Konza Prairie LTERV: Long-Term Research on Grassland Dynamics and Global Change

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PROJECT SUMMARY

This proposal requests funding to continue and expand upon a comprehensive, long-term ecological research program in grassland ecology at Konza Prairie. The 20-year old, broadly-based Konza LTER program encompasses studies across multiple ecological levels and spatial and temporal scales. Since its inception, long-term studies and experiments at Konza Prairie have been linked by an overarching theme that integrates fire, grazing and climatic variability as essential and interactive factors responsible for the structure and function of tallgrass prairie. In contrast to 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, primarily water, light and N. The relative degree of limitation imposed by these key resources varies as a result of both extant and historical fire, grazing and climatic regimes. The interplay of these three disturbances across a heterogeneous landscape leads to the high species diversity and complex, non-linear behavior characteristic of mesic grassland ecosystems. As a result of this complexity, and because grazing and fire are essential elements of natural and managed ecosystems worldwide, results from the Konza Prairie LTER program have relevance not only for understanding grasslands, but for broader ecological issues including human-caused global change. This proposal explicitly builds upon these links with studies that will address consequences of multiple global change phenomena including changes in land-use and land cover, climate change and altered hydrologic regimes, nutrient enrichment, and biological invasions.

Goals for LTER V are: 1) to expand the strong core Konza LTER experiments on fire, grazing and climatic variability begun over 20 years ago, with site-based and intersite studies and synthesis activities; 2) to further develop our mechanistic and predictive understanding of grassland dynamics with particular emphasis on responses of grassland ecosystems to multiple global change factors; and 3) to use our LTER results to develop and test general ecological theory. To accomplish these goals, core long-term studies of land-use (fire and grazing) and responses to climatic variability (natural and manipulated) will be refined and enhanced. This aspect of the proposed research builds upon a long-term database on ecological patterns and processes derived from a fully replicated watershed-level experiment in place on Konza Prairie since 1977. This experimental design includes manipulations of fire frequency (annual fire to fire exclusion), fire season, and grazing (grazed by native or domestic ungulates vs. ungrazed). Studies of climatic controls of ecological processes will be expanded to include multiple climate change factors (changes in precipitation, hydrologic and temperature regimes) in terrestrial and aquatic ecosystems. New studies that address the causes and consequences of land-cover change in the region will be initiated, incorporating both sociological and ecological perspectives to enhance the regional and global relevance of this research. Short-term experiments focused on key processes and mechanisms underlying responses to changing fire, grazing and climatic regimes will continue to be essential components of the Konza LTER program. Other components of human-induced environmental change with particular relevance to these grasslands (nutrient enrichment, invasive species) are incorporated into new LTER V studies. Finally, Konza LTER data will be used to generate and test basic ecological theory in several areas (e.g., diversity-stability relationships, community invasibility, top-down vs. bottom-up controls, soil-plant community feedback models, river continuum model), facilitated by a research group charged with promoting integrative cross-site and synthesis activities.

The intellectual merit of this research will be an increased understanding of the key ecological processes underlying pattern and process in grassland ecosystems, and a predictive understanding of the responses of grasslands to global change. This research will also contribute to the advancement of general ecological theory through synthesis and integration of data from a series of unique long-term studies. The broader impacts of the research include training a future generation of ecologists, contributing to public education, and development of a knowledge base essential for the ecologically sound management of grassland ecosystems worldwide.

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The Konza Prairie LTER Program is a comprehensive, interdisciplinary research program designed to further our understanding of ecological processes in mesic grasslands, particularly tallgrass prairie, as well as contribute to conceptual and theoretical advances in ecology. The focal site for our core LTER research is the Konza Prairie Biological Station, a 3487-ha area of native tallgrass prairie in the Flint Hills of northeastern Kansas. Since its inception in 1981, the Konza LTER program has encompassed studies at, and across, multiple ecological levels and a variety of spatial and temporal scales. These studies have been linked by an overarching theme that considers fire, grazing and climatic variability as essential and interactive factors shaping the structure and function of mesic grassland ecosystems. Research during LTER IV focused on ecological responses to fire, grazing, and the natural climatic variability characteristic of this system, and began to assess the consequences of changes in land-use and climate for these grasslands. To accomplish these goals, we (1) continued the long-term, watershed-level experiments on the role of fire and large herbivores (Bos bison) that form the core of the Konza Prairie LTER experimental design, (2) continued several long-term, plot-level experiments (e.g., the Belowground Plot experiment, Irrigation Transect study), (3) initiated new long-term experiments (e.g., the Fire Treatment Reversal experiment, the Rainfall Manipulation Plot [RaMP] experiment), and (4) broadened our research program with the addition of new investigators and new areas of research emphasis.

From January 1996 (submission of the LTER IV proposal) to January 2002, the Konza Prairie LTER Program produced over 285 publications (see Fig. 1 and Supplementary Documentation) including 177 refereed journal articles, 1 book, 40 book chapters, 49 dissertations and theses, and 19 miscellaneous publications (proceedings, technical reports). During LTER IV, the number of Konza publications in impact journals increased (Fig. 1), as did the mean number of authors per publication, reflecting extensive integration within the program and the interdisciplinary nature of much of our research. LTER funding forms the core of our program, and supports a “research platform” from which we leverage additional extramural funding for shorter-term, mechanistic studies that are integral to achieving our long-term goals. Indeed, our success at securing additional funding from a variety of sources continued to grow (Fig. 2), further broadening our research base. Currently, over $3.7M in active awards (in addition to LTER funding) contributes to ecological research at Konza (see Supplemental Documentation). Finally, we have been successful in attracting new investigators, resulting in additional diversification of our research and publications (Fig. 2). While space constraints prevent a complete listing of research advances in all areas, selected research and publications from LTER IV are highlighted in the following paragraphs.
Ecological Effects of Fire. Fire plays an essential role in the ecology of mesic grasslands worldwide, and the influence of fire regimes on plant and soil processes has been a major focus of the Konza LTER program. We continued our watershed-level treatments of 1-, 2-, 4-, 10- and 20-year fire return intervals, and added experiments to determine the effects of seasonal timing of fires (spring, summer, autumn and winter). We have amassed >25 years of data on patterns of aboveground net primary productivity (ANPP) in annually burned and infrequently burned sites (Fig. 3), and have published several syntheses of these data (Briggs & Knapp 2001, Knapp et al. 1998a,b). These long-term experiments provide unrivaled data on plant and soil responses to burning, and fire exclusion, in mesic grassland ecosystems. Given the high degree of variability inherent in these grasslands, this long-term perspective has been essential for furthering our understanding of the effects of fire on plant community structure and ANPP (Knapp et al. 1998b). Briefly, ANPP is usually stimulated by fire in these grasslands, though this is modulated by water availability and topography (Knapp et al. 1998a). The increase in total ANPP is driven by productivity of a few dominant C4 grasses, while the productivity and diversity of C3 grasses and forbs generally declines under frequent fire regimes (Fig. 3; Collins et al. 1998, Briggs & Knapp 2001). Our long-term studies
of fire clearly demonstrated that the richness and abundance of forbs (critical for plant biodiversity) are reduced by frequent burning (Briggs & Knapp 1995, Knapp et al. 1998b). However, Briggs & Knapp (2001) found that, over 14 years, annual burning did not affect the daily growth rate of forbs, relative to growth rates on a long-term unburned site. This was in contrast to the dominant grasses, which did exhibit a significantly higher daily growth rate on the annually burned site. This suggests that the reduction in forb richness and abundance in response to fire may be more direct (e.g., fire-induced mortality) or that other factors (e.g., recruitment limitation) may play a bigger role in

We continued to assess plant (Collins & Steinauer 1998, Towne & Knapp 1996) and animal (Callaham & Blair 1999, Cavitt 2000, Kaufman et al. 1998, Todd 1996) population and community responses to different fire regimes. An intriguing result emerging from a synthesis of community data was that the plant communities at Konza are undergoing directional trajectories of compositional change that are greatest in annually burned sites and least in unburned sites (Collins 2000). Conversely, animal communities exhibited high inter-annual variability, but showed little or no directional change under any fire regime. This is consistent with previous findings that habitat structure, rather than plant community composition, is key to understanding the dynamics of grassland vertebrate consumers (Zimmerman 1997, Kaufman et al. 1998).

Studies during LTER IV provided new insights into how fire affects soil C and N pools and fluxes. Repeated fires lead to (1) reduced concentrations of inorganic soil N (Turner et al. 1997), (2) lower rates of in situ net N mineralization and nitrification (Blair 1997, Johnson & Matchett 2001), and (3) increased N limitation to plants (Blair et al. 1998). Indeed, plants growing in annually burned prairie exhibit characteristics associated with N limitation (Turner et al. 1997, Blair et al. 1998, Johnson & Matchett 2001). The transient dynamics of soil N resulting from infrequent fires were documented (Fig. 4; Blair 1997), and provided a mechanistic explanation for the “pulse” in ANPP observed when a fire event follows a long period of fire exclusion. The accumulation of available N and increases in foliar N concentration in the absence of fire (Johnson & Matchett 2001) is being investigated with
respect to preferential grazing by bison of newly burned watersheds with long fire-return intervals (>3 yrs). Spring burning increased soil CO₂ flux (Fig. 4). Knapp et al. (1998c) found significantly greater annual soil CO₂ efflux in burned relative to unburned prairie, and showed that increased soil CO₂ efflux could not be explained simply by post-fire changes in soil microclimate. Fire was also shown to alter enzyme activity and microbial biomass in tallgrass prairie soils (Ajwa et al. 1999), as well as the composition of mycorrhizal assemblages (Eom et al. 1999).

The Role of Grazers in Mesic Grasslands. Konza studies showed that bison grazing can influence plant community structure in mesic grasslands (Hartnett et al. 1996), and a recent Science article by Collins et al. (1998) highlighted the role of grazers in modulating plant species diversity in tallgrass prairie. Historically, bison were abundant grazers in these grasslands. They were reintroduced to Konza in 1987 and studies on the effects of bison grazing, and the interaction of fire and grazers, increased substantially during LTER IV. Frequent fires in the absence of grazing lowers plant species richness, but grazing by bison offset the loss of species in frequently burned prairie (Fig. 5; Collins et al. 1998). Long-term plot studies at Konza Prairie showed that aboveground biomass removal by mowing had effects similar to grazing (Fig. 5), suggesting that alleviation of competition for aboveground resources is an important consequence of grazing in mesic grasslands.

LTER IV studies by Johnson and Matchett (2001) documented ecosystem-level responses to bison grazing (Fig. 6), including increased net N mineralization, decreased fine root productivity, and decreased soil CO₂ flux. Bremer et al. (1998) also found lower soil CO₂ flux in grazed prairie and, based on rapid reductions in CO₂ flux after mowing, concluded that reduced canopy photosynthesis and translocation of fixed C to the rhizosphere are important components of this response. Steinauer and Collins (2001) showed how increased nutrient availability due to bison urine deposition (a fine-scale event) could trigger preferential grazing which produces broad-scale patch structure in grasslands. Other recent studies focused on sexual segregation in bison diets (Post et al. 2001), bison wallowing behavior (McMillan et al. 2000), plant community responses to bison vs. cattle grazing (Hartnett et al. 1996), effects of bison grazing on demography of prairie forbs (Damhoureyeh & Hartnett 1997) and cover of woody plant species (Briggs et al. in press), effects of bison on stream macroinvertebrates (Fritz et al. 1999), responses of small mammal populations to bison activities (Matlack et al. 2001), and the role of bison carcasses in generating soil resource heterogeneity.

![Net N mineralization and Soil CO₂ flux](image-url)
In total, these studies suggest that both grazing and non-grazing activities (e.g., wallowing, urine deposition) of bison are important in structuring grassland communities (‘top down’ synthesis of LTER IV results (Knapp et al. 1999) makes a

Fig. 5. Konza LTER studies demonstrated that aboveground biomass removal by grazers can modulate plant community responses to fire and nutrient enrichment in tallgrass prairie. **Left**: In ungrazed prairie, cover of dominant C4 grasses increased with increasing fire frequency, while the cover of forbs decreased, resulting in a loss of diversity (Collins et al. 1998). However, in prairie grazed by bison, the cover of forbs was positively correlated with fire frequency and the cover of grasses was unaffected, resulting in high diversity in spite of frequent fires. **Right**: Similar results were obtained after 8 years in a small-plot experiment where annual burning + fertilization resulted in a marked loss of species richness, while aboveground biomass removal by mowing offset this loss (data from Collins et al. 1998).

Fig. 6. Bison grazing increased rates of net N mineralization (**left**) and net nitrification (**not shown**) in annually burned grasslands, but decreased net root productivity in heavily grazed areas (**right**) as indexed by root ingrowth bag measurements (Johnson & Matchett 2001). Other belowground consequences of bison grazing documented during LTER IV included increased root N content and reduced C:N ratio (Johnson and Matchett 2001), and decreased soil CO2 flux (Knapp et al. 1998c).
Woody Vegetation Expansion into Grasslands. Forest encroachment and the expansion of woody plants into grasslands is a worldwide phenomenon, and an important land-cover change in the grasslands of North America (Archer et al. 2001, Briggs et al. in press). Increases in woody plant cover can be directly attributed to alterations in land management and may be indirectly facilitated by other factors (e.g., altered climate, N deposition, habitat fragmentation). In addition to documenting ongoing changes in woody plant cover associated with long-term fire and grazing treatments on Konza (Fig. 7; Knight et al. 1994, Briggs et al. 1998, Briggs et al. in press), we have begun assessing the causes and consequences of ecosystem conversion from C4 grass to C3 woody plant dominance by initiating studies on (1) the landscape-scale pattern of conversion (Briggs et al. in press), (2) the factors underlying increased woody plant cover, and (3) the ecological consequences of converting this ecosystem from dominance by one growth form to another (McCarron & Knapp 2001). Using Konza LTER data, we initiated studies on the ecological consequences of eastern redbud (Juniperus virginiana) expansion in the grasslands surrounding Konza. The increase in redbud cover was positively correlated to regional increases in human population density (Hoch & Briggs 1999), and changes in land management, especially fire and grazing (Hoch et al. in review). The conversion of grassland to redbud woodland resulted in relatively rapid changes losses of species diversity, increases in NPP, and increases in C and N storage (Norris et al. 2001a,b, Smith & Johnson in review). These changes have the potential to alter C storage and other biogeochemical processes over much of the Midwest.

Terrestrial Ecosystem Responses to Climatic Variability and Climate Change. Climatic variability is a critical factor affecting grassland ecosystems. A recent cross-site synthesis of climate and ANPP data from 11 LTER sites demonstrated that grasslands are among the most responsive of biomes to interannual variability in precipitation (Knapp and Smith 2001). To address the impact of chronic water deficits, we continued a long-term irrigation experiment in which sufficient water is added to replicate transects in annually burned tallgrass prairie to eliminate plant water deficits during the growing season. Results to date indicate that water availability limits ANPP in most (7 of 9) years, and plays an important role in maintaining C4 grass dominance (Knapp et al. 2001). This project was recently expanded to include a nitrogen addition treatment to evaluate potential interactions between precipitation and N limitations (i.e., Hooper and Johnson 1999). A second project, initiated during
LTER IV, utilized field-scale Rainfall Manipulation Plots (RaMPs) in which the timing and amounts of rainfall events can be manipulated, independently and in tandem. This study, established with funding by USDA and DOE, allows us to evaluate the effects of predicted increases in climatic variability by assessing responses in key plant ecophysiological traits, plant community composition, and ecosystem-level processes (Fay et al. 2000, Fay et al. in press).

**Invasive Species Studies.** Worldwide, invasions of ecosystems by exotic species are a critical ecological and economic concern. Smith and Knapp (1999, 2001) used a 15-yr Konza LTER dataset on plant species composition to assess the role of disturbance (fire and grazing) and community structure in determining invasibility by exotic plants in this grassland. They found that frequent fire, which increased the dominance of C₄ grasses and lowered native plant species richness and diversity, also decreased the abundance of exotic species. Grazing, which enhanced native plant species diversity, also increased the abundance of exotic species. Consequently, communities more diverse in native species also had more exotic species (Fig. 8). Their results also suggested that plant community structure was a determinant of invasibility, independent of disturbance regime. Another LTER study of species invasions utilized a long-term study of fire, mowing and nutrient additions to assess the effects of land management on the relative abundance of native and exotic earthworms. European earthworm species have replaced native North American taxa over much of the continent, and differences in the biology of these taxa may alter soil processes (Callaham et al. 2001). Callaham and Blair (1999) found that management practices that increased litter accumulation and soil nutrient status also increased the relative success of exotic earthworm taxa in tallgrass prairie. Kimberly With, a new Konza LTER investigator, participated in a recent synthesis of the population biology of invasive species (Sakai et al. 2001), and is developing a theoretical framework for the ecology of invasive species spread in landscapes (With in press, With in review).

**Fig. 8.** Richness of exotic plant species was negatively correlated with both total (A) and grass (B) ANPP in ungrazed watersheds, across burning treatments (Smith and Knapp 1999). Richness of exotic species was positively correlated with richness of native plant species across burning treatments in both ungrazed (C) and grazed (D) watersheds (Smith and Knapp 1999). These results indicate that similar factors affect richness of both native and exotic species in tallgrass prairie, and support the general hypothesis that species-rich communities are more invasible than species-poor communities.
Plant-Mycorrhizal Symbioses. Symbiotic associations between plants and arbuscular mycorrhizal (AM) fungi are ubiquitous in grasslands and have important effects on plant demography, competition, community structure and ecosystem processes. Multiple LTER IV studies documented important linkages between above- and below-ground communities, and mycorrhizal-mediated responses to fire and grazing in mesic grasslands (Wilson and Hartnett 1997, 1998, Hartnett and Wilson 1999, Eom et al. 1999, 2001). Eom et al. (2000) provided new data suggesting that AM fungi have some degree of host-specificity. The influence of host plant species composition on AM fungal species composition provides support for current feedback models predicting strong regulatory effects of soil communities on plant community structure. A 5-yr experiment on Konza Prairie showed that this symbiosis plays a key role in regulating patterns of dominance and diversity in grassland plant communities (Hartnett and Wilson 1999), and may play a crucial role in post-fire enhancement of ANPP and in offsetting biomass losses to grazers by enhancing compensatory plant growth.

