base - On-line data, descriptio
(meta-data) and List of Investigators
- Konza Prairie Publications
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- List of Konza Publications from 1973 to 1990
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- KSU Ecology Fall 1994 Meeting Schedule
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Fig. 12. Konza Prairie LTER Web Server home page (http://climate.konza.ksu.edu).

A. List of Data Sets On-line.

The preceding examples of results from our LTER III research represents only a selected subset of the studies and data sets completed and ongoing as part of the Konza Prairie LTER Program. We recognize the importance of providing the greater scientific community access to our data and, as a result, we require that all investigators place their data "on-line" after a reasonable period of time (See Data Management section for more details). Below are listed the data sets we have available through our WWW Home Page (http://climate.konza.ksu.edu; Fig. 12).

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All data sets include on-line documentation (meta-data)

1) Ground-Water Chemistry (AGW01; 1991-)
2) National Atmospheric Deposition Program (ANA01; 1982-)
3) Prairie Precipitation (APT01; 1982-)
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12) Bird Checklist (CBC01; 1971-)
13) Bird Dates of Occurrence on Konza Prairie (CBD01; 1971-)
14) Bird Nest (CBN01; 1971-)
15) Bird Populations (CBP01; 1981-)
16) Gall Insects (CGP01; 1991-)
17) Grasshoppers (CGR02; 1982-)
18) Census of Greater Prairie Chickens on Leks (CPC01; 1982-)
19) Soil Microarthropods (CSA01; 1981)
20) Soil Macroarthropod Densities and Biomass (CSA02; 1981)
21) Small Mammal (CSM04; 1981-)

View from a Konza Prairie upland across a watershed dissected by gallery forest. Although a C_4 grass dominated system, the 400 species of forbs, such as the *Echinacia angustifolia* in the foreground, are responsible for the high biodiversity of tallgrass prairie. Forb abundance and plant species richness is typically greatest on uplands on Konza, but productivity on these sites is usually less than on lowlands. Gallery forests represent some of the westernmost extensions of the eastern deciduous forest. With a reduction in fire frequency, expansion of this forest has occurred on Konza (see Fig. 10).

22) Konza Prairie Burn History (1971-)

23) Prairie Litterfall (NPL01; 1981-)

24) Physical and Chemical Characteristics of Soil (NSC01; 1981-)

25) Soil Water Chemistry (NSW01; 1982-)

26) Throughfall (NTF01; 1982-)

27) Aboveground Primary Production (PAB01; 1984-)

28) Gallery Forest Litterfall (PGL01; 1981 -)

29) Plant Phenology (PPH01; 1981-1985)

30) Seed Production and Stem Densities of Grasses (PRE02; 1982-)

31) Root Windows (PRW01; 1986-1989)

32) 1D/UB Transect Studies (PTN01; 1989-)

33) Plant Species Composition (PVC02; 1982-)

34) Mapping of Woody Plants (PWV01; 1972-)

35) Importance Values of Gallery Forest Vegetation (PWV02; 1983)

36) Irrigation Transect Study (WAT01; including: WAT011 (Amount of water added each year; 1991-) WAT012 (Species Composition; 1991-); WAT013 (Aboveground Biomass Data; 1991-) WAT014 (Water Potential Measurements of Big Bluestem; 1991-); WAT015 (Reproductive effort of three grasses; 1991-)

Species Lists:

Flora and Fauna of Konza Prairie

Arbuscular Mycorrhizal Fungi (Glomales) of Konza Prairie

Bryophytes of Konza Prairie (from Merrill 1991)

Vascular Plants of Konza Prairie (compiled by Richard Kazmaier August, 1993)

Terrestrial Insects of Konza Prairie (complied by Philip Fay, Fall 1995)

Aquatic Macroinvertebrates of Konza Prairie (compiled by Ken Fritz, September 1995)

Fishes of the Konza Prairie (compiled by Richard Kazmaier)

Reptiles and Amphibians of Konza Prairie

Phenological Checklist of the Birds of Konza Prairie (from Zimmerman 1985)

Mammals of Konza Prairie

Fig. 13. Right: Estimated pre-settlement extent of tallgrass prairie in North America (from Küchler, 1964). Star represents location of Konza Prairie.

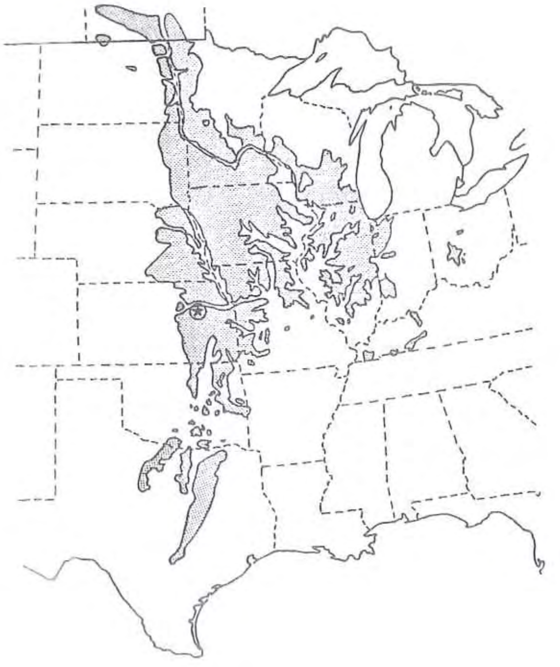


Fig. 13. Left: Regional location of the Flint Hills in eastern KS. This 50,000 km^2 area represents the largest tract of unplowed tallgrass prairie in North America.

Fig. 14. An aerial view of Konza Prairie and the Flint Hills depicting the characteristic geomorphology of the region.

2. Main Body

A. Introduction, Background and Site Description

The Biome.-- Grasslands represent the largest vegetative province in North America (Samson and Knopf, 1994) and the tallgrass prairie is the most mesic and productive grassland type in this biome. Within the contiguous US, historical records indicate that 67.6 million ha of tallgrass prairie once extended from Kansas to Ohio and Texas to Canada (Fig. 13), but today >90% of this once expansive grassland has been turned by the plow, with most states experiencing >98% loss (Samson and Knopf, 1994). One defining characteristic of tallgrass prairies is their fertile soils, a consequence of much greater belowground storage of organic matter than in forests (Seastedt and Knapp, 1993), and a feature that made these ecosystems attractive for row-crop agriculture. Only in the 50,000 km^2 Flint Hills region of Kansas (Fig. 13) do large tracts of unplowed tallgrass prairie persist. In this region, grazing by domestic livestock is the dominant land use because the relatively steep slopes and rocky soils prevented extensive establishment of row-crop agriculture (Fig. 14). Despite the substantial loss of native prairie, >2 million ha of this very productive grassland still exist. In Kansas these grasslands support a livestock grazing industry second only to Texas in animal-unit-months. Near the northern end of the Flint Hills lies the Konza Prairie Research Natural Area (KPRNA), a 3400 ha tract 10 km south of Manhattan, KS and the largest parcel of tallgrass prairie in North America dedicated to ecological research. This site was purchased by The Nature Conservancy in 1970 and is managed by the Division of Biology and Kansas State University.

The Site.-- Konza Prairie is a C_4-dominated grassland with a typical midwestern continental climate characterized by warm, wet summers and dry, cold winters (Fig. 15). Mean annual precipitation (830 mm) is sufficient to support forest or savanna vegetation, but drought, fire and grazing play important roles in maintaining this grassland (Axelrod, 1985; Anderson, 1990). Elevations on Konza range from 320 to 444 m asl and soil type and depth vary substantially with topographic position. Lowland soils (Tully series) are silty clay loams formed from thick colluvial and alluvial deposits and may extend to 2 m. Hillside (Clime and Sogn series) and upland (Florence series) soils are similar, but much more shallow. Chert fragments are common on uplands especially in the B horizon (25 cm) where they comprise 70-80% of the soil (Jantz et al., 1975). These soils overlay as many as 10 distinct layers of alternating limestone and shale (Fig. 16). Limestone layers tend to be permeable to water but shales are not, thus lateral movement of water occurs at interfaces and if these zones surface, seeps and springs occur. Although *Andropogon gerardii* is the dominant grass, there are over 70 species within the Poaceae on the site and over 400 species of forbs (non-graminoid herbs, almost all C_3). Gallery forests (thin bands of forest along stream channels) dissect Konza with the dominant species usually *Quercus macrocarpa*. In total there are over 600 species of plants and bryophytes known on Konza with 32 mammal species, over 200 bird species, greater than 30 herps and 700 invertebrate species identified from terrestrial and aquatic habitats (Species lists are available on our WWW Home Page). There are few species endemic to tallgrass prairie, perhaps reflecting the dynamics of past climates and the relatively recent origin of grasslands in North America (Anderson, 1990), but Konza Prairie serves as a refuge for pristine tallgrass prairie communities. In summary, Konza Prairie has most features representative of the once expansive tallgrass prairie with its deep, rich soils in lowlands, high species richness and diversity and, as described below, fire and large native herbivores incorporated through our experimental manipulations.

Research History.-- The Konza Prairie LTER Program was one of the initial 6 projects funded by NSF in 1980 and, as such, has a data base that spans 15 years. Although Konza was a relatively "new" research facility in 1980 (compared to LTER sites with Forest Service, ARS or IBP research histories), a limited amount of pre-LTER research extends selected data sets back at least

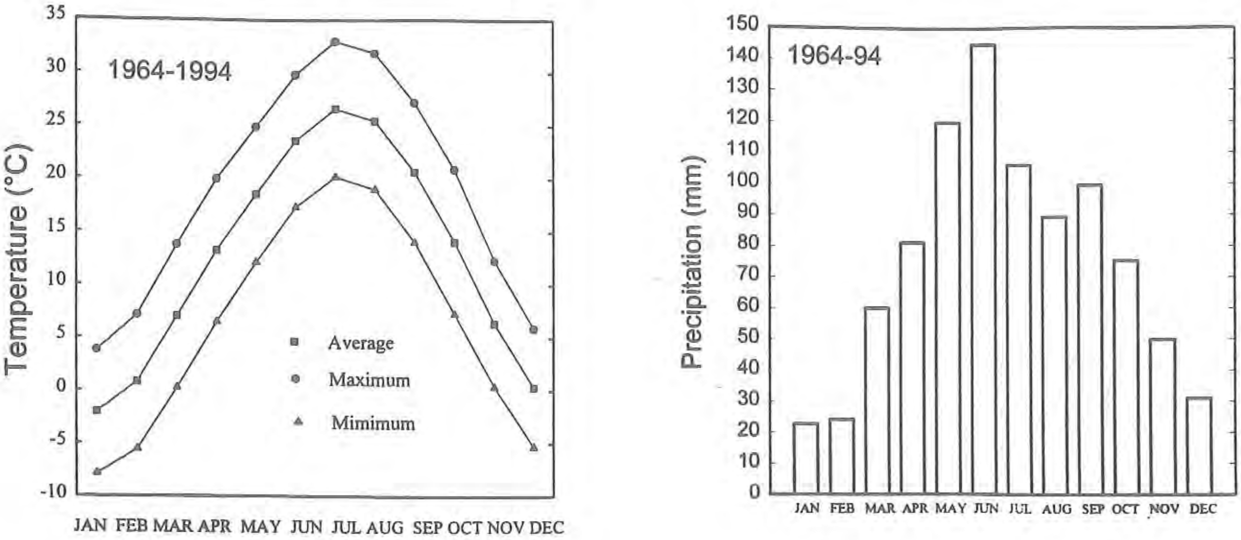


Fig. 15. Left: Monthly average, maximum and minimum temperatures for Manhattan, KS (approx. 10 km from KNZ). Right: Monthly average precipitation for Manhattan, KS.

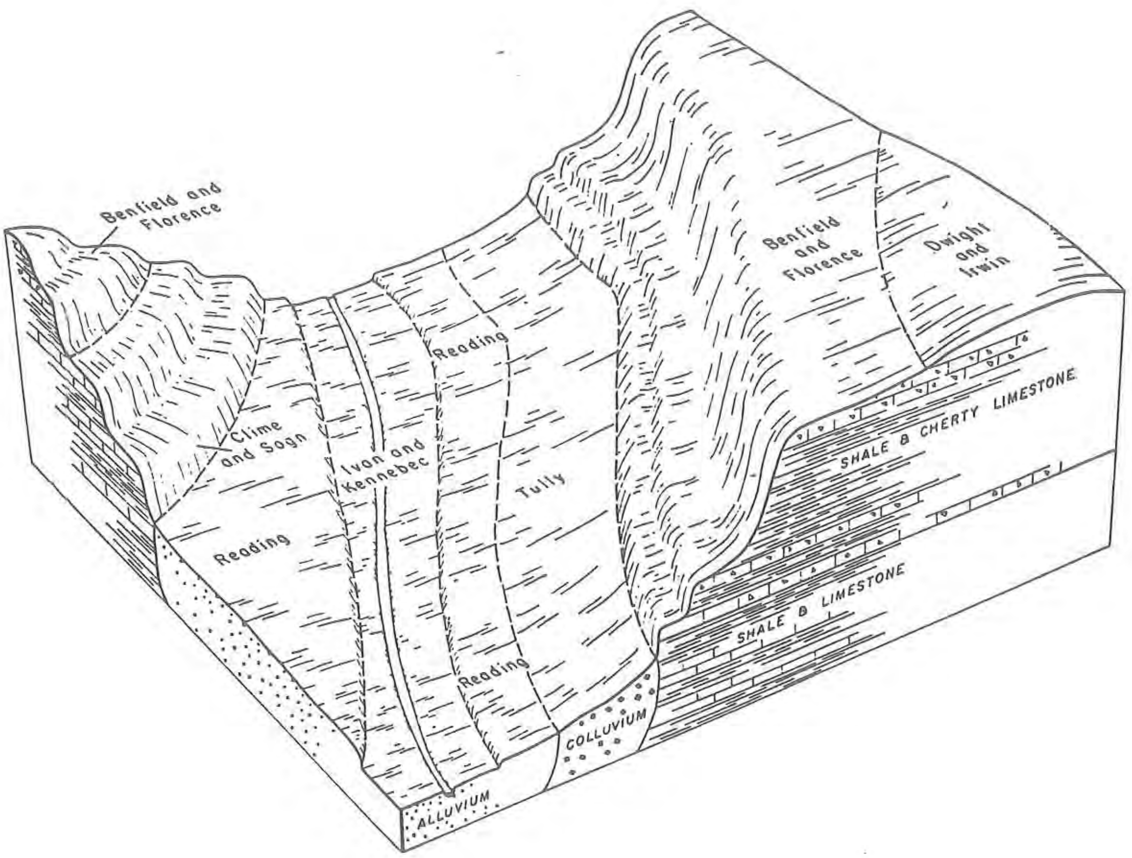


Fig. 16. Idealized schematic of soils and topoedaphic patterns on Konza Prairie watersheds (from Jantz et al., 1975).

20 years. Despite this "late start", research conducted at the site during the 15 years of support by the NSF LTER program has led to over 400 peer-reviewed manuscripts, 3 books and 68 graduate theses and dissertations. Indeed, Konza may be "the most intensively studied grassland on earth" given the LTER effort and the intensity of measurements made during the NASA-FIFE years (Sellers et al., 1992).

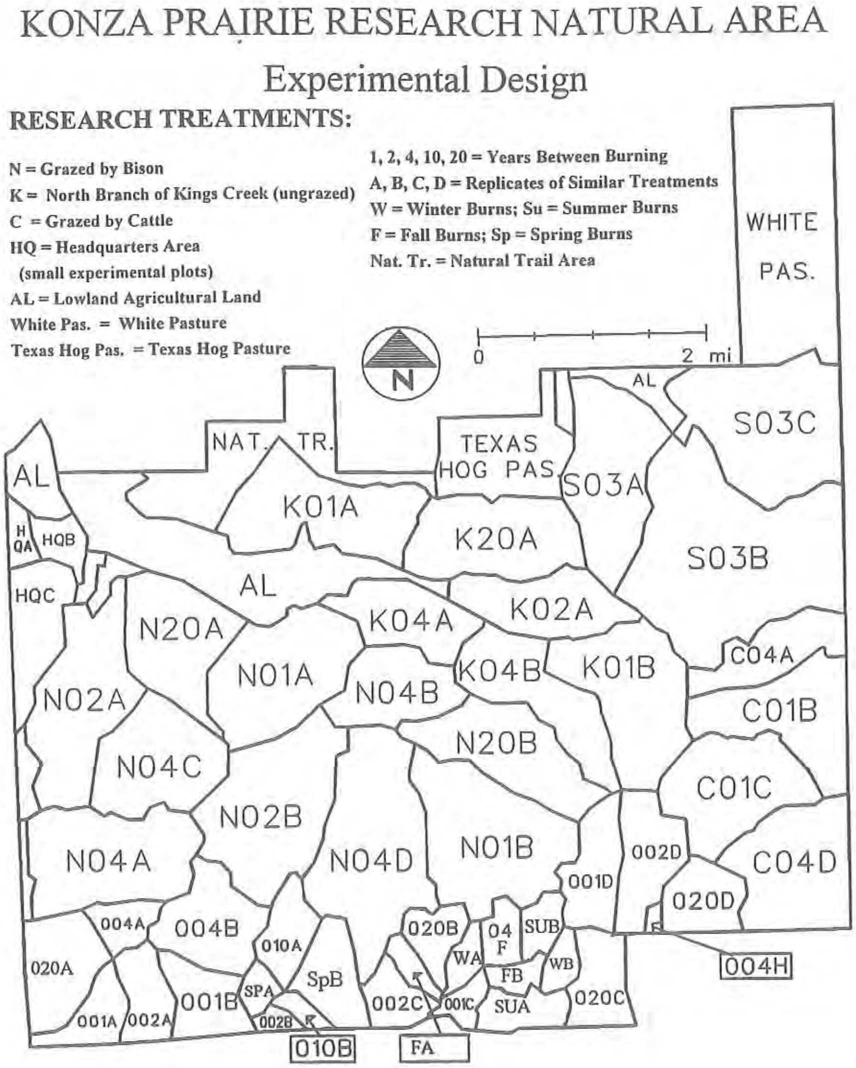
Konza Prairie, and LTER-supported research, provides a valuable link in regional, national and international networks of ecological research. Konza serves as a pristine regional benchmark for studies of land management effects on water and soil quality, Konza is included in a number of cross-site comparative studies of ecological processes through both empirical and modeling approaches, and internationally, Konza LTER PIs have collaborative research projects underway in Hungary, China and Brazil.

As discussed in the "Results from LTER III" section, LTER research on Konza Prairie has expanded over the years from an initial focus on fire extremes to a comprehensive research program on fire, grazing and climatic interactions across the landscape mosaic. Below we describe our conceptual basis for this research paradigm and provide a general overarching theme for our ongoing and proposed studies.

B. Conceptual Framework

Worldwide, grasslands occur where the following three critical system characteristics are present: (1) high intra- and inter-annual precipitation variability (droughts are common), (2) large herbivores are capable of removing a substantial fraction of the aboveground biomass, and (3) fire is (or once was) common and widespread. In contrast with other North American grasslands where shortages of a single resource often dominate system responses (water at the shortgrass CPR LTER site or N in the sandy soils of the Cedar Creek (CDR) LTER), humid tallgrass prairies with soils high in organic matter are best viewed as being limited by multiple resources (water, light, nitrogen; Knapp and Seastedt, 1986; Chapin et al., 1987; Seastedt and Knapp, 1993). The combination of a highly variable continental climate, topoedaphic resource gradients, and a variable grazing and fire regime leads to a very heterogeneous landscape where the relative importance of water, light and nitrogen, and the structural and functional responses of the biota and the ecosystem, vary in space and time (Schimel et al., 1991; Knapp et al., 1993; Benning and Seastedt, 1996). Thus, many ecological patterns and processes in tallgrass prairie are best considered from a non-equilibrium perspective, where frequent shifts in the relative importance of key multiple resources are crucial for maintaining both the diversity and productivity of these ecosystems (Seastedt and Knapp, 1993). We contend that, relative to other grasslands, and indeed most other biomes, these shifting resource limitations are expressed maximally in tallgrass prairie on time scales amenable to ecological study, and affect organismic through ecosystem responses, as well as landscape-level patterns. Thus, our central research theme is that **the structure, function and dynamics of the tallgrass prairie ecosystem are products of multiple limiting resources which vary in importance in space and time. This variability is caused by nonlinear interactions among three key factors: climatic variability, fire regime and grazing pressure, as they are expressed across the landscape.** Clearly, these once inherent features of the system have been significantly altered by human activities either indirectly (atmospheric CO_2 levels) or directly through the management of fire and grazing regimes, species introductions, and fertilization. Long-term field experiments designed to quantify the relative importance of these factors independently and interactively, coupled with short-term mechanistic studies of how critical processes respond to changing resource availability, are necessary to (1) evaluate organismic through ecosystem responses to fire, grazing, and the natural climatic variability characteristic of this system, and (2) assess the consequences of land-use and climate change for

Fig. 17. Watershed-level experimental design of the Konza Prairie Research Natural Area. This 3487 ha site is representative of the Flint Hills region and is owned by the Nature Conservancy. Watershed codes (e.g., K01A) indicate fire frequency and grazing treatment imposed (see legend). Many of the small southern watersheds have been burned since 1971, larger watersheds since 1988. Prescribed burning occurs during the late spring except in watersheds scheduled to be burned in other seasons (winter, summer, fall: see legend). Bison were reintroduced to the native grazer watersheds (denoted by an "N") in 1987 for N02A, N20A, N04C, and N04A, and in the remaining "N" watersheds in 1992. Cattle were introduced to the "C" units in 1992. Weirs are located at the bottom of watersheds N04D, N01B, N02B and N20B. A USGS gauging station is located on Kings Creek in K01A. Kings Creek is notable in that it is the only basin within the USGS network that exclusively drains pristine tallgrass prairie.



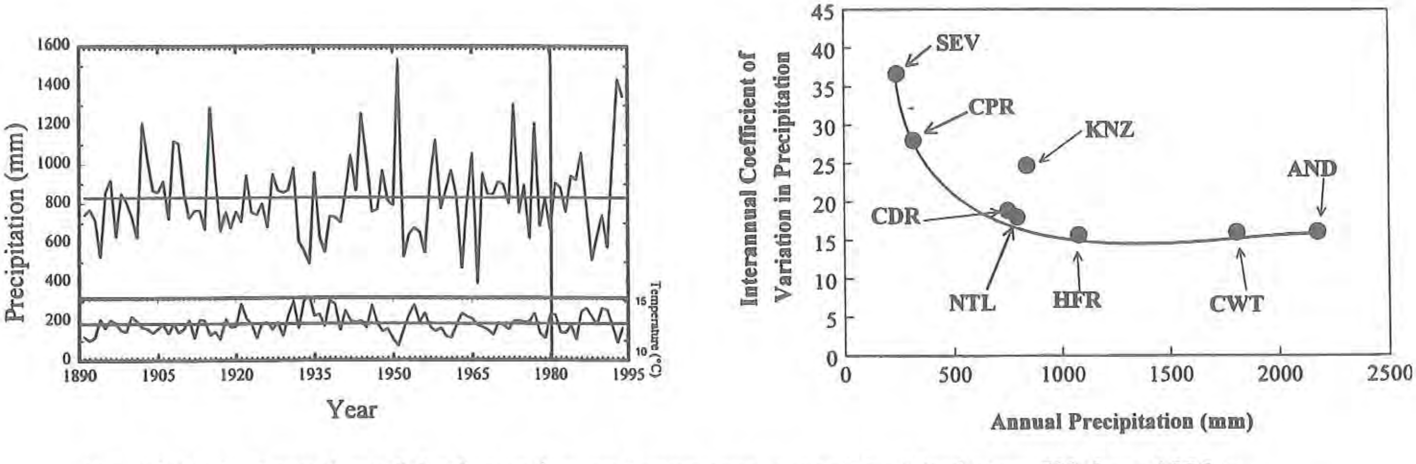


Fig. 18. Left: Annual precipitation and mean temperature record for Manhattan, KS from 1895 to present. The vertical line represents the start of LTER I in 1981 and the horizontal line indicates the 100 yr. mean.
Right: The coefficient of variation (CV) of annual precipitation vs. mean annual precipitation from eight LTER sites. Note that variability for Konza Prairie is distinctively greater relative to the trend for the other sites (i.e., Konza has both high interannual variability in precipitation along with relatively high mean annual precipitation for a grassland site). As a result of these two factors, certain characteristics of tallgrass prairie, such as ANPP, are very responsive to short term climate change.

grasslands. The ongoing and proposed expansion of Konza Prairie LTER research described below is captured within these two goals.

C. Experimental Design & Rationale for Long-Term Research at Konza Prairie

The experimental design of Konza Prairie (Fig. 17), coupled with long-term sampling, incorporates the three critical grassland ecosystem characteristics identified above (fire, grazing and climatic variability). The design is a fully replicated, watershed-level fire frequency and grazing experiment. Within selected "core LTER" watersheds, we have established permanent sampling transects and plots spanning various topographic positions. At these locations, we sample ANPP, plant species composition, consumer populations, nutrient dynamics and aboveground and belowground processes. The co-location of these facilitates integration among our studies. As noted above, fire is critical to the maintenance and functioning of tallgrass prairie (Collins and Wallace, 1990). Since 1981 (and in some areas on Konza since 1971) entire watersheds have been subjected to late spring (April 10 ± 20 days) fire at intervals of 1, 2, 4, 10 and 20 years. This range in fire frequency was designed to encompass natural fire regimes as well as management extremes (annual fire to complete fire suppression). In addition, ongoing small plot studies, begun in 1980, assess the impacts of fire season (the "Hulbert Plot Study", Fig. 44), and in 1994 we added replicate watershed treatments of annual summer, fall and winter fires to the experimental design. The rationale for these studies and a new stochastic fire interval treatment are included in the "New Initiatives" section. Historically, native ungulate grazers (i.e., bison) also were an essential component of these grasslands, and were likely to have significantly influenced ecological processes ranging from plant physiology to whole system nutrient flux (McNaughton, 1985; Detling, 1988). Bison were reintroduced to Konza in 1987 and the herd grew to our target stocking density of 220 animals per 1000 ha in 1994. Domestic cattle were added to other watersheds for comparative studies in 1992. The rationale for these studies of native vs. introduced grazers also is included the "New Initiatives" section.

Although our research emphasis on fire and grazing interactions across the landscape mosaic is clearly appropriate for this grassland, and unique within the LTER network, 15 years of study and ongoing synthesis efforts has given us a new appreciation for the pervasive role of interannual climatic variability in constraining the structure and function of tallgrass prairie. Indeed, interannual precipitation variability at Konza Prairie is distinct from the general trend among LTER sites in which reduced interannual variability occurs as precipitation amount increases from deserts to grasslands to forests (Fig. 18). Moreover, when the average annual moisture deficit (PET- precipitation) is plotted against ANPP, and compared among LTER sites, Konza Prairie occurs where interannual variability in moisture deficit has the greatest influence on ANPP (Fig. 19). In a global comparison of biomes, Frank and Inouye (1994) reached similar conclusions and documented the high degree of variability in AET in grassland biomes. Thus, our contention that both climatic variability and biotic responses to this variability are expressed maximally in tallgrass prairie.