Hydrology and Biogeochemistry of Groundwater and Streams. Grassland streams and groundwater are valuable integrators of terrestrial processes within our experimental watersheds. In LTER IV we expanded the sampling of groundwater wells and continued to study stream discharge and water chemistry in 4 prairie watersheds and several sites along Kings Creek that are subject to anthropogenic impacts. Using 10 yrs of data on Ca, NO₃, and water level, we showed that more dissolved material leaves the watershed during times of high water flow (despite lower concentrations) than low water flow (concentrated chemistry). Strontium isotope ratios indicate that dissolved CaCO₃ is derived mostly from soil rather than Permian bedrock, and likely originates from dry deposition (Wood 2001). Because the greatest factor influencing N export in prairie streams is discharge (Dodds et al. 1998), which is driven by precipitation, these ecosystems will be sensitive to predicted climate changes.

The introduction of bison increased N export by about 30%, but against a 2-3 order of magnitude variation in annual discharge, the effect on annual nutrient export has thus far been minimal (Kemp and Dodds 2001). The strongest biogeochemical effect on groundwater and stream chemistry across the Konza Prairie landscape has been the influence of agricultural cropping in lowland areas (Dodds et al. 1998, Maepherson 1998). Konza scientists provided the first detailed measurements of N flux and transport in a prairie stream (Fig. 9; Dodds et al. 2000), and participated in a cross-site study of N transformations in headwater streams from different biomes (Peterson et al. 2001). In-channel processes retained a substantial amount of N (Kemp & Dodds 2001), but that retention capacity is easily overcome by N influx from fertilized croplands (Kemp and Dodds, in press). Studies of Konza streams have provided a baseline for studies of water quality in other Kansas surface waters.

Ecological Studies within Prairie Streams. LTER IV studies in these historically understudied stream systems focused on the ecology of stream invertebrates (Fritz & Dodds in press, Stagliano & Whiles in press) and fish (Evans-White et al. in press). We found that two omnivorous species (crayfish and stoneroller minnows) were key consumers of N. Other studies provided new data on stream metabolic O₂ dynamics (Mulholland et al. 2001) and the first quantitative food webs and estimates of 2ª productivity for a tallgrass prairie stream macroinvertebrate community. Macroinvertebrate production was high compared to similar-sized streams in other regions of North America (Stagliano and Whiles in press). Most functional groups were well represented (Fig. 10; Dodds et al. 2000), although new evidence suggests that detritivores are food-limited in prairie streams (Stagliano & Whiles in press).
Fig. 9. N fluxes in an upland prairie reach of Kings Creek (Dodds et al. 2000). Size of the arrows corresponds to magnitude of the flux. All fluxes are expressed in mg N m\(^{-2}\) d\(^{-1}\). N uptake by the biota was primarily from the NH\(_4\) pool, while transport of DON was a major flux of N through the system.

Fig. 10. Functional structure of macroinvertebrate assemblages, based on production estimates, from similar-sized streams in different regions of North America and predictions for mid-order streams based on the River Continuum Concept (RCC) model of Vannote et al. (1980). Locations are: Coweeta = southern Appalachian Mountains (forest) (Whiles & Wallace 1995), Kings Creek = Konza Prairie Biological Station (tallgrass prairie) (Stagliano & Whiles in press), and Sycamore Creek = Sonoran Desert (Fisher & Gray 1983).
Synthesis, Cross-Site and LTER Network-Level Activities. The Konza LTER program has matured to the point where syntheses of long-term datasets and results from new analyses in the context of core LTER studies have provided key insights into our understanding of this biome, and of basic underpinnings of ecological patterns and processes in general. Several major synthetic works were produced during LTER IV including the publication of “Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie” (Knapp et al. 1998a), the first book in the Oxford University Press LTER Site Synthesis series. Examples of other synthesis activities during LTER IV (several were already mentioned) included a multi-authored BioScience article on the keystone role of bison in tallgrass prairie (Knapp et al. 1998b), new analyses that provided insight into differential responses to disturbance across trophic levels (Collins 2000), and a synthesis of combined data from long-term plot and watershed-level experiments to determine the relative effects of recruitment limitation and community structure on the invasion success of exotic species (Smith & Knapp 2001).

Konza scientists demonstrated a substantial commitment to cross-site research and synthesis activities, as well. Knapp and Smith (2001) led a cross-site analysis of how temporal patterns of ANPP are influenced by interannual variability in precipitation. This network-wide synthesis, published in Science, included data from 11 LTER sites. Konza scientists (Briggs and Collins) participated in the 2nd East-Asia Pacific Regional Conference on Long-Term Ecological Research in Tsukuba, Japan, and initiated an international cross-site comparison of the effects of fire and grazing on resource availability and heterogeneity in North American (Konza Prairie) and South African (Kruger National Park) grasslands (Knapp, Blair, Hartnett, Briggs, Johnson). Konza Prairie participated in the cross-site LIDET decomposition study (Gholz et al. 2000), and is the primary US site for Collaborative research: Identifying ecosystem controls on biodiversity: A US/UK project (D. Wall, PI). Dodds was a co-investigator on the recent LINX cross-site stream study (Peterson et al. 2001, Mulholland et al. 2001), and currently serves as co-investigator for a new IRCEB intersite stream study (LINX II). The Konza site has been, and continues to be, involved in numerous other cross-site studies, including research on ecological stoichiometry of North American grasshoppers (Joern, PI), nutrient enrichment and mycorrhizae (N.C. Johnson, PI), use of synthetic aperture radar for remotely-sensing ecosystem processes (G. Henebry, PI), earthworm ecology (P.F. Hendrix, PI), stream bacterial community structure (L. Leff, PI), grazing ecology (M. Ritchie, PI), and effects of added N on soil C turnover (Townsend, PI), with Konza scientists collaborating in most of these projects. Contributions to LTER Network activities include service on the LTER Executive Committee (Briggs 1997-98, Knapp 2001-present). Doug Goodin leads the LTER Climate Committee, and is co-editor of a forthcoming LTER book on Climate Variability and Ecosystem Response at Long-Term Ecological Research Sites. Konza LTER scientists also contributed to the recent Oxford Press LTER book on Standard Soil Methods for Long-Term Ecological Research (Blair), and recent LTER workshops on NPP (Knapp) and invasive species (Knapp and Smith).

In summary, the results presented above highlight some of the contributions of the Konza LTER program during LTER IV, and illustrate the breadth of ecological studies comprising our program. These results clearly relate to our overall goal of understanding how fire, grazing and climate variation interact to shape the structure and function of mesic grasslands, and have contributed to the advancement of general ecological knowledge in many areas. During LTER V, we will continue existing core long-term experiments and measurements, and initiate a series of new, integrated experiments to further our understanding of pattern and process in mesic grasslands.
C2. Project Description

A. Introduction and Background. The Konza Prairie LTER Program is a comprehensive, interdisciplinary program addressing long-term research questions relevant to grasslands, and to ecology in general. Since its inception in 1981, the Konza LTER program has encompassed studies across multiple ecological levels (organismic, population, community and ecosystem) and spatial (plot-level, watersheds, regional landscapes) and temporal (days to decades) scales. The unifying conceptual framework guiding this research has been that fire, grazing and climatic variability are essential and interactive factors responsible for the origin, evolution, persistence and function of tallgrass prairie, and other mesic grasslands (Fig. 11). The interplay of these “natural disturbances” across a heterogeneous landscape leads to the high species diversity and complex, non-linear behavior characteristic of these grassland ecosystems (e.g., Seastedt & Knapp 1993, Knapp & Smith 2001, Steinauer & Collins 2001). Because grazing and fire regimes are managed in grasslands worldwide, Konza LTER data are relevant not only for understanding this and other grasslands, but also for addressing broader ecological issues such as productivity-diversity relationships (Waide et al. 1999, Gough et al. 2000, Gross et al. 2000), disturbance and community stability (Collins & Steinauer 1998, Collins 2000, Collins et al. 2001), ‘top down’ vs. ‘bottom up’ controls of ecological processes (Knapp et al. 1998b, 1999, Johnson & Matchett 2001), and the interplay of mutualistic and antagonistic biotic interactions (Hartnett et al. 1993, Smith et al. 1999). We are also poised to use Konza LTER studies and data to address critical issues related to global change, including the ecology of invasions (Smith & Knapp 2001, Grace et al. in press), land-use and land-cover change (Hoch & Briggs 1999, Norris et al. 2001 a,b), human activities and water quality (Dodds et al. 1998, Kemp & Dodds 2001), and ecosystem responses to climate change (Fay et al. 2000, Clark et al. 2001).

History and Growth of the Konza Prairie LTER Program. Konza was one of 6 original LTER sites, and pre-LTER research extends selected datasets back >26 years. Our LTER goals have been refined and expanded over time, but the roles of fire, grazing and climatic variability has remained a central theme. We have built on long-term studies and datasets in each of the 5 original LTER “core areas” (Callahan 1984). Our LTER datasets are essential for assessing long-term changes in the physical, chemical, and biological properties of these grasslands, and their value increases with the length of record (Knapp et al. 1998b). A long-term perspective is essential in these grasslands, given the high interannual variation in abiotic drivers and ecological responses (Knapp et al. 1998a) and apparent directional changes underway in key attributes, such as species composition (Collins 2000, Silletti & Knapp 2001), woody plant cover (Briggs et al. in press), and stream chemistry (Kemp & Dodds 2001).

LTER I (1981-1986) focused on comparative studies of biotic responses to fire and climatic variability. Fire treatments, long-term research sites and sampling protocols were established with emphasis on the extremes of fire frequency and topography. During LTER II (1986-1990), Konza research expanded to encompass a range of fire frequencies and additional ecosystem responses. In conjunction with the collaborative NASA FIFE (First ISLSCP Field Experiment) program (1987-1989), LTER researchers began addressing more complex questions of scale and the use of remotely-sensed data to explore broad-scale issues. LTER III (1991-1996) included more intensive studies of ungulate grazers, and an expanded spatial perspective. The primary focus was on how grazing influences biotic and ecosystem processes and patterns imposed by fire frequency over the Konza landscape mosaic, all of which are subjected to a variable climate. Research foci during LTER IV (1996-2002) included fire-grazer interactions, history and seasonal timing of fires, net ecosystem carbon exchange, restoration ecology and land use/land cover change. In total, the studies in LTER I-IV have encompassed the major abiotic (climate, fire, topoedaphic gradients, hydrology) and biotic (herbivory, competition, mycorrhizal symbiosis) factors influencing this grassland, and led to a non-equilibrium perspective on ecological patterns and processes (Knapp et al. 1998a).
Fig. 11. Conceptual model highlighting the importance of fire, climatic variability and grazing across topographic gradients at Konza Prairie (Knapp et al. 1998a). These three factors influence organismic through ecosystem processes independently and interactively, with responses also dependent on topoedaphic patterns of resource availability. All of the proposed responses shown in boxes are currently being evaluated through long-term watershed-scale and small-scale plot experiments as part of the Konza Prairie LTER program.
The goals of the Konza LTER program are three-fold as we move into LTER V (2002-2008):

1. to continue and expand the strong core LTER experiments on fire, grazing and climatic variability begun over 20 years ago, with the goal of improving our understanding of the major abiotic and biotic factors determining grassland structure and function;

2. to further develop a mechanistic and predictive understanding of grassland dynamics and responses to multiple global change phenomena, using ongoing and new long-term experiments and datasets, coupled with shorter-term supporting studies;

3. to expand our synthesis activities based on LTER results, and use these syntheses to develop and test current ecological theory.

Our experiments incorporate these goals and explicitly consider the major drivers of ecological dynamics in these grasslands, and their interactions with global change phenomena at local and regional scales (Kareiva et al. 1993, Hall et al. 1996, Lubchenco 1998, Chapin et al. 2001). We define global change broadly as human-induced alterations in climate, land-use, hydrologic and biogeochemical cycles, and species introductions. Of these, land-use change has been singled out as the most substantial human alteration of the Earth system, which interacts strongly with all other components of global change (Vitousek et al. 1997). Understanding the mechanisms of response to these changes at the local and regional scales will allow us to generalize our results to other grasslands around the world. In this proposal, we focus on aspects of global change most relevant to grasslands: changes in land use (especially fire and grazing regimes) and land cover (increases in woody cover); climate change; altered nutrient cycles (enhanced N deposition); and biological invasions. We propose to: 1) continue core long-term experiments focused on land-use (fire and grazing) and climatic variability (natural and manipulated); 2) expand climate change studies initiated during LTER IV (precipitation and temperature regimes); 3) initiate new experiments on the consequences of altered hydrologic regimes for stream ecosystems, 4) initiate and continue long-term studies of nutrient enrichment and interactions with land-use practices; 5) conduct new experiments on invasibility in grasslands, and 6) assess the causes and consequences of land-cover change, incorporating sociological and ecological perspectives. We also propose new LTER studies aimed at understanding the mechanisms driving the trajectories and rates of biotic responses to environmental change. Throughout LTER V, we will continue to apply LTER data to the generation and testing of ecological theory, and formal integration and synthesis activities will be elevated to “core area” status with the formation of a “Synthesis/Cross-Site Studies” research group.

B. Conceptual Framework — Grasslands and Global Change. As LTER research at Konza Prairie continues to expand, linking our studies via an overarching theme of global change is a logical next step (Fig. 12). Arguably, grasslands are among the biomes most sensitive to an array of global change phenomenon (Samson & Knopf 1994, Field et al. 2000, Buckland et al. 2001, Reich et al. 2001b), and there is little doubt that responses of grasslands to global change have local, regional and global significance. Temperate grasslands are the potential vegetation of ~36% of the Earth’s surface (Sala 2001), and one of the largest vegetative provinces in North America (Samson & Knopf 1994). In central North America, grassland ecoregions encompass >3M km² (Lauenroth et al. 1999), with tallgrass prairie occupying the most mesic and productive areas (Fig. 13). The productivity and deep, fertile soils of these grasslands resulted in extensive conversion to agriculture (Samson & Knopf 1994). However, expansive areas of native prairie (> 2 M ha) still remain in the western portion of its original range, including the 50,000-km² Flint Hills region, where steep slopes and rocky soils (Fig. 14) prevented extensive plowing. These grasslands lie in an ecotone between more mesic forests and more arid grasslands, and are influenced by large-scale gradients in temperature and precipitation (Fig 15). As a result, these grasslands may show the first signs of climatic- or other human-induced environmental changes, or be especially sensitive to such changes (Knapp & Smith 2001). The occurrence of tallgrass prairie in this ‘tension zone’ also may increase rates of directional change in land cover, such as the increased cover of woody plants already occurring (Knight et al. 1994, Briggs et al. in press).
Fig. 12. Conceptual framework for LTER V. The regionally important components of global change that our LTER V research will address include: changing land-use practices, climate change, nutrient enrichment and biological invasions. The independent and interactive consequences of these changes on tallgrass prairie structure and function will be evaluated, as will the consequences of altered hydrologic regimes, land-cover change and altered biogeochemical cycles and C source/sink relationships. Many feedbacks exist between consequences and drivers of environmental changes, but these are omitted here for simplicity.

Fig. 13. Historic distribution of prairie (light shading) and steppe (dark shading) in North America. The Flint Hills region includes the largest remaining areas of intact, native tallgrass prairie. Konza Prairie Biological Station (star) is located in the northern portion of the Flint Hills in northeastern Kansas.
Tallgrass prairies are complex and dynamic ecosystems, offering unique opportunities for ecological study in the context of human-driven environmental change. In contrast to ecosystems where ecological processes are constrained by chronic limitations of a single resource (e.g., water in arid sites or N in more mesic biomes), patterns and processes in mesic grasslands (e.g., tallgrass prairie) are products of spatial and temporal variability in multiple limiting resources (water, light, N) (Seastedt & Knapp 1993, Knapp et al. 1998b). The relative limitation of these resources varies in space and time as a function of fire, grazing and climatic regimes, as well as site history and position in the landscape (Turner et al. 1997, Blair 1997, Briggs et al. 1998). Thus, many ecological patterns and processes in mesic grasslands are best considered from a non-equilibrium perspective, where frequent shifts in the relative importance of key multiple resources are crucial for maintaining both diversity and productivity (Seastedt & Knapp 1993, Blair 1997). We contend that these dynamics are expressed maximally in tallgrass prairie on temporal and spatial scales amenable to ecological study, affecting organismic through ecosystem responses, as well as landscape patterns. As a result, we expect shifts in relative resource supply and limitations associated with global change to result in significant and tractable responses in these grasslands, with broader ecological implications for other ecosystems that are also defined by non-equilibrium conditions and multiple limiting factors.

Worldwide, grasslands occur where three critical ecosystem characteristics are present: (1) high intra- and inter-annual precipitation variability, (2) presence of large herbivores capable of removing a substantial amount of plant biomass, and (3) recurrent fires, particularly in more mesic grasslands. Long-term research at Konza has established the importance of each of these inherent characteristics and their interactions for determining the structure (physiognomy, life-form dominance, species composition, biodiversity) and function (productivity, nutrient cycling, organic matter storage) of grasslands (Knapp et al. 1998a). However, human activities are directly (management of grazing and fire) and indirectly (changes in atmospheric chemistry and climate) altering these key drivers. Thus, the long-term research program initiated 20 years ago to understand the effects of “natural” disturbances in this grassland, now has additional and immediate relevance for understanding...
and predicting the consequences of global change taking place in the grasslands of North America, and around the world. Examples of key questions we are poised to address include:

1. Are directional changes occurring at the population, community, ecosystem, or landscape scale? What are the trajectories and rates of change? What are the consequences for important ecological and ecosystem services? As the Konza LTER program matures, our long-term datasets (most spanning > 20 yrs) become increasingly valuable as baselines against which to detect and assess consequences of natural and human-induced environmental changes (Knapp et al. 1998b, Silletti & Knapp 2001, Kemp & Dodds 2001, Briggs et al. in press).