In addition to interannual precipitation variability, there are intriguing long-term trends in the precipitation record at this site. For example, both 10-yr (corresponding to solar activity cycles; Perry, 1994) and 30-yr moving averages of annual precipitation show that during the LTER years of study (1980-1995), precipitation has been increasing, and at present, mean annual precipitation is at or near the highest it has ever been (Fig. 20). Indeed, in 1995 the 30-yr mean was over 130 mm greater than the minimum mean in the 1940's. Five-year means (equivalent to the lag time in correlations between solar radiation and precipitation in Kansas; Perry, 1995) show a difference of almost 500 mm from present day to minimum levels. This range spans the precipitation gradient found from mixed-grass prairie in central Kansas (600 mm) to the deciduous forest of Missouri (1080 mm). Historically, such periods of high and low precipitation have been important in setting

Fig. 19. Relationship between aboveground net primary productivity (ANPP; g/m^2/d) and the average annual moisture deficit (PET (potential evapotranspiration) - Precipitation) for 8 LTER sites. Also shown for Konza Prairie is the interannual variability (± 1 and 2 standard deviations) in moisture deficit for the last 26 years. Note that KNZ falls on the steep portion of this curve and that 2 standard deviations approach existing LTER shortgrass and deciduous forest sites. Variability in precipitation (Fig. 17) and PET, and thus moisture deficit, is much less in the forested sites. And, although variability may be just as great in desert sites, short-term production responses in these arid sites are likely limited by a lack of meristems. Thus, **we hypothesize that tallgrass prairie in general, and KNZ in particular, has the greatest interannual variability in ANPP (energy flow) of all LTER sites.** [ANPP data, from LTER sites or published sources, has been expressed for the growing season (defined as the average number of days when minimum temperatures are greater than -5° C). Shallow lake evaporation was used as a surrogate for PET (data from US Army Corps of Engineers).]

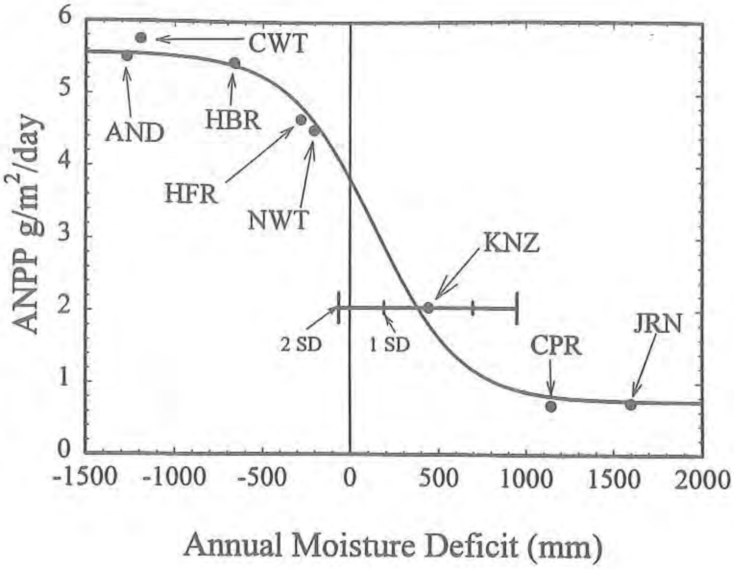
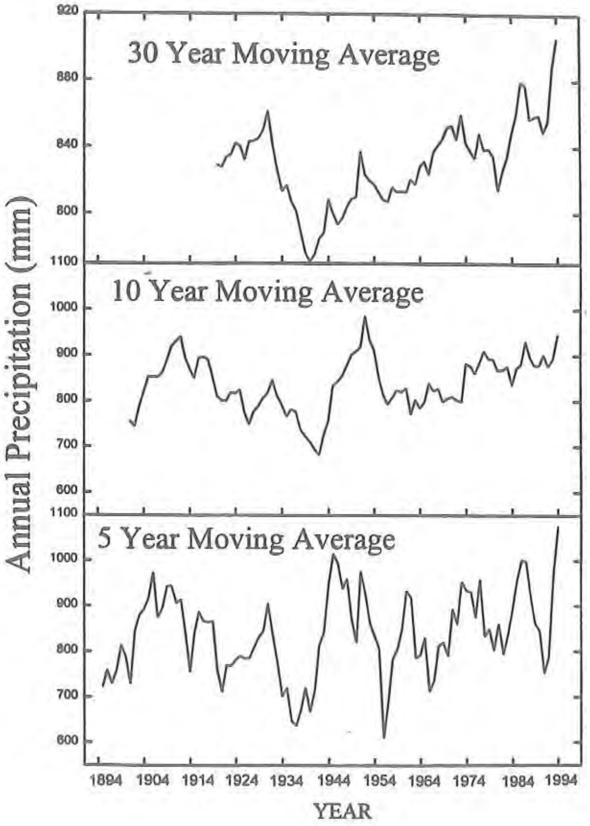


Fig. 20. 30-year moving average (top panel), 10-year moving average (middle panel) and 5-year moving average (bottom panel) of annual precipitation at Manhattan, KS. Note that precipitation has been increasing since the 1950's and that, at present, it is at or near the highest it has ever been. Despite this, significant seasonal water stress occurs and ANPP data from the Irrigation Transect Study (Fig. 27) have shown that additional water increased ANPP in all but 1993 (a year with near record precipitation).



the limits of the distribution of tallgrass prairie (Borchert, 1950) as well as altering a variety of community and ecosystem-level patterns and processes (Weaver, 1954).

The accumulating record of ecosystem and biotic responses to climatic variability coupled with our experimental manipulations of fire and herbivory makes the long-term ecological research at Konza Prairie particularly valuable to the broader ecological community. For example, results from ongoing Konza LTER studies have the potential to clarify debates about equilibrium vs. non-equilibrium models and assumptions in studies of competitive interactions, the maintenance of species diversity, the appropriate spatial and temporal scale for assessing population interactions and community dynamics, stability-diversity issues, and our understanding of complex ecological systems (Tilman, 1987; DeAngelis and Waterhouse, 1987; Huston, 1994; Schulze and Mooney, 1994; Collins, 1995). Konza LTER studies also have shown that the dominant (core) plant species in tallgrass prairie are regulated by competitive (equilibrium) processes (Hartnett, 1993) whereas non-equilibrium processes seem to control the rare (satellite) species (Glenn and Collins, 1992, 1993). Moreover, the role that site and climatic history plays in determining community patterns and critical processes such as energy flow into this ecosystem has been well-documented (Gibson, 1988; Seastedt et al., 1991; Seastedt and Knapp, 1993; Briggs et al., 1994; Briggs and Knapp, 1995). In other words, assumptions that ecological processes in this grassland are in equilibrium with extant forcing factors often leads to poor predictive capabilities (e.g., ANPP in many sites is poorly correlated with current year's precipitation). Only when the system, and the multiple resources constraining its responses, are viewed from a non-equilibrium perspective at the appropriate temporal and spatial scale is our ability to predict process-level phenomena enhanced (Allen and Hoekstra, 1992). Understanding such phenomena will be crucial in future efforts to restore and conserve prairie ecosystems.

On a more regional basis, the tallgrass prairie lies within two major climatic gradients (Burke et al., 1991): a north-south gradient in temperature, which is correlated with a C_3-C_4 plant species composition gradient (Terri and Stowe, 1976), and a west-east precipitation gradient (Fig. 21). Both climatic gradients contribute to historical and present-day fire frequency and grazing intensity gradients across Great Plains grasslands. Konza Prairie lies near the center of the temperature gradient, but at the edge of the precipitation gradient (adjacent to the grassland-forest boundary). Its geographical position makes this LTER site vulnerable to predicted climate changes that may alter site water balance. Models project that such changes will be large in the Great Plains relative to other parts of North America (Mitchell et al., 1990). In addition to projected alterations in precipitation and temperature, increasing CO_2 concentrations will impact plant and soil water status in tallgrass prairie (Knapp et al., 1993; Ham et al., 1995); and all of these will interact with responses to fire and grazing.

Finally, at the broadest scale, research at Konza Prairie and other LTER grassland sites is critical for assessing the role of these ecosystems in the global carbon budget. Grassland soils are superior carbon sinks relative to forest, reflecting fundamental differences between grasses and trees in carbon allocation patterns (Seastedt and Knapp, 1993). As part of LTER IV, hypotheses will be tested that focus on the impacts that climate change and land management (fire, grazing, agriculture) may have on the ability of tallgrass prairie to act as a sink or source for carbon.

In sum, **our conceptual view of this grassland recognizes fire, grazing, and climatic variability as essential and interactive factors responsible for the structure and function of this ecosystem at any point within the landscape mosaic (Fig. 22)**. Indeed, not only are the constraints imposed by these factors interactive, the sequence with which they are imposed is critical. In other words, fire, grazing and climatic history as well as "presence/absence" of these factors at any point in time determine ecological responses. Our LTER goals are to test specific hypotheses relevant and appropriate for the study of this grassland, as well as to conduct research

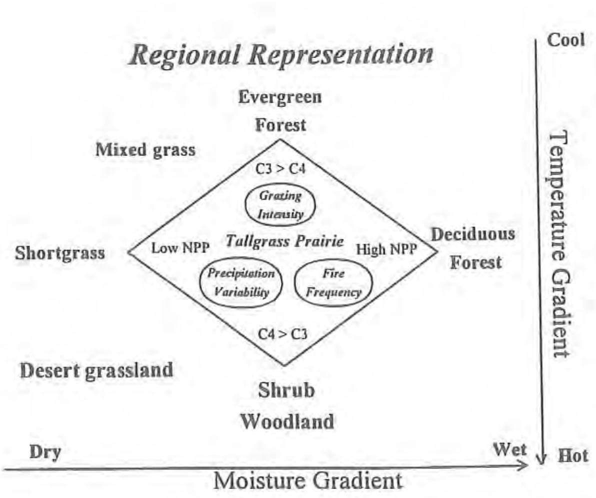
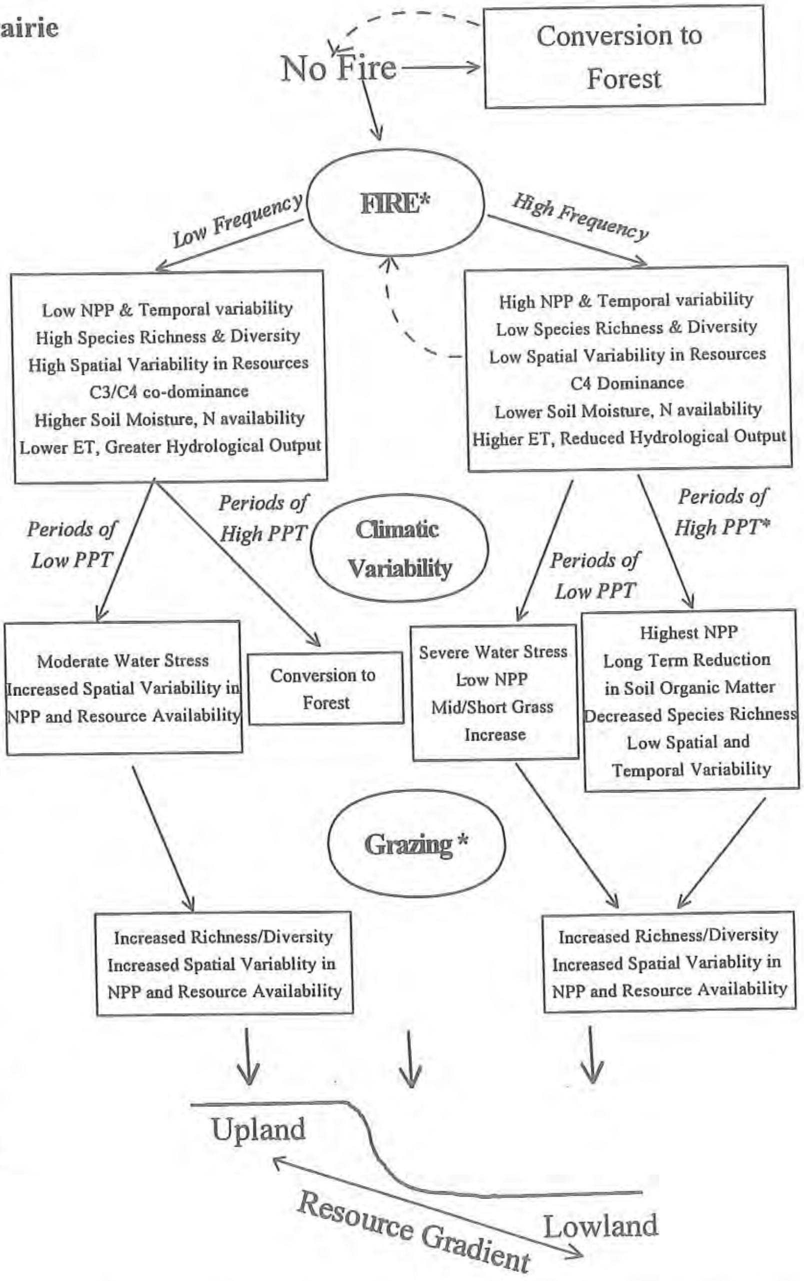


Fig. 21. Tallgrass prairie occurs where strong regional gradients in temperature and moisture occur. These gradients affect species composition and primary production, and gradients in primary production influence grazing intensity and fire frequency. Long term climatic oscillations and directional climate changes, as well as alterations in management (fire, grazing) have the potential to shift the structural and functional attributes of this grassland to states similar to those in adjacent biomes. As noted earlier, extended periods of high or low precipitation are common, but not all structural or functional responses will occur on the same time scale across the tallgrass prairie landscape mosaic. Similarly, shifts in fire frequency or grazing intensity will result in responses at a variety of temporal and spatial scales. Thus, a non-equilibrium perspective is necessary to understand the dynamics of the system.

Central Hypotheses: Konza Prairie

Fig. 22. Flow diagram depicting the central hypotheses of the Konza Prairie LTER Program. Fire, climatic variability and grazing are all factors that can strongly influence organismic through ecosystem responses independently and interactively. We also recognize that these responses are dependent on topographic and landscape position. Fire, grazing and climatic *history* are also important, as is the *sequence* with which these factors occur. For example, fire that occurs in a site with a long grazing history (and associated species composition shifts) will lead to different responses than in a site grazed for only a year. Moreover, burning a site and then grazing it will yield far different responses that if the site is grazed first and then burned. All of the proposed responses (hypotheses) indicated in the boxes are being evaluated through long-term watershed-level experiments or smaller scale studies on Konza Prairie (Fig. 23).



*** denotes experimental manipulations as part of LTER**

that can provide insight into more general ecological phenomenon. Below, we provide a narrative of our ongoing and proposed long-term research program with descriptions of selected short term studies. We have divided our program description into a number of research areas (including some LTER "core areas"), but it should be noted that there are many linkages among these research foci. For example, much of the research in nutrient cycling relates directly to ANPP and plant community dynamics, and community-level studies are closely tied to landscape research efforts. Moreover, all of our short-term and sub-watershed level experiments are linked to multiple research areas as well as to the core grazing-fire watershed experimental design. These studies and their relationship to the core experimental design are depicted in Fig. 23. Finally, one of the original LTER core areas (Callahan, 1984) not explicitly addressed below is "disturbance". We have long debated the definition of this concept in our system due to the high frequency of "disturbances" (fire, herbivory, drought; Evans et al., 1989) in tallgrass prairie. This core area is implicitly incorporated in all of our research areas. (Note: the investigators involved in the research areas below are listed in parentheses; group leaders are underlined; and selected hypotheses are in bold type. Detailed methods for long-term studies can be found in the Methods Manual accessible though the Konza Prairie LTER WWW home page; Fig. 12).

D. Long- and Short-term Experiments

Patterns and Controls of Aboveground Net Primary Production (ANPP) (Knapp, Briggs, Blair, Hartnett, Towne)

ANPP is measured to quantify spatial and temporal variability in energy inputs into the ecosystem, as impacted by fire, grazing and climate, and to assess the role that "bottom-up" control plays in the trophic structure of tallgrass prairie (Hairston et al., 1960; Schmitz, 1993). As one of the original "core areas", substantial effort has been invested to determine the controls of ANPP (Fig. 24). Fire usually leads to an increase in ANPP and we have previously detailed the mechanisms behind this response (Knapp and Seastedt, 1986). As noted earlier, precipitation strongly controls ANPP in burned upland sites (Briggs and Knapp, 1995). This is similar to the control seen across most Great Plains grasslands (Sala et al., 1988). Controls are more complex at burned lowlands and, at present, a "rule-based" conceptual model (Fig. 25) has been developed that incorporates site history, soil moisture and current year climatic factors in predicting positive or negative responses to fire. In addition to refining this model, a goal of LTER IV is to determine the controls of ANPP in unburned sites. Light limitations caused by detrital shading are key in reducing ANPP in unburned sites (Knapp and Seastedt, 1986), but these are fairly constant from year to year. Despite this, ANPP in unburned sites may vary by 2-fold from year-to-year (Fig. 24). Although no significant relationships between any meteorological variables and ANPP were found in unburned sites when the long-term database was analyzed in 1994 (Briggs and Knapp, 1995), **we hypothesize that soil moisture exerts the strongest control of ANPP in the lowlands of unburned watersheds, and similar to burned watersheds, precipitation controls ANPP in upland sites where soils are shallow** (and little storage of water is possible). These relationships are likely not linear, but asymptotic, and are difficult to detect due to the "carry-over" effect of soil moisture from one year to the next. For example, during a 2 year drought period in 1988-89, in the driest year (1988), ANPP actually increased in unburned lowlands (Fig. 24) and ANPP did not decrease until the second year as soil moisture reserves were depleted. Unburned sites always have greater soil moisture than burned sites (Fig. 26; Knapp, 1985; Knapp et al., 1993; Briggs and Knapp, 1995) and the frequency of wetter than average years during the first 15 years of LTER funding (Fig. 18) has made potential relationships between precipitation and ANPP in unburned sites difficult to establish.

Annual spring fire results in high ANPP, dominance by C_4 grasses, and greater interannual and spatial variability in biomass production (Fig. 22, 24; Knapp et al., 1993; Briggs and Knapp,

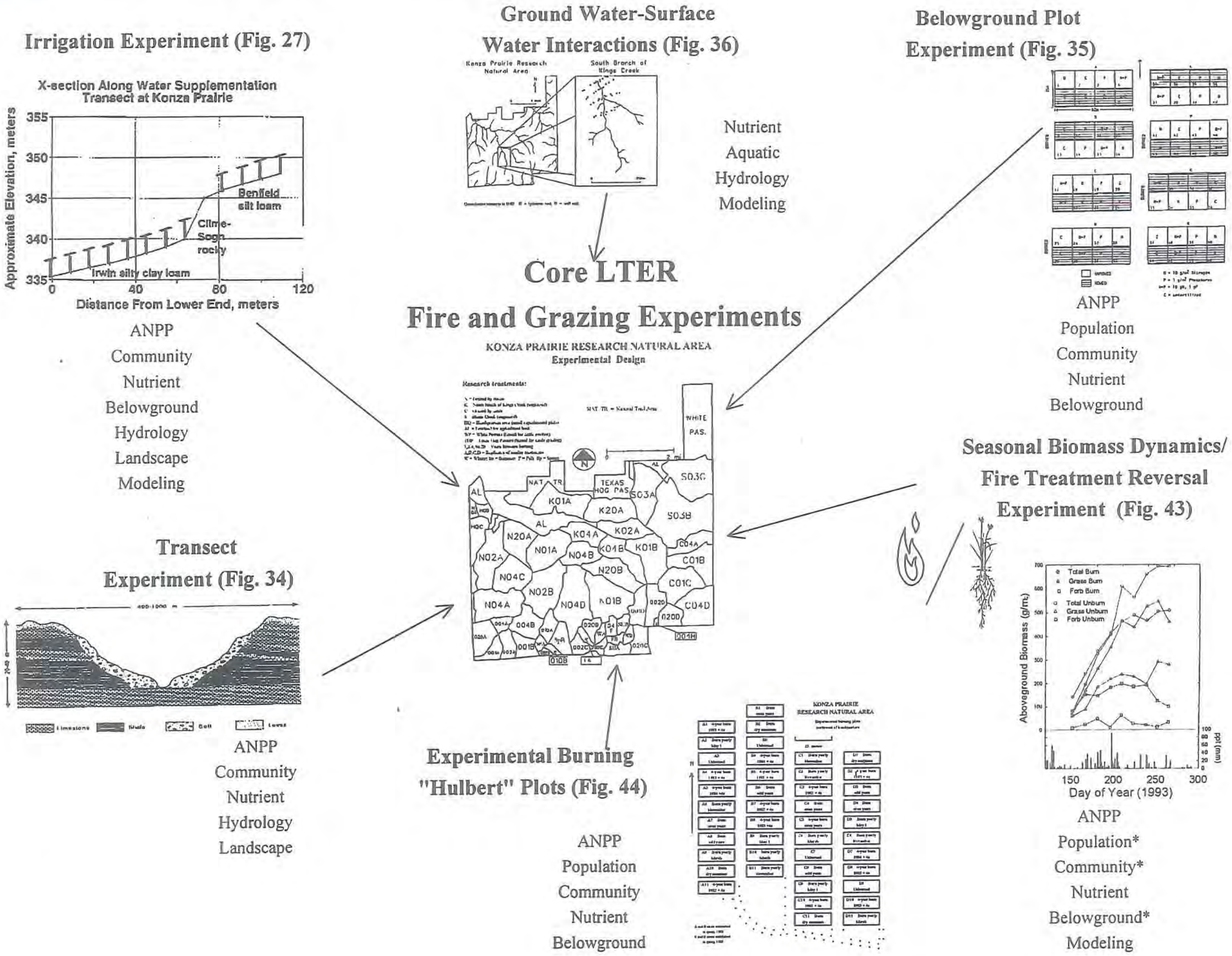


Fig. 23. Ongoing or proposed short-term and/or sub-watershed level experiments that complement the core watershed-level fire frequency/grazing experimental design of Konza Prairie. Each of these studies are described in more detail later. The array of research areas included in each study (ANPP, Population, etc.) is also depicted. * represents new research to be addressed as part of LTER IV.

1995). We hypothesize, and CENTURY model output predicts (Ojima et al., 1990), that **long-term annual burning will reduce soil organic matter and soil N and lead to reduced ANPP** due to C and N losses through volatilization. Long-term estimates of ANPP on annually burned watersheds coupled with soil measurements (see below) provide data to test this hypothesis, but this response is expected to be slow due to the large pool size and stability of soil organic C in grasslands (Burke et al., 1991). After three samples of soil C and N at 5-yr intervals, we have yet to detect a decrease. This may be due to increased allocation to roots by the dominant grasses in annually burned sites that are relatively dry and N-limited (Knapp and Seastedt, 1986; Seastedt et al., 1991; Ojima et al., 1994). In 1991 we initiated an irrigation experiment in an attempt to hasten these responses. The "Irrigation Transect" experiment (Fig. 27) is based on the assumption that maximizing ANPP each year in burned sites (by removing water limitations) will lead to the most rapid loss in site fertility. These replicated transects cross upland and lowland topographic locations and are used to address several other important questions. For example, how important is interannual variability in precipitation to plant species composition? We have preliminary evidence that droughts may be important for maintaining and expanding forb populations in tallgrass prairie (Fig. 28). **We hypothesize that under irrigation and annual fire, dominance by C_4 grasses will be increased and the contribution to ANPP by forbs will be reduced.**

In addition to the importance of water, nutrient availability (primarily N; Seastedt et al., 1991) may also limit ANPP in tallgrass prairie. As part of the "Belowground Plot" experiment (see Belowground Studies section), N, P and N+P have been added to burned, unburned, mowed, and unmowed plots. **We hypothesize that ANPP in burned prairie is N limited in years with adequate precipitation, but that fertilization with N will result in shifts to greater forb (C_3) biomass.** The long-term results of the interaction between annual fire (which reduces forbs; Collins and Gibson, 1990; Gibson et al., 1993; Briggs and Knapp, 1995) and N fertilization (which increases forbs in unburned grasslands; Owensby et al., 1970; McLendon and Redente, 1992) will provide insight into the question of whether forbs (critical for plant biodiversity) are reduced directly by fire (Hartnett, 1991) or indirectly by N or light limitations (Turner and Knapp, 1996) in annually burned sites.

Responses in ANPP to grazing by large ungulates have been extensively documented in the Serengetti by McNaughton and colleagues (e.g., McNaughton, 1979, 1985), as well as in North American grasslands (Detling, 1988; Frank and McNaughton, 1993). Shifts in biomass allocation, sexual vs. asexual reproductive effort, alterations in physiological processes, compensation or even over-compensation for biomass lost have been documented. Earlier studies on Konza indicated that many of these changes occur in response to grazing by bison. In particular, Vinton and Hartnett (1992) found that compensation for biomass lost to herbivory occurred in *Andropogon gerardii* (the dominant grass on Konza) in the first year of grazing, but not in the second year. They suggested that belowground reserves were used, in part, to compensate for aboveground biomass lost in year 1, but that these were depleted by year 2. Our LTER focus for ANPP responses to grazing is on the impact of these herbivores on long-term productivity, and recovery of production potential after cessation of grazing. Studies of the effects of bison grazing on ANPP will be coordinated with proposed studies of grazing impacts on plant community dynamics and belowground processes such as root production and turnover (see Nutrient Cycling and Belowground Studies section). Because bison graze in discrete patches and these patches may be abandoned over time (Vinton et al., 1993), our studies focus on periods of intense herbivory followed by reduced grazing pressure. Since 1992, ANPP has been measured in exclosures that have been protected from bison grazing and compared to adjacent sites previously exposed to ungulate herbivores, but protected from grazing during the years of ANPP estimation (Fig. 29; Hartnett, in press). **We are testing the hypothesis that following cessation of grazing pressure, ANPP will be reduced relative to ungrazed sites for at least one growing season.**

Fig. 24. Patterns in aboveground net primary productivity (ANPP) and precipitation on Konza Prairie from 1975 to 1995 on long-term annually burned and unburned watersheds from deep (lowland) and shallow (upland) soils. Vertical lines represent maximum standard error of the mean. Also shown are yearly total and growing season precipitation for each year. Estimates of ANPP are also made at hillside topographic positions and on replicated 4-yr burned watersheds. Peak season (late August) aboveground biomass is harvested from five 0.1 m^2 quadrats from 4 permanent transects for each topographic position (n = 20 total). Biomass is sorted into graminoid (grasses and sedges), forb and woody plant (usually a minor amount) components along with current year dead biomass and previous years' dead biomass (in unburned sites only). ANPP is estimated as the sum of green and current year dead biomass. Summing biomass increments from sites in which harvests occur every 2 weeks (Fig. 43) does not result in significantly higher estimates of ANPP than employing season end harvests.

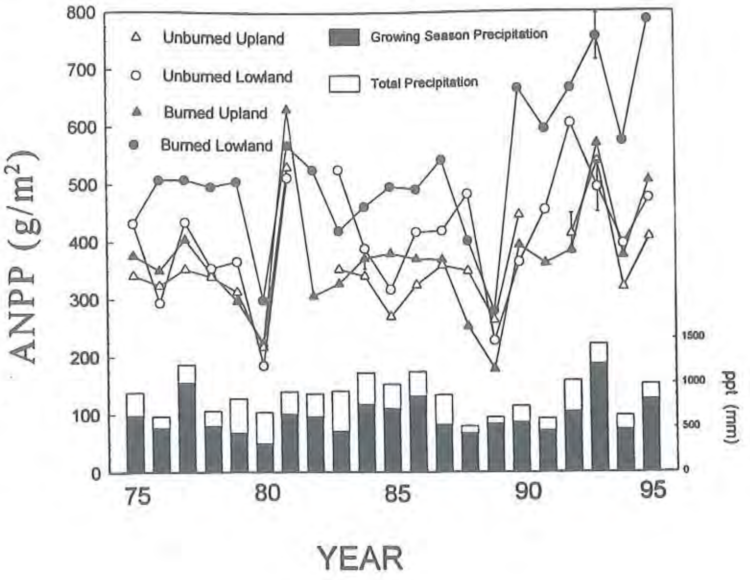
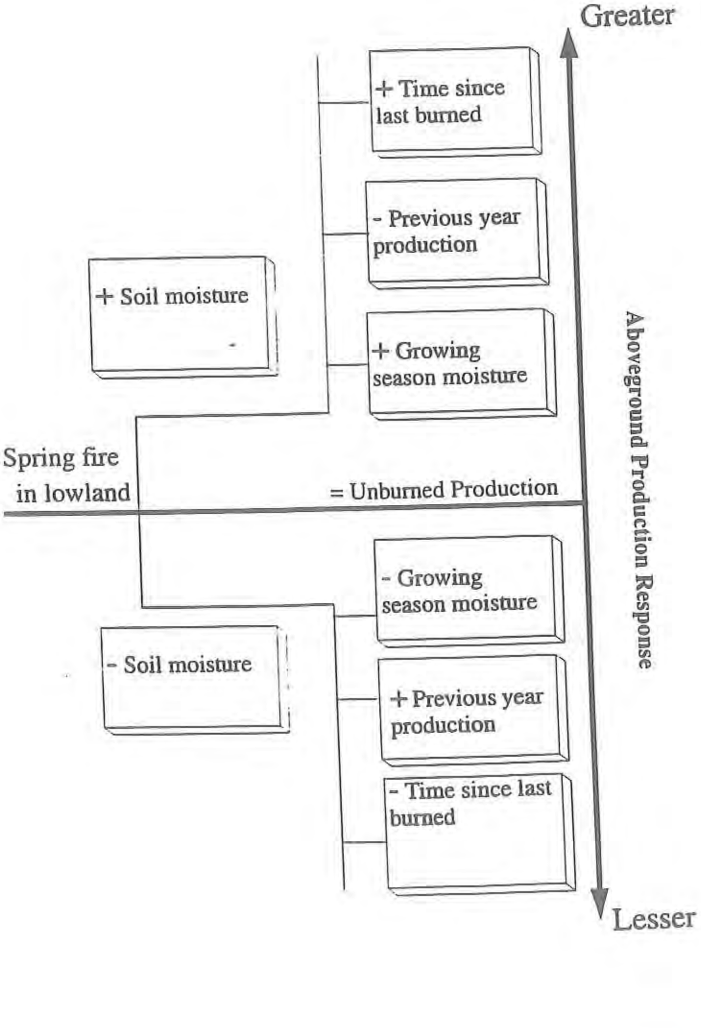


Fig. 25. Contrary to generalizations made in the 1970's, fire does not always result in increased ANPP. Production responses to fire in tallgrass prairie are influenced by a variety of factors and, this "rule-based" model of ANPP responses to fire captures the array of abiotic factors that determines production responses.



We predict that in this first year, allocation to belowground parts will be at the expense of aboveground growth, but that this reduction in ANPP will be short-term. Increased N availability in grazed sites may augment this recovery due to bison-facilitated acceleration of N cycling (see Nutrient Cycling section). Additionally, **we predict that drought will slow the recovery of ANPP** due to reductions in belowground biomass in grazed sites and greater losses of soil moisture caused by the openness of previously grazed canopies.

Plant Populations & Communities (Hartnett, Collins, Towne)

A central focus of proposed plant population and community studies will be to assess the independent and interacting effects of fire, grazing, and climate at multiple scales across the landscape mosaic. We will continue to sample community dynamics by estimating canopy coverage along permanent transects (in place since 1982) that span topoedaphic gradients across a variety of fire and grazing treatments. Both theoretical models (e.g. Milchunas et al., 1988) and preliminary studies suggest that grazing increases floristic and spatial diversity in tallgrass prairie (Hartnett et al., in press; Table 1), and suggest significant grazing X fire interactions (Hobbs et al., 1991). Fire influences plant responses to grazing (Vinton and Hartnett, 1992) and patterns of bison grazing at multiple scales from diet selection to the landscape (Pfeiffer and Hartnett, 1995; Vinton et al., 1993). Grazing also influences fire distribution and intensity by altering spatial patterns of plant biomass (fuel). Significant fire X grazing X climate interactions are predicted based on effects of annual climatic variability on grazing and fire patterns mediated through ANPP, as well as trade-offs between palatability and xerophytism in grassland plants. Community change in response to climate may be mediated through differential species palatability and drought tolerance, coupled with selective herbivory. We hypothesize that **the interacting influences of native ungulate grazers and fire across the landscape mosaic will result in unique, scale-dependent patterns in plant species relative abundances, distribution, and diversity**. Specifically, we hypothesize that **moderate intensities of ungulate grazing will increase floristic diversity and spatial heterogeneity at multiple scales, and the magnitude of these effects will increase with increasing fire frequency.** These diversity and spatial responses will be linked to complementary studies of spatial heterogeneity in nutrient availability (see Nutrient Cycling section).

The value of long-term community studies, such as those on Konza Prairie, has been underscored by renewed interest in diversity-stability relationships in natural communities. Conceptual approaches, and recent empirical studies in various grasslands have suggested a positive relationship between plant species richness and the stability of grassland plant communities (Archer and Smeins, 1991; Frank and McNaughton, 1991; Tilman and Downing, 1994). Among Great Plains grasslands, mechanisms promoting these relationships may be most prominent in the tallgrass prairie, which is characterized by relatively high plant species diversity and large inter-annual climatic variability. Thus, **we hypothesize strong positive relationships between plant species diversity and the compositional and production stability of tallgrass prairie plant communities**. The Konza LTER program is ideal for testing such hypotheses since the core experimental design of Konza Prairie (Fig. 17) provides an array of sites encompassing a wide range in species diversity and productivity.

Proposed studies of individual plant species dynamics and responses to critical resources (water, light, N) will help elucidate the underlying mechanisms causing community-level responses in tallgrass prairie. Our general hypothesis related to our central research theme is that **differential species growth and demographic responses to multiple limiting resources that vary in importance in space and time drive plant community responses to climate variability, fire, and herbivore pressure**. For example, differential responses among legume and other forb species to N limitation under annual burning (Towne and Knapp, 1996) may contribute strongly

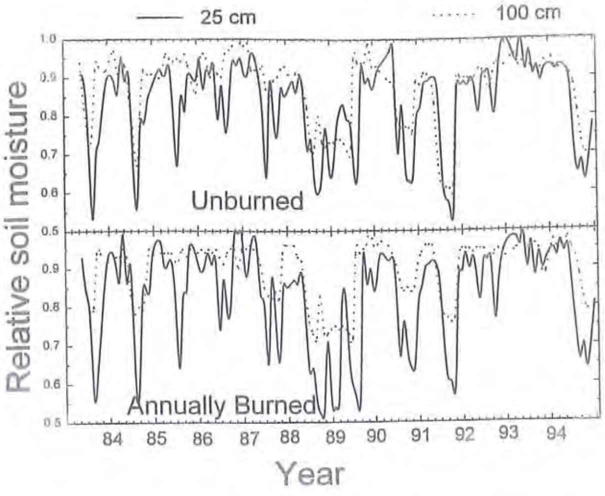


Fig. 26. Monthly mean levels of soil moisture (expressed relative to "saturated" values = 1.0) at two depths (25 cm and 100 cm) on a long-term unburned watershed (020B) and a long-term annually burned watershed (001D) on Konza Prairie. These data are from permanent neutron-probe access tubes (Troxler Electronics) located adjacent to plant species composition and ANPP transects. We also use Time Domain Reflectrometry (TDR; Topp et al., 1980) with rods installed to 15 and 30 cm (where possible) to measure soil moisture in upland sites and across topoedaphic transects on Konza Prairie.

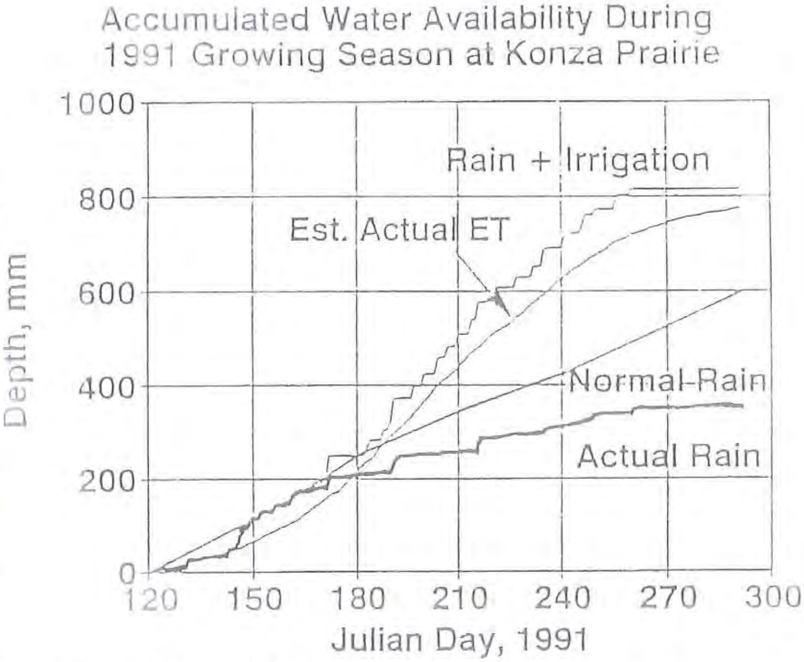


Fig. 27. **Irrigation Transect Experiment**. Photo: looking downhill from the upland portion of the transect. Right: Seasonal course of rainfall, estimated ET and irrigation for 1991.

Justification and description of the study: Water availability can limit ecosystem processes in most years in tallgrass prairie especially in burned sites. In addition, significant seasonal and interannual variability in precipitation is characteristic of tallgrass prairie and is also an important factor affecting grassland structure and key processes from the microbial to the ecosystem level. In 1991, we began experimental supplementation of water across annually burned topoedaphic gradients on Konza Prairie to remove this variability from the system and keep water availability non-limiting. A replicate transect was added in 1993. The minimum planned duration of this study is 10 years. Water supplementation is scheduled to offset evaportranspiration losses and minimize moisture deficits. Responses measured along the transects include: soil moisture, plant water potential, ANPP, plant C and N content, reproductive effort of the dominant grasses, plant species composition, soil organic C and N, soil invertebrate populations, microbial biomass, and litter decomposition. Questions being addressed include: **Can site productivity be maintained under an annual fire regime with ANPP maximized each year? How will decomposition and N mineralization be affected by irrigation? Will C and N pools decrease? Will reproductive effort of the grasses be enhanced by long-term irrigation? Or will allocation to reproduction decline as soil resources become limiting? Will significant shifts in plant species composition occur? Will annual fire be sufficient to keep woody species from increasing along these "wet" transects?**

to effects on plant community structure. Similarly, negative responses of many forb populations to frequent burning may be due to reduced resource availability as competitive effects of the dominant warm-season grasses increase in the post-fire environment (Hartnett, 1991). However, positive responses of some forbs to grazing may result from increased resource availability associated with defoliation of the dominant grasses and subsequent competitive release of the forbs (Fahnestock and Knapp, 1994). Integrative studies in the "Belowground Plots" (see Belowground Studies section) will provide linkages between processes such as N cycling with community responses to Konza LTER fire and grazing treatments.

The local dynamics of prairie plant populations are driven primarily by patterns of vegetative reproduction and rhizome dynamics in response to fire, grazing, and topographic variation. However, physical soil disturbances associated with bison and other animals may influence sexual reproduction and opportunities for seedling recruitment. Variation in these patterns across the landscape may influence both the dynamics and genetic diversity of plant populations. Furthermore, mechanisms controlling plant population dynamics may vary among species and across space and time. Previous studies showing bi-modal patterns of species distribution and abundances (Glenn and Collins, 1990, 1992) suggest different sets of processes regulating the dynamics of core and satellite species. The dominant matrix grasses may be regulated by competition (Hartnett, 1993) whereas non-equilibrium dynamics characterize the rarer interstitial species (Glenn and Collins, 1990). Continued studies will test the hypotheses that **the dynamics and abundances of the dominant matrix grasses and forbs are controlled primarily by competition for limiting resources, whereas the rarer interstitial species are influenced to a greater extent by non-equilibrium dynamics associated with patterns of small-scale (e.g., animal activity) and regional (e.g., fire) disturbance and climatic variability.**

Consumer Populations (D. Kaufman, Fay, G. Kaufman, and Zimmerman)

Since the initiation of the Konza LTER program, studies of consumer populations (small mammals, birds, selected invertebrates) have focused on spatial and temporal variation in their abundance. As one of the original "core areas" of LTER, the primary goals of these studies are to document responses to fire and climatic variability in individual species within these major groups of prairie consumers. Since the reintroduction of bison, studies assessing the impacts of bison grazing on small mammals, birds and insects are now underway. Long-term data sets on mammal and bird populations in particular have been useful in establishing linkages between the abundance of individual species and diversity of the assemblages, describing more completely how prairie fire forces fluctuating patterns of abundance and diversity, documenting uni-directional changes in consumers associated with either frequent or infrequent fire, and assessing the effects of grazing on abundance and diversity.

There is considerable temporal variation in the abundance of individual species of consumers. Because of the overriding impacts of droughts on vegetation and environmental water, we hypothesized that droughts have negative impacts on consumer abundances. There is support for this hypothesis, but more years of data that include additional droughts are needed. The impacts of subtle environmental changes are less obvious and, therefore, it is less apparent which environmental factors influence the abundance of individual species. For example, most species of small mammals exhibit unique temporal patterns of abundance (Fig. 30) which suggest that multiple factors control the population responses of tallgrass prairie consumers. We contend that the interactive, and often subtle, influence that multiple controlling factors may have on consumer populations can only be elucidated by long-term data. For example, past correlative analyses suggested that **shrews are limited by environmental moisture** and that **folivorous rodents are limited by plant productivity**. Because of other interacting environmental factors, hypotheses for temporal patterns of consumer abundance are better stated in terms of conditions that are

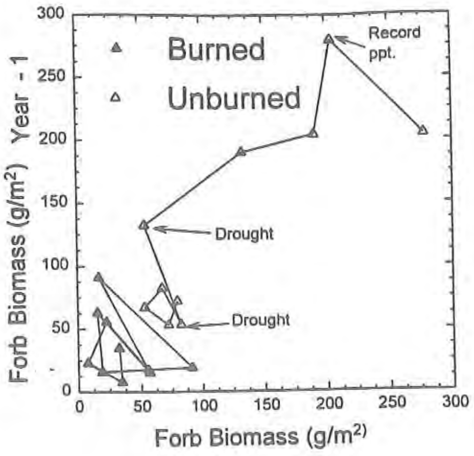


Fig. 28. Temporal dynamics of forb biomass in adjacent annually burned and unburned watersheds on Konza Prairie. Biomass in any year is plotted relative to biomass in the previous year. In burned watersheds, forb biomass is low and variability is low. In unburned watersheds, variability was initially lower during the first 6 years of study, but 2 years of drought and then record levels of precipitation in 1993 led to rapid changes in forb production in this site. The watersheds used for these data are proposed to be part of a new study in which we will schedule 2 annually burned and 2 unburned watersheds to have their treatments switched in 1999 (see New Initiatives section).

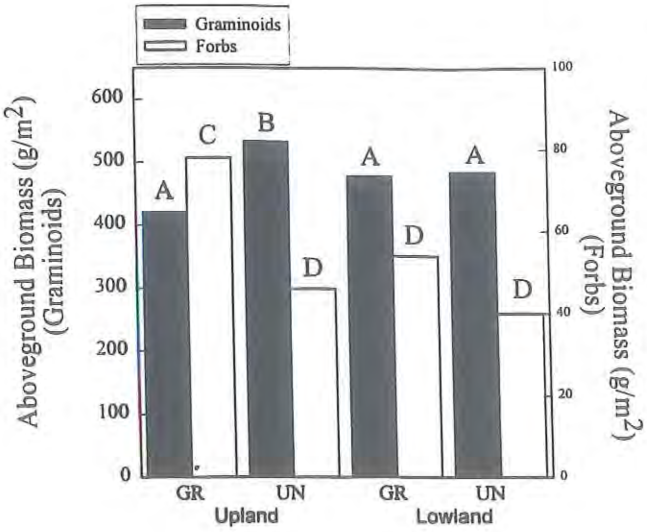


Fig. 29. In watersheds grazed by bison, we use paired permanent and temporary exclosures (5 X 5 m) at all topographic positions to estimate the impacts that grazing by large ungulates may have on site productivity. Peak biomass is harvested annually in the permanent exclosures and compared to that in temporary exclosures that are rotated adjacent to the permanent exclosures at 3 year intervals. Thus, in the temporary exclosures that were subjected to grazing previously, we have estimates of ANPP in 1993 when grazers were excluded. GR = sites grazed by bison from 1987 through 1992 and subsequently allowed to recover using the temporary exclosures. UN = long-term ungrazed sites in permanent exclosures. Different letters above bars indicate significant differences in graminoid and total biomass (P < 0.05). (From Hartnett, in press)

Table 1. Plant diversity components in tallgrass prairie sites. Grazed = sites grazed year-round by bison. Ungr. = ungrazed sites. S = species richness (mean number of species per sampling site). *E* = evenness index = H'/H'_{max} = $H'/\ln S$) H' = Shannon species diversity index ($H' = -\Sigma p_i \cdot \ln p_i$, where p_i = the relative cover of species *i*). . Heterogeneity = spatial diversity = mean percent dissimilarity in species composition among plots within a site, calculated as 1 - Czeckanowski's similarity index): $2\Sigma \min(x_{ij}, x_{ik})/\Sigma(x_{ij} + x_{ik})$, where x_{ij} and x_{ik} are the frequencies of species *i* in quadrats *j* and *k* respectively. (Hartnett et al. 1996. J. Range Manage. In Press).

	S		***E***		**H'**		**Heterogeneity**	
	Ungr.	**Grazed**	**Ungr.**	**Grazed**	**Ungr.**	**Grazed**	**Ungr.**	**Grazed**
Annually burned prairie								
upland sites	27	35	0.42	0.53*	1.40	1.87*	0.41	0.44
lowland sites	28	43*	0.51	0.49*	1.70	1.82*	0.48	0.59*
4-year burn prairie								
upland sites	27	32*	0.53	0.59*	1.76	2.03*	0.33	0.38*
lowlands sites	29	41*	0.38	0.50	1.29	1.85	0.40	0.39

* = significantly different from ungrazed sites at the $p \leq 0.05$ level (Mann Whitney U test).

necessary, but not sufficient to lead to high densities. Thus, the hypothesis for shrews is better stated as **a high level of environmental water (precipitation and/or soil moisture) during the growing season is necessary, but not sufficient, for shrews to reach high densities**. Such hypotheses are developed from the perspective that multiple factors constrain ecological processes in tallgrass prairie and that many of these processes are not in equilibrium with higher or lower trophic level responses. These long-term data sets also provide a baseline for assessing the impacts of humans, including climate change, on small mammals and birds associated with prairie habitats (Kaufman and Kaufman, in press).

Results from LTER I-III have shown that fire alters the abundance of individual species of consumers and, therefore, the composition of assemblages of small mammals and birds. Our data sets for birds and small mammals indicate that most species respond strongly, some negatively and others positively depending on species-specific habitat requirements (birds: Zimmerman, 1993; small mammals: Kaufman et al., 1990; G. Kaufman et al., 1988). Even in those species that respond positively to fire (and hence increased ANPP), there is little evidence of "bottom-up" control. Instead, fire-induced changes in vegetation structure and the amount of plant litter probably are the major influences on populations of both birds (Zimmerman, 1993) and small mammals (Kaufman et al., 1989; Kaufman and Kaufman, 1990; Clark and Kaufman, 1991). Thus, we are testing the hypothesis that **vegetation structure, rather than productivity, controls many small mammal and bird populations.** Long-term studies were begun near the end of LTER III to assess the effects of fire on gall insects that infest prairie forbs and shrubs. These studies are designed to test the hypotheses that **fire reduces the occurrence of gall insects**, and that **distance to unburned sites influences the rate of re-colonization by these insects**.

A subset of the long-term study sites for birds and small mammals were established in areas in which bison were reintroduced after a period of data collection. The interactions of fire, ungulate grazers and a variable climate are most complex in these sites and, as noted above, responses in consumer populations will be mediated by changes in the plant litter, standing dead, vegetation structure and other physical characteristics of the habitat. Thus, in tallgrass prairie, the spatial distributions and temporal dynamics of animals across the landscape are often linked to fire and grazing by changes in habitat structure (Fig. 31). Given the increased vegetation heterogeneity generated by bison (Table 1) and that vegetation structure is altered significantly in grazed sites, we propose the general hypothesis that grazing will alter mammal and bird distribution and abundance patterns at the watershed to landscape level. Specifically, **we will test the hypotheses that grassland bird abundance and diversity decreases with grazing intensity.** In addition to vegetative structural changes, "top-down" control may operate in some cases as a lack of cover in grazed sites leads to increased rates of predation of bird nests (Zimmerman, unpubl. data). **We also predict differential responses of mammal species, changes in species composition, and reduced mammalian diversity with bison-induced habitat changes.** In contrast, insect populations may respond to the taxonomic composition, as well as the physical structure of plant communities. Therefore, **we predict that insect diversity will increase in grazed watersheds due to an increase in plant species richness and spatial heterogeneity.** We also predict that the magnitude of consumer responses will vary significantly with the fire regime in grazed watersheds because fire influences vegetation composition and structure and this influences bison use of the watershed. Thus, linkages between plant community, ANPP and nutrient cycling research and consumer studies in grazed sites are numerous.

Finally, the absence of fire and annual spring burning over long time periods can lead to vegetation changes (Collins and Wallace, 1990) which, in turn, will cause directional changes in consumer populations. For example, long-term absence of fire leads to invasion by woody vegetation which causes shifts in consumer species such that grassland birds and mammals become less common and woodland species become more common. However, different seasons

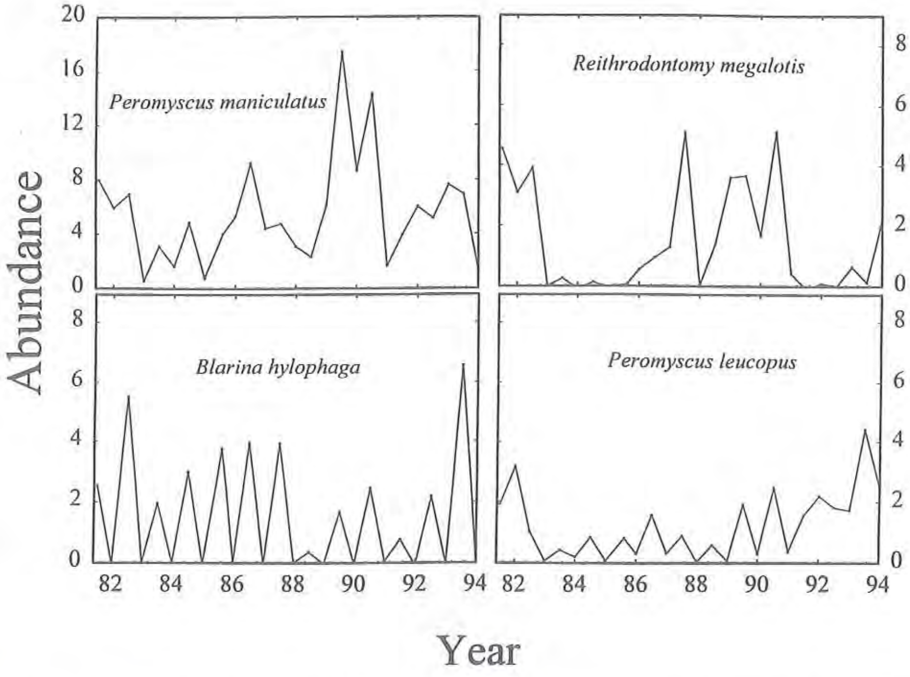


Fig. 30. Temporal patterns of abundance (individuals/trapline) for four common small mammal species in tallgrass prairie (across all fire/grazing treatments). Species were *Peromyscus maniculatus* (deer mouse), *Reithrodontomys megalotis* (western harvest mouse), *Blarina hylophaga* (Elliot's short-tailed shrew), and *Peromyscus leucopus* (white-footed mouse). As with birds and grasshoppers, small mammals are sampled in burned and unburned, grazed and ungrazed prairie. To sample mammals, we use 14 traplines (20 stations, 2 livetraps/station, 4-day periods in both spring and autumn) first established in autumn 1981. By sampling during spring and autumn, we are able to assess abundance during population lows that occur at the end of winter and population highs that occur at the end of the growing season. Since autumn 1993, similar procedures have been used to sample small mammals in eight study sites in seasonal burns.

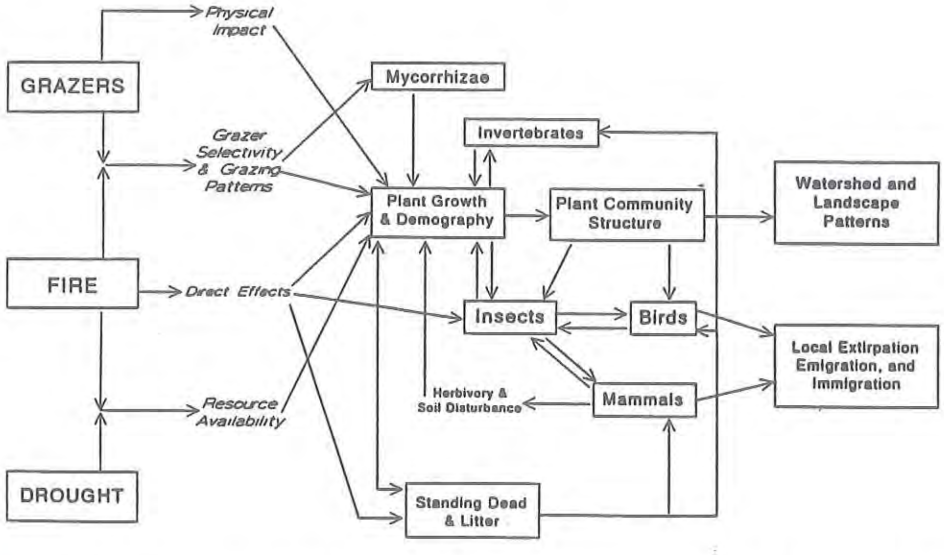


Fig. 31. Primary processes influencing producer and consumer populations in tallgrass prairie. Grazing, fire and climatic variability influence plant and animal populations directly (e.g., physical impact of grazers on plants, direct effects of fire on insect mortality) and indirectly. Habitat structure (e.g., standing dead, litter and vegetation architecture) is the primary *linkage* between these three key processes and patterns of consumer distribution of abundances.

of fire (summer vs. winter for example) may have more direct effects (i.e., mortality) on consumer populations (Fig. 31). As part of the new research proposed in which fire season is varied (see New Initiatives section) we will test the prediction that **summer fires will directly reduce consumer populations, even those that are "grass-dependent" consumer species, whereas fall and winter fires will not negatively impact consumers.** Thus, even though all of these watersheds are annually burned and will likely be dominated by grass species, fire timing *per se* and not vegetation structure will control consumer populations

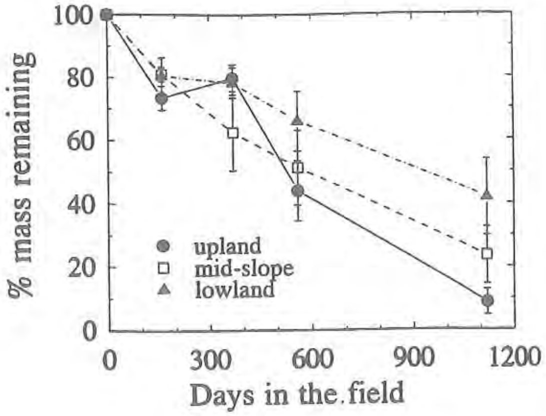
Nutrient Cycling Studies (Blair, Johnson, Ramundo, Rice)

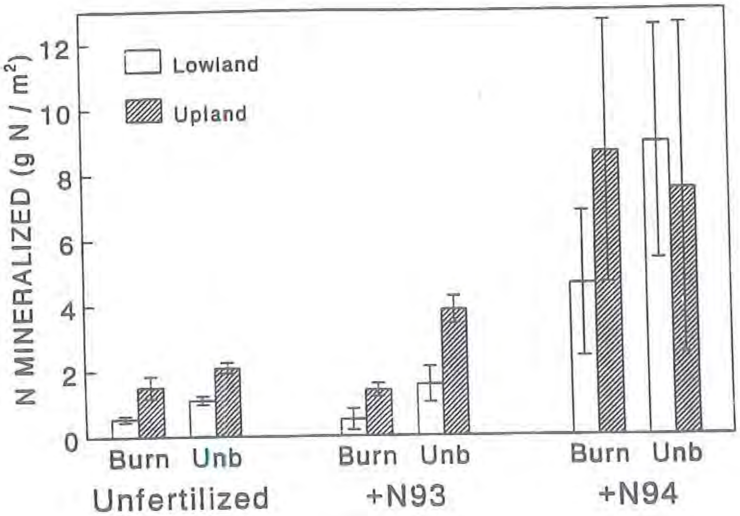
Availability of nutrients, especially N, can limit plant productivity in tallgrass prairie (Seastedt et al., 1991; Ojima et al., 1994), and alter plant community composition (Tilman, 1987; Gibson et al., 1993, Wedin and Tilman, 1993). However, N limitation is not a universal feature of tallgrass prairie, and its relative importance varies with fire, grazing, topography and precipitation. Therefore, understanding the factors controlling N availability and losses is a major focus of our LTER nutrient cycling research. Below we outline some of our ongoing and proposed nutrient cycling research, and its relationships with other ecological phenomena at scales ranging from individual organisms to landscape-level patterns.