2. What are the key natural and anthropogenic drivers of ecological change in tallgrass prairie, and how do they interact? What are the mechanisms underlying observed directional changes? Given the responsiveness of tallgrass prairie to climatic variability and the timing and frequency of natural disturbances (e.g., fire and grazing), we expect these grasslands to have be responsive to, and interact with, altered precipitation regimes, elevated N deposition, and changes in land management. We will explore these and other global change issues with new and ongoing long-term experiments, combined with short-term mechanistic and modeling studies.

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

Konza Prairie Biological Station (KPBS) is a C₄-dominated grassland with a continental climate characterized by warm, wet summers and dry, cold winters (Fig. 16). Mean annual precipitation (835 mm) is sufficient to support woodland or savanna vegetation; consequently, drought, fire and grazing are important in maintaining this grassland (Axelrod 1985, Anderson 1990). The site is topographically complex (320 to 444 m asl), and soil type and depth varying with topographic position. In general, lowland soils are silty clay loams formed from thick colluvial and alluvial deposits and may extend to 2 m. Hillside and upland soils are similar, but much shallower (Ransom et al. 1998). These soils overlay as many as 10 distinct layers of alternating limestone and shale, contributing to the complex subsurface hydrology of the region (Macpherson 1996, Oviatt 1998).

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Fig. 15. Left: Konza lies at the ecotone between deciduous forest and more arid grasslands. Two important gradients influencing grasslands in this region: a north-south temperature gradient, which is correlated with C₃-C₄ plant species composition (Teeri and Stowe 1976), and a west-east precipitation gradient that affects regional patterns of ANPP (Sala et al. 1988, Epstein et al. 2002), N availability (Burke et al. 1997) and soil C storage (Parton et al. 1987). The location of Konza makes this grassland sensitive to a number of important global changes.

Fig. 16. Lower left: Long-term record of climatic variability at Manhattan, KS (vertical line indicates start of LTER studies). Lower right: Mean monthly air temperature and precipitation at Konza.
The vegetation is primarily (>90%) native tallgrass prairie, dominated by perennial C4 grasses, such as Andropogon gerardii, Sorghastrum nutans, Panicum virgatum and A. scoparius. Numerous sub-dominant grasses, forbs and woody species contribute to its high floristic diversity. The KPBS biota includes >600 plant, 40 mammal, >200 bird, 34 reptile and amphibian, 20 fish, and >700 identified invertebrate species (www.konza.ksu.edu/data_catalog/toc.html). Kings Creek, a USGS Benchmark Stream, originates on and traverses 10 km across KPBS. Gallery forests dominated by Quercus spp. and Celtis occidentalis occur along major stream courses. Several agricultural fields and restored prairies occur near headquarters. Overall, the site has most features representative of the pre-settlement tallgrass prairie, with fire and large native herbivores incorporated as a shifting mosaic. Thus, Konza serves as a benchmark for detecting and exploring the causes and consequences of environmental change taking place throughout the grasslands of the eastern Central Plains, with results relevant to mesic grasslands worldwide.

The Konza LTER program continues to build upon a long-term database on ecological patterns and processes derived from a fully replicated watershed-level experimental design, in place since 1977 (Fig. 17). This design includes replicate watersheds subject to different fire and grazing treatments, as well as a number of long-term plot-level experiments (Table 1). The effects of climate are addressed by long-term studies encompassing the natural climatic variability, and possible directional changes, characteristic of this region, as well as manipulations of water availability in field experiments. Within core LTER watersheds, permanent sampling transects are replicated at various topographic positions (n=4/topo. position/watershed), where ANPP, plant species composition, plant and consumer populations, soil properties, and key above- and belowground processes are measured. The collection of diverse data from common sampling locations facilitates integration among our research groups. In total, the Konza LTER Program incorporates explicit study of the major factors influencing mesic grasslands in a long-term experimental setting. It has the essential components of a statistically rigorous ecological research program designed to elucidate patterns and processes inherently important in grasslands, and address the potential impacts of global change in these ecosystems. Below we elaborate on our rationale for focusing on fire, grazing and climate, and describe our core LTER experiments and the impacts of humans on these important system drivers.

Table 1. Brief description of selected long-term, plot-level experiments of the Konza LTER program. Such experiments complement our long-term watershed-scale studies, and provide important information about mechanisms underlying responses at broader scales. These experiments also act as focal points for ecological studies that span multiple disciplines.

<table>
<thead>
<tr>
<th>Experiment and Year Initiated</th>
<th>Treatments</th>
<th>Main Response Variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>Belowground Plot Experiment (1986)</td>
<td>Burning, mowing and nutrient (N, P) additions; 5×5m plots</td>
<td>ANPP, BNPP, plant species composition, plant N and P content, decomposition, soil chemistry, soil biota</td>
</tr>
<tr>
<td>Rainfall Manipulation Plots (RaMPs) (1997)</td>
<td>Timing and amount of ppt; increased temperature treatment to be added for LTER V</td>
<td>ANPP, BNPP, plant species composition, plant ecophysiology, decomposition, soil C and N flux, soil biota</td>
</tr>
<tr>
<td>Irrigation Transect (1991)</td>
<td>Growing season water additions, upland and lowlands; new N treatment added in 1999</td>
<td>ANPP, plant species composition, plant N content, BNPP, decomposition, soil C and N flux, soil biota</td>
</tr>
<tr>
<td>P Addition Experiment (new for LTER V)</td>
<td>P added at 4 rates, +/- N to assess relative N and P limitation</td>
<td>ANPP, species composition, mycorrhizal colonization levels, soil N and P fractions</td>
</tr>
<tr>
<td>Grasshopper Removal Experiment (new for LTER V)</td>
<td>Grasshopper reductions from plots in 1-yr and 4-yr burn uplands, +/- bison</td>
<td>ANPP, plant species composition, plant C/N content, N cycling processes, decomposition, insect communities</td>
</tr>
</tbody>
</table>
Fire. Fire is essential in mesic grasslands worldwide, and human alteration of fire frequency is a key element of global change in these grasslands. Fire was important historically in tallgrass prairie (Daubenmire 1968, Vogl 1974, Bragg 1982, Knapp et al. 1998a, Reich et al. 2001b), and is now managed by humans to limit the growth of woody plants and to promote the cover and productivity of C₄ grasses (Engle et al. 2000, Hoch et al. in review). Fire alters the structure and function of grasslands, and our studies of the ecological consequences of fire have spanned multiple spatial and temporal scales and levels of ecological study. This hierarchical approach has identified many of the mechanisms contributing to responses at higher levels. For example, fire changes the light and soil environment of emerging plants, altering phenology and physiological responses (Knapp et al 1998a), increasing ANPP, increasing competition for light and N. These changes contribute to reduced abundance and richness of C₃ plants and a concomitant decline in biodiversity (Collins et al. 1998, Briggs & Knapp 2001). Changes in vegetation structure, composition and tissue quality elicit responses in aboveground consumers and affect belowground invertebrates (Todd 1996, Blair et al. 2000), mycorrhizae (Eom et al. 1999, 2000) and soil microbes (Rice et al. 1998, Ajwa et al. 1999). The experimental design at Konza (Fig. 17) includes replicate watersheds (avg. size = 60 ha) that, since 1972, have been burned annually or at 2-, 4-, 10- and 20-year frequencies, encompassing a range of likely natural fire frequencies and management extremes. Most watersheds are burned at the end of the dormant season (April), when the greatest frequency of lightning and prescribed burning occurs regionally (Bragg 1995). However, fires historically occurred at other times (Engle & Bidwell 2001), and during LTER IV we initiated a “season of fire” experiment, with replicate watersheds burned in the spring, summer, fall or winter. To address trajectories following a change in fire regime and the role of fire history (legacy effects), we began (in 2001) a long-term “fire treatment reversal” experiment (annual and 20 yr fire treatments switched on replicate watersheds). This new experiment will provide insights into the temporal scales over which plant and soil processes respond to changing fire regimes, and the role of site history in affecting responses to fire. We also incorporate fire into smaller plot-scale plot experiments on Konza, where mechanisms underlying effects of fire are more readily addressed (Benning & Seastedt 1997, Blair 1997, Ajwa et al. 1999, Eom et al. 1999)
**Grazing.** Grazing, like fire, was historically important in tallgrass prairie, but is now largely under human control, with grazing by cattle the dominant land use in the Flint Hills. In fact, changes associated with the management of megaherbivores are among the most significant in the recent history of mesic grasslands worldwide (Fuhlendorf & Engle 2001, McNaughton 2001, Walker 2001). Understanding the role of grazers in these grasslands is crucial (Collins et al. 1998, Knapp et al. 1999). To address the role of native grazers and important fire × grazing interactions (Hobbs et al. 1991, Johnson & Matchett 2001), bison were reintroduced in 1987 to a 1000-ha area of Konza that includes replicate watersheds burned at 1-, 2-, 4- and 20-year intervals and a range of topography and vegetation types. Comparative studies of native (bison) vs. introduced (cattle) ungulates are also needed to understand the impacts of changing land use in North American grasslands. Functional similarities and differences in the effects of bison and cattle on grasslands are being assessed by long-term comparisons of bison and cattle grazing at both the watershed and small enclosure (5 ha) scales.

**Climate.** North American grasslands were formed by climate changes originating during the Miocene-Pliocene transition (Axelrod 1985), and their present day distributions depend on regional temperature and precipitation gradients (Sala et al. 1988, Lauenroth et al. 1999). Although our emphasis on fire and grazing interactions is clearly appropriate, and unique within the LTER network, >20 yrs of study has underscored the pervasive role of interannual climatic variability in this ecosystem. For mesic grasslands, the mean and extremes of precipitation (e.g., floods and droughts) affect most ecosystem processes (Anderson 1990, Hayden 1998). On a continental scale, variability in precipitation affects productivity more in grasslands than in other North American biomes (Knapp & Smith 2001). Thus, responses to altered temperature and precipitation regimes will be an important component of global change. Climate change predictions for the Central Plains include increased temperatures (Gregory et al. 1997, IPCC 2001) and increased temporal variability in rainfall (i.e., larger storm events and longer intervening dry periods; Groisman et al. 1999, Easterling et al. 2000). Changes in temporal patterns of precipitation are predicted impact grasslands more than changes in precipitation quantity alone (IPCC 2001). We are just beginning to understand how grasslands will respond to more extreme rainfall patterns (Fay et al. 2000). Longer-term studies, and those considering multiple, interacting factors (i.e., temperature and precipitation) are needed. New experiments for LTER V will assess grassland responses to climate change over short- and long-time scales.

**In summary,** our conceptual framework recognizes fire, grazing, and climatic variability as essential and interactive factors shaping the structure and dynamics of grasslands across landscape mosaics. Our LTER goals are to test specific hypotheses regarding the independent ecological effects of these factors in mesic grasslands, and to evaluate the potential consequences of multiple global change phenomena. Our research will also elucidate the role of biotic interactions (competition, mutualism, predation, herbivory) in grassland communities and ecosystems, and provide insight into more general ecological phenomenon. For example, Konza studies of above- and belowground herbivores, plants, and mycorrhizal fungi address current issues of linkages and feedbacks between plant and soil communities (e.g., Bever 1999). Our long-term studies also provide tests of theories regarding community structure and stability (e.g., Collins and Glenn 1997a,b, Collins 2000).

**D. Long- and Short-Term Experiments.** Below, we describe the ongoing and proposed new research comprising the Konza LTER program. The program description, organized according to areas addressed by “research groups” (see Konza LTER Management), includes the original LTER “core areas” and additional research foci based on our specific programmatic needs. Many linkages exist among these research groups and their foci, and our short-term and plot-level experiments are integrated with core LTER experiments (Fig. 18). Given the high frequency of “disturbances” (fire, herbivory, drought; Knapp et al. 1998a) in tallgrass prairie, this core area is implicitly incorporated in all of our research areas. (Note: investigators involved in specific research areas are listed in parentheses; group leaders are underlined. Detailed methods for long-term studies are associated with individual datasets on the Konza Prairie LTER WWW [home page]).
Integration of Konza LTER Research

Patterns and Controls of Aboveground Net Primary Production (ANPP) (Briggs, Blair, Fay, Hartnett, Johnson, Knapp, Koelliker). Net primary productivity is an integrated measure of energy capture and assimilation by ecosystems. Global change is expected to alter terrestrial NPP (Running et al. 2000, Schimel et al. 2000), and long-term ANPP measurements are essential to understand grassland dynamics and responses to global change. We will continue to assess spatial and temporal patterns, and controls, of ANPP, with estimates (based biomass harvests; Briggs and Knapp 1995) from replicate transects on 17 watersheds (Fig. 3). We also will continue measuring ANPP in other experiments (e.g., Irrigation Transects, Belowground Plot Experiment, RaMPs), and quantifying annual litterfall in gallery forest sites. These data are essential for our evaluation of the relative importance of factors controlling grassland ANPP (Briggs & Knapp 1995), for comparing rates and patterns of ANPP across sites (Knapp & Smith 2001), and for testing ecological theory on the effects of productivity on community structure and dynamics (Waide et al. 1999, Collins et al. in review). Our ANPP datasets, some > 25yr long, also provide a benchmark for validating ecological models of grasslands. These data are available to the modeling community through our web site, and the Oak Ridge National Laboratory Distributed Active Archive Center NPP Database.
ANPP responses to fire and grazing. Our long-term data demonstrate that fire increases ANPP in years with adequate rainfall, and the greatest increases in ANPP occur following infrequent fires (Seastedt & Knapp 1993). We have identified several mechanisms driving these responses (Briggs & Knapp 1995, Blair 1997, Knapp et al. 1998b), and will continue to refine our resource-based models (Fig. 19) and evaluate the long-term effects of frequency and season of fire on resource limitation and ANPP. New research for LTER V will focus on ANPP responses to changing fire regimes and the legacies of historical fire frequency (Fire Treatment Reversal experiment). We hypothesize that differences in species composition and belowground meristem densities, legacies of past fire regimes, will constrain ANPP responses to changing fire regimes. This is important for predicting responses to changing land use in these grasslands. New LTER V research will link population and ecosystem processes by examining potential demographic mechanisms driving patterns of ANPP and the relative roles of plant growth vs. meristem limitation in regulating ANPP (see next section).

ANPP responses to grazing by large ungulates have been documented in many grasslands (e.g., Detling 1988, Frank and McNaughton 1993, Frank et al. 1994). Shifts in biomass allocation, sexual vs. vegetative reproduction, alterations in physiological processes, and compensatory growth patterns have been reported in response to grazing, and many of these occur in tallgrass prairie (Hartnett et al. 1996, Knapp et al. 1999). During LTER V, we will quantify the cumulative impacts of bison or cattle on production potential (recovery of productivity after cessation of grazing), and relate these responses to grazer-induced changes in plant community composition and belowground processes (i.e., nutrient availability, root dynamics and belowground meristems). Because bison graze in discrete patches that shift over time (Vinton et al. 1993, Knapp et al. 1999), a focus on alternating periods of herbivory and reduced grazing pressure captures the dynamics of this grazing pattern. Since 1992, we have measured ANPP in 98 exclosures (5 × 5m), protected from bison grazing, and compared these data with estimates from adjacent sites historically exposed to grazing, but protected from grazing for 3 year periods. We predict that ANPP will be reduced relative to ungrazed sites for at least one growing season following cessation of grazing, as allocation to belowground parts occurs at the expense of aboveground growth. However, we recognize that grazer-facilitated increases in N availability may augment this recovery (see Nutrient Cycling Studies) and that grazer-induced changes in plant species composition and meristem densities, as well as interactions with other global change phenomena (e.g., elevated N deposition and altered rainfall patterns), complicate predictions of ANPP responses. Interpreting ANPP responses to grazing in this complex milieu requires longer-term measurements and will be facilitated by integration with other LTER studies.
Responses to climate and nutrients. Contrary to the Great Plains as a whole (Sala et al. 1988), ANPP is not strongly correlated with precipitation amounts at Konza (r²=0.37 across all sites; Briggs and Knapp 1995), a consequence of multiple resource limitations (Knapp et al. 1998b). Light limitation caused by detrital shading of emerging shoots contributes to lower ANPP in unburned sites (Knapp and Seastedt 1986), while either water or N can limit ANPP in burned sites (Seastedt et al. 1991, Turner et al. 1997). The lack of strong correlation between in climatic variables and temporal variability in ANPP (Briggs and Knapp 1995, Briggs and Knapp 2001) suggests that other factors (e.g., N) are important. Two new complementary experiments will contribute greatly to understanding the effects of climate and nutrient enrichment on ANPP in grasslands. To examine the role of water-N interactions in controlling ANPP in burned sites, we will expand upon an irrigation experiment initiated in 1991. The Irrigation Transect is a replicated watering experiment, encompassing upland and lowland topographic positions. It is designed to assess the extent of water limitation, and the effects of interannual variability in precipitation, on ANPP, plant species composition, and belowground responses. Thus far, supplemental water has increased ANPP in 7 of 9 yrs but, contrary to our initial hypothesis, has not increased the dominance of C₄ grasses nor reduced the contribution of forbs to total ANPP (Knapp et al. 2001). We propose a new N addition treatment on the irrigation transects (see New Cross-Cutting Initiatives), with ANPP as a key response variable. In addition, the role of climate change in controlling ANPP will be evaluated through experimental manipulation of precipitation and temperature (see RaMPs study in New Cross-Cutting Initiatives).

Plant Populations and Communities (Hartnett, Briggs, Collins, Ferguson, Garret, Towne). Our plant population and community studies are designed to link organismic responses to ecosystem-level phenomena, document the impacts of land use, climate and global change on biodiversity and ecosystem function (Hooper and Vitousek 1997, Loreau et al. 2001), and provide mechanistic explanations for these responses. We will continue long-term measurements of plant species composition (modified Daubenmire cover method; Collins 1992), densities and fecundity on LTER watershed transects, and in numerous plot-level experiments (Belowground Plot Experiment, Irrigation Transect, RaMPs, etc.). These studies, along with new research, will assess the independent and interacting effects of changing land use (e.g., fire and grazing) and climate on plant populations and communities at multiple scales, and test current theories on community structure and biotic interactions.