A continuing objective is to quantify "patterns of inorganic input and movement through soils, groundwater, and surface waters to evaluate the interaction of geochemical and biological processes" as defined in the original LTER nutrient cycling "core area." As a National Atmospheric Deposition Program (NADP) site, wetfall samples are analyzed weekly for pH, NO_3, NH_4, SO_4, PO_4 and major cations. In addition, N and P inputs (NO_3-N, NH_4-N, PO_4-P, total N and total P) are measured in bulk precipitation using collectors located on 4 LTER watersheds. These data provide critical information on nutrient inputs (annual inputs of N and P in bulk ppt are substantially higher than those in wetfall only), and allow us to assess directional changes in nutrient loading at our site. We also will continue to measure N and P concentrations in stream water (four gauged watersheds) and groundwater (groundwater wells on N04D, porous cup lysimeters in the belowground plot experiments, and wells in riparian areas; see Aquatic and Hydrological Studies for details) to provide linkage between terrestrial and hydrologic N studies.

Research during LTER II and III demonstrated the key role that fire frequency plays in determining N limitation to plant productivity in tallgrass prairie (Knapp and Seastedt, 1986; Seastedt et al., 1991; Ojima et al., 1994), and provided some mechanistic explanations for the effects of fire by documenting changes in biologically active soil N pools (Garcia and Rice, 1994; Rice and Garcia, 1994) and net N mineralization rates (Ojima et al., 1994; Turner et al. submitted). Most recently, greater in situ N mineralization rates have been documented in infrequently burned prairie, compared to annually burned prairie (Fig. 6). Presumably, the "pulse" in ANPP following an infrequent fire is due to a build up of labile soil N in the absence fire, and its subsequent mineralization. However, information is lacking on the nature of these labile soil N pools, and on the temporal scale over which these pools accumulate and are depleted. New research in LTER IV will further examine the influence of fire on N cycling by assessing soil N dynamics and plant responses in watersheds subject to a reversal of fire treatments (see New Initiatives section, Fig. 43). **We hypothesize that N mineralization rates will be significantly increased when previously unburned sites are first burned, but that this response will decrease rapidly in subsequent years as labile N pools are exhausted. We also hypothesize that labile N pools, and net N mineralization rates, will increase as previously annually burned sites are protected from fire, but we expect this response to occur more slowly than the decrease in unburned sites switched to an annual fire treatment.** This experiment will provide a unique opportunity for us to address the time scales over which soil N pools and

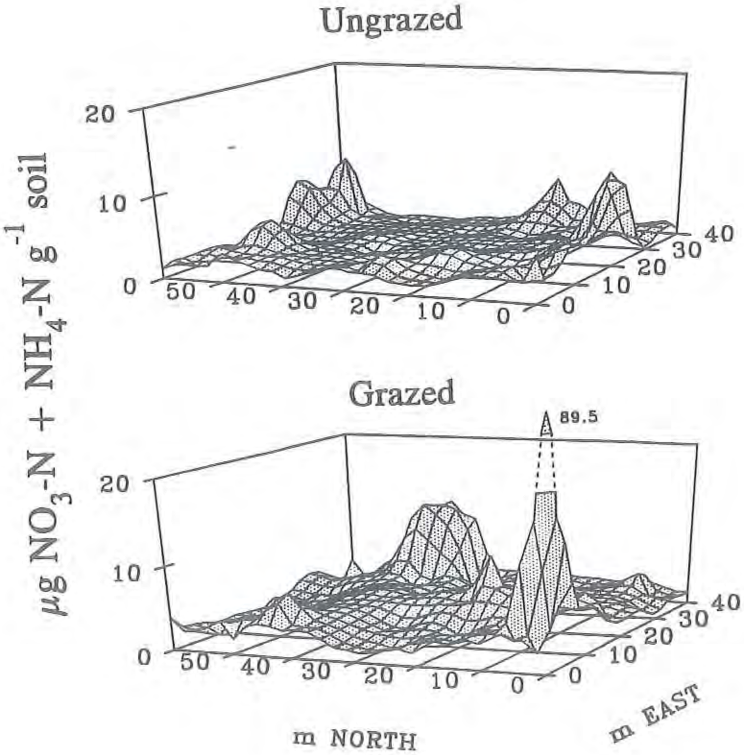
Fig. 32. Right: Effect of topographic position on the decay rates of buried wood dowels (from O'Lear et al., 1996). Decay rates were significantly higher at upland and mid-slope sites, compared to lowlands, in spite of generally greater soil moisture at the lowland sites.





Left: Net soil N mineralization (0-10 cm) measured during the 1994 growing season at upland and lowland topographic positions in plots that were fertilized (10 g N/m^2) in 1993 (+N93), in 1994 (+N94), or left unfertilized (from Turner et al., submitted). Net N mineralization in both the unfertilized and +N93 plots was significantly greater in the upland sites, relative to lowland sites. Mineralization rates in newly fertilized plots (+N94) were highly variable. Results of these studies suggest faster decomposition and greater N mineralization at upland sites, in spite of the shallower, and generally drier soils, which can limit ANPP at these sites.

Fig. 33. Spatial patterns of available (KCl-extractable) soil inorganic N in ungrazed and bison-grazed areas of annually burned watersheds. Two 40x60 m grids consisting of 118 spatially-referenced sampling points were established in a grazed and an ungrazed watershed in the summer of 1995. Soil samples were collected and analyzed for available N, total N, micobial biomass N, potentially mineralizable N, total C, extractable P, and pH. Bison appeared to increase both mean N availability and the "patchiness" of available soil N. Studies planned for LTER IV will focus on both spatial and temporal dynamics of soil and plant responses to bison grazing.



transformation rates respond to changing fire regimes, along with concurrent changes in ANPP and plant species composition.

The need to quantify soil nutrients and plant responses in more spatially explicit ways became apparent during LTER III, as we documented some unexpected landscape level patterns in soil processes (Fig. 32; O'Lear et al., 1996; Benning and Seastedt, 1996; Turner et al. submitted). Based on these studies, we hypothesize that **different factors control aboveground (ANPP) and belowground (decomposition, N mineralization) processes, resulting in a "decoupling" of these processes across topoedaphic gradients**. This explains, in part, why patterns of ANPP are not well correlated with patterns of N availability across the tallgrass prairie landscape (Fig. 7). We hypothesize that **these differences are driven by quantity and quality of belowground plant inputs, as well as by abiotic factors (soil moisture and temperature)**. We will test this by quantifying in situ N mineralization (buried cores; Raison et al., 1987), root production, root decomposition, root tissue chemistry, and fractionating soil N pools across topoedaphic gradients (Transect Experiment, Fig. 34) where ANPP, plant species composition and soil moisture data are being collected. Soil temperature measurement will be added to these sites. These data will also be useful for our ongoing N mineralization modeling efforts (see Modeling section).

Spatially explicit sampling (Fig. 33) will also be critical as we expand our nutrient cycling studies in LTER IV to address the effects of large ungulate grazers (bison). Ungulate grazers can disproportionately affect nutrient cycling and energy flow in grasslands (McNaughton et al., 1988; Holland and Detling, 1990; Frank and McNaughton, 1992) by 1) altering the quantity and quality of belowground inputs (Detling et al., 1979) and 2) locally accelerating N cycling by returning labile forms of N (i.e., dung and urine) to the soil (Ruess and McNaughton, 1984, 1988). Both the quantity and quality (C:N ratio) of root inputs, and the inputs of labile N will determine N mineralization/immobilization dynamics and, ultimately, N availability. Although responses of plants and soils to grazing vary in different grasslands (Milchunas and Lauenroth, 1993), in our system we hypothesize that **grazing will reduce root productivity, lower the C:N ratio of root tissue, decrease N immobilization and increase N availability. The N inputs from dung and urine also will influence landscape patterns of N availability and fluxes. Therefore, grazing lawns will have locally greater N mineralization leading to a patchy distribution of N availability with the landscape.** We will test these hypotheses by measuring belowground processes in 'grazing lawns' and in ungrazed watersheds, and in 'grazing lawns' prior to and after the placement of bison exclosures. Response variables will include plant (root biomass, productivity, C:N) and microbial (total N, net N mineralization, microbial biomass N, soil respiration) processes. Spatially explicit measurements of soil N cycling (N mineralization, N availability, NH_3 volatilization) also will be made. These LTER studies will be augmented by proposed mechanistic studies (for which we will seek additional funding) on the effects of bison grazing on gross N mineralization and rates of N transfer using stable isotope techniques. The ultimate goal of these studies is to determine if, and over what spatial and temporal scales, bison regulate fundamental ecosystem processes such as N cycling and energy flow in the tallgrass prairie landscape ('top down' regulation) and how the resultant spatial variability may relate to patterns in population and community responses.

Although N appears to exert the greatest control of all nutrients on plant productivity, and possibly species composition, we recognize the potential importance of P in these grasslands, especially with respect to plant-mycorrhizal interactions. Patterns of P input and export will continue to be quantified, and long-term experiments (the Belowground Plot studies below, Fig. 35) on the effects of chronic N and P additions in these grasslands will continue. In addition, experiments are underway in which mycorrhizal fungi are manipulated in the field through the use of biocides to determine their effect on both productivity and species interactions (see Related Research).

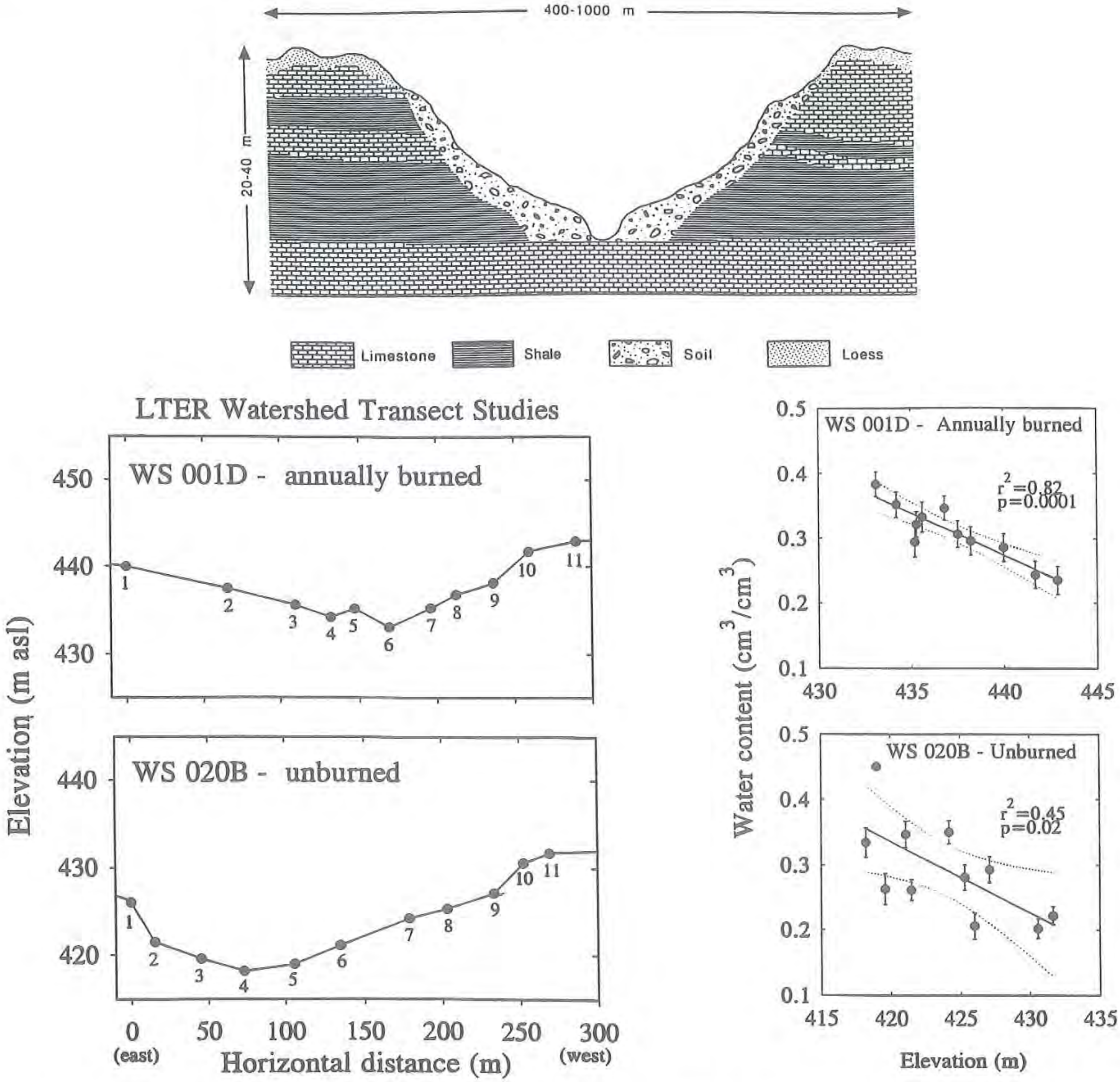


Fig. 34. **LTER Watershed Transect Experiment.** Top: An idealized cross section through a Konza watershed (from Schimel et al., 1991). Bottom left: Location of permanent sampling points along cross-watershed transects which span annually burned (001D) and unburned (020B) watersheds. Bottom right: Relationship between topographic position and mean growing season soil water content (1993, 0-15 cm) on burned and unburned watershed transects.

Justification and description of the study: Much of the landscape-level variation in resource availability and ecological processes at Konza is related to topographic position in the landscape and the accompanying variability in soils (edaphic factors). Soil depth generally increases down slope. Water availability also generally increases down slope, although this relationship can be attenuated as surface litter accumulates in unburned watersheds. In order to document topoedaphic patterns in resource availability and biotic responses, we established permanent east-west transects in 1989 which span elevational gradients across an annually burned (001D) and a long-term unburned (020B) watershed. Each transect is ca. 300 m in length and has 11 permanently marked sampling locations. Soil moisture (TDR, 0-15 cm at all positions + 0-30 cm at lowlands only) and ANPP (replicate 0.1 m^2 quadrats) are routinely quantified at each position. Additional measurements in prior studies along these transects have included: stomatal conductance, light availability, net photosynthesis, plant tissues chemistry, inorganic and total soil N, and litter decomposition. Studies to be implemented in LTER IV will add new measurements of belowground processes (net N mineralization, root productivity, root and rhizome tissue chemistry) to address the hypothesis that **patterns and controls of above- and belowground processes are "decoupled" across these transects.**

We will continue to quantify accumulations of N and P in aboveground live and dead plant biomass as a response variable (upland and lowland sites of LTER watersheds, transect studies, and belowground plots). These measurements are based on replicate 0.1 m^2 quadrats, clipped and separated into live and dead grasses, forbs and surface litter, with each component analyzed for N and P content. Tissue samples are archived for additional future analyses. We propose initiating new measurements of plant tissue chemistry in the "Irrigation Transect" experiment (Fig. 27), where we hypothesize that **alleviating chronic moisture deficits by irrigating will lead to increased N limitation and lower tissue N concentrations (greater NUE) in annually burned prairie, which ultimately may lead to decreased productivity and shifts in species composition.**

Belowground Studies (Rice, Blair, Johnson, Todd)

The "Belowground Plot" experiment (Fig. 35) was established in 1986 to provide a common area for research focused on the response of aboveground (ANPP, plant species composition, etc.) and belowground processes to fire, fertilizer inputs (N, P or N+P) and mowing. This experiment allows us to evaluate the long-term effects of annual burning, aboveground biomass removal and chronic nutrient additions on a suite of plant and soil properties and processes. Response variables measured during LTER II and III included plant productivity, species composition, root biomass, tissue chemistry, soil invertebrates, mycorrhizal fungi, litter decomposition, N mineralization, soil microbial biomass, soil solution chemistry and changes in selected soil nutrient pools. Treatments (fire, mowing, fertilization) will be maintained throughout LTER IV, as will annual estimates of ANPP, tissue chemistry, species composition and soil solution chemistry (porous cup lysimeters). However, we propose reducing our intensive sampling of belowground properties to once every five years in order to minimize the effects of destructive sampling, and to allow us to expand some belowground sampling efforts to the more topographically diverse LTER watersheds.

The belowground plots have been a focal point for research on the effects of burning and nutrient additions on soil microbial and mineralizable C and N pools (Rice and Garcia, 1994; Garcia and Rice, 1994). Microbial biomass C and N will continue to be measured annually using a fumigation-incubation method modified from Jenkinson and Powelson (1976). Changes in potentially mineralizable C and N will be determined less frequently using long-term (>200 days) laboratory incubations of undisturbed soil cores (Stanford and Smith, 1972; Garcia, 1992). Total soil organic C and N will then be fractionated into pools of different biological activity (stable, active and microbial biomass C and N). During LTER III we expanded our on-site analytical capabilities to include stable isotope analyses. In 1994, an ^{15}N addition experiment (as $^{15}NH_4$ or $^{15}NO_3$) was initiated in the belowground plots to determine the effects of fire on plant-microbial competition for added N. Our hypothesis is that **plant-microbial competition for N is dependent on the form of available N (NH_4 vs. NO_3) and is most intense in annually burned prairie.** Initial results indicate preferential plant uptake of NO_3, and greater microbial immobilization in burned prairie (Dell and Rice, 1995). Based on these initial data, we intend to pursue additional external funding to expand the use of stable isotopes for N cycling research at our site.

Although most of the energy flow and cycling of nutrients occurs belowground in tallgrass prairie, little is known about belowground plant productivity or consumers. Hayes and Seastedt (1987) used a combination of soil cores and "root windows" to estimate root biomass and turnover in burned and unburned sites and found that root production was generally higher in burned sites, and was significantly enhanced during drought. A major expansion of our belowground research in LTER IV will include new studies on root dynamics using a minirhizotron system (as suggested during our last site review). Initially, these studies will be done in selected treatments (burned and

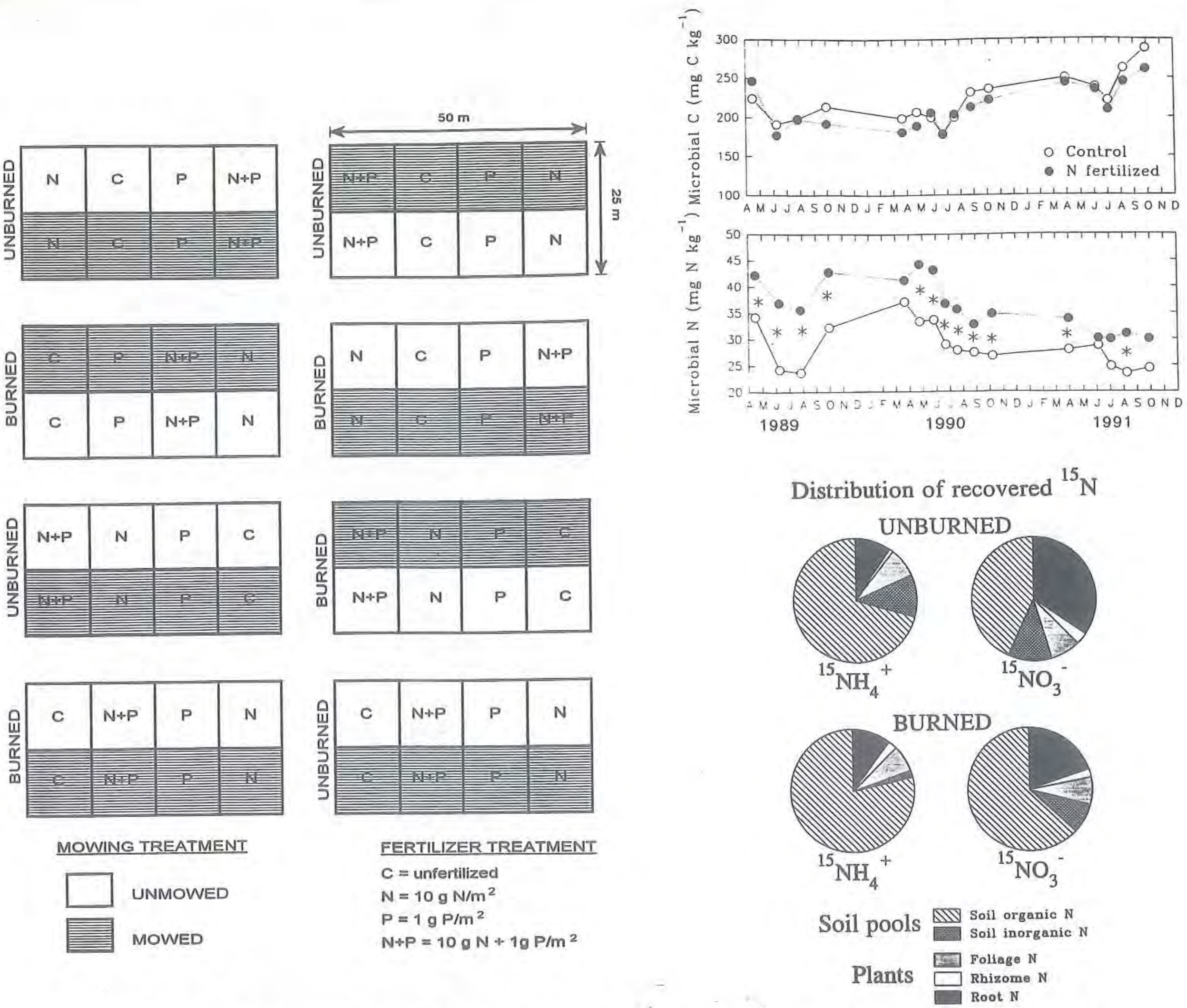


Fig. 35. The Belowground Plot Experiments. Left: Experimental design of the "belowground plots." These long-term plots were established in 1986 in a replicated split-split plot design, with the following manipulations: burning (annually burned vs. unburned), aboveground biomass removal (semi-annually mowed vs. unmowed) and annual fertilization (N only, P only, N+P, and no fertilizer). Top right: Temporal dynamics of soil microbial biomass C and N in control and N-fertilized plots, showing seasonal changes and longer-term trends (from Garcia and Rice, 1994). Bottom right: Partitioning of recovered ^{15}N added to 20 cm diam. microplots in burned and unburned, non-fertilized plots. Plants assimilated more ^{15}N when added in the form of NO_3. Regardless of form, more ^{15}N was immobilized in soils of the annual burned plots where we expect microbial demand to be greatest.

Justification and description of the study: Tallgrass prairie soils are characterized by large accumulations of organic matter and nutrients, high belowground productivity and a large and diverse assemblage of microbes and invertebrates. Much of the energy flow and nutrient cycling in grassland takes place belowground, and aboveground responses to fire, grazing and drought are often mediated by belowground processes. The "belowground plots" allow us to examine the mechanisms responsible for tallgrass prairie responses to fire, grazing and nutrient limitation. Response variables include: plant species composition, ANPP, root and rhizome biomass, plant tissue chemistry, litter decomposition, soil nutrients and transformations, mycorrhizal fungi and soil invertebrates. Some key questions being addressed include: **How does species composition change with burning, mowing and chronic nutrient addition? Will changes in plant species composition affect mycorrhizal fungi and soil invertebrate communities? How does annual burning affect specific fractions of soil C and N? Will annual mowing have a similar effect by reducing allocation of carbon to roots and rhizomes? How do soil invertebrate communities respond to changes in C and N poools? What are the seasonal and longer-term dynamics of soil microbial biomass under different treatments, and how do they relate to patterns of nutrient availability and plant uptake?**

unburned) in the "belowground plots" and in conjunction with new grazing studies (see Nutrient Cycling section). Minirhizotron access tubes already have been installed to 1 m in replicate plots, and a back-pack mounted camera system (Bartz Tech. Co. model BTC-2) is being used to record video images of roots by depth. Measurements will be made at 1-4 week intervals depending on root phenology. Video images will be digitized and analyzed using ROOTS software and appropriate digitizing hardware. Analysis of the images will provide data on root distribution and turnover at depths not feasible with root windows or root ingrowth bags. Thus, **we hypothesize that fire affects not only biomass and turnover of roots, but also phenology (earlier spring growth) and depth distribution (greater productivity at depth in burned sites). In contrast, we expect grazing to reduce root productivity and depth distribution.** Soil invertebrate studies at Konza have also indicated significant effects of fire and/or mowing on earthworms (James 1988, 1992), and nematode communities (Todd et al., 1992, in press). One current hypothesis is that **herbivorous nematode abundances are limited by quality (N and P content) of live grass roots**. In 1995 the spatial extent of soil invertebrate studies was expanded. Initially, this involved an analysis of the effects of experimentally altered soil moisture on soil invertebrate numbers and composition (the "Irrigation Transect" and a reciprocal core transplant experiment). However, we will also extend these studies to the main LTER watersheds during LTER IV to encompass a range of topoedaphic conditions.

Aquatic and Hydrological Studies (Dodds, Gray, Guy, Koelliker, Macpherson, Oviatt)

Surface water hydrology will continue to be studied using precipitation gauges and discharge at N04B, N02B, N01B, and N20B weirs. These data will allow us to refine estimates of water yield of tallgrass prairie. Konza studies have encompassed 5-7 years of moderate precipitation, an equal period of moderately dry conditions, and then 4 years of extremely high discharge. Consequently, it is difficult to define a "typical" hydrological year. The largest gap in knowledge of the area's hydrology is in regard to shallow groundwater movement. **We predict that shallow groundwater movement of nutrients becomes more important than deep groundwater flow when soil is saturated, except during extreme rainstorms when surface flow of both dissolved and particulate nutrients predominates**. These flow patterns constrain the movement of dissolved matter from the surface into streams. We propose to continue our focused studies of the well transects on N04D (Fig. 36) and add a number of new wells in under-represented strata to increase understanding of horizontal flow dynamics. Finally, benchmarks have been installed in watershed N04D to allow measurement of changes in geomorphology.

We will also continue to sample wells in N04D to assess long-term trends in subsurface nitrogen in relation to surface fires and precipitation. These data will be related to those collected from the streams, and integrate with terrestrial nutrient cycling research. The water chemistry monitoring will continue on watersheds N04B, N02B, N01B, and N20B. Total solid and conductivity analyses will be discontinued, and dissolved organic C analysis (Shimadzu TOC 5000 analyzer) will be added to quantify stream water C dynamics and potential C export.

Additional stream monitoring sites will be sampled in an effort to better understand regional water quality patterns: 1) where Kings Creek leaves Konza (some agricultural influence); 2) in Edler Spring (an independent estimate of prairie shallow groundwater chemistry); and 3) in the EPSCoR cropland (strong agricultural influence) and grassland wells. These wells were drilled with funding from other sources, but have been incorporated into our LTER research. In the first 1½ years of sampling these wells, extreme variations in groundwater chemistry were noted, with spikes of nitrate moving through the cropland subsurface at times not coincident with surface fertilization. Long-term data are needed to understand the conditions that lead to pulses of nitrate moving through the groundwater.

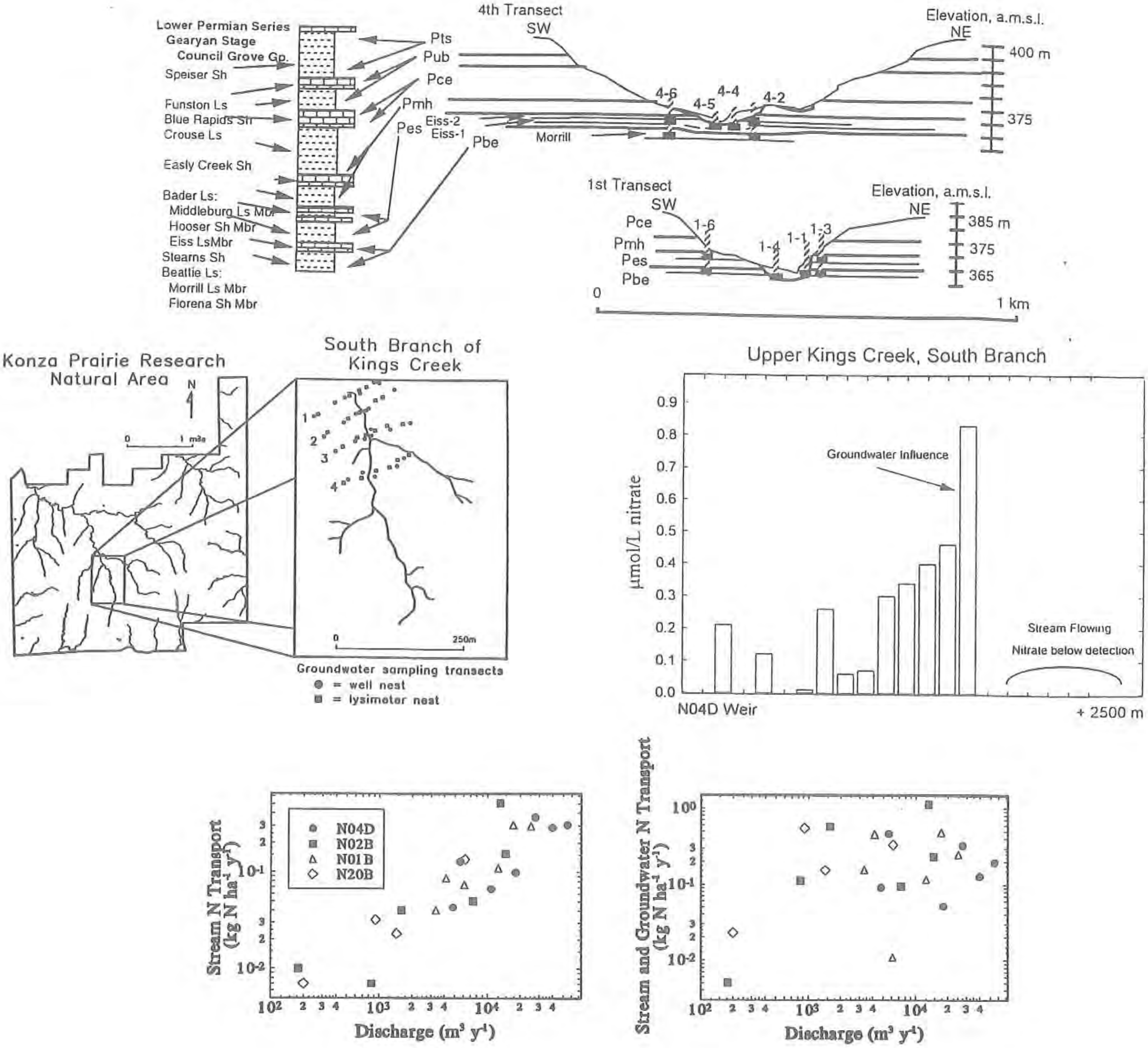


Fig. 36. **Ground Water-Surface Water Interactions**. Top: A schematic of the position of the limestone and shale layers in watershed N04D and of the geology of two of the four well transects. Middle Left: Map of position of four well transects. Middle Right: In the stream adjacent to well transect 4, there is a strong influence of groundwater on the stream nitrate concentrations. This water enters the stream channel through the Eiss limestone series. Above this zone of influence nitrate is below detection. Downstream, the nitrate concentration decreases as in-channel biotic processes remove it. The weir at the bottom of N04D is at the downstream end. Bottom: Nitrogen transport from the N04D and 3 other adjacent watersheds in streams and in streams+groundwater.

Justification and description of the study: Little is known about factors influencing nitrogen concentrations in pristine tallgrass prairie streams. There are obvious influences of landscape and topography but the hydrogeology of the ecosystem is complex. Groundwater influences stream nitrogen concentrations, but we only have the most basic idea of how. As we move downstream nitrate concentrations increase, markedly so in areas with agriculture (Fig. 8). We seek to understand why the nitrate levels increase, and to what extent anthropogenic factors influence this increase.
Questions being addressed include: **Does shallow groundwater movement become more important than deep groundwater flow when soil is saturated, except during extreme rainstorms when surface flow predominates? Are anthropogenic and precipitation inputs the primary influences on N transport and concentrations in streams and groundwaters?**

Our understanding of N dynamics in streams and their links to terrestrial ecosystems is increasing. Collaboration between Blair, Johnson, and Rice (terrestrial N dynamics) and Macpherson, Gray and Dodds (aquatic N dynamics) is allowing us to piece together a picture of N dynamics that includes linkages between landscape units. **We hypothesize that anthropogenic and precipitation inputs are the primary influences on N transport and concentrations in streams and groundwater.** The aquatic group is also involved with cross-site efforts to understand stream solute dynamics (Meyer et al., 1993), organic matter processing (Gray, in press), and N transformations through additions of stable isotopes. We plan to continue these synthetic collaborations.

The streams at Konza are among the most ephemeral habitats in the variable tallgrass prairie biome. Drying and flooding are a regular part of the annual abiotic regime. Nonetheless, algae, invertebrates and fish are found in the channels within a few weeks after flow resumes. It is not known if these organisms come from permanent spring-fed pools above, disperse aerially (not likely for the fish), arise from drought resistant propagules, or move up from below. We are testing the hypothesis that **biological colonization of streams following floods and drying is dominated by colonization from permanent upstream spring-fed pools**. In addition, manipulative experiments are underway in artificial stream troughs and stable isotopes are being used to document foodwebs in the streams. We hypothesize that **crayfish and stoneroller minnow herbivory are major pathways for processing stream primary production**. Ultimately we hope to understand the aquatic communities well enough to set up long-term studies of key indicator organisms and establish a longer term view of community structure and energy flow through aquatic ecosystems in order to detect significant alterations in pattern and process.

Landscape Ecology (Briggs, Goodin, Henebry, Nellis)

The experimental design of Konza Prairie (Fig. 17) provides a mosaic of experimental units for addressing landscape-level questions (cf. Nellis et al., 1992). The NASA-FIFE project provided a wealth of TM and SPOT imagery for 1987-1989 and we have augmented this collection with additional images (Fig. 37). These data, coupled with our GIS database, enable us to sample areas either selectively or synoptically to address questions at specific scales and to investigate the importance of spatial scales in measurements of various ecological phenomena (Nellis and Briggs, 1989; Henebry, 1993).

Landscape-level research in Konza Prairie is motivated by two hypotheses: (1) **position *within the landscape* places fundamental constraints on ecological processes**, and (2) **expressions of these constraints *across the landscape* yield quantifiable patterns that capture treatment and disturbance effects**. Given the topographic relief of the Flint Hills, position within drainage and depositional networks is a major determinant of the dynamics of primary production, organic matter, and nutrients. For example, plant responses to fire, grazing, and recent weather are strongly modulated by soil moisture dynamics, which is a function of both soil depth and landscape position (Knapp et al., 1993; Schimel et al., 1991). The dynamic interaction of plant and soil processes translates into spatial and spatio-temporal patterns across the landscape. These patterns and canopy dynamics can be quantified using NDVI images at spatial resolutions ranging from 20 m to 1 km.

During LTER IV the landscape ecology group will focus on refining our understanding of process-pattern linkages, especially with regard to topoedaphic constraints on ANPP and their interactive effects with management practices and climatic conditions. Tallgrass prairie vegetation exhibits strong temporal patterning associated with species composition and phenology (Fig. 38, 39), and strong spatial patterning related primarily to topography and land use. Areas dominated by C_3 vegetation exhibit two temporally distinct pulses of activity (and greenness) whereas areas

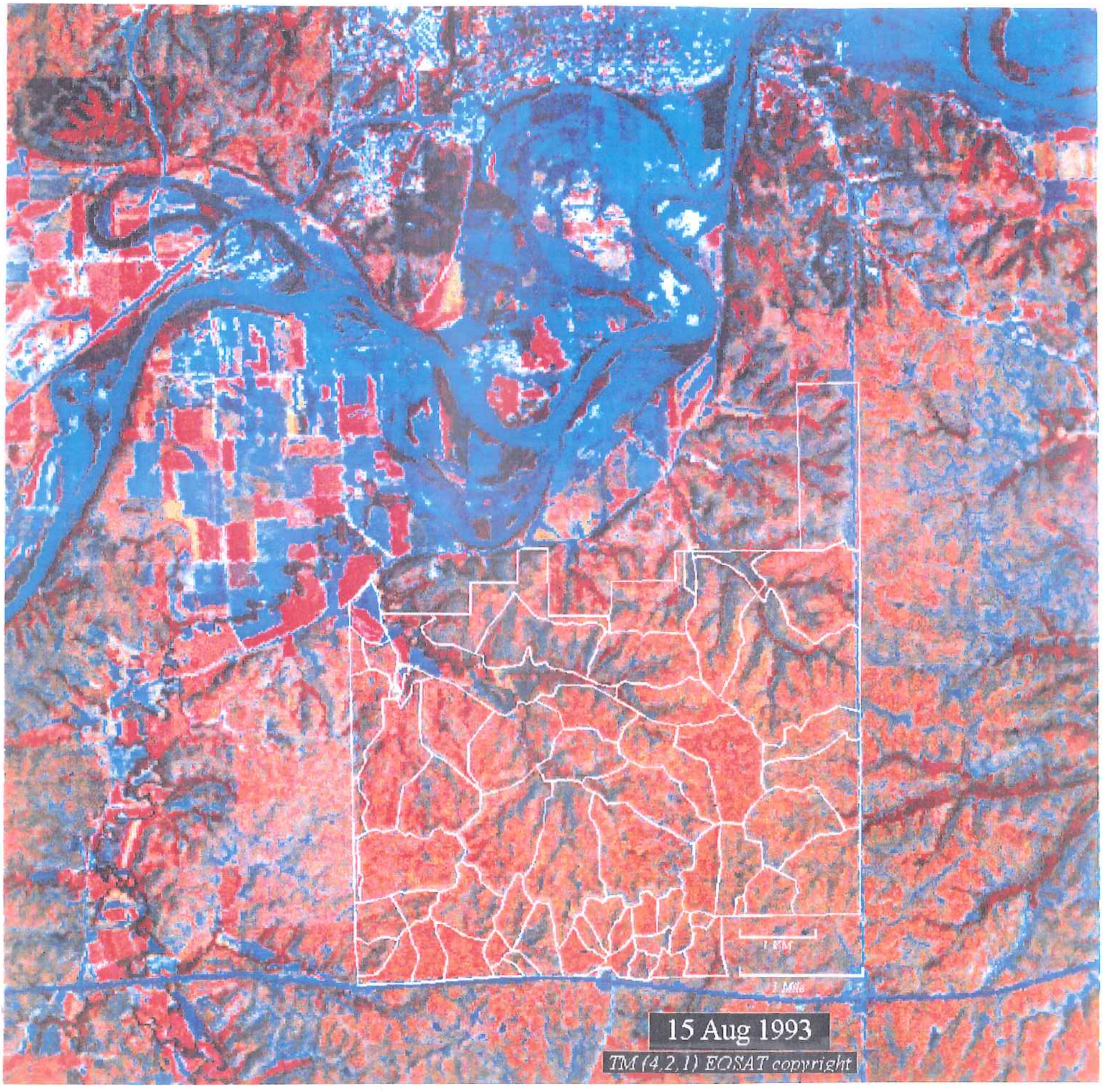


Fig. 37. False color composite of a TM image (15 August 1993) with the KNZ experimental design overlaid. Red color denotes areas with high plant biomass, while blue color denotes areas with little vegetation. 1993 was a year of near record precipitation; note the effect of flooding in the Kansas river valley just north (top of photo) of Konza.

dominated by C_4 vegetation exhibit a single pulse of activity and maximum greenness at midseason (Fig. 39). Grazing by ungulates can remove much aboveground biomass and expose bare soil, thus, NDVI values on grazed areas are generally lower than on ungrazed areas (Turner et al., 1992). Grazing also introduces variability in reflectance characteristics that is driven by stocking rates, grazing intensity, regrowth responses of the vegetation, and recent weather. Thus, information derived from satellite data will be used to assess the constraints that landscape position, species composition and land management (fire, grazing) place on energy flow (measured as ANPP) into the system. Part of this research is synthetic and retrospective and some requires new data collection; in particular, we will introduce the use of ground level spectroradiometry to measure spectral reflectance in areas sampled for aboveground biomass and plant community composition to provide better links with spaceborne sensor estimates.

Our proposed use of remotely sensed data extends beyond tracking canopy dynamics. For example, plant productivity and N trace gas fluxes in tallgrass prairie can be linked because both are controlled by water and N availability providing the opportunity for remotely sensed estimates of trace gas flux (Groffman and Turner, 1995). Although temporal variability in soil moisture, N availability, and trace gas flux within a single growing season is relatively high, an annual time scale integrates this variability. Variation in ANPP across the landscape is also an integrated product of variation in water and N availability over the entire growing season. Thus, strong relationships between point estimates of ANPP and N trace gas flux (Fig. 40) provide a means of estimating processes across landscapes. We will continue to explore these linkages and evaluate new technologies that can strengthen our process-level understanding of these phenomenon. One such technology is Synthetic Aperture Radar, which has the potential to provide synoptic soil moisture estimates across the landscape. Henebry and Knapp are currently supported by an NSF cross-site grant to implement this technology at Konza Prairie and the Sevilleta LTER site.

Modeling (Seastedt, Henebry, Blair, Johnson)

Interactions between empirical studies and modeling exercises at Konza Prairie have produced significant insights into the ecosystem's dynamics. While some scientists see the main purpose of modeling as predictive, others argue that its function is primarily heuristic (Oreskes et al., 1994). Either way, the science can benefit. For example, in the mid '80s, the CENTURY model predicted that intermediate fire frequencies had the potential to produce pulses of plant productivity due to interactions among limiting resources (Ojima, 1987). Subsequent empirical work verified this finding (Seastedt et al., 1991), which led, in turn, to a general theory of nonequilibrium ecosystem behavior, the Transient Maxima Hypothesis (Seastedt and Knapp, 1993) which states that maximum rates of many ecosystem processes are non-sustainable and are caused by the simultaneous release from more than one limiting resource.

During LTER IV we propose to explore the consequences of variations in the multiple limiting factors operating in tallgrass prairie across a range of spatio-temporal scales, from site and watershed (1-1000 m^2) to landscape and regional scales (10-100,000 km^2). This objective requires linking models of canopy dynamics based on plant and soil processes with models of landscape dynamics. Accomplishments during LTER III provide us with both modeling frameworks. Here we describe the components of the plant-soil models, some data needs that will be addressed during LTER IV, and our intended linkage between the two approaches. General goals rather than specific hypotheses are posed since most modeling hypotheses overlap significantly with those stated in previous sections.

The overall goal of the LTER modeling effort is to build upon the Konza Prairie database, integrate across disciplines and identify research needs. The Konza Prairie LTER database already includes a wealth of imagery (from the NASA-FIFE Program and LTER purchases) and ground level data. From this database, we have developed a completely new analytical approach to image time series

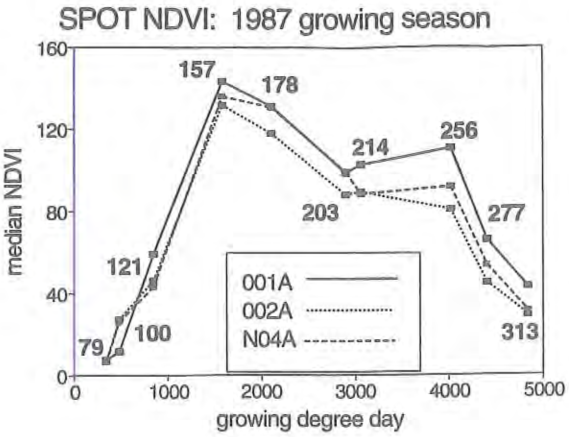
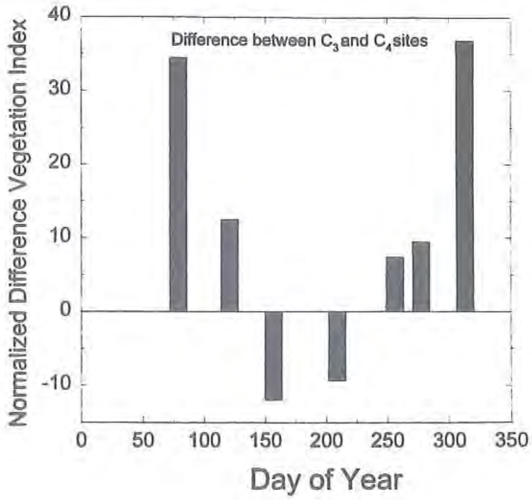


Fig. 38. Watershed median NDVI as a function of growing degree day for 1987. Labels denote day of year of SPOT image acquistion.

Fig. 39. Seasonal NDVI values illustrating the differences between C_3 and C_4 dominated grassland sites in eastern Kansas. The C_3 grasses have a bimodal distribution with peaks occurring in spring and fall, while the C_4 grasses have a single peak in the summer. If a stress is placed on the system or if land use practices (i.e., fire and/or grazing) alter C_3/C_4 ratio, the timing and magnitude of these peaks would change, and would be easily detected using remote sensing techniques.



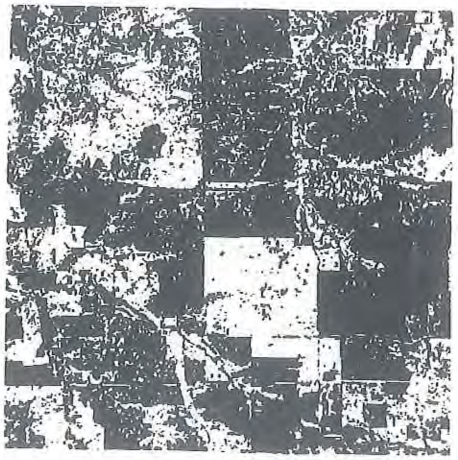


Fig. 40. Estimated annual denitrification for the entire 15 X 15 km NASA FIFE site which included Konza Prairie. High values are indicated by light shades and low values by dark shades. KNZ is in upper left quadrant. (From Groffman and Turner, 1995)

(Henebry, 1993; Henebry and Su, 1993), which lays the foundation for a more quantitative ecological remote sensing of canopies and canopy dynamics.

The canopy integrates abiotic and biological processes across the landscape and yields information relevant to many ecological patterns and processes such as primary production, nutrient fluxes, organic matter dynamics, species composition, habitat structure, population dynamics, and disturbance effects. Our canopy model (output in Fig. 41) modifies the expolinear growth equation (Goudriaan, 1994) to incorporate three major constraints on growth in tallgrass prairie: availability of light, water and N. Specifically, (1) growing degree day serves as a surrogate for net radiation and hence PAR; (2) when soil moisture falls below 90% of field capacity, it affects daily growth increments; and (3) growth occurs only when sufficient N is available from the pool of N stored in belowground plant tissue and net N mineralized in the soil. The difference between burned and unburned canopies is handled through a light extinction coefficient and adjustment of a temperature threshold. The time step is daily and the spatial resolution is nominally 1 m^2, but the simple structure of the model makes it computationally feasible to rescale spatially, given appropriate data layers, such as topography, soils, synoptic soil moisture, etc. Model calibration has relied on the biweekly biomass measurements from watersheds 001A and 020A (Fig. 41).

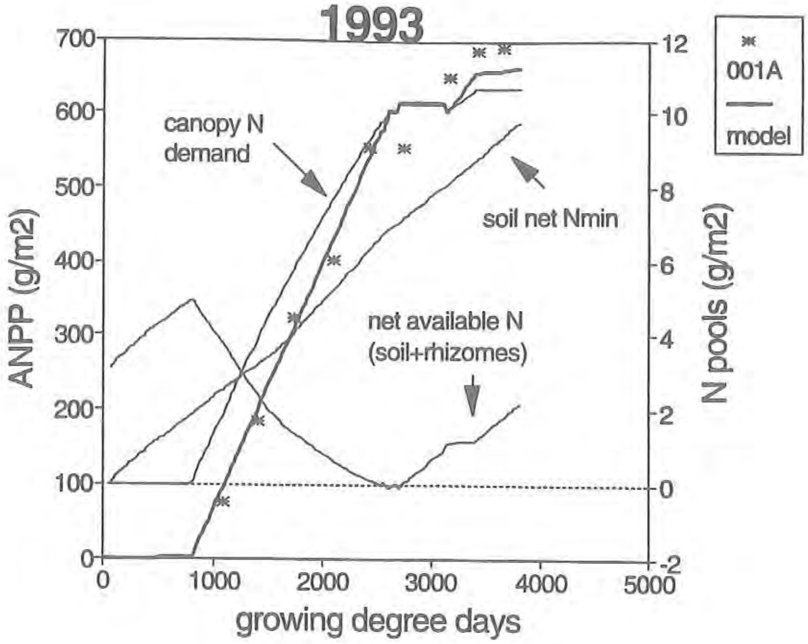
We are also developing a model of net N mineralization (Nmin) to be coupled with our canopy model. The basic Nmin model is a nonlinear curve fit to cumulative Nmin data from long-term incubations (Rice et al., unpubl. data). A Q_{10} scaling of Nmin rates produces a nonlinear temperature response which can lead to significant divergence between Nmin estimates in burned vs. unburned sites, if diel temperature fluctuations are considered (Das et al., 1995) . Accordingly, the model operates at a hourly time step and has a variable number of depth layers, depending on availability of data on N_0 (mineralizable N) pools, moisture and temperature dynamics by depth or horizon. Rate dependence on soil moisture was based on in situ N mineralization studies at Konza (Blair et al., in prep.; Fig. 42). Model intercomparisons with CENTURY are being conducted during the final months of LTER III.

While the coupled models are simple, flexible, and informative, they do not, at this point, address adequately several aspects of the system. There is large uncertainty in estimates of N_0 pools -- more data are needed and will be collected in LTER IV. Rhizome N dynamics are largely unknown but may serve as an important lagged factor in N availability, especially under grazing (Vinton and Hartnett, 1992). Neither the effect of wetting-drying cycles on Nmin nor the seasonal dynamics of the labile (microbial + mineralizable) N pool are addressed. Belowground biomass dynamics are not currently incorporated but will be, once sufficient minirhizotron data accumulate. Extension of the model to incorporate grazing effects is critical to the project and will be pursued during LTER IV. Thus, this modeling exercise has helped us prioritize research needs.

Rescaling the models from stand to watershed to region requires a change in data requirements and in model evaluation procedures. For example, the most difficult input variable to measure spatially is soil moisture: its spatio-temporal dynamics can be modeled interactively by coupling topography models with hydrological models, but the fractured geology of the Flint Hills makes this difficult. An alternative approach is to model spatial relationships by using synoptic soil moisture estimates derived from Synthetic Aperture Radar data. Similarly, the canopy model can simulate growth in terms of biomass or LAI. While Konza has extensive biomass data, NDVI is more directly related to LAI. A collateral NASA study (Briggs, local PI) is underway to measure LAI-biomass relationships at Konza Prairie. Maps of soil properties, land cover and land use, and coarse resolution (1 km^2) remote sensing data will be used to stratify the landscape to aid regional modeling.

We further propose to involve investigators from a number of other LTER sites to use empirical data obtained at Konza for modeling activities (as has been the case for CENTURY model validation). This "win-win" scenario will produce more robust models while generating insights into the behavior of the prairie. Seastedt will coordinate this activity. He remains active in graminoid studies due to his current

Fig. 41. Simulation model output of the dynamics of canopy development, cumulative canopy N demand, cumulative net N mineralization, and net available N on an annually burned watershed in 1993, an exceptionally wet year. After a temperature threshold of 800 growing degree days (GDD), canopy growth responds almost linearly to GDD, a surrogate for net radiation. The model predicts that N limitation is the primary constraint on ANPP, since soil moisture was never strongly limiting during the year. Mean values from biweekly biomass harvests on 001A are presented from comparison.



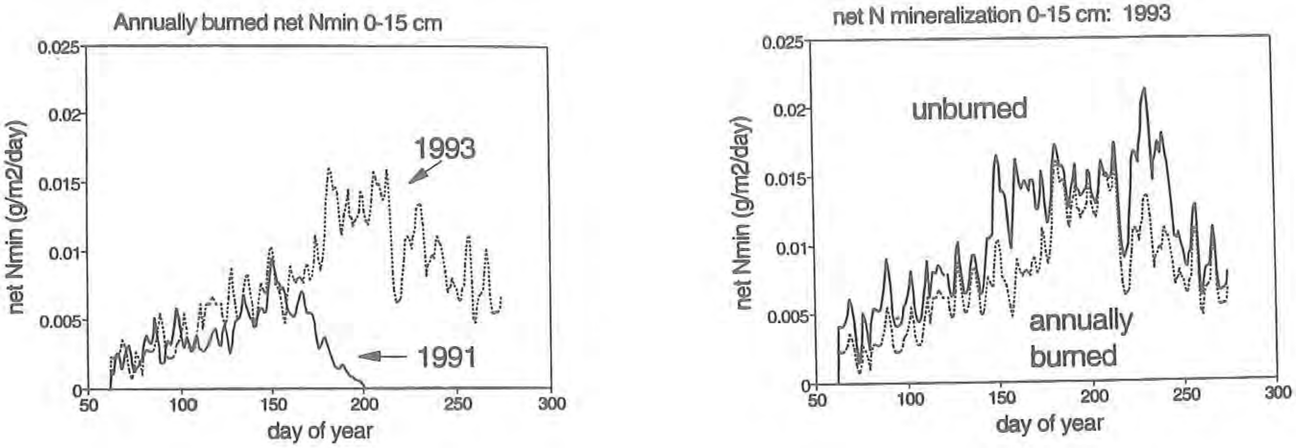


Fig. 42. Left: Simulated net N mineralization dynamics in the upper 15 cm of soil during March through September on an annually burned watershed. Note the cessation in net mineralization during the dry period of 1991 relative to the increased mid-season activity in the very wet year of 1993.

Right: Simulated net N mineralization dynamics in the upper 15 cm of soil during March through September of 1993 comparing annually burned to long-term unburned treatments. Soil moisture was not a limiting factor during 1993; instead the relative size of N_0 mineralizable pools drives the difference in net Nmin rates. (Note the mid-season period when annually burned rates are nearly equal to those of unburned: this corresponds to a relatively sunny period. Thus, the nonlinear scaling of the Q_{10} temperature response differentially enhances net N mineralization in the annually burned treatment.)

interests in Colorado alpine and grassland sites. Scientists involved in modeling efforts of nonforested sites (e.g. Coffin at CPR and Moorhead at MDV) also have indicated their interest in developing and validating models using Konza data. The first project involves documenting and modeling spatial patterns in plant and microbial responses to the switching of limiting resources (i.e. nutrients, light and water) on landscape patterns of ANPP and carbon storage. A developing, system-level species competition model (Rastetter, pers. comm.), an expansion of Rastetter and Shaver (1992), is available to contrast with findings from STEPPE, CENTURY, and other validated models.

E. New Initiatives

Although several areas of expansion within the LTER program have been proposed, there are a number of new initiatives we plan to include within LTER IV. Given the fiscal constraints of an anticipated flat budget, it is difficult to propose expansion at the level of previous LTER proposals without reducing resources available for ongoing long-term studies. This is something we are hesitant to do. However, some funds for new initiatives are available through personnel turnover, reduced frequency of sampling in some experiments, increased cost-sharing by Kansas State University, and the purchase of some major pieces of equipment through other funding sources. We have also tried to be innovative in proposing relevant new studies that are low cost.