Plant population studies. New research for LTER V will address: 1) demographic mechanisms underlying trajectories of community change in response to global change, 2) linkages among plant demography, species diversity and ecosystem function (ANPP), and 3) responses to changes in multiple interacting resources (water, N, P). Community dynamics in these grasslands depend on vegetative reproduction and tillering, as successful establishment from seed is rare (Benson 2001, Elder 2001, Rogers & Hartnett 2001). Thus, the rhizome “bud bank,” the reserve of dormant belowground meristems (Harper 1977), is a critical component of these grasslands and a better predictor of community responses and temporal change than soil seed banks (Benson 2001). Additionally, ANPP is the product of both plant/tiller size (ecophysiological response to resource availability) and plant numbers (demographic processes). Thus, “meristem limitation” can constrain ANPP to varying degrees under different land uses (Table 2) and in different grasslands. Lower variability in ANPP in arid grasslands may result from meristem limitation, whereas larger belowground meristem banks in mesic grasslands may allow greater positive responses to periods of abundant resources (Knapp and Smith 2001). We hypothesize that ANPP is strongly linked to the demography of vegetative reproduction in mesic grasslands, and that the density and dynamics of belowground rhizome meristem pools is the best predictor of spatio-temporal variability in ANPP and responses to fire, grazing, and climate. We predict that 1) fire and grazing increase belowground meristem densities, allowing greater ANPP responses to changing resource availability; and 2) belowground bud banks are positively correlated with the CV of ANPP across fire×grazing treatments. To address these hypotheses, we will expand our LTER studies to include sampling of belowground meristem banks (censusing grass and forb rhizomes/rhizome buds in 10×15 cm deep cores) and aboveground tiller densities along LTER plant sampling transect. We will initially sample
monthly to determine seasonal dynamics, and thereafter annually at peak meristem population densities. Long-term study of belowground meristem dynamics in the core LTER watersheds, fire treatment reversal experiment, Irrigation Transects, and RaMPs will provide important insights into the demographic processes driving grassland vegetation responses to global change.

Table 2. Rhizome bud bank density and aboveground stem density (mean ± 1 SE) as affected by fire at Konza Prairie (from Benson and Hartnett submitted). The effects of land use (fire and grazing) on relative meristem limitation may play a key role in determining mesic grassland responses to future global change, an issue our proposed LTER studies will address.

<table>
<thead>
<tr>
<th>Plant attributes</th>
<th>Annually burned</th>
<th>Unburned</th>
</tr>
</thead>
<tbody>
<tr>
<td>Buds / m² (1997)</td>
<td>1830 ± 330</td>
<td>733 ± 33</td>
</tr>
<tr>
<td>Stems / m² (1998)</td>
<td>1369 ± 158</td>
<td>1063 ± 124</td>
</tr>
<tr>
<td>Meristem Limitation Index (ratio of buds:stems)</td>
<td>1.3:1.0</td>
<td>0.7:1.0</td>
</tr>
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**Plant community studies.** Community-level research for LTER V will use long-term Konza studies (some > 20 yrs) on community responses to fire, grazing and climatic variability, to assess rates and trajectories of community change, and relate these to changes in other ecosystem components (e.g., ANPP, nutrient dynamics, soil biota). This information will be crucial for accurately assessing and predicting grassland responses to global change. Other new LTER V plant community studies will focus on 1) relative roles of local and regional processes in community structure, 2) relationships between plant species diversity and community stability in space and time, and 3) community invasibility. Plant community responses are also integrated into other new and ongoing studies, including the Belowground Plot Experiment, RaMPs, Irrigation Transect, P addition experiment (Nutrient Cycling), and grasshopper removal experiment (Consumer Studies).

**Local vs. regional processes.** We will use LTER species composition datasets to determine the degree to which local richness (10 m²-scale) is related to broad-scale richness in grazed and ungrazed watersheds. Local diversity results from the interplay between local species interactions and regional species pools (Cornell & Lawton 1992, Srivastava 1999). We will test Huston's (1979) hypothesis that effects of regional diversity vary with productivity by comparing the strength of the local-regional relationship in sites on Konza that differ in long-term ANPP potential. We predict that richness responses will reflect meristem dynamics, linking results from the bud-bank studies to grassland community responses.

**Diversity-stability.** Long-term community studies are needed to address questions on community stability (Frank & McNaughton 1991, Tilman & Downing 1994, Collins 2000). Heterogeneity is a measure of spatial variation, whereas stability is measured as lack of directional change over time (Collins 2000). Previous LTER studies showed that community heterogeneity and stability increased with decreasing fire frequency (Collins 1992, 2000), and revealed significant relationships between plant species diversity and community stability (Collins & Benning 1996) in ungrazed uplands. However, since species diversity co-varies with local grazing intensity, and grazing intensity varies in space and time, further analyses are needed to understand the interplay between community diversity, disturbance, and stability. Using core LTER data we will test the following hypotheses: 1) grazing increases the rate of community change over time, but the rate of change varies with fire frequency, and 2) spatial heterogeneity (measured as compositional similarity among plots) is related to temporal variability (measured with time-lag analysis Collins et al. 2001) in ungrazed, but not grazed, grasslands. We will test these hypotheses during LTER V as the temporal coverage of this dataset
lengthens in the grazed areas. We will also use long-term data from the Irrigation Transects and RaMPs to assess how diversity affects temporal stability under different environmental conditions.

**Species invasions.** Invasibility is an important aspect of community stability, and invasion by exotic species is an increasingly important aspect of global change (Dukes & Mooney 1999), often with substantial ecosystem consequences. We will expand our studies of grassland invasibility (Smith & Knapp 1999, 2001) and test the hypothesis that plant species diversity (regional species pool size) and disturbance (fire and grazing) regimes influence the invasibility of tallgrass prairie by exotic species (Fig. 20). We predict that invasibility in mesic grasslands is associated with a minimum threshold of below-ground meristem density, based on traits of prairie grasses including high tiller production and integration, regulated tiller spacing, and rapid and efficient space-filling, all of which can contribute to low space and resource capture by exotic invaders (Davis et al. 2000). We will expand studies of two exotic species (*Sericea lespedeza* and *Andropogon bladhii*) to clarify 1) traits contributing to successful invasions of closed canopy grassland communities, 2) influence of land use and climate on patterns of invasion, and 3) community and ecosystem consequences of invasion.

**Terrestrial Consumers** *(D. Kaufman, Horne, Joern, G. Kaufman, Sandercock, With, Zolnerowich).* Terrestrial consumers in grasslands include invertebrate herbivores, small mammals and grassland birds, groups that often respond strongly to global change phenomenon (Kareiva et al. 1993). Our goals in LTER V are: 1) to continue to evaluate the ecological role of consumers in grasslands, 2) to understand the mechanisms underlying the dynamics of consumer populations and communities, and 3) to provide predictions of consumer responses to global change. Past LTER research has focused on spatial and temporal variation in abundance of terrestrial consumers, and selected taxa have been studied for >20 years on permanent transects across watersheds at Konza (Kaufman et al. 1998, Zimmerman 1993). We will continue these surveys to document long-term trends and variability in consumer populations, and to assess the effects of fire, grazing and climatic variability on population dynamics (Turchin 1999, Turchin & Ellner 2000, Perry et al. 2000). We will expand our studies to include amphibians and reptiles, as widespread declines in amphibian numbers are a conservation issue of international concern. New research for LTER V will include: 1) new analyses and synthesis of consumer datasets to assess spatial and temporal patterns of response by key consumer populations, and predict their direct and indirect demographic responses to environmental change; 2) more comprehensive studies of the role of grasshoppers and other invertebrate herbivores, and 3) evaluation of the impact of land-use practices on two threatened species of grassland birds.

**Consumer population dynamics in response to fire and grazing.** Consumer populations are highly variable in tallgrass prairie (Kaufman et al. 1998). Multiple, interacting factors limit consumer populations in these grasslands (Belovsky & Joern 1995), and we hypothesize that multiple factors must concurrently reach threshold levels for populations to reach high abundances. We will identify factors driving consumer population dynamics, particularly for those populations that do not vary in synchrony *(e.g.,* shrews can respond positively to environmental moisture, provided other factors are at threshold levels, while folivorous rodents respond positively to ANPP; Kaufman et al. 1998). Our
research has uncovered many such species-specific relationships between consumers and grassland attributes or function (Evans 1984, Kaufman et al. 1988, 1990, 1998b, Clark & Kaufman 1990, Zimmerman 1993), and many of these relationships have additional complexity that links climate, fire and grazing effects (Fig. 21; Matlack et al. 2002).

Developing higher-order general rules that determine consumer dynamics is a major challenge, but predicting consumer responses to global change requires that we understand their collective responses to multiple environmental factors. For example, fire and grazing alter vegetation heterogeneity and structure, species composition, and ANPP in grasslands. Vertebrates, as a group, appear to respond primarily to vegetation structure and litter accumulation (Kaufman et al. 1989, Kaufman & Kaufman 1990, Clark & Kaufman 1991, Zimmerman 1993), while insects may respond to changes in richness or abundance of host plants (Strong et al. 1984, Lawton & MacCarvin 1986), escape space (Otte & Joern 1977, Jeffries & Lawton 1984), or habitat traits that optimize physiological processes (Huey & Kingsolver 1989, Lactin & Johnson 1998). Our goal is to develop and test specific hypotheses regarding the mechanisms driving these responses. We expect significant fire × grazing interactions with all consumer groups, since fire regimes influence broad-scale grazing patterns (Knapp et al. 1998b). Because multiple, proximate ecological factors typically interact to determine species-specific habitat selection and population abundances in grasslands, we will subject our long-term datasets to structural equation analyses (sensu Wooton 1994; also Johnson et al. 1991, Grace & Pugasek 1997) and for all consumer groups, we will construct species-based trait groups or assembly rules (Weiher & Keddy 1999), to develop predictive insights into consumer responses to land use change. We will link consumer data with those of other Konza research groups (e.g., plant composition and structure, ANPP and tissue chemistry, soil nutrients, etc.) to test multi-variate hypotheses regarding direct and indirect effects of multiple environmental factors on consumer populations in a synthetic way.

**Influence of grasshoppers on grassland dynamics.** Grasshoppers are abundant consumers in tallgrass prairie. Yet, like other insect herbivores, their impact on grassland ecosystems is poorly known (Hunter 2001). Because grasshopper abundance varies widely with climate and management (fire and grazing), rates of plant consumption also vary, often reaching high levels in years and sites
with high grasshopper biomass. Compared with megaherbivores, grasshoppers consume small, high quality bits of many leaves, and their feeding often results in significant ‘greenfall’ (Davis et al. 1992, Lactin & Johnson 1995). Fecal material (frass) is spread broadly and continuously in the habitat as small, readily decomposable (high nutrient) packets, with production of frass scaled to size- and temperature-based digestion rates (Yang & Joern 1994a,b, Harrison & Fewell 1995, Lactin & Johnson 1995). To assess grasshopper effects on nutrient dynamics and plant responses, we propose a new long-term grasshopper removal experiment (combination of insecticides and removal by sweep netting), complemented by small-scale manipulations of grasshopper feeding, as well as frass, cadaver and greenfall deposition. These manipulations will be done in grazed and ungrazed watersheds under annual and 4 yr fire frequencies to address interactions of land use with insect herbivory. We will answer several questions: 1) By what mechanisms, and to what degree, do grasshoppers regulate grassland processes? 2) What are the relative contributions of grasshopper herbivory to slow (plant species composition, litter quality and decomposition rate) vs. fast (frass, cadaver and green-litter addition) nutrient cycling? 3) How does variability in grazing, fire and climate influence the magnitude of these responses?

**Land use change and grassland birds.** In addition to maintaining long-term surveys of bird abundance, we propose a new study on habitat selection by two threatened species of grassland birds—upland sandpipers, a neotropical migrant, and greater prairie chickens, a resident gamebird. Like many grassland birds, both species are declining due to habitat loss and changing land use (Peterjohn & Sauer 1999). Both species are also sensitive to habitat fragmentation and require large tracts of grassland for breeding (Vickery et al. 1994). Konza offers a unique opportunity for studies of habitat requirements of these declining species, with experimental watersheds that span the natural range of vegetative cover in grassland ecosystems. Our objectives are: 1) to quantify habitat selection at different stages of the breeding cycle, and 2) to obtain habitat-specific estimates of fecundity and survival that will be used to model population dynamics. Birds will be captured in early spring and marked with leg bands and radio-transmitters. Foraging birds, nests and broods will be located by radio-telemetry, and mapped with GPS receivers. Habitat-specific demography will provide insights into the population responses of these indicator species to changes in land use and land cover.

**Nutrient and Carbon Cycling Studies** (Blair, Ham, Johnson, Knapp, Pierzynski, Rice). Changes in biogeochemical cycles are both a cause and consequence of global change (Schlesinger 1997), with feedbacks on ecosystem processes, atmospheric chemistry, and water quality. Konza LTER studies will 1) quantify rates of nutrient input and export, 2) evaluate the effects of land-use (fire and grazing) and climate on nutrient cycles, and 3) mechanistically link changes in nutrient cycling to ecosystem and community responses. We focus primarily on N, P, and C. We will continue long-term studies of atmospheric deposition (described below) and hydrologic export of nutrients (see Aquatic Studies), soil chemistry (5 yr sampling along LTER transects and in long-term plot experiments), and nutrient content of plant biomass (from ANPP samples). New research during
LTER V will fill gaps in the N cycle of these grasslands (Fig. 22) by providing estimates of dry deposition and N fixation, and examine the potential for uptake of dissolved organic N by prairie plant (separate funding to be sought by Johnson and Evans). We will assess soil C and N flux in responses to changes in fire frequency and ungulate grazing (outlined below) and climatic variability (see New Cross-Cutting Initiatives). Mediation of P availability by mycorrhizae is also important in grasslands (Johnson et al. 1997, Hartnett & Wilson 1999), and we propose a new P addition experiment to address controls of P availability and responses of grassland communities to added P. **Nutrient inputs and outputs.** Long-term records of nutrient inputs are essential for constructing nutrient budgets, calculating weathering rates, as inputs for modeling efforts, and for assessing interannual variability and directional changes in nutrient loading (Gilliam 1987, Blair et al. 1998). In conjunction with the National Atmospheric Deposition Program, we will continue documenting inputs of NO₃, NH₄, SO₄, PO₄, H⁺ and major cations in wetfall. We will also continue long-term measurement of N and P inputs (NO₃, NH₄, PO₄, total N and P) in bulk precipitation. A new long-term dataset will include measurement of dry deposition as part of the CASTNet program (www.epa.gov/castnet), which will provide weekly average atmospheric concentrations of SO₄, NO₃, NH₄, SO₂, and HNO₃, hourly concentrations of ambient O₃ and meteorological data to calculate dry deposition rates. We will also quantify N and P concentrations in stream water, soil water and groundwater to provide linkage between terrestrial and hydrologic studies. Symbiotic N fixation is an unquantified, but potentially important, N input in these grasslands. A new LTER investigator (Crews) will provide expertise in terrestrial N fixation (Crews 1999, Crews et al. 2000) to assess symbiotic N fixation and responses to land use. Tallgrass prairie includes a variety of legumes, and our LTER fire and grazing treatments provide a unique matrix for testing hypotheses about effects of land use/land-cover on symbiotic N fixation. This research will address: 1) **Basic questions of N fixation:** What legumes fix N and at what rates? How does N fixation compare to other inputs? 2) **Effects of fire on legume N fixation:** Several legume species are most abundant in burned prairie (Towne & Knapp 1996). Based on how fire affects N limitation (Turner et al. 1997) and P availability (Eisle et al. 1990), we hypothesize that N fixation rates will be highest in frequently burned sites and lowest in unburned sites; 3) **Effects of grazing on legume N fixation:** Selective grazing of grasses increases forb abundance (Collins et al. 1998), which may increase the abundance and productivity of N fixing legumes. At the same time, grazing also stimulates net N mineralization and nitrification (Johnson & Matchett 2001), which might reduce the N fixation of legumes. We propose to estimate N fixation by legumes using a natural abundance of ¹⁵N approach (based on 6¹⁵N values of soil- vs. atmosphere-derived N; Shearer & Kohl 1986, Hogberg 1997), but will also evaluate other complementary methods (¹⁵N₂ chamber method, acetylene reduction, xylem ureide methods) to verify and calibrate our estimates. We will derive legume-specific N fractionation values by growing legumes inoculated with native *Rhizobium* in N-free solution. Once tested and refined, we will conduct large-scale sampling of legumes and reference plants in watersheds with different combinations of fire and grazing. We also plan small-scale experiments to assess the regulation of N fixation in prairies, and investigate N transfer from legumes to grasses using in situ labeling of legumes with ¹⁵N (McNeill et al. 1997). This research will provide new data on symbiotic N fixation in these grasslands, the responses of symbiotic N fixation to different land use regimes, and the ecological regulation of N fixation (Vitousek & Howarth 1991, Crews 1999). **Soil N fluxes in responses to fire.** Konza LTER studies have provided much new information on the effects of fire on biologically active soil N (Rice & Garcia 1994), net N mineralization rates (Blair 1997, Johnson & Matchett 2001), and N limitation to ANPP in tallgrass prairie (e.g., Seastedt et al. 1991, Ojima et al. 1994, Turner et al. 1997). Available and mineralizable soil N accumulates in the absence of fire, which provides a mechanistic explanation for the pulse in ANPP following infrequent fires (Blair 1997), and may contribute to increased species diversity under reduced fire frequencies (Collins et al. 1998). During LTER V we will continue to document short- and long-term changes in soil N transformations in response to different fire regimes, using in situ estimates of net N mineralization (Blair 1997), and laboratory assays of potentially mineralizable N (Robertson et al. 1999). We will focus on changes in soil N pools and availability in the “reversal of fire treatments”
experiment, and with respect to the expansion of woody vegetation associated with reduced fire frequency in these grasslands (i.e., shrub island expansion and redcedar woodland encroachment).