Fire Treatment Reversal Experiment. Seasonal dynamics of ANPP in two adjacent watersheds (one annually burned and one unburned) have been measured for 11 years (the "Seasonal Biomass Dynamics" study, Fig. 23). We propose switching the treatments in these two watersheds (and in additional replicates) in 1999 to study the transition in ecosystem structure and function as the fire regime cycles between two extremes (Fire Treatment Reversal Experiment, Fig. 43). We will quantify a variety of population, community, and ecosystem properties for 2 years prior to and immediately after the switch, and thereafter at a decreasing intensity. This will be a relatively low cost study since no new treatments are being added. Blair, Briggs, Collins, Johnson, Hartnett, Knapp, Rice and Towne will participate in this new study.

Season of Fire Treatment. In response to long-term interest in "season-of-fire" effects on tallgrass prairie (Fig. 44), some watershed-level fire treatments have been switched from late spring fire to summer, fall and winter annual fire treatments. Season-of-fire effects on soil moisture, ANPP, plant species composition, small mammal populations and belowground processes will be quantified. Howe (1994) recently reported that season-of-fire can strongly influence plant species composition in restored, mesic prairie although abiotic and biotic mechanisms behind these changes have not been documented. The timing of fire as a management tool in restored or recovering tallgrass prairie is a critical aspect of natural area management, and these studies will provide insights into this issue. Investigators involved include: Blair, Collins, Hartnett, Johnson, D. Kaufman, G. Kaufman, Knapp and Towne.

Stochastic Fire Treatment. Similarly, we have long recognized that natural fires did not occur at regular intervals (Axelrod, 1985) as dictated by our experimental design (Fig. 17). Thus we propose to switch four watersheds to a stochastic fire regime. The watersheds to be burned in any given year will be determined by a stochastic model incorporating estimated fuel loads, with a fixed long-term fire return interval of 3 years. None of these watershed treatment alterations will impact the number of replicates (four) of our "core" LTER watershed treatments (annually burned, 4-yr burned, unburned). Moreover, established LTER protocols for measuring response variables (species composition, ANPP, etc.) will be used.

Native vs. Domestic Ungulate Studies. In addition to assessing plant community responses to grazing, we are interested in comparing the effects of native (bison) versus introduced ungulates (cattle) on tallgrass prairie. Addressing this issue is important because replacement of native with introduced ungulates, and the landscape changes associated with their management, has been one

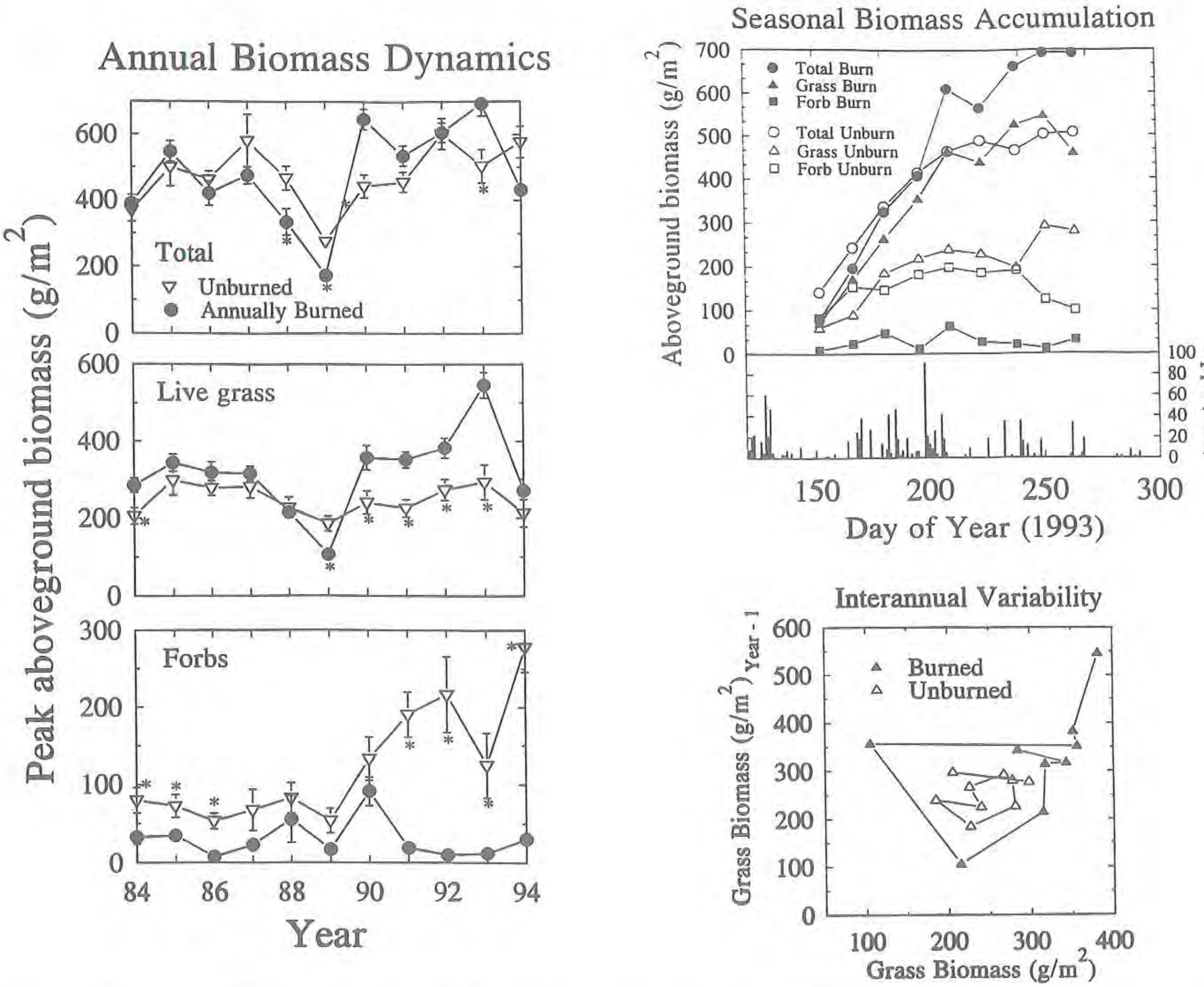


Fig. 43. **The Fire Treatment Reversal Experiment.** Left: A 10-year record of aboveground biomass on two adjacent watersheds which have been annually burned (001A) or unburned (020A) since 1974. Top right: Seasonal patterns of biomass accumulation in these same watersheds, documented using biweekly harvests since 1984. Bottom right: Temporal dynamics of grass productivity, plotted as grass biomass in year$_x$ vs. grass biomass in year$_{x-1}$, showing greater interannual variation in the annually burned watershed.

Justification and description of the study: For some areas of Konza, we have >20 years of data comparing annually burned and long-term unburned watersheds. While continuing these studies is essential for understanding both the short-term dynamics and long-term trajectories of ecological processes under different fire frequencies, a new "reversal of fire treatments" on selected watersheds, proposed for LTER IV, will enhance our understanding of the effects of both fire frequency and site history. Watersheds in which prescribed fire treatments (annually burned or unburned) will be reversed are 001A, 020A, 001C and 020D (Fig. 17). This experiment will provide new insights into the temporal scales over which plant and soil processes respond to altered fire regimes, and will aid in interpreting the role of "site history" in affecting population, community and ecosystem soil responses to fire. Most of Konza was burned frequently prior to its establishment as a research site. These new treatments will allow us to determine how annual burning affects the trajectories of tallgrass ecosystems that begin in a different initial state. In addition, a switching of fire treatments will allow us to capture the short-term soil and plant responses to a change in fire frequency. The following variables will be measured both prior to and following the treatment reversals: plant species composition, ANPP, root and rhizome biomass, plant tissue chemistry, soil C and N pools and transformations (soil CO_2 flux, net N mineralization) and soil invertebrates. Some key questions include: **Will annual burning of previously unburned watersheds result in a convergence of species composition with other annually burned watersheds? or will an established forb and woody plant community be able to persist in spite of annual fire? How long will the expected "pulse" in aboveground productivity persist? Will belowground productivity mirror this pattern? Based on prior studies and model predictions, we expect a period of high N availability following the burning of a previously unburned watershed. How long will increased N availability persist? Conversely, how long will it take for specific soil C and N pools to accrue in the absence of fire?**

of the most significant changes in North American grasslands in recent history. Based on significant differences between bison and cattle in (1) dietary preferences, (2) grazing patterns at different scales, (3) patterns of non-grazing activities and disturbances, and (4) management constraints (Hartnett et al., in press; Table 2), we hypothesize that **bison and cattle are not functionally equivalent herbivores and produce unique patterns in plant communities at different spatial and temporal scales**. Hartnett has received USDA funding to establish this experiment and LTER IV will support sampling in the long-term.

Carbon Flux Studies. As noted earlier, grasslands are characterized by soils high in stored C and tallgrass prairies are among the most C-rich of grasslands (Jenny, 1930; Stevenson, 1986). These grasslands are relatively recent in origin (Axelrod, 1985; Anderson, 1990) and this implies that the ecosystem has been a strong sink for C historically. However, recent changes in both climate and land-use have the potential to alter source/sink relationships in these grasslands (Burke et al., 1991; Vitousek, 1992, 1994). Questions that will be addressed as part of LTER IV include whether or not these grasslands are still sequestering C and **how fire, grazing, climatic variability and conversion to agriculture affect the C budget of these systems?** Clearly, this new initiative will require the greatest fiscal and personnel commitment of those proposed, but this study will address questions of fundamental importance to grassland ecology and will be relevant for global issues as well. Through the efforts of Drs. Jay Ham and Knapp, funding (from DOE, USDA and NSF) has been secured to purchase micrometeorological equipment to measure continuously CO_2, H_2O and energy fluxes over tallgrass prairie and quantify annual budgets. Towers will be permanently placed in annually burned and 4-yr burned, ungrazed watersheds on Konza Prairie, in a grazed site on an KSU-owned cattle ranch (Rannels Ranch) adjacent to Konza, and at the Agronomy Research Farm where annual fluxes will be measured for an irrigated corn crop. Eddy correlation and eddy accumulation techniques will be utilized and with the installation of belowground bunkers (for protecting equipment from temperature extremes and fire) and the use of solar panels, we are confident that these measurements can be made year round (Fig. 45). Bunkers, solar panels, computers, etc. have already been purchased or funds are available from non-LTER sources. Indeed, the proposed system has been field tested via temporarily placed towers on Konza and the data are encouraging (Fig. 46). In addition to these budgets, soil respiration, microbial biomass, plant photosynthesis and respiration, individual plant stem water flux, soil moisture and site characteristics (plant community and soils data) will be assessed to provide information about the partitioning of these fluxes. Ham will lead this effort with Blair, Johnson, Knapp and Rice participating.

Gallery Forest Soil C Studies. We propose new studies to investigate the role of changing land management (i.e., decreased fire frequency and intensity) in increasing tree cover and subsequently altering soil C dynamics. This research (supported by LTER after which we will seek additional funds) will expand on recent work of Knight et al. (1994) that documented an expansion of gallery forest over prairie at Konza. Such vegetation cover changes can have important consequences for soil C storage. As noted above, grassland soils, compared to forest soils, typically contain ~50% more C and that C is evenly distributed within the soil profile rather than concentrated at the soil surface (Brady, 1974). **We hypothesize that plant cover changes associated with forest expansion into prairie will decrease the quantity, quality and distribution of organic matter and plant C input to soil, alter N mineralization/ immobilization dynamics and N availability, and ultimately decrease long-term soil C storage**. We will estimate the rate and distribution of new C input from trees and turn-over of residual tallgrass prairie soil C by taking advantage of the naturally-occurring differences in the abundance of ^{13}C in C_3 trees ($\delta^{13}C$~-27) and C_4 grasses ($\delta^{13}C$ ~-13) and in the soils derived from these plants (Balesdent and Mariotti, 1987; Martin et al., 1990). Johnson will lead these studies with Blair, Briggs and Knapp participating.

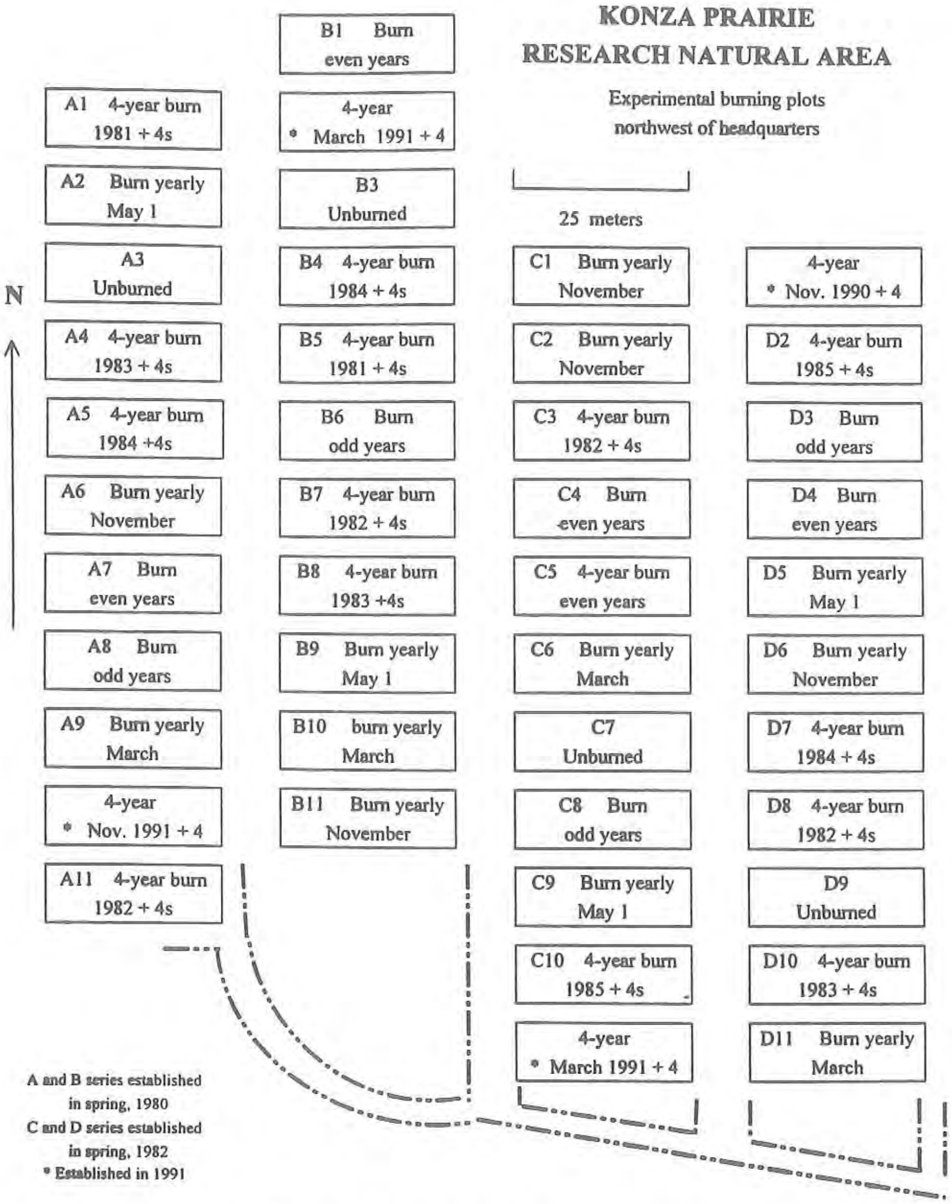


Fig. 44. The "Hulbert Plot Study"is a replicated small plot study designed to determine the effects of fire frequency and season of fire on plant species composition. These experimental plots, which were established in 1980-82 by the late Dr. Lloyd C. Hulbert, are located on one soil type, and span a moderate upland-lowland gradient. Treatments include some of the same fire treatments imposed on the LTER watersheds (1, 2, and 4 year fire intervals; unburned plots), as well as some novel treatments which focus on the effects of season of fire (early spring (March), late spring (May), and autumn (November). The primary research focus in the plots has been on plant species composition, although we also have documented plant reproductive effort and mycorrhizal spore abundance (Gibson and Hetrick 1988). The proximity of these plots to the headquarters area also makes them valuable as demonstration plots for illustrating the effects of fire in tallgrass prairie.

Regional Studies. Two additional new initiatives will be led by non-KSU investigators. Dr. Mary Ann Vinton (a new faculty member at Creighton University) has interests in regional gradients in functional traits of species and ecosystems. A network of satellite sites has been established for measurements of ANPP with the goal of determining if the models and factors we identify as controlling ANPP at Konza are appropriate at a broader spatial scale. These sites include the Ross Natural Area south of Konza near Emporia, KS (E. Finck, local PI), the Quivera Wildlife Refuge, SW of Konza (J. Frye, local PI) and the Nine Mile Prairie near Omaha, NE (T. Bragg, local PI). All of the sites have a prescribed burning regime and the local PIs have agreed to provide ANPP data to our data base (including some long-term data sets). Vinton will be in charge of coordinating this effort. In addition, Vinton will initiate new experiments in common gardens to evaluate species vs. environmental controls of functional traits of widely-distributed plants in the tallgrass prairie region. Rhizomes will be collected from the satellite sites and across other environmental gradients, and functional traits (tissue quality, root:shoot ratio; productivity; response to fire, drought, grazing) that are potentially important constraints on ecosystem processes will be compared. The working hypothesis is that **ecotypes, not species, are the best units to define traits important to ecosystem function.** A modest subcontract to defray costs for this research will be part of LTER IV.

Biodiversity. We view Konza Prairie as a "research platform" from which a variety of studies from disciplines complementary to the core LTER experiments are encouraged. Indeed, we believe that our past breadth of research is a strength of the program (Fig. 1). We will continue to actively encourage additional investigators to use the site and the resources available through our LTER program. For LTER IV, Dr. Robert Holt (University of Kansas) has agreed to serve as liaison between the scientists at the Museum of Natural History at KU and the Konza LTER Program. The goal of this interaction is to merge the talents and expertise of the systematists at the Museum with the more ecologically oriented research group at Konza Prairie to address biodiversity issues. Although we have species lists, and measure the responses to fire, grazing, etc. for many taxa, there are many more groups deserving of study. Dr. Holt has identified Dr. Steve Ashe, an arthropod systematist, as an initial collaborator in this effort. Dr. Ashe will advise a student (funded by the Konza LTER) to study arthropod responses to our treatments on Konza. In addition to this role, Holt and the Konza LTER PIs have submitted proposals to begin additional regional studies of ecological responses across environmental gradients.

F. Related Research, Regionalization and Cross-Site Studies

There are a large number of related research projects associated with the LTER program as well as intersite and regional projects that include Konza. Summaries of these are listed in Table 3. Below, one project is highlighted as an example of how short-term projects can complement LTER goals and initiate new long-term studies.

Arbuscular mycorrhizal fungi (AMF) play key roles in tallgrass prairie, and most plant species are obligate or facultative mycotrophs. Plant responses to AMF differ among species and among plant life history stages (Hetrick et al., 1992; Hartnett et al., 1994). AMF in tallgrass prairie strongly influence plant growth, competition, and responses to grazers and fire (Bentivenga and Hetrick, 1992b; Hartnett et al., 1993; Hetrick et al., 1994). Grazing and fire, in turn influence the development of the AMF symbiosis (Bentivenga and Hetrick 1992b; Hartnett et al., in press). Given differential plant species responses to AMF, and important interactions between AMF, plant resources, and fire and grazing, **we hypothesize that mycorrhizae influence tallgrass prairie plant community structure by mediating plant biotic interactions (competition and plant-grazer interactions) and responses to limiting resources**. Related short-term NSF-funded studies are examining these mechanisms, and a newly initiated long-term study involving mycorrhizal suppression in the field will assess the influence of AMF on plant community

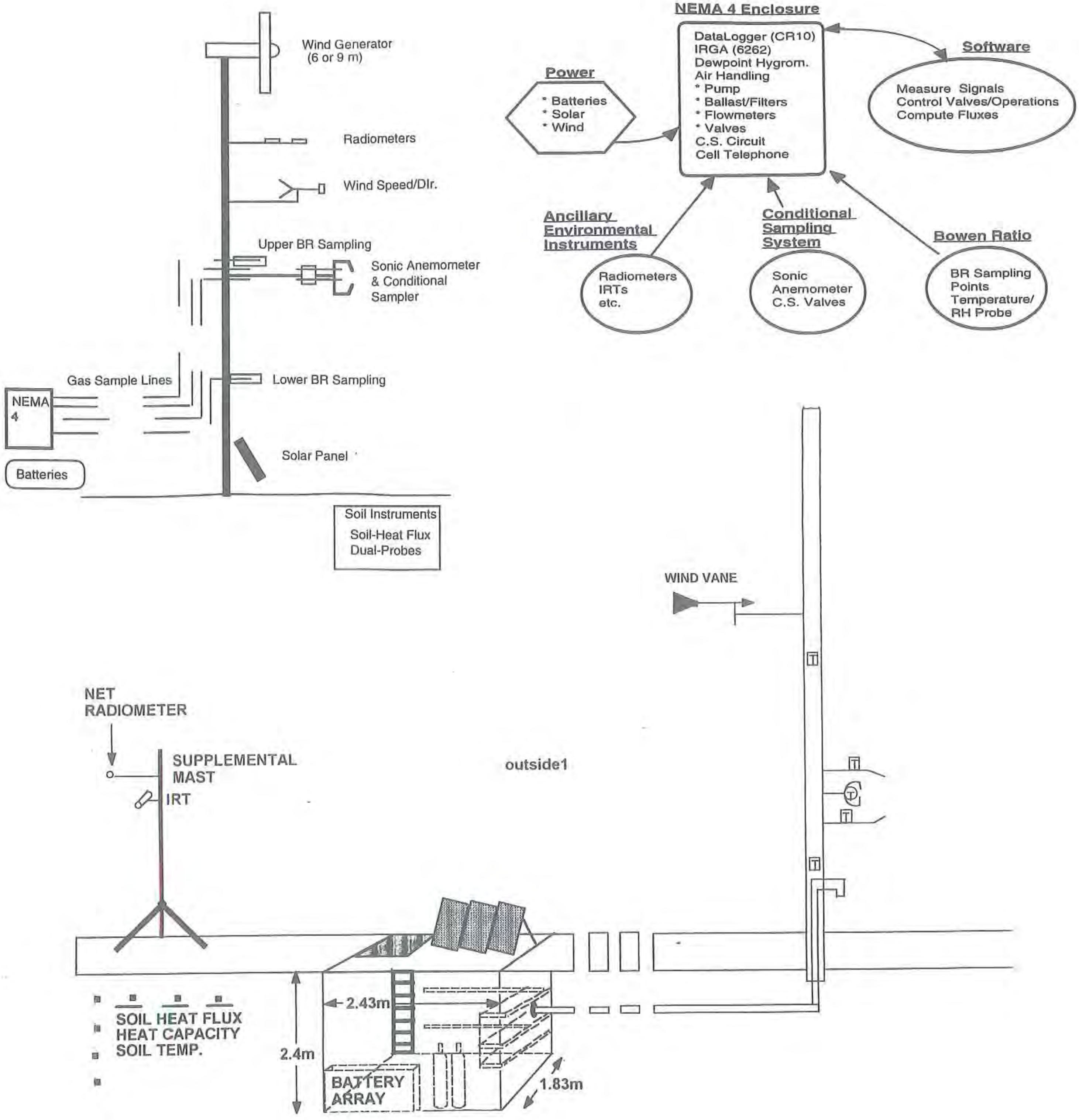


Fig. 45. A new initiative for LTER IV will focus on continuously measuring CO_2, water vapor and energy fluxes from tallgrass prairie sites subjected to different fire frequencies, grazing and agriculture. Long-term data on annual budgets will allow us to assess how climatic variability and directional climate change may interact with landuse to impact the C storage capabilities of this ecosystem. Top left: a schematic diagram of the instrument mast. Top right: a block diagram of the major components within the instrument package. Bottom: schematic of the entire system with approximate placement of instruments above and belowground (in bunkers).

structure. Plant communities will be sampled in plots treated bi-weekly with fungicide (benomyl) and control plots in grazed and ungrazed watersheds burned at different frequencies.

G. Synthesis of Research Results

We continue to be very active in synthesis efforts that focus on the Konza LTER database. A variety of formats have been used for the publication of these works. For example, a large fraction of a book on fire in grasslands (Collins and Wallace, 1990) was based on Konza data and, as noted earlier, Briggs and Knapp (1995) synthesized, in a journal article, 19 years of ANPP data focusing on the role that fire, topography and climatic variability play in explaining temporal and spatial patterns of ANPP in this grassland.

Although the NASA FIFE program was conducted in the late 80's (LTER II), synthesis efforts on this massive database are still ongoing and a major synthesis involving Konza investigators was published in 1992 as a special issue of the Journal of Geophysical Research.

Several books have been published in which Konza investigators have authored synthesis chapters. Examples include a grassland book by Joern and Keeler (1995) with chapters by Hartnett, Collins and Seastedt; a book on ecosystem responses to elevated CO_2 (Koch and Mooney, 1996) with a chapter by Owensby, Rice, Ham and Knapp; and a book on information analysis (Brunt et al., 1994) with a chapter by Briggs and Su.

Dr. John Zimmerman, an avian ecologist, published a major synthetic effort on the avifauna of Konza Prairie with much of the data derived from LTER research (Zimmerman, 1993). Indeed, a central focus of the book was the identification of relationships of bird populations with the vegetative communities of Konza, as well as avian community responses to fire and climatic variability. Data from 208 species are included.

Valuable synthetic analyses of long-term data can occur both within and across disciplines. Most of our accomplishments to date have been within discipline as described above. However, the length and breadth of the Konza LTER data base is now sufficient to allow us to test more general and integrative predictions that cross disciplines. For example, patterns of animal community structure and dynamics can be examined relative to theoretical models that predict relationships between diversity and stability. Preliminary analyses by Collins (unpubl.) of mammal and insect communities reveal opposing relationships between their temporal stability and plant species richness (Fig. 47). Similarly, plant species composition changes in response to fire are being evaluated in light of results from our nutrient cycling studies. Efforts in these and other synthetic and integrative studies will increase during LTER IV as our database grows.

Finally, our most ambitious synthetic effort is near completion. In 1994, Knapp and Briggs outlined a synthesis volume for the entire Konza Prairie LTER program and in 1995, 15 chapters were written (3 are still to be completed). The outline and selected chapters have been externally reviewed by Oxford Press and a contract offer to publish this book has been made. Subsequently, Oxford Press has agreed to serve as the publisher for a series of LTER site syntheses and our plans are to complete this volume in the spring of 1996. This volume will include not only syntheses at the "core area" level (i.e. patterns and processes in ANPP) by all group leaders (Fig. 48), but also synthesis across disciplines. This latter effort is being led by Collins. Although the completion of this volume will represent a major accomplishment for the Konza Prairie LTER group, the process has also been invaluable in identifying critical research needs and new research directions. At least two of these new research areas have been incorporated into pending research proposals. Thus, we have come to view synthesis exercises not as a means of closure for data sets and studies, but as an integral part of our evolving long-term research program in grassland ecology.

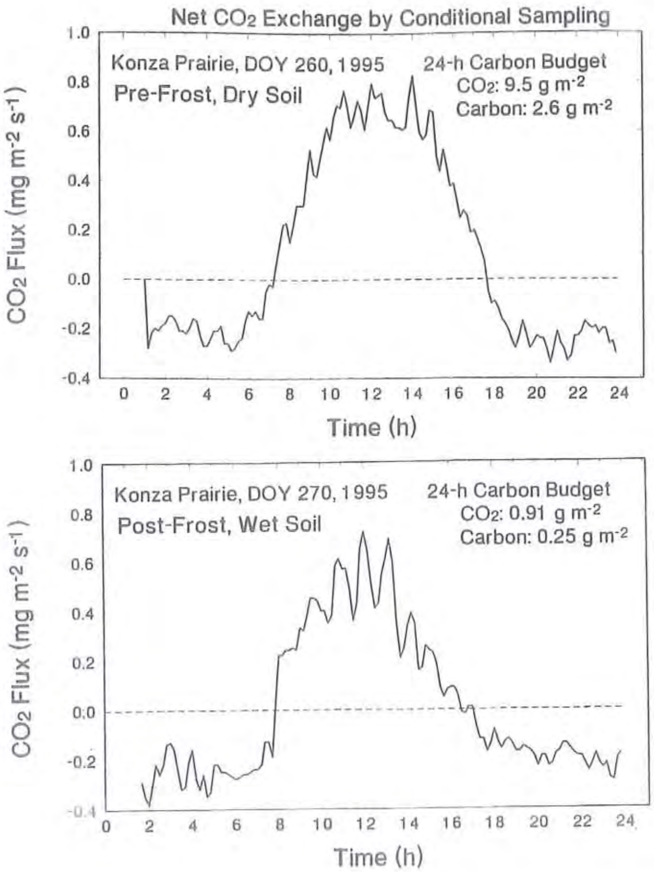


Fig. 46. Examples of diurnal CO_2 flux data measured by conditional sampling for two days in an annually burned watershed on Konza Prairie. Conditional sampling (i.e. relaxed eddy accumulation) is accomplished by using a sonic anemometer to detect upward vs. downward moving eddies and high speed conditional valves to sample each separately. Both CO_2 and H_2O concentrations are quantified in the air streams from upward and downward eddies. The difference between the upward and downward movement is the mass flux. An independent Bowen ratio estimate of water vapor flux will be used to verify the conditional sampling technique. In the late season data shown, the influence that a frost has on this C_4 grass dominated system can clearly be seen. In midseason, > 30 g/m^2/day of CO_2 uptake occurs in tallgrass prairie (Ham, unpubl. data.).

Photo: A temporarily placed measurement system operating in an annually burned watershed on Konza Prairie in 1995.

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† REU student

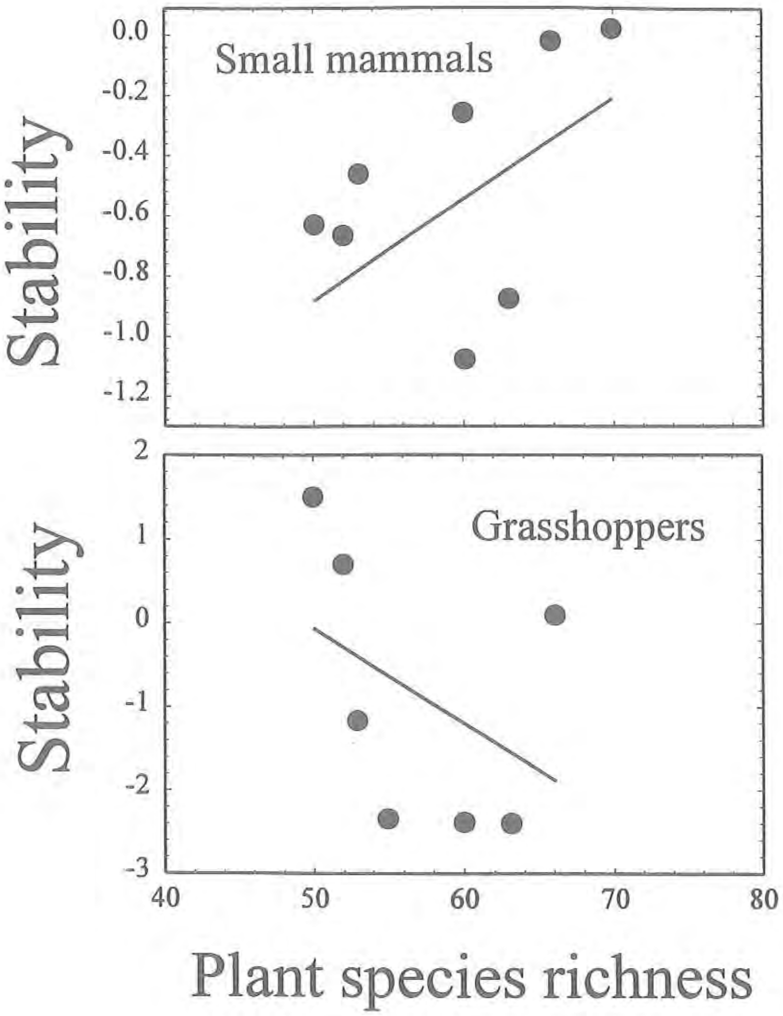

Fig. 47. Relationship between temporal stability of small mammals (top) and grasshopper populations (bottom) and plant species richness in a variety of experimental watersheds on Konza Prairie. Different fire regimes imposed in each watershed lead to changes in plant communities, and this preliminary analysis of the long-term data suggest that these two consumer groups are responding to different factors. Small mammal population stability is greatest in sites with highest plant species richness (typically infrequently burned or unburned sites) and these sites have the lowest interannual variability in ANPP and vegetative structure (see Figs. 24, 43). Grasshopper populations are most stable in sites with low plant species richness (annually burned sites where grasses dominate). Thus, small mammals may be responding more to community structure whereas grasshoppers may be more responsive to the taxonomic composition of the vegetation (see Consumer Populations section).

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Table 2. Qualitative Comparison of Foraging Ecology Traits of Bison and Cattle. (Hartnett et al. In Press)

Trait	Bison	Cattle	References[a]
Forage plant selectivity	lower	higher	1,9
Use of forbs and browse (% of diet)	lower (<10%)	higher (10-20%)	1-9
Use of graminoids (% of diet)	higher	lower	1-9
Diet niche breadth (number of available species/growth forms consumed)	lower	higher	4
Time allocated to grazing (during the growing season)	lower	higher	9
Time allocated to nonfeeding activities	higher	lower	9
General diet quality (crude protein, digestibility, cell wall constituents)	lower	higher	1,4,9
Digestibility of C_3 and C_4 graminoids	higher	lower	9
Mean digesta retention time	higher	lower	3

[a] [1]Peden et al. 1974, [2]Kautz and Van Dyne 1978, [3]Schaefer et al. 1978, [4]Schwartz and Ellis 1981, [5]Bennett and Dahlgren 1982, [6]Coppock et al. 1983, [7]Wydeven and Dahlgren 1985, [8]Krueger 1986, [9]Plumb and Dodd 1993.

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Table 3. Ongoing related research projects and cross site studies on Konza Prairie (KNZ).

PI(s)	Title	Location	Group
Blair, Knapp, Todd and Rice	Effects of altered soil moisture on soil communities, primary production and ecological processes in grasslands	KNZ, Fort Hays, KS	Nutrients, NPP, Belowground
Briggs, Blair, Dodds, Goodin, Henebry, Knapp, Nellis	Use of remotely sensed data on phenological activity and heterogeneity to detect changes in grassland	Flint Hills	Landscape, NPP
Cully, Heibert & Godfrey	Effects of size, fragmentation and management of prairie remnants on biodiversity and sustainability	KNZ, & Great Plains	Population Comm.
Cully et al.	Kansas GAP analysis	State of Kansas	Pop/Comm., Landscape
Frank	The influence of large herbivores on nitrogen cycling using natural 15N abundance.	KNZ& Yellowstone	NPP& Nutrients
Gibson et al.	The capacity of Ft. Riley tallgrass prairie to support military training activity.	KNZ & Fort Riley, KS	NPP,Belowground, Pop/Comm.
Harmon et al.	LIDET	KNZ and other LTER sites	Belowground
Ham and Knapp	Carbon, water, and energy fluxes from a tallgrass prairie: a long-term investigation of environmental, biological and land management factors.	KNZ, & agricultural/grazing fields	NPP, Organic matter
Hartnett and Hetrick	Mycorrhizal mediation of grass biotic interactions and plant community structure.	KNZ & Range Research Unit	Pop/Comm. & Belowground
Hendrix et al.	Cross-site collaborative research Earthworms and soil processes in North America.	KNZ, CWT, LUQ	Belowground Nutrient
Hartnett and Cochran	Grazing effects on plant community, biodiversity and stability.	KNZ & Range Research Unit	Pop/Comm.
Knapp and Henebry	Cross-site collaborative research: Spatio-temporal dynamics of canopy and soil moisture: Linking synthetic aperture radar image phenomenology with ecosystem processes.	KNZ &SEV	NPP, Landscape
Jastrow, Rice, Miller, Boutton	Controls of soil carbon retention under elevated atmospheric CO_2.	KNZ, Texas	Belowground
Rice, Owensby.	Sequestration of carbon dioxide into soil organic carbon pools under elevated dioxide environment.	KNZ	Belowground
Owensby, Ham ,Knapp, Rice	Rangeland ecosystem response to CO_2 enrichment: a carbon balance approach.	KNZ	NPP, Belowground
Rice and Owensby	Sequestration of carbon dioxide into soil organic carbon pools under elevated dioxide environment.	KNZ	Belowground
Richie et. al.	Cross-site collaborative research: Effects of different-size herbivores on grassland plant diversity.	KNZ, CDR, CPR, Badlands Nat. Park	Consumers
Stueter et al.	Relationship between landscape patterns, ecological processes and biological diversity in the Great Plains.	Great Plains	Pop/Comm. & Landscape
Tieszen and Ojima	Cross-site collaborative research: Analysis of past and current changes in grassland ecosystem dynamics in Asia and North America	KNZ, CPR, Mongolia	Organic matter
Vinton, Finck, Frye, and Knapp	Regional ANPP.	KNZ, Emporia, McPherson, KS & Omaha, NE.	Regional NPP

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† REU Student

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Fig. 48

LTER III ORGANIZATION

Principal Investigators:

John M. Briggs* David C. Hartnett Donald W. Kaufman Alan K. Knapp**
(*Data Manager)
(** Project Coordinator)

LTER STAFF

Gene Towne (Field Coordinator); Geoff Henebry (Modeling); Rosemary Ramundo (Lab Coordinator)

LTER RESEARCH GROUPS

ABIOTIC FACTORS
John Briggs
Alan Knapp
Doug Goodin*

NET PRIMARY PRODUCTION
John Briggs
David Hartnett
Alan Knapp*
Duane Nellis

POPULATION/ COMMUNTIES
Ted Evans (USU)
David Hartnett*
Barbara Hetrick
Scott Collins
Don Kaufman
Tim Todd
John Zimmerman
David Gibson (Southern Illinois University)

NUTRIENT STUDIES
Walter Dodds
Jim Koelliker
Chuck Rice
Paul Schwab
John Blair*
Tim Seastedt

ORGANIC MATTER STUDIES
Walter Dodds*
Jim Koelliker
Jack Oviatt
Chuck Martin
Wendy Macpherson (KU)
Larry Gray*

AQUATIC STUDIES
Walter Dodds*
Jim Koelliker
Larry Gray (Ottawa University)*
Jack Oviatt
Wendy Macpherson

BELOWGROUND STUDIES
Barbara Hetrick(NIU)
Chuck Rice*
Paul Schwab
Tim Todd
John Blair
Tim Seastedt

CONSUMERS
Don Kaufman*
David Hartnett
Ted Evans
John Zimmerman

LANDSCAPE ECOLOGY
John Briggs*
Duane Nellis*
Geoff Henebry

* = Group Leaders

(Continued on next page)

4. Program Management

One of the original goals of the architects of the LTER Program was that long-term, site-based research programs with a relatively stable funding base would be managed in such a way that turnover of individual investigators and/or completion of scientific careers would not be detrimental to the central goals, experiments established, and the data collection efforts of the LTER sites (Callahan, 1984). The Konza Prairie LTER site has served as a test of this model. The original experimental design of Konza Prairie as a watershed-level fire frequency-grazing experiment in tallgrass prairie was designed by the late Dr. Lloyd Hulbert prior to LTER I. The program has remained focused on this experimental design and flourished despite different administrative PIs coordinating each renewal, and a significant turnover of investigators over the past 15 years. Indeed, our plan is to continue to rotate administrative leadership as untenured faculty rise in rank, have proven their commitment to the long-term goals of the program, and feel comfortable assuming the responsibilities. Dr. John M. Blair has, or will soon have fulfilled these criteria, and has agreed to serve as administrative PI near the midpoint of LTER IV with Knapp continuing in an advisory role.

Such turnover of the administrative role is possible because our management model depends on shared intellectual leadership and group decision-making. The organizational scheme we have used in LTER III and a proposed scheme for LTER IV are depicted in Fig. 48. In practice, Knapp serves as responsible PI at the local (University) and LTER Network level. For day-to-day financial decisions, Knapp and Briggs share responsibility and coordinate activities. Interactions are at a daily level and Blair has been increasingly involved in the past year. For decisions of greater magnitude, such as personnel contracts, research subcontracts, major purchases, etc., Kaufman (a former administrative PI) and Hartnett (current Konza Prairie Site Director) are also consulted. Such interactions occur as necessary. LTER group leaders (Fig. 48) are consulted as required either individually or as a group when more major research decisions must be made or when specific requests for data, information, or collaboration are received. The willingness of group leaders to deal with these latter types of requests reduces the work load on the administrative PI substantially.

Turnover in the administrative PI role at Konza Prairie is also possible because of the long-term commitment that Dr. John Briggs has made to the program. Briggs, with 13 years of continuous full-time activity in the Konza LTER program, provides "memory" and perspective that is critical to success of the program. In addition to his LTER role, Briggs is active on the faculty at KSU. The Division of Biology has secured Graduate Faculty status for Briggs and provides teaching opportunities and salary augmentation when possible.

A third key in this model is maximizing the involvement of other personnel in LTER activities. Knapp serves as Konza's LTER Coordinating Committee member and when CC meetings allow additional site representatives to attend, group leaders are always given the opportunity. Blair, Hartnett and Briggs have participated recently. Minutes from these meetings are always distributed to the entire group. Workshop participation is encouraged and supported when possible.

Fig. 48 (cont).

LTER IV ORGANIZATION

Principal Investigators:

John M. Briggs* John M. Blair**, Walter K. Dodds, David C. Hartnett, Loretta Johnson, Donald W. Kaufman Alan K. Knapp***

(*Data Manager) (** Project Coordinator 2000-2002) (*** Project Coordinator 1997-1999)

LTER STAFF

Gene Towne (Grazing & Fire Management); Rosemary Ramundo (Lab Coordinator); Amanda Kuhl (Field Coordinator)

LTER RESEARCH GROUPS

ABIOTIC FACTORS
John Briggs
Alan Knapp
Doug Goodin*†
Jay Ham†

NET PRIMARY PRODUCTION
John Briggs
David Hartnett
Alan Knapp*
Duane Nellis

POPULATION/ COMMUNTIES
Jack Culley†
David Hartnett*
Chuck Rice
Scott Collins
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Bob Holt*†

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John Blair*
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ORGANIC MATTER STUDIES
Walter Dodds*
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Larry Gray*
Jay Ham†

MODELING
Tim Seastedt*
Geoff Henebry
John Blair
Chuck Rice
Loretta Johnson†

AQUATIC STUDIES
Walter Dodds*
Jim Koelliker
Larry Gray *
Jack Oviatt
Wendy Macpherson
Chris Guy†

BELOWGROUND STUDIES
Loretta Johnson†
Chuck Rice*
Gail Wilson†
Tim Todd
John Blair*
Tim Seastedt

CONSUMERS
Don Kaufman*
David Hartnett
Phil Gibson†
John Zimmerman
Jack Culley†
Glennis Kaufman†
Phil Fay†

LANDSCAPE ECOLOGY
John Briggs*
Duane Nellis*
Geoff Henebry
Loretta Johnson†
Doug Goodin†

REGIONAL NPP
MaryAnn Vinton*†
Elmer Finck†
Jonathan Frye†
Alan Knapp
John Briggs

SYNTHESIS
Scott Collins*
Alan Knapp
John Briggs
John Blair
Bob Holt†
David Hartnett

* = Group Leaders
† = new investigator for LTER IV

Interactions among investigators are fostered, and scientific and programmatic information disseminated in a variety of ways. All investigators (at Kansas State University and at other campuses) are on e-mail lists through which Briggs (data manager) distributes information and requests input. For example, LTER network office e-mail communications sent to "PI-list" (which includes Knapp and Briggs) are routinely forwarded to the entire group. During the academic year, a bi-weekly research meeting is held for all Konza scientists and graduate students. General announcements and research presentations comprise the format of these meetings with minutes distributed group-wide and made available on our WWW home page. On an annual basis, we host a Konza Prairie LTER Workshop (the 7th was held in 1995). These all-day workshops are usually attended by off-campus researchers as well as the local scientists. Faculty, Post-doc, graduate and undergraduate students present research results as oral or poster presentations and late afternoons usually include a group leaders meeting. Abstracts with figures are disseminated to the entire group and are made available on our WWW home page.

Although we follow a distributed model in terms of scientific/intellectual leadership and decision making, we recognize the need for external input into our research program. In addition to the NSF-led site reviews that occur once each funding cycle, we have had informal review teams evaluate our program in the past, as well as "targeted" individual visits by non-Konza LTER scientists. In the past, the NSF review team has provided us with overall guidance that often overlapped substantially with our informal review team report. Thus, we have found it more valuable for our program to utilize targeted individual visits by external scientists. These provide more in-depth review of one or more aspects of our program. Often we can combine these visits with a Division of Biology seminar presentation to reduce costs. Our goal is for each research group to invite an outside expert to review their program over the LTER IV funding cycle.

Finally, one of the benefits of the distributed management of the Konza Prairie LTER is the broadly based research program that results when such a large group of scientists is actively involved in a common program. This "scientific diversity" (Fig. 1) will grow significantly in LTER IV. In addition to the new faculty in Biology at Kansas State mentioned earlier, a new National Biological Service Wildlife Coop Unit has been established at KSU and the three federally supported scientists, Drs. Phil Gipson (predator ecology), Jack Culley (vertebrate ecology) and Chris Guy (aquatic ecology) have already begun research programs that include Konza Prairie. Also on campus are new faculty in Agronomy (Dr. Jay Ham, micrometeorology) and Geography (Dr. Doug Goodin, remote sensing) participating in both new initiatives and established research areas. Off campus, Dr. Bob Holt (U. of Kansas) will lead efforts to enhance our knowledge of site biodiversity and participate in regional and synthesis efforts. Also involved in regional efforts and our "satellite-site" program are Drs. Mary Ann Vinton (Creighton University), Jon Frye (McPherson College) and Elmer Finck (Emporia State University). Attracting additional scientists to participate in the research at Konza Prairie is an ongoing goal of our program.

5. Data Management

Konza Prairie Data Management

The overall objectives of the Konza Prairie LTER Data Management (KPLDM) plan are **to assure data integrity (correctness, at all times, of all items in the database), improve security (protection against loss of data), and facilitate use of data by the original investigator(s) as well as by future researchers**. Our goal is the development of a research database to address scientific questions ranging from local to global scales. The development of our database system has been summarized by Briggs and Su (1994).

Since its inception in 1981, the KPLDM program has evolved from serving a local research group at Kansas State University (most in the Division of Biology) to working with a multi-disciplinary team of over 30 investigators from a variety of universities and government agencies. During the early 1980's, considerable effort was made by the Konza LTER staff to implement a base-level research data management plan. Its primary goal was to allow all interested researchers to locate, interpret and use Konza data. This plan was designed using guidelines established by Gorentz et al. (1983) and is documented in Gurtz (1986). At our site, the Data Manager (Briggs) is also a PI on the LTER grant and thus has been highly involved in the design and execution of research projects as evident from the Konza Publication list.

The design of the current Konza Prairie LTER database is straightforward. All data sets are in ASCII format (with exception of GIS coverages and remote sensing data). The entire database resides on a Novell Network (Version 3.1), running on a Pentium server with 6 gigabytes of disk space. (The disk's are mirrored, thus we always have two copies of the database on two separate drives). The database is divided into subdirectories which correspond to specific Konza research groups or which represent the nature of the data set.

For consistency, most LTER data sets have the first 16 columns of each line organized as:

1. Datacode	1-5	A5
2. Rectype	6	I1
3. Year	7-8	I2
4. Month	9-10	I2
5. Day	11-12	I2
6. Watershed	13-16	A4

Thus, each line has a data set code associated with it. Although, this was originated in the "days of computer cards" when it was important to have the data set code on each card, it is now useful to have this information in case of hardware failures (disk crashes, bad tapes, etc.). We have linked the personal microcomputers of KSU LTER researchers directly to each other and the Konza Prairie data bank using the Novell Network. All PC's have direct access to the internet and thus the World Wide Web (WWW). We use the Novell network primarily for data entry, other local data management activities (i.e. updates of software) and for local data access for KSU investigators. This allows data, reports and manuscripts to be transferred among local researchers. For non-local investigators, we have established a WWW server on a local UNIX machine (http://climate.konza.ksu.edu). The Konza Prairie data bank on our WWW server

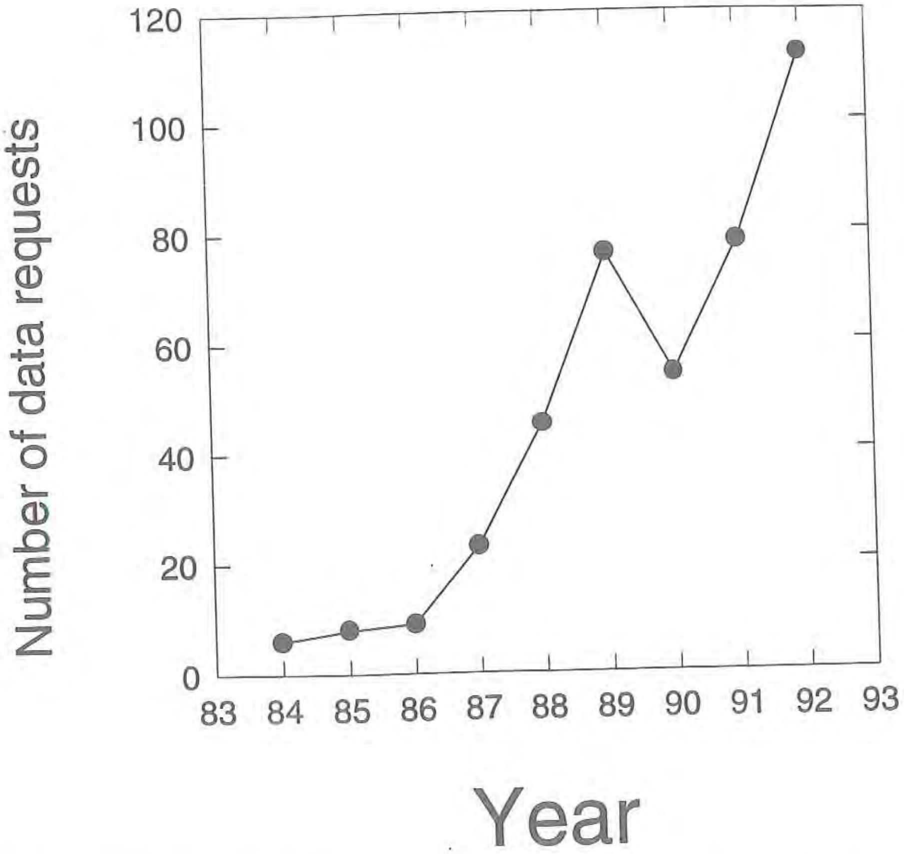


Fig. 49. Data requests to the Konza Prairie LTER Data Manager from 1984 to 1992 from non-KSU investigators (From Briggs and Su, 1994).

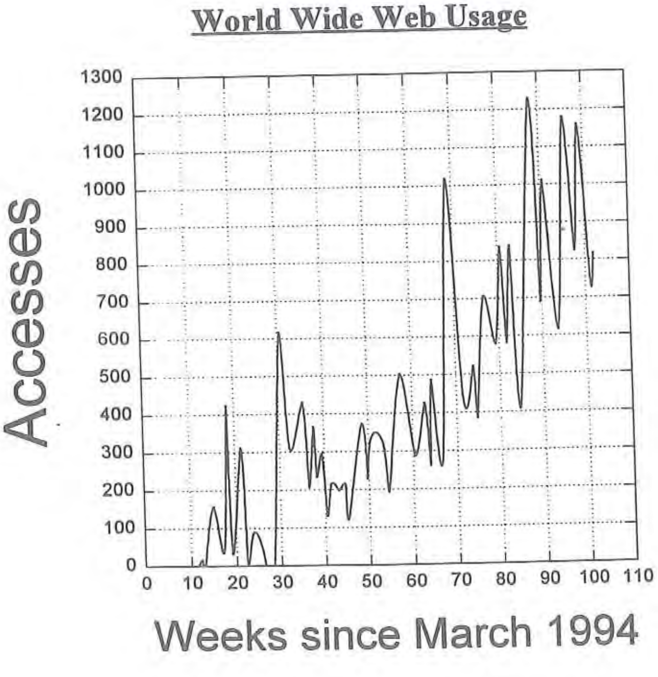


Fig. 50. Trends in the use of the Konza Prairie LTER WWW server. At present (Jan. 1996), we are averaging about 1000 requests per week.

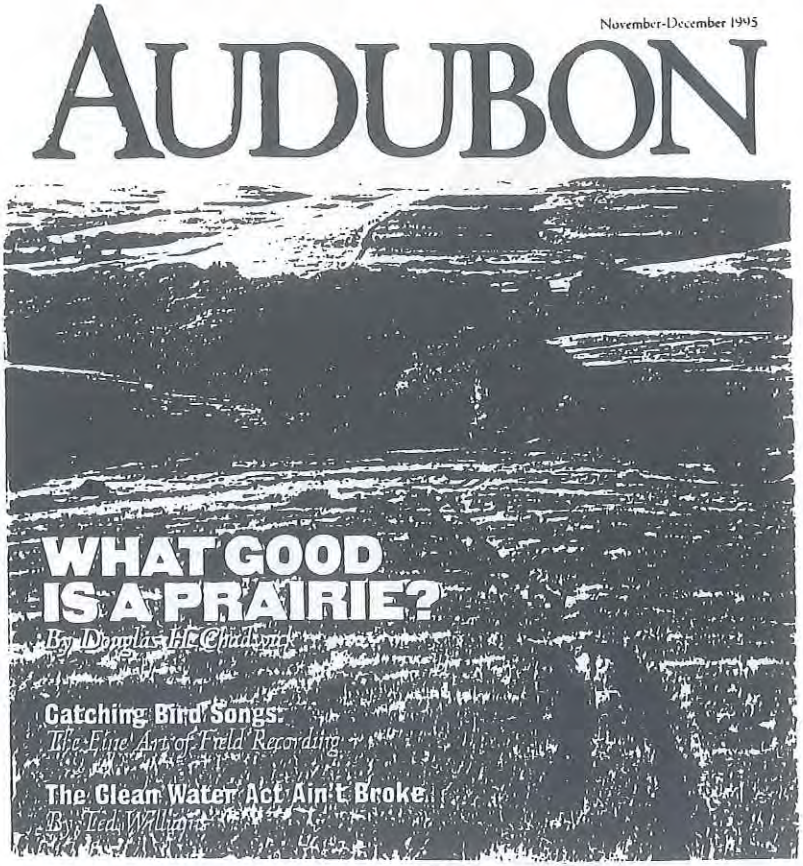
includes the same archived LTER data, meta data and our Methods Manual (see below) that is on our Novell server. This allows anyone the same complete access to all of the Konza LTER data that KSU investigators have.

Like most LTER sites, we have found that storing data in flat ASCII files is the most efficient way to allow multiple investigators, using a variety of platforms and software, complete access to all of the data. Prior to the development of our server, we tested various mechanisms to allow non-KSU LTER scientists direct remote access to the Konza Prairie LTER data base. This included an Oracle data base system modeled after the FIFE Information System (Strebel et al., 1990). However this system did not handle graphic images very well and the user needed to learn Structured Query Language (SQL). Furthermore, getting data into the system was very time consuming. In addition, the Data Manager personally addressed many data requests (Fig. 49) that the Oracle data base system could not handle. By 1992, the time required to respond to these data requests became excessive. Thus, it was necessary to find a more interactive and user-friendly data base interface.

The WWW server at our site has been in operation since April 1994. Features such as graphic display capabilities and hyper links have greatly facilitated development of a user-friendly interface to a large and complex information base. In this short time, it has become the main avenue for handling data requests. The use of our WWW server has increased by a factor of 100 and we now average over 100 daily requests for data and other information on the Konza Prairie LTER program. (Fig. 50). We also exploit the features of our WWW server to facilitate the collection and organization of information (such as metadata) within our research group. In addition to research, we are using the WWW server to facilitate communication among researchers interested in Konza Prairie. News, upcoming seminars, etc. are all posted on the WWW server and over 200 different (non-KSU) users have accessed the Konza Prairie Publication records in 1995.