**Responses to grazing.** Large herbivores affect energy flow and nutrient cycling in grasslands (Detling 1988, Frank & Evans 1997, McNaughton et al. 1997). The reintroduction of bison to Konza provides us with a unique opportunity to address the effects of native grazers on N cycling in mesic grasslands. Changes in N cycling can provide mechanistic explanations for feedback among grazers, soil and plants (Hamilton & Frank 2001), and changes in plant community structure (Steinauer & Collins 2001). Our studies indicate that bison grazing increases net N mineralization and nitrification rates as reported in other grasslands (Frank et al. 2000), decreases net root productivity, and increases root tissue N content (Fig. 6; Johnson & Matchett 2001). We will continue to measure and compare belowground processes and plant responses in grazed and ungrazed areas, and will complete a long-term study of the transformations and fate of N additions in 15N-labeled bison dung and urine. In LTER V, we will initiate research on how grazers fundamentally alter the path and magnitude of C cycling belowground (Hamilton and Frank 2001). Using isotopic tracers, we will investigate how grazing 1) changes plant processes (root mass and productivity, turnover, and root exudation) 2) affects soil attributes and processes (microbial biomass and activity, soil organic matter quality and quantity, and 3) reduces soil CO2 flux in grazed areas. Determining how grazing affects C fluxes belowground is critical, considering that nearly ¼ of the earth’s surface is grassland and much of that is managed for grazing. We predict that bison will also increase spatial and temporal heterogeneity of soil N availability in grazed and non-grazed areas, and to relate these to plant community dynamics and the spread of invasive species.

**P addition experiment.** N exerts substantial control on plant productivity, but P is also an important resource, especially with respect to plant-mycorrhizal and plant-plant interactions (Hartnett et al. 1993, Johnson 1993, Johnson et al. 1997). This is especially true in grasslands where competition for P will increase as atmospheric N inputs increase. For LTER V, we propose to establish a new long-term P fertilization experiment (led by Collins) to assess the effects of altered relative P limitation on grassland community dynamics. This experiment will complement studies on the irrigation transects and the belowground plots. Given that mycorrhizae are important in P acquisition by grassland plants (Hetrick et al. 1994, Hartnett and Wilson 1999, Smith et al. 1999), we will test the hypothesis that P addition leads to a decoupling of above- and belowground community linkages, leading to divergent above- and belowground community trajectories. To test this hypothesis, we will add 4 levels of P (0, 2.5, 5, and 10 g P/m2), crossed with 2 levels of N (0 and 5 g/m2) in replicated plots to assess potential interactive effects of competition for N and P. An upland site burned every 2-yrs will provide a mix of plant functional groups and high initial plant species diversity. We expect that alleviation of N limitations will maximize competition for P, and that plant community responses to P will be contingent on varying degrees of mycorrhizal dependencies of grassland plants (Hetrick et al. 1994, Wilson & Hartnett 1998). Using this experiment and other manipulations (fire × grazing treatments, RaMPs), we will test the hypothesis that shifting resource limitations associated with global change (e.g., altered P:N or carbon:nutrient limitation) will alter symbiotic function and cost-benefit relationships between AM fungi and plants, resulting in mycorrhizal-mediated plant community responses. A detailed characterization of changes in soil P and N fractions will assess short- and long-term changes in soil P and N pools (led by Pierzynski).

**Net ecosystem C exchange.** Effects of global change on net C exchange in grasslands are important locally and globally (e.g., Houghton et al. 1999). Grasslands soils are high in C, and tallgrass prairies are among the most C-rich of grasslands (Jenny 1930, Parton et al. 1987). These grasslands are relatively recent in origin (Axelrod 1985, Anderson 1990), implying that the ecosystem has been a strong sink for C historically. However, recent changes in both climate (means and variability) and land-use have the potential to alter source/sink relationships in grasslands, as well as other ecosystems (Barford et al. 2001, Schimel et al. 2000). To address this issue, we installed eddy flux
towers for continuous measurement of net ecosystem C exchange (Ham & Knapp 1998) at Konza Prairie, on two nearby KSU-owned cattle grazed sites, and in a nearby redcedar stand where the biogeochemical consequences of regional land-cover change are being studied (Norris et al. 2001a,b). We will explore if these grasslands are still sequestering C and how changing land-use, land-cover and climatic variability affects the C budgets of these ecosystems. We also will continue to evaluate the influence of land-use and climate on key component fluxes (e.g., soil CO2 flux).

**Belowground Studies** *(Johnson, Blair, Hartnett, Jumpponen, Rice, Todd, Whiles)*. Mesic grasslands support some of the highest densities of fine roots (1.5 kg/m², Jackson et al. 1997) among ecosystem types, and rivals tundra in the storage of soil carbon (19.2 kg C/m², Schlesinger 1997). Given the importance of belowground components and processes in these ecosystems, belowground responses to global change are predicted to have substantial impacts on these grasslands. We focus on 1) patterns and controls of belowground NPP (BNPP) and root-derived inputs of organic matter and nutrients, 2) soil biota (invertebrates and microbes), 3) transformations of organic matter and nutrients by the biota, and 4) nutrient uptake by plants and mycorrhizae. For LTER V, our efforts will concentrate on addressing how belowground processes respond to multiple global change phenomena (changes in land-use, land cover, and climate) and their interactions (e.g., interactions between increased N deposition and changing precipitation regimes).

Much of our past research focused on the Belowground Plot (BGP) Experiment established in 1986 to provide a common platform for research belowground processes and responses to fire, nutrient inputs (N, P or N+P) and mowing (Fig. 23). Response variables included ANPP, species composition, root dynamics, soil invertebrates, mycorrhizae, decomposition, soil microbial biomass and activity, soil solution chemistry and selected soil nutrient pools. We will maintain the BGP treatments for LTER V, as well as annual estimates of ANPP and minirhizotron studies (see below). However, we propose reducing intensive sampling of other variables to once every 5 yrs to minimize destructive sampling, and to allow us to initiate new belowground studies within the theme of global change.

**Roots**. Most of the energy flow and cycling of nutrients occurs belowground in tallgrass prairie, but there have been few studies of BNPP. We hypothesize that fire and grazing have opposing effects on BNPP and root biomass: Fire increases BNPP and 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 BNPP and depth distribution. Major expansion of our research in LTER IV included new studies on root dynamics using a minirhizotron system. Initially, these studies were done in selected treatments in the BGP experiment. Minirhizotron data from the BGP experiment (Fig. 24) was complemented by research using root ingrowth cores as an index of productivity (Johnson & Matchett 2001) in selected fire and grazing treatments. Annual burning increased BNPP compared to unburned sites, while grazing reduced BNPP compared to ungrazed sites (Fig. 6). We will continue minirhizotron studies in the BGP experiment to develop a unique and valuable long-term dataset on root dynamics (analogous to our long-term ANPP dataset) which will allow us to address questions regarding inter-annual variability in root processes, and the relative sensitivity of above- and belowground plant processes to climatic variability. We also will expand root studies to LTER watersheds and new plot experiments (RaMPs and redcedar woodland studies).

**Soil invertebrate studies**. Soil invertebrates are important components of belowground food webs in grasslands, and they respond to changes in belowground inputs (roots), as well as environmental factors (Blair et al. 2000). We expect that nutrients, frequent fire, and increased water availability will positively affect the abundance of most soil invertebrates, while mowing or grazing (by reducing BNPP) will reduce soil fauna. There may be exceptions to these generalization, as well as important fire × grazing × climate interactions. We have examined how altered soil water content affects soil invertebrate communities (Todd et al. 1999, O’Lear & Blair 1999), and how cicadas, an abundant and important belowground herbivore in grasslands, respond to burning and mowing, and fluxes of nutrients associated with their emergences. Cicada emergence represents a substantial flow of energy and N (3g N/m²/yr) from below- to aboveground. Emergence traps will be used in new studies of cicada responses to land use and climate along the LTER watershed transects. We predict significant fire × grazing interactions, due to effects of land use on plant species composition, belowground
allocation and resource quality. We also propose new studies of microarthropod and nematode response to combined changes in water and N and the Rainfall Manipulation Plot experiment (see New Cross-Cutting Initiatives).

**Microbial dynamics.** Microbial biomass and activity in grassland soils are regulated by substrate quantity and quality as well as water and temperature (Garcia & Rice 1994, Rice et al. 1998, Ajwa et al. 1999). Fire and grazing (or mowing) directly or indirectly affects substrate quality and quantity. We hypothesize that grazing reduces microbial biomass and activity due to reduced root inputs, while frequent fires increase microbial biomass and activity. We will quantify temporal dynamics of microbial biomass C and N (Garcia & Rice 1994), and assess responses to treatments in the BGP using a fumigation-incubation (modified from Jenkinson 1988). Changes in mineralizable C and N will be determined less frequently using long-term (>200 days) laboratory incubations of soil cores (Stanford & Smith 1972, Garcia 1992). For LTER V, we will expand initial studies of soil microbial responses to added water on the Irrigation Transect (Williams 2001) with a new water-N experiment (see New Cross-Cutting Initiatives) to assess the interactions of increased N deposition and water availability on belowground properties and processes. Other new studies will focus on changes in belowground processes as a result of climate change and woody plant expansion (New Initiatives).

Fig. 23. **Right column:** Photograph and experimental design of the Belowground Experimental Plots, initiated in 1986 to provide a platform for studying linkages between above- and belowground responses to fire, mowing and nutrient additions in mesic grasslands.

Fig. 24: **Below:** The Belowground Plot Experiment includes minirhizotron studies of root dynamics and responses to burning and aboveground biomass removal by mowing. Burning significantly increased peak root length density and total root length production, but reduced root turnover.
Aquatic and Hydrological Studies (Dodds, Guy, Gido, Koelliker, Macpherson, Whiles). Globally, about 1/3 of all runoff originates from grasslands and savannas, with many of these streams being intermittent (Dodds 1997). Increased hydrological variability (climate change) and changes in riparian vegetation (land-cover change) are likely to alter biogeochemistry, ecosystem metabolism, and invertebrate productivity of grassland streams (Grimm 1993). Konza streams exhibit high spatial and temporal variability in hydrologic conditions (Dodds et al. 1996) and a variety of riparian plant cover, thus providing a useful model for assessing grassland stream responses to global change. We will continue long-term hydrological and chemical measurements of groundwater and stream water in these grasslands (4 gauged upland watersheds, 3 downstream sampling sites, 46 groundwater wells). New LTER V research will: 1) assess effects of hydrological variability on stream species composition and ecosystem function, and 2) evaluate the effects of altered hydrological variability and riparian vegetation on stream macroinvertebrate community structure and productivity.

Effects of climate change and species composition on intermittent streams. Drought and flooding are major events that structure stream communities and regulate ecosystem processes. We will assess how changes in hydrology will interact with stream biota to regulate ecosystem functioning in intermittent prairie streams. In particular, experimental stream units will be used to evaluate how changes in drought duration and flood frequency interact with the presence or absence of a key grazer to regulate stream metabolism (O₂ production/consumption) and nutrient retention. We hypothesize that increased drought duration will increase retention of organic matter (OM) and nutrients in pools (Butturini & Sabater 1998, Larned 2000), but decreased water volume will reduce whole-stream metabolism. In contrast, we expect flooding to reduce particulate OM (e.g., Buzby & Perry 2000), and lower nutrient retention (Mulholland et al. 1985, Grimm 1987) and respiration. We also expect primary production associated with epilithic algae to recover quickly. Macroinvertebrates can be dislodged or displaced by flooding, altering species composition (Holomuzki & Biggs 1999) and we will assess the effects of flood severity and timing (Boulton & Lake 1992) on resilience of assemblages (i.e., post-flood recovery rates). Flooding and drought may also eliminate or reduce the abundance of fish (Closs & Lake 1996). We predict that the loss of a dominant grazer (central stonerollers, Campostoma anomalum) has potential to further influence stream ecosystem responses to disturbance. Campostoma reduces algal and bacterial biomass, alters algal composition, reduces macroinvertebrate density, and increases material cycling rates (Power et al. 1985, Gelwick & Matthews 1992), all of which affect the resistance and resilience of streams (Gelwick & Matthews 1997). We expect biotic interactions involving Campostoma to be greatest during periods of moderate drought (e.g., Grimm 1993), but we expect Campostoma to be eliminated by longer droughts. We hypothesize that grazing minnows will increase the resistance and resilience of prairie streams to moderate disturbance (flooding or drought) by preventing the accumulation of algae.

We will use experimental stream units (Fig. 25) to test the interactive effects of abiotic disturbance (drought duration and flood frequency) and species composition on stream function. These units have been used successfully to mimic natural systems (Gido et al. 1999, Gido & Matthews 2001), and allow replication for rigorous testing of climate-change scenarios (Hogg & Williams 1996). We also will track temporal variation in productivity in two intermittent streams on Konza, and focus on periods of prolonged drought and flooding to compare with results from experimental streams. We will interpret our results in light of regional climate change scenarios to understand how climate change will interact with species composition to affect metabolism and nutrient retention in grassland streams. Specifically, we will assess the effects of increased drought duration and flood frequency on stream metabolism, and how this affects and is affected by the resident animal communities.
Spatial and temporal patterns of macroinvertebrate production in grassland streams. We will assess how landscape and hydrological variation affects stream invertebrate community production. Prairie streams differ from forested streams due to their intermittency and patterns of energy inputs. Upstream reaches have limited canopy cover and algal production dominates carbon inputs whereas downstream reaches are covered by gallery forest canopy and receive substantial inputs of leaf litter (Gurtz et al. 1988, Gray & Dodds 1998). These differences in allochthonous vs. autochthonous energy inputs should lead to distinct patterns of functional feeding groups (e.g., Vannote et al. 1980), but this has not been investigated with secondary production estimates and quantified food webs. Estimates of secondary (2°) productivity are an integrated measure of the “success” of consumers, because they incorporate abundance, biomass, growth, and survivorship (Benke 1993) and they allow quantitative estimates of the role of consumers in material and energy cycling. New research during LTER V will quantify macroinvertebrate community 2° production and food webs. Initially, we will compare stream reaches with similar hydrology but different riparian vegetation. We will then focus on the influence of hydrologic variability on functional structure and energy flow.

Understanding relationships between riparian vegetation and stream ecosystem function is important in light of changes in riparian plant cover (Knight et al. 1994). We will compare reaches of Kings Creek bordered by open prairie, shrubs, and gallery forest. Estimates of 2° productivity, along with estimates of stream organic resources and gut content analyses of consumers, will be used to establish energy flux through food webs for each stream reach. We hypothesize that functional structure and energy and nutrient cycling will change substantially with riparian vegetation type. We predict that functional feeding groups (e.g. leaf shredders, periphyton scrapers) will respond to riparian vegetation as predicted by the River Continuum Concept (Vannote et al. 1980), but that the lack of canopy in upland reaches will alter the longitudinal patterns initially observed for forested streams.

Temporal patterns, climate, and groundwater geochemistry. Groundwater chemistry and flux are affected by climate, land use and land cover. In turn, groundwater affects stream hydrology and productivity, and links terrestrial and stream ecosystems. We will continue long-term studies of groundwater at Konza to 1) evaluate the long-term effects of watershed treatments and climatic variability on groundwater chemistry and nutrient flux, and 2) develop estimates of weathering rates (part of an LTER cross-site study) and 3) quantify contributions to stream water chemistry. At Konza, chemical weathering strongly influences carbonates (95% of the dissolved mass in stream water), which originate from limestone bedrock and carbonates in dry deposited material (Wood 2001). We will quantify chemical weathering rates through continued stream and groundwater monitoring, combined with data on nutrient inputs in precipitation and dry deposition (see Nutrient Cycling studies). We will quantify subsurface flow patterns in gauged LTER watersheds with short-term, periodic monitoring of stream flow rates in selected watersheds in addition to those already monitored to calculate a water mass balance. Stream and groundwater flow estimates will link hydrological studies to mass balance of terrestrial ecosystems, allowing predictions of climate change effects on downstream water quality and material transport.
Landscape Ecology (With, Blair, Briggs, Brock, Goodin, Johnson, McKane, Price). Changes in disturbance regimes have significant consequences at both fine and broad spatial scales (Turner et al. 1993). The scope of landscape ecological research at Konza will be expanded in LTER V to address spatial heterogeneity and responses to global change at a variety of scales. This will require a shift in emphasis from the traditional broad-scale view of ‘landscapes’ on Konza, to a more general perspective of landscapes as spatially heterogeneous areas defined by the scale(s) at which the ecological process of interest operates (e.g., Wiens 1989). Quantifying spatial pattern is critical for any landscape ecological investigation (Turner & Gardner 1991, Klopatek & Gardner 1999), and will be necessary to understand how global change alters patterns and processes in grasslands. Expanding the scope of our current landscape studies will allow us to focus on how spatial pattern affects ecological processes across a range of scales (Turner 1989). This will require 1) application of landscape metrics and spatial statistics to the analysis of patterns (e.g., soil types, nutrient concentrations, vegetation, species distributions) across a range of scales; 2) multiscale analyses to identify scaling domains, the spatial and temporal scales that bound a given ecological phenomenon or process; 3) explicit consideration of how spatial patterns affect ecological processes.