Since the inception of the Konza LTER, all Konza Prairie LTER investigators have been required to submit their data and meta data to the Konza Prairie data bank. The KPLDM has developed specialized data entry and data checking programs to reduce errors and time spent entering data, and maintain data integrity. We store all archived files (files that have been entered and thoroughly checked) on a variety of electronic media from 1/2" magnetic tapes, 8mm tapes, hard disks and re-writeable optical disks. Our goal is to have at least three copies of our data base stored in different physical locations.

The most difficult and time consuming component of our data management plan has been the proper documentation of data sets such that they can be used by investigators who did not originally collect the data (Tate and Jones, 1991). This is especially critical for a long-term research program considering the turnover of personnel coupled with the changes that occur in data collection due to technology enhancements (i.e., new laboratory equipment, etc.). As noted previously, we have had turnover of senior personnel which, when coupled with the usual succession of post-docs and graduate students, has increased our need for proper data documentation. A key component of this documentation has been development of a Methods Manual describing our procedures. The Konza Prairie LTER program has maintained a Methods Manual since 1981 (currently a 172 page document; on-line via our WWW server), which details how each LTER data set is collected. It includes items such as maps with locations of sampling sites and transects, sample data sheets, and very detailed procedures on instrument installation and use. This manual provides the necessary details to interpret the more extensive data



November-December 1995

AUDUBON

WHAT GOOD IS A PRAIRIE?

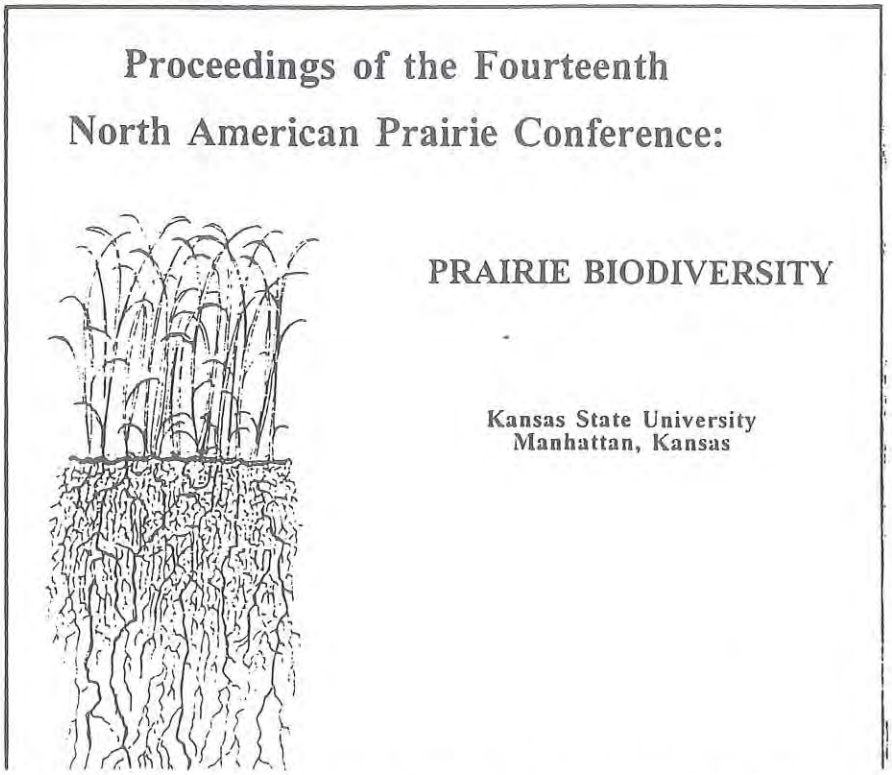
By Douglas H. Chadwick

Catching Bird Songs:

The Fine Art of Field Recording

The Clean Water Act Ain't Broke

By Ted Williams



Proceedings of the Fourteenth

North American Prairie Conference:

PRAIRIE BIODIVERSITY

Kansas State University

Manhattan, Kansas

Fig. 51 A) Konza Prairie and the Konza LTER Program have been featured in several publications, including in a 12-page cover story in *Audubon* magazine, written by National Geographic Author, Douglas Chadwick.

documentation files maintained for each data set. This document is updated yearly and a completely revised manual is produced every 5 years.

One of the goals of the Konza Prairie LTER program is to support, as much as possible, collaborative and independent research efforts on Konza Prairie. Thus, we have developed a highly successful protocol (implemented in 1983) that allows outside (non-Konza LTER) investigators access to the LTER data. We have three levels of access restrictions: unrestricted, limited restriction, and full restriction. Briefly, *unrestricted*--archived data sets accessible to all researchers. This is read-only access and it is understood that any errors discovered (or suspected) in an unrestricted data file must be brought to the immediate attention of the Data Manager, who will confer with the investigator (These are the data we have on our WWW server; most Konza LTER data fall in this category). *Limited restriction*--archived data sets with read-only access available to current Konza LTER researchers or to outside researchers upon written permission of the current LTER PI(s) and the data set investigator. The PI(s) may deem that the investigator approval is not necessary if he/she has waived that privilege, is deceased, or cannot be reached within a reasonable amount of time. This restriction is mostly used for short-term projects (i.e. graduate students theses, short-term exploratory research, etc.) *Restricted*--these data are accessible only to the investigator or persons designated by the investigator. These may be raw data or other data files which are considered incomplete, unchecked, or have proprietary rights (e.g. commercial remote sensing data). Our goal is to have all LTER data archived, on our WWW server and in the unrestricted category within one year after the last datum is collected. As soon as any data set is placed in the unrestricted category, it is placed on our WWW server. Thus we are constantly updating the data base on our WWW server. In addition, we ask investigators who use Konza Prairie LTER data to follow these guideline for the release and citation of data collected as part of the Konza Prairie LTER project:

1) Manuscripts using the data are to be provided to the Principal Investigator, LTER, Division of Biology, Ackert Hall, Kansas State University, Manhattan, KS 66506 so that he/she may notify the appropriate investigators. 2) Acknowledgment should be made to recognize the contribution of data by Konza Prairie LTER. We request that the following statement be included in any manuscript or proposal. "Data from the Konza Prairie Research Natural Area were collected as part of the Konza Prairie LTER program (NSF grants DEB-8012166, BSR-8514327 and BSR-9011662), Division of Biology, Kansas State University, Manhattan, KS. Data and supporting documentation are stored (Data Set Code(s)=_____) in the Konza Prairie Research Natural Area LTER Data Bank." Additionally, specific investigators may be cited for their contributions to the paper.

Coleman donates $15,000 for Konza improvements

The Coleman Company of Wichita has awarded $15,000 to Konza Prairie Research Natural Area to improve the public nature trails and create a public education facility at the site.

David Hartnett, Konza director, said the Coleman Company Charitable Trust is contributing $5,000 a year for three years toward the improvements. "The Coleman Company is interested in supporting Kansas outdoor-related projects and conservation efforts," he said.

"Konza is first of all a biology research site, but there are also three public-access nature trails of varying length on the prairie preserve. Gifts like this one from Coleman will allow us to open up the facilities and increase the opportunities for public use and public education on the prairie," Hartnett said.

New information signs at the trailhead kiosk and interpretive trail markers will be put in this year with the Coleman grant. Trail improvements, including replacing the bridge across King's Creek which washed out twice this spring, will be completed during the first year. A public education facility, restrooms and shelter house will be added near a stone barn at an abandoned home site along the nature trail.

Hartnett said matching funds are being sought to help carry out additional public use area improvements.

The Friends of Konza Prairie is assisting with facility use planning and fund raising for the public education aspects of Konza.

The Konza Praire will soon see some improvements thanks to the Coleman Company of Wichita.

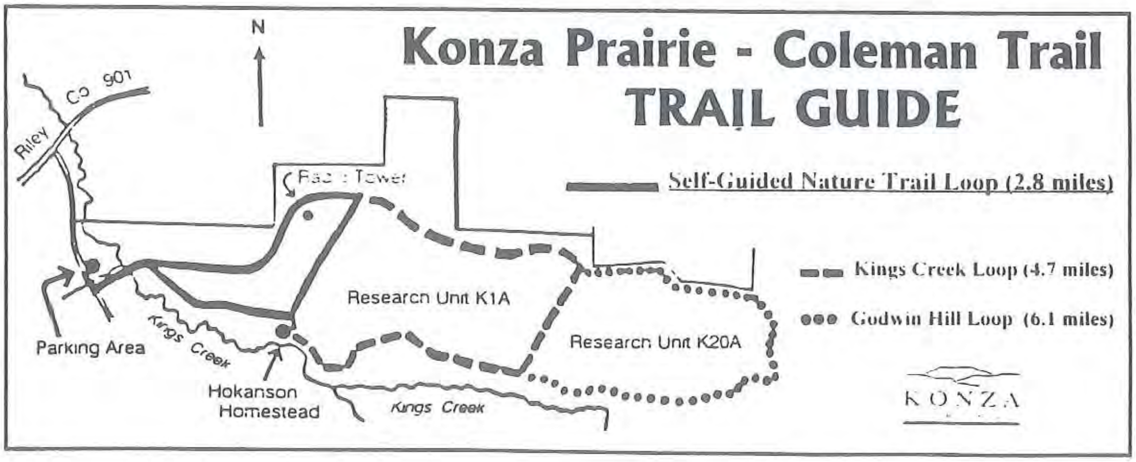


Fig. 51 B) A 3-year grant from the Coleman Company provided support to enhance public educational facilities and programs on Konza Prairie.

6. Outreach Activities

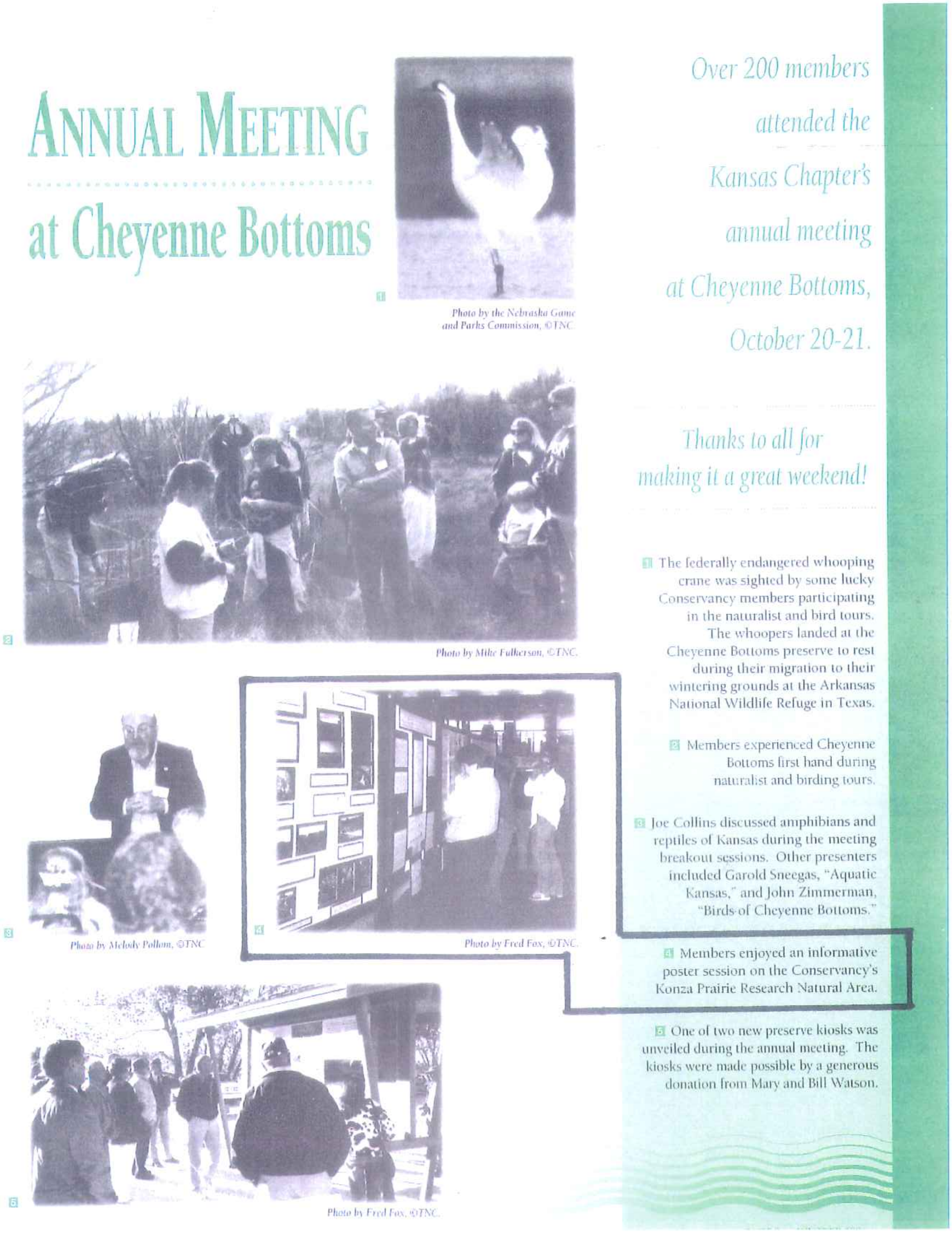
Konza Prairie programs and activities in public education, service, and professional training increased significantly during LTER III. During 1995, the number of site visitors involved in organized educational programs and tours numbered over 2,000, and over 3,000 visitors used the self-guided nature trails and educational facilities (Table 4). During the bi-annual KPRNA Visitors' Day, an additional 2,000 people participate in public educational programs.

KPRNA researchers have hosted numerous science education programs involving primary, secondary, and post-secondary students, and teacher training. Konza faculty, post-doctoral, and graduate researchers have participated in training individuals for the Konza Prairie Docent Program. During the past year, 24 docents have been involved in leading school field trips and educational programs in conjunction with various school districts throughout Kansas. Other programs have provided research experience opportunities for high school students. For example, in 1995 Dr. Walter Dodds received NSF funding to involve 4 high school students and 2 teachers in a summer LTER-related research project on Konza stream water quality. At the college level, KPRNA serves as an outdoor educational laboratory for university classes and visiting field courses from numerous institutions each year. Information about these opportunities on KPRNA are made available through its membership in the Organization of Biological Field Stations, Association of Ecological Research Sites, and other organizations. Adult education programs on Konza Prairie include an Elderhostel course offered each summer through the KSU Division of Continuing Education and team taught by Konza-LTER Scientists, and a program for senior citizens on Konza offered through The Botanica, the Wichita Botanical Gardens.

KPRNA and the LTER program have actively integrated undergraduate students into research and have provided many training opportunities through the REU programs and the employment of undergraduate assistants. Collectively, Konza LTER investigators have received 5 REU supplements during LTER III to support 13 undergraduates. These student projects have resulted in 7 published papers, 4 with REU students as senior authors. Five additional manuscripts based on REU projects are currently in preparation or submitted. In 1995, a REU site grant to the KSU Division of Biology supported 10 additional undergraduates from institutions throughout the US. LTER investigators lectured in an introductory seminar and served as mentors for student research projects.

A major facilities renovation program, currently in progress, will greatly enhance the capacity of KPRNA to provide research opportunities and science education programs. With support from the NSF Field Stations and Marine Laboratories Program, the Kansas Agricultural Experiment Station, and KSU, major site improvements and building renovations including a prairie education center, teaching laboratory, exhibits, meeting rooms, and bedroom and dormitory facilities for visiting students and scientists will be completed by July, 1996. In addition, a grant from the Coleman Company in 1995 supported enhancements to the public trails facilities including trail guide printing, interpretive signage and kiosks, and the construction of an outdoor education center (Fig. 51).

Konza Prairie scientists deliver numerous presentations and talks about KPRNA research and educational programs throughout the year to various conservation organizations (e.g. The Nature Conservancy, The Audubon Society), civic groups, educational organizations, and professional organizations and agencies (e.g. KS Wildlife & Parks Grassland Management Workshop, Kansas Rangeland Field Day, Kansas Agricultural Experiment Station). During LTER III, we hosted



ANNUAL MEETING at Cheyenne Bottoms

Photo by the Nebraska Game and Parks Commission, ©TNC.

Photo by Mike Fulkerson, ©TNC.

Photo by Melody Pollom, ©TNC

Photo by Fred Fox, ©TNC.

Photo by Fred Fox, ©TNC.

Over 200 members attended the Kansas Chapter's annual meeting at Cheyenne Bottoms, October 20-21.

Thanks to all for making it a great weekend!

1 The federally endangered whooping crane was sighted by some lucky Conservancy members participating in the naturalist and bird tours. The whoopers landed at the Cheyenne Bottoms preserve to rest during their migration to their wintering grounds at the Arkansas National Wildlife Refuge in Texas.

2 Members experienced Cheyenne Bottoms first hand during naturalist and birding tours.

3 Joe Collins discussed amphibians and reptiles of Kansas during the meeting breakout sessions. Other presenters included Garold Sneegas, "Aquatic Kansas," and John Zimmerman, "Birds of Cheyenne Bottoms."

4 Members enjoyed an informative poster session on the Conservancy's Konza Prairie Research Natural Area.

5 One of two new preserve kiosks was unveiled during the annual meeting. The kiosks were made possible by a generous donation from Mary and Bill Watson.

Fig. 51 C) Konza Prairie Long-term Ecological Research has been featured in several meetings and workshops, including the 1995 annual meeting of the Kansas Chapter of The Nature Conservancy, and the 1995 North American Prairie Conference.

several professional meetings and workshops, including the Amer. Soc. of Mammalogists meeting (1991) and the 14th N. Amer. Prairie Conference (1994). Konza will host The Nature Conservancy's Great Plains Biodiversity Workshop in March, 1996.

National visibility of the Konza LTER program has increased significantly in recent years as the site has attracted numerous journalist and has been the focus of several major projects. In August, 1995 Konza LTER researchers hosted nature writer Douglas Chadwick who produced a 12-page cover story on the tallgrass prairie and the Konza long-term research published in *Audubon* magazine (Fig. 51). In 1994 Konza served as a filming site for a 2-hr nationally televised BBS educational documentary film on the Oregon Trail. In addition, Konza Prairie has recently served as the focal site for photography and/or text production of a number of books (Table 5).

KPRNA Scientists and the LTER program have provided valuable resources and consultation to government agencies and organizations. For example, in 1995 Konza LTER investigators assisted the National Park Trust in developing an interim management plan for the Spring Hill/Z-Bar Ranch, an 11,000 acre tract that has been proposed as a Tallgrass Prairie National Park. National Parks Service project directors from the developing Walnut Creek National Wildlife Refuge in Iowa also made several visits to Konza for assistance and consultation in developing their tallgrass prairie restoration, management, and public education programs. The Konza LTER program also provided valuable resources and input for management of Weaver's historical 9-mile Prairie near Lincoln, NE. In addition, Konza LTER scientists have been actively involved with the Kansas Department of Transportation in designing an educational facility (interpretive signage and handicapped-accessible walkway) for a tallgrass prairie scenic overlook on a state highway bordering Konza Prairie.

International outreach during LTER III has taken several forms. (1) Based on image analysis techniques developed with LTER support, Henebry received a Fulbright Research Award to travel to the Brazilian National Institute for Space Research to conduct ecological remote sensing studies on the Pantanal, a disturbance-maintained ecosystem, like Konza, and the largest wetland habitat on earth. The INPE-Konza connection has been fruitful (Henebry and Kux 1995, Henebry and Batista 1994, Krug and Henebry 1994, 1995, Kux and Henebry 1994). (2) Henebry was awarded a COBASE Project Development Grant by NAS/NRC to travel to Hungary and work with Hungarian colleagues to study recent landscape change in the Kiskunsag grassland region. This research team includes ecologists, climatologists, remote sensing and GIS experts. Funding is being sought from NSF, NSERC, and NATO. (3) Other international linkages developed during LTER III include interactions with long-term ecological research programs in China (CERN; Briggs), and the development of a collaborative project on mycorrhizal ecology of Australian grasslands (Hartnett [KNZ] and D. Orr [Queensland).

Table 4. Participants in KPRNA public education programs and use of educational facilities during 1995.

Activity/Program	Number of Events	Number of Participants
Docent Training	15	210
Individual visitors (seminar speakers, university visitors, etc.)	23	78
Organized Groups (not associated with educational institutions)	24	435
Conference Groups	8	240
Elementary School Classes	23	1097
High School Classes	4	104
Kansas State University Classes	10	289
College/University Classes (non KSU)	10	178
Self-Guided Public Nature Trails		3346
TOTAL	117	5977

Table 5. Educational books/publications featuring Konza Prairie Research Natural Area.

Chadwick, D.H. 1995. What Good Is a Prairie? Audubon 97:36-46.

Knopf, F.L. and F.B. Samson. (In Press). Great Plains Vertebrates and Their Habitats. Springer-Verlag.

Ladd, D. and F. Oberle. 1995. Tallgrass Prairie Wildflowers. Falcon Press. Helena, MT. 262 pp.

Madson, J. and F. Oberle. 1993. Tallgrass Prairie. Falcon Press, Helena, MT. 112 pp.

Reichman, O.J. 1987. Konza Prairie: A Tallgrass Natural History. University Press of Kansas. Lawrence, KS. 226 pp.

Reichman, O.J. and S. Mulligan. 1995. Living Landscapes of Kansas. Falcon Press. Helena, MT. 157 pp.

Zimmerman, J. L. 1993. The Birds of Konza: The Avian Ecology of the Tallgrass Prairie. University Press of Kansas, Lawrence, KS. 186 pp.

8A. List of Collaborators

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Patrick J. Bohlen
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B. A. D. Hetrick
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N. Huntly
R. Hutson
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S. Johnson
Stephen R. Johnson
D. Karentz
K. H. Keeler
M. L. Kelrick
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10. Facilities and Equipment

In addition to the 3,487 ha field site, KPRNA includes several buildings in the headquarters area that are used for LTER research. The Konza Prairie Laboratory includes a 430 ft^2 analytical lab, equipped with a fume hood, DI water system, and standard laboratory equipment (balances, drying ovens, refrigerator, growth chamber, etc.). The building also houses a 430 ft^2 sample processing lab with bench space, large sinks and soil traps for processing plant, soil and rhizome/root samples, wood and metalworking shops, and a garage for storage of two fire trucks and miscellaneous equipment. In addition, we have ample on-site equipment storage facilities for individual investigators/projects. KPRNA maintains two general purpose vehicles on-site, as well as specialized equipment (tractors, fire trucks, etc.). Recently, KPRNA was awarded an NSF facilities improvement grant which is being used to renovate the original stone house and barn (built in 1912). The lower level of the house will be used as a visitors center (with exhibits and a teaching lab), the main floor will house computing facilities and offices and have a meeting room, while the upper floor will be used to accommodate visiting researchers and students. The headquarters area also includes the bison coral and handling facilities, which are essential for our grazing studies, and the main meteorological station, which is linked by phone line to the computer room at Bushnell Hall.

Additional laboratory facilities are located on the KSU campus, approximately 15 km from the Konza site. The majority of LTER laboratory space and analytical equipment are located in Bushnell Hall (Biology), including space and equipment for preparing plant, soil and water samples for analysis (drying ovens, grinders, shaker tables, block digestors, vacuum filtration systems). Bushnell Hall also houses an extensive collection of prairie plant specimens in the KSU Herbarium. Some specific equipment and facilities are located within other Departments (Agronomy, Plant Pathology, Geography), reflecting the multidisciplinary nature of our research. Some of the major analytical equipment available for LTER research includes: 2 Alpkem autoanalyzers (FlowSolution and RFA500) for liquid samples, a Carlo-Erba 1500 automated C/N analyzer for solid samples, a Shimadzu TOC 500 analyzer for dissolved C, a Hitachi UV2000 automated dual-beam spectrophotometer, a Europa stable isotope ratio mass spectrometer for ^{13}C and ^{15}N analyses (with optional trace gas module), several gas chromatographs with electron capture, flame ionization and thermal conductivity detectors, a Nikon compound microscope with epi-flouresence and video imaging capabilities, 1 LiCor 6400 and 3 LiCor 6200 Portable Photosynthetic Systems (1/4 and 1 L cuvettes), a LiCor 6200 system dedicated for soil CO_2 flux measurements, a LiCor 1600 null-balance porometer for stomatal conductance, and 3 pressure chambers (PMS model 1000) for measuring plant water status, 4 Tektronix cable testers (model 1502B) coupled to Campbell CR10 data loggers for TDR soil moisture measurements, a Troxler (model 3221) neutron probe gauge for soil moisture determinations, and a back-pack mounted minirhizotron (Bartz Technology Co. BTC-2) camera system. We also have access to a shared Hewlett Packard HPLC and GC/MS system for characterizing soluble organic compounds. Field-equipment associated with our new system-level C flux studies are detailed in Fig. 45. In addition, other "typical" laboratory equipment (balances, microscopes, etc.) is available in individual investigator laboratories.

Presently LTER has available three 1981 jeeps and four pickup trucks which range in model year from 1977-1994. Hence, funds are requested for replacement vehicles during LTER IV.

Most laboratories, and all PI offices, have personal computers, linked to a local area network, as well to the Sun workstations and KSU mainframe computers. Descriptions of computer hardware and software available to the Konza LTER program are provided below.

Computer Software and Hardware Equipment List: Konza Prairie LTER Program

Image Processing and GIS Laboratory:

1-SUN Sparcstation workstation (Climate) with two SuperSPARC processors and Supercache, GX 8-Bit accelerated 2-D/3-D color graphics workstation, 19" color monitor, 64 MB RAM, 12GB Hard disk; Running ARC/INFO 5.0 and 6.0, SAS 6, KHOROS

1-SUN 4/110 color workstation (Andro) with 32 Mb RAM, 900Mb disk, 8mm tape drive.

1-SUN IPC Color workstation (Bison) with 24 Mb RAM, 1.2 Gigabyte hard drive, 600 Mb optical drive, and CD-ROM Reader; Running Oracle

1-Postscript Laser Printer
1-Calcomp 8-pen plotter
1-Altek 32" X 24" hand digitizer
1-Ultra Comp 486/50, 16 Mb RAM, 1.2 Gigabyte hard disk, 660 Mb optical drive running ERDAS 7.5 with PC/ARC/INFO with 1024 X 1024 color imaging board, with video digitizer, ½" magnetic tape drive and color jet printer.

(Also have IDRISI, P-Map, MAP, GRASS).

PC-Network

Hardware:

Novell 3.1 on Pentium/100mhz with 32 Mb RAM and 4.4 Gigabyte hard disk.
HP Laser Jet IV Printer
HP 7475 Color plotter
Okidata 24-pin dot matrix printer
Film Recorder (works with Slide Write, Sigma Plot, AXUM, SAS/Graph, HPGL)
CD-ROM and Map Assist

Software:

Network—PC/SAS, PC ARC/INFO, Word Perfect 5.1 (6.0, both Windows and DOS) MS-WORD, Slide Write, Kedit.

Indvidual Copies -- (Sigma Plot, Word Star, Lotus, Freedom of Press, Alchemy, Frame Maker, Excel, Paradox, DBASE IV, Surfer, Basic, Pascal, C, Assemble, Fortran).

Special Software—CAPTURE, PELANAL, TRANSECT, HEP, RASKER, McPAAL, DECORANA, COMPAS, SPAN, ECOLOGICAL MEASURES

Spatial analysis software

(FORTRAN codes developed by G.M. Henebry and tested on PCs, workstations, and Crays.)

GLCMWIN calculates Grey Level Co-occurrence Matrix measures for grey-scale spatial lattice data at multiple scales.

IWREST calculates Intra-Window Range in grey-scale spatial lattice data.

LACUNAE and LACURAN calculate a lacunarity index in grey-scale spatial lattice data using exhaustive sampling and random resampling, respectively.

SOFEST estimates correlation lengths and areas in grey-scale spatial lattice data using scale of fluctuation methodology.