Use of multiscale analyses and scaling domains in remote sensing. Identifying scaling domains can reveal critical transitions in the underlying process(es) or process constraints responsible for the pattern (King et al. 1991, Wiens et al. 1993). For example, the Normalized Difference Vegetation Index (NDVI), is widely used to estimate plant biomass or ANPP, and is important for monitoring and evaluating effects of global change in grasslands. Research during LTER IV assessed the extent to which fine-scale NDVI data (<1m) could be rescaled to estimate NDVI data obtained at broader scales (e.g., 6-m resolution). Rescaled data did not retain the spatial structure of the measured data, revealing that techniques used to rescale image data were not sensitive to scaling domains. Thus, estimates derived from rescaled NDVI data must be interpreted with caution (Goodin & Henebry in press). This study, supported in part by the Kansas NASA Space Grant Consortium, will be expanded during LTER V, using spectral and NDVI data collected from close-range, aircraft- and satellite-borne sensors coordinated with extensive ground data to obtain coordinated, nested observations at multiple spatial scales within selected LTER sampling sites. These data will be used to develop and test methods for modeling across-scale dynamics in NDVI, which will be important for quantifying and forecasting grassland responses to changes in climate, land use or woody plant expansion.

Spatial patterns and ecological processes. A landscape approach can address how spatial pattern (of nutrients, resources, disturbances, habitat, or species) affect flows of nutrients, energy, or water across or between watersheds (e.g., identification of sources/sinks), movement patterns or dispersal of organisms, population structure and persistence (extinction risk), gene flow and genetic structure of populations, community dynamics, and invasive spread and invasibility of communities. Assessing how spatial pattern affects ecological processes in grasslands will complement efforts of other Konza research groups. For example, a landscape approach can contribute to understanding how patterns of vegetation complexity (e.g., meristem density, plant species composition) affect community invasibility (Plant Populations and Communities studies), or the relationship between heterogeneity of soil resources (Nutrient Cycling studies) and plant responses to grazing. Consideration of how pattern influences processes will complement the current research program, which is mechanistically based and generally focused on how process gives rise to patterns. Both perspectives are required to develop the pattern-process linkages underlying grassland dynamics, and to understand and predict the responses of grasslands to global change. Below, we provide an example of how spatial pattern will be incorporated into studies of ecological processes in these grasslands.

Fire-mediated landscape constraints on spatial and temporal patterns of bison grazing: Bison are important keystone species in grasslands (Knapp et al. 1999), which exert top-down effects on ecosystem processes. However, bison activities are not distributed uniformly across the landscape. Local nutrient enrichment (i.e., urine patches) affects bison grazing preferences at fine scales (Steinauer & Collins 2001), but spatio-temporal patterns of fire drive bison grazing patterns at a broad scale (Fig. 26; Knapp et al. 1998c, Vinton et al. 1993, Nellis & Briggs 1997). The mechanisms responsible for this grazing preference have not been fully explored. We hypothesize that fire-
mediated control over foliar N explains the observed temporal and spatial patterns of bison grazing at Konza. In LTER IV, satellite imagery and semi-weekly ground observations of bison grazing patterns in burned watersheds were related to patterns of foliar N content. These data indicated that bison preferentially graze burned watershed, but they do not graze among these areas uniformly. Instead, bison appear to selectively graze burned watersheds with long (>3 yr) return intervals. Within watersheds burned in the spring, bison were recorded most frequently, and grazing activity (removal of aboveground biomass) was most intense, on the watershed with the longest fire return interval (Fig. 26). Similarly, foliar N of *A. gerardii* also was higher on this 4-yr burned watershed, compared to the annually burn watershed, as predicted by the transient maxima hypothesis (Blair 1997). These data suggest that this fire-mediated pattern of variability in N availability and plant quality (*i.e.*, N content) is a critical determinant of the processes driven by bison grazing activities. We will test this hypothesis over longer time scales, and determine what ecosystem attributes affect short vs. long-term (intra- vs. inter-seasonal) spatial patterns of bison grazing. Linking this analysis to concurrent invertebrate consumer studies (see Terrestrial Consumers section) will allow us to develop a fine-scale, predictive model that incorporates ecosystem controls on herbivore patterns.

![Fig. 26](image)

There are strong interactions between fire and bison grazing. *Left:* Bison grazing reduces the accumulation of detritus, affecting the extent and intensity of fire on fine scales. *Below:* Fire affects broad-scale patterns of bison grazing activities. LTER studies indicated that bison preferentially grazed burned watersheds, especially those that burned infrequently (> 3-yr fire-return interval). Note the higher kernel density (red) of bison observations in the burned watersheds with 6 yr (2000) and 3 yr (2001) intervals between fires. Grazing preferences appear to be related to higher foliar N content in burned watersheds with longer fire return intervals.
E. New Cross-Cutting Initiatives. New LTER V research that falls primarily under the domain of specific research groups was outlined in the preceding sections. However, we also propose to initiate, or expand, other projects with cross-cutting themes that will involve the coordinated research efforts of multiple groups. Rather than list these under multiple research groups, we highlight them here.

Rainfall Manipulation Plots (RaMPs) (Knapp, Blair, Fay, Collins and others). Climate change predictions for the Central Plains include increases in mean temperatures and more variable and extreme precipitation patterns, with increased frequency of large precipitation events and extended drought periods. Research during LTER V will address these two important aspects of climate change, and their interactions, simultaneously within a unique experimental facility capable of temperature and precipitation manipulations. Our central hypothesis is that warming and more extreme rainfall patterns (larger precipitation events with longer inter-rainfall droughts, but no change in total precipitation amount) will significantly alter temporal patterns and depth distributions of soil moisture and, consequently, plant, community and ecosystem attributes and processes. Combined effects of more extreme precipitation patterns and warmer temperatures are predicted to be additive in most instances, but more complex interactions are likely for several key processes such as decomposition and soil CO₂ flux (Luo et al. 2001). These responses will be key to explaining changes in the structure and function of grasslands under a future climate that includes both directional changes and greater variability. This research builds on an existing field study initiated with non-LTER funding, the Rainfall Manipulation Plot (RaMPs) experiment (Fig. 27; Fay et al. 2000). Beginning in 2002, we will add an increased temperature treatment (IR lamps) to the ongoing manipulations of the amount and timing of precipitation events. This will allow us to assess the effects of projected changes in temperature and precipitation, individually and in tandem, in an intact grassland in a fully replicated factorial design. We predict that alterations in the depth distribution of soil moisture and its temporal dynamics will lead to growth-form specific responses in leaf-level gas exchange, water relations and productivity, longer-term changes in plant community composition (affecting biodiversity) and decomposition, as well as alterations in the dynamics of fine roots and C and N cycling processes (Fig. 28). Understanding ecosystem responses to changes in both climate means (temperature) and variability (precipitation) is critical for detecting and predicting consequences of climate change. Ties to other LTER experiments at this site will create a unique, multifactor and hierarchical study of grassland ecosystem responses to altered climatic regimes.

We initiated this research with short-term funding, but some of our most important results have emerged only after 10 yrs or more of study (Collins et al. 1998, Knapp et al. 1998b, Knapp & Smith 2001). We plan to continue the temperature/precipitation experiments with RaMPs for at least 10 yrs, with a significant LTER support for this project. Supplemental funding from other sources (e.g., regional NIGEC funding) has been secured, and additional funding will be sought as needed, for more focused, and costly, measurements (e.g., minirhizotron and root biomass data).

Water and N limitations of grassland ecosystem function (Johnson, Koelliker, Knapp, Blair, Briggs). Periods of water limitation are a defining characteristic of this and most grasslands, although the degree to which N co-limits productivity and plant community dynamics varies (Hooper & Johnson 1999). The addition of N fertilization treatments to the long-term Irrigation Transect experiment (Fig. 29) will allow us to assess the relative limitations of water and N and to test for water × N interactions. Understanding how grasslands respond to N additions, especially in combination with water, is critical given predicted increases in anthropogenic N inputs and climate change. This study will provide a research platform for several research groups. Our objectives are to 1) determine the relative importance of water and N limitations to ANPP and BNPP and identify thresholds of response, 2) test for water × N interactions on ecosystem processes, 3) identify differences in responses of functional group (C₄ and C₃ grasses, legume and non-legume forbs) and relate these to plant community-level changes, 4) assess responses in soil biota and nutrient cycling processes and provide linkages between above- and belowground responses, and 5) determine how these responses vary with topography. We will address questions such as: Is the ability of prairie to respond to N limited by water availability? To what extent does prairie respond to anthropogenic N
additions in dry years? Is the NPP response to released from both N and water limitation greater than when water and N are added separately (i.e., is there a water × N interaction)? What is the relative importance of water and N in affecting community composition and the distribution and abundance of grass and forb functional groups? What is the relative importance of water and N in controlling belowground processes (e.g., nutrient cycling, soil respiration, and soil fauna dynamics)?

Fig. 27. RaMPs are intact grassland plots beneath fixed-location rainout shelters that exclude and collect natural rainfall, and allow experimental control of the quantity, timing, and variability in rainfall inputs. Shelters (14 x 9 m) consist of clear (UV transparent) poly-ethylene roofs, reservoirs to collect and store rainfall, and an overhead irrigation system. The 6 x 6 m central sampling area has a substantial buffer zone, and 1.2 m deep subsurface barrier limits lateral water movement. For more details see Fay et al. (2000).

Fig. 28. Responses in aboveground net primary production (ANPP), seasonally averaged soil CO₂ flux, plant species diversity (Shannon-Weiner, H') and relative canopy cover of a suite of 9 drought tolerant species in grassland plots exposed to either ambient or altered rainfall patterns. Data for ambient and altered rainfall treatments were combined from three years of experimental manipulation for ANPP and CO₂ fluxes. Plant species defined as drought tolerant are those whose cover in xeric uplands in annually burned Konza Prairie watersheds was significantly (P<0.05) higher than in mesic lowlands. Plant community responses are after three years of experimental treatments.

Fig. 29. The Irrigation Transect experiment includes replicate irrigation and control transects spanning upland to lowland topographic positions to address the controls of water limitations in these grasslands (Knapp et al. 2001). These studies will be expanded in LTER V by inclusion of a N treatment to address important water-N interactions.
The experiment includes 3 levels of water (mean of 0, 150 and 250 mm/yr in excess of natural ppt.) combined factorially (n=6) with 4 levels of N (0, 2.5, 5, 10 g/m²/yr). Responses include ANPP, grass, legume and non-legume forb mass and N content; and plant species composition measured annually. We will also assess selected belowground responses (soil enzymes, soil respiration, decomposition, BNPP (root ingrowth bags), soil fauna, and microbial diversity). We hypothesize that a strong water × N interactions and synergistic effects of water and N supplementation greater than response to either water or N alone. We expect relative responses to water and N to be contingent on topographic position and natural climatic variability. We also hypothesize that grasses will respond more than forbs to water and N additions, resulting in long-term changes in plant community composition, and that belowground responses will be more sensitive to increased water than increased N. Linkages between this new study and other LTER experiments will provide new insights into the interactive effects of water and N limitation in mesic grasslands, and responses to changes in these resources.

Woody plant expansion in grasslands (Johnson, Briggs, Blair, Knapp, Price). Woody plant expansion is increasing in grasslands of the Great Plains (Schmid & Leatherby 1995) and worldwide (Archer et al. 2001), yet the causes and ecosystem consequences of this change life form are poorly understood (Houghton et al. 1999). Increases in woody plant cover may affect land-atmosphere interactions more than previously thought (Schimel et al. 2000), and drive rates of C accumulation in some terrestrial ecosystems (Caspersen et al. 2000). We will expand studies of the causes and consequences of woody plant expansion, focusing on eastern red cedar expansion in the Central Plains and expansion of shrub cover on Konza. This research aims to assess and predict local and regional impacts of redcedar expansion on biogeochemical processes. In as little as 40 yrs, redcedar encroachment doubled ANPP and C stocks (Fig. 30), and reduced plant species diversity, compared to grassland. Changes in grazing and prescribed burning are likely the main drivers of this important life-form shift. Indeed, the expansion of redcedar was positively related to human population density (Hoch & Briggs 1999) and resulting changes in land use. Fire-induced mortality of trees was nearly 3 times higher on ungrazed sites than on grazed sites, because grazing reduced fuel loads in tallgrass prairie (Hoch et al. in review). Shrub expansion studies at Konza also illustrate the interactions between fire and grazing for woody expansion into tallgrass prairie (Briggs et al. in press). Tree density increased 2- to 10-fold over a 15-yr period, except on watersheds that are burned annually. Woody vegetation increased in bison-grazed watersheds regardless of fire frequency, presumably due to increased tree survivorship as the intensity and extent of fire were reduced.

For LTER V, we will focus on comparisons of net C exchange in redcedar woodlands and prairie using eddy covariance techniques and a detailed investigation of the mechanisms responsible for differences in C balance. A related project on “ecosystems in transition” (NSF funding to Briggs and Knapp) will identify the mechanisms responsible for long-term patterns of shrub expansion on Konza and establish pattern-process linkages across a range of scales from the leaf to the landscape. At the regional scale, our LTER efforts will be enhanced by a recent NASA grant (Johnson, Price, Blair, McKane) using remote-sensing methods and modeling to ‘scale-up’ extensive plot-scale studies of biogeochemical consequences of redcedar expansion to the regional level, and to develop predictive models of woody encroachment. These complementary studies demonstrate continued efforts to place Konza within the regional context of the Flint Hills and Great Plains.

Integration of social science and ecology (Bloomquist, Middendorf, and others). Humans have altered all major processes affecting terrestrial ecosystems (Vitousek et al. 1997). Thus, integrative approaches involving social scientists and ecologists are necessary to characterize extant grasslands, and to understand and predict grassland responses to global change (Grimm et al. 2000, Redman 1999). KSU sociologists (Bloomquist and Middendorf) have begun, with LTER support, to address the human dimensions of global change as they relate to changing land use practices in the Flint Hills. Our initial emphasis is on identifying and defining the social drivers of land-use change, as well as elements that limit the range of possible land use decisions. Research questions to be addressed are 1) What is the relationship between the changing structure of land ownership and heterogeneity of land-use? 2) What are the long-term ecological consequences of the spread of human populations into adjacent rural areas? Konza researchers have already documented a
correlation between the expansion of redcedar woodlands and county-level population growth (Fig. 30). Specifying land use decisions and other actions that make population growth such an important social driver in the region’s land-cover is the focus of this aspect of our research. 3) How do people in the region perceive their environment; and, how does this perception impact their environmental decisions? People’s perception of their surroundings affects their actions and the policies they support vis-à-vis the environment. Of particular relevance are people’s understanding and attitudes of grasslands in the Central Plains. (e.g., How does an understanding of the role of fire and grazing affect attitudes toward land use? What valuation models shape individual perceptions of the environment?). Addressing these questions will require data from several sources and multiple analytical methods, such as comparative farm/ranch level analysis and county-level Census of Agriculture data. Research on long-term socio-demographic changes will be conducted at the county (pre-1990 social demographic data) and sub-county levels (post 1990 data). A social demographic profile of the region will be developed, and a database on environmental perceptions and decision-making will be used to understand the factors driving regional land-use.

**Biodiversity studies.** We will continue to encourage grassland biodiversity studies at Konza. For LTER V, we will support insect surveys (Zolnerowich) of hymenopteran parasitoids (Superfamily Chalcidoidea). Hymenopterans account for ~75% of all insect parasites (Eggleton & Belshaw 1992), and food webs involving plants, insect herbivores, and parasites contain more than half of all known metazoan species (Hawkins & Lawton, 1987). Parasitoids can regulate populations of phytophagous insects, affect herbivore diversity, and alter herbivore-plant interactions (LaSalle & Gauld 1993). Abundance and diversity of these important insects will be assessed using Malaise traps across fire

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Fig. 30. **Upper left:** Aerial photos showing the rapid expansion of redcedar woodlands (dark areas) into adjacent grassland. Note light-colored grassland across fence line in upper portion of photos, illustrating effects of land use on woodland expansion. **Upper right:** Relationship between county-level human population growth and cover of redcedar. **Right:** Summary of measured C stocks (kg C/ha) and fluxes (kg C/ha/yr) in grassland and redcedar woodlands (FR=fine roots). Note the shift in distribution of biomass C from belowground in prairie to aboveground in the woodland. Soil respiration in woodlands was ~30% lower than in grassland.
and grazing treatments and vegetation types. Systematists from other Universities will be provided
with non-hymenopteran specimens from these collections. Ferguson and Mayfield will develop, with
outside support, a specimen database for the KSU Herbarium (~180,000 specimens with emphasis on
Central Plains), which will include taxonomic type specimens and plants occurring at KPBS. They
also will pursue interests in taxonomy and genetic relationships of invasive plants in these grasslands.
Finally, we will support preliminary studies (Jumpponen) of molecular approaches to identify soil-
and rhizosphere-inhabiting fungi and assess community responses to environmental change.

F. Synthesis, Integrative Studies and Cross-Site Research (Knapp, and all others as appropriate).
The maturation of the Konza LTER program, and the LTER network as a whole, provides new
opportunities for synthetic and integrative analyses to address ecological issues of fundamental
importance. New analyses may focus on a particular dataset from one site, a suite of studies at one
site, or similar datasets across sites. Multiple studies originally initiated for other purposes also may
be integrated to answer new questions. Such syntheses are not a means of closure for data collection
and analyses, but instead often generate innovative new research. The formation of a formal
Synthesis Research Group (see Management Plan) as part of the Konza LTER program is emblematic
of our commitment of time and resources to this goal.

Synthetic, integrative and cross site research during LTER IV varied from analyses of single long-
term datasets (Briggs & Knapp 2001, Kemp & Dodds 2001) to our most ambitious site-based
synthetic effort to date – “Grassland Dynamics, Long-Term Ecological Research in Tallgrass
Prairie” (Knapp et al. 1998a). In addition, long-term data from 11 LTER sites were integrated by
Konza researchers to answer questions regarding continental scale patterns and controls of ANPP that
could not have been addressed without a network of LTER sites (Knapp & Smith 2001). Many
individual datasets are now of sufficient duration for meaningful temporal analysis and these will be
the focus of much activity during LTER V (i.e., consumer population datasets, results from the
belowground plot experiment). In addition, exciting opportunities exist for new and innovative
integration of datasets from Konza and throughout the network. A few specific examples follow.

Synthesis and modeling responses to global change (McKane and others). We will use the Marine
Biological Laboratory-General Ecosystem Model (GEM; Rastetter et al. 1991) as a tool to integrate
and synthesize Konza LTER data, to extrapolate Konza results in time and space, and to predict the
responses of C, N and water cycles to natural and human-induced environmental change. GEM is a
process-based model of ecosystem C, N and water dynamics, which has been used to simulate the
effects of global change on temperate forests (Rastetter et al. 1991, McKane et al. 1997c), tropical
forests (McKane et al. 1995), and arctic tundra (McKane et al. 1997a,b, Rastetter et al. 1997, Hobbie
et al. 1998). The model will 1) integrate data across sites and experiments, 2) provide a process-based
analysis of ecosystem response to global change, and 3) predict global change effects across scales of
plots to regions and years to centuries. Our goals include evaluating how C-nutrient-water inter-
actions affect ecosystem C dynamics in response to global change, and predicting historical and
future responses to environmental drivers of NPP and ecosystem C storage. Key questions include:
Will mesic grasslands be a net source or sink of atmospheric CO2 in response to projected global
changes? How will changes in NPP and C storage be distributed across land cover types (grassland
vs. woodland)? What biogeochemical processes control those responses? In order to synthesize
LTER data collected over the past 20 yrs, as well as new data, we will derive a single parameter-
ization of GEM that simulates changes in ecosystem C, N and water dynamics in response to climatic
variability and past manipulations of atmospheric CO2, N, water, and disturbance (fire and grazing).
This will be similar in scope and purpose to the parameterization of GEM for the Arctic LTER site
(McKane et al. 1997a). We will link GEM to a GIS (based on spatial data on soils, vegetation and
catchment topography) and a hillslope hydrology model to spatially and temporally extrapolate
global change effects across the topographically complex Konza landscape, providing additional
linkages between our terrestrial and aquatic studies. Once parameterized, GEM will be used to
analyze how resources, or interactions among resources, may limit NPP and ecosystem C storage and
assess how C-N interactions constrain responses of NPP and net C storage to global change.
**Integrative studies of community structure (Holt, Foster, Collins and others).** The experimental design and long-term database of the Konza LTER provide a unique opportunity to address the mechanisms of species coexistence in a landscape context. Understanding the determinants of community structure, and in particular the relative importance of alternative mechanisms of coexistence, and of local and regional processes, is a major challenge in ecology. Deterministic processes resulting from an imposed fire and grazing regime clearly influence between-watershed variation in plant community structure (Collins 2000). Within watersheds, topographic position also influences community structure. Recent studies in a variety of systems (e.g., Zobel 1997) have highlighted the importance of species pool phenomena (e.g., regional diversity, proximity to propagule sources) in governing community composition. The ‘mass effect’ (Shmida & Wilson 1985) arises when dispersal permits species to persist in local communities because of recurrent immigration from external sources. We will take a multi-pronged approach to addressing the importance of local and regional processes. First, we will determine the relationship between local and regional richness under different levels of productivity (See Plant Community Studies section). We will also use the existing LTER database to examine the impact of landscape context (e.g., the composition, diversity and productivity of landscape units, surrounding focal landscape units) on plant diversity and composition. Next, we will complement existing data by collecting fine-scale spatial data along transects of contiguous 1×1 m quadrats, slicing across experimental landscape treatments. If mechanisms of coexistence involving dispersal (e.g., colonization-competition tradeoffs) are important, there should be ‘spillover’ between habitats, which will vary as a function of distance along the transect. Finally, we will develop spatial simulation models, tailored to Konza, to assess affects of potential mechanisms structuring local communities. Recent theoretical studies (e.g., Chase et al. 2002) suggest qualitative differences in community structure can arise from different combinations of coexistence mechanisms. The simulation models will be grid-based models that have been successfully applied in other grasslands (e.g., Moloney & Levin 1996, Wiegand et al. 1998), in which knowledge about the environment-dependent life-history attributes, dispersal biology, disturbance, sensitivity to herbivory by large mammals, and local competitive interactions is integrated into simple transition rules, which then drive the simulations.

**New cross-site studies (Hartnett and others).** Konza scientists continue to address ecological questions that span LTER sites. As one example, we propose to test the hypothesis that soil seed banks and belowground meristem pools switch in relative importance across regional precipitation/productivity gradients (Fig. 31). As noted earlier, a prediction borne out of a cross-site synthesis of ANPP data (Knapp & Smith 2001) is that the ability of ecosystems to respond to resource pulses may be constrained by meristem limitations on a larger scale (Plant Population and Community studies). We plan to address this via a separate cross-site study involving the CDR, KNZ, SGS, and SEV.

![Fig 31.](image-url) **Left:** ANPP data from 11 LTER sites indicated that grasslands (KNZ, CDR, SGS) were the most responsive to pulses in resource (i.e., water) availability. **Right:** A conceptual model illustrates that the responsiveness of mesic grasslands may be due to a combination of high meristem densities and high climatic variability (from Knapp & Smith 2001).
LTER sites. We will sample bud bank and seed bank dynamics and aboveground tiller and genet densities and relate patterns of meristem limitation (ratio of aboveground ramet:belowground bud densities) to LTER data on temporal variability of ANPP at each site. Such studies can provide a mechanistic basis for patterns borne of synthetic analyses and is one example of why we view these integrative activities as integral to our evolving long-term research program in grassland ecology.

Summary. We propose a broad and integrated research program that builds on a legacy of long-term studies in mesic grasslands. This research will expand the scope and breadth of a productive LTER program, to provide new insights into the ecological drivers of grassland dynamics and the responses of these important ecosystems to multiple global change factors. An emphasis on applying our LTER data to the generation and testing of ecological theory, and a continued commitment to education and training, will contribute the advancement of ecology.

C3. Konza Prairie LTER 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 been a successful test of this model. A group of KSU faculty led by G. Richard Marzolf initiated LTER I (1981-1986), implementing the site-based fire and grazing experiment designed by Lloyd Hulbert. The Konza LTER program was greatly expanded during LTER II (1986-1990), under the leadership of Don Kaufman and Tim Seastedt (Co-PIs during LTER I). Following Seastedt’s departure in 1991, Alan Knapp and John Briggs provided leadership and administration for LTER III (1991-1996), with co-PIs David Hartnett and Don Kaufman serving in advisory roles. Leadership during LTER IV (1996-2002) was provided by Alan Knapp, John Blair and John Briggs, with co-PIs Hartnett, Kaufman, Dodds and Johnson. Briggs left KSU in 1998, but has kept a strong research presence and will remains a Co-PI for LTER V. Blair assumed administrative responsibilities at the midpoint of LTER IV, and will serve as lead PI of LTER V, with Knapp, Briggs, Hartnett and Johnson, Dodds and Kaufman as Co-PIs. The program has remained focused on a unifying central theme and site-based experimental design, and has flourished despite different administrative PIs coordinating each renewal and turnover, and expansion of LTER investigators over the past 20 years. An important reason for this has been shared intellectual leadership, and continuity of Co-PIs with substantial advisory roles. In addition, Konza investigators who were on the KSU faculty (e.g., Briggs, Seastedt, Whiles) have continued their involvement in the Konza LTER program despite changing institutional affiliations.

The turnover of administrative PIs is possible, and even desirable, because our management model depends on shared intellectual leadership and group decision-making. Our current LTER organizational scheme is depicted in Fig. 32, page C-46). In practice, Blair serves as PI-of-record and primary LTER point-of-contact at the local (University) and LTER Network level. For day-to-day administrative decisions, Blair and Knapp share most responsibility and coordinate activities. For decisions of greater magnitude (personnel contracts, research subcontracts, major purchases, etc.), Kaufman (a former administrative PI), Hartnett (current Konza Prairie Site Director), and other members of the Konza LTER Executive Committee are consulted. Such interactions occur as necessary. The LTER Scientific Steering Committee, consisting of all LTER Co-PIs plus other key Senior Personnel, meets as needed to make decisions regarding scientific direction of the LTER research program. LTER researchers are divided into research groups, based on specific research interests, with a designated leader for each group (Fig. 32). Group leaders are consulted as required either individually or as a group when 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 workload on the administrative PI substantially, and allows for greater coordination of this diverse research program. Finally, we invite all Konza senior investigators, staff and students to an annual Konza LTER workshop, generally held in the fall of each year (see below).

Another feature of this model is maximizing the involvement of other personnel in LTER Network activities. Blair serves as Konza’s Coordinating Committee member for LTER network meetings, with Knapp currently serving on the LTER network Executive Committee. When CC meetings allow additional site representatives (e.g., scientific theme meetings), group leaders or other senior Konza investigators are given the opportunity to attend. Minutes from these meetings are always distributed to the entire group. Other LTER workshop participation is encouraged and supported whenever possible.

Interactions among Konza LTER 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 included on appropriate e-mail lists through which information and requests are distributed. For example, LTER network office e-mail communications sent to “PI-list” (which includes Blair and Knapp) are routinely forwarded to the Executive or Scientific Steering Committees. In addition, a Konza listserv (Konza-l) was created to provide an improved method of broadcasting announcements and information of interest to Konza researchers. 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 13th was held in 2001). Both off-campus researchers and local scientists attend these all-day workshops. 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 (our most recent was in September 1999), we have also 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 major research group to invite an outside expert to review their program over the LTER V funding cycle.

Finally, one of the benefits of the distributed management of the Konza LTER program is the broad-based research program that results when such a large group of scientists is actively involved in a common program. We have been very successful at attracting additional scientists, from both KSU and other institutions, to participate in Konza research and this “scientific diversity” is poised to grow significantly as we begin LTER V. In addition to the new faculty with LTER interests recently hired in Biology (Ari Jumpponen, Fungal Ecology, 1999; Kimberly With, Landscape Ecology, 2000; Brett Sandercock, Avian Ecology, 2000; Carolyn Ferguson, Plant Systematics, 2001; Keith Gido, Aquatic Ecology, 2001), we have encouraged, and supported where possible, new Konza research by faculty in other departments at KSU (Karen
Garrett, Plant Pathology; Greg Zolnerowich, Entomology; Gary Pierzynski, Agronomy; Leonard Bloomquist and Gerad Middendorf, Sociology) and researchers from other institutions (Tim Crews, Prescott College; Bob Holt, Bryan Foster, Kevin Price and Valery Terwilliger, KU; Tony Joern, NU; Bob McKane, EPA; Matt Whiles, SIU). The use of Konza LTER data has proven to be invaluable in attracting non-KSU investigators and is possible only due to the cooperation of all Konza LTER scientists. We will continue to encourage use of the Konza site and Konza LTER data by additional investigators as opportunities arise, through a variety of mechanisms, including on-site research support, LTER “seed money” and, where feasible, more formal subcontracts.
Fig. 32 – Organizational structure of the Konza Prairie LTER Program

Konza Prairie LTER Organization

Executive Committee


Scientific Steering Committee


Konza LTER Staff

Brent Brock (Information Manager); Amanda Kuhl (Field Coordinator); Rosemary Ramundo (Lab Coordinator); Gene Towne (Plant Sampling and Bison Management); Valerie Wright (Schoolyard LTER Coordinator)

Konza LTER Research groups

<table>
<thead>
<tr>
<th>Physical Environment</th>
<th>Net Primary Productivity</th>
<th>Plant Populations and Communities</th>
<th>Terrestrial Consumers</th>
<th>Nutrient and Carbon Cycling</th>
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<td>S. Ashe</td>
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<td>K. Garrett</td>
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<th>Landscape Ecology</th>
<th>Synthesis/ Cross-Site Studies</th>
<th>Human Dimensions</th>
<th>Education and Outreach</th>
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<td></td>
<td>K. With*</td>
<td>D. Kaufman</td>
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*Group Leaders
C4. Konza Prairie LTER Data and Information 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 data security (protection against loss of data), and facilitate use of data by the original investigator(s) as well as by future researchers. Our goal has been 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) and Briggs (1998). At our site, the Data Managers (initially J. Briggs, and now B. Brock) also have been scientists and active participants in the design and execution of research projects, as evident from the Konza Publication list. Having a scientist as a data manager is a model that has worked well for the Konza LTER program.

During the early 1980's, the Konza LTER staff developed and implemented a base-level research data management plan to allow all interested researchers to locate, interpret and use Konza data. This plan was designed using guidelines established by Gorenzt et al. (1983) and is documented in Gurtz (1986). Since its inception, the KPLDM program has evolved from serving a local research group at KSU (most in the Division of Biology) to functioning with a multi-disciplinary team of over 40 investigators from a variety of universities and government agencies. The design of the current Konza Prairie LTER database is straightforward. All datasets are in ASCII format (with exception of GIS coverages and remote sensing data). The storage of data in ASCII format has proven to be easily transferred from computer operating systems from CPM, UNIX, and Windows®. The entire database resides currently on a Novell Network (Version 5.0), running on a Pentium server with 24 gigabytes of disk space. (The disks are striped over a RAID 5 array, thus data is protected in case of hard drive failure). The database is divided into subdirectories which correspond to specific Konza research groups or which represent the nature of the data set.

Since the inception of the Konza LTER program, all investigators have been required to submit their data and metadata 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 on a variety of electronic media from DAT 24 magnetic tapes, RAID hard disk arrays, and compact disks. Our goal is to have at least three copies of our database stored in different physical locations with a 6-month daily backup window. For consistency, the first 16 columns of each line of most Konza LTER datasets code for similar information (Table 3). Thus, each line is associated with a data set code, which helps maintain data security and integrity. Like most LTER sites, we find 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. ASCII files currently provide the most stable format for long term data archiving, and all Konza LTER data (except spatial data) will continue to be archived in this format. However, recent advances in WWW technology and data integration require Relational Database Management Systems (RDBMS) to realize their full capabilities. During LTER V, KPLDM will test and deploy RDBMS and structured language formats for Konza LTER data and metadata (see below). We have already converted two datasets (Konza LTER bibliography, and Konza burn history) to RDBMS and provided WWW query forms that have improved data access and management.

The computers of all KSU LTER researchers are connected via 100 mbps network lines on the KSU campus and by T1 from the Konza Prairie research site. These PCs have direct access to the Novell Network and to the Internet and World Wide Web (WWW). We use the Novell network primarily for data entry, application services (e.g., statistics, virus protection, GIS, and productivity software), FTP, secure storage of data, and other local data management activities (i.e., updates of software, group mailing lists, etc.). This allows transfers of data, reports and manuscripts among researchers regardless of their location. A WWW server on a local Windows 2000 machine (http://www.konza.ksu.edu) serves as our primary access point for Konza LTER
data. The data bank on our WWW server includes archived LTER data, metadata and our Methods Manual (see below), allowing anyone complete access to all Konza LTER data. Like the Novell Network server, our WWW server contains a RAID 5 disk array that provides seamless data protection in the event a hard drive should fail. The WWW server at our site has operated since April 1994, and is our main avenue for data requests and acquisition. Since June 1999, over 172,000 visitors from 41,000 unique hosts have accessed the Konza WWW server. Ninety percent of all accesses originated from outside KSU and represent 113 countries. Thus, demand for Konza LTER data is substantial. Our WWW server also facilitates collection and organization of information (such as metadata) within our research group, as well as communication among researchers. News, upcoming seminars, etc. are all posted on the WWW server.

The most difficult and time-consuming component of our data management plan is the proper documentation of datasets so that they can be used by investigators other than those who originally collected 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 in data collection due to technology enhancements (i.e., new analytical equipment) and methodological changes. A key component of our documentation has been development of an LTER Methods Manual describing our procedures. We have maintained a Methods Manual since 1981 (currently a 150 page document; on-line via our WWW server), which details how each LTER data set is collected. It includes maps with locations of sampling sites and transects, sample data sheets, and detailed procedures on instrument installation and use. This manual provides the details necessary to interpret the more extensive data documentation files maintained for each data set. This document is updated annually and a completely revised manual is produced every 5 years.

One of the goals of the Konza LTER program is to support, as much as possible, collaborative and independent research on Konza Prairie. Thus, we have developed a highly successful protocol (implemented in 1983) that allows outside (non-Konza LTER) investigators complete and unrestricted access to archived LTER data. We have three levels of access restrictions: unrestricted, limited restriction, and full restriction. Briefly, ‘unrestricted’ refers to archived datasets accessible to all researchers as read-only files (these are the data on our WWW server). Most Konza LTER data are in this category. ‘Limited restriction’ refers to archived datasets with read-only access available to current Konza LTER researchers or to outside researchers upon written permission of the 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 used mostly for short-term projects (i.e., graduate students theses, short-term exploratory research, etc.). ‘Restricted’ refers to data accessible only to the responsible 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. Once a data set is placed in the unrestricted category, it is immediately placed on our WWW server. Thus, the database on our WWW server is continuously updated.

We ask that manuscripts prepared using LTER data be provided to the LTER so that appropriate investigators may be notified, and we may have a record of publications using Konza LTER data. We also request that investigators using LTER data adhere to the following guidelines (available on our website): We ask that all publications, reports and proposals using any data from KNZ acknowledge the KNZ program using the following statement: "Data for XXX was supported by the NSF Long Term Ecological Research Program at Konza Prairie Biological Station"; where XXX is the list of datasets used in the publications, reports or proposals.
Five specific enhancements to the KPLDM program are planned for LTER V:

1. We will migrate our entire metadata catalog to a structured standard, most likely EML, following guidelines and “best practices” established by the LTER information management community. Migration to EML will greatly improve efficiency and accessibility of the Konza LTER database, due to the ability to provide customized metadata based on structured query results, flexibility in choosing metadata output formats, and by allowing inclusion of the Konza LTER data catalog in global searchable metadata database catalogs such as Metacat.

2. We will test, and where appropriate implement, RDBMS for data storage and retrieval. RDBMS provides powerful tools for data management and retrieval, particularly providing potential for on-the-fly subsetting and concatenation of datasets, essentially making the Konza LTER database a seamless dataset that can be customized to individual researcher needs. However, we recognize that any implementation of RDBMS must accommodate output in the currently available ASCII format to allow researchers to use existing tools (i.e., SAS programs) to parse and analyze data. We have already successfully implemented RDBMS with our site bibliography and burn treatment history datasets. Management of these datasets was significantly simplified and accessibility was improved by the addition of search capabilities. As an alternative to RDBMS, we will also test the potential to “reverse engineer” datasets from EML queries allowing us to realize the benefits of RDBMS while continuing to maintain datasets as ASCII flat files.

3. We will continue to improve and develop our GIS and Remote Sensing database. Many Konza GIS and Remote Sensing data layers are available on the Web via ArcIMS as interactive maps, or by FTP as compressed binary files. We plan to develop our online GIS capabilities to enhance the value of our spatial data for data mining, visualization and synthesis. Our goal is to move our online spatial database beyond its current role as a simple map visualization and query tool to a powerful data analysis tool that is integrated with our tabular datasets whenever possible. A first step will be to place our entire spatial database onto our ArcIMS server.

4. We will develop a wireless LAN at the KPBS research site. This is an inexpensive way to greatly enhance data collection and management. During LTER IV we installed a dedicated network connection to our meteorological station, which greatly improved temporal resolution of the data, simplified data collection through increased automation, improved QA/QC of data, and decreased response time for detecting and repairing problems. A wireless LAN would extend similar capabilities to remote locations throughout the site (i.e., stream dataloggers, RaMPs project, and CO2 flux tower) and would be a cost effective option (compared with trenched cable) for connecting additional equipment near the headquarters area. Finally, real-time connectivity to data collection devices opens opportunities for education and outreach activities via interactive Web sites.

5. We plan to add a half-time position to our information management staff. Currently all information management activities (Data management, Network administration, GIS, and assisting with other activities) are the responsibility of one person in addition to his independent research activities. It is unlikely that a single person can accomplish the goals set forth for LTER V while retaining all of the current responsibilities. The addition of a half-time position will bring new expertise and skills to the KPLDM program and allow the current information manager to concentrate on data management and program enhancements.
Table 3. Data elements in the first 16 columns of Konza LTER data.

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<th>Element Name</th>
<th>Columns</th>
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<td>Rectype</td>
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<tr>
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<td>I2</td>
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</tr>
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<td>Watershed</td>
<td>13-16</td>
<td>A4</td>
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* Data Format (A=ASCII, I=integer). The numeral equals the number of digits occupied by the element.

**C5. Outreach and Educational Activities.**

Educational activities associated with the Konza LTER program have increased greatly during LTER IV. Undergraduate and graduate student training is a central activity of the Konza LTER program. Forty-nine graduate student thesis and dissertations were completed during LTER IV. A Konza Prairie site-based REU program was maintained (http://www.konza.ksu.edu/general/reu.html), supporting an average of 10 undergraduates per year in addition to several LTER- and other grant-supported REU students annually. An education director was hired in 1996 (Dr. Valerie Wright) to lead the Konza Environmental Education Program (KEEP) in its two-fold mission of increasing appreciation and understanding of natural ecosystems and the process and value of science among K-12 students and the public (www.ksu.edu/konza/keep). A Konza Prairie Schoolyard LTER program was initiated in 1998, with emphasis on the development of realistic and relevant long-term research activities for K-12 students and their teachers as a means of educating students about the science of ecology. SLTER and KEEP conduct over 125 programs annually, serving > 4,000 K-12 students, teachers, and other adults from throughout Kansas (Fig. 33). Numerous Konza LTER scientists participate in KEEP and SLTER student and teacher training. Other Konza Prairie programs provide research experience opportunities for high school students. For example, KPBS hosted 12 students through Landmark Volunteers, a national summer program that provides experience in research and conservation for high school students. The Konza LTER site was also used as part of the KSU Girls Researching Our World Program. This program, funded by the NSF Gender Equity in SMET initiative, provides 6th-8th grade girls with exposure to careers science using environmental stewardship as a theme (www.ksu.edu/grow/). At the college level, KPBS serves as an outdoor educational laboratory for university classes and visiting field courses from numerous institutions each year. Information about these opportunities on KPBS is made available through its membership in the Organization of Biological Field Stations, Association of Ecosystem Research Centers, and other organizations.

KPBS and the LTER program have actively integrated undergraduates into research and have provided many training opportunities through the REU program and employment. During LTERIV, 28 Konza Prairie undergraduates have published papers (as senior author or co-author) in national peer-reviewed journals. Also, the majority of Konza REU students have completed senior honors theses and/or presentations at national meetings based on their KPBS research. In addition, results from Konza LTER studies are increasingly utilized in undergraduate ecology texts and other teaching materials. For example, Konza LTER studies demonstrating the role of fire and grazing in grasslands are prominently featured in *General Ecology, 2nd* edition by D.T. Krohne, and a recent Konza study by Collins et al. is a featured “case study” in the on-line supplement to *Ecology. Theory and Applications*. 3rd edition by Stiling. Case studies from Konza Prairie have also been incorporated into an educational CD on ecosystems, targeted at high school and undergraduate college courses (part of the Electric Biology series produced by Digital Studios, Aptos, CA) and Konza LTER studies on effects of fire and grazing were featured in *Cricket* magazine, an educational periodical for elementary students.
Konza Prairie scientists deliver numerous presentations and talks each year to various civic groups and educational, professional, and conservation organizations and agencies (e.g., The Nature Conservancy, National Parks Conservation Association, National Bison Association, KS Dept. of Wildlife & Parks). During LTER IV, we hosted several professional meetings and workshops, including The Nature Conservancy’s Great Plains Biodiversity Workshop (1997), USDA Sustainable Agriculture Conference (1997), National Park Service Biodiversity Workshop (1998), Soil Ecology Society Annual Meeting (1997), and the American Scientific Affiliation Annual Meeting (2001).

Konza Prairie LTER scientists, and the Konza LTER database, have continued to contribute to a number of important outreach activities of local, regional, national and international significance. At a local level, Konza scientists participate in Kansas Agricultural Experiment Station public education events, and host a biannual Visitors’ Day at the Konza Prairie site (~2000 people/yr), featuring LTER research and results. Konza LTER scientists have been actively involved at the state level in two major projects: 1) Konza researchers designed interpretive materials for a tallgrass prairie scenic overlook (including handicapped-accessible prairie walkway and information/viewing kiosk, completed in 1997) on a state highway bordering Konza Prairie, and 2) Konza LTER PIs are currently involved in the planning and design of a Flint Hills Tallgrass Prairie Interpretive Center, planned for construction on the Interstate 70 corridor adjacent to KPBS. At the regional level, we hosted a National Park Service (NPS) workshop and a training session in tallgrass prairie ecology and management for NPS Rangers at the National Preserve. The Konza LTER database on the effects of fire and grazing on tallgrass prairie ecosystems has been instrumental to the NPS in their development of a scientifically sound management plan for this newest unit in the National Park system. In addition, results from the Konza LTER program were used at The Nature Conservancy's (TNC) Midwest District Ecosystem Management Workshop to develop management and conservation strategies for grassland preserves throughout the region. The “Flint Hills Initiative” is a new program initiated by TNC to utilize and incorporate findings of Konza LTER and other research to develop ecologically sound management and preservation strategies for the Flint Hills and broader tallgrass prairie region. Brian Obermeyer, the new leader of that program, interacts extensively with KPBS scientists to summarize and incorporate LTER results into regional grassland management.

At a national level, Konza scientists served as advisors for a Smithsonian Museum of Natural History exhibit on grasslands and agriculture (Forces of Change). National visibility of the Konza LTER program has also increased significantly in recent years as it has been the focus of several major projects. An educational documentary film entitled Last Stand of the Tallgrass Prairie, funded by NSF, EPA, NEA, and several corporate sponsors, was aired nationally by PBS in 2001. Numerous Konza LTER researchers and other grassland scientists worked with Inland Sea Productions to produce this program, which was filmed principally on Konza Prairie and prominently featured the Konza LTER research program. A companion educational book of the same title, also highlighting Konza prairie research, was published by Friedman Fairfax publishers in April 2001. Konza LTER scientists contributed several sections to the book on topics ranging from global carbon cycling, to fire ecology, to adaptations of grassland plants. Concurrently, Konza scientists were involved in production of a major educational exhibit entitled “Listening to the Prairie” which premiered at the Smithsonian Institution in March 2001 and will be traveling to libraries and museums throughout the U.S. over the next 2 years.

In the international arena, Konza LTER scientists participated in a South African National Park Service workshop on fire and grasslands at the Kruger National Park, Skukuza, South Africa, in April 2000, and hosted a return visit by South African Scientists in April 2001. The Konza LTER program has also attracted visiting scientists and natural resource managers from Tanzania, Namibia, Australia, and Hungary, with many of these visits focusing on resource management issues of public concern.

Our goals for LTER V are to maintain our strong tradition of education and outreach, and to continue to expand the educational activities of the Konza program. A major facilities renovation program,
currently in progress, will greatly enhance the capacity of KPBS to provide research opportunities and science education programs. With $1.0M in support from the NSF Field Stations and Marine Laboratories Program, the Kansas Agricultural Experiment Station, KSU, and private foundations, major site improvements and building renovations including a prairie education center (Fig. 33), new research and teaching laboratories, exhibits, meeting rooms, and dormitory housing facilities for visiting students and scientists were completed during LTERIV, and a recent NSF-FSML grant has provided funding for two new 2-bedroom housing units for visiting scientists and students. In addition, numerous grants from state agencies (e.g. KS Dept. of Travel and Tourism, Eisenhower Professional Development Program) and private foundations (e.g. Emma Balsinger Foundation, Timmons Foundation, Wallace Foundation) have supported enhancements to the public interpretive trails facilities, educational materials, and the construction of an outdoor education center.

Fig. 33: Activities of the Konza Schoolyard LTER (SLTER) program. The Hulbert Research Center (upper left) houses laboratory and classroom facilities for the SLTER Program. Students and their teachers participate in SLTER studies, and add to their own long-term datasets, as a means of learning about grassland ecology and the enterprise of science.
D. Literature Cited


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H. Facilities and Equipment
In addition to the 3,487-ha field site, KPBS includes several buildings in the headquarters area that are used for LTER research. With support from KSU and three NSF-FSML facilities improvement grants, several major building and facilities improvements were completed during LTER IV (www.ksu.edu/konza/facilities.htm). Current station facilities include the 4,650 ft.\(^2\) Hulbert Center housing a library/conference room, classroom, offices, teaching laboratory, reference herbarium and animal collections, and dormitory-style housing for 15 visitors. The 2,400 ft\(^2\) Ecology Laboratory houses 2 analytical laboratories (with fume hood, DI water, balances, drying ovens, refrigerators, freezers, growth chambers), a soil and root processing lab (large sinks and soil traps), a computer room, and researchers’ shop. Other station buildings include a fire station and shop/maintenance building, storage building for research equipment, materials, and archived samples, and a residence for on-site staff. All KPBS headquarters buildings have T1 Internet connectivity to the KSU campus.

A recent NSF-FSML grant and additional KSU funds will support construction of two new 2-bedroom housing units to expand the accommodation capacity to 25 visiting researchers by next year. Planned additional improvements over the next 5 years include a 2,000 ft.\(^2\) on-site greenhouse facility, and the renovation of the large (10,000 ft.\(^2\)) limestone barn as a meeting and research facility with lecture auditorium, dining room, computing center, and offices. The headquarters area also includes the bison corral and handling facilities (holding chute, electronic scales, etc.), which are essential for LTER grazing studies, and the main meteorological station, which is linked to the LTER network. Other field equipment and instrumentation at the site includes an eddy flux tower for quantifying ecosystem-level C flux, four weirs and associated stream gauging equipment, 46 wells for monitoring groundwater levels and chemistry, numerous TDR probes and neutron access tubes for soil water measurements. Recent and planned new on-site monitoring instrumentation, including a CIMEL Sun Photometer, a seismometer (USGS), and a dry-deposition monitoring facility (CASTNet), will add significantly to the data available for LTER research and education programs.

Additional laboratory facilities are located on the KSU campus, approximately 15 km from KPBS. 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). Two walk-in controlled environment chambers (Conviron PGV 36) are located in Bushnell Hall and available for LTER use. 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, Biological and Agricultural Engineering, Plant Pathology, Geography), reflecting the interdisciplinary 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, several gas chromatographs with electron capture, flame ionization and thermal conductivity detectors, a Nikon compound microscope with epifluorescence 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. Cold
storage facilities for holding samples are available, as are sample preparation rooms for drying and grinding plant and soil samples. Climate controlled greenhouse space is available on the KSU campus. In addition, other “typical” laboratory equipment (balances, microscopes, etc.) is available in individual investigator laboratories.

A Stable Isotope Mass Spectrometry Laboratory (www.ksu.edu/simsl/) was established in the Division of Biology at Kansas State University in 2001, under the direction of Drs. Loretta Johnson and Roxane Fagan. The laboratory is dedicated to the isotopic (‰) and elemental (%) analysis of carbon (C), nitrogen (N), oxygen (O) and hydrogen (H) in organic and inorganic phases (solids, liquids and gases). The facility features a Finnegan Delta Plus SIRMS for the high precision measurement of relative isotope abundances of $^{13}$C, $^{15}$N, $^{18}$O, $^{34}$S, and hydrogen (H/D). This also includes the Con-flow II-Elemental Analyzer Interface for the fast, efficient and precise analysis of $^{13}$C and $^{15}$N in bulk soils, plant tissues. The Gas Bench II allows isotopic analysis of gaseous species (e.g., CO$_2$ and N$_2$O). This facility will be utilized for new LTER V stable isotope studies of N fixation, grazer-facilitated N cycling, and soil C dynamics associated with conversion from C$_4$ grasslands to C$_3$ woodlands.

Presently LTER has available four pickup trucks, ranging in model year from 1992-1997, and one 2001 crew cab pickup. We have access to two 1981 jeeps, which are no longer road-worthy and can only be used on-site. Hence, funds are requested for two replacement field vehicles during LTER V.

**Computer Software and Hardware - Konza Prairie LTER Program**

Most laboratories, all PI offices, and KPBS buildings have personal computers, linked to a local area network, as well to the KSU UNIX system. Descriptions of computer facilities available at the Konza site are provided under the “Other Resources” category. A list of computer hardware and software available to the Konza LTER program are provided below.

**Image Processing and GIS Laboratory:**

1. Windows 2000® Workstation with 500 MHz Pentium II processor, 312 Mb RAM, 19” monitor, and mirrored 40 Gb hard drives; Running ArcGIS 8.1, ArcView 3.2.
2. Windows 2000® Server with 400 MHz Pentium II processor, 256 Mb RAM, RAID 5 SCSI disk array, dual 100 Mbit NIC’s, and DAT 24X6 tape autoloader for network workstation backup; Running ARC IMS 3.1 and Arc/Info license server.

**PC-Network**

**Hardware:**

Novell 5.0 on dual Pentium/400 Mhz with 1 Gb RAM and 24 Gigabyte hard disk storage in RAID 5 array with hot swap spare.

Windows 2000 WWW Server on Pentium/400 Mhz with 256 Mb RAM and 27 Gigabyte hard disk storage in RAID 5 array with hot swap spare (runs IIS with Front Page extensions, ArcIMS, and Reference Web Poster)

HP Laser Jet® IV Printer
HP Design Jet® 1055CM Large Format Color Plotter
Epson Stylus Photo 700 Color Inkjet Printer
Film Recorder (works with PowerPoint, Sigma Plot, AXUM, SAS/Graph, HPGL, ArcGIS)
CD-ROM and Map Assist
Epson 1650 Flatbed Scanner
Nikon Coolscan® III Slide Scanner
Software:
Network—PC/SAS, ArcGIS, MS Office, Sigma Plot, Kedit.
Special Software—FRAGSTATS, 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 gray-scale spatial lattice data at multiple scales.
IWREST calculates Intra-Window Range in gray-scale spatial lattice data.
LACUNAE and LACURAN calculate a lacunarity index in gray-scale spatial lattice data using exhaustive sampling and random resampling, respectively.
SOFEST estimates correlation lengths and areas in gray-scale spatial lattice data using scale of fluctuation methodology.
Supplemental Documentation — Konza LTER Publications and Datasets

I. Publications of the Konza Prairie LTER Program (1996-2001)

A. Refereed journal articles.


B. Books.


C. Book chapters.


D. Proceedings and other publications.


E. Dissertations and theses.


II. Datasets available online at Konza Prairie LTER\textsuperscript{1,2}

<table>
<thead>
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<th>Dataset Name</th>
<th>Dataset Code</th>
<th>Years Included</th>
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<td>Ground-Water Chemistry</td>
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<td>Soil Moisture</td>
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<td>Root Windows</td>
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**On-line GIS data**

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Soils\textsuperscript{5}  \quad \text{KZGIS006} \quad \text{Current}  \\
TIN \quad \quad \quad \quad \text{KZGIS007} \quad \text{Current}  \\
Digital Elevation Model \quad \text{KZGIS008} \quad \text{Current}

**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 (compiled by Philip Fay, Fall 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
- Diatom species of Kings Creek (compiled by Walter Dodds 1999)

\textsuperscript{1}Table includes only data available online and represents only a selected subset of the studies and data sets completed and ongoing as part of the Konza Prairie LTER Program
\textsuperscript{2}Available at: http://www.konza.ksu.edu
\textsuperscript{3}All data sets include on-line documentation (meta-data)
\textsuperscript{4}All layers include FGDC compliant metadata and are downloadable as Arc Exchange files and available online via interactive map server. 
\textsuperscript{5}Second order soil surveys (1:24,000) are available for the site (Jantz et al. 1975). Digital soil maps were created using SSURGO data. In addition, a detailed soils map (1:2000 scale) is available for a 125-ha watershed that is the focus of our hydrologic and geochemical studies.
### III. WWW Data Accesses Since June 15, 1999

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<td>RaMPs</td>
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<td>Belowground Studies</td>
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<td>Mammals of Konza Prairie</td>
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IV. WWW Accesses By Domain Since June 15, 1999

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1The total number of foreign countries accessing the Konza LTER Web site.
IV. Partial List of Konza Prairie LTER-Related Extramural Funding During LTER IV


